

BIOGEOGRAPHIC PATTERNS OF BENTHIC INVERTEBRATE MEGAFUNA ON SHELF AREAS WITHIN THE SOUTHERN OCEAN ATLANTIC SECTOR

S.J. Lockhart and C.D. Jones✉
 US Antarctic Marine Living Resources Program
 NOAA Southwest Fisheries Science Center
 8604 La Jolla Shores Drive
 La Jolla, CA 92037, USA
 Email – chris.d.jones@noaa.gov

Abstract

Bioregionalisation of Antarctic and Southern Ocean shelf communities ideally incorporates a range of data on physical, environmental and biological properties. Analysis of the benthic invertebrate megafaunal assemblages of shelf habitats within the Atlantic sector, from scientific survey trawl catches, reveals distributional patterns. For the northern Antarctic Peninsula and the South Shetland Islands, the data indicate a two-layered pattern based on standardised total biomass data and the composition of phyla that contribute to that biomass. An examination of physical oceanographic data reveals a pattern of shelf faunal zonation: the benthic invertebrate communities on the northern shelves of the South Shetland Islands and the northern Antarctic Peninsula can apparently be separated into zones based on the physical properties of the Antarctic Circumpolar Current and the Weddell water masses that meet and mix in this region. Evident at smaller spatial scales are the effects of disturbance regimes, whether by iceberg scouring or historical commercial bottom trawling. Patterns of benthic invertebrate biomass are also described for the South Orkney Islands, as well as general patterns of phylum-level composition for South Georgia, the South Sandwich and Bouvet Islands. These regions are generally echinoderm-dominated, compared to the hexactinellid sponge-dominated northern Antarctic Peninsula region.

Résumé

La biorégionalisation des communautés de l'Antarctique et du plateau de l'océan Austral comporte idéalement une variété de données sur des caractéristiques physiques, environnementales et biologiques. L'analyse des assemblages d'invertébrés de la mégafaune benthique des habitats du plateau dans le secteur Atlantique, à partir des captures effectuées lors de campagnes scientifiques au chalut de fond, révèle des schémas de répartition. Pour le secteur nord de la Péninsule Antarctique et les îles Shetland du Sud, les données indiquent un schéma à deux niveaux fondé sur des données de biomasse totale normalisées et sur la composition des phyla représentés dans cette biomasse. Un examen des données océanographiques physiques aboutit à un schéma de zonation faunistique des plateaux : les communautés d'invertébrés benthiques sur les plateaux nord des îles Shetland du Sud et du secteur nord de la péninsule antarctique peuvent apparemment être séparés en fonction des propriétés physiques du courant circumpolaire antarctique et des masses d'eau de Weddell qui se rencontrent et se mélangent dans cette région. À des échelles spatiales plus faibles, les effets des régimes de perturbation, comme le labourage du fond par les icebergs ou les anciennes activités commerciales de chalutage de fond sont mis en évidence. Les schémas de la biomasse d'invertébrés benthiques sont également décrits pour les Orcades du Sud, de même que le sont les schémas généraux de la composition au niveau du phylum pour la Géorgie du Sud, les îles Sandwich du Sud et l'île Bouvet. Ces régions sont généralement dominées par les échinodermes, alors que ce sont les éponges hexactinellides qui prédominent dans la région nord de la péninsule antarctique.

Резюме

При биорайонировании шельфовых сообществ Антарктики и Южного океана в идеале используется ряд данных о физических, экологических и биологических свойствах. Анализ бентических ассоциаций мегафауны беспозвоночных, обитающих на шельфе атлантического сектора, по данным о траловых уловах, полученных в ходе научных съемок, позволил выявить характер распространения. Данные, основанные на стандартизованных данных об общей биомассе и составе входящих в эту биомассу типов, свидетельствуют о двухуровневой структуре в районе северной части Антарктического п-ова и Южных Шетландских

о-вов. Анализ физико-океанографических данных выявил картину зонального распределения шельфовой фауны: сообщества бентических беспозвоночных на северных шельфах Южных Шетландских о-вов и на севере Антарктического п-ова, по-видимому, могут быть разделены на зоны исходя из физических свойств водных масс Антарктического циркумполярного течения и моря Уэдделла, которые сходятся и смешиваются в этом регионе. В более мелких пространственных масштабах проявляется воздействие аномальных режимов, таких как повреждение дна айсбергами или коммерческое донное траление в прошлом. Также описываются характеристики биомассы бентических беспозвоночных у Южных Оркнейских о-вов и общие особенности состава на уровне типа в районе Южной Георгии, о-ва Буве и Южных Сандвичевых о-вов. В этих районах обычно доминируют иглокожие, в отличие от района северной части Антарктического п-ова, где преобладают шестилучевые губки.

Resumen

La biorregionalización de las comunidades que habitan en las plataformas antárticas y del Océano Austral idealmente toma en cuenta una variedad de datos sobre las propiedades físicas, ambientales y biológicas. El análisis de las comunidades de invertebrados bentónicos de la megafauna en la plataforma del sector atlántico del Océano Austral –presentes en las capturas de arrastre de campañas científicas– reveló patrones de distribución. Los datos revelaron que al norte de la Península Antártica y las Islas Shetland del Sur, existe un patrón de dos capas basado en los datos normalizados de la biomasa total y en la composición de la fila que contribuye a esa biomasa. El examen de los datos oceanográficos físicos de la región revela una zonación característica de la fauna de la plataforma: las comunidades de invertebrados bentónicos de la plataforma al norte de las Islas Shetland del Sur y de la Península Antártica aparentemente pueden separarse en zonas según las propiedades físicas de las masas de agua de la Corriente Circumpolar Antártica y del Mar de Weddell que confluyen y se mezclan en esta región. En escalas espaciales más pequeñas se aprecian los efectos de regímenes de perturbación, ya sea por la erosión causada por icebergs o los arrastres de fondo de la pesca comercial a través de los años. Se describe además la distribución característica de la biomasa de invertebrados bentónicos de las Islas Orcadas del Sur, y las características generales de la composición de la fauna de invertebrados a nivel de filo en las Islas Georgia del Sur, Sándwich del Sur y Bouvet. En estas regiones por lo general predominan los equinodermos, en comparación con la zona norte de la Península Antártica donde predominan las esponjas de la clase Hexactinellidae.

Keywords: bioregionalisation, benthic invertebrates, megafauna, zonation, water masses, Antarctic Circumpolar Current, iceberg scouring, hexactinellid, CCAMLR

Introduction

The invertebrate megafauna and benthic habitats of the Antarctic and Southern Ocean archipelagos are among the least well known of the world's oceans. A greater understanding of the benthic environment and megafaunal communities is essential for elucidating relationships between different components of the Antarctic ecosystem, identifying seabed areas which may be highly vulnerable to anthropogenic disturbances, as well as successful and sound monitoring of the ecosystem and its resources. Knowledge of spatial characteristics of Antarctic benthic assemblages at fine- and meso-scales can also provide information on biogeographical boundaries, and furnish insight toward optimal bioregionalisation of Southern Ocean shelf provinces.

Attempts to delineate benthic invertebrate assemblages of Southern Ocean habitats into

zoogeographical provinces date back to the early 20th century (Koehler, 1912; Hedgpeth, 1969). Such attempts have been plagued by difficult and perplexing taxonomy or thwarted by sparse records. Even where advances in both have been so great as to allow the delineation of provinces for some taxa (e.g. Linse et al., 2006; Rodríguez et al., 2007), such regionalisation has yet to be proven applicable to other taxa (Clarke et al., 2007).

At the community level, few studies have attempted to characterise megafaunal assemblages beyond localised shallow embayments in the vicinity of land-based stations, and have been limited by very small spatial scales with little attention given to larger bio-geographic provinces. Those that have attempted a characterisation at these larger scales have usually been restricted to qualitative descriptions only, or limited to quantification via video or photographic transect data.

The ideal bioregionalisation of Antarctic and Southern Ocean shelf communities incorporates a range of data on physical, environmental and biological properties, as well as the interaction of these properties.

Here, benthic invertebrate megafaunal assemblages collected through scientific survey trawl catches from shelf habitats within the Atlantic sector of the Southern Ocean were analysed in order to identify and characterise communities for comparative purposes, with an ultimate aim of identifying and understanding broader-scale patterns of distribution. Of the regions covered in this study, by far the greatest sampling effort and resolution of data was from the northern Antarctic Peninsula and the South Shetland Islands, and thus is the primary focus of this paper. Survey data is either lacking, as in the case of the South Orkney Islands, or sparse, as in the case of the island groups in the northern study region, and is presented from these additional regions for the purpose of qualitative comparisons only and for a more holistic view of the Atlantic sector of the Southern Ocean. Large-scale patterns identified from the data across the northern Antarctic Peninsula and the South Shetland Islands region are further discussed in the context of physical oceanographic properties.

Materials and methods

The sampling and characterisation of benthic invertebrates in this study was conducted using information collected from four research cruises from 1999 to 2006, across five CCAMLR statistical subareas within the Atlantic sector of the Southern Ocean (Figure 1, Table 1). Sampling design during all cruises was based on a random stratified survey design. Sampling from the southern regions of the study area (South Shetland Islands, northern Antarctic Peninsula and South Orkney Islands) and the northern regions (South Georgia and Shag Rocks, the South Sandwich Islands and Bouvet Island) employed different trawl gear and likely demonstrate very different sampling selectivities, and thus will be treated separately throughout this paper.

For the South Shetland Islands, northern Antarctic Peninsula (Subarea 48.1) and South Orkney Islands (Subarea 48.2), a four-panel bottom trawl (HBST) with vented V-doors (Net Systems Inc., Bainbridge Island, WA, USA) was deployed. The trawl codend was fitted with a 38 mm (stretched) mesh three-strand nylon web liner. The headrope transducer platform of the trawl was instrumented with a SimRad FS25 sonar system used to monitor the geometry of the mouth of the

trawl during each deployment and to record the period of trawl bottom contact. Trawl mouth width and height was measured for each deployment, and averaged 17.9 m and 9.1 m respectively. The target time for a gear deployment was 30 min on the bottom. Geographic coordinates were recorded throughout the period the trawl was in contact with the bottom.

Sampling in the southern region of the study area was conducted on board the RV *Yuzhmorgeologiya*, as part of the US Antarctic Marine Living Resources (US AMLR) Program's demersal research cruises. Sampling for the South Shetland Islands region took place in March 2003, and consisted of 68 stations (deployments) stratified by five depth strata: 50–100 m, 100–200 m, 200–300 m, 300–400 m and 400–500 m respectively, and positioned to account for as wide a geographic range as time, sea and ice conditions determined. The northern Antarctic Peninsula samples were collected in February–March 2006, and consisted of 63 stations. Sampling along the northern Antarctic Peninsula was depth-stratified similarly to the South Shetland Islands, although it included a small number of hauls (3) within 700–800 m. Station locations for all hauls in the South Shetland Islands and Antarctic Peninsula are set out in Figure 2(a). Sampling at the South Orkney Islands was carried out in March 1999, and consisted of 64 stations positioned similarly to the depth-stratified sampling design previously described. Station locations for the South Orkney Islands are set out in Figure 2(b).

Sampling for South Georgia and Shag Rocks (Subarea 48.3), the South Sandwich Islands (Subarea 48.4) and Bouvet Island (Subarea 48.6) in the northern regions of the study area was undertaken primarily by means of a 'Blake' trawl, which includes a 2 m wide rigid steel frame, and a limited number of bottom otter trawl hauls (mouth width 9.14 m). The codends of these trawls consisted of a 38 mm (stretched) three-strand nylon web. The target time for a gear deployment was 30 min on the bottom. Time on the bottom was measured by means of a time-depth recorder mounted on the trawl, and geographic coordinates were recorded throughout the deployment.

All sampling in the northern region of the study area was carried out in May–June 2004 on the RV/IB *Nathaniel B. Palmer* as part of the ICEFISH 2004 research cruise. Sampling for the South Georgia Island/Shag Rocks consisted of 14 stations (11 taken by Blake trawl and three by bottom otter trawl) stratified by depth similar to the previously described design. Station locations for the South Georgia and Shag Rocks region are set out

Table 1: Cruise and sampling details for benthic invertebrate collections analysed in this paper.

Location	Vessel	Date	Gear type	Number of stations
South Shetland Islands (Subarea 48.1)	RV <i>Yuzhmorgeologiya</i>	March 2003	HBST	68
Northern Antarctic Peninsula (Subarea 48.1)	RV <i>Yuzhmorgeologiya</i>	February–March 2006	HBST	63
South Orkney Islands (Subarea 48.2)	RV <i>Yuzhmorgeologiya</i>	March 1999	HBST	64
South Georgia Island/Shag Rocks (Subarea 48.3)	RV <i>Nathaniel B. Palmer</i>	June 2004	Blake/Otter	17
South Sandwich Islands (Subarea 48.4)	RV <i>Nathaniel B. Palmer</i>	June 2004	Blake/Otter	8
Bouvet Island (Subarea 48.4)	RV <i>Nathaniel B. Palmer</i>	June 2004	Blake/Otter	12

in Figure 2(c). Sampling for the South Sandwich Islands area consisted of six depth-stratified stations, all using the Blake trawl. Sampling for the Bouvet Island area consisted of six depth-stratified stations, three using the Blake trawl, and three using the bottom otter trawl.

Biomass

For all samples used in this study, the trawl catch was secured on deck, shovelled into baskets and moved off the back deck. The contents of each basket were emptied onto sorting tables, the fish removed, and the remaining benthos then sorted or, as necessary, returned for weighing and random subsampling. In some instances, particularly in regions along the northern shelf of the Antarctic Peninsula, the biomass of the hauls was so great that only a portion of the catch could feasibly be transferred into baskets for weighing and sorting. In these cases, fish were removed while the catch was on the back deck and the benthos was shovelled into baskets. Up to 20 baskets of benthos were transferred to the sorting area for weighing. Additional basket loads were counted and discarded. In this way, an average weight per basket was calculated for extrapolation to the entire haul.

Biomass of megafaunal invertebrates by sampling station was standardised by prorating nominal pooled catch of the station's swept area to 1 n mile². The area of sampled seabed at each station was determined by the latitude/longitude coordinates taken with GPS from the start to the end of bottom trawling (seabed contact), and the average trawl mouth width while the trawl was on the bottom. In the case of the northern study area, invertebrate densities were computed by standardising the area swept using only Blake trawl deployments, since this gear has a fixed mouth width.

Contrary to deployments in the study area to the south, a mechanism for recording the dynamic geometry of the otter trawl was unavailable for the northern area. Thus, such comprehensive measurements from the otter trawl were unavailable for biomass calculations. Calculations of biomass for all stations excluded only inorganic matter. Standardised biomass interpolation shading was generated by means of geostatistical gridding of biomasses using kriging assuming a linear variogram model (Cressie, 1991).

Despite the fact that data were collected during four separate cruises, deviations from the above protocol for the treatment and analysis of each haul were minor and not considered to affect the results presented here.

Megafaunal assemblage characterisation

With the exception of the South Orkney Islands study, from which only pooled biomass data are presented here, the benthic invertebrate catch was compositionally analysed by sorting into operational taxonomic units. Although only data at the level of phyla are visually presented here, sorting and data recording were conducted with greater complexity and resolution. However, identification to species-level for all benthic invertebrates encountered was not considered feasible in terms of available time and personnel. The practicality of identification to species (or even morphospecies) level for benthic invertebrates of the Southern Ocean was considered limited due both to the confused state of the taxonomy of many difficult taxa, and also the state of flux in species diversities. Such flux is exemplified by the few available population-level molecular datasets that indicate the possible existence of multiple cryptic species within long-considered circumpolar species, e.g. the isopods *Ceratoserolis*

trilobitoides (Held, 2003) and *Glyptonotus antarcticus* (Held, 2005) and the crinoid *Promachocrinus kerguelensis* (Wilson et al., 2007). Nevertheless, where a particular taxon was often found to be dominant and was instantly recognisable, it was identified to genus (e.g. the isopod genus *Glyptonotus*, the polychaete genus *Laetmonice*). Thus, with maximisation of shelf area sampled a priority, the catch was sorted into an average of approximately 50 operational taxonomic groupings per region. Weights for each were recorded and individuals were counted where appropriate. Any dead or unsortable organic matter was also weighed and, for the latter, characterised (e.g. 60% bryozoan fragments, 30% ophiuroid arms, 10% organic matter) where possible. Algae were also weighed and recorded. Inorganic matter and incidentally caught pelagic invertebrates were only weighed in cases where subsampling was necessary. When excessive biomass prevented complete analysis of a haul, weighed baskets of benthos were numbered and a subset (maximum feasible) randomly chosen.

For the purpose of meso-scale comparisons of benthic invertebrate composition between stations, standardised weights were pooled within each phylum to calculate the proportion each contributed to the total biomass. These calculations excluded the dead uncharacterisable portion of the unsortable organic matter (described above), as well as inorganic material, pelagics and algae.

Results

Northern Antarctic Peninsula and the South Shetland Islands

Standardised biomass (tonnes n mile⁻²) of total benthic invertebrate assemblages encountered off the northern Antarctic Peninsula and the South Shetland Islands (Figure 3) illustrates extremes. Despite the fact that the assemblages supporting the greatest (257.1 tonnes n mile⁻²) and the smallest (0.03 tonnes n mile⁻²) benthic biomass – a difference of four orders of magnitude – were both recorded from the shelf north-northeast of Joinville Island, it is the more general contrast in patterns between the northern shelves of the Peninsula with those of the South Shetland Islands that is most immediately striking. The enormous biomass of benthos encountered along the Peninsula, indicating long- and well-established communities, stands in stark contrast to the relative paucity consistently encountered along the South Shetland Island chain. Superimposed on this broad geographic pattern in biomass is a greater complexity of habitats revealed for the shelves of Elephant Island and north-northeast of Joinville Island epitomised by the extremes

stated above. This pattern is particularly evident at those stations located beyond the easterly limits of Joinville Island's coast, the majority of which support less than 0.5 tonnes n mile⁻² of benthic megafauna. By comparison, stations located along the Peninsula support communities of benthos larger by an order of magnitude or more, many with over 100 tonnes n mile⁻² of invertebrate biomass. Only five stations are exceptions to this pattern of high Peninsula biomass. The westernmost station supports a community biomass that resembles those encountered at the easternmost stations. This stands, on the one hand, in stark contrast to the communities immediately to its east, while on the other hand appears to parallel the sparsely populated communities found on shelves to the north and across the Bransfield Strait. The depths of this station and the four additional stations along this shelf that indicate low biomass were all greater than 400 m.

The shaded regions overlaid on Figure 3 were constructed by kriging the discrete standardised invertebrate biomass permitting a visually explicit broader-scale delineation of shelf regions where high levels of benthic invertebrate biomass are likely to be encountered. This interpolation indicates that the entire region along the shelf of the Peninsula, as well as eastern and southeastern shelf areas of Elephant Island, are considerably higher in total invertebrate biomass than other areas of the shelf observed.

Patterns in the composition of benthic megafaunal invertebrate assemblages can also be seen along these shelf habitats (Figure 4). The proportions contributed by each phylum to the total benthic invertebrate biomass at station localities are illustrated in the form of piegraphs. For visual simplicity, composition data from stations in close vicinity, and at similar depths, were pooled. The depth range and other details each piegraph represents can be referenced in Table 2.

A broad geographic pattern in megafaunal invertebrate dominance is apparent; those shelves west and north of the main South Shetland Island chain are, relative to those shelves east of the main chain including Elephant Island and those north of the Antarctic Peninsula, dominated more often by Echinodermata, while the main component of the benthos along the latter shelves are Porifera (primarily massive hexactinellid sponges). Again, superimposed on this general pattern of invertebrate composition, are regions of greater compositional complexity: north of King George Island, west and northwest of Elephant Island and north-east of Joinville Island.

Table 2: Depth range of stations pooled for benthic invertebrate composition of the northern Antarctic Peninsula and South Shetland Islands. Number codes refer to composition piegraphs illustrated in Figure 4. Stations pooled per piegraph (*n*) are parenthesised. The totality of seabed area trawled (n miles²) and analysed for benthic megafaunal invertebrate catch is indicated in **bold font**.

Piegraph	Depth range (m)	Area of seabed (n mile ² × 10 ⁻³) sampled	Piegraph	Depth range (m)	Area of seabed (n mile ² × 10 ⁻³) sampled
1	300–400	10.60 (1)	26	450–500	10.40 (1)
2	100–200	21.70 (2)	27	300–500	47.08 (3)
3	100–250	33.96 (3)	28	100–300	15.18 (2)
4	300–450	37.80 (3)	29	50–100	8.18 (1)
5	100–200	70.34 (6)	30	700–800	5.32 (1)
6	300–450	42.80 (3)	31	300–400	18.84 (2)
7	50–200	54.70 (5)	32	100–300	17.16 (2)
8	100–200	11.63 (1)	33	300–500	19.91 (2)
9	200–300	50.30 (4)	34	700–800	12.00 (1)
10	300–450	23.79 (2)	35	400–500	28.86 (2)
11	200–300	40.12 (3)	36	100–300	17.60 (2)
12	300–400	23.10 (2)	37	100–200	15.88 (2)
13	400–500	19.19 (2)	38	200–300	5.46 (1)
14	150–300	51.90 (4)	39	100–300	50.49 (6)
15	300–400	22.90 (2)	40	300–500	48.49 (5)
16	50–100	21.67 (2)	41	300–500	41.57 (4)
17	100–200	24.30 (2)	42	200–300	88.96 (9)
18	200–300	39.91 (3)	43	100–200	65.00 (8)
19	50–200	36.76 (3)	44	50–100	6.01 (1)
20	50–100	22.00 (2)	45	700–800	10.20 (1)
21	300–500	21.10 (2)	46	300–500	48.42 (5)
22	100–200	21.04 (2)	47	200–300	10.00 (1)
23	350–400	12.10 (1)	48	200–300	13.90 (1)
24	50–150	40.95 (3)	49	50–100	14.50 (1)
25	150–200	24.70 (2)	Total seabed area		1.40 n mile²

Despite the fact that this region can be geographically delimited quite clearly either by extremes in total benthic biomass or by which phyla, Echinodermata or Porifera, has the greatest influence on that biomass, the resulting demarcations are not the same. Although habitats supporting enormous amounts of biomass can be used to predict the dominance of Porifera, a benthic community dominated by Porifera in terms of biomass does not necessarily predict the magnitude of that community's total biomass. Likewise, a benthos dominated by echinoderms could never represent a total community biomass of the magnitude seen along the northern Peninsula.

Only in terms of depth is there a general trend (see also Lockhart and Jones, 2006). Piegraphs 30, 34 and 45 in Figure 4 represent the only off-the-shelf stations (500–800 m). In terms of composition, an increase in the contribution of Cnidaria to the total biomass of these off-the-shelf communities is noted and can be attributed to an abundance of very large (and heavy) anemones. Not surprisingly, total biomass is lower than that generally found on

the shelf. Nevertheless, more than a few of the shelf habitats sampled exhibited a paucity of megafaunal biomass by comparison.

South Orkney Islands

The standardised biomass of the benthic invertebrate assemblages encountered on the shelves of the South Orkney Islands (Figure 5) presents a complex, though relatively well-defined, picture. Two general trends are discernible. Moderate to low densities of benthos appear to typify the outer southern shelf extension. However, in the vicinity of the islands themselves the trend is west to east, whereby a region of low biomass on the western shelf contrasts with a concentration of the greatest biomass recordings documented for this island group to the east and southeast.

As the sampling strategy and gear type deployed here was the same as that off the Antarctic Peninsula and the South Shetland Islands, a direct comparison of standardised biomass is permissible. Noted

first is the absence of the extreme biomass observations that typify the shelves north of the Peninsula and west of Elephant Island. Benthic invertebrate biomass observed for the shelves around the South Orkney Islands never exceeded 50 tonnes n mile^{-2} . In contrast are the regular recordings off the Peninsula of biomass 2- to 6-fold greater. However, the contrast is not as great as that seen between the shelves of the Peninsula and those north of the main South Shetland Island chain. The complex distribution, and scale, of invertebrate biomass most greatly resembles that observed around Elephant Island. An examination of the overlaid shaded regions of continuous standardised densities in Figure 5 demonstrates four areas across the shelf that may support higher levels of biomass relative to other areas. However, it should be noted that there is no data between the three areas from the south to the east shelf, and that this may be one continuous region of relatively high biomass.

Compositional data on the benthic invertebrate communities encountered on the shelves of the South Orkney Islands is not available. However, with the Peninsula and South Shetland Island data for reference, there is the opportunity for some degree of inference. As no echinoderm-dominated assemblages were recorded to have a biomass greater than 10 tonnes n mile^{-2} , it would be reasonable to assume that the shelves immediately to the south and to the west of the South Orkney Islands support a sponge-dominated benthos.

South Georgia

As previously indicated, the substantially different gear types deployed at South Georgia, the South Sandwich Islands and Bouvet Island (northern region), confound direct comparison with the results presented for the Antarctic Peninsula, the South Shetland Islands and the South Orkney Islands (southern region), and any comparisons between these broad study regions must be made with caution. Gear selectivity for the northern regions may include an under-representation of Mollusca due to the ability of octopods to dart more easily out of the path of the smaller trawl mouth width compared to the commercial-sized bottom trawl gear deployed at the southern regions. On the other hand, total standardised biomass will be greater due to retention of finer material, because the frame of the Blake trawl collects and retains smaller organisms.

Standardised benthic invertebrate biomass recorded for the shelf habitats sampled off South Georgia and Shag Rocks varied (Figure 6) but was consistently high on the northwest shelf of the

former. The greatest biomass of the region was recorded from a shallow bay (50–100 m) on the northwest coast of South Georgia.

The relative contributions of benthic invertebrate phyla to the total standardised biomass recorded at each station are illustrated in Figure 7. A general trend in megafaunal distribution is indicated. At two of the three Shag Rocks stations, the benthos is dominated by tunicates. However, echinoderms are a significant component of the community at all three stations. The megafaunal invertebrate assemblages encountered on the northwestern shelf of South Georgia are dominated by Echinodermata but biomass dominance is replaced further east along the northern shelf by Porifera. Hexactinellid sponges make up the majority of the two northernmost Porifera-dominated communities, whereas the more southerly stations were dominated by demosponges. A benthic assemblage of large anemones was encountered at a relatively deep station (~300 m).

South Sandwich Islands

Standardised benthic invertebrate biomass of the South Sandwich Island chain is illustrated in Figure 8. A distribution trend for the benthic invertebrate composition is not easily discernable, possibly due to the different depths sampled. At Zavodovski Island to the north, the two hauls were conducted at the same depth (330 m) and the invertebrate fauna composition (Figure 9) very much resembled that seen at South Georgia sites. A diverse assemblage of echinoderm fauna was encountered around Candlemas Island (118 m) further south. The greatest depth sampled for invertebrates along this island chain was at Montague Island further south (400 m) where cnidarians share dominance with echinoderms. Bryozoa was the dominant phylum at the southernmost island sampled, Bristol Island, which also represented the shallowest station at this island group (85 m).

Bouvet Island

The greatest standardised benthic invertebrate biomass recorded, not only for Bouvet Island but also for the other island groups in the northern study area sampled with this gear type (i.e. South Georgia and the South Sandwich Islands), was on the eastern shelf (Figure 10). However, the great biomass at this location was not a result of Porifera but rather the phyla Annelida, principally sabellid polychaete tubes (Figure 11). North and south of this station these polychaetes and their tubes still account for a significant portion of the benthos

even though a consortium of Echinodermata dominate overall at these, and all, stations. Echinoderm dominance is most pronounced at the deepest stations on the west and south shelves.

Discussion

The greatest potential for understanding and identifying the key aspects shaping the benthic invertebrate megafaunal communities of Southern Ocean shelf habitats lies with the data presented here for the northern Antarctic Peninsula and the South Shetland Islands. The data may be basic but the sampling is intensive and has allowed some coarse but clear patterns in biomass and composition to be identified. Although a relationship with depth is indicated, sampling has not been extensive and patterns at slope depths should be considered separately and will not be addressed further here.

Observations of both biomass and composition reveal broad geographic patterns along the shelves, within which regions of greater complexity can be identified. In terms of biomass, the shelves north of the Antarctic Peninsula represent an extreme compared to the relatively sparse South Shetland Island shelf. The situation is reversed at either region's easternmost shelves. In terms of composition, the demarcation occurs where the sponge-dominated communities most frequently encountered on both shelf systems, rather abruptly subside westwards on the shelf north of the South Shetlands off western King George Island. In broad terms, this demarcation corresponds to the two 'core communities' of Antarctic macrobenthos identified by Gutt (2007): one dominated by sessile suspension feeders and the other dominated by mobile epifauna and infauna. Again, at the eastern extremes of both shelf systems a greater complexity is indicated.

The role iceberg scouring plays in shaping the Antarctic benthos to depths of up to 600 m (Gutt, 2001) has received a recent surge of interest (Gutt and Starman, 1998; Brey et al., 1999; Peck et al., 1999; Gutt, 2000; Gutt, 2001; Gutt and Starman, 2001; Gutt and Piepenburg, 2003; Teixidó et al., 2004). Different levels of iceberg disturbance, which various parts of this region might experience, are a possible explanation for the observed patterns. Those stations to the northeast of Joinville Island are those most likely to be affected by Weddell Sea gyre currents and the loading of icebergs that this major system carries with it in its clockwise circulation. Large icebergs grounding on this outer shelf at a relatively high frequency would prevent the massive biomass that typifies the invertebrate community of the northern Antarctic Peninsula shelf from becoming established. The contrast in exposure between

the northern shelves of the South Shetland Islands and those of the Antarctic Peninsula at first consideration appears to lend itself to an iceberg-scouring hypothesis also. However, is the frequency of icebergs travelling with the Antarctic Circumpolar Current (ACC), parallel with the coast of the main South Shetland Island chain, really as intense as that being carried northeast past Joinville Island as to prevent any high biomass refuge from remaining? Such refugia were encountered at Elephant Island and are reported also from the intensely ice-scoured shelves of the eastern Weddell Sea (Gutt and Piepenburg, 2003). And for that matter, is the density of icebergs north of the South Shetland Islands really that much greater than within the Bransfield Strait? In fact, it is precisely the low iceberg density of this whole region that facilitated such intense sampling. Furthermore, the low biomass region northeast of Joinville Island represents the eastern and southern limits to sampling due to a high density of icebergs.

Iceberg scouring is not the only possible source of disturbance that Antarctic shelf habitats might experience. The degree to which these two coastlines have been affected by historical commercial fishing activities differs. The shelf northwest of Joinville Island was exploited at irregular intervals from 1978 to 1989 (Kock et al., 2004). Likewise, commercial bottom trawl fishing activities once occurred along the northern coast of the South Shetland Islands including Elephant Island (Kock, 1992) in the late 1970s and early 1990s (Kock and Jones, 2005). In contrast, the shelf areas off the northern Antarctic Peninsula within the Bransfield Strait that support the greatest biomass of benthos are also those that have escaped focused commercial activities.

Seabed disturbance can also arise from the impact of demersal sampling gear used in scientific surveys and the sampling conducted in this region for this study is no exception. Although the 2006 cruise off the Antarctic Peninsula represents the first comprehensive survey of this region, the South Shetland Islands, including Elephant Island, have been surveyed several times (Kock and Jones, 2005). Nevertheless, such surveys impact a negligible area of seabed within the area sampled. The total number of gear deployments undertaken at this primary study region impacted 1.4 n miles² of seabed, whereas the total area of seabed within the 50–500 m survey region is 14 540 n miles² (6 832 n mile² for the South Shetland Islands (Jones et al., 1999) and 7 709 n mile² for the Antarctic Peninsula (Smith and Sandwell, 1997)). Hence, the two surveys examined in this part of the study collectively impacted a mere 0.0096% of the targeted

seabed within the survey area. In order to disturb 1% of this region's seabed, 208 scientific surveys of this magnitude would need to be conducted. Unfortunately, catch and effort information for the commercial bottom trawl fishery that occurred in this region is not reliably documented; comparative data regarding the number of vessels participating, or the amount of fish taken, during the seasons that fishing occurred, is scarce (Kock et al., 2004).

Even considering a severe disturbance regime resulting from the combined effects of iceberg scouring and fishing activities, these questions remain: (i) was this combined disturbance regime intensive enough to leave no refuge of high biomass along the main South Shetland Island chain?; (ii) how did such refugia survive around Elephant Island, including those parts of the shelf targeted by fishing, when the combined disturbance regime at this island and at the rest of the South Shetland chain was likely similar? Moreover, no disturbance regime, severity or source can be invoked to explain the abrupt delimitation along the main South Shetland chain, in the vicinity of the mid-King George Island coast, of sponge-dominated communities regardless of total biomass recorded. Indeed, the existence of unidentified key factors influencing the population growth and presence of sponges, other than physical disturbance and predation, has been acknowledged (Gutt, 2007).

It appears that this southern portion of the South Shetland Island chain shelf simply does not have the potential to support the enormous benthic biomass seen across the Bransfield Strait and also at Elephant Island, even given a complete absence of disturbance. Such enormous megafaunal biomasses in the Southern Ocean are achieved by, and most likely can only be achieved by, the presence of a community of massive hexactinellid sponges. All along the northern Antarctic Peninsula, large communities of these sponges (most likely of the genus *Rossella*) were regularly encountered, individuals of which reached approximately 1 m in diameter with a barrel volume large enough to easily accommodate a large man (pers. obs.). Only at South Georgia were comparatively impressive specimens observed: a refuge of hexactinellids (almost as massive) was encountered on this shelf system that has nevertheless been subject to commercial bottom trawl fisheries still active at South Georgia up until the 1989/90 season (Kock, 1992). Not surprisingly, these slow growing hexactinellids (Dayton, 1978) are indicative of a stable Antarctic environment (Gutt, 2000). Gutt and Starman (2001) use the presence of these sponges in studies of successional recovery after iceberg scouring events to indicate and define the final of four stages of benthic

assemblage succession, labelled UD (undisturbed). However, the percentage of cover and the dimensions of these sponges in a 1 m² photographic subsample required for a UD categorisation was just 3% coverage (Teixidó et al., 2004) and an average diameter of approximately 20–30 cm (Gutt and Starman, 2001; Gutt and Piepenburg, 2003; Teixidó et al., 2004). Hexactinellids of this size – a fraction of those encountered off the northern Antarctic Peninsula – were used to estimate the time since last disturbance as >500 years (Gutt and Starman, 2001; see also Figure 4(a) in Gutt and Piepenburg, 2003). Extrapolating further to estimate the age of what must represent the Antarctic shelf benthos at successional climax encountered in the present study would be formidable.

Regardless of total biomass, shelf regions demonstrating sponge-dominated communities are areas in which this hexactinellid can be found, and presumably have the potential to reach successional climax, as defined by the Antarctic Peninsula communities, if not for disturbance. The severity of disturbance regime, whether by icebergs or by fishing or both, required to explain the biomass densities seen on King George Island's northwest shelves and around Elephant Island is greatly reduced by this more normalised scale (i.e. climax communities are considered such a rare occurrence that they serve only to skew the examination of disturbance). Sponge components of the otherwise echinoderm-dominated communities off the southern islands in the South Shetland chain are, with only one exception, demosponges (non-hexactinellid).

Two major water masses meet in this region, and are vastly different in their physical properties (Orsi et al., 1995). The ACC flows west to east along the Antarctic Peninsula, past the South Shetland Islands and through the Scotia arc (Orsi et al., 1995). The Weddell Gyre off the eastern coast of the Antarctic Peninsula also flows west to east in a clockwise direction. Thus, separated by the Antarctic Peninsula they meet in this region at its tip. Both major water masses can be subdivided further (Orsi et al., 1995). However, in this region, at shelf depths, the Weddell water mass can be differentiated from the ACC water mass by colder temperatures and lower salinity (Orsi et al., 1995). Figure 12 shows the 10-year average sea bottom temperature of the region (C. Hewes, unpubl. data) from CTDs taken during annual US AMLR research cruises.

Cold Weddell water flows around Joinville Island and into the Bransfield to the west until it meets the ACC water mass (Hofmann et al., 1996; Gordon et al., 2000). Cold Weddell water also flows

up between Elephant Island and the rest of the South Shetland Island chain to meet and mix again with the ACC water mass. A third flow of cold Weddell water passes between Elephant Island and Clarence Island to its east (Hofmann et al., 1996; Gordon et al., 2000). This pattern effectively mirrors the distribution of *Rossella*(?) hexactinellid sponges, as shown in Figure 4. This sponge reaches its upper temperature limit at mixed ACC and Weddell waters of $\sim 0.75^{\circ}\text{C}$.

Warm ACC water hugs the Antarctic Peninsula until it reaches the colder Weddell waters of the Bransfield Strait and is deflected north at the southernmost South Shetland Islands, where it continues east along this coast only to be deflected north once again by Weddell waters around King George and Elephant Islands (Hofmann et al., 1996; Gordon et al., 2000). This pattern effectively mirrors the distribution of echinoderm-dominated communities as shown in Figure 4, including those encountered on Elephant Island's northwest shelves. Thus, even without going beyond the level of phyla, it appears that these community assemblages would be largely made up of fauna with sub-Antarctic and Scotia arc affinities. A cursory comparison with the compositional data for the northern regions studied (Figures 7, 9 and 11) is additionally persuasive, whereby the vast majority of sub-Antarctic benthic shelf communities is shown as dominated by Echinodermata. The hexactinellid communities north of South Georgia are very likely to be the sub-Antarctic sister species (apparently with a lower temperature tolerance of $\sim 1^{\circ}\text{C}$) to the hexactinellid communities of the Bransfield Strait and Weddell Sea, and may even replace the ecological niche of this species on the Antarctic Peninsula shelf immediately to the west of the region studied here.

The fauna of the Scotia arc island shelves is widely accepted as having sub-Antarctic affinities (e.g. Koehler, 1912; Hedgpeth, 1969) and may, in the context of the findings presented here, be more appropriately described as ACC fauna. Finer-scale bioregionalisation, for the purpose of successful and sound monitoring of the ecosystem and its resources, among Antarctic islands situated within the path of the ACC, should rely on supplementary data, such as measures of benthic biodiversity.

Conclusions

The benthic invertebrate megafaunal assemblages on the northern shelves of the South Shetland Islands and the northern Antarctic Peninsula can apparently be separated into two zones based on the physical properties of the ACC and the Weddell water masses that meet and mix in this region.

Super-imposed on this geographic pattern are the effects of disturbance regimes, whether by iceberg scouring or historical commercial bottom trawling, which work at smaller spatial scales.

That such zoogeographic zones based on basic water-mass data can separate benthic assemblages described only at the level of phyla indicates the strength of the pattern and suggests that the pattern may hold across multiple taxa. In fact, in the context of this zonation, one of the authors (S. Lockhart) re-examined detailed distribution maps of cidaroid echinoid morphospecies for the same areas covered here. Not only is the pattern of cold Weddell to warm ACC and sponge-dominated to echinoderm-dominated community composition mirrored in these distributions, but in addition, molecular phylogenetic data collected and analysed (S. Lockhart, unpubl. data) supports the scenario hypothesised here for the hexactinellids of the Weddell Sea and the sub-Antarctic. Moreover, the complex distribution re-examined in the context of this zonation hints at providing the key to clarifying the complex nature of the taxon's systematics.

Elegant in its simplicity, such a zonation has the potential to describe complex distributions and, as such, has far-reaching possibilities not only for the bioregionalisation of other Antarctic shelf regions but also as a key to elucidating such classic long-standing mysteries like that of circumpolar species. The most essential next step in research would be to expand the kind of data presented here to other regions of the Antarctic shelf system where the ACC water mass may meet and mix with other high-Antarctic water masses, such as the South Orkney Islands and further west down the Antarctic Peninsula.

Acknowledgements

The authors wish to thank the captains and crews of the RV *Yuzhmorgeologiya* and RV/IB *Nathaniel B. Palmer*. This research could not have been conducted without the assistance of many on board whose cheerful and untiring assistance in sorting the massive amounts of benthos is gratefully acknowledged. Proving critical to the formation of the ideas presented here, we are most grateful to Christian Reiss for his descriptions of the physical oceanographic characteristics of our study area, and also for putting together Figure 12 from unpublished data. Constructive manuscript review was provided by K. Linse, J. Gutt and B. Fernholm, for which we are most appreciative. US National Science Foundation Grant OPP-0132032 awarded to H. William Detrich contributed funding for the ICEFISH cruise.

References

- Brey, T., D. Gerdes, J. Gutt, A. Mackensen and A. Starmans. 1999. Growth and age of the Antarctic bryozoan *Cellaria incula* on the Weddell Sea shelf. *Ant. Sci.*, 11 (4): 408–414.
- Clarke, A., H.J. Griffiths, K. Linse, D.K.A. Barnes and J.A. Crame. 2007. How well do we know the Antarctic marine fauna? A preliminary study of macroecological and biogeographical patterns in Southern Ocean gastropod and bivalve molluscs. *Diversity and Distributions*, 13 (5): 620–632.
- Cressie, N. 1991. *Statistics for Spatial Data*. John Wiley and Sons, New York: 900 pp.
- Dayton, P.K. 1979. Observations of growth, dispersal and population dynamics of some sponges in McMurdo Sound, Antarctica. In: Lévi, C. and N. Boury-Esnault (Eds). *Sponge Biology*. Colloques internationaux du Centre National de la Recherche Scientifique, Paris, 291: 271–282.
- Gordon, A.L., M. Mensch, Z. Dong, W.M. Smethie Jr and J. de Bettencourt. 2000. Deep and bottom water of the Bransfield Strait eastern and central basins. *J. Geophys. Res.*, 105 (C5): 11337–11346.
- Gutt, J. 2000. Some 'driving forces' structuring communities of the sublittoral Antarctic macrobenthos. *Ant. Sci.*, 12 (3): 297–313.
- Gutt, J. 2001. On the direct impact of ice on marine benthic communities, a review. *Polar Biol.*, 24 (8): 553–564.
- Gutt, J. 2007. Antarctic macro-zoobenthic communities: a review and an ecological classification. *Ant. Sci.*, 19 (2): 165–182.
- Gutt, J. and A. Starmans. 1998. Structure and biodiversity of megabenthos in the Weddell and Lazarev Seas (Antarctica): ecological role of physical parameters and biological interactions. *Polar Biol.*, 20 (4): 229–247.
- Gutt, J. and A. Starmans. 2001. Quantification of iceberg impact and benthic recolonisation patterns in the Weddell Sea (Antarctica). *Polar Biol.*, 24 (8): 615–619.
- Gutt, J. and D. Piepenburg. 2003. Scale-dependent impact on diversity of Antarctic benthos caused by grounding of icebergs. *Mar. Ecol. Prog. Ser.*, 253: 77–83.
- Hedgpeth, J.W. 1969. Introduction to Antarctic zoogeography. *Antarctic Map Folio Series*, Folio 11: 1–9.
- Held, C. 2003. Molecular evidence for cryptic speciation within the widespread Antarctic crustacean *Ceratoserolis trilobitoides* (Crustacea, Isopoda). In: Huiskes, A.H.L., W.W.C. Gieskes, J. Rozema, R.M.L. Schorno, S.M. van der Vies and W.J. Wolff (Eds.). *Antarctic Biology in a Global Context*. Backhuys Publishers, Leiden, The Netherlands: 135–139.
- Held, C. 2005. Cryptic speciation in the giant Antarctic isopod *Glyptonotus antarcticus* (Isopoda, Valvifera, Chaetiliidae). *Scientia Marinae*, 69 (2): 175–181.
- Hofman, E.E., J.M. Klinck, C.M. Lascara and D. Smith. 1996. Water mass distributions and circulation west of the Antarctic Peninsula and including the Bransfield Strait. In: Ross, R.M., E.E. Hofman and L.B. Quetin (Eds). *Foundations for Ecological Research West of the Antarctic Peninsula*. AGU Ant. Res. Ser., 70.
- Jones, C.D., S.N. Sexton, and R.E. Cosgrove III. 1999. Surface areas of seabed within the 500 m isobath for regions within the South Shetland Islands (Subarea 48.1). *CCAMLR Science*, 6: 133–140.
- Kock, K.-H. 1992. *Antarctic Fish and Fisheries*. Cambridge University Press, Cambridge: 359 pp.
- Kock, K.-H. and C.D. Jones. 2005. Fish stocks in the Southern Scotia Arc region – a review and prospects for future research. *Rev. Fish. Sci.*, 13: 75–108.
- Kock, K.-H., L. Pshenichnov, C.D. Jones, K. Shust, K.E. Skora, Zh.A. Frolkina. 2004. Joinville–D'Urville Islands (Subarea 48.1) – a former fishing ground for the spiny icefish (*Chaenodraco wilsoni*), at the top of the Antarctic Peninsula – revisited. *CCAMLR Science*, 11: 1–20.
- Koehler, R. 1912. Échinodermes (Astéries, Ophiures et Échinides). In: *Deuxième Expedition Antarctique Française (1908–1910) Commandée par le Dr Jean Charcot*. Masson et Cie, Paris: 270 pp. (in French).
- Linse, K., H.J. Griffiths, D.K.A. Barnes and A. Clarke. 2006. Biodiversity and biogeography of the Antarctic and sub-Antarctic mollusca. *Deep-Sea Res.*, II, 53: 985–1008.

- Lockhart, S.J. and C.D. Jones. 2006. Benthic bycatch composition and characterization of the Northern Antarctic Peninsula. In: Lipsky, J.D. (Ed.). *US AMLR 2005/2006 Field Season Report: Objectives, Accomplishments and Tentative Conclusions*. NOAA-TM-NMFS-SWFSC-397.
- Orsi, A.H., T. Whitworth III and W.D. Nowlin Jr. 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Res.*, I, 42 (5): 641–673.
- Peck, L.S., S. Brockington, S. Vanhove and M. Beghyn. 1999. Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica. *Mar. Ecol. Prog. Ser.*, 186: 1–8.
- Rodríguez, E., P.J. López-González and J.M. Gili. 2007. Biogeography of Antarctic sea anemones (Anthozoa, Actiniaria): What do they tell us about the origin of the Antarctic benthic fauna? *Deep-Sea Res.*, II, 54: 1876–1904.
- Smith, W.H.F. and D.T. Sandwell. 1997. Global sea-floor topography from satellite altimetry and ship depth soundings. *Science*, 277: 1956–1962.
- Teixidó, N., J. Garrabou, J. Gutt and W.E. Arntz. 2004. Recovery in Antarctic benthos after iceberg disturbance: trends in benthic composition, abundance and growth forms. *Mar. Ecol. Prog. Ser.*, 278: 1–16.
- Wilson, N.G., R.L. Hunter, S.J. Lockhart and K.M. Halanych. 2007. Multiple lineages and absence of panmixia in the ‘circumpolar’ crinoid *Promachocrinus kerguelensis* from the Atlantic sector of Antarctica. *Mar. Biol.*, 152 (4): 895–904.

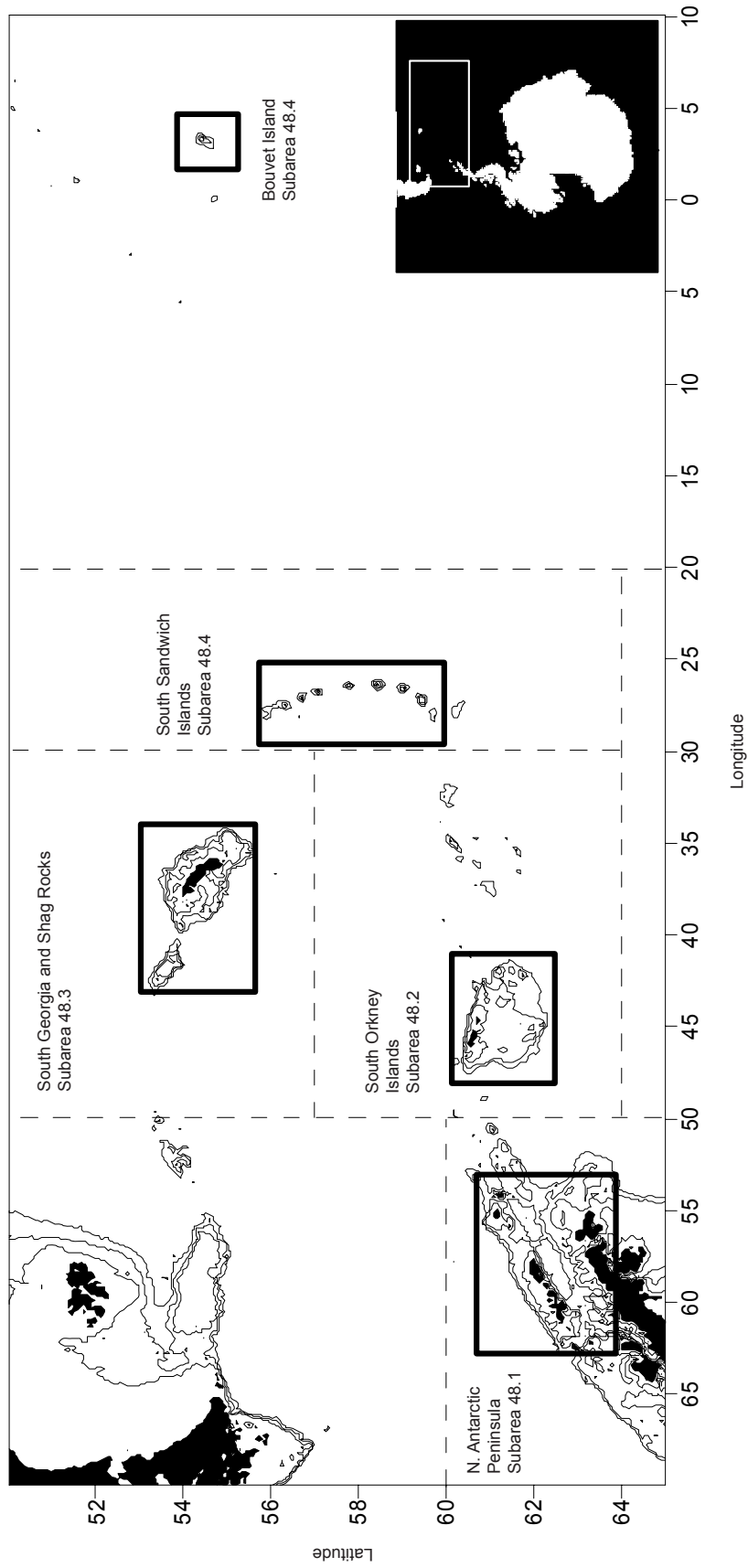


Figure 1: Shelf areas within the Atlantic sector of the Southern Ocean sampled as part of this study, with CCAMLR statistical boundaries.

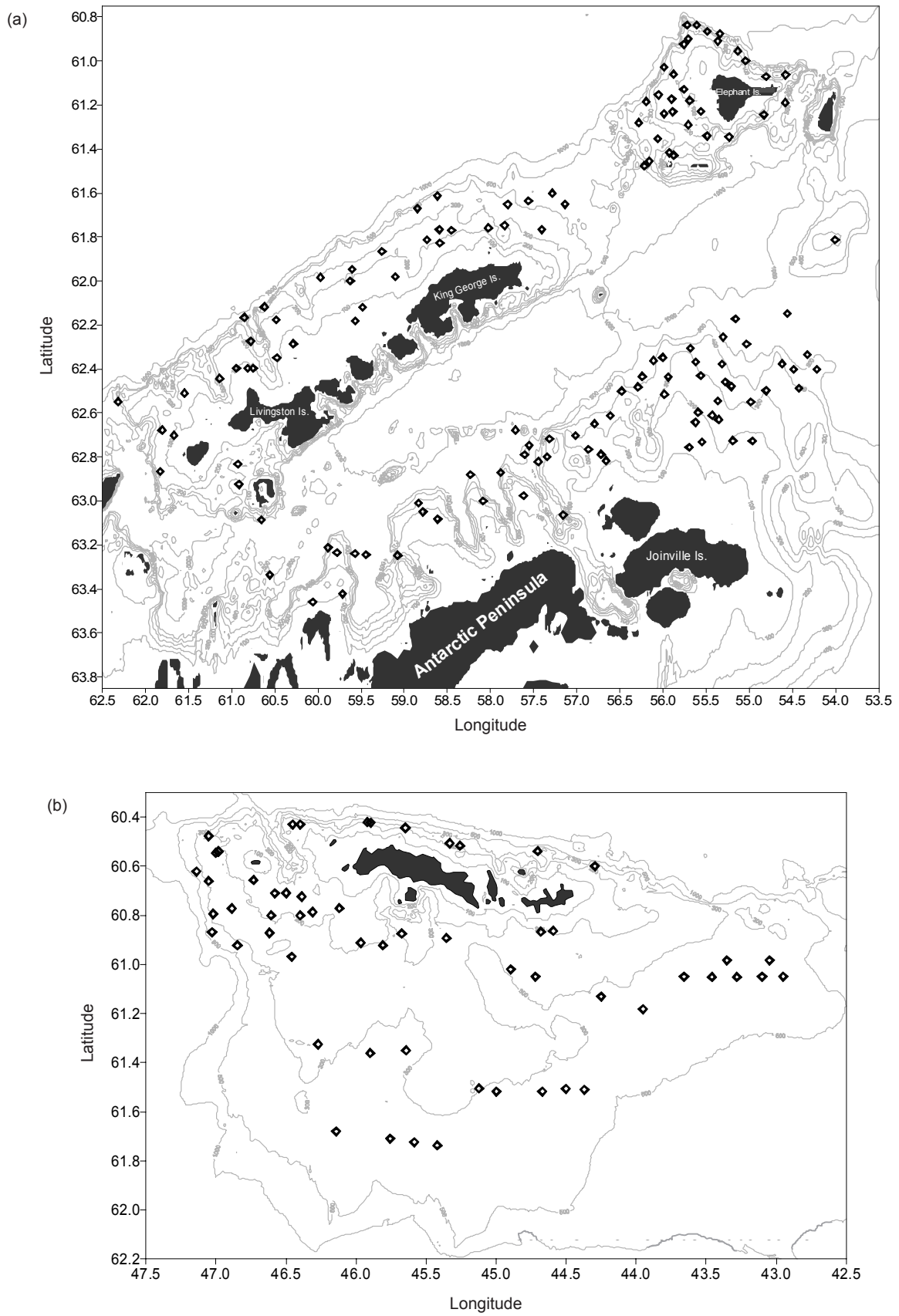


Figure 2: Sampling station locations for: (a) the northern Antarctic Peninsula and South Shetland Islands (Subarea 48.1); (b) the South Orkney Islands (Subarea 48.2).

(continued)

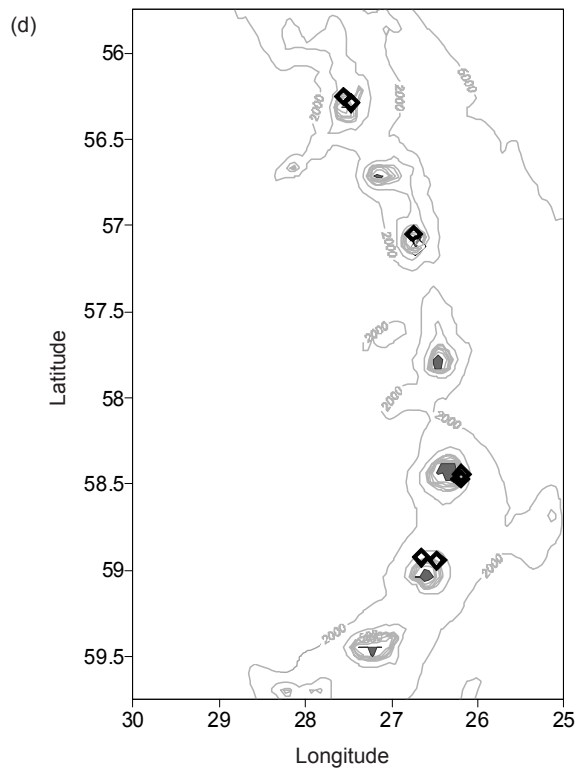
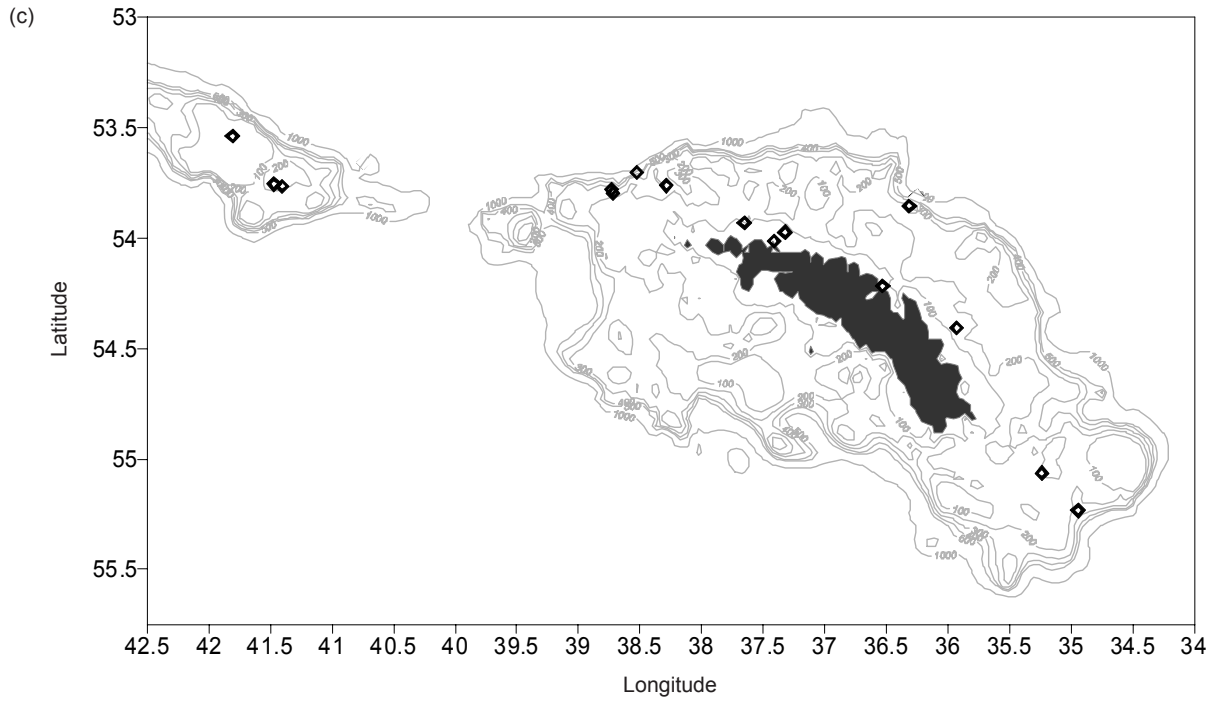


Figure 2 (continued): Sampling station locations for: (c) South Georgia Island and Shag Rocks (Subarea 48.3); (d) the South Sandwich Islands (Subarea 48.4).

(continued)

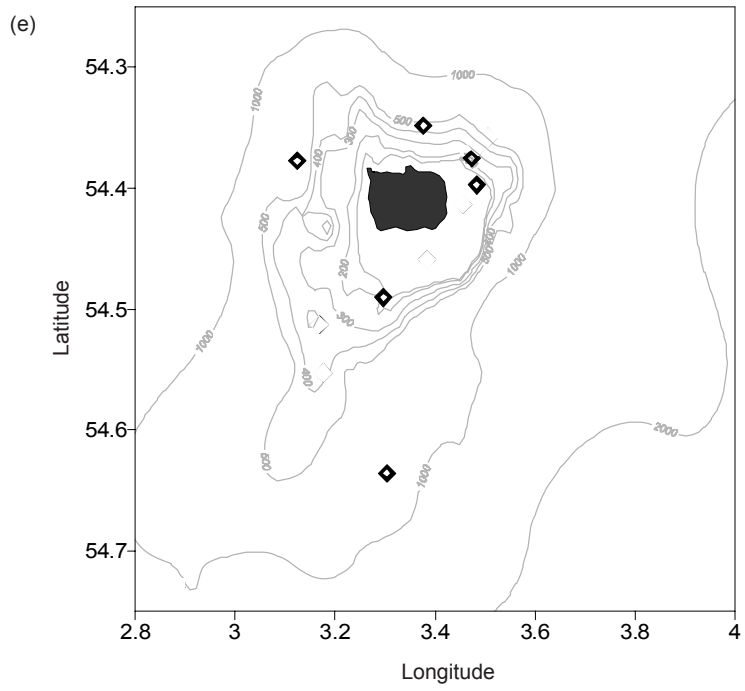


Figure 2 (continued): Sampling station locations for: (e) Bouvet Island (Subarea 48.6).

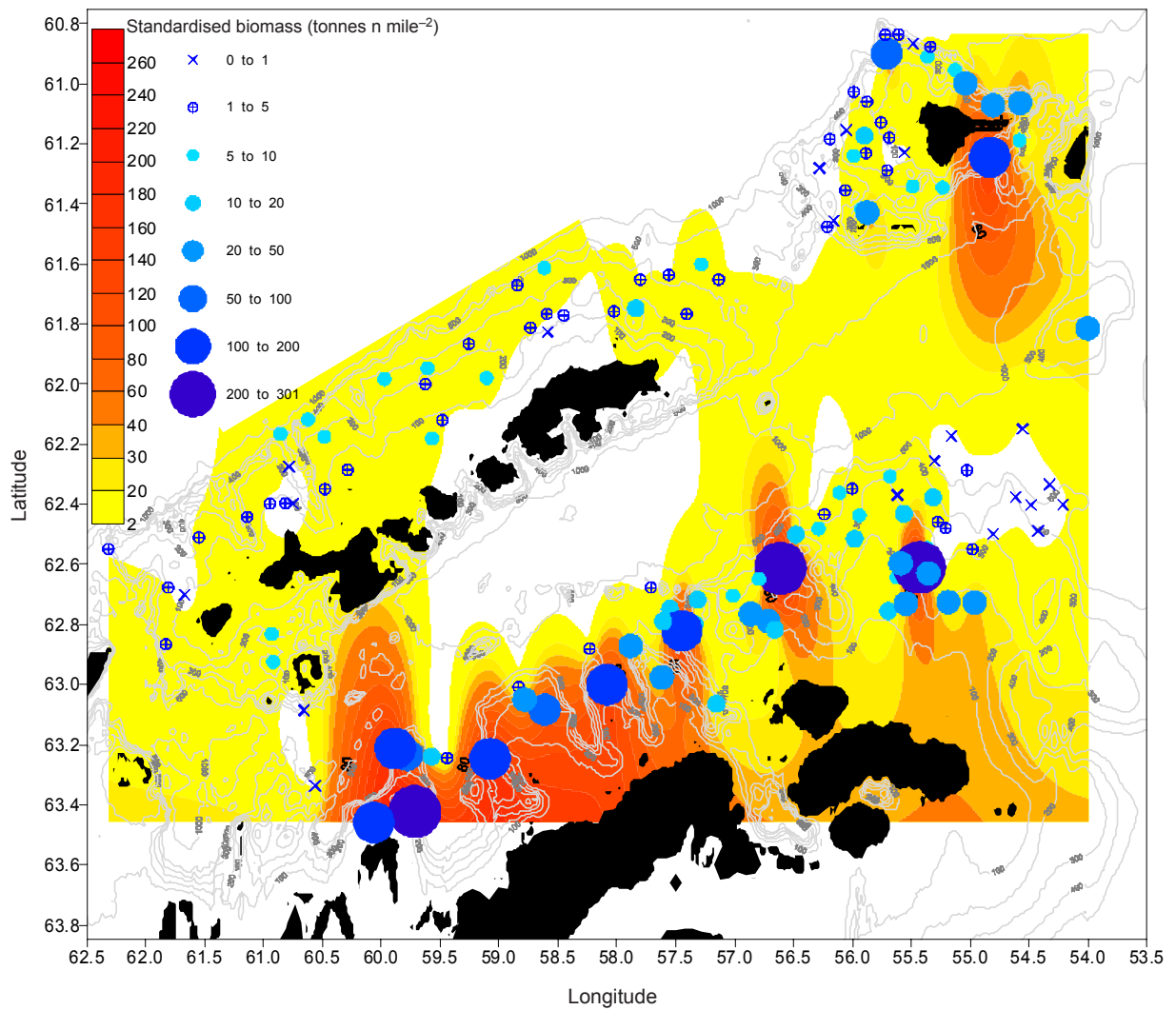


Figure 3: Standardised biomass of benthic invertebrate catch (tonnes n mile⁻²) across the northern Antarctic Peninsula and South Shetland Islands. Overlaid shaded regions were generated through geostatistical gridding of densities using kriging (smoothed interpolation).

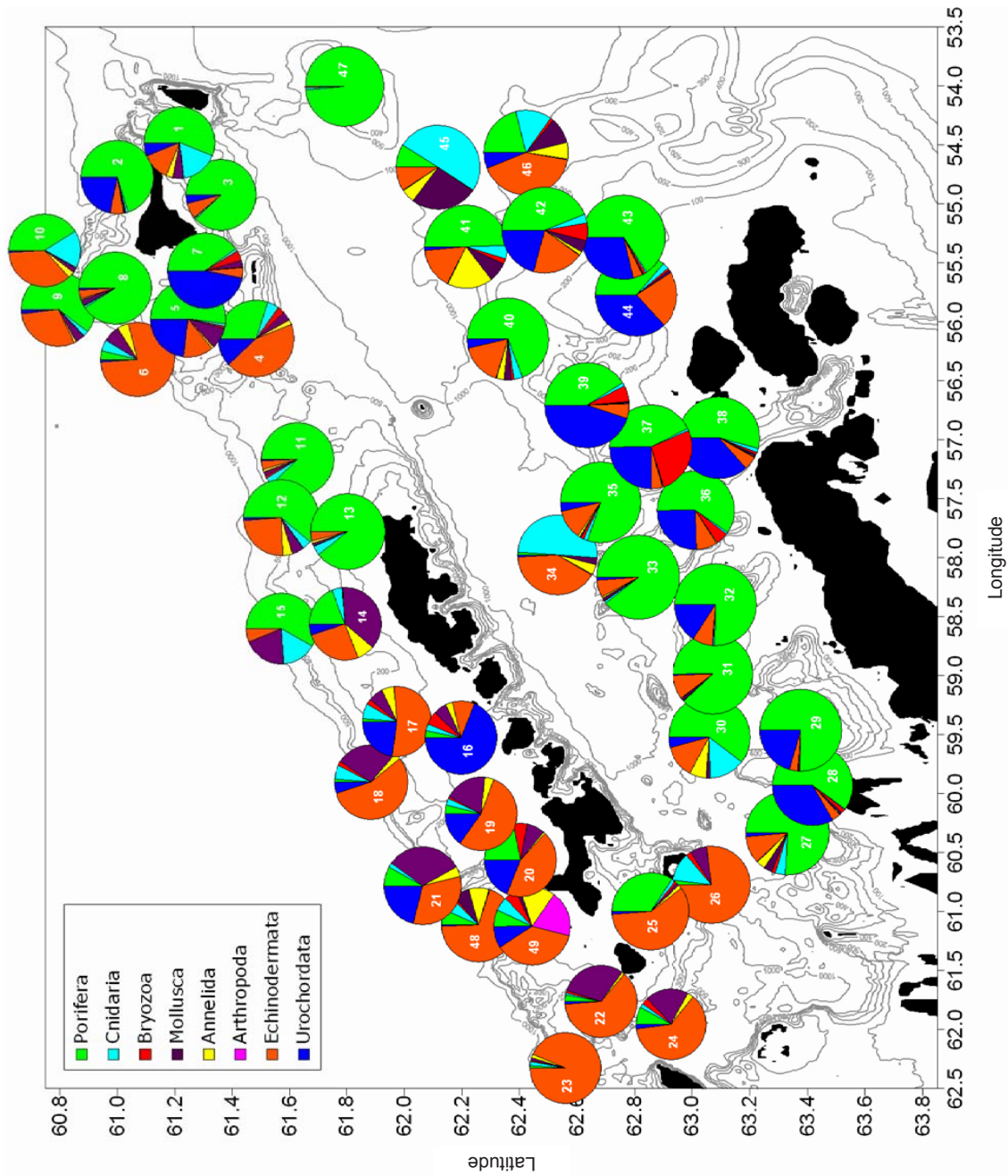


Figure 4: Relative contributions by invertebrate phyla to benthic composition across the northern Antarctic Peninsula and South Shetland Islands shelf areas. Only those phyla represented by at least 1% are graphically represented.

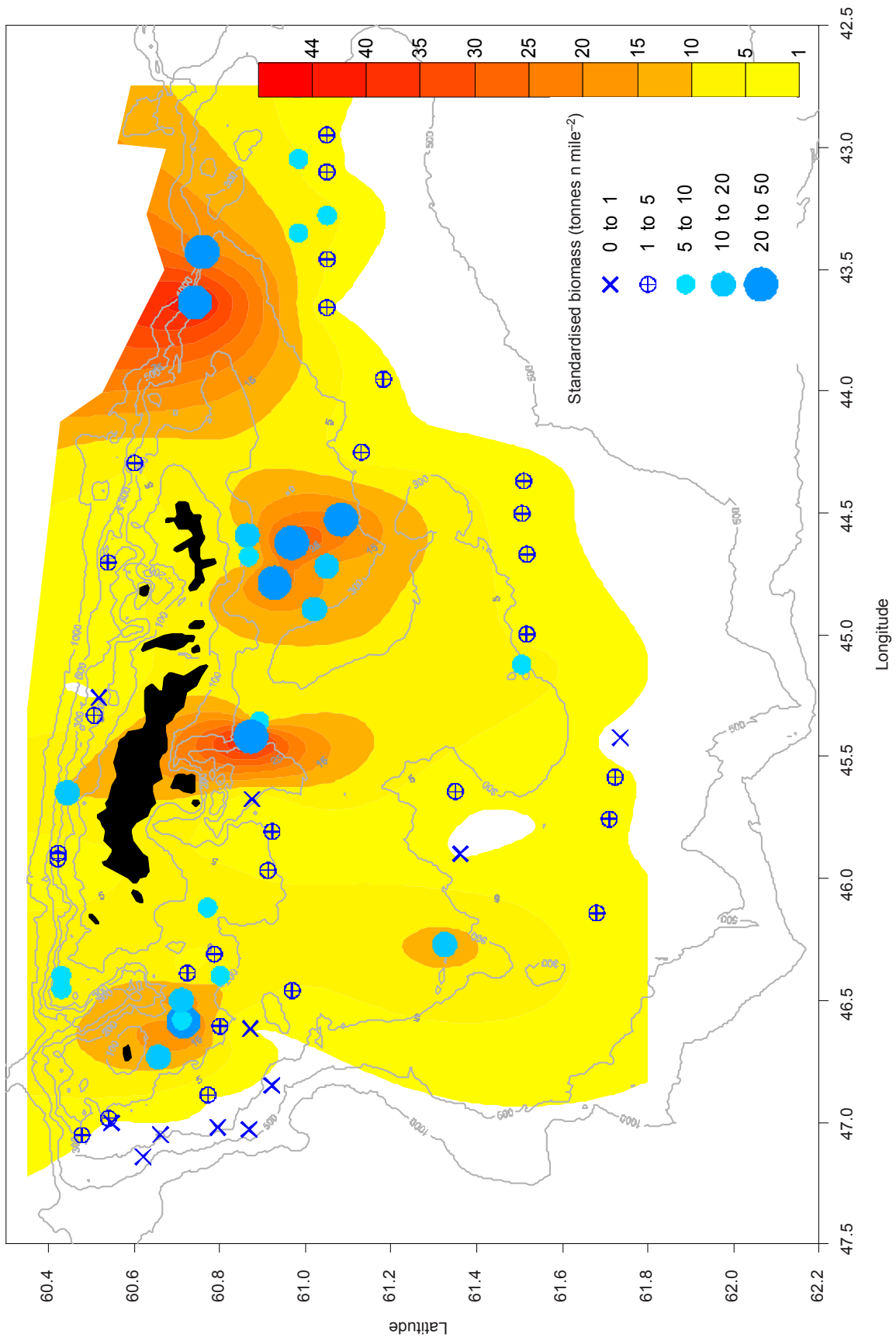


Figure 5: Standardised biomass of benthic invertebrate catch (tonnes n mile⁻²) across the South Orkney Islands shelf area. Overlaid shaded regions were generated through geostatistical gridding of densities using kriging (smoothed interpolation).

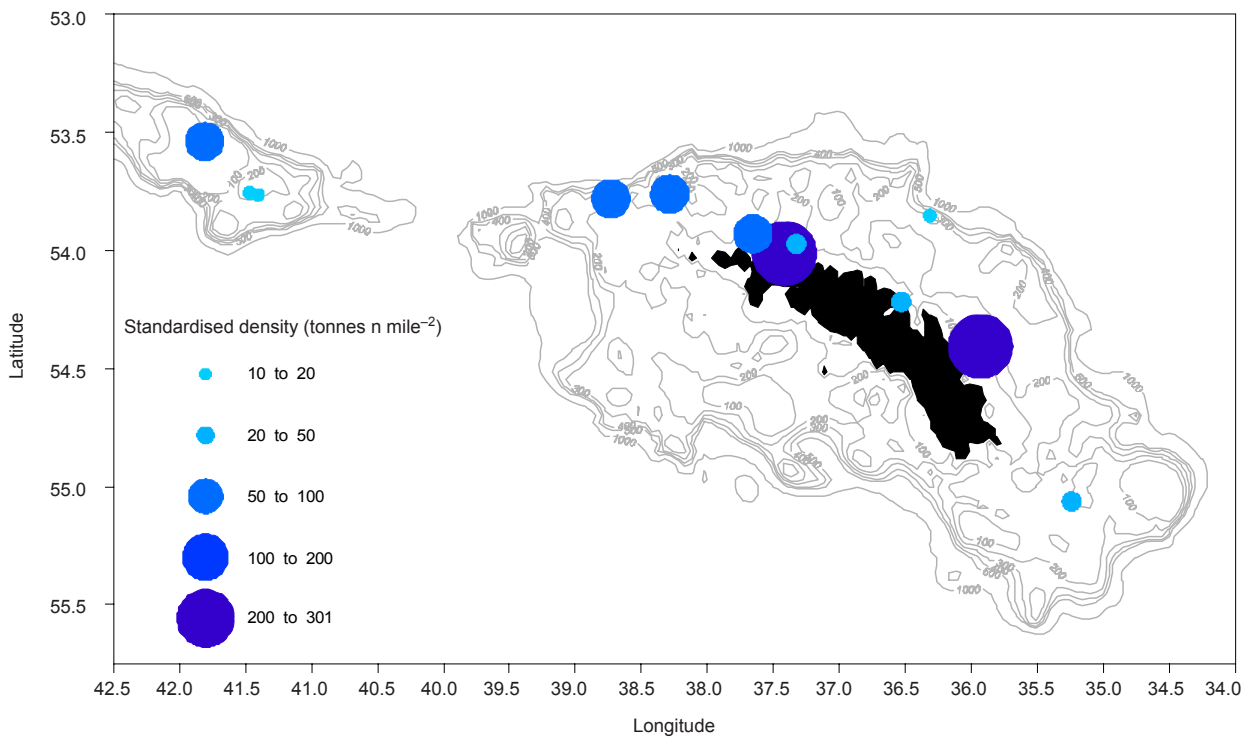


Figure 6: Standardised biomass of benthic invertebrate catch (tonnes n mile⁻²) across the South Georgia Island and Shag Rocks shelf areas.

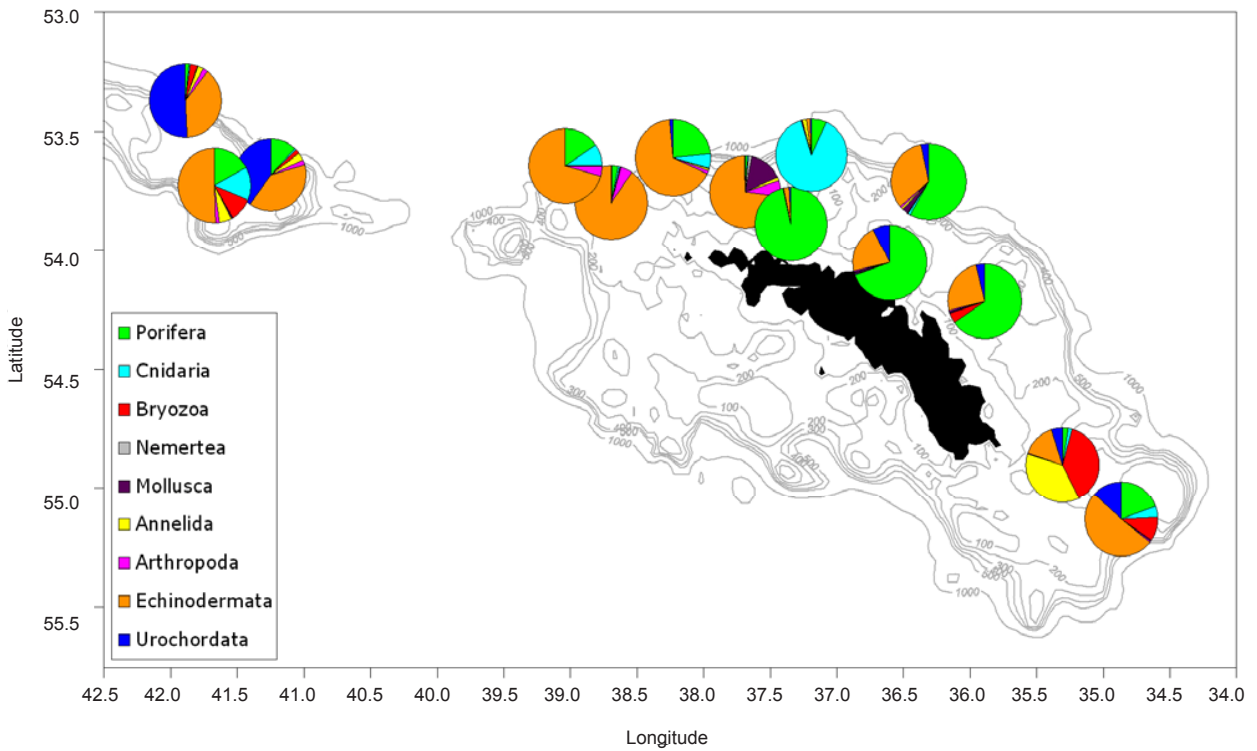


Figure 7: Relative contributions by invertebrate phyla to benthic composition across the South Georgia Island and Shag Rocks shelf areas.

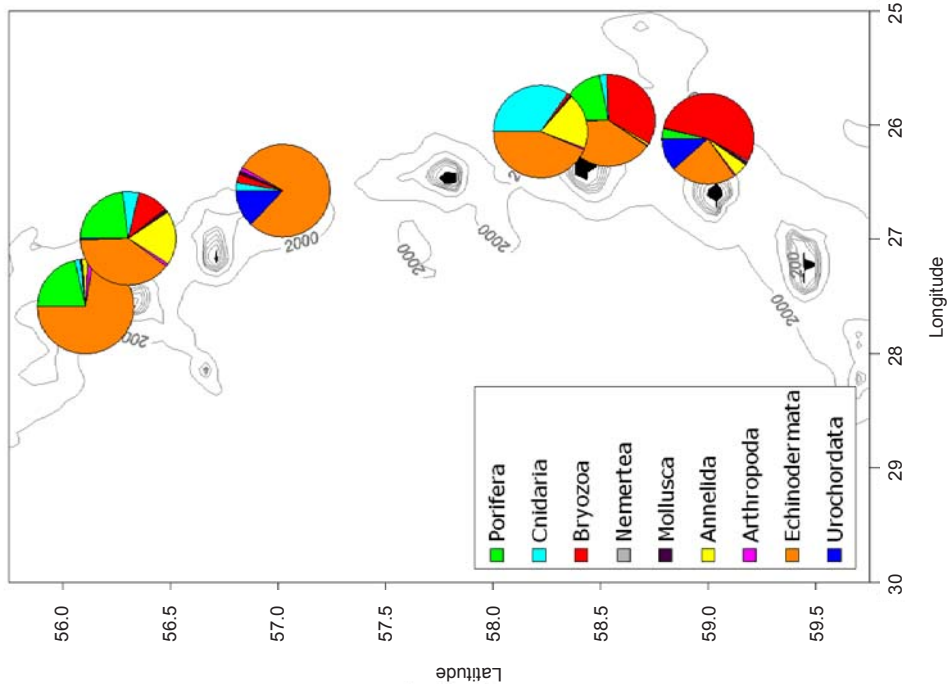


Figure 9: Relative contributions by invertebrate phyla to benthic composition across the South Sandwich Islands shelf areas.

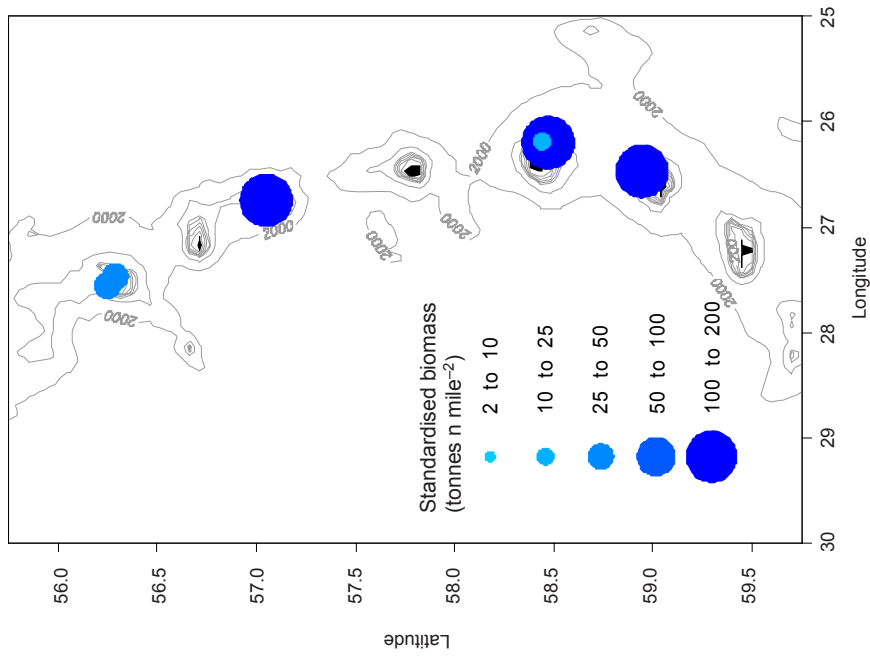


Figure 8: Standardised biomass of benthic invertebrate catch (tonnes n mile⁻²) across the South Sandwich Islands shelf areas.

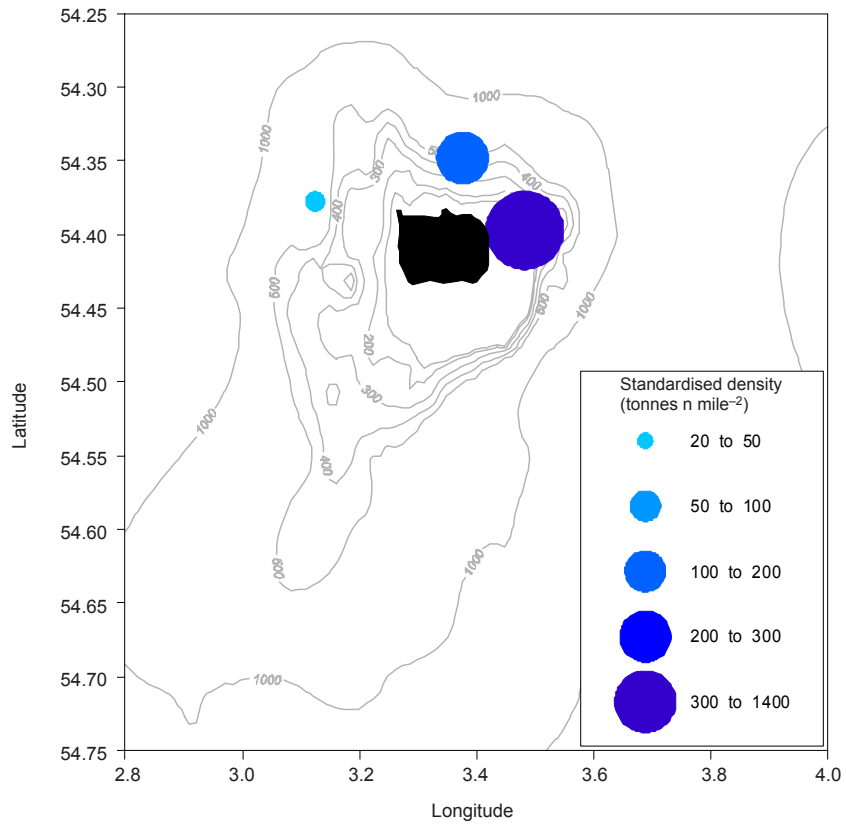


Figure 10: Standardised biomass of benthic invertebrate catch (tonnes n mile⁻²) across the Bouvet Island shelf area.

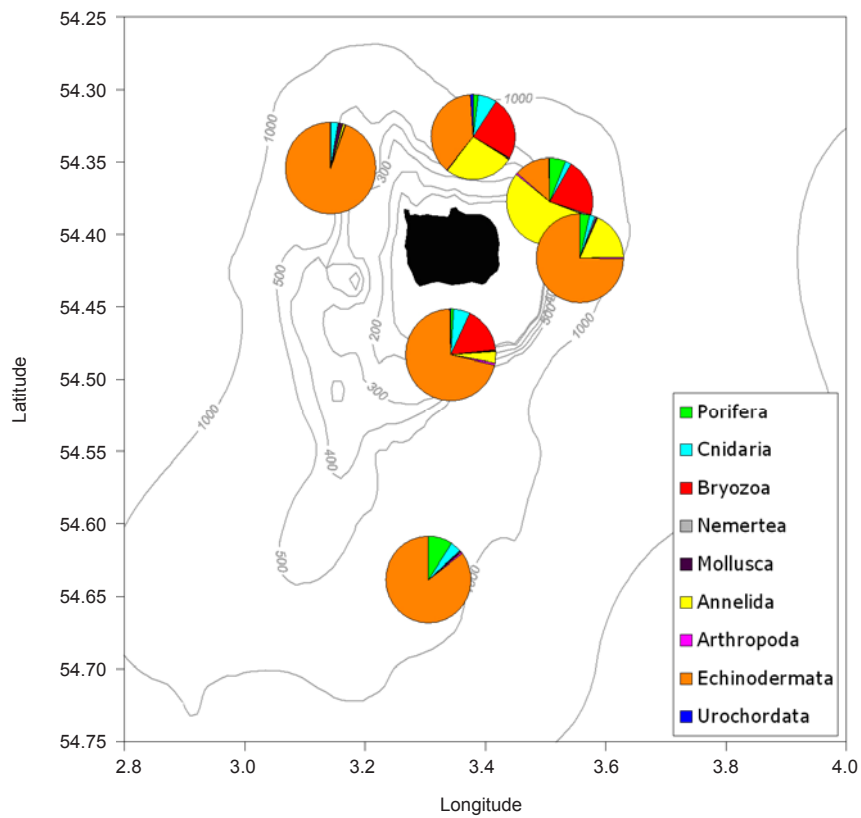


Figure 11: Relative contributions by invertebrate phyla to benthic composition across the Bouvet Island shelf area.

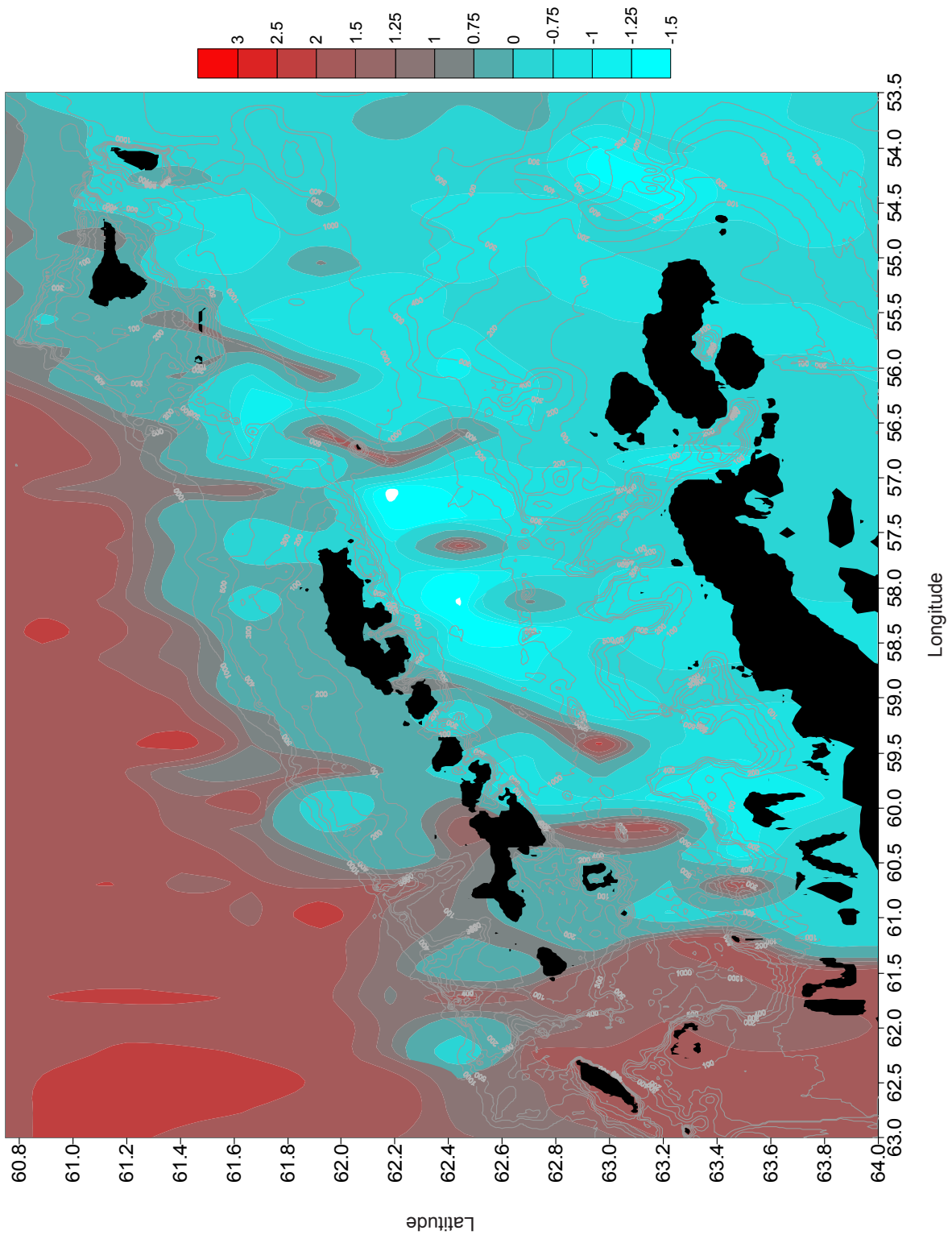


Figure 12: Ten-year average sea bottom temperature of the northern Antarctic Peninsula and South Shetland Islands shelf areas. Data derived from CTD casts taken January–March from 1997 to 2007 as part of the US AMLR survey grid.

Liste des tableaux

- Tableau 1: Informations sur les campagnes et l'échantillonnage réalisés pour la collecte des invertébrés benthiques analysés dans l'article.
- Tableau 2: Intervalle de profondeur des stations regroupées pour la composition d'invertébrés benthiques du secteur nord de la péninsule antarctique et des îles Shetland du Sud. Les codes numériques correspondent aux graphiques de composition en camembert illustrés sur la figure 4. Les stations regroupées par graphique en camembert (*n*) sont entre parenthèses. La totalité des aires de fond marin ayant fait l'objet de chalutage (milles carrés) et analysées pour la capture d'invertébrés de la mégafaune benthique est indiquée en **caractère gras**.

Liste des figures

- Figure 1: Zones de plateau dans le secteur Atlantique de l'océan Austral échantillonnée dans le cadre de cette étude, avec limites statistiques de la CCAMLR.
- Figure 2: Lieux des stations d'échantillonnage pour : (a) le secteur nord de la péninsule antarctique et les îles Shetland du Sud (sous-zone 48.1) ; (b) les îles Orcades du Sud (sous-zone 48.2) ; (c) la Géorgie du Sud et les îlots Shag (sous-zone 48.3) ; (d) les îles Sandwich du Sud (sous-zone 48.4) ; et (e) l'île Bouvet (sous-zone 48.6).
- Figure 3: Biomasse normalisée de la capture d'invertébrés benthiques (tonnes par mille nautique carré) sur l'ensemble du secteur nord de la péninsule antarctique et des îles Shetland du Sud. Les zones foncées superposées ont été générées par une analyse géostatistique consistant à interpoler les densités sur une grille au moyen de la méthode du krigeage (interpolation lissée).
- Figure 4: Importance relative des phyla d'invertébrés dans la composition benthique de l'ensemble du secteur nord de la péninsule antarctique et des secteurs de plateau des îles Shetland du Sud. Seuls les phyla représentés à plus de 1% sont illustrés graphiquement.
- Figure 5: Biomasse normalisée de la capture d'invertébrés benthiques (tonnes par mille nautique carré) sur l'ensemble du secteur du plateau des îles Orcades du Sud. Les zones foncées superposées ont été générées par une analyse géostatistique consistant à interpoler les densités sur une grille au moyen de la méthode du krigeage (interpolation lissée).
- Figure 6: Biomasse normalisée de la capture d'invertébrés benthiques (tonnes par mille nautique carré) sur l'ensemble des secteurs de plateau de la Géorgie du Sud et des îlots Shag.
- Figure 7: Importance relative des phyla d'invertébrés dans la composition benthique de l'ensemble des secteurs de plateau de la Géorgie du Sud et des îlots Shag.
- Figure 8: Biomasse normalisée de la capture d'invertébrés benthiques (tonnes par mille nautique carré) sur l'ensemble des zones de plateau des îles Sandwich du Sud.
- Figure 9: Importance relative des phyla d'invertébrés dans la composition benthique de l'ensemble des zones de plateau des îles Sandwich du Sud.
- Figure 10: Biomasse normalisée de la capture d'invertébrés benthiques (tonnes par mille nautique carré) sur l'ensemble du secteur de plateau de l'île Bouvet.
- Figure 11: Importance relative des phyla d'invertébrés dans la composition benthique de l'ensemble du secteur de plateau de l'île Bouvet.
- Figure 12: Température moyenne du fond de la mer sur 10 ans dans le secteur nord de la péninsule antarctique et dans les zones de plateau des îles Shetland du Sud. Les données sont dérivées de lancers de CTD effectués de janvier à mars de 1997 à 2007 dans le cadre du quadrillage des campagnes d'évaluation de l'US AMLR.

Список таблиц

- Табл. 1: Информация о рейсах и сборе коллекций образцов бентических беспозвоночных, которые анализируются в данной статье.
- Табл. 2: Диапазон глубин станций, объединенных в целях определения состава бентических беспозвоночных у северной части Антарктического п-ова и Южных Шетландских о-вов. Номера относятся к круговым диаграммам состава, показанным на рис. 4. В скобках показано количество объединенных станций (*n*) для каждой диаграммы. **Жирным шрифтом** показана общая площадь протраленного морского дна (мор. миль²), по которой был проведен анализ улова бентической мегафауны беспозвоночных.

Список рисунков

- Рис. 1: Районы шельфа атлантического сектора Южного океана, обследованные в рамках этой работы, и статистические границы АНТКОМа.
- Рис. 2: Расположение станций сбора образцов: (а) северная часть Антарктического п-ова и Южные Шетландские о-ва (Подрайон 48.1); (b) Южные Оркнейские о-ва (Подрайон 48.2); (c) о-в Южная Георгия и скалы Шаг (Подрайон 48.3); (d) Южные Сандвичевы о-ва (Подрайон 48.4); и (e) о-в Буве (Подрайон 48.6).
- Рис. 3: Стандартизованная биомасса улова бентических беспозвоночных (т/мор. миля²) для северной части Антарктического п-ова и Южных Шетландских о-вов. Темным цветом показаны районы, полученные путем геостатистического гридирования плотностей с использованием кригинга (сглаженной интерполяции).
- Рис. 4: Относительная доля типов беспозвоночных в составе бентоса шельфовых районов – север Антарктического п-ова и Южные Шетландские о-ва. Показаны только типы, составляющие по крайней мере 1%.
- Рис. 5: Стандартизованная биомасса улова бентических беспозвоночных (т/мор. миля²) для района шельфа Южных Оркнейских о-вов. Темным цветом показаны районы, полученные путем геостатистического гридирования плотностей с использованием кригинга (сглаженной интерполяции).
- Рис. 6: Стандартизованная биомасса улова бентических беспозвоночных (т/мор. миля²) для районов шельфа о-ва Южная Георгия и скал Шаг.
- Рис. 7: Относительная доля типов беспозвоночных в составе бентоса шельфовых районов – о-в Южная Георгия и скалы Шаг.
- Рис. 8: Стандартизованная биомасса улова бентических беспозвоночных (т/мор. миля²) для районов шельфа Южных Сандвичевых о-вов.
- Рис. 9: Относительная доля типов беспозвоночных в составе бентоса шельфовых районов – Южные Сандвичевы о-ва.
- Рис. 10: Стандартизованная биомасса улова бентических беспозвоночных (т/мор. миля²) для района шельфа о-ва Буве.
- Рис. 11: Относительная доля типов беспозвоночных в составе бентоса шельфовых районов – о-в Буве.
- Рис. 12: Осредненная за 10 лет температура придонных вод в районах шельфа на севере Антарктического п-ова и Южных Шетландских о-вов. Данные получены по станциям СТД, выполненным в январе–марте 1997–2007 гг. в рамках съемочной сети США AMLR.

Lista de las tablas

- Tabla 1: Detalles de la prospección y toma de muestras para la colección de invertebrados del bentos analizados en este trabajo.

Tabla 2: Intervalo de profundidad de las estaciones agrupadas para determinar la composición de invertebrados del bentos al norte de la Península Antártica y de las Islas Shetland del Sur. Los códigos numéricos se refieren a los gráficos de tartas de la composición ilustrados en la figura 4. El número de estaciones combinadas por gráfico de tartas (*n*) figura entre paréntesis. El área total de lecho marino barrida (millas náuticas²) y analizada para determinar la captura de invertebrados de la megafauna del bentos se indica en **negrita**.

Lista de las figuras

- Figura 1: Áreas de la plataforma del sector atlántico del Océano Austral muestreadas para este estudio, con los límites de las áreas estadísticas de la CCRVMA.
- Figura 2: Posición de las estaciones de muestreo: (a) al norte de la Península Antártica y de las Islas Shetland del Sur (Subárea 48.1); (b) en las Islas Orcadas del Sur (Subárea 48.2); (c) en la Isla Georgia del Sur y Rocas Cormorán (Subárea 48.3); (d) en las Islas Sándwich del Sur (Subárea 48.4); y en (e) Isla Bouvet (Subárea 48.6).
- Figura 3: Biomasa normalizada de la captura de invertebrados del bentos (toneladas por milla náutica²) al norte de la Península Antártica e Islas Shetland del Sur. Las regiones sombreadas superpuestas fueron generadas mediante el método geoestadístico kriging aplicado a los valores de densidad (interpolación suavizada).
- Figura 4: Contribución relativa de varios filos de invertebrados marinos a la composición del bentos al norte de la plataforma de la Península Antártica y de las Islas Shetland del Sur. Sólo se han incluido en el gráfico aquellos filos que contribuyen por lo menos en un 1% a la biomasa.
- Figura 5: Biomasa normalizada de la captura de invertebrados del bentos (toneladas por milla náutica²) en el área de la plataforma de las Islas Orcadas del Sur. Las regiones sombreadas superpuestas fueron generadas mediante el método geoestadístico kriging aplicado a los valores de densidad (interpolación suavizada).
- Figura 6: Biomasa normalizada de la captura de invertebrados del bentos (toneladas por milla náutica²) en las áreas de la plataforma de la Isla Georgia del Sur y de las Rocas Cormorán.
- Figura 7: Contribución relativa de varios filos de invertebrados marinos a la composición del bentos en las áreas de la plataforma de la Isla Georgia del Sur y Rocas Cormorán.
- Figura 8: Biomasa normalizada de la captura de invertebrados del bentos (toneladas por milla náutica²) en las áreas de la plataforma de las Islas Sándwich del Sur.
- Figura 9: Contribución relativa de varios filos de invertebrados marinos a la composición del bentos en las áreas de la plataforma de las Islas Sándwich del Sur.
- Figura 10: Biomasa normalizada de la captura de invertebrados del bentos (toneladas por milla náutica²) en el área de la plataforma de Isla Bouvet.
- Figura 11: Contribución relativa de varios filos de invertebrados marinos a la composición del bentos a lo largo de la plataforma de la Isla Bouvet.
- Figura 12: Promedio de la temperatura del fondo del mar en áreas de la plataforma al norte de la Península Antártica y de las Islas Shetland del Sur, de un período de 10 años. Los datos provienen de muestras de CTD tomadas entre enero y marzo de 1997 a 2007 en el área de estudio del programa AMLR de Estados Unidos.