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5.17. Biogeographic patterns of Southern Ocean benthic Amphipods

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1. Introduction

Amphipod crustaceans are well represented in all three macrohabitats of the Southern Ocean: the sea floor with Gammaridea and Corophiidea, the water column with Hyperiidea and pelagic and bentho-pelagic Gammaridea, and the sea ice with epontic Gammaridea. With more than 853 described species (801 benthic and bentho-pelagic species) of Gammaridea and Corophiidea currently recorded south of the Sub-Tropical Front (*i.e.* in the Southern Ocean *sensu lato*), amphipod crustaceans rank as the second most speciose macrobenthic group - after the Gastropoda (Linse *et al.* 2006) - in Antarctic and sub-Antarctic waters.

Currently 564 amphipod species (530 benthic and bentho-pelagic) are known in the Antarctic region, south of the Polar Front, and 417 species (398 benthic and benthopelagic) in the sub-Antarctic region, between the Sub-Tropical Front and the Polar Front. Both regions share 129 species, *i.e.*, 23% of the Antarctic fauna or 31% of the sub-Antarctic fauna (De Broyer *et al.* 2007, updated). Moreover, in addition to ongoing identification of new records and taxonomic revisions of several genera, recent molecular studies revealed a number of cryptic species increasing the known species richness (*e.g.*, Lörz *et al.* 2007, 2011, 2012; Baird *et al.* 2011, 2012; Havermans 2012, Havermans *et al.* 2010, 2011, 2013) and this trend should obviously continue.

Amphipods present a high diversity in terms of life styles (Steele 1988, Bousfield & Shih 1994), trophic types (e.g., Dauby et al. 2001), habitats (e.g., De Broyer et al. 2001; Jażdżewska 2011), and size spectra (De Broyer 1977; Chapelle & Peck 1999, 2004). They constitute a significant resource for a number of Southern Ocean fish, invertebrates, seabirds and mammals (reviewed in Dauby et al. 2003). In terms of composition, the Antarctic and sub-Antarctic amphipod fauna is mostly dominated by representatives of Lysian-assoidea (165 spp. in 58 genera and 18 families), Eusiroidea (109 spp. in 27 genera and 4 families), Stenothoidae (68 spp. in 16 genera), Ischyroceridae (49 spp. in 7 genera), Iphimediidae (46 spp. in 13 genera), Phoxocephalidae (35 spp. in 18 genera) and Epimeriidae (30 species in 5 genera).

This chapter aims at characterising the main geographical and bathymetrical patterns of the Southern Ocean benthic amphipods and at comparing them with other macrobenthic groups.



Photo 1 Epimeria rubrieques De Broyer & Klages, 1991. Weddell Sea: Atka Bay (*Polarstern* ANT-XXIV/2 (ANDEEP-SYSTCO); stn. PS71/048-1, Agassiz Trawl; Date: 2008-01-12; Time: 10:33; Lat: -70.40000; Long: -8.32860; Depth: 602 m). Image © Henri Robert (RBINS).

2. Methods 2.1. Occurrence dataset

The amphipod occurrence data were extracted from the comprehensive compilation of taxonomic and ecological literature (>945 references up to the end 2005) by De Broyer *et al.* (2007), databased in SCAR-MarBIN (www.scarmarbin.be / www.biodiversity.aq ; De Broyer & Danis 2013). This extensive dataset was updated by newly published information (90 references post 2005), in particular taxonomic revisions, molecular results and new deep-sea records, and completed by museum collection records validated by the authors, as well as by the authors' unpublished data. Records of new undescribed morphospecies (see De Broyer *et al.* 2004) have been taken into account. The dataset comprises 10,760 occurrence records of benthic and benthopelagic gammarid and corophiid species from about 2000 unique stations (*i.e.*, unique combination of geographic coordinates, irrespective of the date).This georeferencing effort had to deal with data with various coordinate precisions. For biogeographic mapping purposes, when precise locality coordinates were missing in literature records, geographic coordinates of collecting stations have been searched in original station lists of relevant expeditions when available. When only a locality name was given the general coordinates were extracted from the relevant gazetteers (in particular SCAR: https://data.aad.gov.au/aadc/gaz/scar/, USGS: http://geonames.usgs.gov/antform.html, and GEBCO: http://www.ngdc.noaa.gov/gazetteer/).

2.2. Data coverage area

The area considered in the present biogeographic analysis covers the entire Southern Ocean (SO) in its wide sense, as used by oceanographers (*e.g.* Deacon 1984, Longhurst 2007, Rintoul 2007, Carter *et al.* 2009), extending from the Sub-Tropical Front (STF) zone in the north (located between 41°S and 48°S according to longitude; Orsi *et al.* 1995) to the coast of the Antarctic continent in the south (the southernmost record being under the Ross Ice Shelf at 82°S; Bruchhausen *et al.* 1979). It includes the Antarctic continental shelf, the peri-Antarctic and sub-Antarctic islands as well as the southern tip of South America (from 43°S on the Argentinian coast and from 41°S on the Chilean coast; see De Broyer *et al.* 2007) and the Campbell Plateau south of New Zealand. This vast area presents contrasting oceanographic conditions, from shallow to deep-sea and cold temperate to true polar environments.

The extra-limital occurrences of species present in the SO *s.l.* were also systematically recorded. For facilitating data retrieval from existing databases, convenient operational limits of the area of interest have been defined, fitting as closely as possible, when justified, to the statistical areas used by the Convention for the Conservation of Antarctic Marine Living Resources (see De Broyer & Danis 2011: fig. 2 and table 1).

2.3. Geospatial distribution mapping

A selection of frequently recorded species (with at least 50 records in the SO *s.l.*) was used for mapping the recurrent spatial distribution patterns. The distribution maps of all species can be visualised on the SCAR-MarBIN/ANT-ABIF portal (www.biodiversity.aq), which however includes records that may not have been validated for this study.

2.4. Biogeographical analysis

To detect biogeographical affinities of the different regions/areas of the Southern Ocean, the SO was divided into 27 operational geographic/hydrographic units (Map 1). To allow pertinent comparisons, this division was partly based on previous schemes (Knox & Lowrv 1977: Linse *et al.* 2006: Barnes &



Amphipods Map 1 Geo-hydrographic units used in the biogeographical analysis (occurrence records limited to 1000 m depth). SC: South Chile. SA: South Argentina. TdF: Tierra del Fuego. Fal: Falkland Islands. Sha: Shag Rocks. SG: South Georgia. TdC: Tristan da Cunha and Gough Islands. PEd: Prince Edward and Marion Islands. Cro: Crozet Islands. Ker: Kerguelen Islands. Hea: Heard and McDonald Islands. Mac: Macquarie Island. Cam&Auc: Campbell and Auckland Islands. Boun&Ant: Bounty and Antipodes Islands. SS: South Sandwich Islands. WS: Weddell Sea. DML: Queen Maud Land. EL: Enderby Land. PB: Prydz Bay. DS&WL: Davis Sea and Wilkes Land. AC&OL: Adélie Coast and Oates Land. RS: Ross Sea. AS: Amundsen Sea. BS: Bellingshausen Sea.







Griffiths 2007, Griffiths *et al.* 2009; Pierrat *et al.* 2013), with some complements and adjustments. A multivariate analysis was conducted to measure the similarity of the different geo-hydro units (with the same method used for the bathymetric analysis, see below). The detailed results of this biogeographical affinities analysis and an amphipod-based biogeographical regionalisation of the Southern Ocean will be presented elsewhere (Jażdżewska & De Broyer in prep.).

2.5. Bathymetric distribution

The shelf depth range considered here is standardized at 0-1000 m around the continent (Clarke & Johnston 2003), at 0-500 m around the South Orkney Islands (Kaiser et al. 2011), and at 0-200 m for the Scotia Arc Islands as well as around the sub-Antarctic islands and within the Magellan region. This range includes in some places the upper part of the slope. Depth occurrence data were grouped by 100 m range units and, for measuring their similarity, a Bray-Curtis similarity coefficient was calculated based on the presence/absence data matrix, using Primer for Windows v.5 (Plymouth Marine Laboratory: Clarke & Warwick 1994). The dendrogram was built using group average method. To allow detecting bathymetric patterns around the Antarctic continent itself, the dataset was restricted to occurrences on the shelf (<1000 m), slope (1000-3000 m) and adjacent abyssal basins of the continent (>3000 m), including the Peninsula and the adjacent South Shetland Islands (with a shelf break between 400 and 1000 m), but excluding the other Scotia Arc, peri-Antarctic or sub-Antarctic island occurrences (these regions having their shelf break at about 200 m). This restricted dataset comprised 503 species. It must be kept in mind that the deep-sea amphipod records resulting from the successful ANDEEP expeditions are still very incomplete and may change significantly our view of the deep-sea bathymetric patterns (see De Broyer et al. 2004; Brandt et al. 2012).

2.6. Some definitions

In the present chapter, we refer to the following geographic entities, defined as follows (see also Map 1): *West Antarctic*: the area comprising the Antarctic Peninsula (AP) and the Scotia Arc Islands south of the Polar Front (PF), thus including South Georgia and Shag Rocks. The limits of the Peninsula are set up at 75°W on its western side (WAP), and at 70°S (south of Larsen Ice Shelf) on its eastern side (EAP). To facilitate the distinction of South Georgia and Shag Rocks in the analysis, we use the code "W" for the West Antarctic without South Georgia and Shag Rocks, which are separately coded "SG".

Continental High Antarctic (or East Antarctic) (code: E): the circum-continental shelf region of high latitude, excluding the AP, extending eastward from the eastern border of the Weddell Sea to the eastern border of the Ross Sea. (Note that this is a restricted definition in comparison with the use of "East Antarctic" by De Broyer *et al.* (2007), where the Weddell and the Bellingshausen Seas were included in the East Antarctic region).

Circum-Antarctic: distributed all around the Antarctic continent in the High Antarctic zone, and in the West Antarctic zone, including or not the Weddell Sea (code: WS) and the Bellingshausen Sea (code: BS), [i.e., E+W (+SG), (+WS), (+BS)]. We consider a species to be circum-Antarctic when it is distributed in at least 3 widely separate localities around the continent (e.g., in any West Antarctic locality or/and Weddell Sea, in the Ross Sea and in another East Antarctic locality, such as Adélie Coast, Davis Sea or Prydz Bay).

Pan-Antarctic: distributed in the whole Antarctic region, i.e. in the High Antarctic and West Antarctic zones, the Weddell Sea, as well as around South Georgia (i.e., E+WS+W+SG).

Circum-sub-Antarctic: distributed in the whole sub-Antarctic zone around the sub-Antarctic islands (code: S) and in the Magellanic area (code: M).

Amphipods Maps 2a–2b Number of sampling sites of benthic amphipods (per grid 1°x1°); Map 2b. Species richness of benthic amphipods (per grid 1°x1°).

3. Biogeographic patterns

3.1. Hotspots of species richness and sampling effort

Map 2a displays the distribution of all sampling stations of benthic amphipods. It reveals the relative concentration of sampling sites around South Georgia, in the Scotia Sea, on the Western Antarctic Peninsula, in the eastern Weddell Sea, the Prydz Bay region, and in the Ross Sea, as well as in the Magellan region and around the sub-Antarctic islands of Prince Edward and Marion, Crozet and Kerguelen. Four sampling "hotspots" can be detected: South Georgia, the South Shetland Islands: King George Island (see Sicinski *et al.* 2011) and Elephant Island, the north-eastern Weddell Sea around Kapp Norvegia, and the Prince Edward Islands. Comparison of maps of sampling effort (number of stations: Map 2a) with the hotspots of species richness (Map 2b) suggests that these hotspots clearly reflect the sampling intensity, except for the Prince Edward Islands (see Chapter 2.2).

3.2. Recurrent distribution patterns in shelf and upper slope zone

On the basis of current knowledge, the following (recurrent) distribution patterns for benthic and bentho-pelagic amphipods can be distinguished:

Circum-Antarctic pattern

One hundred and seventeen species (or 22% of all Antarctic benthic and bentho-pelagic species) present a circum-Antarctic distribution, occurring around the continent, around the Peninsula and the Scotia Arc, extending or not to extra-Antarctic locations. Among them, 88 species (16.6% of Antarctic species) are restricted to this zone, *e.g., Oediceroides calmani* Walker, 1906 (E+W: Map 3); *Waldeckia obesa* (Chevreux, 1905) (E+W+BS: Map 4).

Within the circum-Antarctic fauna, 53 species (10% of Antarctic species) present a *pan-Antarctic* distribution, occurring in the entire Antarctic region, around the continent, around the Peninsula and the Scotia Arc Islands including South Georgia. Thirty five species (abt 7%) are restricted to this area, *e.g.*, E+W+SG: *Paramoera walkeri* (Stebbing, 1906) (Map 5), E+W+WS+SG: *Ampelisca richardsoni* Karaman, 1975 (Map 6), *Echiniphimedia echinata* Walker, 1906, *Melphidippa antarctica* Schellenberg, 1926, or *Prostebbingia gracilis* (Chevreux, 1912) (all cited species with at least 50 records). The endemic genus *Iphimediella* with 11 species is also restricted to this area (Map 7).

The circumpolar distribution has long been recognised as a characteristic of the Antarctic benthos (Hedgpeth 1969, 1970, 1971; Dell 1972; Arntz et al. 1994, 1997; Clarke & Crame 1997), shared by the amphipods. It was usually explained by the homogenising effect of the strong circumpolar current system - the Antarctic westward-flowing Coastal Current (AcOC, formerly East Wind Drift) close to the continent and the more northern eastward-flowing Antarctic Circumpolar Current (ACC) - as well as by the relatively similar environmental conditions (such as isothermal waters or the continuous shelf), all of these factors facilitating gene flow. However, recent in-depth taxonomic revisions of some amphipod genera (e.g., Conlan 1990: Jassa; Udekem d'Acoz 2008, 2009: Liljeborgia; Krapp-Schickel & De Broyer 2014: Leucothoe) and, mainly, the detection by molecular methods of cryptic species with restricted distribution in previously considered wide-ranging species (Lörz et al. 2009; Havermans 2012; Havermans et al. 2013; see Chapter 10.5) have challenged the circumpolarity paradigm for benthic amphipods. This was also the case in a number of other benthic groups, and was first shown in the polymorphic isopod Ceratoserolis trilobitoides (Eights, 1833) by Held (2003). On the other hand, true circumpolarity has been confirmed by molecular studies in several benthic and benthopelagic amphipods (e.g. Abyssorchomene sp. 1, Pseudorchomene rossi (Walker, 1903), and Waldeckia obesa clade B; see Havermans 2012 and Chapter 10.5: maps 5, 4, 7 respectively) as well as in species from various other groups (e.g., pycnogonids: Arango et al. 2011; shrimps: Raupach et al. 2010).

Continental High Antarctic (or East Antarctic) pattern

Two hundred and sixteen species (40.7% of all Antarctic spp.) have been recorded so far in the High (or East) Antarctic region. Among them 35 species (about 7% of all Antarctic spp.) seem to be endemic of this zone, but it must be noted that all but 7 species are rare species, known only from one or two records. Examples of Antarctic regional endemics (Map 8) for the Davis Sea (12 spp.) are: *Calliopiurus excellens* Bushueva, 1986, *Allogaussia galeata* Schellenberg, 1926 and *A. paradoxa* (Schellenberg, 1926); for the Ross Sea (11 spp.): *Epimeria larsi* Lörz, 2009, *E. rimicarinata* Watling & Holman, 1980 (also recorded in Davis Sea), and *E. schiaparelli* Lörz, Maas, Linse & Fenwick, 2007; for the Adélie Coast (5 spp.): *Lepidepecreella emarginata* Nicholls, 1938, and *Nototergum bicarinatum* Bellan-Santini 1972; for Queen Maud Land (2 spp.): *Neoxenodice hoshiai* Takeuchi & Takeda, 1992.

West Antarctic pattern

A total of 355 species (67% of all Antarctic spp.) have been collected so far around the Peninsula region and on the shelf of Scotia Arc islands south of the PF. Among them, 126 species (23.7%) seem to be endemic of this region (W or W+SG), *e.g., Bovallia gigantea* Pfeffer, 1888 (Map 9), *Eurymera monticulosa* Pfeffer, 1888, and *Paradexamine fissicauda* Chevreux, 1906 (Map 10), among the frequently recorded species.

This relatively high proportion of endemic species indicates that a discrete West Antarctic amphipod fauna can be distinguished from the continental Antarctic fauna. This implies that a "single Antarctic province", without east-west sub-division, which was suggested by Griffiths *et al.* (2009), does not hold true for the amphipods. A clear distinction between the "Antarctic Peninsula and Scotia Sea Province" and the "Continental High Antarctic Province" (Clarke *et al.* 2007) was also observed in a number of other macrobenthic groups, *e.g.*, Hydrozoa (Peña Cantero 2004), Gastropoda (Linse *et al.* 2006) and less clearly in Bryozoa (Barnes & De Grave 2000).

The Weddell Sea case

The amphipod fauna of the eastern and, to a lesser extent, the southern Weddell Sea has been particularly intensively studied (Gutt et al. 2000; see De Broyer et al. 2007 for references) and comprises 191 recorded species (36% of all Antarctic spp.), with 16 apparent endemics. The analysis of its biogeographic affinities (Fig. 1) indicates its transitional position between West and East Antarctic, obviously reflecting its geographical and hydrographical location, but it also shows that it shares significantly more species with the Peninsula-Scotia Sea fauna than with the High Antarctic fauna (e.g., WS+W: Liouvillea oculata Chevreux, 1912 (Map 11); WS+W+SG: Ampelisca bouvieri Chevreux, 1912 (Map 12) and Paraceradocus miersii Pfeffer, 1888. This is in contrast with the results of biogeographic analyses of other macrobenthic groups that clustered the Weddell Sea within the continental High Antarctic (e.g., Gutt et al. 2000; gastropods and bivalves: Linse et al. 2006, Clarke et al. 2007; pycnogonids: Munilla & Soler-Membrives 2009; Soler Membrives et al. 2009). However, strong affinities between the Weddell Sea fauna and the West Antarctic fauna have been detected in other groups (e.g., Zelaya 2005; Pierrat et al. 2013) and the role of the Weddell Sea gyre as a potential barrier to gene flow has been suggested (Linse et al. 2006). Moreover, we have to keep in mind that a number of groups remain to be subject to a detailed multivariate biogeographical analysis at a pertinent resolution level.

The Bellingshausen and Amundsen Seas cases

The Bellingshausen Sea remains poorly sampled with only 22 recorded amphipod species. On this limited basis, its faunal affinities mostly indicate its transitional nature between the West and the East Antarctic fauna, with however stronger links with the Peninsula fauna. On the other hand, the Amundsen Sea has been until very recently a complete white spot in Antarctic biogeography. A recent investigation of its macro- and megabenthos indicated that the benthic assemblages are clearly different from the Weddell, Scotia or Ross seas (Linse *et al.* 2013). First studies of the Amundsen Sea isopod fauna revealed many species new to science. Additionally the genera found there on the shelf were generally found elswhere in the deep-sea (Kaiser *et al.* 2009). *The* preliminary identifications of the recorded amphipods (<10 spp.) do not allow us to detect any biogeographic or bathymetric pattern.



Figure 1 Biogeographical affinities of the benthic amphipod fauna of the Weddell Sea. end.: endemics; Ant: Antarctic ; Sub: sub-Antarctic ; WS, E, W, SG, BS, S: see text.

The South Georgia case

One hundred and seventy five species (33% of all Antarctic spp.) have been recorded around South Georgia and/or Shag Rocks, with 132 of these species also occurring at West or High Antarctic localities, confirming the dominant Antarctic character of the South Georgia fauna (see Barnes et al. 2006; Hogg et al. 2011). South Georgia appears to be the northernmost occurrence locality for 78 of these aforementioned species (e.g., Ampelisca bouvieri Chevreux, 1912: Map 12 , A. richardsoni Karaman, 1975: Map 6, Iphimediella spp. Map 7, Bovallia gigantea Pfeffer, 1888: Map 8, Paradexamine fissicauda Chevreux, 1906: Map 9, Paramoera walkeri Stebbing, 1906: Map 5). On the other hand, it appears to be the southernmost extension (or more exactly the coldest water occurrence) of 19 sub-Antarctic (Magellanic, or more widely South America or Southern Hemisphere ranging) species (e.g., SG+M+S+: Dodecas elongata Stebbing, 1883: Map 13), all of these species potentially being at their respective thermal tolerance limit (see Barnes et al. 2010). The overall biogeographical affinities of the South Georgia fauna clearly reflect its position as a transitional zone between the Antarctic and sub-Antarctic regions (Fig. 2) and may justify its "district" status within the West Antarctic fauna given by Hedgpeth (1969) and Dell (1972). Twenty six species appear endemic to South Georgia. This 14.8% endemism rate is much higher than the rate recorded from spong





Figure 2 Biogeographical affinities of the benthic amphipod fauna of South Georgia. end.: endemics; Ant : Antarctic (= E, W, WS, BS); Sub: sub-Antarctic (= S, M). (+) and (++) indicate extra SO records.

es (2.7%) but significantly lower than the rate observed in molluscs (bivalves and gastropods: 45.9%) or cheilostome bryozoans (55.6%) (Hogg *et al.* 2011).

Southern Ocean s.l. or across Polar Front distribution

One hundred and six species (20% of all Antarctic benthic and benthopelagic species) are found in both Antarctic and sub-Antarctic waters, on either side of the Polar Front. Typical examples are: for the E+W+G+S+M pattern: *Caprellinoides mayeri* (Pfeffer, 1888) (Map 14), *Atyloella magellanica* (Stebbing, 1888) (non SO endemic) (Map 15); for E+W+SG+S: *Schraderia gracilis* Pfeffer, 1888 (Map 16), *Uristes gigas* Dana, 1852 (bentho-pelagic) (Map 17) *Cheirimedon femoratus* (Pfeffer, 1888), *Hippomedon kergueleni* (Miers, 1875); for E+W+SG+M: *Rhachotropis antarctica* K.H. Barnard, 1932 (Map 18), *Heterophoxus videns* K.H. Barnard, 1930 (non SO endemic) (Map 19); for W+SG+S: *Prostebbingia brevicornis* (Chevreux, 1906) (Map 20), *Djerboa furcipes* Chevreux, 1906; for W+SG+M: *Gondogeneia antarctica* (Chevreux, 1906) (Map 21); for SG+M+S+: *Dodecas elongata* Stebbing, 1883 (Map 13).

These different types of distribution can result from various biogeographical drivers such as the SO geodynamic history, the prevalence of the ACC system in faunal dispersal, the palaeo-ceanographic context with the late Cenozoic shifts of the Polar Front, and the relevant biological processes (speciation, extinction,...), which have to be considered at the level of the particular taxa (see below).

Circum-sub-Antarctic pattern

Few species exhibit a circum-sub-Antarctic pattern, being recorded on the southern shelf of South America and around the sub-Antarctic islands of the southern Indian Ocean as well as around Macquarie Island and/or the New Zealand sub-Antarctic islands. Only 3 species present the "M+S" pattern, e.g. *Stomacontion pepinii* (Stebbing, 1888) (Map 22), and 9 others are also found at some other Southern Hemisphere locations ("M+S+" pattern), e.g. *Parawaldeckia kidderi* (S.I. Smith, 1876), a non SO endemic species (Map 23) and *Acontiostoma marionis* Stebbing, 1888 (Map 24).

Considering the limited dispersal capacities of these species, this distribution pattern might be explained either by vicariance (*e.g.* continental drift of Gondwanian relicts) or by dispersal and colonisation with some supports (mostly driven by the ACC). *P. kidderi* is an obligate kelp-dweller, which is commonly found on *Durvillea antarctica* and *Macrocystis pyrifera* holdfasts (Edgar 1987). Studies of molecular genetic markers have suggested that its circumpolar distribution may be best explained by post-glacial colonisation of the sub-Antarctic islands through macroalgal rafting by the ACC, but a potential source region could not be identified (Nikula *et al.* 2010).

Sub-Antarctic Islands

Two hundred and nine species (comprising 80 endemics or 38.2%) have been recorded around the sub-Antarctic islands (S) as a whole. These islands can be clustered in two faunistic groups: on one hand, the south Indian Ocean group of Prince Edward and Marion, Crozet, Kerguelen (and Heard) islands with the addition of Macquarie Island, and, on the other hand, the New Zealand sub-Antarctic islands: Auckland, Campbell, Antipodes, Bounty and Snares islands. Heard Island on the Kerguelen Plateau (but presently separated from Kerguelen Islands by the PF; Moore et al. 1999) shares 8 of its 14 species (which include 3 endemics) with Kerguelen Islands. Macquarie Island (33 spp.), although close to the New Zealand sub-Antarctic islands and connected by the Macquarie Ridge (see O'Hara 1998), shares two-thirds of its species (21 spp.) with the Kerguelen plateau or other south Indian Ocean islands, but only 9 species with the New Zealand sub-Antarctic islands. The latter islands (which together host 76 spp., with 22 endemics) exhibit strong affinities with the New Zealand shelf (mostly South Island), sharing 37 species, and much less affinities with the south Indian Ocean group (with only 9

spp. in common).

Examples of regional endemics on sub-Antarctic islands for Kerguelen Islands (95 spp. recorded, 28 endemics) are: *Cicadosa cicadoides* (Stebbing, 1888), *Kerguelenia compacta* Stebbing, 1888, *Lysianella morbihanensis* (Bellan-Santini & Ledoyer, 1974), *Orchomenella (Orchomenella) guillei* De Broyer, 1985; for Macquarie Island (33 spp., 3 endemics): *Aurometopa aurorae* (Nicholls, 1938), *Pagetina monodi* Nicholls, 1938; for Auckland and Campbell Islands (63 spp., 21 endemics): *Ceradocopsis carnleyi* (Stephensen, 1927), *Elasmopus wahine* J.L. Barnard, 1972, *Kakanui punui* Lowry & Stoddart, 1983, *Parawaldeckia vesca* Lowry & Stoddart, 1983.

The Kerguelen fauna sets apart from the other sub-Antarctic Islands by its strong Antarctic component sharing 43% of its species with the Antarctic fauna. The past connectivity of the Kerguelen plateau with the Antarctic region due to the paleo-oceanographical conditions, in particular the northern shift of the PF (Gendron-Badou *et al.* 1997; Kemp *et al.* 2010), may likely explain the strong Antarctic affinities of the present Kerguelen amphipod fauna.

Magellanic distribution

The benthic amphipod fauna of the Magellanic area ("M", including here south Chile, south Argentina and Tierra del Fuego: see Map 1), comprises 174 (described) benthic species (De Broyer & Rauschert 1999, updated). The Falkland Islands, located on the same wide Patagonian shelf, counts 104 species (with 23 endemics, or 22%) and shares 67 species (64.4%) with the Magellanic area.

The zoogeographical affinities of these southern South America faunas were analysed by De Broyer & Rauschert (1999: fig. 3) and Lopez Gappa *et al.* (2006). They have shown that the fauna from south Chile, south Argentina, Tierra del Fuego, the Falkland/Malvinas Islands and the Burdwood Bank can be grouped under a distinct Magellanic Biogeographic Province, represented by 204 amphipod species, comprising 92 endemics (45%).

The Magellanic fauna shares only 30 species (14.7%) with the more northern parts of South America (mostly with the Argentinian shelf, see Lopez Gappa et al. 2006), e.g. Tryphosites chevreuxi Stebbing, 1914 (Map 25). It shares 37 species (18.1%) with the sub-Antarctic islands fauna. In comparison, bivalve, gastropod, and bryozoan faunas of the south Indian Ocean group comprising Prince Edward and Marion, Crozet, and Kerguelen islands show stronger affinities with the Magellanic fauna, exhibiting a "South American signature" (Griffiths et al. 2009). This trend is poorly visible in the amphipods with only 24 species (11.7%) of southern South America species shared by the south Indian Ocean island group, and only 9 spp. exhibiting a restricted "Magellanic + south Indian Ocean group" distribution. In contrast, the Magellanic fauna shows much stronger affinities with the Antarctic fauna, sharing 67 species (32.8%), including 10 species extending only to South Georgia. This trend, observed in other macrobenthic taxa has been explained by the past connection and potential migration route offered by the Scotia Arc linking the southernmost South America with the Antarctic Peninsula (see discussion in Chapter 10.9)

3.2.2. Endemism

In terms of endemism, the Antarctic region shows a level of 66.6% of benthic endemic species. The genus endemism level attains 27.6%. The Antarctic amphipod fauna is characterised by the presence of one (small) endemic family, Clarenciidae, whereas two other (small) families, Didymocheliidae and Pagetinidae, are restricted to Antarctic and sub-Antarctic waters.

The sub-Antarctic region is characterized by a lower level of benthic species endemism of 47.9%, mostly reflecting the links with adjacent regions (e.g. South America for the Magellan province and New Zealand for the New Zealand sub-Antarctic islands). The rate of genus endemism attains 15.6%. If the entire Southern Ocean *s.l.* is considered, the level of species endemism reaches 83.6% for benthic and benthopelagic species.

These high levels of endemism are common to a number of Antarctic macrobenthic groups (Arntz *et al.* 1997, White 1984, Griffiths *et al.* 2009) and reflect the long isolation of the SO by the ACC front system but also implies significant speciation and radiation events within Antarctic waters (see Watling & Thurston 1989).

4. Bathymetric distribution

Using the standard bathymetric partitioning retained for this Atlas, the Antarctic continental shelf fauna (0-1000 m) comprises 450 species and largely dominates the Antarctic species records (89.4% of 503 spp.). The slope fauna (1000-3000 m) is represented by 80 species (15.9%) and the abyssal fauna (3000-6000 m) by only 23 species (4.5%) (Fig. 3)

In comparison with other benthic groups, the species richness distribution over depth appears quite similar to the pattern observed in Gastropoda, another highly species Antarctic taxon (Brandt *et al.* 2009: fig. 2b). However, in contrast to gastropods, the amphipod species richness shows a regular decrease in the number of species from 0-100 m to 101-200 m (from 258 spp. to 236 spp.) and a slight increase in the 201-300 m zone (from 236 to 260 spp.), increase that can also be detected in the 4 groups studied by Brandt *et al.* (2009): Bivalvia, Gastropoda, Isopoda, and Polychaeta. This slight increase in species richness may possibly be linked to an increase in seafloor area at corresponding depths (see Griffiths 2010: fig. 2).



120°W

• Paramoera walkeri

Map 5









Amphipods Maps 3-8 Distribution patterns of benthic amphipods. Circum - Antarctic: Map 3 Oediceroides calmani; Map 4 Waldeckia obesa s.l.; Map 5 Paramoera walkeri; Map 6 Ampelisca richardsoni; Map 7 Iphimediella spp. High Antarctic endemics: Map 8 Allogaussia galeata; Calliopiurus excellens; Epimeria rimicarinata; Lepidepecreella emarginata; Neoxenodice hoshiai; Nototergum bicarinatum. Stars indicate the respective type localities.





Figure 3 Overall species richness per 100 m depth range (includes all SO s.l. species)



Figure 4 Bathymetric clusters (Antarctic continent and Peninsula species).

4.1. Bathymetric clusters

A Bray-Curtis similarity analysis focused on the depth distribution was performed based on 100 m depth range units (503 spp.) and resulted in the detection of five distinct bathymetric clusters around the continent: the shelf fauna (0-800 m) with two potential subdivisions (0-100 m, 101-800 m), the upper slope fauna (801-2200 m), the lower slope-upper abyssal fauna (2201-3700 m) and the (deep) abyssal fauna (3701-5000 m) (Fig. 4).

The shelf fauna (0-800 m)

This bathymetric cluster comprises 449 species. A significant part of these shelf bound species (146 spp. or 32.5%) extend their distribution from the shallow (less than 100 m) to the deep shelf without occurring deeper than 800 m, *e.g. Ampelisca richardsoni* (15-634 m); *Echiniphimedia echinata* (10-547 m); *Melphidippa antarctica* (4-750 m); *Oediceroides calmani* (15-550 m); *Prostebbingia gracilis* (10-385 m).

Fifty-nine spp. (or 13.1%) of the shelf-occurring species extend their distribution to the upper slope zone (800-2200 m), *e.g. Waldeckia obesa* (0-1030 m); *Pseudorchomene rossi* (7-1453 m); *Parschisturella carinata* Schellenberg,

 Table 1
 Potential Antarctic continental slope species

1926 (14-2081 m). In addition, 11 species (2.4%) occur deeper than 2200 m showing obvious eurybathy (see below), *e.g. Byblisoides juxtacornis* K.H. Barnard, 1931 (160-2315 m); *Pseudorchomene coatsi* (Chilton, 1912) (0-2889 m). Among the remaining (truly) shelf fauna two groups can be distinguished:

a. The coastal / upper sublittoral fauna (0-100 m): Among the 258 species occurring between 0-100 m, 80 species (30.8%) are restricted to these depths, with 48 species (18.5%) restricted to 0-50 m (algal zone). The majority of these shallow waters species (65 spp.) occur in the WAP region (30 exclusively) and 28 species (13 exclusively) in the East Antarctic. Not unexpectedly, this group includes the algal dwellers and phytophagous amphipods such as the eusiroid *Gondogeneia* spp., *Paramoera* spp., *Oradarea* spp., *Schraderia* spp., *Atylopsis* spp., *Eurymera monticulosa* Pfeffer, 1888 (0-40 m), but also the predator-omnivore *Bovallia gigantea* (0-80 m). These coastal amphipods are remarkably abundant in the Western Peninsula region (see *e.g.*, Jazdzewski *et al.* 2001; Huang *et al.* 2007).

b. The (deep) shelf fauna (101-800 m): 355 species occur in this depth range. Many of these species (151 spp. or 42.5%) do not extend their distribution deeper than 800 m and seem to be restricted to this depth zone: *e.g., Byblis securiger* K.H. Barnard, 1931 (199-750 m); most *Iphimediella* spp.: *I. bransfieldi* K.H. Barnard, 1932 (200-419 m); *I. cyclogena* K.H. Barnard, 1930 (178-889 m); *I. dominici* Coleman, 1996 (421-429 m); *I. georgei* Watling & Holman, 1980 (316-735 m); *I. microdentata* (Schellenberg, 1926) (216-720 m); *I. rigida* K.H. Barnard, 1930 (256-625 m); *I. ruffoi* Coleman, 1996 (242-264 m); and the *Adeliella* spp. (*A. laticornis* Nicholls, 1938: 216-620 m; *A. olivieri* De Broyer, 1975: 200-600 m).

The upper slope fauna (801-2200 m)

Eighty-six species occur on the upper slope: among them 65 species are also present on the shelf, and 11 species extend their distribution deeper than 2200 m. Twenty species (including 9 undescribed spp.) are restricted to this zone, possibly representing a distinct slope fauna (see discussion in Kaiser *et al.* 2011), however all of these species but 1 are rare species collected only once (Table 1).

The lower slope / upper abyssal fauna (2201-3700 m)

Among the 40 species occurring in this depth zone, 9 species also occur in the two upper bathymetric zones (shelf and upper slope) and 26 species are restricted to this zone (*e.g. Alexandrella martae* Berge & Vader, 2005: 2608-3175 m; *Rhachotropis anoculata* J.L. Barnard, 1962: 2315-3725 m; most others are rare species known from single records).

The abyssal fauna (3701->4500 m)

Only 12 species have been currently recorded in the Antarctic abyssal below 3700 m, including 1 species below 4500 m (the bentho-pelagic *Abyssorchomene chevreuxi* (Stebbing, 1906)). These numbers may change significantly after the completion of the ANDEEP material identification.

4.2. Eurybathy

Among the 503 species here considered (occurring around the Antarctic continent and Peninsula), 34 species (6.7%) from 16 families (mostly Lysianassidae: 7 spp., Uristidae: 5 spp., Stilipedidae: 4 spp., Epimeriidae: 3 spp., Ampeliscidae, Liljeborgiidae, Phoxocephalidae: 2 spp. each) exhibit a depth range wider than 1000 m, and 10 species (2.2%) a depth range wider than 2000 m, with 5 species spanning over 3000 m (Table 2).

Recent molecular studies have demonstrated that some apparently extreme eurybathic species were in fact composed of different (pseudo)cryptic species: *e.g., Orchomenella (O.) cavimanus* (Stebbing, 1888) - of which morphological differences were already detected (personal observations) – consisting in fact of 3 well supported species-level lineages with only one being truly eurybathic (lineage C, Havermans 2012; see Chapter 10.5). On the other hand, the same studies confirmed the wide eurybathy of *Abyssorchomene scotianensis* (Andres, 1983) *and A.* sp. 1.

Described species	Family	Depth min.	Depth max.	N. records	Reference
Ampelisca antarctica Ren, 1991	Ampeliscidae	1098	1098	1	De Broyer <i>et al.</i> 2007
Epimeria larsi Lörz, 2009	Epimeriidae	1954 1990 1		1	Lörz 2009
Pontogeneoides abyssi Nicholls, 1938	Pontogeneidae	1566	1566	1	De Broyer <i>et al.</i> 2007
Lepechinelloides weddellensis Andres & Brandt, 2001	Lepechinellidae	1983	1983	1	De Broyer <i>et al.</i> 2007
Paralepechinella occultolongicornis Andres & Brandt, 2001	Lepechinellidae	1645	1645	1	De Broyer et al. 2007
Leucothoe longimembris Krapp-Schickel & De Broyer, 2014	Leucothoidae	1030	1030	1	De Broyer et al. 2007
Liljeborgia bathysciarum d'Udekem d'Acoz, 2009	Liljeborgiidae	1579 1584		1	Udekem d'Acoz, 2009
Liljeborgia cnephatis d'Udekem d'Acoz, 2008	Liljeborgiidae	2372	2375	1	Udekem d'Acoz, 2008
Andaniexis ollii Berge, De Broyer & Vader, 2000	Stegocephalidae	1444	1444	1	De Broyer et al. 2007
Stegomorphia watlingi (Berge, De Broyer & Vader, 2000)	Stegocephalidae	1153	1153	1	De Broyer et al. 2007
Alexandrella australis (Chilton, 1912a)	Stilipedidae	884	2609	3	De Broyer et al. 2007













Amphipods Maps 9-13 West Antarctic pattern: Map 9 Bovallia gigantea, Map 10 Paradexamine fissicauda. Weddell Sea: Map 11 Liouvillea oculata; Map 12 Ampelisca bouvieri. South Georgia: Map 13 Dodecas elongata. Stars indicate the respective type localities.



Table 2 Antarctic extreme eurybathic species

Species	Family	Depth min. (m)	Depth max. (m)	Depth range (m)	N records	Habitat	Source
Byblisoides juxtacornis K.H. Barnard, 1931	Ampeliscidae	160	2315	2155	>6	В	De Broyer et al. 2007
Liljeborgia homospora Udekem d'Acoz, 2008	Liljeborgiidae	1180	4392	3212	15	В	Udekem d'Acoz 2008
Orchomenella (Orchomenopsis) cavimanus (Stebbing, 1888) s.l.*	Lysianassidae	6	3683	3677	35	В	Havermans 2012 and Chapter 10.6
Pseudorchomene coatsi (Chilton, 1912) s.s.	Lysianassidae	0	2889	2889	45	В	Udekem d'Acoz & Havermans 2012
Abyssorchomene scotianensis (Andres, 1983)	Uristidae	385	3408	3023	26	BP	Havermans 2012 and Chapter 10.6
Abyssorchomene sp. 1	Uristidae	310	4409	4099	10	BP	Havermans 2012 and Chapter 10.6
Parschisturella carinata (Schellenberg, 1926)	Uristidae	14	2081	2067	>35	В	De Broyer et al. 2007
Necochea pardella J.L. Barnard, 1962	Pardaliscidae	170	3725	3555	2	В	De Broyer et al. 2007
Bathypanoploea schellenbergi Holman & Watling, 1983	Stilipedidae	340	2889	2549	30	В	De Broyer et al. 2007
Dodecasella elegans K.H. Barnard, 1931	Caprellidae	68	2894	2826	16	В	De Broyer <i>et al.</i> 2007

* comprises 3 (pseudo)cryptic species (see Havermans 2012)

Although our results indicated that eurybathy does not seem a common feature among Antarctic benthic amphipods, this biogeographical trait has been frequently detected among the Antarctic macrobenthos, e.g., in demosponges and hexactinellids, hydrozoans, bivalves, polychaetes,...(see respective chapters in this volume).

This phenomenon has been explained by the presence of the isothermal water column from the shelf to the deep around the continent (but see Kaiser et al. 2011 and references therein for details on distinct water masses), and the formation of deep water at shelf depths which may bring shelf species to the deep (e.g., Strugnell et al. 2008). Its evolutionary origin has been attributed to the effect of the Pleistocene glacial-interglacial cycles of extension and retreat of the continental ice over the shelf, which pushed the shelf species downwards along the slope during glacial maxima (Brey et al. 1996). **Concluding remarks**

Most of the various distribution patterns observed in amphipods remain to be tentatively explained at the individual genus or even species level, attempting to disentangle the respective roles of the geodynamic, oceanographic, and biological driving processes. In contrast to some other macrobenthic taxa, in particular molluscs (Crame 1997; Linse et al. 2006), amphipods are characterized by a (quasi total) absence of fossil records, which limits the interpretation of the vicariance and dispersal roles in the shaping of the present amphipod biogeography. Many of the recurrent distribution patterns exhibited by the amphipods are shared by a number of other macrobenthic groups (see the relevant Atlas chapters) and can be likely explained by the same main driving factors. The distribution of the Southern Ocean biota has been shaped by the unique tectonic, oceanographic, and climatic history of the Antarctic, as well as by biological drivers such as adaptive radiation and diversification, dispersal or extinction, acting in various temporal and spatial contexts (see e.g., Rogers 2012; reviewed in Chapter 10.9).

The database of georeferenced amphipod records (De Broyer et al. 2007, updated) is one of the most extensive among Antarctic invertebrates, and has been thoroughly validated. Like in other benthic taxa (see Chapter 2.2), there are still significant gaps in the SO sampling or in the database coverage (Map 2a), in particular in the East Antarctic, in Bellingshausen and Amundsen seas, as well as, more critically, in the Antarctic and sub-Antarctic deep sea. On the other hand, it is obvious that some more identification and record validations are needed, especially for apparently circumpolar, widespread species (e.g., Eusirus antarcticus Thomson, 1880, Atyloella magellanica, Heterophoxus videns), which may in fact represent species complexes. The refinement of the taxonomic resolution (by finer morphological and molecular approaches) and the completion of the sampling coverage may undoubtedly improve the accuracy of the identification of biogeographical patterns at regional or local levels but should probably not modify the long established general patterns.

There is an obvious need for more molecular phylogeographic studies few have been conducted so far on amphipods. In conjunction with detailed morphological and cladistic studies, they will be key to elucidating the biogeographical history of the Southern Ocean amphipod fauna.

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Amphipods Maps 14-19 Southern Ocean s.I. (across Polar Front) pattern: Map 14 Caprellinoides mayeri ; Map 15 Atyloella magellanica ; Map 16 Schraderia gracilis ; Map 17 Uristes gigas ; Map 18 Rhachotropis antarctica ; Map 19 Heterophoxus videns. Stars indicate the respective type localities.

30°E

120°E

Amphipods Maps 20-25 Southern Ocean s.I. (across Polar Front) pattern: Map 20 Prostebbingia brevicornis; Map 21 Gondogeneia antarctica. Circum-sub-Antarctic pattern: Stomacontion pepinii; Map 23 Parawaldeckia kidderi; Map 24 Acontiostoma marionis. Magellanic pattern: Map 25 Tryphosites chevreuxi. Stars indicate the respective type localities.

Sea: macrozoobenthic species (demersal fish included) sampled during the expedition

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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.

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AnT-ERA)

Ant Eco

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