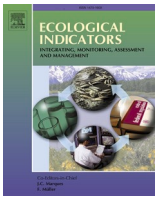
Ecological Indicators 128 (2021) 107832

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Drivers of abundance and spatial distribution in Southern Ocean peracarid crustacea

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ARTICLE INFO

Keywords:
Macrobenthos
Environmental factors
Benthic environment
Marine invertebrates
Peracarida
Depth

ABSTRACT

The Southern Ocean (SO) continental shelf and deep sea are environments characterised by different benthic communities. Their structure and composition are driven and shaped by different variables: whilst on the continental shelf physical environmental variables are the main drivers shaping faunal abundance, structure and composition, the deep-sea fauna is most probably driven by biological variables such as predation and competition. Among shelf and deep-sea benthic communities, peracarids (e.g. amphipods and isopods) are one of the most dominant groups, showing high levels of abundance and diversity in both environments. Knowledge on their assemblage structure and composition in the SO remains limited, as well as the knowledge of the environmental variables that influence them. Therefore, the aim of our study was to investigate peracarid assemblages from the SO continental shelf and deep sea and to assess the main drivers shaping their assemblage structure along a wide bathymetric gradient (from 160 m to about 6000 m depth) and at a large geographic scale. We analysed the spatial distribution of 183,606 peracarids sampled using an epibenthic sledge (EBS) during nine different expeditions in the SO, covering a latitudinal range of 77° to 41° South. Depth was identified as the main driver shaping peracarid abundance pattern, their assemblage structure from the continental shelf (<1499 m) was dissimilar to that from the deep sea (>1500 m). Also, depth was differently correlated with different peracarid orders: while isopod abundances increased with depth, amphipods and mysids were negatively correlated; no correlation was found with cumaceans and tanaidaceans. The dissimilar peracarid assemblage structure between the SO continental shelf and the SO deep sea can be due to the assumption that there are different driving forces shaping benthic assemblages from these two environments (physical variables on the continental shelf, biological interactions in the deep sea). As a result, we also suggest that environmental changes due to climate change (e.g. temperature, ice coverage, productivity) would have different consequences depending on the bathymetric range considered.

1. Introduction

The SO, here defined as the area within the Polar Front, is the largest polar marine ecosystem on Earth, comprising near-shore, shallow-water, continental-shelf and deep-sea habitats (Knox, 2006; David and Saucède, 2015). The near shore and shallow water habitats will not be covered in the context of this study as the sampling gear used, the epibenthic sledge (EBS), is usually deployed at greater depths on the continental shelf and in the deep sea (Linse et al., 2002; Brenke, 2005; Brandt et al., 2007c; Kaiser et al., 2008). A unique characteristic of the Antarctic continental shelf is that the weight of the extensive ice mass suppresses the continent isostatically, increasing the depth of the shelf (Clarke et al., 2009). Ice-sheet meltwater current flows and scouring events caused erosions of the continental shelf and led to the formation of local troughs and basins down to 1500 m depth (Clarke et al., 2009). The area of the Antarctic continental shelf not covered by ice shelves and perennial sea ice represents 11% of continental shelves of our planet (Clarke et al., 2004). This percentage will probably increase in the near future considering the rate at which ice shelves are calving and summer sea ice is decreasing, for example along the Antarctic Peninsula and in the Weddell Sea (e.g. Rott et al., 1996; Rack and Rott, 2003; Cook et al., 2016; Turner et al., 2020).

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https://doi.org/10.1016/j.ecolind.2021.107832
Received 27 January 2021; Received in revised form 26 April 2021; Accepted 10 May 2021
Available online 1 June 2021
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In this century, benthic sampling effort in the SO has increased, improving our knowledge on SO biodiversity (Brandt et al., 2007a; Kaiser et al., 2013; Schiaparelli et al., 2013; Gutt et al., 2018), however sampling distribution is still rather patchy and some areas are still under-sampled because they are difficult to reach or deploy gear in (e.g. ice-covered places and deep sea) (De Broyer and Jazdzewska, 2014; Gutt et al., 2011; Kaiser et al., 2013). For example, the Amundsen Sea is the least accessible area due to its distance from nearby continents; the western Weddell Sea and the eastern Ross Sea are very difficult to access because of the conspicuous sea-ice coverage and high number of icebergs (Griffiths, 2010).

While sampling in the SO has been performed from the intertidal to the abyss (Brandt et al., 2009; Griffiths, 2010), the effort differs depending on the sampling depth: only about 30% of benthic samples have been taken at depths below 1000 m (Griffiths, 2010). The SO deep sea covers an area of about 27.9 million km^2, representing 80% of the SO seafloor (Brandt et al., 2007a; Clarke, 2008). It is still under sampled and very little is known about its benthic fauna (Brandt et al., 2014a, 2014b). International initiatives and research programs like CEAMARC, CAML and ANDEEP largely contributed to expand our knowledge of the SO deep-sea benthic fauna. The CAML and CEAMARC aimed to investigate SO communities in relation to climate change from the continental shelf down to the slope (Hosie et al., 2011; Schiaparelli et al., 2013). The ANDEEP I-III expeditions revealed the presence of a largely underestimated biodiversity in the SO deep sea (Brandt et al., 2007b). With only 48 stations sampled in the Weddell Sea, the South Sandwich Islands and the Western Antarctic Peninsula, >700 new species were recorded in bathyal, abyssal and hadal depths (Brandt et al., 2007b, 2007c).

The SO continental shelf is dominated by two main communities: 1) sessile suspension feeders that mainly rely on food supplies derived from strong near-bottom currents and are associated with coarse-grained glacial substrates, and 2) infauna and mobile epifauna controlled by vertical phytodetritus fluxes (Clarke et al., 2004; Gutt, 2007). On the SO continental shelf, the number of dropstones and the coarse glacial substrates increase the habitat heterogeneity representing an optimal substrate for many benthic taxa (Clarke, 1996).

Many species of benthic invertebrates from the SO continental shelf show an extended eurybathy compared to non-Antarctic shelf fauna (Brey et al., 1996), this can be explained as a consequence of the unusually higher depths of the SO continental shelf which is on average 500 m, but can reach down to > 1000 m (Clarke, 2003). Several species of polychaetes, gastropods, bivalves, and foraminiferans were exhibit a wide bathymetric range, from the shelf to the deep sea, as much as 5000 m in certain cases (Hilbig et al., 2006; Brandt et al., 2007b, 2009; Schwabe et al., 2007). Despite this, the deep-sea benthos differs significantly from that from the continental shelf, for example the isopod diversity at abyssal depths is different to that of the continental shelf (Brandt et al., 2007b).

In the deep sea, sessile suspension feeders are reduced in terms of biomass and abundance leaving space to the predominant motile fauna (Clarke, 2003; Brandt et al., 2007a). Holothurians, ophiuroids, asteroids, polychaetes, isopods and amphipods are among the most dominant and species-rich groups of the SO deep sea (Brandt et al., 2007a).

The general pattern of biomass and abundance of the SO deep-sea benthos is food limited since the amount of organic matter reaching the seafloor is reduced. This is due to the low sedimentation rate (100–200 m d^{-1}; Suess, 1980; Gooday, 2002; Veit-Köhler et al., 2011) and to the disaggregation and heterotrophic consumption of the organic matter in the water column (Nelson et al., 1996). The limited organic input influences benthic faunal abundance, which is typically reduced (Clarke, 2003). However, the SO deep sea has been shown to be highly diverse and unique: during the ANDEEP I-III expeditions 674 of isopod species were found with about 90% being currently unknown outside the SO (Brandt and Gutt, 2011) and represent double the number of species previously reported from the entire SO continental shelf (Brandt et al., 2007b). The extraordinary diversity recorded in the deep sea extended from 2000 m to abyssal depths (including trenches and fracture zones).

One of the most dominant and species-rich groups in the SO benthos is represented by the crustacean superorder Peracarida (Brandt et al., 2007a; De Broyer and Jazdzewska, 2014; De Broyer and Koubbi, 2014). In general, peracarids are a key taxon in benthic communities. They serve as important links between low trophic levels and top predators (Mouat et al., 2001; Padovani et al., 2012; Xavier et al., 2020), as well as important converters of biomass and organic matter in biogeochemical cycles (Karlson et al., 2007; Dunn et al., 2009). Specimens of five orders, Amphipoda, Cumacea, Isopoda, Mysidacea, Tanaidacea can be found in the benthic peracarid assemblages of the SO, from nearshore waters to the deep sea (Jazdzewski et al., 1991; Arntz and Gutt, 1999; Jazdzewski et al., 2001; Brökeland et al., 2007).

The study of peracarid abundance and distribution increased thanks to the development of fine-meshed epibenthic sledges (Brattegard and Fosså, 1991; Brandt and Barthel, 1995; Brenke, 2005) that enable the collection of small-sized, epibenthic and swimming taxa. Among these, the epibenthic sledge (EBS) has been successfully used to sample peracarid crustaceans from the continental shelf and the deep sea of the SO (Linse et al., 2002; Lörz and Brandt, 2003; Brandt et al., 2007c; Kaiser et al., 2008; Di Franco et al., 2020). Moreover, sampling was performed using a Rauschert Dredge (Rehm et al., 2007). Small-sized peracarids collected by EBS and Rauschert Dredge improved our understanding of the evolutionary history of benthic deep-sea species from the SO (Brandt et al., 2007b; Raupach et al., 2009; Rehm et al., 2020).

To date little is still known about the influence that environmental drivers have on the abundance and distributional patterns of peracarids in the SO. Previous studies showed contrasting results, they showed different patterns and correlations between environmental variables and peracarid abundances (Brandt et al., 2007c; Meyer-Löbbecke et al., 2014), which might be explained by different environmental conditions between study areas (Di Franco et al., 2020).

Here we present the results based on 109 EBS collections from locations in the Atlantic and Pacific sector of the SO, ranging from 160 m depth on the continental shelf to 6348 m in the hadal South Sandwich Trench. The objective of our study is to expand our knowledge on SO benthic peracarid assemblages. After collating all available data on peracarid abundances collected by EBS in and near the Weddell Sea region of the SO, we aim to investigate the influence of environmental variables on peracarid abundance and assemblage patterns. This will allow us to assess whether benthic assemblages from the continental shelf and the deep sea are shaped by the same drivers. Also, it will provide useful information to improve our knowledge and predict the influence of environmental changes on benthic assemblages at a wide bathymetrical range and at a large spatial scale.

2. Material and methods

2.1. Abbreviations

The following abbreviations will be used in this paper: South Atlantic Ocean (SAO); Eastern Polar Front (PFE); Western Polar Front (PFW); South Orkney Islands (SOI); South Sandwich Islands (SSI); Deep Weddell Sea Abyssal Plain (DWS); Filchner Trough and Kapp Norvegia (FT-KN); Eastern Antarctic Peninsula (EAP); Western Antarctic Peninsula (WAP); Prince Gustav Channel (PGC).

2.2. Study area

The present study is based on peracarid data collected by 109 EBS deployments in the Atlantic and Pacific sectors of the SO and SAO during previous expeditions: ANTARKTIS XV/3 (EASIZ II, Arntz and Gutt, 1999), ANTARKTIS-XIX/3–4 (ANDEEP I and II; Fütterer et al., 2003; Brökeland et al., 2007), ANT-XXII/3 (ANDEEP III; Fahrbach, 2006; Brökeland et al., 2007), ANT-XXVIII/3 (SYSTCO; Wolf-Gladrow, 2013;

Brandt et al., 2014b) and PS118 (Dorschel, 2019) on board of RV *Polarstern*, and JR144 (BIOPEARL I), JR275, JR15005, JR17003a (Linse, 2006, 2018; Kaiser et al., 2008; Griffiths, 2012, 2016) on board of RRS *James Clark Ross* (Supplementary Table S1). The study area comprised stations located in the Southern Atlantic Ocean, north of the Polar Front, in the Polar Frontal Zone (PFE and PFW), on the continental shelf of the SOI, off the SSI, in the DWS, on the eastern Weddell Sea continental shelf between the FT-KN, the EAP on the western Weddell Sea shelf, and the WAP in the Pacific SO sector (Fig. 1A). The EAP includes a subdivision into the PGC, which until 1995 was partly covered by the Prince Gustav Ice Shelf (Rott et al., 1996), and the remaining stations in the area for the analysis of Weddell Sea EBS deployments only (Fig. 1B). In total, 109 stations were analysed, encompassing samples from depths ranging between 160 m and 6348 m, and latitudes ranging from 77° to 41° South (Table 1).

2.3. Environmental data

Environmental data were downloaded from the "global environmental datasets for marine species distribution modelling" Bio-ORACLE (http://www.bio-oracle.org/; Tyberghein et al., 2012; Assis et al., 2018) with a resolution of 5 arcminutes. Data were assembled by a combination of satellite and in situ observations, for a period of 14 years (2000–2014; Assis et al., 2018). Bio-ORACLE offers data recorded at the maximum depth (benthic layers) and data recorded at the surface (surface layers). For the present study, the layers downloaded included data about annual-mean value at the maximum depth recorded of salinity, temperature (°C), chlorophyll-a (mg/m^3), silicate (mol/m^3), current velocity (m^{-1}), iron (μmol/m^3), oxygen concentration (mol/m^3), nitrate (mol/m^3), primary production (g/m^3d^{-1}), phosphate (mol/m^3), and phytoplankton biomass (μmol/m^3).

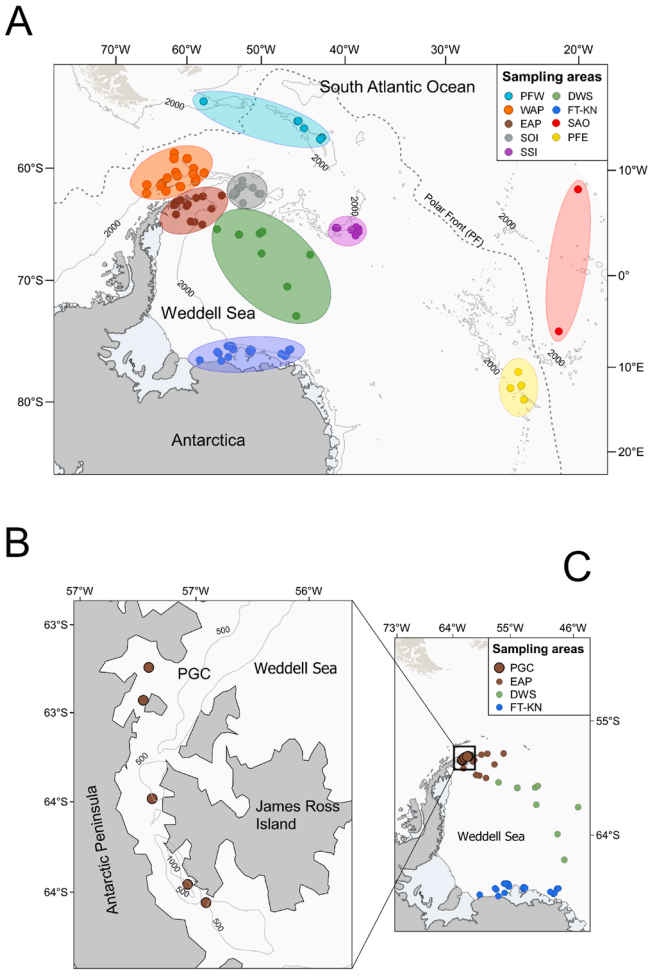

Fig. 1. Map of the study area at a wide geographical scale showing all stations at which EBS peracarid samples were collected (A); map showing stations from the Prince Gustav Channel within the EAP (B) and those from the Weddell Sea (C). Abbreviations: South Atlantic Ocean (SAO), Eastern Polar Front (EPF), Western Polar Front (WPF), South Orkney Islands (SOI), South Sandwich Islands (SSI), deep Weddell Sea Abyssal Plains (DWS), area confined between the Filchner Trough and the Kapp Norvegia (FT-KN), Western Antarctic Peninsula (WAP), Eastern Antarctic Peninsula (EAP), Prince Gustav Channel (PGC).

Table 1
Studies sampling areas of the EBS samples analysed. Precise locations of all stations are available in Supplementary Table S1.

Sampling area	N. of stations	Depth range (m)	Latitudinal range	Longitudinal range
PFW	8	193–1508	54° 18′ – 53° 15′ S	56° 40′ – 37° 53′ W
WAP	20	100–5191	63° 19′ – 59° 22′ S	64° 39′ – 53° 57′ W
EAP	16	432–3405	65° 20′ – 62° 11′ S	58° 30′ – 49° 27′ W
SOI	15	204–1984	62° 09′ – 60° 13′ S	47° 27′ – 42° 30′ W
SSI	10	307–6348	59° 31′ – 58° 14′ S	27° 27′ – 23° 57′ W
DWS	9	4069–4976	68° 03′ – 62° 58′ S	48° 03′ – 20° 31′ W
FT-KN	21	201–4382	77° 21′ – 70° 31′ S	35° 21′ – 13° 58′ W
SAO	2	4577–4720	47° 39′ – 41° 07′ S	4° 15′ – 9° 55′ E
PFE	7	2736–4327	53° 00′ – 51° 59′ S	12° 03′ – 8° 00′ E

2.4. Data analysis

The analysed peracarid abundance data, based on the collation of published datasets (references as above), were already standardized to 1000 m haul distances for comparative analyses between stations. The influence of environmental variables on the composition and distribution pattern of peracarid crustaceans was investigated on abundance data at a large geographic scale (from the SAO to the SO; Fig. 1A) and by means of ordinate analyses. The present study aimed to investigate whether peracarid assemblage structure from continental shelf areas recently covered by ice shelves or perennial sea ice resembled those from the DWS. The Weddell Sea, with its ice shelves, areas of perennial sea ice and deep-sea plains, was chosen for the analysis (Fig. 1B). Abundances from the PGC were compared to the remaining EAP stations, to those from the DWS and from the FT-KN (Fig. 1B). For the comprehensive, full study area analysis (Fig. 1A) stations from the PGC were considered as EAP stations. For ordinate analysis, the standardized abundance data were square root transformed. An ANSOSIM 1-way permutation test was performed on a Bray-Curtis similarity matrix to give the significance level of differences between samples. Draftsman plot analysis based on the Pearson correlation coefficient checked for multicollinearity between environmental variables and assessed variable skewness. When required, a transformation was applied to correct the skewness following Clarke and Gorley (2006). Depth, chlorophyll-a, current velocity, oxygen, iron, phytoplankton and primary productivity were log transformed; phosphate, salinity and silicate concentration were inversely transformed. According to Pearson's correlation coefficients (Supplementary Table S2) the following environmental variables were removed for the presence of multicollinearity: phytoplankton, nitrate and silicate. In subsets of variables with Pearson correlation coefficient averaging between > 0.90 and < -0.90 only one of the two variables was kept for further analyses (Supplementary Table S2). The distribution pattern of peracarid crustaceans in relation

to environmental variables and similarities between stations were visualized using non-metric multidimensional scaling (nMDS) plots based on Bray-Curtis similarity matrices. In order to assess the correlation between explanatory environmental variables and samples, a Redundancy Analysis (RDA) was used. Prior to RDA, environmental variables were normalized to make them comparable with each other and a Detrended Corrispondence Anlaysis (DCA) was performed to assess whether taxa responses were best explained by unimodal or linear models. Linear models are accepted if the gradient length of the first axis is<3 SD (Lepš and Šmilauer, 2003). A Monte Carlo permutation test was performed to determine if the variance explained by environmental variables was significant (999 permutations).

After RDA, BIO-ENV (BEST analysis) was used in order to investigate which environmental variables best explained the abundance patterns, assuming that more than one variable influenced peracarid assemblages. The analysis was statistically tested through the global BEST match permutation test (999 permutations). Ordinate analyses were performed in Primer 6 (Clarke and Gorley, 2006), analyses DCA, RDA and Pearson correlation were performed using the statistic software RStudio package "ggpubr" and "vegan" were used (Kassambara, 2017; Oksanen et al., 2017).

SIMPER analysis was used to identify which peracarid order contributed most to the dissimilarities between samples (Clarke and Gorley, 2006). Correlations between environmental variables and abundances were also analyzed by Pearson correlation analyses.

In general, the deep sea is defined to begin at the continental shelf break towards the continental slope and in non-Antarctic regions starts at about 200 m. In the SO, the Antarctic continental shelf is usually deeper, with an average of 500 m depth, due to the weight of the ice sheet, but also has deeper troughs and basins (Clarke, 2003; Clarke et al., 2009). It was shown that a shift between shelf and deep-sea isopod and sponge communities occurred only at about 1500 m in the Powell Basin (Brandt et al., 2007c; Gocke and Janussen, 2013). Therefore we considered as shelf stations those belonging to a depth range between 0 and 1499 m and deep stations those deeper than 1500 m.

2.5. Results

For the present study, peracarids collected at 109 EBS stations were analysed and a total of 183,606 specimens were counted and identified (Supplementary Table S1). Peracarid fauna included five orders, of which 75,367 were amphipods, 41,580 were cumaceans, 49,073 isopods, 9559 mysidaceans and 8027 were tanaidaceans. In each station the abundance of the different peracarid orders varied from 0 to a maximum of 7555 ind./1000 m haul among amphipods, 9823 ind./1000 m haul among cumaceans, 7828 ind./1000 m haul among isopods, 2805 ind./1000 m haul among mysidaceans, 1170 ind./1000 m haul among tanaidaceans (Supplementary Table S1).

2.6. Peracarid distribution pattern in the SO

The 1-way ANOSIM test performed on the abundance dataset including all sampled stations showed that differences between peracarid assemblages at different stations are significant ($p = 0.001$), although the R value of 0.262 indicated a certain degree of overlap between sampling areas. In the nMDS, sampling sites clustered in two main groups at 40% of similarity (Fig. 2A), two smaller clusters were on the left side of the graph. The assemblagés structure of these two latter was dissimilar to that of the main clusters because of their very low abundances. Among all environmental variables, depth was the one which best explained the abundance patterns shown on the nMDS. The plot showed a clear dissimilarity in assemblage structure between deep-sea stations and those from the continental shelf (Fig. 2A). Shelf and slope stations (0–1499 m) clustered together on the right side of the graph, while deep-sea stations (>1500 m) clustered on the left side.

DCA analysis indicated that the gradient length of the first axis was<3 (1.93 SD), confirming that RDA analysis would be appropriate. This latter analysis showed that canonical axes explained 47% of the variance and that the first axis was the most significant, explaining 41% of the variance (λ axis 1 = 394.62, p = 0.001; 999 permutations). Depth, iron and chlorophyll-a were strongly correlated with the first axis and were the environmental variables that best explained the variation in

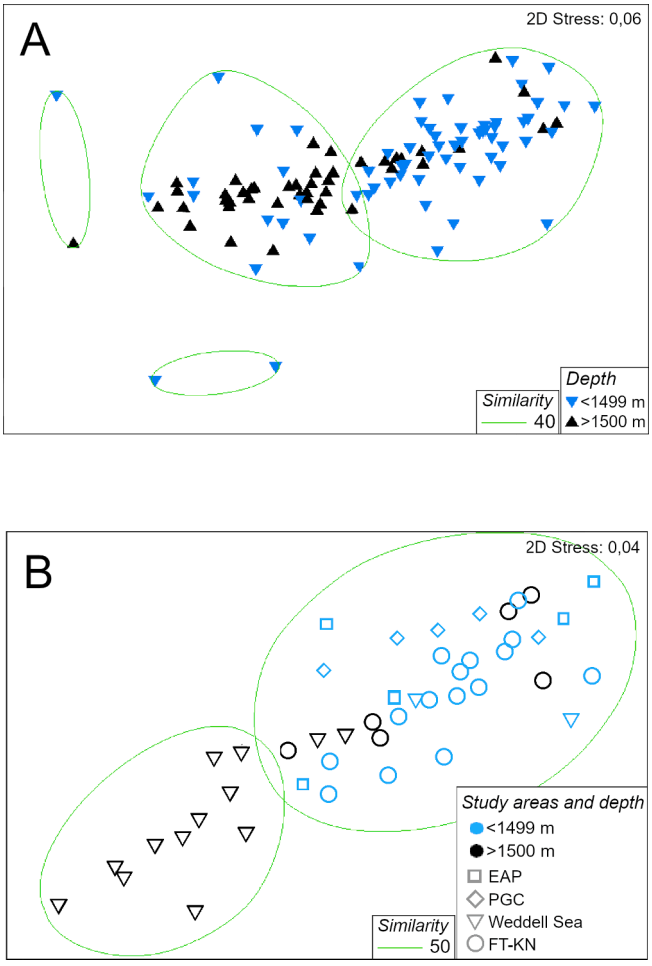

Fig. 2. Non-metric multidimensional scaling (nMDS) plot of peracarid abundance from all sampling areas and in relation to depth (A); nMDS plot of depth of peracarid abundance from the Weddell Sea (B). Abbreviations: Eastern Antarctic Peninsula (EAP), Prince Gustav Channel (PGC), area confined between the Filchner Trough and the Kapp Norvegia (FT-KN). Stations < 1499 m are from the SO continental shelf while stations > 1500 m are from the SO deep sea.

Table 2
Plot scores for constraining variables for all sampling areas and for the Weddell Sea. Plot scores higher than 0.7 are indicated in bold. Only statistically significant axes are shown (p < 0.05). Abbreviations: Chl-a = chlorophyll-a; Cv = current.

	All sampling areas	Weddell Sea
Variable	RDA1	RDA1
Depth	**−0.7183**	**−0.86725**
Chl-a	**0.7092**	0.64064
Cv	0.3394	0.53403
O2	0.5183	0.33129
Fe	**0.719**	0.62479
PO4	0.1727	**−0.80264**
PP	0.446	0.53016
Sal	0.239	−0.32612
T	−0.1721	0.01294
Ice	0.4355	−0.17597

peracarid composition (Table 2; Fig. 3A). While depth showed a negative correlation with peracarid assemblages, iron and chlorophyll-a were positively correlated (Fig. 3A). BIOENV (BEST) analysis indicated depth and chlorophyll-a as main drivers shaping the abundance patterns ($p = 0.1\%$; $\rho = 0.328$). The dissimilarity between peracarid abundances from the continental shelf and those from the deep sea was confirmed also through SIMPER analysis, which indicated Amphipoda as the main peracarid order driving the abundance patterns observed (Higher % of contribution; Table 3). The dissimilarity was significantly high between abundances from the continental shelf and those from abyssal and hadal depths (4000–6000 m), while the dissimilarity between abundances from the continental shelf and those from intermediate depths (1500–4000 m) was less significant (Table 3). Ultimately, no significant dissimilarity was observed between abundances from intermediate and abyssal depths. Statistical analyses by means of Pearson correlation showed a positive correlation between depth and isopod abundance, while amphipods and mysids were negatively correlated. No correlation was found between the other peracarid orders and depth (Table 4).

South Atlantic Ocean (SAO), Eastern Polar Front (PFE), Western Polar Front (PFW), South Orkney Islands (SOI), South Sandwich Islands (SSI), deep Weddell Sea Abyssal Plains (DWS), area confined between the Filchner Trough and the Kapp Norvegia (FT-KN), Western Antarctic Peninsula (WAP), Eastern Antarctic Peninsula (EAP), Prince Gustav Channel (PGC).

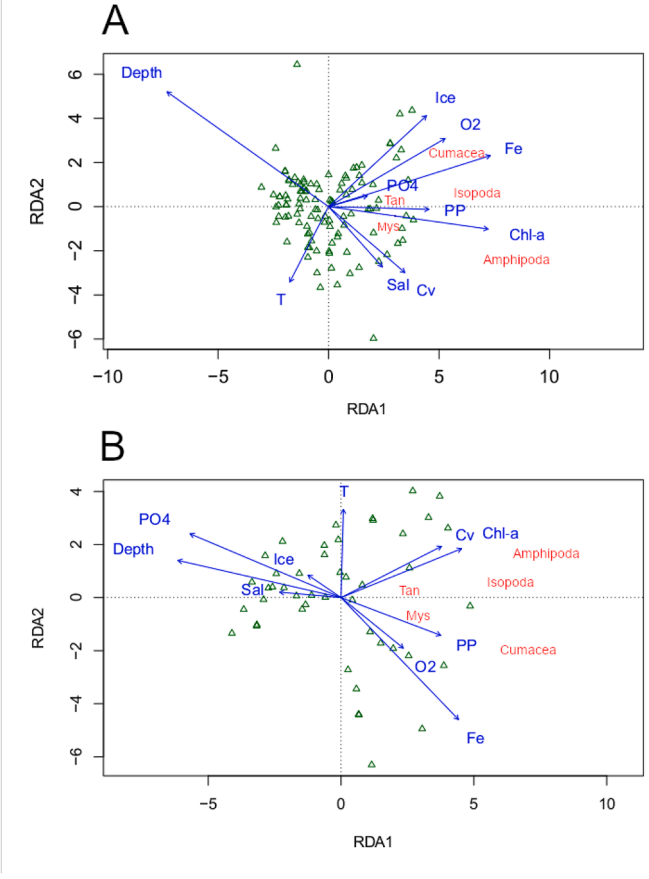

Fig. 3. RDA plot of peracarid assemblages and environmental variables from all sampling areas (A); RDA plot of peracarid assemblages and environmental variables from the Weddell Sea (B). Abbreviations: Chl-a = chlorophyll-a; Cv = current velocity; O2 = oxygen; Fe = iron; PO4 = phosphate; PP = primary productivity; Sal = salinity; T = temperature; Ice = ice concentration.

Table 3
Results of SIMPER ("similarity percentage") analysis to determine which order of peracarid drives the different patterns of abundance at a wide geographical scale and bathymetrical range. Stations < 1499 m are from the SO continental shelf while stations > 1500 m are from the SO deep sea.

Groups 0–1499 and 1500–4000	Group 0–1499	Group 1500–4000		
Average dissimilarity = 56,12	Av.Abund	Av.Abund	Contrib %	Cum. %
Orders				
Amphipoda	24.11	14.53	32.45	32.45
Isopoda	17.65	13.59	24.35	56.8
Cumacea	14.23	10.41	20.88	77.68
Mysidacea	7.43	3.48	11.38	89.05
Tanaidacea	7.63	4.54	10.95	100
Groups 1500–4000 and 4000–6000	Group 1500–4000	Group 4000–6000		
Average dissimilarity = 51,71	Av.Abund	Av.Abund	Contrib %	Cum. %
Orders				
Amphipoda	14.53	3.32	29.83	29.83
Isopoda	13.59	6.13	29.62	59.45
Cumacea	10.41	1.8	21.44	80.89
Tanaidacea	4.54	1.83	10.99	91.88
Groups 0–1499 and 4000–6000	Group 0–1499	Group 4000–6000		
Average dissimilarity = 64,77	Av.Abund	Av.Abund	Contrib %	Cum. %
Orders				
Amphipoda	24.11	3.32	34.44	34.44
Isopoda	17.65	6.13	23.73	58.17
Cumacea	14.23	1.8	18.3	76.47
Tanaidacea	7.63	1.83	12.11	88.59
Mysidacea	7.43	0.48	11.41	100

Table 4
Pearson's correlation analyses of environmental variables and peracarid abundances. Significant results are highlighted in bold ($p < 0.05$).

Taxon	R	p value
Amphipoda	−0.66	**9.3e-06**
Cumacea	−0.26	0.12
Isopoda	0.78	**1.6e-08**
Mysidacea	−0.51	**0.0011**
Tanaidacea	−0.087	0.61

2.7. Peracarid distribution patterns within the Weddell sea

The 1-way ANOSIM test showed significant dissimilarity between peracarid abundances from different areas ($R = 0.46$; $p = 0.1\%$). Based on the draftsman plots results, depth, chlorophyll-a, current velocity, oxygen, iron, phytoplankton and primary productivity were log transformed and according to Pearson correlation coefficients (Supplementary Table S3), the following environmental variables were removed due to their multicollinearity: phytoplankton, silicate and nitrate. The nMDS results showed two main clusters in which sampling sites were grouped at 50% of similarity (Fig. 2B). The cluster on the left side of the graph included sampling sites from the DWS, except for one single sampling site from the EAP characterized by very low peracarid abundance. The environmental variable that better explained the pattern observed in the nMDS was depth. Based on the latter, the graphs showed a clear dissimilarity in peracarid assemblagés structure between deep-sea and continental-shelf sampling sites. Peracarid assemblagés structure from the PGC was similar to that from the continental shelf (FT-KN, EAP) and dissimilar to values from the deep sea (>1500 m; Fig. 2B). To investigate the correlation between environmental parameters and peracarid assemblages a RDA was used. Canonical axes explained 55% of the

variation in peracarid composition. The eigenvalue of axis 1 was statistically significant ($\lambda = 668.8$; $p = 0.001$; 999 permutations) and explained 49% of the total variance. Depth was the main explanatory variable followed by phosphate concentration (Table 2, Fig. 3B). Both latter variables were negatively correlated with peracarid assemblage composition (Fig. 3B). DCA results confirmed that RDA analysis would be appropriate (gradient length of the first axis = 0.97 SD). Results from the BIOENV (BEST) analysis indicated depth and current velocity as main drivers shaping the abundance patterns ($p = 0.1\%$; $\rho = 0.328$). SIMPER analysis showed that isopods and cumaceans were the main orders driving the dissimilarities observed (Table 5).

3. Discussion

Studies investigating the influence of environmental variables on SO peracarids from the continental shelf and from the deep sea are still limited (Brandt et al., 2005, 2007c, 2009; Kaiser et al., 2007; Rehm et al., 2007; Meyer-Löbbecke et al., 2014; Brandt et al., 2016). These studies mainly focused on one single peracarid order, the Isopoda, while very little is known about the influence of the environment on abundances and distributional patterns of all five orders represented in the SO. A recent study investigated the influence of environmental variables on the abundance and assemblage structure of five peracarid orders including only 28 stations from the continental shelf of the Weddell Sea and Atlantic Sector of the SO (Di Franco et al., 2020). The results of the study showed that ice coverage and chlorophyll-a concentration strongly influenced peracarid abundance and assemblage structure. The aim of the present research was to expand our knowledge on the distributional pattern of peracarid crustaceans, investigating the influence of a larger set of environmental variables at larger bathymetrical and geographical scales. Furthermore, we aimed to investigate the peracarid order being responsible for such differences between different geographic regions.

The distribution and abundance of benthic communities and assemblages are the result of the interaction between several factors, depending also on the investigated local, regional or global scale (Kaiser et al., 2007). At wider geographic scales differences between environmental variables are pronounced and different areas can be characterized by very different abiotic factors and conditions (e.g. water bodies, primary productivity rate, presence/absence of ice, current regimes). The analyses carried out in our study showed multiple environmental variables as possible drivers of the peracarid assemblage structure, nevertheless depth was the main abiotic factor responsible for the pattern observed. However, the transition between the continental shelf and deep sea is not always distinct, some abyssal species were reported also from the continental shelf at 1000 m (Clarke, 2003). In our study the unusual depth of the SO continental shelf was confirmed, peracarid assemblage structure from shallower stations (<1499 m) was dissimilar to that from deeper ones (>1500 m). This distinction was also observed in another study (Brandt et al., 2016) where the ANOSIM tests showed that main differences in composition of isopod assemblages were between shallower stations (<2000 m) and deeper ones (>4000 m), while no difference was reported between assemblages from intermediate stations (2000–4000 m). Similarly, Kaiser et al., 2007 observed no significant effect of depth on the variability of isopod abundances among stations from the deep sea (from about 2000 m to almost 5000 m; only three stations were shallower at a depth < 1900 m).

Differences between shelf and deep-sea in other peracarid orders were shown in studies based on species composition, a Bray-Curtis similarity analysis performed in De Broyer and Jazdzewska (2014) showed a clear distinction in amphipod species composition with depth, where shelf and upper slope fauna (0–800 m and 801–2200 m respectively) were dissimilar to lower slope and abyssal fauna (2201–3700 m and 3701->4500 m respectively). Also, species composition of cumaceans and tanaidaceans from the SO continental shelf differ from that from the SO deep sea. For example, 43% of tanaidaceans species and

Table 5
Results of SIMPER ("similarity percentage") analysis on peracarid abundance from the Weddell Sea and at a wide bathymetrical range.

Groups EAP and DWS	Group EAP	Group DWS				
Average dissimilarity = 63,33	Av. Abund	Av. Abund	Av. Diss	Diss/ SD	Contrib %	Cum. %
Orders						
Isopoda	29.25	3.58	17.76	1.42	28.05	28.05
Amphipoda	25.12	6.77	16.33	2.15	25.79	53.83
Cumacea	20.51	1.82	12.59	1.34	19.87	73.71
Mysidacea	9.9	0.36	9.39	1.16	14.83	88.54
Tanaidacea	10.38	1.59	7.26	1.65	11.46	100
Groups EAP and FT-KN	Group EAP	Group FT-KN				
Average dissimilarity = 44,93	Av. Abund	Av. Abund	Av. Diss	Diss/ SD	Contrib %	Cum. %
Orders						
Isopoda	29.25	30.16	14.01	1.66	31.17	31.17
Cumacea	20.51	25.06	11.61	1.4	25.84	57.01
Amphipoda	25.12	27.2	10.09	1.42	22.46	79.47
Mysidacea	9.9	8.31	4.62	1.12	10.29	89.77
Tanaidacea	10.38	9.76	4.6	1.18	10.23	100
Groups DWS and FT-KN	Group DWS	Group FT-KN				
Average dissimilarity = 70,22	Av. Abund	Av. Abund	Av. Diss	Diss/ SD	Contrib %	Cum. %
Orders						
Isopoda	3.58	30.16	22.21	3.17	31.63	31.63
Cumacea	1.82	25.06	18.53	2.25	26.39	58.02
Amphipoda	6.77	27.2	16.07	1.89	22.89	80.9
Tanaidacea	1.59	9.76	6.96	1.8	9.91	90.81
Groups EAP and PGC	Group EAP	Group PGC				
Average dissimilarity = 45,66	Av. Abund	Av. Abund	Av. Diss	Diss/ SD	Contrib %	Cum. %
Orders						
Cumacea	20.51	31.55	13.76	1.43	30.14	30.14
Amphipoda	25.12	30.77	10.17	1.35	22.26	52.4
Isopoda	29.25	17.35	9.95	1.25	21.79	74.19
Mysidacea	9.9	13.04	5.89	1.34	12.91	87.1
Tanaidacea	10.38	13.97	5.89	1.23	12.9	100
Groups DWS and PGC	Group DWS	Group PGC				
Average dissimilarity = 74,11	Av. Abund	Av. Abund	Av. Diss	Diss/ SD	Contrib %	Cum. %
Orders						
Cumacea	1.82	31.55	22.07	2.05	29.78	29.78
Amphipoda	6.77	30.77	17.96	2.13	24.23	54.01
Mysidacea	0.36	13.04	12.06	1.94	16.27	70.28
Tanaidacea	1.59	13.97	11.7	2.21	15.79	86.07
Isopoda	3.58	17.35	10.32	2.35	13.93	100
Groups FT-KN and PGC	Group FT-KN	Group PGC				
Average dissimilarity = 36,37	Av. Abund	Av. Abund	Av. Diss	Diss/ SD	Contrib %	Cum. %
Orders						
Cumacea	25.06	31.55	10.79	1.43	29.68	29.68
Amphipoda	27.2	30.77	8.84	1.26	24.32	54
Isopoda	30.16	17.35	8.19	1.37	22.51	76.51
Mysidacea	8.31	13.04	4.62	1.18	12.71	89.23
Tanaidacea	9.76	13.97	3.92	1.3	10.77	100

67% of cumaceans species were never found below 900 m and 1000 m respectively (Błażewicz-Paszkowycz, 2014).

In light of all this, it is likely that in the bathyal deep sea beginning from > 1500 m down to the abyss and hadal zone (3500–6000 m), depth and other physical parameters no longer influences benthic communities, the environment is generally more homogeneous and becomes more stable in the deep sea (Thistle, 2003). For example, Di Franco et al., 2020 showed that ice coverage influence peracarid assemblagés structure only within a certain depth range (down to ~ 1000 m). At deeper depths, other mechanisms are probably more responsible for structuring the benthos, for example food availability, feeding mode, reproductive adaptations along with biological interactions such as competition and predation (Rex, 1976, 1981; Brandt et al., 2007a).

The link between depth and benthic faunal abundances has been generally attributed to the rate at which food particles reach the seafloor (Thistle, 2003). Benthic faunal abundance generally decreases with depth, due to the reduction of food supply (McClain, 2004; Carney, 2005). Disaggregation and heterotrophic consumption contribute to the decrease of organic matter down the water column and only a small fraction of food particles reaches the deep-sea benthos (e.g. Gerlach, 1994; Nelson et al., 1996). A negative correlation between abundances and depth in peracarid assemblages was shown from the SO in a recent study (Di Franco et al., 2020), where peracarid abundances linearly decreased from the continental shelf down to the deep sea (from about 400 m to about 6000 m). A similar trend was observed for amphipods and mysids in the present study, conversely isopod abundances significantly increased with depth, as previously shown by Dahl, 1954. On one hand, this could be a reflection of the different species composition between peracarid orders, on the SO continental shelf isopods are less species-rich compared to the deep sea, while amphipods, tanaidaceans and cumaceans show a higher number of species on the shelf (Błażewicz-Paszkowycz, 2014; De Broyer and Jażdżewska, 2014; Mühlenhardt-Siegel, 2014; Brandt et al., 2016). On the other hand, the absence of a correlation between depth and abundances of cumaceans and tanaidaceans suggests that the abundance within Peracarida may also depend on other factors such as their functional traits rather than the composition in species of their communities. Expanding our investigation to species level will likely provide a better understanding of such patterns. It is worth mentioning also that a better comprehension of the interdependence between peracarid abundances and number of species can be affected by the limited knowledge of species composition of the deep-sea. For instance, during the ANDEEP expeditions, carried out in the SO deep sea, >85% of the collected isopod species were new to science (Brandt et al., 2007b).

We aimed to investigate whether abundances from the DWS were similar to those from the PGC, which was formerly covered by the Prince Gustav Ice Shelf (Larsen A) that almost completely collapsed in 1995 (Rott et al., 1996). Five years after the collapse, first scientific expeditions were led to the newly ice-free area in order to study the benthic communities which lived beneath the former shelf; their findings showed an impoverished benthic fauna characterized by the presence of typical deep-sea species (Gutt et al., 2011). The higher statistical significance in the results of the second part of our study supports the assumption that at large geographical scales benthic communities are affected by a wider range of abiotic variables, thus making more difficult the interpretation of results (Kaiser et al., 2007). However, regardless the geographical scale, depth was confirmed as the main factor shaping benthic peracarid composition and abundance, with a clear distinction between assemblages from the continental shelf and those from the deep sea. Confirming that in the latter, the structure of benthic communities is probably regulated by different mechanisms compared to those dominating the shelf (Rex, 1976, 1981; Brandt et al., 2007a). The difficulty in interpreting the results can be attributed to the lack of environmental data at different depths within the water column. Improved data availability could reveal additional information addressing the relationship between peracarid assemblage composition and the variation of physical variables in the water column and/or changes in seasonality. The latter can play an important role, especially in the deep sea. For example, deep-sea isopod species can show an opportunistic feeding strategy, being dependent on seasonal pulses of fresh phytodetritus on the seafloor (Brökeland et al. 2010).

The dissimilarity between peracarid assemblage structure from the PGC continental shelf and that from the DWS showed in our study did not confirm our initial assumption that peracarid assemblage structure from shelf areas recently covered by ice shelves or perennial sea ice are similar to deep sea ones. However, the observed dissimilarity can be the result of the high taxonomical level used for our analyses. Further studies at species level will probably give us a better resolution and it will be possible to investigate whether the composition in species of peracarids from the PGC is similar to that of the deep sea.

4. Conclusions and future outlooks

Our study confirmed depth as the main environmental variable shaping the assemblage structure and abundance pattern of SO peracarids at wide geographic scales and at wide bathymetric ranges, from the continental shelf to hadal depths. At smaller geographic scales, physical parameters vary less within the same area and their influence on benthic assemblages is easier to assess. At larger geographical scales, the influence of a greater variability of physical parameters on benthic assemblages becomes more difficult to evaluate.

The similarity between peracarid assemblages along a bathymetric range from ~ 100 m to 1499 m, confirmed the exceptional depth of occurrence of SO continental shelf assemblages at depth assigned to the deep sea in non-SO settings. Our findings confirmed that different peracarid orders show different abundance patterns along a wide bathymetric range. Further investigations at species level will allow us to have a better understanding of the correlation between peracarid abundances and species richness in the SO, from the continental shelf to the deep sea. It will be possible to investigate the role played by functional traits of the different peracarid species and assess the trait correlations with depth. This will allow us to better understand the dynamics ruling benthic peracarid assemblages in the deep sea as well as to assess existing hypotheses which try to explain the origin of the structure of benthic faunal deep sea communities.

CRediT authorship contribution statement

Davide Di Franco: Conceptualization, Formal analysis, Writing - original draft, Visualization. **Katrin Linse:** Conceptualization, Supervision, Funding acquisition, Writing - review & editing. **Huw J. Griffiths:** Conceptualization, Supervision, Funding acquisition, Writing - review & editing. **Angelika Brandt:** Conceptualization, Supervision, Funding acquisition, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to the captains and crews of RV *Polarstern* and RRS *James Clarke Ross* for their support, especially for our EBS deployments, during multiple expeditions. We acknowledge our expedition leaders' stamina in handling our requests for "just one more EBS station". This work was done thanks to the support and funding of the Deutsche Forschungsgemeinschaft (DFG; Br1121/51-1) in the framework of the project Larsen-C PEARL. Katrin Linse and Huw Griffiths are part of the British Antarctic Survey Polar Science for Planet Earth Programme. It was funded by The Natural Environment Research Council (NERC) [NC-

Science], and included the funding for the RSS *James Clark Ross* expeditions JR275 and JR15005. The RSS *James Clark Ross* expedition JR17003a was funded by the NERC urgency grant NE/R012296/1. Multiyear ice data from 15/10/1978 to 15/03/2019 were obtained from Q20 https://www.meereisportal.de (grant: REKLIM-2013-04).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107832.

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