



Abundance and Distributional Patterns of Benthic Peracarid Crustaceans From the Atlantic Sector of the Southern Ocean and Weddell Sea

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Climate change is influencing some environmental variables in the Southern Ocean (SO) and this will have an effect on the marine biodiversity. Peracarid crustaceans are one of the dominant and most species-rich groups of the SO benthos. To date, our knowledge on the influence of environmental variables in shaping abundance and species composition in the SO's peracarid assemblages is limited, and with regard to ice coverage it is unknown. The aim of our study was to assess the influence of sea ice coverage, chlorophyll-a, and phytoplankton concentrations on abundance, distribution and assemblage structure of peracarids. In addition, the influence of other physical parameters on peracarid abundance was assessed, including depth, temperature, salinity, sediment type, current velocity, oxygen, iron, nitrate, silicate and phosphate. Peracarids were sampled with an epibenthic sledge (EBS) in different areas of the Atlantic sector of the SO and in the Weddell Sea. Sampling areas were characterized by different regimes of ice coverage (the ice free South Orkney Islands, the seasonally ice-covered Filchner Trough and the Eastern Antarctic Peninsula including the Prince Gustav Channel which was formerly covered by a perennial ice shelf). In total 64766 individuals of peracarids were collected and identified to order level including five orders: Amphipoda, Cumacea, Isopoda, Mysidacea, and Tanaidacea. Amphipoda was the most abundant taxon, representing 32% of the overall abundances, followed by Cumacea (31%), Isopoda (29%), Mysidacea (4%), and Tanaidacea (4%). The Filchner Trough had the highest abundance of peracarids, while the South Orkney Islands showed the lowest abundance compared to other areas. Ice coverage was the main environmental driver shaping the abundance pattern and assemblage structure of peracarids and the latter were positively correlated with ice coverage and chlorophyll-a concentration.

We propose that the positive correlation between sea ice and peracarid abundances is likely due to phytoplankton blooms triggered by seasonal sea ice melting, which might increase the food availability for benthos. Variations in ice coverage extent and seasonality due to climate change would strongly influence the abundance and assemblage structure of benthic peracarids.

Keywords: the Weddell Sea, Southern Ocean, ice coverage, environmental variables, Peracarida, Crustacea, abundance, distribution pattern

INTRODUCTION

Peracarids play an important role in marine ecosystems; they can influence the structure and composition of benthic communities (Duffy and Hay, 2000) and they are an important converter of biomass and organic matter in the biogeochemical cycles (Karlson et al., 2007; Dunn et al., 2009). Burrows built by sediment-living peracarids allow oxygenated water to pass through the sediment layer, consequently promoting the mineralization of organic matter by other organisms (Pelegri and Blackburn, 1994; Lehtonen and Andersin, 1998). Furthermore, peracarid crustaceans can also directly consume organic matter as deposit-feeders and also feed on dead organisms from the sea bottom as scavengers; the assimilated biomass can be then transferred to the higher trophic levels via direct consumption (Jeong et al., 2009; Thiel and Hinojosa, 2009; Duffy et al., 2012). Peracarids are also an important source of food for benthic organisms as well as pelagic fauna such as fish and squid (Mouat et al., 2001; Padovani et al., 2012; Xavier et al., 2020). For example, amphipods represent a large percentage in the diet of many Antarctic species, from benthic invertebrates such as the polynoid polychaete *Harmothoe spinosa*, to benthic and bathy-pelagic predators such as cephalopods (e.g., *Galiteuthis glacialis*), notothenioid fish (e.g., *Notothenia coriiceps*), and megafaunal predators like penguins (e.g., *Eudyptes chrysolophus*), and baleen whales (e.g., *Balaenoptera borealis*) (Dauby et al., 2003). It has been estimated that about 60 million tons of amphipods are consumed every year within the Antarctic food web (Dauby et al., 2003).

Among invertebrates from the SO, Peracarida are one of the dominant and most species-rich groups of benthic fauna (De Broyer and Jazdzewski, 1996; Brandt et al., 2007b; De Broyer and Jazdzewska, 2014; De Broyer and Koubbi, 2014; Kaiser, 2014; Legezyńska et al., 2020). They show high levels of endemism, ranging from 51% (Cumacea) to 88% (Amphipoda) (Brandt, 2000; Brökeland et al., 2007). This might be because the SO's peracarids are characterized by low dispersal ability due to their reproductive biology (Brandt, 1999). Peracarids have undergone a long period of isolation during their evolution, which was strongly influenced by geological and climatic events over the last 40 Ma (Clarke and Crame, 1992; Lawver et al., 2011). During the Eocene-Oligocene, the opening of a seaway between Australia and East Antarctica and the subsequent opening of the Drake Passage in the Northern Antarctic Peninsula initiated the onset of the Antarctic Circumpolar Current (Lawver et al., 2011). The Antarctic Circumpolar Current is the largest current in the world and promoted the biogeographic isolation of the

SO by forming a dispersal barrier for marine species (Barker et al., 2007). Furthermore, during the glacial period of the late Cenozoic, the variation in size and extent of the continental ice sheet influenced the benthic community by forcing the organisms to take refuge on the shelf, and/or to shift their distribution ranges into the deep sea (Thatje et al., 2005). Such events caused a reduced gene flow between the newly separated communities and enhanced speciation. As a result, new species from the deep sea could then recolonize the shallow waters following the glacial retreat (Brey et al., 1996; Hodgson et al., 2003). For example, recent studies showed that different families of isopods underwent multiple colonization events from the shelf to the deep sea; some hypotheses also supported these using molecular experiments (Brandt et al., 2007c; Raupach et al., 2009; Riehl et al., 2020). Cooling events likely caused the extinction of some groups of decapods in the SO (Thatje and Arntz, 2004; Aronson et al., 2009). Consequently, the lack of benthic predators such as lobsters or brachyuran crabs in Antarctica offered new ecological niches to the peracarid crustaceans (Brandt, 1999).

The success of the SO's peracarids can be further explained by their highly diverse lifestyle and feeding biology (Brökeland et al., 2007; Thiel and Hinojosa, 2009; Brusca et al., 2016). For example, mysidaceans are strictly distributed in the water column, isopods and amphipods have benthic, pelagic, or benthopelagic lifestyle (Brökeland et al., 2007). Isopods and amphipods are one of the most dominant components of the emerging benthos (Aldredge and King, 1985; Vallet and Dauvin, 2001; Kiljunen et al., 2020). They perform vertical migrations into the water column during the night, moving benthic resources to the pelagos, thus playing an important role in the benthic-pelagic coupling (Vallet and Dauvin, 2001; Pacheco et al., 2013; Kiljunen et al., 2020). Peracarids include mobile swimmers, bottom-dwelling, and sediment-living species feeding on a wide variety of different food sources. Besides being prey by themselves, they can also be predators, scavengers, suspension-feeders and, among isopods and amphipods (e.g., whale lice), there even are ectoparasites. Cumaceans and tanaidaceans represent a smaller range of lifestyles being more strictly related to the sediment type, they mainly include suspension-feeders and deposit-feeders, but also predators (Thiel and Hinojosa, 2009; Brusca et al., 2016). Despite their high abundance and dominance, the composition pattern of the orders of Peracarida along the SO is still far from being comprehensively understood.

Sediment characteristics and depth have been identified as the most important factors driving faunal abundance and composition patterns in the SO's peracarids (Brandt et al., 2007b; Rehm et al., 2007). In addition, temperature, oxygen, salinity,

primary productivity, and quantity of food influence their diversity and community structure (Brandt et al., 2007a; Ingels et al., 2012; Meyer-Löbbecke et al., 2014). Some of these factors in turn could be affected by sea-ice dynamics: the extent and duration of ice coverage affect the amount of light penetrating the water column, which can positively influence phytoplankton activity (Dayton et al., 1994; Runcie and Riddle, 2006; Clark et al., 2017). Moreover, ice melting can also influence the salinity of the upper water column (Haumann et al., 2016).

Apart from sea ice, SO's peracarids can also be affected by glacial ice, in particular by floating ice shelves, icebergs, or marine terminating glaciers. Ice shelves around Antarctica cover more than 1.561 million km² (Rignot et al., 2013; Smith et al., 2019) creating conditions of permanent limited light penetration and food depletion, which can last for millennia (Domack et al., 2005; Pudsey et al., 2006). Benthic communities living beneath the ice shelf rely on the lateral advection of food particles (Riddle et al., 2007; Gutt et al., 2011; Smith et al., 2019). Due to limited food and light, benthic communities that live under the ice shelves are more similar to those living in the deep sea (Rose et al., 2015). Icebergs calving from ice shelves can play an important role as a source of physical disturbance in shallow Antarctic benthic marine systems (Gutt and Starman, 2001; Rack and Rott, 2004; Barnes and Souster, 2011). Iceberg scouring events are one of the main physical processes affecting shallow benthic communities which can be catastrophic (Gutt et al., 1996; Peck et al., 1999; Barnes and Souster, 2011; Valdivia et al., 2020). Iceberg calving events are episodic. Although, in the recent decades rising temperatures and in particular the regional warming along the Antarctic Peninsula caused destabilization leading to disintegration and break-up of several ice shelves (e.g., Larsen A and B and most recently Larsen C in the Eastern Antarctic Peninsula; Rott et al., 1996; Rack and Rott, 2003). Consequently, this caused an increase in the rate of iceberg calving events in the area (Rack and Rott, 2004; Massom et al., 2018).

Sea ice coverage (pack and fast ice) is characterized by strong seasonality, forming in winter and retreating or breaking out during austral summer, and it has a strong influence on the biota underneath. As aforementioned, during its retreat sea ice disperses and allows more light penetration into the upper water column, strongly increasing primary production and triggering phytoplankton blooms. Furthermore, when the ice melts, sea-ice biota are released and enhance the primary productivity and the organic matter input in the water column (e.g., fecal pellets produced by zooplankton). Released algae and fecal pellets can ultimately sink to the sea floor serving as food for the benthos, being able to reach also greater depths (Vanhove et al., 1995; Boetius et al., 2013; Wing et al., 2018). In addition, the land-fast sea ice along the coast prevents drifting icebergs from scouring the seabed (Smale et al., 2008; Smith, 2011; Collares et al., 2018).

Satellite observations show that the overall ice coverage in the Weddell Sea experienced a gradual increase since the early 1980s, particularly in summer. However, long-term trends are superimposed by large multi-year variability, with a recent strong decline beginning in 2016 (Parkinson, 2019; Vernet et al., 2019).

The sea ice development is somewhat contradictory to the strong warming experienced by the Antarctic Peninsula region, which is considered one of the most rapidly warming regions of the world (Hansen et al., 2010).

In light of all this, improving our knowledge on composition and distribution of Antarctic benthic communities and their interactions with the environmental abiotic factors is important for prediction of the potential ecological impact induced by ongoing climate change. The knowledge of its influence in shaping abundances and species composition in benthic communities of the deep sea is limited and in peracarid crustaceans still remains unknown. This study therefore aims to describe the composition of peracarid crustaceans in different areas of the Weddell Sea, and to investigate the importance of ice coverage and potential driving environmental variables on their abundance, distribution patterns and assemblage structure.

MATERIALS AND METHODS

Study Area

The peracarid samples were collected from different areas of the Atlantic sector of the SO, mainly in the Weddell Sea, during expeditions of the RRS *James Clark Ross* and RV *Polarstern* (Figure 1). The entire area of the Weddell Sea is dominated by the cyclonic Weddell Gyre, which branches off from the warmer and more saline Antarctic Circumpolar Current north of the Antarctic Peninsula going southwards into the Antarctic continental shelves (Fahrbach et al., 1995). In this area, colder deep and bottom waters (Weddell Sea Bottom Water) are produced, released into the gyre and transported back to the north along the Eastern Antarctic Peninsula. Another water mass that contributes to the formation of the Weddell Gyre is the Weddell Sea Deep Water, which originates by mixing processes between surface water masses and a component of the Antarctic Circumpolar Current, the Circumpolar Deep Water (Fahrbach et al., 1995; Vernet et al., 2019).

The expedition JR15005 with the RRS *James Clark Ross* worked at the South Orkney Islands in February–March 2016, a small archipelago located in the Northeast of the Antarctic Peninsula (Figures 1A,B, Griffiths, 2017). It is characterized by a great variability in the duration of ice coverage (Murphy et al., 1995; Meredith et al., 2011), the presence of the Antarctic Circumpolar Current in the north and the Weddell Sea Deep Water in the south (Meredith et al., 2011).

During the expedition JR17003a on the RRS *James Clarke Ross*, sampling was carried out in February–March 2018 in the Prince Gustav Channel, situated in the Eastern Antarctic Peninsula (Figures 1A,C) because the Larsen-C ice shelf, where iceberg A68 calved off in July 2017 (Hogg and Gudmundsson, 2017), could not be reached as originally planned due to heavy pack-ice conditions (Linse, 2018). The Prince Gustav Channel was formerly covered by ice shelf but in 1995, an almost total collapse of the ice shelf (Rott et al., 1998; Pudsey et al., 2001) exposed the area to new environmental conditions, leading to an increase in primary production (Bertolin and Schloss, 2009). The area, especially in the deeper parts, is characterized by drapes

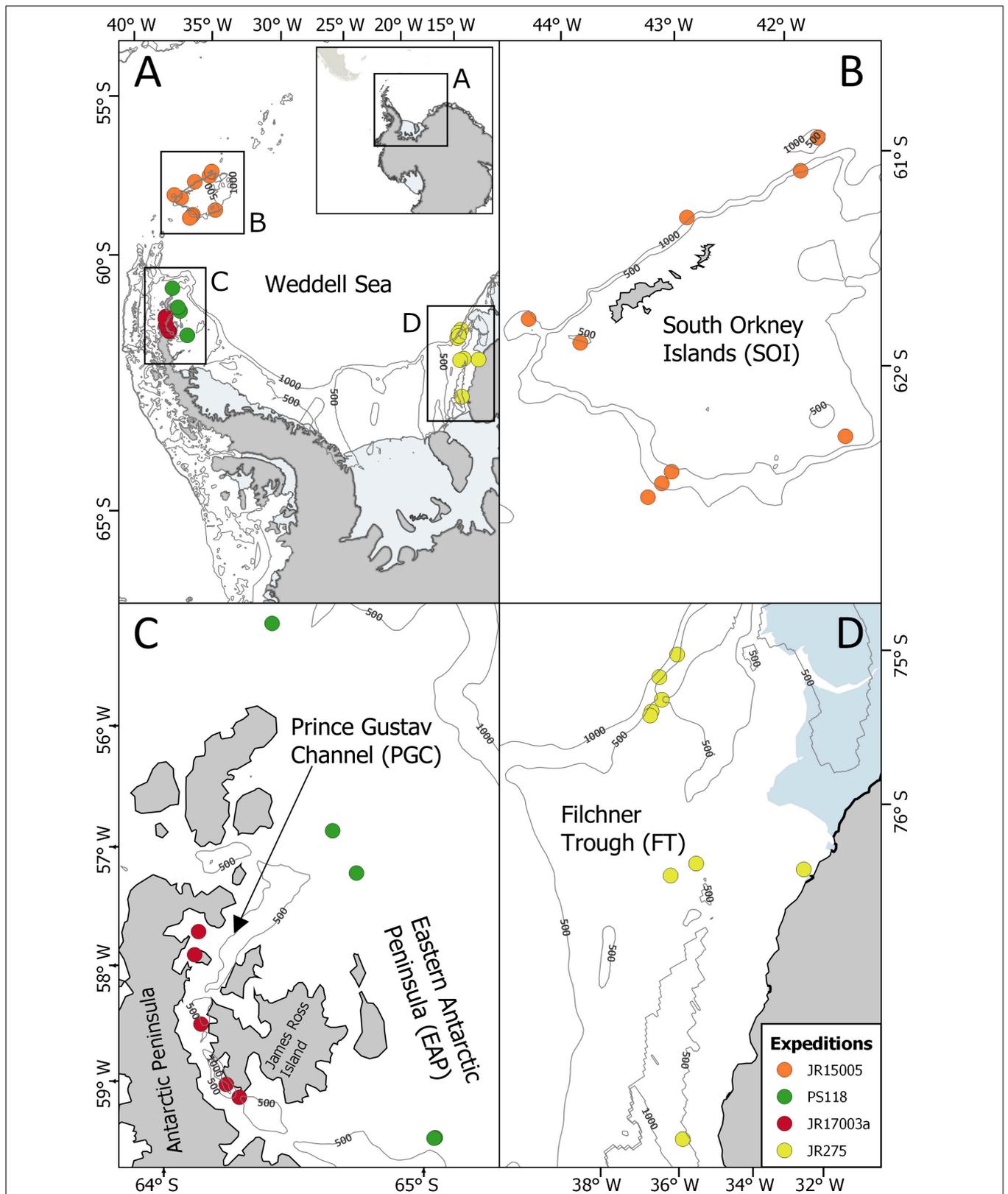


FIGURE 1 | Locations of the EBS stations sampled during the expeditions in the SO (A); JR15005, South Orkney Island, SOI (B); PS118, Eastern Antarctic Peninsula, EAP (C); JR17003a, Prince Gustav Channel, PGC, (C); JR275, Filchner Trough, FT, (D).

of diatom-bearing glacial marine mud, which are typical of the presence of floating ice shelves (Pudsey et al., 2001).

The PS118 expedition of the RV *Polarstern* in February/March 2019 aimed to reach the Larsen-C ice shelf but also failed to reach this area as well due to very heavy sea-ice conditions (Dorschel, 2019). Therefore, sampling was done to the east of James Ross Island along the Eastern Antarctic Peninsula following a latitudinal gradient transect at an average depth of about 400 m from 63° to 64° south (Figures 1AA,C).

Previously, epibenthic sledge (EBS) samples were taken during the expedition JR275 on the RRS *James Clark Ross* (February–March 2012) in the Filchner Trough area (South-Eastern Weddell Sea), located in front of the Filchner Ice Shelf (Figures 1A,D) (Griffiths, 2012). The South-Eastern Weddell Sea is relatively inaccessible and under-sampled as it is mostly covered with perennial sea ice and is characterized by the presence of very large icebergs (Årthun et al., 2013; Darelius and Sallée, 2018). The sampled area, situated in the north of the Filchner Ice Shelf, is characterized by seasonality in the ice coverage (Yi et al., 2011) and is affected by super-cooled Ice Shelf Water. The latter originates from the Filchner Ice Shelf and flows northwards mixing with the Weddell Sea Bottom Water, contributing to the formation of the Weddell Gyre (Gordon et al., 2001). Ice Shelf Water and Weddell Sea Bottom Water are characterized by very low temperatures (with Ice Shelf Water reaching -2.3°C) and high level of oxygen concentration (Orsi et al., 1993; Makinson et al., 2011).

Sampling Protocol

During each expedition, peracarid crustaceans were collected using an EBS which consisted of a suprabenthic- and an epibenthic net with a mesh size of 500 μm (cod-ends 300 μm) and was deployed as described by Brenke (2005). The epibenthic net extended from 27 to 60 cm above the seafloor, while the suprabenthic net extended from 100 to 133 cm above the bottom. The sledge was provided with an opening-closing mechanism so that box supra- and epibenthic meshes would immediately close once the gear was lifted (Brenke, 2005). The deployment was carried out for 10 min at a mean velocity of about one knot. Trawling distances were then calculated on the basis of velocity of ship and winch from the start of the trawling until the sledge left the ground, following the equation #4 reported in Brenke (2005). Since the trawling distance between stations was not always the same, in order to compare the different stations, numbers of individuals were standardized to 1000 m haul distances (Tables 1, 2).

In order to make station numbers more intuitive and easier to read, original station IDs were changed and reported in Table 1 as “New Station ID.” Nevertheless, original station names from each expedition were included as well (Table 1; “Original Station ID”) to make our results comparable with published data in which the original names were used. A total of 28 EBS and 26 CTDs were deployed at 28 stations in the areas of the Filchner Trough (9 EBS/7 CTDs), the Prince Gustav Channel (5/5), the Eastern Antarctic Peninsula (4/4) and the South Orkney islands (9/9) (Table 1). CTD sensors attached to the EBS collected data about temperature and salinity, except for station F6 and F9 in the

Filchner Trough. The characterization of the type of sediment was derived from the analysis of video footage, following the same protocol as in Brasier et al. (2018) for the geomorphologic classification (Table 1). Video footage was recorded using the Shallow Underwater Camera System during expeditions JR15005 and JR17003a, the Deep Water Camera System during JR275 and the Ocean Floor Observation and Bathymetry System during the expedition PS118 (Table 1).

On board samples were sieved with a mesh size of 300 μm and/or directly transferred into precooled (-20°C) 96% ethanol. All ethanol-preserved samples were then stored at -20°C for at least 48 h before further processing, to avoid DNA degradation. On board and later in the laboratory, ethanol-preserved peracarids were further sorted to order level. The number of individuals per sample was counted (raw data; Supplementary Table 1) and compared with the number of individuals standardized to 1000 m haul distance.

Environmental Data

Environmental data not collected during the expeditions were obtained from the “global environmental datasets for marine species distribution modeling” Bio-ORACLE¹ (Tyberghein et al., 2012; Assis et al., 2017) with a resolution of 5arcmin (0.0833°). The latter were compiled from combinations of satellite and *in situ* observations, gathering data for a period of 14 years (2000–2014; Assis et al., 2017).

The layers downloaded for the present paper included data about annual-mean value of chlorophyll-a (mg/m^3), current velocity (m^{-1}), oxygen concentration (mol/m^3), iron ($\mu\text{mol}/\text{m}^3$), nitrate (mol/m^3), silicate (mol/m^3), phosphate (mol/m^3), phytoplankton ($\mu\text{mol}/\text{m}^3$), primary production ($\text{g}/\text{m}^3\text{d}^{-1}$). All values referred only to the maximum depth at the sea bottom except for primary production which included only the pelagic data. Besides, ice concentration data (fractions from 0 to 1), salinity, and temperature ($^{\circ}\text{C}$) were also downloaded in order to assess the reliability of Bio-ORACLE data in comparison with the CTD data. Bio-ORACLE data were used to replace the two missing values of CTD data of temperature and salinity in station F6 and F9 from the Filchner Trough. Ice concentration data from all study areas since the year 1978 were obtained from the meereisportal data base of the Alfred Wegener Institute² (Grosfeld et al., 2016). Ice concentration is given using the unit interval (fractions) from 0 to 1, where 0 indicates absence of ice and 1 indicates a completely ice-covered area.

Data Analysis

To determine the distribution patterns of the assemblage of peracarid crustaceans between stations and in relation to environmental variables, abundance data were analyzed by means of ordination analysis. Prior to analyses, a draftsman plot was used to check for multicollinearity between environmental variables and to assess the presence of heavily skewed ones. Heavily skewed variables were then transformed following Clarke and Gorley (2006). The following variables were removed:

¹<http://www.bio-oracle.org/>

²meereisportal.de

TABLE 1 | Station list of analyzed EBS deployments ordered by depth, CTD and environmental data measured at seafloor.

Original station ID	New station ID	Date	Depth range	Latitude (S)	Longitude (W)	Haul	T	S	O2	Device	Sediment (%)		
			(m)	Start - End	Start - End	length (m)	(°C)	(psu)	(ml/l)		Soft	Hard	Biogenic
JR275	JR275									DWCS			
45	F1	22/02/2012	429 – 428	75° 45.72' – 75° 45.85'	30° 26.56' – 30° 27.08'	536	–1.96	34.66	–	✓	88.6	1.6	9.8
94	F2	29/02/2012	478 – 491	74° 41.51' – 74° 41.36'	29° 29.27' – 29° 29.05'	426	–1.75	34.40	–	✓	41.0	4.3	54.7
40	F3	21/02/2012	549 – 539	76° 10.01' 76° 09.94'	27° 48.23' – 27° 48.44'	508	–1.84	34.38	–	✓	65.7	0.2	34.1
50	F4	22/02/2012	583 – 587	75° 44.60' – 75° 44.75'	31° 14.77' – 31° 15.21'	684	–1.98	34.67	–	✓	69.8	2.3	5.5
89	F5	29/02/2012	642 – 657	74° 40.30' – 74° 40.24'	29° 23.93' – 29° 23.30'	575	–1.56	34.42	–	✓	16.3	13.8	70.0
23	F6	19/02/2012	654 – 656	77° 21.42' – 77° 21.47'	35° 21.64' – 35° 21.90'	701	–	–	–	–	–	–	–
99	F7	01/03/2012	977 – 963	74° 38.05' – 74° 38.14'	29° 00.49' – 28° 59.97'	741	0.18	34.60	–	✓	48.7	15.6	35.7
83	F8	28/02/2012	1582 – 1580	74° 29.12' – 74° 29.08'	8° 46.48' – 28° 47.08'	1172	0.33	34.67	–	✓	98.0	0.0	2.0
78	F9	26/02/2012	2021 – 2026	74° 24.28' – 74° 24.39'	28° 05.09' – 28° 04.62'	1251	–	–	–	✓	98.0	0.0	2.0
JR15005	JR15005									SUCS			
12	S1	02/03/2016	516 – 519	61° 31.85' – 61° 31.80'	46° 55.89' – 46° 56.20'	662	0.25	34.66	7.98	✓	100.0	0.0	0.0
133	S2	16/03/2016	527 – 521	60° 40.38' – 60° 40.35'	42° 30.74' – 42° 31.02'	670	0.34	34.67	7.96	✓	83.3	16.7	0.0
34	S3	06/03/2016	561 – 524	62° 09.61' – 62° 09.45'	44° 58.92' – 44° 59.00'	780	0.12	34.66	8.00	✓	80.2	19.8	0.0
115	S4	15/03/2016	588 – 590	60° 45.16' – 60° 45.14'	42° 57.75' – 42° 58.08'	780	0.07	34.66	8.02	✓	20.3	79.7	0.0
18	S5	03/03/2016	782 – 786	61° 32.20' – 61° 32.08'	47° 07.99' – 47° 08.24'	850	0.22	34.67	7.98	✓	88.1	11.9	0.0
103	S6	14/03/2016	788 – 817	60° 28.53' – 60° 28.41'	44° 25.38' – 44° 25.61'	819	0.09	34.66	8.01	✓	19.9	80.1	0.0
86	S7	12/03/2016	795 – 794	60° 13.07' – 60° 13.11'	46° 44.54' – 46° 44.87'	937	0.16	34.66	8.00	✓	100.0	0.0	0.0
57	S8	09/03/2016	798 – 835	60° 33.33' – 60° 33.44'	46° 30.92' – 46° 31.12'	898	0.23	34.65	7.98	✓	100.0	0.0	0.0
27	S9	04/03/2016	1461 – 1471	61° 31.92' – 61° 31.80'	47° 23.49' – 47° 23.68'	1456	–0.02	34.66	8.03	✓	100.0	0.0	0.0
JR17003a	JR17003a									SUCS			
53	P1	07/03/2018	470 – 445	63° 36.97' – 63° 37.00'	57° 30.23' – 57° 30.40'	508	–1.64	34.48	–	✓	28.4	62.5	5.7
35	P2	05/03/2018	787 – 727	64° 02.86' – 64° 02.95'	58° 27.71' – 58° 28.01'	937	–1.84	34.53	–	✓	3.1	0.1	0.1
34	P3	04/03/2018	843 – 850	64° 07.70' – 64° 07.64'	58° 30.31' – 58° 29.96'	851	–1.85	34.53	–	✓	90.5	2.4	7.4
47	P4	06/03/2018	874 – 872	63° 48.44' – 63° 48.57'	58° 04.12' – 58° 04.34'	898	–1.77	34.48	–	✓	99.0	0.2	0.9
5	P5	01/03/2018	1079 – 1081	63° 34.47' – 63° 34.51'	57° 17.08' – 57° 17.41'	937	–1.84	34.54	–	–	–	–	–
PS118	PS118									OFOBS			
9-5	E1	12/03/2019	403 – 401	64° 01.18' – 64° 01.35'	55° 54.08' – 55° 54.90'	459	–1.64	34.55	6.88	✓	99.0	0.7	0.3
38-9	E2	22/03/2019	428 – 427	63° 03.79' – 63° 03.92'	54° 18.56' – 54° 18.75'	579	–0.88	34.56	6.11	✓	94.6	4.4	1.0
6-5	E3	05/03/2019	432 – 433	64° 58.43' – 64° 58.60'	57° 47.20' – 57° 48.24'	854	–1.86	34.58	6.91	✓	97.0	1.4	1.7
6-6	E4	05/03/2019	438 – 438	64° 58.25' – 64° 58.35'	57° 47.89' – 57° 48.63'	640	–1.86	34.58	6.91	✓	97.0	1.4	1.7
12-7	E5	14/03/2019	445 – 444	63° 49.40' – 63° 49.48'	55° 40.67' – 55° 40.21'	334	–1.21	34.54	6.63	✓	98.8	0.5	0.7

SWCS, Shallow Underwater Camera System; DWCS, Deep Water Camera System; OFOBS, Ocean Floor Observation and Bathymetry System.

TABLE 2 | Standardized abundance of peracarid orders from all stations.

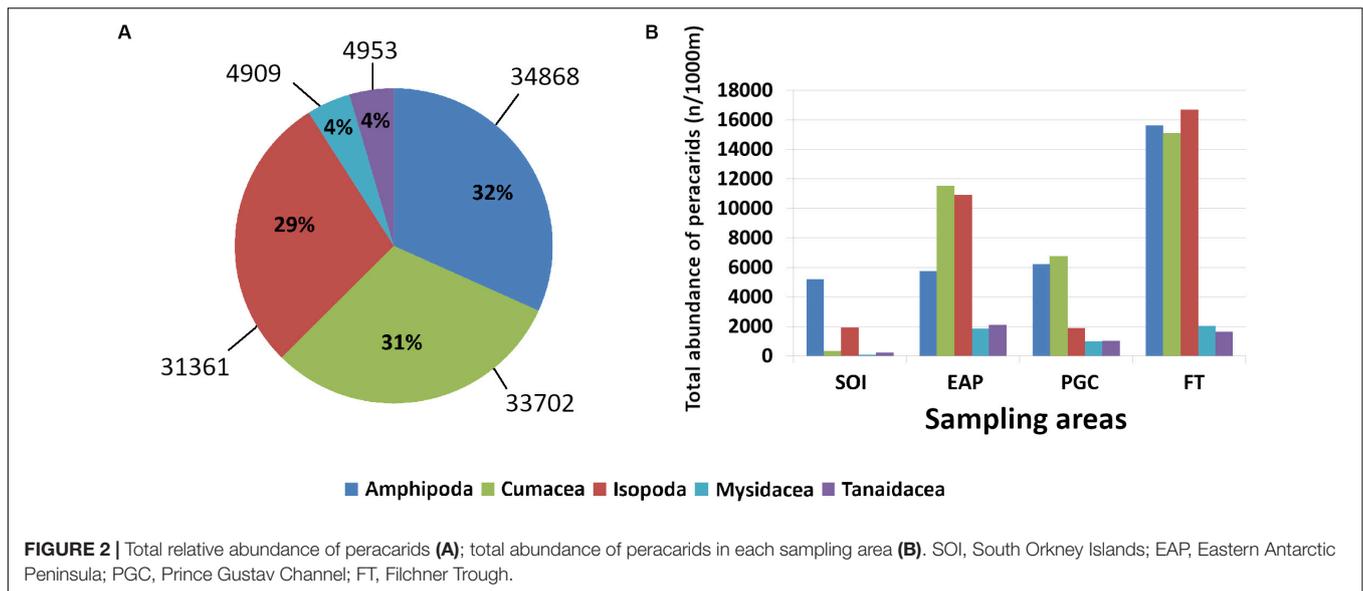
Taxon	Amphipoda	Cumacea	Isopoda	Mysidacea	Tanaidacea	Total
Station	Standardized 1000 m trawl length					
JR275						
F1	1681	5132	2073	274	56	9216
F2	2955	531	3085	33	164	6768
F3	1778	2081	963	646	384	5852
F4	1259	3466	1789	598	175	7287
F5	7555	553	5210	97	325	13740
F6	407	1083	531	150	23	2194
F7	1644	1254	1976	161	147	5182
F8	368	974	918	54	350	2664
F9	40	35	119	22	18	234
JR15005						
S1	195	59	142	11	33	440
S2	2249	63	213	4	9	2538
S3	739	1	253	6	33	1032
S4	823	18	326	12	10	1189
S5	259	49	218	0	74	600
S6	889	110	758	20	26	1803
S7	17	10	10	0	22	59
S8	2	3	2	0	2	9
S9	26	3	11	0	1	41
JR17003a						
P1	502	156	175	461	211	1505
P2	940	2930	653	186	106	4815
P3	612	1243	161	222	160	2398
P4	4018	2369	840	37	318	7582
P5	160	52	39	83	213	547
PS118						
E1	2815	1441	2699	619	1770	9344
E2	377	38	14	503	41	973
E3	269	184	303	75	68	899
E4	70	41	52	25	8	196
E5	2219	9823	7828	610	206	20686

phytoplankton, nitrate, oxygen, silicate. In addition, depth, chlorophyll-a, current velocity, iron and primary productivity were log transformed. When a couple of variables presented mutual Pearson correlation coefficients averaging more than 0.90 and less than -0.90 , only one for each couple was selected for further analyses (**Supplementary Table 2**).

Ordinate analysis was performed using the non-metric multidimensional scaling (nMDS) based on Bray–Curtis dissimilarity matrix and on square rooted transformed abundance data in order to visualize dissimilarities in assemblages' structure among samples. The similarity profile permutation test (SIMPROF) was used to visually identify significant dissimilarities among samples by superimposing significant SIMPROF clusters on nMDS plots. Principal Component Analysis (PCA) based on normalized environmental data was used to graphically represent correlations between peracarid assemblages and environmental parameters.

The BIOENV procedure (BEST) was used to identify the subset of variables that best explained the dissimilarity patterns observed. BIOENV computed a Spearman rank correlation (Rho) between the Bray–Curtis similarity matrix of peracarid's abundances and the similarity matrix of transformed and normalized environmental variables based on Euclidean distance. In order to examine the statistical significance of observed correlation, the global BEST match permutation test (999 permutations) was used.

The seriation with replication test of the RELATE routine was used to test whether the dissimilarity in assemblages' structure observed in the nMDS followed a sequential pattern of change. This analysis applies a Spearman rank correlation (Rho) between dissimilarities among samples and a perfect seriated model matrix based on a linear sequence of values equally spaced along a line (Clarke and Gorley, 2006). A Spearman rank correlation coefficient Rho close to one indicates high seriation,



while a coefficient Rho close to zero corresponds to the null hypothesis of no seriation. To reject the null hypothesis of a complete absence of seriation, a permutation test was applied to the matching coefficient (Rho; 999 permutations). The null hypothesis was rejected at a significance level of at least 1 in 10000 ($p < 0.0001$).

Ordination analysis including nMDS and PCA, BIOENV and RELATE analyses were performed using the multivariate software PRIMER v6 (Clarke and Gorley, 2006).

Ultimately, correlations between environmental variables and total peracarid abundances were analyzed by Pearson correlation analyses using the statistic software RStudio and the package “ggpubr” (Kassambara, 2017).

Statistical analyses by means of Pearson correlation were carried out on selected stations from the continental shelf (depth range 400–899 m) excluding those from the deep sea. The latter usually starts at about 200 m but in the SO where the continental shelf is usually deeper, it starts at a depth of 1000 m (Clarke, 2003). It was also 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). The depth range 400–899 m was chosen because it allowed us to have the larger dataset having the smallest difference in depth.

RESULTS

Peracarid Abundance

A total of 64766 peracarids were sorted and identified to order level, five orders were identified (Amphipoda, Cumacea, Isopoda, Mysidacea, Tanaidacea; **Table 2**). Standardized abundance data showed that the sampled areas had different levels of maximum abundance per station. Noteworthy was station F5 in the Filchner Trough which had the highest abundance with 13740 peracarid ind./1000 m haul, while abundance from station F9 was the lowest with only 234 ind./1000 m haul (**Table 2**).

In total, amphipods were the most abundant taxon with 34868 ind./1000 m haul, representing 32% of the total abundance, while Mysidacea and Tanaidacea were the least abundant with 4909 and 4953 ind./1000 m haul respectively, each only representing 4% of the total abundance (**Figure 2A**).

The number of individuals in each order of peracarids varied regardless of the depth in all sampling areas. In the Eastern Antarctic Peninsula, abundances from station E5 (445 m depth) were the highest with 20686 ind./1000 m haul, while abundances from station E4 (438 m) were only 196 ind./1000 m haul (**Table 2** and **Figure 3C**). The other stations from the same area and with similar depth showed a much lower number of peracarids (**Table 2** and **Figures 3A,E,G**).

The total abundance of the five peracarid orders varied between different areas. Whilst in the Filchner Trough amphipods, isopods, and cumaceans were similar in abundance, in the Prince Gustav Channel isopods were less abundant (**Figure 2B**). In the Eastern Antarctic Peninsula and in the South Orkney Islands the least abundant of these three taxa were the amphipods and cumaceans, respectively (**Figure 2B**).

One of the most striking results was the very high abundance of cumaceans at station E5 off the Eastern Antarctic Peninsula, dominating with 9823 ind./1000 m haul (**Figure 3C**), while at station S3 off the South Orkney Islands only one single ind./1000 m haul was found (**Table 2**). A similar trend was observed also for the other groups; although, none of them showed such high abundance in one single station. Cumaceans were also dominant at five of nine stations in the Filchner Trough and at two stations from the Prince Gustav Channel (**Figures 3E–H**).

Relative abundances showed different patterns between the different areas and regardless of depth. In the South Orkney Islands amphipods were the most dominant group, representing up to more than 80% of the total in the different stations (**Figure 3B**). A consistent relationship between depth and the abundance of amphipods was not observed. In the Eastern

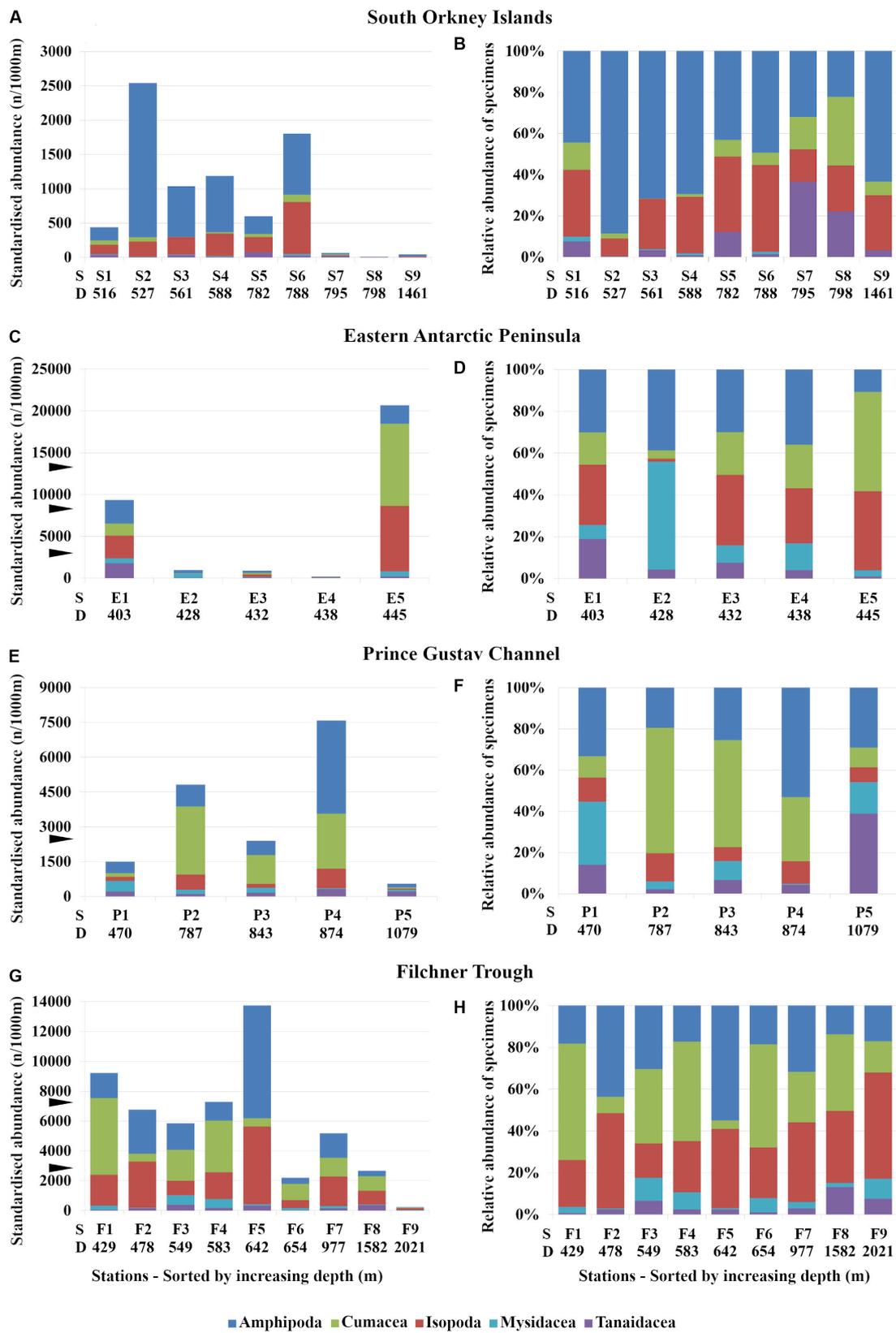
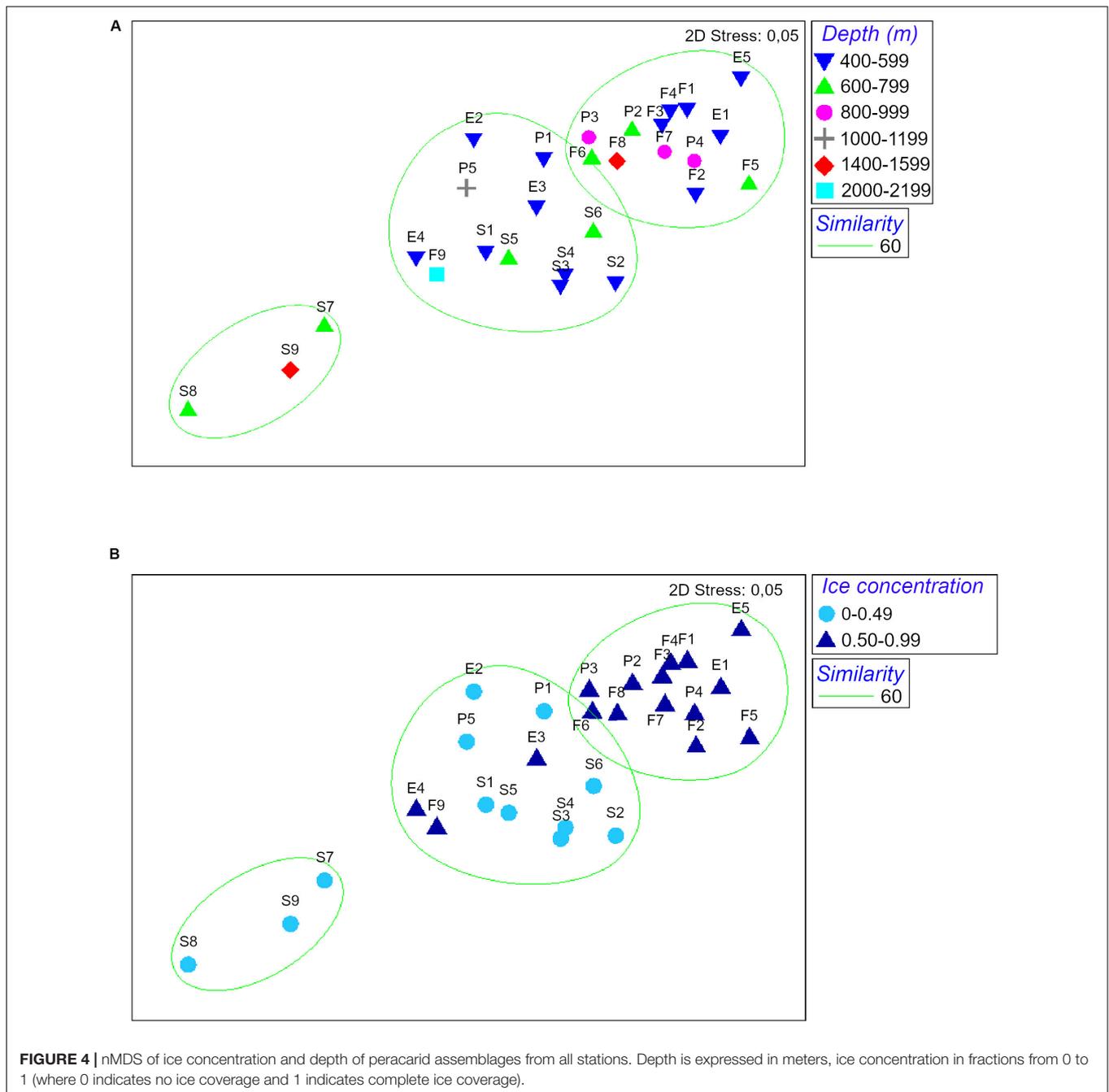


FIGURE 3 | Standard (A,C,E,G) and relative abundance (B,D,F,H) of peracarid orders in the study areas. (A,B) South Orkney Islands, (C,D) Eastern Antarctic Peninsula, (E,F) Prince Gustav Channel, (G,H) Filchner Trough. ▶, maximum standardized abundance at comparative regions; S, station number; D, depth (m).



Antarctic Peninsula amphipods showed a similar pattern between stations (**Figure 3D**). In the Prince Gustav Channel, Cumacea were the dominant order, representing up to 61% of the total abundance among the different stations (**Figure 3F**). In the Filchner Trough almost all orders showed similar abundance patterns at all stations (**Figure 3H**).

Peracarid Assemblages and Environmental Variables

In order to assess the abundance, distribution patterns and assemblage structure of peracarids between the different stations

and in relation to environmental variables, ordinate statistical analyses were performed.

The nMDS analysis showed a dissimilarity in assemblages' structure among sampling sites gradually increasing from low ice concentration (<0.5) to high ice concentration (>0.5). Stations S7, S8, S9 were very dissimilar compared to the rest of the cluster due to their extremely low abundances (59, 9 and 41 ind./1000 m haul, respectively; **Figure 4** and **Table 2**). In contrast, depth did not explain the patterns of dissimilarity in assemblages' structure observed. Stations from the same depth ranges were evenly distributed among the different clusters (**Figure 4**).

Principal Component Analysis produced a total of five principal components, the first three of which explained 80.1% of the total variance (eigenvalue > 1). Analysis of the eigenvectors showed that the major contribution in the first PCA axis (PC1) was given by phosphate concentration and temperature, while the predominant variables in the second axis (PC2) were salinity and primary productivity. Ice coverage and depth were the most significant variables in the third axis (PC3; **Table 3**; **Figure 5**). BIOENV analysis showed that the ice coverage was the variable which was most highly correlated with the similarity matrix derived from peracarid abundances ($p = 0.008$; $\rho = 0.334$). The presence of a gradual change of dissimilarities in assemblage's structure among samples with increasing/decreasing ice concentration was tested using the "seriation with replication" test implemented in the RELATE routine. The analysis showed a significant result ($p = 0.0001$; $\rho = 0.355$). The same test carried out on a depth gradient did not show any significant result ($p = 0.17$; $\rho = 0.077$).

Total abundance of peracarids from all the stations investigated in the present study (400–2021 m) decreased with depth ($R = -0.67$, $p = 0.033$; **Figure 6A** and **Table 4**). When the correlation was tested including only stations from the continental shelf (400–899 m) the result was not significant ($R = -0.82$, $p = 0.092$; **Table 4**), showing that the correlation between abundances and other environmental variables was not affected by the depth intervals (100 m) chosen in the analysis.

A negative correlation was found with increasing temperature and salinity ($R = -0.53$, $p = 0.013$ and $R = -0.52$, $p = 0.018$ respectively; **Figures 6C,E** and **Table 4**). Peracarids showed higher abundances at lower values of the two parameters. Conversely, peracarid abundances significantly increased with increasing ice and chlorophyll concentration (**Figures 6B,D** and **Table 4**). No significant correlation with the other environmental parameters investigated in this study (current velocity, iron, phosphate, primary productivity; **Table 4**) was found.

When comparing Bio-ORACLE data with shipboard CTD measurements, both sources produced similar results.

DISCUSSION

Abundance of Peracarid Crustaceans

Results from this study showed that peracarid abundances varied in different study areas and between stations within the same area. Such a trend is in line with a previous study from the SO continental shelf, in which Kaiser et al. (2008) reported that total abundance of peracarids between different stations (South Sandwich Islands) ranged from 11 to 4123 ind./1000 m haul (samples collected with an EBS, the deepest station was about 1000 m). In our study, overall, shelf stations from the Filchner Trough showed much higher abundances compared to those recorded in the South Orkney Islands. A similar result was observed when comparing the Filchner Trough with the South Sandwich Islands (Kaiser et al., 2008). Total abundances of peracarids from the latter (4361 ind./1000 m haul) more closely resembled those from the South Orkney Islands (**Table 2**). The higher abundances in the Filchner Trough could be explained by

TABLE 3 | Eigenvectors for the first five principal components (PCA) from environmental variables.

Variable	PC1	PC2	PC3	PC4	PC5
Depth	0.311	0.066	0.648	0.262	0.333
Ice	-0.36	0.038	0.554	0.225	-0.07
T	0.421	-0.294	0.101	-0.135	-0.211
S	0.227	-0.54	-0.039	0.265	0.474
Chl-a	-0.341	-0.098	0.371	-0.575	-0.019
Cv	0.226	0.455	-0.125	-0.424	0.607
Fe	-0.407	-0.174	-0.327	0.298	0.214
PO4	0.451	0.189	-0.036	0.124	-0.447
PP	-0.092	0.578	-0.02	0.42	0.032

PP, primary productivity; Chl-a, chlorophyll-a; S, salinity; T, temperature; Fe, iron; Cv, current velocity; PO4, phosphate; Ice, ice concentration.

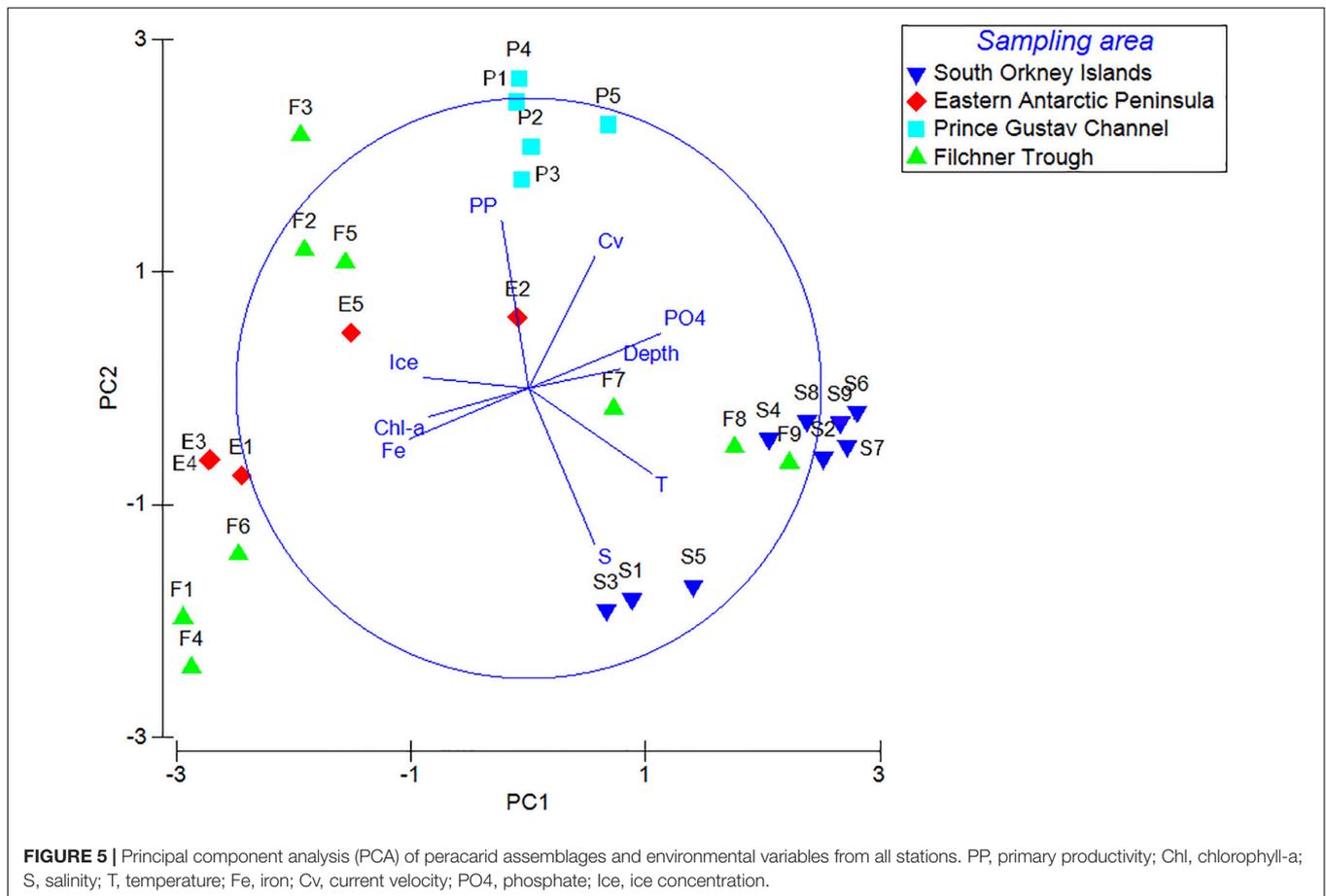
the high frequencies of icebergs that can lead to more open water, broken-up ice, enhanced primary productivity and also impact benthic communities promoting the spread of opportunistic species, which in turn can become very abundant (Gerdes et al., 2003; Årthun et al., 2013). Our finding is in line with a previous study in which Brandt et al. (2007c) indicated an increase in abundance and species richness from the Scotia Arc area toward the Southern Weddell Sea.

Amphipods showed the highest relative abundance compared to other peracarid orders, which corresponds to previous studies where amphipods were also the most abundant group sampled in the SO (Brökeland et al., 2007; Kaiser et al., 2008). Nevertheless, a striking result was the high abundance recorded for cumaceans from many stations and from different areas (Filchner Trough, Prince Gustav Channel, Eastern Antarctic Peninsula). This is unusual, as in previous studies, cumaceans were rarely dominant, except for two stations sampled in the Ross Sea (Rehm et al., 2007).

Besides, the high relative abundance of cumaceans recorded in our study (31%) was never reported before. In Brandt (2001; Eastern Weddell Sea), they represented about 21%, in Brökeland et al. (2007; different areas of the SO) 16%, in Rehm et al. (2007; Ross Sea) 7%, in Kaiser et al. (2008; South Sandwich Islands) they represented only the 2% of the entire peracarid assemblage. The high abundance of cumaceans recorded in the present study may be explained by their life style. Cumaceans are inbenthic (only males move into the water column during circadian migrations; Mühlenthaldt-Siegel, 2014), they specially occur in very fine and silty sediments which characterized most of the sampling sites.

Influence of Environmental Variables Temperature, Salinity, Depth, Sediment Type

Previous studies that investigated the influence of environmental parameters on peracarid assemblages' abundance and composition in the SO mainly considered factors such as depth, salinity, temperature and sediment type. However, previous results did not always show the same patterns or correlations between peracarid assemblages and environmental parameters. Meyer-Löbbecke et al. (2014) suggested that salinity, temperature, chlorophyll-a, and depth might influence the



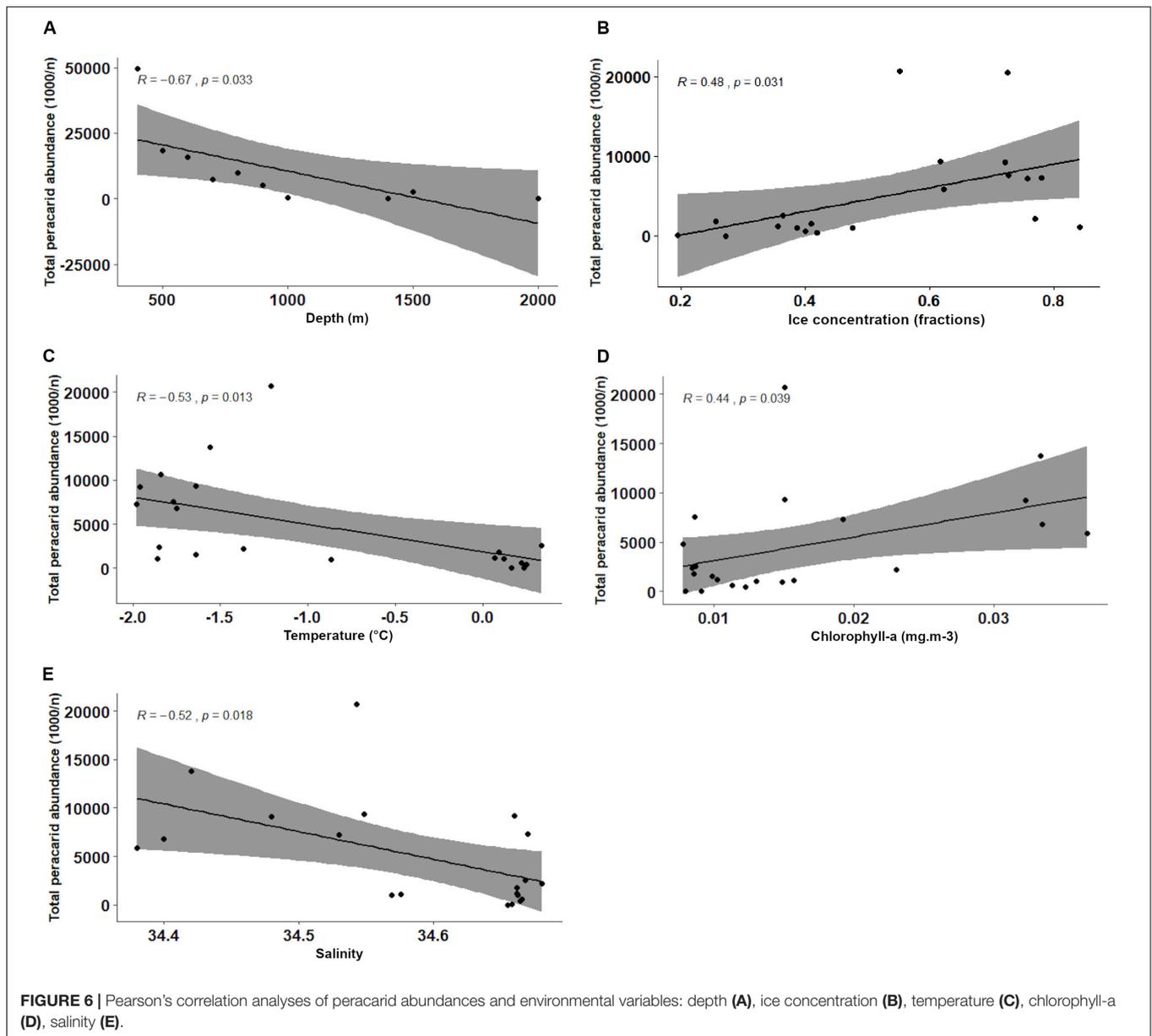
number of isopod specimens and the isopod assemblages, while in Brandt et al. (2007a) depth was the main driver shaping the structure of isopod assemblages. These different results could be due to the fact that sampling was done in areas influenced by different water bodies and thus by different environmental conditions, besides the different number of stations and depth range. A full understanding of the dynamics governing the composition of benthic communities is difficult, since general distribution patterns can result from several different factors and from the spatial scales investigated (e.g., if local or regional scale; Kaiser et al., 2007).

In our study, the abundance of peracarids from all stations (depth range 400–2021 m) was negatively correlated with temperature, salinity, and depth. The negative correlation with the latter can be explained by a decrease in food availability and quality from shallower to deeper waters (Hessler, 1974; Gage and Tyler, 1991; Schnack-Schiel and Isla, 2005; Brökeland et al., 2007). The high number of peracarids recorded at stations from the deep sea showed that depth is not the only factor affecting food availability at the bottom (Brökeland et al., 2007). This possibly documents the importance of the Antarctic bottom-water production, which might enhance food availability in deeper waters (Brandt et al., 2007b). For example, in East Antarctica regions it was shown that downslope flow of Antarctic bottom-water rich in organic matter and generated

in shelf polynyas can supply food to seafloor slope benthos (Jansen et al., 2018). It was shown to be also one of the key factors sustaining benthic communities from the continental shelf, down to about 900 m (Post et al., 2010).

Ice Coverage and Chlorophyll-a Concentration

In our study, ice concentration was the parameter which best explained the pattern of dissimilarity in assemblages' structure of peracarids. Dissimilarities among samples increased with decreasing percentage of ice concentration. In spite of the lack of studies in this regard in the Southern Ocean, the influence of sea ice on peracarid assemblages was reported in a previous study performed in the Northern Hemisphere (Greenland; Brandt, 1995). Composition, abundance and diversity of benthic peracarids reflected the availability of food (phytoplankton and ice algae) which was linked to the presence of a polynya and ice-edge primary production. The polynya opened in spring and enhanced the primary productivity of the area throughout the summer months. The increased primary productivity in the water column affects the benthos by the increasing amounts of organic matter reaching the seafloor. For example, Brandt (1995) linked the presence of high isopod abundances to the availability of fresh phytoplankton material on the seafloor, derived from phytoplankton blooms initiated by melting sea ice. In our study, noteworthy was the significant positive correlation observed



between sea ice concentration and peracarid abundance and between chlorophyll-a and peracarid abundance. In the SO a previous study investigated the correlation between deep-sea isopod assemblage and chlorophyll-a concentration, although a clear pattern was not observed (Meyer-Löbbecke et al., 2014). An explanation for this result could be the use of surface chlorophyll-a in the analysis. The organic matter produced at the surface could be rapidly consumed by the zooplankton communities and in part also be laterally transferred by currents. Therefore, only a small amount of organic matter might reach the seafloor and be available for the benthic communities. A consideration of the concentration of chlorophyll-a and organic matter at the bottom might thus yield a more reliable result.

Mean sea ice concentration and peracarid abundances of continental shelf stations from present and previous studies

combined (same sampling protocol and data standardization; Arntz and Gutt, 1999; Fütterer et al., 2003; Fahrbach, 2006; Linse, 2006; Brökeland et al., 2007; Kaiser et al., 2008) also showed a significant correlation. In contrast, the same analysis carried out at deeper stations did not show any significant result (Table 4). This suggests that benthic communities may be more strongly influenced by the presence of sea ice only within a certain depth range (up to about 1000 m from results of the present study). The reason could be the different response between deep-sea and shelf communities to seasonal organic inputs derived by the release of ice biota in the water column. Benthic shelf communities can show a quick response to the input of organic matter in productive shallow waters (Covazzi Harriague et al., 2007; Zhang et al., 2015); whereas, in the deep sea, results can be contrasting. Several studies showed that the benthic macrofauna

TABLE 4 | Pearson's correlation analyses of environmental variables and peracarid abundances.

Environmental Variables	Present study		Present and previous studies	
	<i>R</i>	<i>p</i> value	<i>R</i>	<i>p</i> -value
Depth (400–899 m)	–0.82	0.092	–0.86	0.061
Depth (400–2021 m)	–0.67	0.033	–0.66	0.014
Depth (400–6348 m)			–0.55	0.011
Se ice concentration 1978–2019	0.48	0.031		
Sea ice concentration Bio-ORACLE	0.44	0.043	0.53	0.0023
Sea ice concentration Bio-ORACLE (977–6348 m)			0.24	0.067
Temperature (CTD)	–0.53	0.013		
Temperature Bio-ORACLE + CTD	–0.47	0.027	–0.51	0.0037
Salinity (CTD)	–0.52	0.018		
Salinity Bio-ORACLE + CTD	–0.46	0.033	–0.42	0.023
Chlorophyll-a (max depth)	0.44	0.039	0.36	0.045
Current velocity	–0.098	0.66	–0.18	0.35
Iron	0.34	0.12	0.5	0.0045
Phosphate	–0.4	0.068	–0.08	0.67
Primary productivity	0.13	0.56	0.16	0.39

Significant results are highlighted in bold ($p < 0.05$).

from abyssal depths can quickly react to phytodetritus pulses (Sorbe, 1999; Aberle and Witte, 2003; Witte et al., 2003), although in other studies no clear response was observed (Pfannkuche, 1993; Gooday, 2002).

Concentration of chlorophyll-a in the water column can be influenced by sea ice, the break-up and melt of the latter might trigger phytoplankton blooms and enhance the production of sea-ice algae in the surrounding environment (Gradinger, 1996; Jin et al., 2007; Gradinger, 2009). In a previous study, it was also shown that the contribution of sea-ice algae to the general primary production in the water column increased in areas with more extensive ice coverage, reaching up to 57% of the total primary productivity in the ice of the Central Arctic Ocean (Leu et al., 2011). Besides, sea ice melting processes may cause a stabilization of the surface mixed layer, which can lead to higher primary production (Dunbar et al., 1998; Vernet et al., 2019) and thus higher abundances and more diverse benthic communities. In marginal sea ice zones or polynyas, higher abundances of benthic fauna were reported due to the enhanced primary productivity (Brandt, 1995, 1996; Fonseca and Soltwedel, 2007). This also proved true for peracarid assemblages from the continental shelf in the North Atlantic, where higher abundances were recorded in response to an increase in sedimentation of phytoplankton and ice algae to the sea floor (Brandt, 1995, 1996).

Sea ice retreat influences primary productivity also indirectly by the increase of open water areas whose ice-free surface is affected by wind action. During ice-free periods winds can change the depth of the mixed layer in the water column leading to a mixed-layer deepening, which in turn decreases the mean value of light available per water volume for phytoplankton photosynthesis, thus reducing the chlorophyll-a concentration (Ikeda, 1989; Dunbar et al., 1998; Montes-Hugo et al., 2009; Rainville et al., 2011). These results highlight the importance of seasonal ice coverage variations. Włodarska-Kowalczyk et al. (2004) showed, for example, that areas characterized by seasonal ice coverage had higher abundances of the benthic macrofauna

compared to areas characterized by perennial ice coverage. Moreover, the lack of sea ice break-up events strongly alters the benthic food-web structure, causing a shift on the diet of the benthic organisms (Michel et al., 2019).

Sea ice is characterized not only by seasonality but also by an interannual variability, which can drive changes in the annual rate of primary production in different regions of the SO (Arrigo et al., 2008). The latter authors showed an interannual variability in annual primary production in the Weddell Sea for the period range 1997–2006. They addressed higher annual primary production rates to anomalies in sea ice extent. Sea ice coverage around the Antarctic Peninsula has undergone a gradual increase during the last three decades and a strong decline starting from 2014 (Parkinson, 2019). In light of this, it is possible that the peracarid distribution pattern, abundance and assemblage structure observed in our study could be also explained by different sampling years (from 2012 to 2019), which may have experienced different interannual productivity rates due to changes in ice cover extent. Similarly, Meyer-Löbbecke et al. (2014) indicated the difference in sampling years as a possible factor explaining the different patterns observed in their study on isopod abundance.

CONCLUSION

Our study suggests that varying regimes of ice coverage and chlorophyll-a concentration strongly influence the abundance and assemblages' structure of benthic peracarids from the continental shelf of the SO. On one hand, the sea-ice break-up and retreat in summer is a key element for peracarid abundance and distribution since the ice-melting process releases a large amount of ice algae in the water column. These, in turn, increase the local primary productivity and thus enhance the amount of organic matter available for the benthic communities. On

the other hand, ice shelves with their continuous ice coverage allow the existence of a benthic fauna adapted to live in an environment characterized by very low sedimentation rate and which resembles that of the deep sea.

The retreat of sea ice and the disintegration of ice shelves caused by the increase of temperatures (Rott et al., 1996; Rack and Rott, 2003; Cook et al., 2016) can alter these equilibriums and impact the composition and abundance of the benthic fauna. Peracarid assemblages are subject to change drastically in the future due to such variations. Given the important role that peracarid crustaceans play among benthic communities, the complete retreat of sea ice and the consequent strong decrease of their abundance would negatively impact the benthic ecosystem. For a better understanding of interactions between sea-ice coverage and benthic communities, it is fundamental to study the ecological impact of such events on faunal compositions. Only if we understand these correlations might we be able to predict faunal alterations induced by climate change.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

AB, KL, and HG developed and designed the study. DD, AB, KL, and HG collected the samples. DD, AB, and KL sorted the samples and identified the specimens to order level. CH provided the sea ice analyses. HS provided the environmental data and helped with the statistical analyses. DD prepared the figures and tables, performed the statistical analyses, and drafted the original manuscript which was revised and improved by AB, KL, HG, CH, and HS. All the authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2020.554663/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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