Diversity and biogeography of Southern Ocean peracarid crustaceans in a changing environment

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“You don’t try to build a wall. You don’t set out to build a wall. You don’t say ‘I’m going to build the biggest, baddest, greatest wall that’s ever been built.’ You don’t start there. You say ‘I’m gonna lay this brick as perfectly as a brick can be laid,’ and you do that every single day, and soon you have a wall.” – Will Smith

I finally achieved to lay one more brick to my wall, I am not sure if it is going to be the biggest, baddest, greatest wall that has ever been built, but I am sure that I will always give 100% to build that wall I have always dreamt about.

I want to dedicate this thesis to all the people that like me have worked hard to achieve their goals despite the uncertainties of life always knocking at our door. I hope the work I am doing and the goals I achieved will inspire people to never give up on their dreams. In particular, this thought goes to the students I supervised during these three years as well as those that I will supervise in the future, because as Will Smith said: “if you’re not making someone else’s life better, then you’re wasting your time”.

Table of contents

Geographic units

Region	Southern Ocean; Atlantic sector of the Southern Ocean; South Atlantic Ocean
Areas	Filchner Trough, Antarctic Peninsula, Prince Gustav Channel
Locations	Sampling stations

Abbreviations

SO	Southern Ocean
ACC	Antarctic Circumpolar Current
EBS	Epibenthic Sledge

1. Summary

The Southern Ocean (SO) is one of the most pristine regions of our Planet, characterised by high levels of biodiversity (5% of the global diversity) (David and Saucède 2015) and hosting a unique fauna (up to 90% of SO species are endemic) (De Broyer and Danis 2011; Chown et al. 2015). Yet, the knowledge on SO biodiversity is still far from being completed. In addition, the knowledge on the impact that changing environments have on SO species-richness is very little and for some groups, it is still totally unknown. For instance, most of studies generally focus on one single species such as Antarctic krill (Kawaguchi et al. 2011), *Clio pyramidata* Linnaeus, 1767 (Orr et al. 2005), *Globigerina bulloides* d'Orbigny, 1826 (Moy et al. 2009), or only on a high taxonomic level (e.g. phylum, class): Echinodermata, Crustacea, Mollusca, Porifera, Bryozoa, Brachiopoda, Hydrozoa, Ascidiacea, Holoturoidea (Barnes 1999; Rowden et al. 2015; Post et al. 2017; Gutt et al. 2019; Vause et al. 2019; Pineda-Metz et al. 2020). Ultimately, the influence of sea-ice coverage on benthic species diversity was totally unknown prior to this study. In light of this, the **objectives** of the thesis are:

1. To expand the knowledge on shelf and deep-sea peracarid assemblage structure and abundance on a small regional (Weddell Sea) and on a large regional (Atlantic sector of the SO and South Atlantic Ocean) geographic scale.
2. To assess the environmental variables driving peracarid assemblage structure and abundance from the above mentioned areas.
3. To investigate SO benthic isopod species diversity from the Atlantic sector of the SO and assess the influence of environmental variables on their species-richness and composition.

4. To describe new possible peracarid species by means of integrative taxonomy, using morphological descriptions and whole genome sequencing analyses to support the species identification.

Objective outcomes: The present thesis provides new information on the abundance and assemblage structure based on 64766 peracarid crustaceans from different 28 locations within the Atlantic sector of the SO continental shelf and deep sea (**Chapters I-II**). These locations are characterised by different environmental conditions, for instance different sea-ice concentrations. Results from **Chapters I-II** confirmed the dominance of peracarid assemblages in the benthos, with amphipods being the most abundant group, followed by isopods. Sea ice was identified as the main driver shaping benthic peracarid assemblage structure (**Chapter I**). On a larger geographic scale and wider bathymetric range (e.g. including sampling locations from previous studies performed in the South Atlantic Ocean and at a depth range from 160 to ~6000 m), depth was the main physical variable driving peracarid assemblage structure (**Chapter III**). In addition, 16157 isopod specimens from the Atlantic sector of the SO were identified to species level at a smaller scale (**Chapter IV**). In this case, sea ice was identified as the main physical driver affecting isopod diversity and composition among sampling locations (**Chapter IV**). Reduced concentration of sea ice causes a decrease in isopod biodiversity, thus climate change was identified as a huge threat for this taxon and for SO benthos in general. During the identification process, two new isopod species were discovered (**Chapter V**). The two new species (*Notopais sp.1* n. sp. and *Notopais sp.2* n. sp.) were accurately described and identified by means of integrative taxonomy. This provided the first whole genome sequencing of benthic isopods from the SO and the first complete mitochondrial genome of the genus *Notopais* (**Chapter V**).

Thanks to the collaboration with the University of Genoa (Dipartimento di Scienze della Terra dell'Ambiente e della Vita, DISTAV, Italy) and the National Antarctic Museum (MNA) in Genoa, two new SO species of the suborder Valvifera G. O. Sars, 1883 were described by means of classical taxonomy. In this case, a molecular approach could not be used because both new species were represented by a single specimen, therefore it was important to preserve the integrity of the holotypes (**Chapters VI-VII**).

2. Zusammenfassung

Der Südliche Ozean (SO) ist eine der ursprünglichsten Regionen unseres Planeten. Er zeichnet sich durch eine hohe Biodiversität (5 % der weltweiten Vielfalt) aus (David und Saucède 2015) und beherbergt eine einzigartige Fauna, von der bis zu 90 % der Arten endemisch für den SO sind (De Broyer und Danis 2011; Chown et al. 2015). Dennoch ist das Wissen über die biologische Vielfalt des SO noch lange nicht vollständig. Der Effekt von Umweltveränderungen auf die Artenvielfalt des SO ist nur wenig erforscht und für einige Gruppen gänzlich unbekannt. So konzentrieren sich die meisten Studien im Allgemeinen auf eine einzige Art wie den Antarktischen Krill (Kawaguchi et al. 2011), *Clio pyramidata* Linnaeus, 1767 (Orr et al. 2005), *Globigerina bulloides* d'Orbigny, 1826 (Moy et al. 2009) oder nur auf höhere taxonomische Ebenen (z. B. Phylum, Klasse): z. B. Echinodermata, Crustacea, Mollusca, Porifera, Bryozoa, Brachiopoda, Hydrozoa, Ascidiacea, Holoturoidea (Barnes 1999; Rowden et al. 2015; Post et al. 2017; Gutt et al. 2019; Vause et al. 2019; Pineda-Metz et al. 2020).

Peracaride Krebse sind eine der dominantesten und artenreichsten Gruppen des SO-Benthos. Im SO gibt es fünf rezente Ordnungen: Amphipoda, Cumacea, Isopoda, Mysidacea und Tanaidacea. Sie weisen einen hohen Grad an Endemismus auf, der von 51 % für die Ordnung Cumacea bis zu 88 % für die Amphipoda reicht (Brandt 2000). Der Erfolg der Peracariden des SO lässt sich durch ihre äußerst vielfältige Lebensweise, Ernährungsbiologie (Brökeland et al. 2007; Brusca 2016) und geringe Ausbreitungsfähigkeit erklären (Brandt 1999). Peracarida sind Brüter, sie tragen ihre Nachkommen in einem ventralen Marsupium, das Fehlen eines freischwimmenden Larvenstadiums schränkt somit ihre Ausbreitungsfähigkeit ein (Brandt 1999). Zu den Peracariden gehören mobile schwimmende, bodenbewohnende und im Sediment lebende Arten, die sich von einer Vielzahl unterschiedlicher Nahrungsquellen ernähren. Sie können Räuber, Aasfresser, Suspensionsfresser, Ablagerungsfresser und Parasiten sein (Thiel und Hinojosa 2009). Während Isopoden und Amphipoden benthische, pelagische und bentho-pelagische Lebensweisen haben, sind Mysidaceen ausschließlich in der Wassersäule verbreitet (Brökeland et al. 2007). Cumaceen und Tanaidaceen sind stärker an das Substrat gebunden, jedoch verlassen Cumaceen-Männchen und -Weibchen den Boden zur zirkadianen Migration bzw. zur Paarung (Mühlenhardt-Siegel 2014). Der Erfolg der SO-Peracariden wird auf ihre lange evolutionäre Geschichte zurückgeführt (Kaiser 2014). Während des Eozän-Oligozäns leitete die Öffnung eines Seewegs zwischen Australien und der Ostantarktis und die anschließende Öffnung der Drake-Passage auf der Nördlichen

Antarktischen Halbinsel das Entstehen des Antarktischen Zirkumpolarstroms ein (Lawver et al. 2011). Der Antarktische Zirkumpolarstrom ist die größte Strömung der Welt und förderte die biogeografische Isolierung des SO, indem er eine Ausbreitungsbarriere für marine Arten bildete (Barker et al. 2007). Darüber hinaus bot das Aussterben der benthischen Zehnfußkrebse (z. B. Brachyurenkrabben) in der Antarktis aufgrund von Abkühlungsereignissen (Thatje und Arntz 2004; Aronson et al. 2009) den peracariden Krebsen wahrscheinlich freie ökologische Nischen (Brandt, 1999).

Ziel dieser Arbeit war es, neue Daten über SO-Peracariden zu liefern, sowie den Einfluss einer sich verändernden Umwelt auf ihre Zusammensetzung, Verbreitung, Häufigkeit und Artenvielfalt zu untersuchen. Der Fokus lag insbesondere auf folgenden Punkten:

1. Erweiterung des Wissens über die Struktur und Häufigkeit von Peracariden-Gemeischaften auf dem Schelf und in der Tiefsee, auf kleiner (Weddellmeer) und großer regionaler (atlantischer Sektor des SO und Südatlantik) Ebene.
2. Bewertung der Umweltvariablen, die die Struktur und Häufigkeit der Peracariden-Assemblage in den oben genannten Gebieten beeinflussen.
3. Untersuchung der Artenvielfalt benthischer Isopoden aus dem atlantischen Sektor des SO und Bewertung des Einflusses von Umweltvariablen auf deren Artenreichtum und Zusammensetzung.
4. Beschreibung neuer möglicher Peracariden-Arten mittels integrativer Taxonomie, unter Verwendung morphologischer Beschreibungen und Genomsequenzanalysen zur Unterstützung der Artbestimmung.

Ziele und Ergebnisse: Die Ergebnisse der vorliegenden Arbeit liefern neue Informationen über die Häufigkeit und die Struktur der Peracariden. Diese wurden in verschiedenen Gebieten des SO gesammelt, welche durch unterschiedliche Umweltbedingungen gekennzeichnet sind. Im Einzelnen entstammt das Material von den eisfreien Süd-Orkney-Inseln (Expedition JR15005), östlich der Antarktischen Halbinsel (Expedition PS118), aus dem Prinz-Gustav-Kanal, wo 1995 das Schelfeis kollabierte, (Expedition JR17003a) und dem saisonal eisbedeckten Filchner Graben (Expedition JR275). Alle Proben wurden mit einem Epibenthosschlitten (EBS) gefangen. Dieser wird zu dem Sammeln kleiner epibenthischer und suprabenthischer Makrofauna in marinen Lebensräumen verwendet. Er besteht aus zwei waagerecht übereinander angeordneten Netzkästen, an denen das Epi- und Supranetz befestigt sind. Diese bestehen aus Nylon und haben eine Maschenweite von 500 µm, zum hinteren Ende der Netze hin ist die Maschenweite auf 300 µm reduziert (Brenke, 2005).

Insgesamt konnten 64766 peracaride Krebe von 28 verschiedenen Probenahmestellen im atlantischen Sektor des SO-Kontinentalschelfs und der Tiefsee identifiziert werden (Kapitel I-II). Unter diesen 64766 identifizierten Peracariden waren Amphipoda mit 32 % der Gesamthäufigkeit das häufigste Taxon, gefolgt von Cumacea (31 %), Isopoda (29 %), Mysidacea (4 %) und Tanaidacea (4 %). Das Gebiet des Filchner Graben waren das Gebiet mit der höchsten Abundanz an Peracariden, während die Süd-Orkney-Inseln im Vergleich zu den anderen untersuchten Gebieten durch die geringste Abundanz an Peracariden gekennzeichnet wurden. Die Eisbedeckung war der wichtigste Umweltfaktor, der das Abundanzmuster und die Gemeinschaftsstruktur der Peracariden beeinflusste. Es konnte eine positive Korrelation von Eisbedeckung und Chlorophyll-a-Konzentration festgestellt werden. Aus den Ergebnissen dieser ersten beiden Kapitel lässt sich schließen, dass eine künftige Verringerung der Meereiskonzentration aufgrund des Klimawandels wahrscheinlich Auswirkungen auf die Zusammensetzung und Abundanz benthischer Peracariden im Weddellmeer haben wird. Angesichts der wichtigen Rolle, die die Peracariden Krebse im antarktischen Ökosystem spielen, wird dies wahrscheinlich auch Auswirkungen auf das antarktische Nahrungsnetz haben. Wie in Kapitel I hervorgehoben wurde, stellen Peracaride Krebse aus dem SO eine sehr wichtige Nahrungsquelle für viele Tiere des SO dar (z. B. Meeressäuger, Vögel, benthische und bentho-pelagische Räuber wie Tintenfische und Fische) und tragen darüber hinaus zum Recycling organischer Stoffe und zu deren Weitergabe im antarktischen Nahrungsnetz bei.

In einem größeren geografischen und bathymetrischen Untersuchungsmaßstab (z. B. unter Einbeziehung von Probenahmestellen aus früheren Studien im Südatlantik und in einem Tiefenbereich von 160 bis ~6000 m) war die Tiefe die wichtigste physikalische Variable, die die Struktur und Häufigkeit der Peracariden-Assemblage bestimmte (Kapitel III). Aus dem letztgenannten Ergebnis lässt sich schließen, dass der Einfluss einer größeren Variabilität physikalischer Parameter auf benthische Gemeinschaften auf großen geografischen Skalen schwieriger zu bewerten ist. Dies ist möglicherweise auf die größere Umweltheterogenität zurückzuführen (z. B. Wasserkörper, Primärproduktivität, Eisausdehnung, Strömungsregime) (Kapitel III). Darüber hinaus zeigten die Ergebnisse, dass verschiedene Peracaridenordnungen entlang eines bathymetrischen Gradienten unterschiedliche Abundanzmuster aufweisen: Die Abundanz von Isopoden war positiv mit der Tiefe korreliert, während sie bei Amphipoden und Mysidaceen negativ korreliert war. Bei Cumaceen und Tanaidaceen wurde kein

Zusammenhang festgestellt. Die Zunahme der Abundanz von Isopoden in der Tiefsee hängt mit der höheren Anzahl von Arten zusammen, die primär in der Tiefsee vorkommen im Vergleich zu den Arten, die auf dem Schelf leben, im Vergleich zu den Amphipodenarten, die im Gegensatz häufiger auf dem Schelf anzutreffen sind (De Broyer und Jazdzewska 2014; Kaiser 2014). Darüber hinaus wird in Kapitel III ein deutlicher Unterschied in der Abundanz zwischen Peracaridengemeinschaften vom Kontinentalschelf und denen aus der Tiefsee gezeigt. Es war möglich, das Vorkommen der Peracaridenfauna des Kontinentalschelfs bis zu einer Tiefe von 1500 m zu bestimmen, während die Gemeinschaften aus der Tiefsee in einer Tiefe von mehr als 1500 m identifiziert wurden.

Die außergewöhnliche Tiefe des SO-Kontinentalschelfs kann auf die geomorphologische Geschichte des SO zurückgeführt werden. Das Gewicht der antarktischen Eiszeit Eismassen sowie Erosionsprozessen führten zu einer isostatischen Absenkung des Kontinentalschalfes (Clarke et al. 2009). In Kapitel IV wird die Artendiversität einer ausgewählten Ordnung von Peracariden Krebsen sowie der Einfluss von Umweltvariablen auf ihren Artenreichtum und ihre Zusammensetzung untersucht. Insgesamt wurden 16157 Isopoden aus dem atlantischen Sektor der SO bis auf Artniveau bestimmt (Kapitel IV). Das Meereis wurde als wichtigster physikalischer Faktor identifiziert, der sich auf die Vielfalt und Zusammensetzung der Isopoden an den verschiedenen Probenahmestandorten auswirkt. Ein Rückgang der Meereiskonzentration führte zu einer geringeren biologischen Vielfalt der Isopoden. In Gebieten mit höherer Meereiskonzentration wurde eine größere Anzahl seltener Arten und spezialisierter Arten gefunden. Der Zusammenhang zwischen abnehmender Meereiskonzentration und benthischer Artenvielfalt und -zusammensetzung erklärt sich durch das Vorhandensein großer Populationen sympagischer Algen (Lizotte 2001; Thomas und Dieckmann 2002), die unter dem Meereises leben (Kapitel IV). Die Bewegung von Meereis bewirkt einer Umschichtung von gelösten Nährsalzen. Dies führt insbesondere im Bereich der Eiskanten zu einer Erhöhung der Primärproduktivität, wodurch die Verfügbarkeit von organischem Material für das Benthos erhöht wird (Jin et al. 2007; Gradinger 2009). Aus den Ergebnissen dieses Kapitels konnten wichtige Schlussfolgerungen zu den möglichen Auswirkungen zukünftiger Umweltveränderungen durch den Klimawandel gezogen werden. Zum ersten Mal in der Wissenschaft des Südlichen Ozeans wurde der Nachweis erbracht, dass die benthischen Arten des Südlichen Ozeans durch den zukünftigen Klimawandel gefährdet sind.

Im Südlichen Ozean (SO) gilt die Antarktische Halbinsel als eine der sich an den schnellsten erwärmenden Regionen der Welt, mit einem durchschnittlichen jährlichen Anstieg der atmosphärischen Temperatur von 2 bis 4 °C und einem Anstieg der Temperatur im Winter von 5 bis 6 °C seit den 1950er Jahren (Hansen et al. 2010; Ingels et al. 2021). Diese Veränderungen haben zu drastischen Schwankungen in der regionalen Meereisausdehnung beigetragen (Turner et al. 2015). Ein Rückgang der Meereiskonzentration aufgrund der Klimaerwärmung würde die Vielfalt der benthischen Isopoden des SO stark gefährden. Spezialisierte und seltene Arten sind am anfälligsten, sie können entweder abwandern, um günstigere Bedingungen zu finden, oder würden aussterben (Griffiths et al. 2017). Dies könnte zu einer Artenverschiebung in Richtung opportunistische Arten führen, die dann von einem Rückgang der Meereiskonzentration profitieren würden.

Während des Bestimmungsprozesses wurden vier neue Isopodenarten entdeckt und identifiziert (Kapitel V-VII). Zwei neue Arten von Valvifera wurden mit Hilfe der klassischen Taxonomie auf der Grundlage morphologischer Unterscheidungen beschrieben, während zwei neue Arten der Gattung *Notopais* (Munnopsidae, Asellota) mit Hilfe der integrativen Taxonomie beschrieben und identifiziert wurden. Darüber hinaus lieferte Kapitel V die erste vollständige Genomsequenzierung von benthischen Isopoden aus dem SO und das erste vollständige mitochondriale Genom der Gattung *Notopais*.

Im letztgenannten Kapitel wird erörtert, wie neuere Sequenzierungsmethoden in der integrativen Taxonomie nützlich sein können. So ist die Gewinnung qualitativ hochwertiger DNA von Isopoden ist oft eine Herausforderung, was auf das Vorhandensein aktiver Enzyme zurückzuführen ist, die ihre DNA schnell zersetzen (Riehl et al. 2014). Im Zuge dieser Doktorarbeit wurde versucht, COI-Sequenzen von *Notopais*-Arten mit spezifischen Primern zu erhalten, wie in Riehl et al. 2014 berichtet, dies allerdings ohne Erfolg. Dank neuer Sequenziermethoden konnte das gesamte Genom und das vollständige Mitogenom der genannten Gattung erhalten werden. Daraus konnte die DNA-Barcoding-Analyse benötigten COI-Sequenzen extrahieren werden. Die letztgenannte Analyse bestätigte die Unterscheidung der beiden neu beschriebenen *Notopais*-Arten. Die Arten dieser Gattung lassen sich leicht durch das Muster der dorsalen Stacheln der Pereoniten unterscheiden. Die neue Art *Notopais* sp.1 ist die einzige beschriebene SO-Art von *Notopais*, die keine Dorsalstacheln auf Pereonit 4 hat, mit Ausnahme der beiden kleinen Stacheln auf dem dorsomedialen Paar der vier Tuberkel. *Notopais* sp.2 unterscheidet sich durch das Vorhandensein von sechs Dorsalstacheln auf Pereonit 4 und zwei Tuberkeln auf Peronit 5, einzigartige Merkmale, die diese Art charakterisieren. Die beiden neuen Arten sind nur von ihrem *Locus typicus* bekannt, während alle anderen SO *Notopais*-Arten eine zirkumantarktische Verbreitung aufweisen. Der Grund für diese weite Verbreitung kann durch das Vorhandensein eines Seewegs erklärt werden, der das Weddellmeer und das Rossmeer im späten Quartär verband (Barnes und Hillenbrand 2010). Weitere genetische Studien zu dieser Gruppe sind jedoch erforderlich, um diese Möglichkeit zu untersuchen.

Zusammenfassend lässt sich sagen, dass die vorliegende Arbeit einen wichtigen Beitrag zum Wissen über die Zusammensetzung und Verteilung von Peracariden im atlantischen Sektor des SO leistet. Außerdem stellt sie einen wichtigen ersten Schritt in der SO-Wissenschaft zu einem besseren Verständnis der Folgen dar, die der Klimawandel auf die benthischen Arten des SO haben kann. Es ist daher von größter Bedeutung, diese Studie auf andere Peracaridengruppen und geografische Gebiete des SO auszuweiten, um die Auswirkungen des Klimawandels auf einer breiteren taxonomischen und geografischen Skala zu bewerten. Dadurch können wir besser verstehen, wie verschiedene Arten oder Taxa von Umweltveränderungen (z. B. Meereiskonzentrationen) betroffen sein können. Während der Klimawandel für einige Arten eine Bedrohung darstellen kann (z. B. für spezialisierte Arten), kann er für andere Arten von Vorteil sein (z. B. für opportunistische Arten). In der Zukunft werden weitere Analysen notwendig sein, um zu verstehen welche SO-Taxa mehr oder weniger anfällig für Veränderungen der Meereiskonzentration sind. Darüber hinaus sollte der Effekt von physischen Barrieren für Genfluss im SO untersucht werden, um die genetische Konnektivität zwischen verschiedenen Gebieten des SO (z. B. dem Rossmeer und dem Weddellmeer) bewerten zu können.

3. General Introduction

3.1. The Southern Ocean: source of marine biodiversity and endemism

The SO is considered as one of the largest ecosystems of the Planet (Knox 2006), characterised by unique oceanographic and geomorphological features. This uniqueness is the result of a long evolutionary history. The dominant circulation patterns and water mass distributions in the SO were established at least 20 million years ago (Knox 1980, 2006; Borrelli et al. 2014). During the Eocene-Oligocene, the South Tasman Rise (Australia) separated from the Victoria Land (Antarctica), while the Drake Passage formed between South America and the Antarctic Peninsula (Knox 2006; Lawver et al. 2011). These two events determined the onset of the largest current in the world, the Antarctic Circumpolar Current (ACC) (Figure 1) (Carter et al. 2008). The ACC has isolated the Antarctic continent and its marine continental shelf environments. Thus, it has shaped much of the recent faunal distribution of SO marine fauna by acting as a strong dispersal barrier (Clarke et al. 2005; Thatje et al. 2005; Griffiths et al. 2017).

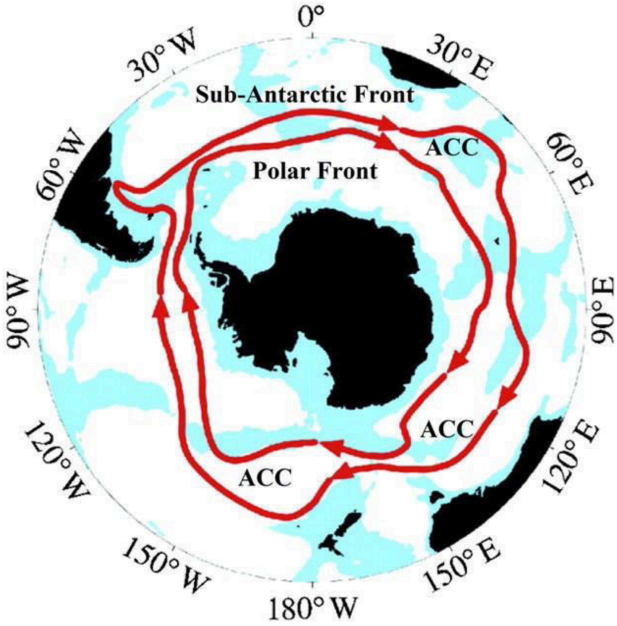


Figure 1. Schematic representation of the ACC (Constantin and Johnson 2016).

More than 8000 species have been discovered around the Antarctic continent and 50-97% of these are endemic (including various taxa such as sponges, tube worms, peracarid crustaceans, molluscs, sea spiders) (Chown et al. 2015). SO species diversity was enhanced further by cyclic variations in size and extent of the continental ice sheet, during the past glacial events (Clarke and Crame 1992). Fragmentation and isolation, during glaciation cycles led to a reduction of gene flow in species, resulting in a change in the population genetic structure and to genetically distinct populations or sister species (Brey et al. 1996; Hodgson et al. 2003).

The habitat fragmentation forced benthic communities to find refuge on the continental shelf or migrate to deeper waters (Figure 2A) (Thatje et al. 2005). During the last glacial period, multiannual sea-ice cover contributed to a wide-scale reduction in primary production, causing starvation among benthic communities; nevertheless, open-ocean polynyas are likely to have played a key role in maintaining the starved benthos through the supply of organic matter fluxes (Figure 2B) (Thatje et al. 2008). Studies on benthic communities under present-day ice shelves have shown that they largely depend on lateral advection of food particles, which can nourish communities of benthic organisms up to 100 km away from the ice edge (Riddle et al. 2007).

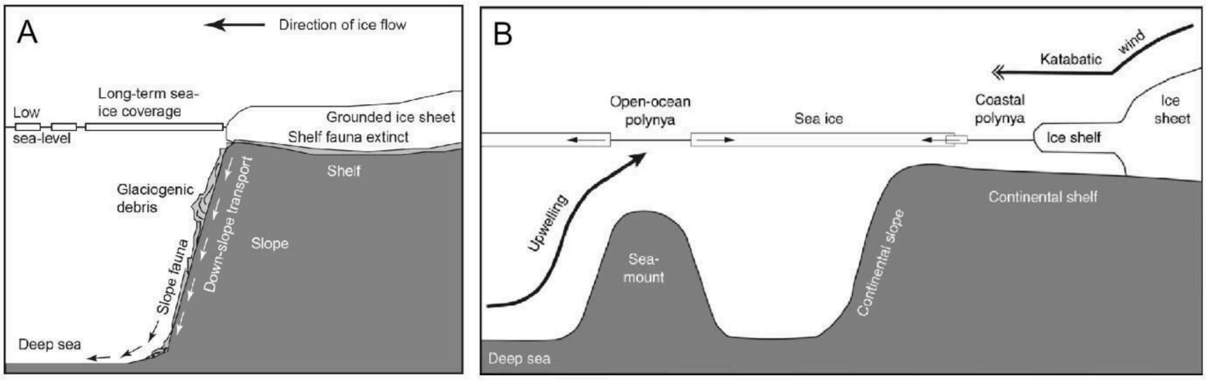
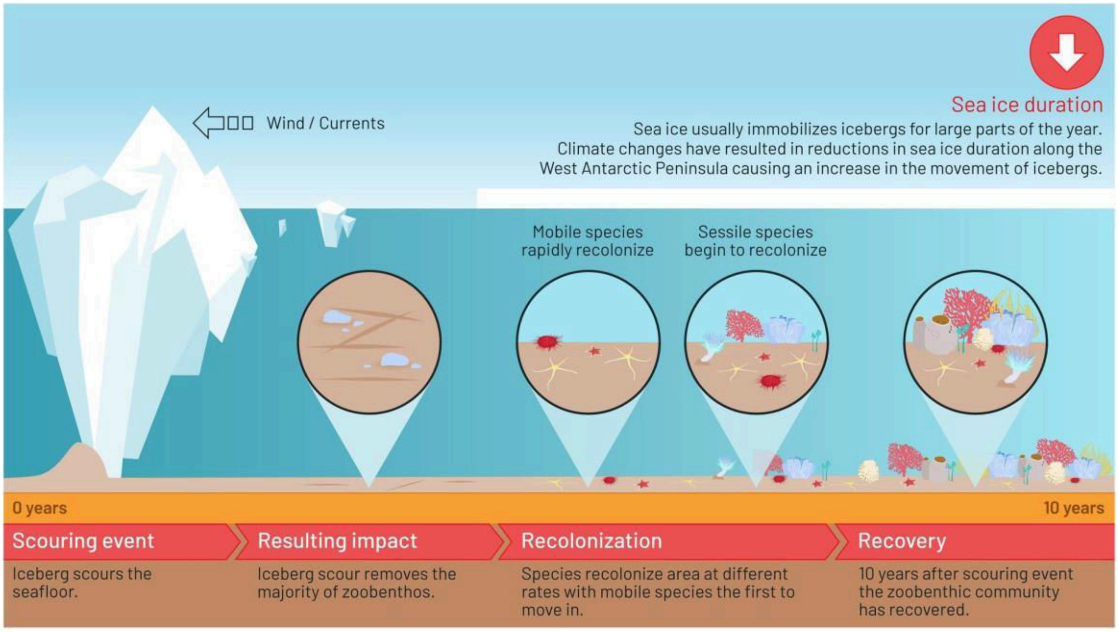


Figure 2. A) The ice-shelf conditions on the Antarctic margins during glacial maxima and its effects on benthic communities (Thatje et al. 2005); B) representation of the mechanisms that form open-ocean polynyas (Thatje et al. 2008)

Shelf shelters are believed to have provided several taxa with refuges during the last glacial period: for instance, macrostylid isopods (Riehl and Kaiser 2012), amphipods of the genus *Eusirus* (Baird et al. 2012), the sea urchin *Sterechinus neumayeri* (Meissner, 1900) (Díaz et al. 2018), the crinoid *Promachocrinus kerguelensis* Carpenter, 1879 (Hemery et al. 2012), and the sea spider *Nymphon australe* Hodgson, 1902 (Arango et al. 2011).

After the glacial retreat, new species from the deep sea could recolonise the continental shelf. For example, different families of isopods were able to colonise the shelf from the deep sea (hypothesis supported by molecular experiments) (Brandt et al. 2007c; Raupach et al. 2009). These processes therefore may represent one of the drivers in the mechanisms of allopatric speciation in Antarctic taxa, potentially acting as a taxonomic diversity pump (Clarke and Crame 1989). Watling and Thurston described the SO as an “incubator” for species as the cooling of the Antarctic waters promoted the diversification of the amphipod genus *Iphimedia* (Watling and Thurston 1989). Today, more than 70% of the Antarctic coastline are bordered by ice shelves that cover over 1.5 million km^2 of seafloor and about 30% of Antarctica’s continental shelf (Ingels et al. 2018). Similarly to long term glaciation cycles, the recent ice shelves have a strong impact on SO benthic community diversity and composition but on a much shorter time scale. For instance, due to the accumulation of snow on the continent, the ice shelves continue to move seaward at a rate of about 1 m per day; their successive progression towards the open ocean exposes them to waves that eventually crack and calve some of them into floating icebergs (Knox 2006). Iceberg scouring is one of the main physical processes affecting benthic shelf communities in the SO, sometimes with catastrophic effects (Ingels et al. 2021). At a small spatial scale, iceberg scouring is destructive, drastically reducing the benthic diversity of the impacted area (Figure 3) (Gutt and Piepenburg 2003). In areas that are heavily impacted by continuous iceberg groundings, communities can be held at early successional stages by the chronic ice scouring (McCook and Chapman 1993; Pugh and Davenport 1997; Smale et al. 2008). However, at large geographical scales and at intermediate levels of disturbance, iceberg scouring may promote biodiversity by preventing the monopolisation of space by dominant competitors and increasing habitat heterogeneity and niche separation (Arntz et al. 1994; Brenner et al. 2001; Gutt and Piepenburg 2003; Smale et al. 2008). The intermediate-disturbance hypothesis predicts a high diversity at intermediate levels of disturbance (Huston 1979): when the disturbance is frequent, only few species will persist, mostly the opportunistic ones; if disturbance is rare, only those species who can efficiently exploit the limited resources and the most robust competitors will survive. Thus, diversity is expected to be higher at intermediate levels of disturbance.



Sea ice usually immobilizes icebergs for large parts of the year. Climate changes have resulted in reductions in sea ice duration along the West Antarctic Peninsula causing an increase in the movement of icebergs.

Iceberg scours the seafloor.

Iceberg scour removes the majority of zoobenthos.

Species recolonize area at different rates with mobile species the first to move in.

10 years after scouring event the zoobenthic community has recovered.

Figure 3. Representation of the effects of iceberg scouring on benthic communities and the recolonization/recovery process of these latter (Zwerschke et al. 2021).

3.2. Sampling effort in the SO

The sampling effort in the SO of the last century has improved our knowledge on SO biodiversity (Brandt et al. 2007c; Schiaparelli et al. 2013; Kaiser et al. 2013; Broyer and Koubbi 2014; Gutt et al. 2018). Sampling campaigns such as CEAMARC, CAML largely contributed to the discovery of SO continental shelf and slope communities (Hosie et al. 2011; Schiaparelli et al. 2013). The ANDEEP I-III expeditions investigated SO from the slope down to the hadal zone at 6348 m depth, revealing an incredibly underestimated benthic diversity. For example, during ANDEEP expeditions, 674 isopod species were identified with more than 85% of these being new to science (Brandt et al. 2007c). However, sampling records around the Antarctic continent are still patchy and some areas are still under-sampled (e.g. areas characterised by high sea-ice coverage and deep sea) (Gutt et al. 2011; Kaiser et al. 2013). Most of the sampling in the SO has been performed from the intertidal to the abyss (Brandt et al. 2009; Griffiths 2010) and only about 30% of benthic samples have been taken at more than 1000 m depth (Griffiths 2010).

To ensure an efficient sampling process from a qualitative and quantitative point of view, it is crucial to use the most adequate sampling gear. Among these, the epibenthic sledge (EBS) has been successfully used to sample epibenthic and suprabenthic macrofauna from the continental shelf and deep sea worldwide, including the SO (Brandt et al. 2013, 2015; Moreau et al. 2013; Yasuhara et al. 2014; Lins and Brandt 2020). The EBS consists of two nets, a suprabenthic- and an epibenthic-net of a mesh size of 500 µm. At one end of each net is a cod end equipped with a net of 300 µm mesh size (Figure 4). At the opposite end, each net presents a net box a width of 1,0 m and a height of 0,35 m and it is inclined at the openings at a 45° angle. The epibenthic net extends from 27 to 60 cm above the seafloor, while the suprabenthic net extends from 100 to 133 cm above the bottom (Brandt and Barthel 1995). The EBS is equipped with an opening-closing device consisting of a simple lever- and spring mechanism. This mechanism allows the suprabenthic- and epibenthic net to immediately close once the EBS has left the bottom (Brandt and Barthel, 1995). Compared to other devices such as the anchor-box dredge or box dredge (Macintyre 1964; Carey and Hancock 1965), the EBS has good hydrodynamic properties, maintaining a stable position in the water column. Its robust construction and steel frame minimise mechanical damage during sampling, allowing to sample on hard substrates among rocks and slopes (Brandt and Barthel 1995; Brenke 2005).

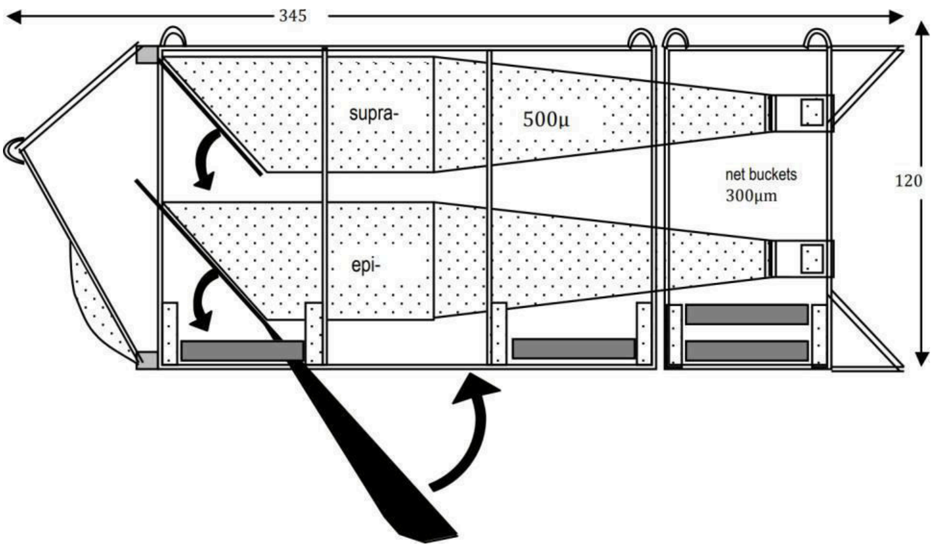


Figure 4. Schematic illustration of an EBS (Brandt et al. 2013, in Wolf-Gladrow 2013).

3.3. SO continental-shelf and deep-sea benthos

The benthos inhabiting SO continental shelf and deep sea is represented by different communities as a result of the different physical features that characterise these two different environments; the continental shelf is an heterogeneous environment, dominated by sessile suspension feeders that mainly rely on food supplies derived from strong near-bottom currents and infauna and mobile epifauna controlled by vertical phytodetritus fluxes (Clarke and Johnston 2003; Clarke et al. 2004; Gutt 2007). The heterogeneity of the SO continental shelf is enhanced by the presence of drop-stones released by floating icebergs and the glacial substrates; these represent an optimal substrate for many benthic taxa (Clarke 1996). In the deep sea, physical parameters are generally more homogeneous and stable (Thistle 2003). Deep-sea benthic communities are food limited because of the lower amount of organic matter reaching the seafloor compared to shallower waters. The deep sea presents low sedimentation rate (100-200 m d^{-1}; (Suess 1980; Gooday 2002; Veit-Köhler et al. 2011, p.) and most of the organic particles are directly consumed in the water column by heterotrophic pelagic organisms (Nelson et al. 1996). For this reason, deep-sea benthic fauna is less abundant (Clarke 2003) and it is mostly dominated by motile fauna, while sessile suspension feeders are reduced in terms of biomass and abundance (Clarke 2003; Brandt et al. 2007b). In the SO deep sea, Holothurians, ophiuroids, asteroids, polychaetes, isopods and amphipods are among the most dominant and species-rich groups (Brandt et al. 2007b).

Overall, SO continental shelf and deep sea host very high level of biodiversity and endemism, with more than 8.000 valid species, representing 5% of global marine biodiversity (De Broyer and Danis 2011; David and Saucède 2015) and 50-97% of them being endemic (Chown et al. 2015). In particular, the SO deep sea has been shown to be highly diverse and unique, ANDEEP expeditions revealed the presence of a largely underestimated deep-sea biodiversity with more than 700 new species recorded in bathyal, abyssal and hadal depths (Brandt et al. 2007c, a).

3.4. SO peracarid crustaceans

The subphylum Crustacea is the most dominant taxon in the SO benthos with the superorder Peracarida (Figure 5A-D) being the most abundant and species-rich group (Brandt et al. 2007a; De Broyer and Danis 2011). Amphipods are the second most speciose macrobenthic group in the SO, they are represented by more than 853 described species (De Broyer and Jazdzewska 2014), followed by isopods (~441 spp.), tanaidaceans (~160 spp.), cumaceans (~90 spp.) and mysidaceans (~70 spp.) (Błażewicz-Paszkowycz 2014; De Broyer and Jazdzewska 2014; Kaiser 2014; Mühlenhardt-Siegel 2014; Petryashov 2014).

SO peracarids show high levels of endemism, ranging from 51% for the Order Cumacea to 88% for the Amphipoda (Brandt 2000). Their dominance and success in the SO benthos can be attributed to their evolutionary history and their extremely diverse lifestyle and feeding biology (Brökeland et al. 2007; Brusca 2016), as well as their reproductive biology. The Cenozoic glaciation determined the extinction of some crustaceans groups such as brachyuran decapods, leaving ecological niches available for peracarids (Brandt 1999). These latter are brooders, the presence of a synapomorphic ventral marsupium (Figure 5E) protecting their offspring is probably one of the most important adaptations that allowed them to survive the glacial maxima and become one of the most dominant SO benthic groups (Brandt 1999). Females keep their eggs inside the ventral marsupium until these develop to the manca stage II (juvenile forms similar to adults) (Wägele 1991; Brandt et al. 1994; Johnson et al. 2001; Bauer 2015).

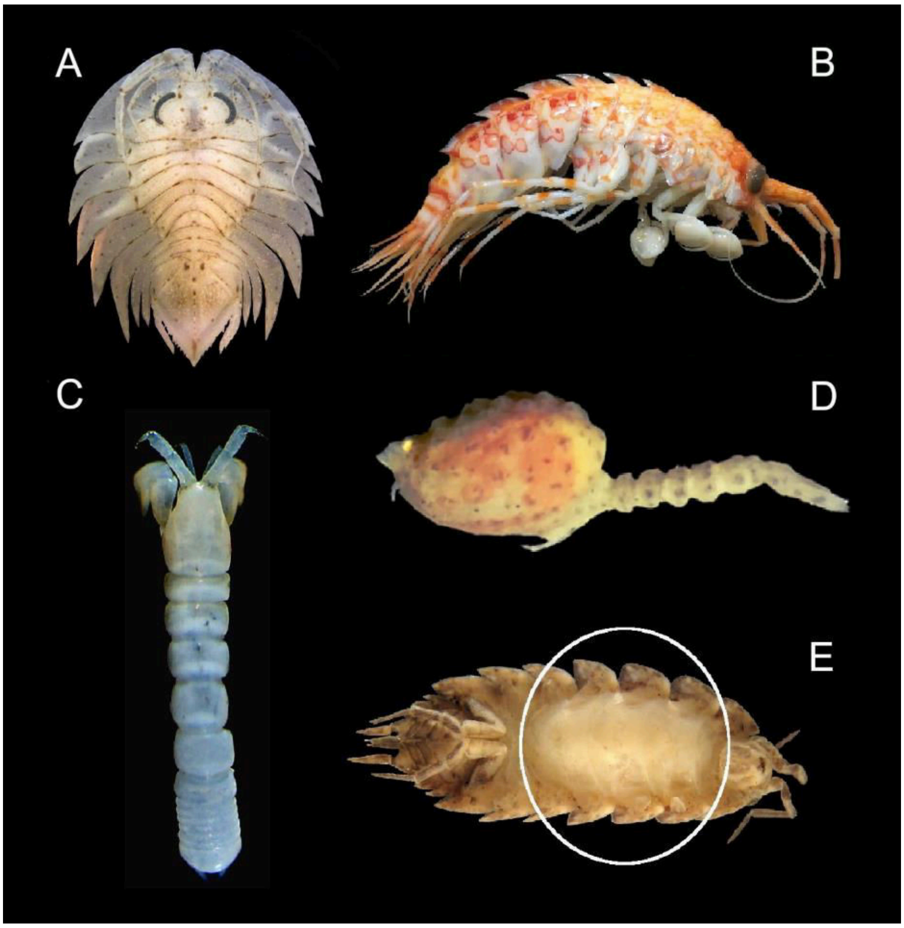


Figure 5. Examples of peracarid species: A) Isopoda, *Ceratoserolis trilobitoides* (Eights, 1833); B) Amphipoda, *Eusirus perdentatus* Chevreux, 1912; C) *Tanaella quintanai* Morales-Núñez and Ardila, 2019 (photo: Morales-Núñez and Ardila 2019; D) Cumacea, Campylaspidae; E) example of an isopod´s ventral marsupium in a terrestrial oniscid isopod (white circle), photo: (Appel et al. 2011).

Thanks to their highly diversified lifestyle, peracarids play a very important ecological role in SO benthos. For instance, scavengers feeding on dead organisms and deposit-feeders processing the deposited organic matter represent a source of biomass that is transferred to higher trophic levels via direct consumption through the food web (Thiel and Hinojosa 2009; Jeong et al. 2009; Duffy et al. 2012). In this respect, peracarids are a very important food source for many marine pelagic and bentho-pelagic animals such as fish, squids, (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*) (Mouat et al. 2001; Dauby et al. 2003; Padovani et al. 2012). Sediment-living peracarids build burrows causing oxygenated water to flow through them, thus promoting the mineralization of organic matter (Pelegrí and Blackburn 1994; Lehtonen and Andersin 1998). On one hand, amphipods and isopods have benthic, pelagic, bentho-pelagic lifestyles (Brökeland et al. 2007) and include a large variety of trophic groups such as filter-feeders, deposit-feeders, scavengers, parasites, predators, suspension-feeders (Thiel and Hinojosa

2009). On the other hand, the other peracarid groups present a smaller variety of lifestyle, for example mysidaceans are exclusively distributed in the water column while cumaceans and tanaidaceans are more related to the sediments. In particular, cumaceans are inbenthic, females leave the bottom only for mating while males migrate through the water column through circadian migration (Mühlenhardt-Siegel 2014). These two latter peracarid taxa (cumaceans and tanaidaceans) are mainly represented by suspension-feeders and deposit-feeders, although predators have been reported as well (Thiel and Hinojosa 2009).

In the SO, peracarid crustaceans are distributed from the continental shelf to the deep sea (Arntz and Gutt 1999; Jazdzewski et al. 2001; Brökeland et al. 2007). However, peracarid composition and species richness varies with depth and between the different orders. Differences between shelf and deep-sea amphipod species composition were shown in De Broyer and Jazdzewska (De Broyer and Jazdzewska 2014) where shelf and upper slope fauna (0-800 m and 801-2200 m respectively) were shown to be dissimilar to lower slope and abyssal fauna (2201-3700 m and 3701->4500 m respectively). While isopod families such as Santiidae and Paramunnidae have been found almost exclusively on the shelf, families like Haploniscidae, Ischnomesidae and Macrostylidae dominate in the deep sea (Brandt 1991; Kaiser 2014). Similarly, species composition of SO continental-shelf cumaceans and tanaidaceans differ from SO deep-sea species, with 43% of tanaidaceans species and 67% of cumaceans species found exclusively up to 900 m and 1000 m respectively (Błażewicz-Paszkowycz 2014).

Concerning species diversity, the number of amphipod species decreases with depth, ranging from more than 400 species on the SO continental shelf, to the he slope (~80 species) and the abyss (~23 species) (De Broyer and Jazdzewska 2014). About 60% of SO Tanaidacea species were recorded on the shelf, while the other 39% are represent by deep-sea species (Błażewicz-Paszkowycz 2014); about 67% of cumacean species described were recorded exclusively on the shelf from 1 to 900m (Mühlenhardt-Siegel 2014). In contrast, isopod species-richness increases with depth, showing a peak at around 2000-4000 m (Brandt et al. 2016).

Given their dominance among benthic communities and their important role played in the Antarctic food web, peracarid crustaceans are a key taxon to expand the knowledge on SO diversity. In addition, their brooding nature reduces their migration potential in response to a changing environment, making peracarid crustaceans an ideal model group to study the influence of changing environments on marine biodiversity.

3.5. SO peracarid crustaceans: Order Isopoda

The order Isopoda is a heterogeneous and diverse group, including more than 10300 species widely distributed in all realms, from freshwater environments to terrestrial and marine ones (Kaiser 2014). Most of isopod species occur in the sea and are adapted to a benthic lifestyle, while only few taxa are able to swim (e.g. Munnopsidae) (Hessler and Strömberg 1989). Isopods (after amphipods) are the most diverse peracarid crustaceans and represent one of the most abundant and species-rich group among SO benthic communities, with more than 441 species recorded (Kaiser 2014). Asellota is the isopod suborder showing the highest number of species; they are well represented across all depths, from the continental shelf to the deep sea where they represent the majority of the total isopod abundance and diversity (Wilson 1998; Brandt et al. 2007a; Kaiser 2014). This suborder has been very useful to study the consequences of glacial cycles on the SO benthos; as aforementioned, these cycles probably forced SO benthic species to take refuge on the continental shelf and/or in the deep sea; recent studied supported by molecular analyses showed that asellotan isopods were able to survive these climatic events and underwent multiple colonization events into the deep sea (Raupach et al. 2004, 2009). Isopods have been proved to be a useful taxon for evolutionary, ecological, and biogeographic studies (Brandt 1992; Wilson 1998). Like all peracarids, isopod crustaceans are brooders and are characterized by low dispersal mobility. Thus, studying their actual distribution can be useful to better understand their origins and radiation events (Kaiser 2014).

3.6. DNA barcoding and next generation sequencing as tools for integrative taxonomy

Increased use and innovation of molecular techniques can expand our knowledge on SO biodiversity. For example, new methodologies such as COI barcoding have been successfully tested, leading to the development of the Barcode of Life Data System (BOLD), a digital support for the acquisition, storage, analysis and publication of DNA barcode records (Hebert et al. 2003; Ratnasingham and Ebert 2007). Until relatively recently, the DNA barcodes available for SO marine species were limited. In 2009 genetic data were only available for 2.6% of marine invertebrate species (Grant and Linse 2009), but the number of SO DNA barcodes rapidly increased from 432 to 20355 between 2009 and 2011 (Grant et al. 2011).

DNA barcode analyses revealed to be a very useful and successful tool complementing the morphological identification of species (Bucklin et al. 2011; Leray and Knowlton 2015). COI sequences have been used with success also among SO isopods, although at date studies are not numerous (Leese et al. 2010; Riehl et al. 2014). One of the possible reasons is the difficulty in obtaining high-quality DNA sequences from isopods (Osborn personal communication; Riehl et al. 2014). In addition, this latter study showed that the rate of success of COI gene sequencing using universal primers varies between different isopod families, ranging from ~40% to ~80% of success, suggesting the creation of new taxon−specific primers to guarantee a higher rate of success. Universal primers were designed by (Folmer et al. 1994), however these have been frequently replaced with new sets of primers that are specific for a certain taxon (Rach et al. 2017).

In light of this, it is important to expand the technological tools available to increase the probabilities of sequencing success. Among these, next generation sequencing techniques can be very useful through the generation of complete genome and mitochondrial genome sequences. These new techniques have been successfully used among different taxa (Jue et al. 2016; Chen et al. 2019; Köhler et al. 2021) and can be extremely helpful when it is difficult to obtain COI sequences from a specimen using universal or newly designed primers. Mitogenome generation does not require the use of primers, and COI sequences are amplified as part of mitogenome amplification. These COI sequences can then be used to design new specific primers for the problematic taxon (e.g. the aforementioned isopod crustaceans).

4. Thesis Objectives

Despite the great diversity and dominance in terms of abundance shown by SO peracarids, the knowledge on their composition, abundance and distribution in the SO is still limited (Brandt et al. 2004; Rehm et al. 2007; Brökeland et al. 2007; Błażewicz-Paszkowycz 2014; Kaiser 2014). For example, ANDEEP expeditions revealed a remarkably underestimated diversity among deep-sea isopods. More than 85% of the species sampled were new to science. In addition, at date there are not many studies investigating the role that environmental variables play on peracarid assemblage structure and species richness. Above all, before the present thesis, the influence of sea-ice coverage, an environmental variable affected by climate change, on benthic isopods from the SO was not investigated at all. In light of all this, the aim of the present thesis is to expand the knowledge on the composition and distribution patterns of peracarid crustaceans on a small (Atlantic sector of the SO) and large (Atlantic sector of the SO and South Atlantic Ocean) geographic scale. The present thesis aims to discover the link between peracarids and environmental variables and provide useful information to predict the consequences of a warming ocean. Such link was investigated to species level using peracarid isopods as model group.

The species diversity of peracarid isopods from the Atlantic sector of the SO was studied not only to evaluate their link with possible driving physical variables but also to expand the knowledge on SO isopod diversity and possibly discover new species. When possible, newly described species were investigated by means of integrative taxonomy to provide molecular support to the morphological descriptions and provide genetic data of the paratypes. The thesis aims to provide the first whole genome sequencing and whole mitochondrial assembly of isopod species from the SO.

5. Thesis Outline

The thesis comprises a total of seven chapters. The first chapter (**Chapter I**) aims to investigate the distribution and composition of peracarid assemblages from the Atlantic sector of the SO and assess the link with influencing environmental variables. The knowledge on the influence of environmental variables on SO peracarid assemblage is still limited and fragmented. For this reason, **Chapter I** aims to overcome this limitation and provide a comprehensive view on the link between SO peracarid assemblages from the continental shelf and slope and their environment, including a large number of assessed variables. In particular, the following variables were investigated: chlorophyll-a (mg/m^3), current velocity (m^{-1}), oxygen concentration (mol/m^3), iron ($mmol/m^3$), nitrate (mol/m^3), silicate (mol/m^3), phosphate (mol/m^3), phytoplankton ($mmol/m^3$), primary production (g/m^3d^{-1}). For comparability between sampling locations, the study was based on standardised abundances per 1000 m/haul. Amphipods were the most abundant group, followed by isopods, cumaceans, tanaidaceans and mysidaceans. Among all physical variables, sea-ice concentration was the main one driving peracarid assemblage structure and abundance. In **Chapter II**, raw peracarid abundance data from the Atlantic sector of the SO are provided to highlight the importance of improving the availability of scientific data that can be freely accessible to the scientific community. In particular, samples from remote regions such as the SO are very valuable therefore it is of the outmost importance to ensure their availability. **Chapter III** investigates the abundance and distributional pattern of peracarid assemblages on a larger scale, including sampling data from previous studies and investigating an area ranging from 77° to 41° South. This is explained by the presence of a higher environmental heterogeneity (e.g. different water masses and wider depth ranges) that reduces the resolution of the results obtained, making more difficult their interpretation. In **Chapter IV** SO benthic isopods from the Atlantic sector of the SO are investigated to improve the knowledge on their diversity and composition, as well as to assess the influence of changing sea-ice concentrations and other possible environmental variables. This chapter provides new data on SO isopod diversity, increasing the number of known isopod species from this region with two new species discovered. In addition, for the first time in SO science it provides valuable information on the impact of reducing sea-ice extent on SO isopod species and highlights the threat that climate change pose on SO benthic species diversity. New species discovered in **Chapter IV** were drawn for subsequent morphological descriptions. In particular, two new species of the genus *Notopais* Hodgson, 1910 are described in **Chapter V**. The morphological description was complemented by COI barcoding analyses to confirm the identity of the two newly described species. COI sequences were extracted from whole genome assemblies of the two species, providing thus valuable information on the genomic structure of this taxon. At date studies investigating SO benthic isopods from a genetic point of view are only few and there are no other studies investigating their whole genome, this is the first time that whole genome sequencing is performed on SO isopods. **Chapter VI** and **VII** describe two new species of the suborder Valvifera, *Pseudidothea* sp. nov. and *Chaetarcturus* sp. nov. (Noli et al. under review); while the first species was collected in the Atlantic sector of the SO (Burdwood Bank, South Orkney Islands), the second species was sampled in the Ross Sea. In both cases, only one single specimen was found. The two new species were described on the basis of their morphology, while integrative taxonomy was not used to preserve the holotypes.

6. Thesis Chapters

6.1. Chapter I

Chapter I

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

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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.

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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 (Pelegrí 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 bentho- 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; Legezyñska 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 bentho-pelagic lifestyle (Brökeland et al., 2007). Isopods and amphipods are one of the most dominant components of the emerging benthos (Alldredge 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 phytoplanktonic 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 km^2 (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 Starmans, 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 on-going 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

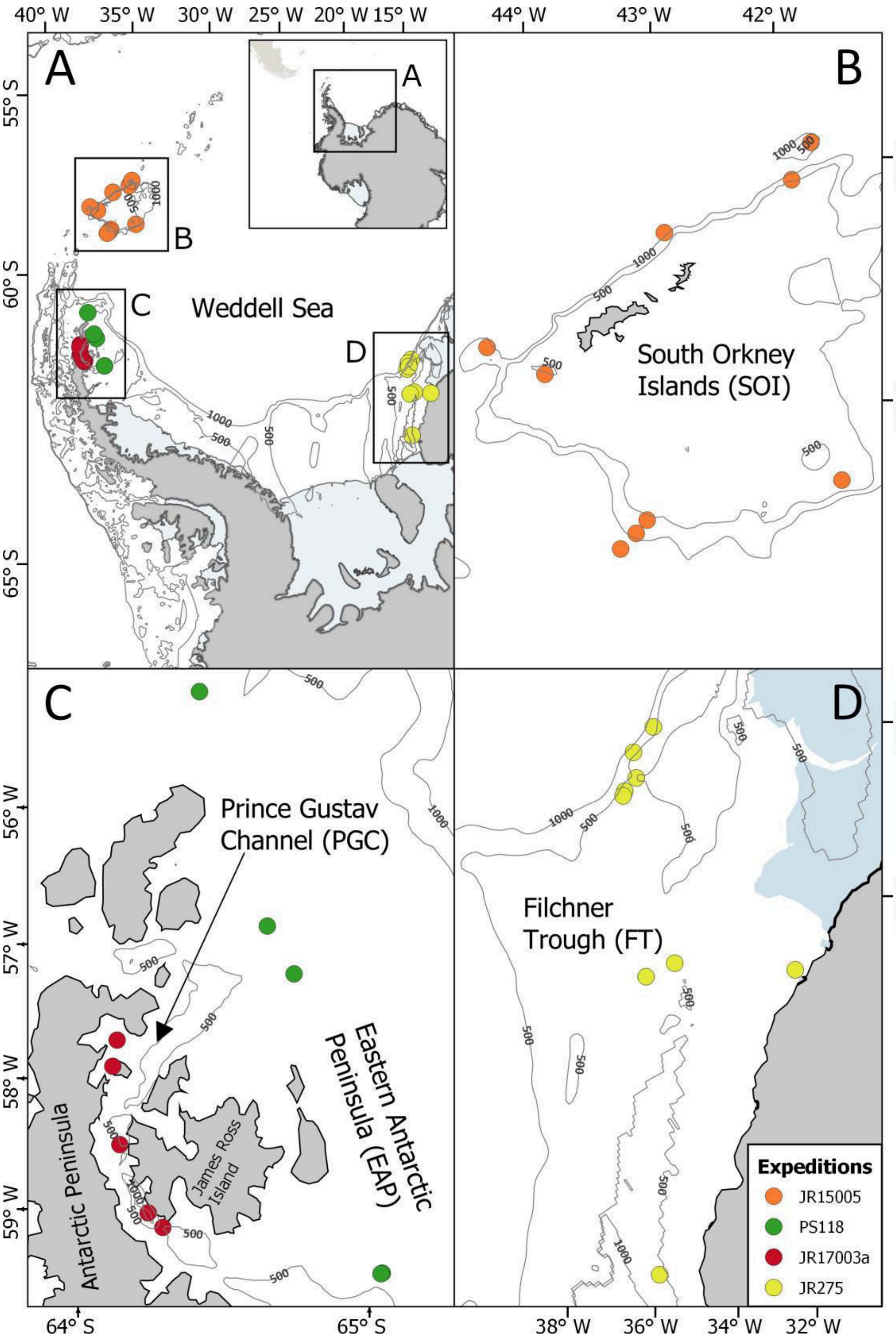

FIGURE 1 | Locations of the EBS stations sampled during the expeditions in the SO (A); JR15005, South Orkney Island, SOI (B); PS118, Eastern Antarctic Peninsula, EAP (C); JR17003a, Prince Gustav Channel, PGC, (C); JR275, Filchner Trough, FT, (D).

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 where 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-ORACLE[1] (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 (μmol/m^3), nitrate (mol/m^3), silicate (mol/m^3), phosphate (mol/m^3), phytoplankton (μmol/m^3), primary production (g/m^3d^{-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 (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 Institute[2] (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:

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[1] http://www.bio-oracle.org/

[2] meereisportal.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^{r} – 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^{r} – 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^{r} – 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^{r} – 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^{r} – 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^{r} – 35° 21.90′	701	–	–	–	–	–	–	–
99	F7	01/03/2012	977 – 963	74° 38.05′ – 74° 38.14′	29° 00.49^{r} – 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^{r} – 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^{r} – 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^{r}	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^{r}	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 θ.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^r 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,

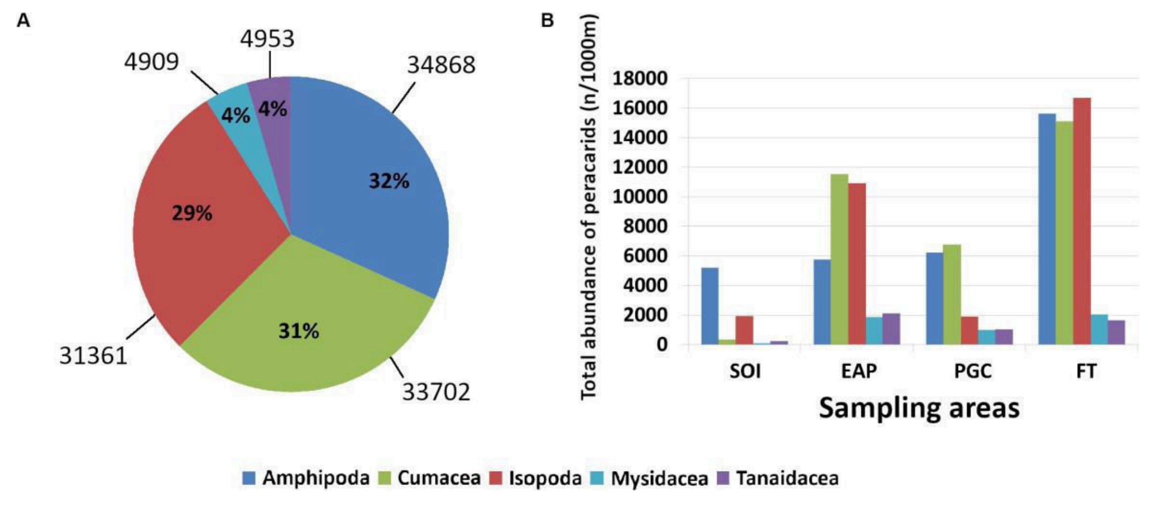

FIGURE 2 | Total relative abundance of peracarids (A); total abundance of peracarids in each sampling area (B). SOI, South Orkney Islands; EAP, Eastern Antarctic Peninsula; PGC, Prince Gustav Channel; FT, Filchner Trough.

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

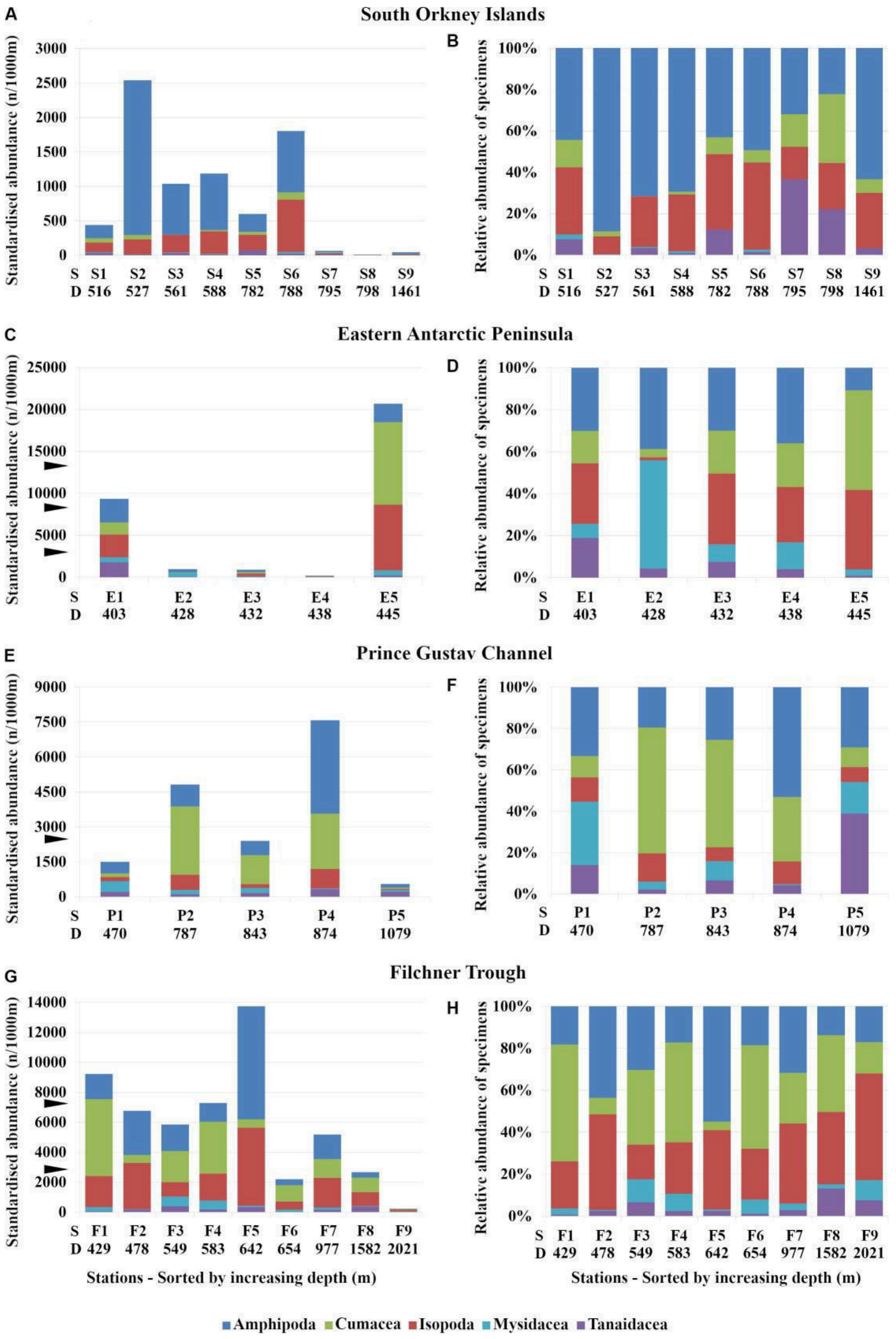

FIGURE 3 | Standard (A,C,E,G) and relative abundance (B,D,F,H) of peracarid orders in the study areas. (A,B) South Orkney Islands, (C,D) Eastern Antarctic Peninsula, (E,F) Prince Gustav Channel, (G,H) Filchner Trough. ❯, maximum standardized abundance at comparative regions; S, station number; D, depth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

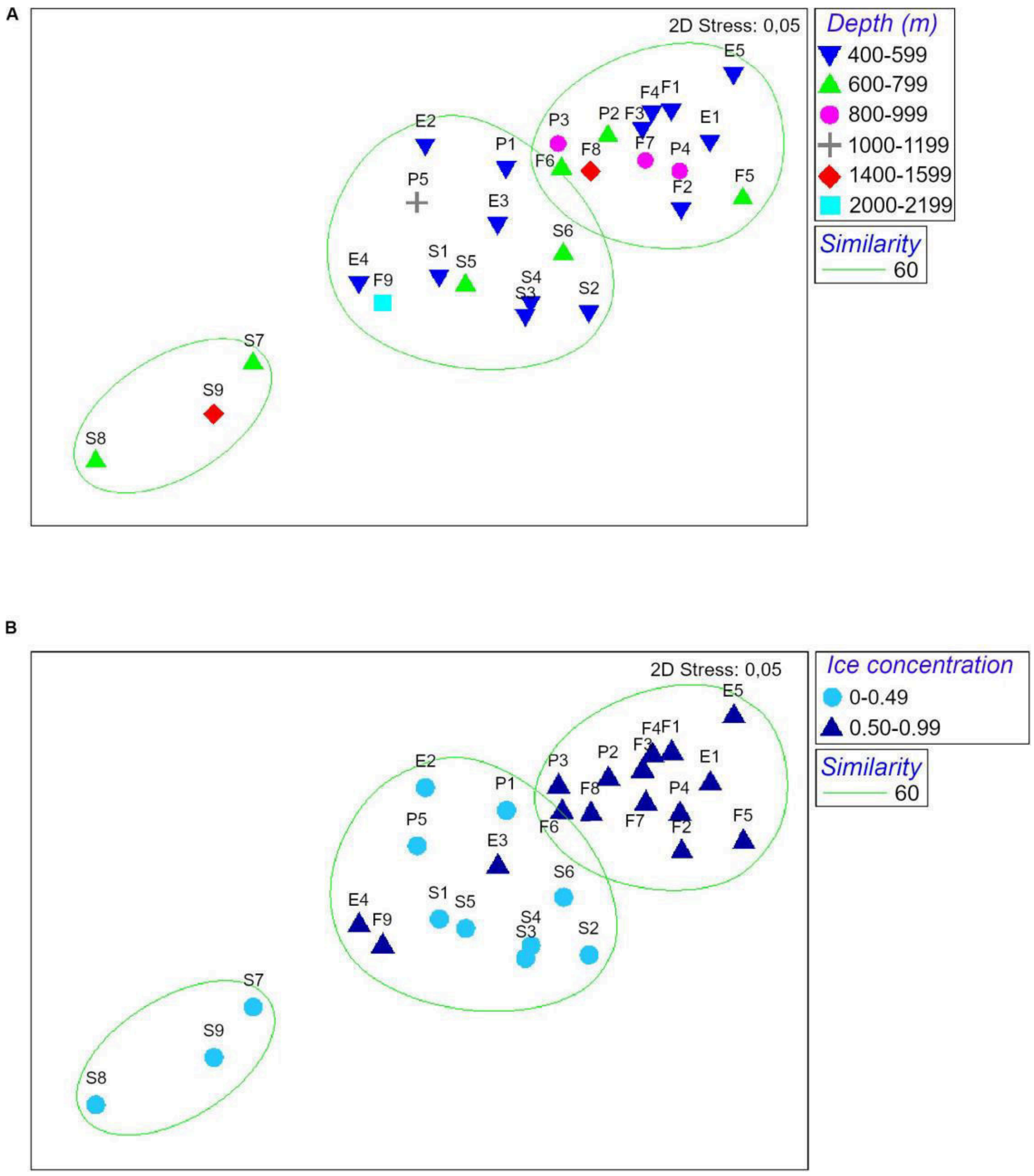

FIGURE 4 | nMDS of ice concentration and depth of peracarid assemblages from all stations. Depth is expressed in meters, ice concentration in fractions from 0 to 1 (where 0 indicates no ice coverage and 1 indicates complete ice coverage).

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; ρ = 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; ρ = 0.355). The same test carried out on a depth gradient did not show any significant result (*p* = 0.17; ρ = 0.077).

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.

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 clorophyll 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 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 circadial migrations; Mühlenhardt-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^r 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

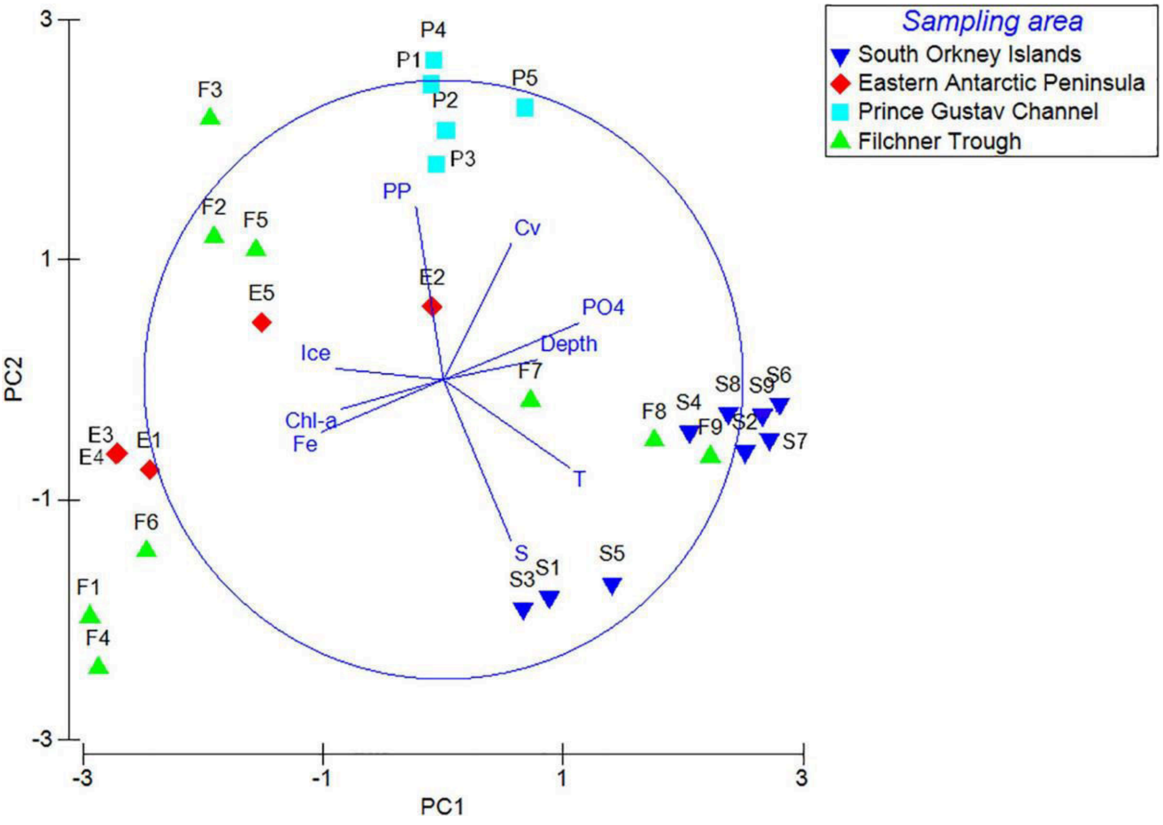

FIGURE 5 | Principal component analysis (PCA) of peracarid assemblages and environmental variables from all stations. PP, primary productivity; Chl, chlorophyll-a; S, salinity; T, temperature; Fe, iron; Cv, current velocity; PO4, phosphate; Ice, ice concentration.

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

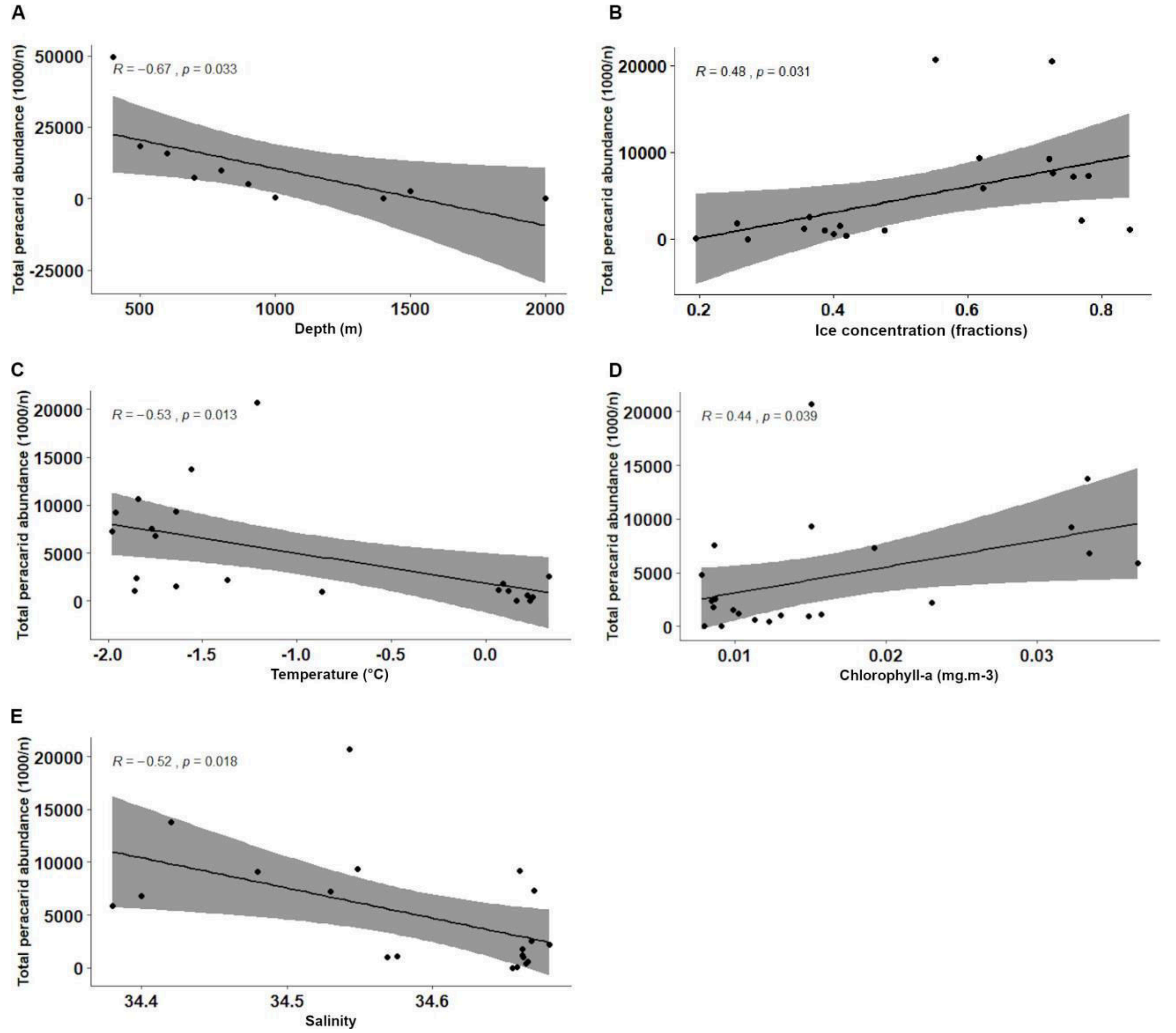

FIGURE 6 | Pearson's correlation analyses of peracarid abundances and environmental variables: depth (A), ice concentration (B), temperature (C), chlorophyll-a (D), salinity (E).

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	Present study		Present and previous studies	
Variables	*R*	*p* value	*R*	*p*-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. Wlodarska-Kowalczuk 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.

6.2. Chapter II

Chapter II

Abundance data of benthic peracarid crustaceans from the South Atlantic and Southern Ocean

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Data Article

Abundance data of benthic peracarid crustaceans from the South Atlantic and Southern Ocean

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Peracarid data were collected in the Southern Ocean and South Atlantic Ocean. Sampling was performed during nine different expeditions on board of RRS *James Clark Ross* and RV *Polarstern*, using epibenthic sledges (EBS) at depth ranging between 160–6348 m at 109 locations. The correlation between environmental variables and peracarid abundance was investigated. Abundance data comprise a total of 128570 peracarids (52366 were amphipods, 28516 were cumaceans, 36142 isopods, 5676 mysidaceans and 5870 were tanaidaceans). The presented data are useful to investigate the composition and abundance patterns of peracarid orders at a wide depth range and spatial scale in the Southern

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Ocean. They can also be reused to compare their abundance with that of other taxa in broader ecological surveys.

Specifications Table

Subject	Biodiversity
Specific subject area	Biogeography and benthic assemblage composition
Type of data	Table
How data were acquired	Abundance data were available with peer-reviewed articles and as unpublished material. Environmental variables were available from the "global environmental datasets for marine species distribution modelling" Bio-ORACLE [1,2].
Data format	Raw Analyzed
Parameters for data collection	For data collection, data had to include peracarid abundances from the Atlantic sector of the Southern Ocean and the Weddell Sea at a wide range of depth (from the continental shelf to the deep sea). Environmental variables had to be recorded at the maximum depth (benthic layers).
Description of data collection	Primary data – unpublished primary (raw) data were collected by the authors during the expedition JR144 (BIOPEARL I) [3]. Published secondary data were collected from peer-reviewed articles. When sampling locations presented standardised abundances to 1000 m haul only, raw abundances were calculated using the haul length recorded at each station. Environmental data were downloaded from Bio-ORACLE. The latter offers only data recorded at the maximum depth (benthic layers) and data recorded at the surface (surface layers); benthic layers were chosen for the study.
Data source location	Primary data sources: primary data are partly available on PANGAEA data repository (https://doi.org/10.1594/PANGAEA.811814) and on the cruise report of the expedition JR144 (BIOPEARL I) [4]. In total, BIOPEARL I comprised 26 sampling locations from depths ranging between 160 m and 1655 m, and latitudes ranging from 53° to 62° South (Table 1). Published secondary data are available in the following peer-reviewed articles: [4–9]. Environmental data are available at http://www.bio-oracle.org/.
Data accessibility	With the article
Related research article	D. Di Franco, K. Linse, H.J. Griffiths, A. Brandt, Drivers of abundance and spatial distribution in Southern Ocean peracarid Crustacea, Ecol. Indic. In Press.

Value of the Data

- Unpublished raw peracarid abundances reported in the present manuscript provide important and valuable data to the previous published datasets. These data are valuable because they come from remote areas (the Southern Ocean continental shelf and deep sea), difficult to access for logistic reasons.
- They can be useful to taxonomists and ecologists who investigate the Southern Ocean benthos and study geographical distribution patterns of benthic taxa in the Southern Hemisphere. They allow to better assess the assemblage structure and composition of peracarid orders and improve the knowledge on peracarid distribution in the Atlantic sector of the Southern Ocean.

- The comparison between peracarid abundance data and abundance data of other taxa can have further applications on broader ecological studies from the same area. Raw data from our results can also be used together with published data to investigate the influence of environmental variables on peracarid assemblage structure and composition through modelling, based on future climatic scenarios and on a larger geographic scale.

1. Data Description

The present study includes abundance data of peracarid crustaceans collected during nine different expeditions at a depth range between 160–6348 m (Table 1). Sampling was performed in the Southern Atlantic Ocean, north of the Polar Front, in the Polar Frontal Zone (the Eastern and Western Polar Front – PFE, PFW), on the continental shelf of the South Orkney Islands (SOI), off the South Sandwich Islands (SSI), in the deep Weddell Sea Abyssal Plain (DWS), on the eastern Weddell Sea continental shelf between the Filchner Trough and Kapp Norvegia (FT-KN), the East Antarctic Peninsula (EAP) on the western Weddell Sea shelf, and the West Antarctic Peninsula (WAP) in the Pacific SO sector (Table 1). The EAP includes a subdivision into the Prince Gustav Channel (PGC). A total of 109 stations were analysed, with latitudes ranging from 77° to 41° south (Table 1).

Twelve different environmental data from the Southern Ocean Weddell Sea (and South Atlantic Ocean) were obtained for each sampling location (Table 2): chlorophyll-a (mg/m3), current velocity (m-1), oxygen concentration (mol/m3), iron (μmol/m3), nitrate (mol/m3), phosphate (mol/m3), phytoplankton biomass (μmol/m3), primary production (g/m3d-1), salinity, silicate (mol/m3), temperature (°C), sea-ice concentration (expressed in fractions from 0.1 to 1, where 0.1 indicates very low concentration/absence of ice and 1 indicates a completely ice-covered area.

2. Experimental Design, Materials and Methods

Abundance data were collected from peer-reviewed articles and cruise reports of the expeditions that were performed in the Southern Ocean and South Atlantic Ocean. All acquired data are from peracarid crustaceans collected using epibenthic sledges (EBS) following the design by Brandt and Barthel [10]. The latter consists of a suprabenthic- and an epibenthic net with a mesh size of 500 mm (cod-ends of 300 mm). The sledge possesses an opening-closing mechanism, which only opens at bottom contact. Therefore, supra- and epibenthic samplers would immediately close once the gear was lifted [11].

Environmental data were downloaded as ASCII file from Bio-ORACLE. Files were loaded into the open-source software QGIS as layers and used to extract environmental data from each sampling point.

Table 1
Expeditions and stations of the analyzed EBS samples.

Area	Original station ID	Date	Depth	Latitude	Longitude	Amphipoda	Cumacea	Isopoda	Mysidacea	Tanaidacea
			(m)	Start - End	Start - End	Raw peracarid abundances				
	Expedition JR275									
FT-KN	23	19/02/2012	654 – 656	77° 21.42' S – 77° 21.47' S	35° 21.64' W – 35° 21.90' W	285	759	372	105	16
FT-KN	40	21/02/2012	549 – 539	76° 10.01' S – 76° 09.94' S	27° 48.23' W – 27° 48.44' W	903	1057	489	328	195
FT-KN	45	22/02/2012	429 – 428	75° 45.72' S – 75° 45.85' S	30° 26.56' W – 30° 27.08' W	901	2751	1111	147	30
FT-KN	50	22/02/2012	583 – 587	75° 44.60' S – 75° 44.75' S	31° 14.77' W – 31° 15.21' W	861	2371	1224	409	120
FT-KN	78	26/02/2012	2021 – 2026	74° 24.28' S – 74° 24.39' S	28° 05.09' W – 28° 04.62' W	50	44	149	28	22
FT-KN	83	28/02/2012	1582 – 1580	74° 29.12' S – 74° 29.08' S	28° 46.48' W – 28° 47.08' W	431	1141	1076	63	410
FT-KN	89	29/02/2012	642 – 657	74° 40.30' S – 74° 40.24' S	29° 23.93' W – 29° 23.30' W	4344	318	2996	56	187
FT-KN	94	29/02/2012	478 – 491	74° 41.51' S – 74° 41.36' S	29° 29.27' W – 29° 29.05' W	1259	226	1314	14	70
FT-KN	99	01/03/2012	977 – 963	74° 38.05' S – 74° 38.14' S	29° 00.49' W – 28° 59.97' W	1218	929	1464	119	109
	Expedition JR15005									
SOI	12	02/03/2016	516 – 519	61° 31.85' S – 61° 31.80' S	46° 55.89' W – 46° 56.20' W	129	39	94	7	22
SOI	18	03/03/2016	782 – 786	61° 32.20' S – 61° 32.08' S	47° 07.99' W – 47° 08.24' W	220	42	185	0	63
SOI	27	04/03/2016	1461 – 1471	61° 31.92' S – 61° 31.80' S	47° 23.49' W – 47° 23.68' W	38	4	16	0	2
SOI	34	06/03/2016	561 – 524	62° 09.61' S – 62° 09.45' S	44° 58.92' W – 44° 59.00' W	576	1	197	5	26
SOI	57	09/03/2016	798 – 835	60° 33.33' S – 60° 33.44' S	46° 30.92' W – 46° 31.12' W	2	3	2	0	2
SOI	86	12/03/2016	795 – 794	60° 13.07' S – 60° 13.11' S	46° 44.54' W – 46° 44.87' W	16	9	9	0	21
SOI	103	14/03/2016	788 – 817	60° 28.53' S – 60° 28.41' S	44° 25.38' W – 44° 25.61' W	728	90	621	16	21
SOI	115	15/03/2016	588 – 590	60° 45.16' S – 60° 45.14' S	42° 57.75' W – 42° 58.08' W	642	14	254	9	8
SOI	133	16/03/2016	527 – 521	60° 40.38' S – 60° 40.35' S	42° 30.74' W – 42° 31.02' W	1508	42	143	3	6
	Expedition JR17003a									
PGC	5	01/03/2018	1079 – 1081	63° 34.47' S – 63° 34.51' S	57° 17.08' W – 57° 17.41' W	150	49	37	78	200
PGC	34	04/03/2018	843 – 850	64° 07.70' S – 64° 07.64' S	58° 30.31' W – 58° 29.96' W	345	586	71	164	43
PGC	35	05/03/2018	787 – 727	64° 02.86' S – 64° 02.95' S	58° 27.71' W – 58° 28.01' W	881	2745	612	174	99
PGC	47	06/03/2018	874 – 872	63° 48.44' S – 63° 48.57' S	58° 04.12' W – 58° 04.34' W	3606	2126	754	33	285
PGC	53	07/03/2018	470 – 445	63° 36.97' S – 63° 37.00' S	57° 30.23' W – 57° 30.40' W	255	79	89	234	107
	Expedition PS118									
EAP	6-5	05/03/2019	432 – 433	64° 58.43' S – 64° 58.60' S	57° 47.20' W – 57° 48.24' W	230	157	259	64	58
EAP	6-6	05/03/2019	438 – 438	64° 58.25' S – 64° 58.35' S	57° 47.89' W – 57° 48.63' W	45	26	33	16	5

(*continued on next page*)

Table 1 (*continued*)

Area	Original station ID	Date	Depth	Latitude	Longitude	Amphipoda	Cumacea	Isopoda	Mysidacea	Tanaidacea
			(m)	Start - End	Start - End	Raw peracarid abundances				
EAP	9-5	12/03/2019	403 – 401	64° 01.18’S – 64° 01.35’S	55° 54.08’W – 55° 54.90’W	1291	661	1238	284	812
EAP	12-7	14/03/2019	445 – 444	63° 49.40’S – 63° 49.48’S	55° 40.67’W – 55° 40.21’W	742	3284	2617	204	69
EAP	38-9	22/03/2019	428 – 427	63° 03.79’S – 63° 03.92’S	54° 18.56’W – 54° 18.75’W	218	22	8	291	24
	Expedition ANDEEP I									
WAP	41-3	26/01/2002	2370	59° 22.24’S – 59° 22.57’S	60° 04.06’W – 60° 04.05’W	108	34	217	10	10
WAP	42-2	27/01/2002	3689	59° 40.30’S – 59° 40.32’S	57° 35.42’W – 57° 35.64’W	548	477	906	19	110
WAP	43-8	03/02/2002	3962	60° 27.13’S – 60° 27.19’S	56° 05.12’W – 56° 04.81’W	225	77	196	0	29
WAP	46-7	30/01/2002	3894	60° 38.33’S – 60° 38.06’S	53° 57.38’W – 53° 57.51’W	3090	2707	1449	158	203
WAP	99-4	12/02/2002	5191	61° 06.40’S – 61° 06.40’S	59° 16.57’W – 59° 17.61’W	11	5	32	0	5
WAP	105-7	12/02/2002	2308	61° 24.16’S – 61° 24.25’S	58° 51.56’W – 58° 51.56’W	26	9	6	3	0
WAP	114-4	17/02/2002	2921	61° 43.54’S – 61° 43.51’S	60° 44.21’W – 60° 44.43’W	94	85	448	13	18
WAP	129-2	22/02/2002	3640	59° 52.21’S – 59° 52.20’S	59° 58.75’W – 59° 58.63’W	94	41	90	4	24
	Expedition ANDEEP II									
EAP	131-3	05/03/2002	3053	65° 19.83’S – 65° 19.99’S	51° 31.61’W – 51° 31.23’W	419	64	917	36	25
EAP	132-2	06/03/2002	2086	65° 17.75’S – 65° 17.62’S	53° 22.81’W – 53° 22.86’W	33	3	33	15	0
EAP	133-3	07/02/2002	1121	65° 20.17’S – 65° 20.08’S	54° 14.30’W – 54° 14.34’W	321	547	742	13	75
DWS	134-3	09/03/2002	4069	65° 19.20’S – 65°19.05’S	48° 03.77’W – 48° 02.92’W	23	14	50	0	5
DWS	135-4	10/03/2002	4678	65° 00.05’S – 65° 59.97’S	43° 03.02’W – 43° 00.82’W	31	11	413	3	8
DWS	136-4	12/03/2002	4747	64° 01.54’S – 64° 01.51’S	39° 06.88’W – 39° 06.88’W	5	5	37	0	5
DWS	137-4	14/03/2002	4976	63° 44.98’S – 63° 44.74’S	38° 47.75’W – 38° 48.23’W	18	5	69	0	9
DWS	138-6	17/03/2002	4542	62° 58.08’S – 62° 57.99’S	27° 54.10’W – 27° 54.28’W	75	8	191	0	17
SSI	139-6	20/03/2002	3950	58° 14.10’S – 58° 14.15’S	24° 21.20’W – 24° 21.21’W	19	26	65	0	6
SSI	140-8	21/03/2002	2970	58° 15.98’S – 58° 16.28’S	24° 53.73’W – 24° 54.09’W	92	71	138	0	54
SSI	141-10	23/03/2002	2312	58° 25.07’S – 58° 24.63’S	24° 00.78’W – 24° 00.74’W	229	93	37	37	28
SSI	142-6	24/03/2002	6348	58° 50.78’S – 58° 50.44’S	23° 57.75’W – 23° 57.59’W	0	0	0	0	0
SSI	143-1	25/03/2002	774	58° 44.69’S – 58° 44.45’S	25° 10.28’W – 25° 10.66’W	190	13	58	9	13
	Expedition ANDEEP III									
SAO	16-10	26/01/2005	4720	41° 07.55’S – 41° 07.020S	09° 55.94’E – 09° 54.85’E	90	58	224	3	22
SAO	21-7	29/01/2005	4577	47° 39.87’S – 47° 38.520S	04° 15.79’E – 04° 14.94’E	15	12	70	0	6
FT-KN	74-6	20/02/2005	1032	71° 18.42’S – 71° 18.330S	13° 58 .21’W – 13° 57.65’W	1057	984	738	31	392

(*continued on next page*)

Table 1 (*continued*)

Area	Original station ID	Date	Depth	Latitude	Longitude	Amphipoda	Cumacea	Isopoda	Mysidacea	Tanaidacea
			(m)	Start - End	Start - End	Raw peracarid abundances				
FT-KN	78-9	22/02/2005	2149	71° 09.52'S – 71° 09.340S	14° 00.76'W – 13° 58.85'W	416	642	411	19	78
FT-KN	80-9	23/02/2005	3100	70° 38.45'S – 70° 39.180S	14° 42.86'W – 14° 43.43'W	516	158	615	11	27
FT-KN	81-8	24/02/2005	4382	70° 31.08'S – 70° 32.230S	14° 34.82'W – 14° 34.90'W	194	50	376	3	94
DWS	88-8	27/02/2005	4931	68° 03.84'S – 68° 03.640S	20° 31.39'W – 20° 27.49'W	94	21	269	0	31
DWS	94-14	02/03/2005	4891	66° 39.08'S – 66° 37.160S	27° 09.26'W – 27° 10.13'W	70	7	90	0	3
DWS	102-3	06/03/2005	4801	65° 33.18'S – 65° 34.320S	36° 33.24'W – 36° 31.05'W	20	3	92	0	7
DWS	110-8	10/03/2005	4695	64° 59.20'S – 64° 00.910S	43° 02.05'W – 43° 02.10'W	55	15	499	3	23
EAP	121-11	14/03/2005	2659	63° 38.27'S – 63° 37.310S	50° 37.16'W – 50° 38.04'W	323	109	375	8	88
EAP	133-2	16/03/2005	1584	62° 46.73'S – 62° 46.330S	53° 02.57'W – 53° 04.14'W	7602	88	2842	7	196
EAP	142-5	18/03/2005	3405	62° 11.36'S – 62° 11.360S	49° 27.62'W – 49° 29.57'W	99	36	92	0	2
SOI	150-6	20/03/2005	1984	61° 49.13'S – 61° 48.520S	47° 27.51'W – 47° 28.16'W	270	113	312	24	28
SOI	151-7	21/03/2005	1183	61° 45.67'S – 61° 45.420S	47° 07.19'W – 47° 08.07'W	394	47	109	17	40
WAP	152-6	23/03/2005	1998	62° 20.64'S – 62° 19.910S	57° 53.12'W – 57° 53.68'W	2	0	6	0	2
WAP	153-7	29/03/2005	2096	63° 19.82'S – 63° 19.180S	64° 36.44'W – 64° 37.53'W	266	152	215	6	72
WAP	154-9	30/03/2005	3803	62° 32.52'S – 62° 31.310S	64° 39.45'W – 64° 38.66'W	109	53	25	0	20
	Expedition BIOPEARL I									
PFW	FT-EBS-1	27/02/2006	193 – 194	54° 18.90' S – 54° 18.82' S	56° 40.92' W -56° 41.17' W	9	0	5	0	0
WAP	LI-EBS-1	03/03/2006	1455 – 1502	62° 16.54' S – 62° 16.42' S	61° 35.82' W -61° 36.06' W	0	2	0	0	0
WAP	LI-EBS-3	04/03/2006	557 – 624	62° 23.73' S – 62° 23.70' S	61° 46.25' W – 61° 46.60' W	12	4	6	0	6
WAP	LI-EBS-4	04/03/2006	189 – 191	62° 31.52' S – 62° 31.52' S	61° 49.86' W – 61° 50.21' W	63	14	20	5	6
WAP	DI-EBS-1	05/03/2006	160 – 160	62° 56.81' S – 62° 56.95' S	60° 39.38' W – 60° 39.18' W	1473	3	81	1644	0
WAP	EI-EBS-1	12/03/2006	1490 – 1503	61° 36.72' S – 61° 36.84' S	55° 13.05' W – 55° 13.31' W	100	21	161	10	93
WAP	EI-EBS-2	04/03/2006	1000 – 1000	61° 34.38' S – 61° 34.44' S	55° 14.55' W – 55° 14.88' W	216	98	219	12	43
WAP	EI-EBS-3	04/03/2006	493 – 491	61° 23.14' S – 61° 23.19' S	55° 11.66' W – 55° 11.99' W	80	0	8	2	0
WAP	EI-EBS-4	04/03/2006	199 – 204	61° 20.13' S – 61° 20.18' S	55° 12.23' W – 55° 12.54' W	2475	155	402	108	9
WAP	EI-EBS-5	14/03/2006	544 – 521	60° 58.20' S – 60° 58.34' S	55° 57.88' W – 55° 57.99' W	13	0	0	0	0
SOI	PB-EBS-1	17/03/2006	1638 – 1655	61° 02.06' S – 61° 01.89' S	46° 57.35' W – 46° 57.35' W	20	17	20	5	6
SOI	PB-EBS-2	17/03/2006	967 – 1027	61° 02.03' S – 61° 01.87' S	46° 52.01' W – 46° 52.00' W	2	0	0	0	0
SOI	PB-EBS-3	18/03/2006	505 – 506	60° 59.44' S – 60° 59.60' S	46° 49.91' W – 46° 49.91' W	486	132	608	35	97

(*continued on next page*)

Table 1 (*continued*)

Area	Original station ID	Date	Depth	Latitude	Longitude	Amphipoda	Cumacea	Isopoda	Mysidacea	Tanaidacea
			(m)	Start - End	Start - End	Raw peracarid abundances				
SOI	PB-EBS-4	18/03/2006	201 – 211	60° 49.31’ S – 60° 49.45’ S	46° 29.10’ W – 46° 28.94’ W	750	95	250	91	27
SSI	ST-EBS-1	28/03/2006	1569 – 1580	59° 31.40’ S – 59° 31.46’ S	27° 27.97’ W – 27° 28.25’ W	3	1	2	0	5
SSI	ST-EBS-2	28/03/2006	1007 – 1040	59° 30.42’ S – 59° 30.40’ S	27° 18.16’ W – 27° 18.47’ W	0	0	5	0	16
SSI	ST-EBS-3a	27/03/2006	518 – 544	59° 28.85’ S – 59° 28.85’ S	27° 16.69’ W – 27° 17.01’ W	3	0	12	0	21
SSI	ST-EBS-3b	28/03/2006	501 – 507	59° 28.80’ S – 59° 28.80’ S	27° 17.35’ W – 27° 17.67’ W	11	1	12	0	55
SSI	ST-EBS-4	27/03/2006	294 – 305	59° 28.23’ S – 59° 28.28’ S	27° 16.57’ W – 27° 16.88’ W	1418	50	196	9	318
PFW	SG-EBS-2	06/04/2006	988 – 971	53° 34.59’ S – 53° 34.59’ S	37° 53.11’ W – 37° 53.37’ W	62	4	5	0	2
PFW	SG-EBS-3	05/04/2006	496 – 477	53° 35.85’ S – 53° 35.85’ S	37° 54.18’ W – 37° 54.47’ W	575	232	516	39	4
PFW	SG-EBS-4	05/04/2006	221 – 221	53° 36.66’ S – 53° 36.66’ S	37° 53.10’ W – 37° 53.37’ W	360	150	325	25	3
PFW	SG-EBS-5	09/04/2006	316 – 315	53° 47.37’ S – 53° 47.27’ S	37° 58.68’ W – 37° 58.88’ W	122	4	5	251	3
PFW	S’-EBS-4	11/04/2006	203 – 201	53° 37.68’ S – 53° 37.60’ S	40° 54.46’ W – 40° 54.69’ W	2279	13	600	0	31
PFW	S’-EBS-5	12/04/2006	501 – 505	53° 19.27’ S – 53° 19.27’ S	42° 14.05’ W – 42° 13.79’ W	293	6	222	16	31
PFW	S’-EBS-6	12/04/2006	1016 – 1027	53° 15.19’ S – 53° 15.19’ S	42° 08.63’ W – 42° 08.89’ W	22	0	14	0	7
	Expedition ANTXV/3-EASIZ II									
FT-KN	48-171	12/02/1998	231 – 231	74° 31.72’S – 74° 31.87’S	27° 12.80’W – 27° 13.18’W	666	254	211	27	17
FT-KN	48-111	06/02/1998	397 – 397	73° 38.32’S – 73° 38.43’S	22° 11.61’W – 22° 12.23’W	476	89	194	44	19
FT-KN	48-107	06/02/1998	934 – 924	73° 34.77’S – 73° 34.92’S	22° 38.29’W – 22° 38.89’W	310	350	269	10	80
FT-KN	48-142	10/02/1998	1573 – 1535	74° 36.13’S – 74° 36.30’S	27° 16.13’W – 27° 15.50’W	140	45	276	4	11
FT-KN	48-089	04/02/1998	1639 – 1633	73° 27.26’S – 73° 27.27’S	22° 45.67’W – 22° 46.52’W	200	111	271	11	45
FT-KN	48-130	08/02/1998	1982 – 1973	73° 23.99’S – 73° 23.83’S	22° 08.24’W – 22° 08.65’W	349	98	35	13	2
FT-KN	48-272	26/02/1998	2076 – 2003	71° 28.8’S – 71° 29.0’S	15° 10-4’W – 15° 10.3’W	102	92	34	0	31
FT-KN	48-133	09/02/1998	2043 – 2029	74° 31.72’S – 74° 1.87’S	27° 12.80’W – 27° 13.18’W	56	9	40	8	2
	Expedition SYSTCO									
PFE	81-17	20/01/2012	3744 – 3763	52°0.18’ S – 10°0.72’ E	51°59.61’ S – 9°59.10’ E	12	0	12	4	4
PFE	81-18	20/01/2012	3706 – 3757	52°0.36’ S – 10°1.47’ E	51°59.89’ S – 9°59.55’ E	24	0	81	0	24
PFE	84-25	23/01/2012	4327 – 4046	53°0.89’ S – 10°3.55’ E	53°0.22’ S – 10°2.12’ E	18	5	41	0	9
PFE	85-15	27/01/2012	2736 – 2732	52°0.23’ S – 8°0.48’ W	52°0.56’ S – 8°0.55’ W	18	8	26	0	10
PFE	86-20	31/01/2012	3935 – 3959	51°59.83’ S – 12°3.17’ W	51°59.58’ S – 12°4.13’ W	4	4	4	0	4
PFE	86-24	01/02/2012	3934 – 3994	52°0.07’ S – 12°2.94’ W	51°59.21’ S – 12°4.52’ W	22	26	48	0	13
PFE	86-25	01/02/2012	3936 – 3945	52°0.49’ S – 12°2.05’ W	51°59.31’ S – 12°3.70’ W	5	5	18	0	9

Table 2

Bio-ORACLE environmental variables for each station. Abbreviations: Chl-a = chlorophyll-a; Cv = current velocity; O2 = oxygen; Fe = iron; PO4 = phosphate; Phy = phytoplankton; PP = primary productivity; Sal = salinity; SiO4 = silicate; T = temperature; Ice = sea-ice concentration.

Area	OriginalstationID	Chl-a	Cv	O2	Fe	NO3	PO4	Phy	PP	Sal	SiO4	T	Ice
	Expedition JR275												
FT-KN	23	0.0231	0.0129	318.8007	0.0010	30.6439	2.1523	0.0618	0.0043	34.6804	90.6264	-1.3667	0.6986
FT-KN	40	0.0367	0.0490	281.5575	0.0005	31.7545	2.2068	0.1017	0.0078	34.5287	101.4170	-0.3774	0.4562
FT-KN	45	0.0323	0.0132	311.5363	0.0010	30.9466	2.1669	0.0866	0.0018	34.5439	92.7902	-1.2677	0.7664
FT-KN	50	0.0193	0.0068	315.8773	0.0013	30.7393	2.1630	0.0517	0.0017	34.6520	92.1030	-1.2402	0.8009
FT-KN	78	0.0139	0.0163	254.5854	0.0004	32.5347	2.2639	0.0412	0.0038	34.6659	117.3688	0.7451	0.7322
FT-KN	83	0.0156	0.0230	255.4485	0.0004	32.4478	2.2560	0.0456	0.0037	34.6706	115.7917	1.0104	0.7449
FT-KN	89	0.0334	0.0433	278.4321	0.0005	31.8212	2.2103	0.0927	0.0031	34.6300	102.5980	0.0482	0.7589
FT-KN	94	0.0335	0.0438	278.6671	0.0005	31.8162	2.2100	0.0930	0.0030	34.6050	102.3797	0.0321	0.7626
FT-KN	99	0.0207	0.0310	260.5658	0.0004	32.2475	2.2394	0.0592	0.0035	34.6821	111.3769	1.2234	0.7471
	Expedition JR15005												
SOI	12	0.0122	0.0098	258.6483	0.0005	32.1626	2.2369	0.0332	0.0021	34.6734	107.0041	1.0194	0.3336
SOI	18	0.0113	0.0090	258.6371	0.0005	32.2507	2.2443	0.0317	0.0021	34.6505	109.5758	0.9001	0.3295
SOI	27	0.0101	0.0524	257.2589	0.0005	32.4694	2.2636	0.0299	0.0022	34.6471	115.9241	0.1412	0.3309
SOI	34	0.0130	0.0100	262.7820	0.0006	32.1268	2.2351	0.0346	0.0018	34.6814	106.3767	1.0371	0.4087
SOI	57	0.0091	0.0453	243.4282	0.0005	32.4047	2.2535	0.0269	0.0032	34.6870	111.9271	0.8336	0.1995
SOI	86	0.0080	0.0325	240.5603	0.0004	32.5058	2.2629	0.0249	0.0028	34.6706	115.3983	0.5165	0.1515
SOI	103	0.0086	0.0539	250.5930	0.0004	32.5655	2.2705	0.0263	0.0027	34.6498	117.1581	0.2032	0.1683
SOI	115	0.0102	0.0872	250.3204	0.0005	32.3557	2.2505	0.0291	0.0019	34.6803	110.9865	0.8584	0.2691
SOI	133	0.0087	0.0532	253.3008	0.0004	32.5896	2.2733	0.0266	0.0020	34.6560	118.4082	-0.0109	0.2653
	Expedition JR17003a												
PGC	5	0.0094	0.0549	246.6989	0.0006	32.2379	2.2461	0.0274	0.0133	34.6823	114.6415	0.4620	0.2689
PGC	34	0.0084	0.0330	236.0333	0.0005	32.3353	2.2468	0.0259	0.0089	34.7072	113.2353	0.7026	0.4710
PGC	35	0.0078	0.0330	234.8699	0.0005	32.3618	2.2506	0.0247	0.0116	34.7023	116.4606	0.7496	0.3180
PGC	47	0.0087	0.0481	238.0963	0.0006	32.3144	2.2463	0.0263	0.0142	34.7043	113.6021	0.6495	0.2206
PGC	53	0.0099	0.0561	246.8897	0.0006	32.2209	2.2428	0.0284	0.0142	34.7005	112.6604	0.3966	0.2443

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Table 2 (*continued*)

Area	OriginalstationID	Chl-a	Cv	O2	Fe	NO3	PO4	Phy	PP	Sal	SiO4	T	Ice
	Expedition PS118												
EAP	6-5	0.0157	0.0100	292.2677	0.0013	31.2400	2.2039	0.0398	0.0042	34.5444	97.0706	-1.5687	0.7043
EAP	6-6	0.0157	0.0100	292.2677	0.0013	31.2400	2.2039	0.0398	0.0042	34.5444	97.0706	-1.5687	0.7043
EAP	9-5	0.0150	0.0047	286.5737	0.0015	31.4308	2.2182	0.0384	0.0053	34.5671	98.8565	-1.5176	0.4828
EAP	12-7	0.0151	0.0354	285.9884	0.0012	31.4562	2.2105	0.0389	0.0064	34.5723	99.7628	-1.3941	0.4449
EAP	38-9	0.0149	0.0804	273.3957	0.0008	31.8974	2.2244	0.0394	0.0045	34.6166	104.2050	-0.9089	0.3370
	Expedition ANDEEP I												
WAP	41-3	0.0060	0.0586	226.1177	0.0004	32.5007	2.2606	0.0215	0.0034	34.7073	122.0348	0.5823	0.0030
WAP	42-2	0.0069	0.0197	239.1510	0.0004	32.5526	2.2735	0.0227	0.0038	34.6834	121.8985	0.1728	0.0065
WAP	43-8	0.0069	0.0120	239.9987	0.0004	32.5546	2.2736	0.0229	0.0044	34.6757	121.9000	0.1168	0.0254
WAP	46-7	0.0076	0.0076	244.4984	0.0004	32.5340	2.2714	0.0242	0.0043	34.6672	119.6660	0.1648	0.0549
WAP	99-4	0.0044	0.0028	215.7537	0.0003	32.7394	2.2645	0.0200	0.0046	34.7036	145.6740	0.2468	0.0322
WAP	105-7	0.0067	0.0190	235.2405	0.0004	32.5086	2.2669	0.0226	0.0051	34.6929	121.2443	0.3758	0.0411
WAP	114-4	0.0064	0.0073	233.2873	0.0004	32.5215	2.2684	0.0221	0.0048	34.6940	122.5574	0.2964	0.0534
WAP	129-2	0.0064	0.0691	233.7844	0.0004	32.5295	2.2696	0.0220	0.0034	34.6942	122.5498	0.2889	0.0056
	Expedition ANDEEP II												
EAP	131-3	0.0096	0.0278	257.0883	0.0004	32.6324	2.2782	0.0296	0.0017	34.6522	122.0541	-0.2998	0.7987
EAP	132-2	0.0112	0.0490	257.8369	0.0005	32.4189	2.2591	0.0328	0.0021	34.6526	117.3294	0.4782	0.7885
EAP	133-3	0.0133	0.0656	265.4427	0.0006	32.1028	2.2353	0.0371	0.0023	34.6689	110.9404	1.0531	0.7886
DWS	134-3	0.0102	0.0063	263.3558	0.0004	32.6704	2.2896	0.0319	0.0014	34.6520	124.4308	-0.6032	0.7388
DWS	135-4	0.0087	0.0008	265.8650	0.0004	32.8066	2.2952	0.0280	0.0013	34.6432	127.2823	-0.7887	0.6421
DWS	136-4	0.0092	0.0028	267.4208	0.0004	32.8170	2.2951	0.0291	0.0014	34.6468	126.3059	-0.7794	0.5727
DWS	137-4	0.0092	0.0028	267.4208	0.0004	32.8170	2.2951	0.0291	0.0014	34.6468	126.3061	-0.7794	0.5598
DWS	138-6	0.0094	0.0064	266.1975	0.0004	32.7739	2.2950	0.0293	0.0019	34.6463	124.7432	-0.7185	0.5242
SSI	139-6	0.0071	0.0104	257.5859	0.0004	32.7410	2.2982	0.0235	0.0021	34.6521	127.0629	-0.5132	0.1894
SSI	140-8	0.0078	0.0344	255.8512	0.0004	32.7286	2.2903	0.0249	0.0022	34.6561	122.8767	-0.3595	0.2244
SSI	141-10	0.0071	0.0064	258.0052	0.0004	32.7404	2.2986	0.0236	0.0020	34.6490	127.2817	-0.5241	0.1750
SSI	142-6	0.0072	0.0065	258.2807	0.0004	32.7379	2.2981	0.0238	0.0019	34.6490	127.2817	-0.5270	0.1915
SSI	143-1	0.0088	0.0374	250.5798	0.0004	32.6757	2.2802	0.0270	0.0022	34.6691	118.5745	0.0436	0.2719

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Table 2 (*continued*)

Area	OriginalstationID	Chl-a	Cv	O2	Fe	NO3	PO4	Phy	PP	Sal	SiO4	T	Ice
	Expedition ANDEEP III												
SAO	16-10	0.0045	0.0079	214.9538	0.0006	29.8717	2.0303	0.0200	0.0052	34.7844	92.1891	1.2900	0.0000
SAO	21-7	0.0045	0.0120	217.1751	0.0005	31.7258	2.1529	0.0200	0.0027	34.6901	111.3773	0.6794	0.0000
FT-KN	74-6	0.0141	0.0463	253.2647	0.0004	32.5207	2.2619	0.0418	0.0029	34.6696	116.0030	0.9551	0.6513
FT-KN	78-9	0.0130	0.0376	254.8871	0.0004	32.6254	2.2727	0.0388	0.0025	34.6672	118.7248	0.5096	0.6598
FT-KN	80-9	0.0128	0.0117	265.0141	0.0004	32.7316	2.2901	0.0386	0.0019	34.6520	122.5455	-0.4113	0.6779
FT-KN	81-8	0.0128	0.0017	265.8060	0.0004	32.7250	2.2907	0.0386	0.0019	34.6520	122.8277	-0.4639	0.6762
DWS	88-8	0.0128	0.0042	273.5165	0.0004	32.7866	2.2965	0.0394	0.0014	34.6506	125.5550	-0.7124	0.6333
DWS	94-14	0.0121	0.0015	273.2635	0.0004	32.7970	2.2948	0.0373	0.0016	34.6511	125.4371	-0.7731	0.6221
DWS	102-3	0.0100	0.0020	268.6074	0.0004	32.7976	2.2933	0.0315	0.0015	34.6469	126.1360	-0.7844	0.6103
DWS	110-8	0.0087	0.0009	265.8363	0.0004	32.8067	2.2953	0.0279	0.0013	34.6429	127.2823	-0.7889	0.6390
EAP	121-11	0.0101	0.0460	257.0160	0.0004	32.5484	2.2697	0.0304	0.0025	34.6520	120.2742	-0.0437	0.6112
EAP	133-2	0.0110	0.0736	258.2803	0.0005	32.3834	2.2562	0.0319	0.0030	34.6458	115.1296	0.7103	0.4200
EAP	142-5	0.0089	0.0058	256.2522	0.0004	32.6069	2.2777	0.0274	0.0021	34.6520	120.9542	-0.2853	0.4609
SOI	150-6	0.0100	0.0704	257.3563	0.0005	32.4871	2.2651	0.0297	0.0022	34.6478	116.5540	0.0411	0.3673
SOI	151-7	0.0107	0.0482	257.9414	0.0005	32.3673	2.2547	0.0308	0.0021	34.6474	112.8308	0.5437	0.3706
WAP	152-6	0.0069	0.0634	233.8989	0.0004	32.4699	2.2604	0.0230	0.0068	34.7108	119.6696	0.7166	0.1224
WAP	153-7	0.0048	0.0098	215.1420	0.0003	32.5432	2.2555	0.0203	0.0042	34.7080	130.5275	0.6131	0.1130
WAP	154-9	0.0058	0.0156	226.3083	0.0004	32.5340	2.2654	0.0213	0.0031	34.6981	132.0427	0.3477	0.0602
	Expedition BIOPEARL I												
PFW	FT-EBS-1	0.0897	0.1576	288.2635	0.0003	24.3944	1.7121	0.2711	0.0055	34.0882	29.4800	3.9502	0.0000
WAP	LI-EBS-1	0.0053	0.0479	215.6366	0.0004	32.5091	2.2527	0.0209	0.0057	34.7269	123.4480	0.8560	0.0759
WAP	LI-EBS-3	0.0052	0.0555	212.2230	0.0004	32.5109	2.2495	0.0208	0.0059	34.7402	120.2483	0.8847	0.0774
WAP	LI-EBS-4	0.0111	0.0694	227.3546	0.0007	32.2295	2.2375	0.0317	0.0065	34.6676	94.8744	-0.3831	0.0817
WAP	DI-EBS-1	0.0342	0.0473	266.0254	0.0009	31.5668	2.2132	0.0835	0.0082	34.1967	91.6641	-1.2254	0.0983
WAP	EI-EBS-1	0.0078	0.0529	242.0465	0.0005	32.4704	2.2630	0.0245	0.0040	34.6561	117.6464	0.5904	0.1220
WAP	EI-EBS-2	0.0106	0.0702	257.5303	0.0007	32.1398	2.2458	0.0292	0.0043	34.6424	113.3977	0.2268	0.1152
WAP	EI-EBS-3	0.0117	0.0501	261.9873	0.0007	32.0749	2.2381	0.0316	0.0051	34.6782	111.5524	0.0651	0.1086
WAP	EI-EBS-4	0.0117	0.0501	261.9873	0.0007	32.0749	2.2381	0.0316	0.0051	34.6782	111.5524	0.0651	0.1086
WAP	EI-EBS-5	0.0082	0.0932	235.4298	0.0005	32.3787	2.2490	0.0256	0.0050	34.7106	113.6474	0.9389	0.0528
SOI	PB-EBS-1	0.0099	0.0109	254.8230	0.0005	32.4319	2.2601	0.0292	0.0023	34.6537	114.8937	0.3831	0.2675

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Table 2 (*continued*)

Area	OriginalstationID	Chl-a	Cv	O2	Fe	NO3	PO4	Phy	PP	Sal	SiO4	T	Ice
SOI	PB-EBS-2	0.0103	0.0268	255.2434	0.0005	32.3602	2.2535	0.0299	0.0023	34.6566	112.8380	0.6576	0.2668
SOI	PB-EBS-3	0.0109	0.0229	251.0748	0.0005	32.2590	2.2431	0.0305	0.0024	34.6637	108.6968	0.9692	0.2583
SOI	PB-EBS-4	0.0180	0.0187	250.7584	0.0008	32.0988	2.2328	0.0447	0.0028	34.5184	102.1753	0.7513	0.2380
SSI	ST-EBS-1	0.0076	0.0161	241.6533	0.0004	32.6430	2.2804	0.0243	0.0019	34.6659	118.6256	0.1703	0.3306
SSI	ST-EBS-2	0.0085	0.0131	242.8239	0.0004	32.6253	2.2756	0.0260	0.0020	34.6676	116.6997	0.2514	0.3339
SSI	ST-EBS-3a	0.0097	0.0136	234.9417	0.0004	32.5286	2.2626	0.0280	0.0020	34.6780	111.6710	0.5506	0.3254
SSI	ST-EBS-3b	0.0097	0.0136	234.9417	0.0004	32.5286	2.2626	0.0280	0.0020	34.6780	111.6710	0.5506	0.3254
SSI	ST-EBS-4	0.0097	0.0136	234.9417	0.0004	32.5286	2.2626	0.0280	0.0020	34.6780	111.6710	0.5506	0.3254
PFW	SG-EBS-2	0.0058	0.0059	211.0450	0.0004	32.4687	2.2506	0.0211	0.0051	34.6995	109.6219	0.9906	0.0000
PFW	SG-EBS-3	0.0089	0.0125	212.8409	0.0004	32.3960	2.2381	0.0269	0.0052	34.7078	87.3191	1.4410	0.0000
PFW	SG-EBS-4	0.0089	0.0125	212.8409	0.0004	32.3960	2.2381	0.0269	0.0052	34.7078	87.3191	1.4410	0.0000
PFW	SG-EBS-5	0.0187	0.0219	239.0831	0.0005	31.0162	2.1414	0.0496	0.0057	34.4539	64.3489	1.6270	0.0000
PFW	SR-EBS-4	0.0062	0.0128	207.9209	0.0004	32.5871	2.2563	0.0218	0.0026	34.7263	104.0782	1.1853	0.0000
PFW	SR-EBS-5	0.0071	0.0077	206.7518	0.0004	32.6193	2.2550	0.0235	0.0028	34.6733	94.7574	1.4087	0.0000
PFW	SR-EBS-6	0.0070	0.0073	206.6150	0.0004	32.6208	2.2551	0.0234	0.0029	34.6854	94.8750	1.4049	0.0000
	Expedition ANTXV/3-EASIZ II												
FT-KN	48-171	0.0483	0.0091	323.4557	0.0007	30.7678	2.1556	0.1290	0.0076	34.4659	90.9305	-1.6702	0.5499
FT-KN	48-111	0.0294	0.0827	269.0245	0.0005	32.0195	2.2226	0.0827	0.0042	34.6162	105.1463	0.3652	0.6565
FT-KN	48-107	0.0179	0.0598	256.8818	0.0004	32.3809	2.2499	0.0520	0.0040	34.6792	112.4451	1.2269	0.6748
FT-KN	48-142	0.0164	0.0226	256.0208	0.0004	32.4202	2.2534	0.0480	0.0056	34.6699	114.6458	1.1378	0.6930
FT-KN	48-089	0.0144	0.0425	254.7469	0.0004	32.5291	2.2631	0.0426	0.0039	34.6704	116.1008	0.9651	0.6834
FT-KN	48-130	0.0135	0.0329	254.9713	0.0004	32.5884	2.2690	0.0401	0.0042	34.6682	117.6414	0.7137	0.6702
FT-KN	48-272	0.0133	0.0384	254.2244	0.0004	32.5920	2.2692	0.0397	0.0024	34.6686	117.8511	0.6733	0.6698
FT-KN	48-133	0.0140	0.0137	254.6401	0.0004	32.5345	2.2638	0.0415	0.0054	34.6648	117.3599	0.7905	0.6960
	Expedition SYSTCO												
PFE	81-17	0.0059	0.0135	225.9090	0.0004	32.4885	2.2476	0.0218	0.0022	34.6738	118.0993	0.3522	0.0000
PFE	81-18	0.0059	0.0135	225.9090	0.0004	32.4885	2.2476	0.0218	0.0022	34.6738	118.0993	0.3522	0.0000
PFE	84-25	0.0066	0.0287	253.7286	0.0004	32.8336	2.3099	0.0228	0.0027	34.6478	129.3201	-0.6160	0.0024
PFE	85-15	0.0062	0.0051	228.4755	0.0004	32.5836	2.2612	0.0223	0.0021	34.6776	123.5956	0.2052	0.0000
PFE	86-20	0.0059	0.0036	227.9028	0.0004	32.5057	2.2495	0.0220	0.0024	34.6801	117.4531	0.2445	0.0001
PFE	86-24	0.0054	0.0161	226.0687	0.0004	32.4675	2.2399	0.0211	0.0024	34.6722	117.4007	0.2727	0.0001
PFE	86-25	0.0054	0.0161	226.0687	0.0004	32.4675	2.2399	0.0211	0.0024	34.6722	117.4007	0.2727	0.0001

Ethics Statements

The authors declare that the present work did not include experiments on human subjects and/or animals.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships which have or could be perceived to have influenced the work reported in this article.

CRediT Author 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, Formal analysis, Writing – original draft, Visualization.

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6.3. Chapter III

Chapter III

Drivers of abundance and spatial distribution in Southern Ocean peracarid crustacea

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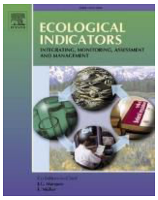

Drivers of abundance and spatial distribution in Southern Ocean peracarid crustacea

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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 problably 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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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).

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

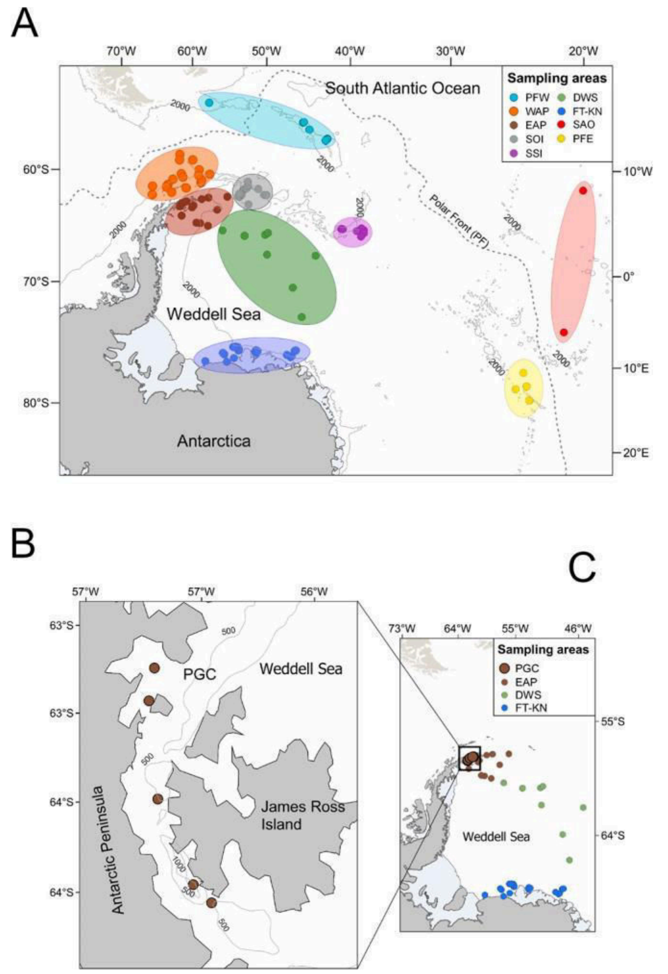

Fig. 1. Map of the study area at a wide geographical scale showing all stations at which EBS peracarid samples were collected (A); map showing stations from the Prince Gustav Channel within the EAP (B) and those from the Weddell Sea (C). Abbreviations: South Atlantic Ocean (SAO), Eastern Polar Front (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).

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 assemblage's 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 axis1 = 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

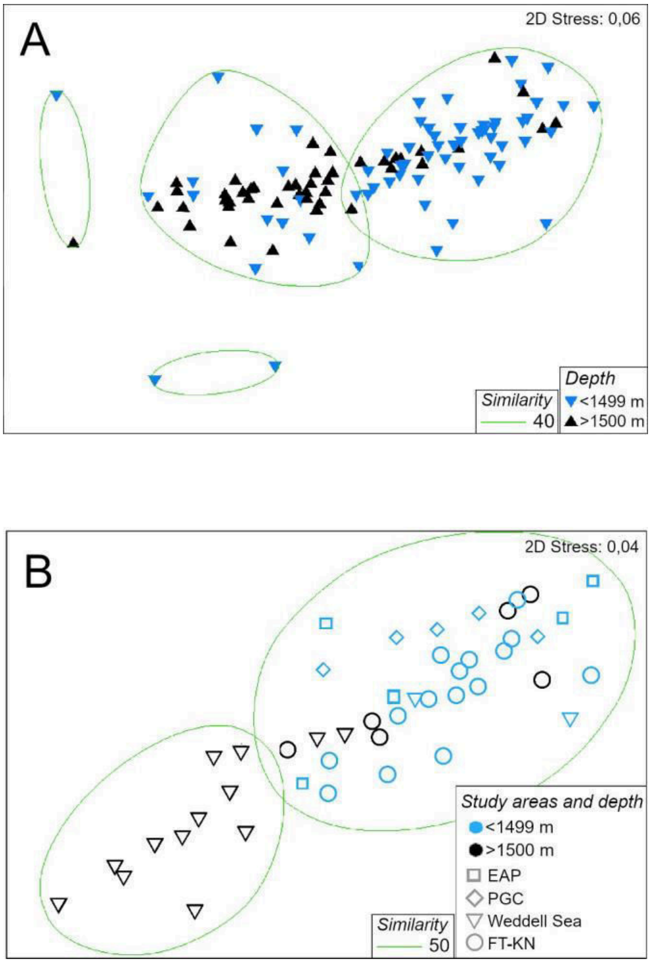

Fig. 2. Non-metric multidimensional scaling (nMDS) plot of peracarid abundance from all sampling areas and in relation to depth (A); nMDS plot of depth of peracarid abundance from the Weddell Sea (B). Abbreviations: Eastern Antarctic Peninsula (EAP), Prince Gustav Channel (PGC), area confined between 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).

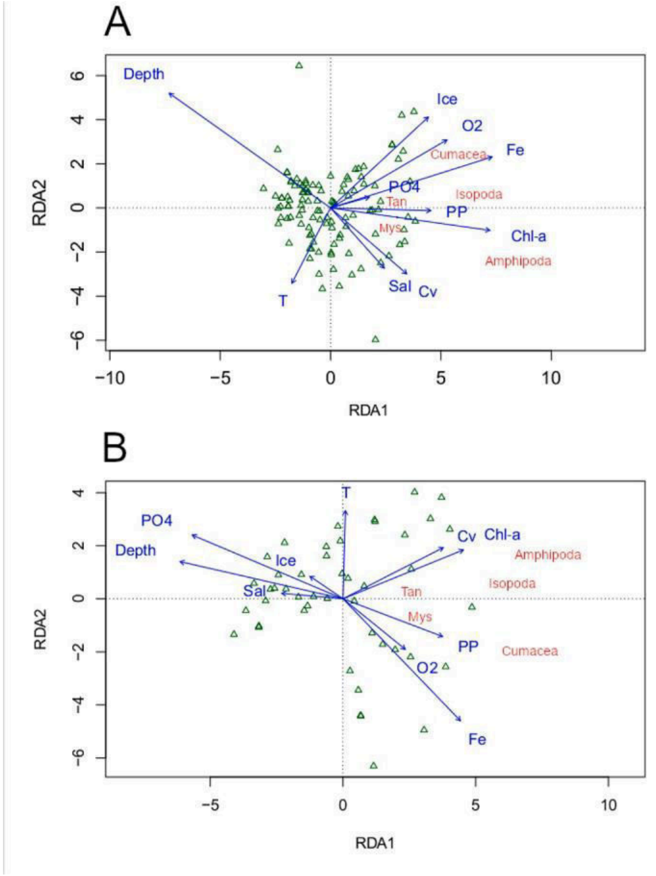

Fig. 3. RDA plot of peracarid assemblages and environmental variables from all sampling areas (A); RDA plot of peracarid assemblages and environmental variables from the Weddell Sea (B). Abbreviations: Chl-a = chlorophyll-a; Cv = current velocity; O2 = oxygen; Fe = iron; PO4 = phosphate; PP = primary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

Table 3
Results of SIMPER (ʽsimilarity percentageʼ) 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
Pearsonʼs 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 assemblages structure between deep-sea and continental-shelf sampling sites. Peracarid assemblages 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 (λ = 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%; ρ = 0.328). SIMPER analysis showed that isopods and cumaceans were the main orders driving the dissimilarities observed (Table 5).

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

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

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 sea- floor (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.

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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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6.4. Chapter IV

Chapter IV

Sea-ice loss threatens Southern Ocean’s benthic species diversity

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Sea-ice loss threatens Southern Ocean's benthic species diversity

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Abstract

For the first time in Southern Ocean (SO) research, we document the vulnerability of benthic species diversity to loss of sea ice. Our model group to test for correlations between environmental variables and benthic species diversity are isopod crustaceans, one of the most dominant taxa of the SO macrofaunal benthos. A total of 12 environmental variables, based on a combination of satellite and *in situ* observations over a period of 14 years, were investigated in the SO between 60° S and 77° S and at depth ranges between 403 – 4976 m. We document a decline in species diversity with declining sea ice on the basis of 214 benthic isopod species representing 78 genera from the Atlantic sector of the SO. Redundancy Analysis (RDA) and Generalised Linear Model analysis (GLMs) analyses identified sea ice as a significant physical driver shaping benthic isopod species richness and composition. Thus, sea ice is one of the physical drivers affecting life in the SO. Future projections of climate warming suggest that the

entire SO will be affected by a strong decline in sea-ice concentration and extent, consequently threatening the current SO benthic species diversity. The SO is a hotspot of biodiversity on a global scale, expanding the knowledge on the effect of sea-ice loss on SO communities is thus imperative. Our results call for an urgent response to climate change by policymakers as this is a tremendous threat for the environment and it has reached the most remote and pristine Polar regions.

1. Introduction

Despite the low temperatures and polar environment, the Southern Ocean (SO) hosts a unique fauna with high levels of diversity and endemism (more than 8,000 valid marine species discovered, 50-97% of which are endemic) (*1*, *2*). These characteristics are the result of an evolution in isolation for > 20 Million years, and strong influence by geologic and climatic events over the last 40 Ma (*3*). Extreme temperatures and oceanographic features such as the Antarctic Circumpolar Current (ACC) have contributed to this isolation by acting as barriers to most marine organisms (*4*). Due to this evolutionary history, several SO benthic taxa have developed peculiar and habitat-specific adaptations such as cold tolerance, stenothermia, slow metabolic rate, long generation times, and brooding as reproductive strategy (*5*–*7*). SO cool-adapted taxa are considered to be particularly vulnerable to changes in their physical environment (*7*, *8*).

Among SO environmental variables, sea ice, is one of the main physical drivers affecting life on the seafloor (*9*), which is home to about 90% of the marine species known from the region (*2*). The variability in sea-ice duration and the seasonal inputs of high quantities of food particles in the SO, led to a niche diversification where benthic species adopted different feeding habits in relation to sea-ice extension and persistence. For instance, up to 95% of Antarctic species that directly consume phytoplankton or benthic algae cease to feed in winter due to the reduced availability of suitable food sources (*6*). Many suspension-feeders that feed throughout the year shift their food target from large particles to smaller ones due to seasonal changes in food availability (*6*). The warming-induced reduction of sea-ice coverage and alteration of its seasonality due to climate change will make vertical food transfer available for longer periods and alter its composition: a decline in sea-ice extent will lead to a decrease of the overall sea-ice algae abundance causing changes throughout the SO food web; in addition, it will reduce the frequency of ice-related phytoplankton blooms with shift in the phytoplankton species composition towards smaller diatoms and flagellates (*10*). This will force benthic taxa to change their feeding habits and/or find alternative food supplies, leading to taxonomic shifts in their communities, migration and even extinction events for those species that are unable to adapt (*11*). Aim of our study is to expand the knowledge on the diversity of benthic isopods from SO areas characterised by different environmental conditions, including sea-ice extent, containing the southernmost marine region of the SO, the Filchner Through area. Thus, we aim to investigate the influence of environmental variables driving SO benthic isopod species richness and assemblage composition.

2. Material and methods

The study is based on isopod samples (Fig. 1a) collected using an epibenthic sledge (EBS) (*12*) during four different expeditions in the Atlantic sector of the SO: JR275, JR15005, JR17003a on board of RRS *James Clark Ross* and PS118 expedition on board of RV *Polarstern* (*13*). Samples were collected in the Atlantic sector of the SO between 60° S and 77° S and at depth ranges between 401 – 2026 m. For comparability, abundance data were standardised to 1000 m haul distances. A total of 16157 isopod specimens were preserved on board in 96% ethanol and subsequently identified and counted in the laboratory. Environmental data were downloaded from the "global environmental datasets for marine species distribution modelling" Bio-

ORACLE (http://www.bio-oracle.org/) (*14*) with a resolution of 5 arcminutes. Bio-ORACLE data are based on a combination of satellite and in situ observations, for a period of 14 years. Layers downloaded included annual-mean values 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^{3}d^{-1}), phosphate (mol/m^3), phytoplankton biomass (µmol/m^3), sea-ice concentration (fractions from 0.1 to 1, where 0.1 indicates very low concentration/absence of sea ice and 1 indicates a completely ice-covered area). Environmental variables were checked for collinearity using a Draftsman plot analysis based on Pearson correlation coefficient through the software PRIMER 6 (*15*). According to the Pearson correlation coefficient, the following variables were removed: silicate, nitrate, phosphate, phytoplankton biomass. The correlation between isopod species and environmental variables was investigated by means of Pearson correlation analyses using the statistic software RStudio and the package "ggpubr"(*16*). A Redundancy Analysis (RDA) and a Generalised Linear Model analysis (GLMs) were performed on square root transformed species abundance data to assess the physical driving variable shaping isopod species community composition and species richness, respectively. Prior to analyses, environmental variables were normalised for comparability. A Detrended Correspondence Anlaysis (DCA) was performed to assess whether taxa responses were best explained by unimodal or linear models, thus to evaluate whether a Hellinger transformation was needed (*17*, *18*). DCA analysis showed that the gradient length of the first axis was greater than 2 (5.25 SD), therefore Hellinger transformation was performed on the dataset to perform the RDA. In addition, a Monte Carlo permutation test was performed to test the significance of the variation in species composition explained by environmental variables and individuate the most significant axis/axes (999 permutations). GLMs analysis was initially fitted with a Poisson distribution, in case over-dispersion the model was subsequently fitted with a quasi-Poisson regression. To check for over-dispersion, the library "qcc" for RStudio was used (*19*). While the RDA analysis was done using the library "vegan" on RStudio (*20*), the GLMs analysis was done using the function "glm ()" on the same software. Species record and environmental data are available from the Polar Data Centre under Di Franco et al. 2021 doi:10.5285/68315d6d-e7bf-4da0-a73a-5d6e0ba242a7.

3. Results and Discussion

The material analysed for our study comprised 37 epibenthic sledge samples collected on the shelf and upper slope of the South Atlantic sector of the SO (including the Weddell Sea) (Fig. 1b), comprising a total number of 214 species.

Among the 214 species recorded, 32% were exclusively found in sampling stations characterised by higher sea-ice concentrations (>0.5 fraction), 53% of which were species that are new to science and 75% were rare species characterised by very limited geographic distributions, including endemics. The reduction or total disappearance of sea-ice coverage is likely to make these species disappear with the risk that many others will get extinct before these are even discovered. Stations with higher sea-ice concentration (>0.5 fraction) presented a higher number of specialist species, e.g. four different species of the selective phytodetritivore family Macrostylidae Hansen, 1916 and seven selective deposit-feeding species belonging to the family Ischnomesidae Hansen, 1916, while only one species of Ischnomesidae and no macrostylids were found at stations of lower sea-ice concentrations. Locations with higher sea-ice concentrations showed a higher abundance of specimens of the specialist, sponge-commensal family Dendrotionidae Vanhöffen, 1914 compared to stations with low sea-ice concentration (137 and seven specimens respectively). This might be explained by a possible correlation with higher abundances of sponges in areas with higher sea-ice concentrations. A longer sea-ice duration was found to be positively correlated with the percent cover of sponges in seasonally ice-covered areas (*21*). In our study, areas with higher concentrations of sea ice and especially those in the southeast Weddell Sea showed the highest number of rare species and species previously known only from their type locality.

3.1. Sea-ice influence on isopod species richness and composition

While salinity, temperature, chlorophyll-a, current velocity, iron, oxygen and primary production did not show any correlation with isopod diversity (Fig. 1c), the number of isopod species increased with increasing sea-ice coverage (Fig. 1d).

The RDA analysis identified current velocity and sea ice as the environmental variables that best explained the variation in isopod species composition (Supplementary Table 1). Canonical axes explained 0,42 % of the variance and the permutation test showed that the first and second axes were the most significant (p = 0,001 and p = 0,002, respectively). These latter explained 0,15 % and 6,5 % of the variance, respectively (Supplementary Table 1).

The GLMs model showed sea ice and chlorophyll-a as the main variables driving species richness variations among sampling sites (p = 0,0025 and p = 0,011, respectively). The model was first fitted with Poisson distribution, however the latter indicated over-dispersion of the data (over-dispersion test p < 0,05), therefore the model was subsequently fitted with a quasi-Poisson regression. The model fit was tested using an ANOVA Chi-square test showing the statistical significance of the model (p = 0,000017 and p = 0,009, respectively).

The influence of sea-ice concentration on benthic species richness and composition shown in these results is explained by sea-ice dynamics and its seasonal break-up. When sea ice melts, large quantities of sympagic algae and animals are released, triggering phytoplankton blooms and thus enhancing the productivity in the column water and the amount of organic matter available for the benthos (*22–24*). In addition, sea-ice melting processes release freshwater, increasing the stratification of the water column that in turn enhances the amount of light availability and thus primary productivity (*25*, *26*).

To evaluate the robustness of our findings for biodiversity patterns in SO deep sea, we included a further 22 epibenthic sledge samples collected during ANDEEP (ANtarctic benthic DEEP-sea biodiversity, colonisation history and recent community patterns) expeditions from bathyal and abyssal depths of the study region (Fig. 1b), enlarging the dataset to a total of 763 nominal species. Again, the number of isopod species per station showed an increase with increasing sea-ice concentration (Fig. 1e). Especially the southeast Weddell Sea, a region characterised by high sea-ice concentration, had a much higher diversity of isopods than the northern region around the Antarctic Peninsula. GLM analysis indicated sea-ice concentration, iron, primary productivity and depth as the main environmental variables driving species richness between sampling stations. The influence of iron on species richness is related to the aforementioned sea-ice dynamics. Large quantities of iron accumulate in sea ice and are released when this latter break-up and melts; sea ice is considered as the dominant source of iron in Polar waters during seasonal melting (*27*). In the Southern Ocean, the growth of phytoplankton is strongly limited by the availability of iron (27, 28), thus large pulses of seasonal iron inputs through sea-ice melting highly increase the productivity in the water column (*29*). Despite the low sedimentation rate that characterises the deep sea (*30–32*) and the reduced quantity of organic matter reaching the seafloor (*33*, *34*), it has been shown that deep-sea benthic communities from abyssal depths can quickly react to phytodetritus pulses (*35–37*); although other studies did not show a clear response (*30*, *38*). It has been assumed that deep-sea isopod species probably present an opportunistic feeding strategy and mainly rely on seasonal pulses of fresh phytodetritus on the seafloor (*39*). Moreover, in the Southern Ocean the number of isopod species increases with depth, reaching the highest value of diversity at about 2000-4000 m (*40*).

A recent study identified sea-ice concentration as the main driver shaping the composition and abundance of SO peracarid orders (*41*). Our new findings expanded these analyses and identified for the first time the link between species richness and sea ice in the SO, highlighting the important role that sea ice plays as driver of benthic diversity. Higher diversity and number of rare/specialist species found in areas with higher sea-ice concentrations provide valuable insight to predict the consequences that a reduction in sea-ice extent would have on SO benthic communities.

Changes in sea-ice extent strongly affect the benthic fauna living underneath, due to changes in food availability and food-web structure (*9*, *21*, *42*); forcing benthic species to change their feeding habits, impacting highly adapted food specialists in favor of food generalist species, which will increase in abundance. In turn, increased abundances and biomass due to the reduction of sea-ice coverage can impact species richness. The theory of competitive exclusion suggests that higher productivity would alter the composition and balance of the benthic community, excluding species better adapted to the sea-ice zone (*43*, *44*). The prominent influence of sea ice on benthic communities was recently reported by Pineda-Metz et al. (*5*): the negative correlation between sea ice and primary productivity directly influence the abundance and biomass of the benthos, at decreasing levels of sea-ice coverage and increasing primary productivity abundances and biomass increase with a total gain of blue carbon. In 2021, Lin et al. showed the decline of plankton diversity with reduced sea ice extent in a study that investigated on genus level a five-year dataset of seven different genera of phytoplanktonic diatoms from the Western Antarctic Peninsula (*45*). However, our findings expand these analyses to the benthic ecosystem and to species level, investigating with the Atlantic sector of the Southern Ocean a much larger area. In contrast to the pelagic ecosystem where short-time environmental changes cause shifts in community composition (*46*), the benthic species are less affected by short-term changes in the overlying water column. The signal of isopod diversity decline with reducing ice concentrations in benthos is very compelling and concerning. Our results suggest that a reduction in sea-ice concentration would highly threaten the striking diversity of SO benthic isopod communities.

Future projections of climate warming suggest that this strong decline in sea ice will eventually affect the entire SO, threatening both regional and global biodiversity, due to the high levels of endemism in the SO (*47*). In a warming climate scenario (RCP 8.5), the SO could lose half of its sea-ice cover by 2100 (*48*) and the Eastern Weddell Sea could record the greatest sea-surface temperature anomaly with respect to preindustrial values (up to 3 °C by 2100) (*49*). More recently, despite the gradual increase of sea ice in the Weddell Sea since the early 1980s, long-term trends showed large multi-year variability, with a recent strong decline beginning in 2016 (*25*, *50*). Our findings suggest that this warming and loss of sea ice clearly endangers the biodiversity of the fauna living on the Weddell Sea continental shelf and deep sea.

Almost half of the sampling locations in the extended dataset including ANDEEP samples were from bathyal and abyssal depths (between ~1500 m and ~4900 m), suggesting that the retreat of sea ice can impact even the deepest parts of the SO. Changes are currently affecting the deep sea, the mean warming rate of the deep Weddell Sea below 2000 m is five times that of the global ocean (*51*). A possible reason to this trend is the variation in sea-ice coverage which can modify the heat loss from ocean to atmosphere and alter radiative fluxes. Recent studies showed the link between sea ice and deep-ocean circulation (*52*) and identified water masses and currents as important physical drivers affecting SO benthos (*53–56*). In the SO, the ANDEEP expeditions showed high level of isopod species diversity down to 5000 m and levels of diversity from 500 and 2000 m similar to those present in many temperate and tropical slopes in the Southern Hemisphere (*57*). The SO is a hotspot of biodiversity, it hosts 5% of the global marine biodiversity, despite representing only the 8% of global ocean surfaces (*58*). Some of the SO marine invertebrates highly contribute to the world´s species richness, for example SO holothurians represent 10% of the world´s holothuroid species diversity, SO pycnogonid are probably the most species-rich on the Planet, with 20% of their total known species found exclusively in Antarctic and/or Sub-Antarctic waters (*59*, *60*). SO benthic fauna shows remarkable level of endemism, for instance 70% of gastropods and pycnogonids and 88% of peracarid amphipods are endemic of the SO (*58*, *61*). In this latter, the main area investigated in this study (the Weddell Sea) is the region with the highest level of endemism (*58*); due to climate change and its consequent warming, 79% of SO endemic species face a reduction in suitable temperature habitat (*11*). Ultimately, it is worth mentioning that the SO diversity is probably still underestimated, for example more than 85% of the isopod species sampled during the ANDEEP expeditions in the SO deep-sea were new to science (*57*). In light of this and of our findings, it is possible to conclude that the remarkable species richness of the continental shelf and deep sea at the highest latitudes in the SO is highly threatened by climate change and the consequent loss of sea ice.

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Author contributions

D.D., K.L., H.G., A.B. developed, designed the study and collected the samples; D.D. and A.B. identified the isopod specimens and A.B. led the ANDEEP campaigns; D.D. performed the analyses and wrote the manuscript with the contribution and revision of all co-authors. All authors approved the final submission of the manuscript.

Competing interests

The authors declare no competing interests.

Fig. 1. Correlation between sea-ice concentration and benthic isopods in the Southern Ocean (SO). a, The exemplary benthic isopod species *Ceratoserolis trilobitoides* (Eights, 1833) from the Weddell Sea (SO). **b**, Map of the study area, pink circles show stations from the shelf and upper slope (expeditions JR275, JR15005, JR17003a and PS118); grey circles are stations from the deep-sea ANDEEP II-III expeditions; ice concentration is given using the unit interval

(fractions) from 0.1 to 1, where 0.1 indicates very low concentration/absence of ice and 1 indicates a completely ice-covered area. **c**, Pearson correlation analysis of environmental variables and isopod species number from the shelf and upper slope. **d**, Pearson correlation analysis of sea-ice concentration and isopod species number from the shelf and upper slope; **e**, Pearson correlation analysis of sea-ice concentration and isopod species number from the shelf, upper slope (pink circles) and deep-sea ANDEEP II-III expeditions (grey circles).

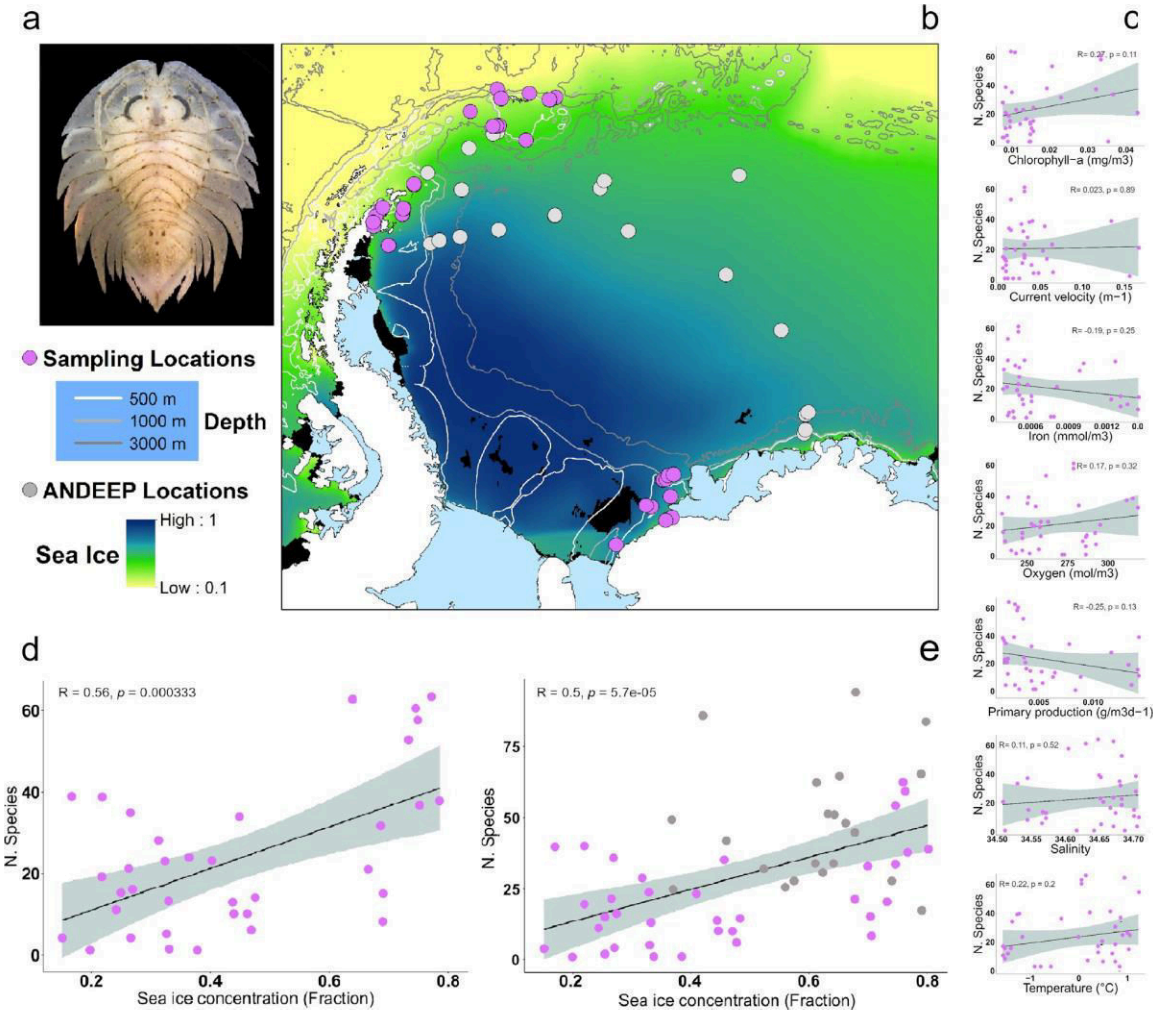

Table S1. RDA analysis on benthic isopod species from the continental shelf and slope of the Weddell Sea. Abbreviations: Chl-a = chlorophyll, Cv = current velocity, O2 = oxygen, Fe = iron, PP = primary productivity, Sal = salinity, Temp = temperature, Ice = sea-ice concentration.

Partitioning of variance

	Inertia	Proportion
Total	0.8085	1
Constrained	0.3374	**0.4173**
Unconstrained	0.4711	0.5827

Eigenvalues and their contribution to the variance

Importance of components

	RDA1	RDA2	RDA3	RDA4	RDA5	RDA6
Eigenvalue	**0.1234**	**0.05261**	0.04007	0.02633	0.02267	0.0224
Proportion	Explained	0.1527	0.06508	0.04956	0.03256	0.02804
Cumulative	Proportion	0.1527	0.21777	0.26733	0.29989	0.32793

Biplot scores for constraining variables

	RDA1	RDA2	RDA3	RDA4	RDA5	RDA6
Depth	-0.29229	-0.12082	0.22178	0.4524	-0.28958	-0.55053
Chl-a	-0.32279	0.56316	-0.18915	0.28004	0.17979	0.50116
Cv	**-0.50894**	-0.279	0.41653	-0.41117	0.03733	-0.42775
O2	-0.08966	0.58446	-0.60217	-0.04533	0.27598	0.16345
Fe	0.22983	0.14628	-0.54425	-0.11074	0.31719	0.34537
PP	0.35732	0.12019	0.07915	0.13504	0.24813	0.30047
Sal	-0.0979	-0.05678	-0.26161	0.01151	0.23913	0.31883
Temp	-0.33216	-0.37322	0.54346	0.01639	-0.36351	-0.01977
Ice	-0.21434	**0.65379**	-0.39022	0.16664	-0.43679	0.2141

6.5. Chapter V

Chapter V

Integrative taxonomy and whole genome sequencing of two new isopod species of the genus *Notopais* Hodgson, 1910 (Crustacea, Malacostraca) from the Southern Ocean

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Integrative taxonomy and whole genome sequencing of two newisopod species of the genus *Notopais* Hodgson, 1910 (Crustacea, Malacostraca) from the Southern Ocean

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Abstract

The genus *Notopais* Hodgson, 1910 is distributed in the Southern Hemisphere and comprises a total of 11 species. In the present study, we describe two new species of the genus, *Notopais sp.1* and *Notopais sp.2* using integrative taxonomy. The two species can be easily identified and distinguished from the other *Notopais* species by the spinal and tubercular pattern on the dorsal surface of their pereonites. The morphological distinction between the two new *Notopais* species was confirmed by a COI barcoding analysis, as well as by their different genome size of 1.44 Gb and 2.59 Gb and large differences in genomic heterozygosity (1.52%/0.70%). In the present work, we provide the first whole genome sequencing of isopod species from the Southern Ocean and the first mitochondrial genome of the genus *Notopais*.

Key words

Southern Ocean, Munnopsidae, genomic, barcode, new species

1. Introduction

The family Munnopsidae is the most abundant and diverse groups of deep-sea isopods. It comprises nine subfamilies and 42 genera, with more than 320 described species (WoRMS Editorial Board 2021), and it is frequently sampled in large numbers in the Southern Ocean (SO) (Brandt et al. 2004; Malyutina and Brandt 2007). In the last decade several new munnopsid species have been described on the basis of morphological characters (Malyutina and Brandt 2014; Malyutina 2015; Merrin 2016). The most comprehensive study on munnopsids based on genetic data was performed in 2009 by Osborn; the author investigated the phylogenetic relationship within the family Munnopsidae using three different genetic markers (18S, 28S and COI) (Osborn 2009). New genetic methodologies (e.g. DNA barcoding) revealed to be a very useful approach for the identification of species and a valid complement to the classic taxonomy based on morphological characters (Bucklin et al. 2011; Leray and Knowlton 2015). However, genetic analyses on SO munnopsids are not numerous due to the difficulties in obtaining high-quality DNA from the isopod specimens, as was shown in a recent study (Riehl et al. 2014). Among munnopsid genera, the genus *Notopais* has only been recorded in the Southern Hemisphere (Merrin 2004) with a total number of 9 formally described species. From the SO, to date the total number of formally described species known is five, comprising *Notopais beddardi* Merrin, 2004, *Notopais magnifica* (Vanhöffen, 1914), *Notopais quadrispinosa* (Beddard, 1886); *Notopais spicatus* Hodgson, 1910, and *Notopais spinosa* (Hodgson, 1902). Further *Notopais* specimens unassigned to known species are present in collections. Species of the genus *Notopais* are mainly distinguished by the presence/absence of spines on their pereonites.

To date, there have been no genetic studies on this genus; Osborn attempted to obtain genetic sequences of Notopais in 2009 without success (2009; Osborn´s personal communication).

The aim of our study is to describe two new species of the genus *Notopais* based upon morphological description and DNA barcoding, to expand the knowledge of the distribution of *Notopais* species in the SO. In addition, we provide data from the nuclear and mitochondrial genome of the two new species. This is the first study reporting the complete nuclear genome of isopods from the Southern Ocean and of the genus *Notopais*.

2. Material and Methods

2.1. Sampling

Samples were collected during the British Antarctic Survey (BAS) expeditions JR275 and JR15005 on board of the research vessel RRS *James Clark Ross*, in the Filchner Trough area, Weddell Sea, (2002) and in the South Orkney Islands (2016) respectively (Griffiths 2002, 2017) (Figure 1). While JR275 was part of the Evolutionary History (EvolHist) work package within BAS's Environmental Change and Evolution Programme (BAS), the expedition JR15005 was performed in cooperation with the Scientific Committee for Antarctic Research (SCAR) in the framework of the AntEco research program (SO-AntEco). *Notopais* specimens were collected using an epibenthic sledge (EBS) (Brenke 2005) and stored into precooled (-20°C) 96% ethanol. For later genetic studies, samples were retained in a -20°C freezer for 48 hours to reduce DNA degradation. Afterwards, they were stored at room temperature.

2.2. Identification and species description

The identification of the new species, taxonomic drawings and comparison with the other species of the same genus were performed using two stereomicroscopes, Leica M60 and Leica MZ8, both equipped with a camera lucida. Appendage drawings were prepared by means of an equally equipped Leica DM750 microscope. In total, ten specimens (Table S1) were used for the illustrations. Whilst the allotype and paratype of two formally undescribed species of *Notopais* were drawn in glycerine ($C_2H_8O_3$), their holotypes and the lectotypes of *N. magnifica* (Vanhöffen, 1914), *N. spicatus* (Hodgson, 1910), *N. spinosa* (Hodgson, 1902) and *N. quadrispinosa* (Beddard, 1886) were drawn in 96% ethanol (C_2H_4O). For the glycerine drawings, specimens were transferred into a 1:1 solution of glycerine and 96% ethanol. After the ethanol volatilized completely, appendages from allo- and paratypes were dissected and transferred onto slides with pure glycerine. Once line drawings were completed, they were digitalized using a Wacom Intuos drawing pad and Adobe Illustrator CS2 on a Toshiba Satellite C50 notebook, following Coleman's method (Coleman 2003). Holotypes were used to make the body descriptions, while the appendages were described from the para- and allotypes (Table S1). Subsequently, the width of pereonites 1-4 was measured from spine to spine, as well as the total body length from the frontal edge of the cephalon to the caudal tip of the pleotelson. The remaining measurements were taken following Hessler (Hessler 1970). The type material of the new, formally described *Notopais* species is held at the Senckenberg Research Institute and Natural History Museum in Frankfurt/M., Germany.

2.3. Comparative plate and biogeographic distribution

Specimens of *Notopais magnifica* (Vanhöffen, 1914), *Notopais spicatus* (Hodgson, 1910), *Notopais spinosa* (Hodgson, 1902) and *Notopais quadrispinosa* (Beddard, 1886) were used to make the comparative plate (Figure 2-3; Supplementary Table 1). These specimens were collected using an EBS on board RRS *James Clark Ross* during the expeditions JR275, JR15005 and JR 17003a (Linse 2018) performed in the Filchner Trough, the South Orkney Islands and the Prince Gustav Channel respectively. Coordinates and depths of the sampling locations were as follow: *Notopais magnifica*, between 60° 28.53'S – 44° 25.38'W and 60° 28.41'S – 44° 25.61'W (788 – 817 m respectively); *Notopais spicatus*, between 76° 10.01'S – 27° 48.23'W and 76° 09.94'S – 27° 48.44'W (549 – 539 m respectively); *Notopais spinosa*, between 63° 48.44'S – 58° 04.12'W and 63° 48.57'S – 58° 04.34'W (874 – 872 m respectively); *Notopais quadrispinosa*, between 75° 14.46'S – 27° 51.72'W and 75° 14.55'S – 27° 52.26'W (413 – 416 m respectively).

The distribution of the genus *Notopais* in the Southern Ocean shown in Figure 1 is based on data retrieved from the databases GBIF (Global Biodiversity Information Facility) (https://www.gbif.org/) (GBIF.org 2021) and OBIS (Ocean Biodiversity Information System) (https://obis.org/).

2.4. Genetic analysis

Genetic analyses were performed on two paratype specimens (one single specimen each) to preserve the integrity of the holotypes. The whole specimens had to be used for DNA isolation in order to obtain sufficient amounts of DNA. The paratype of *Notopais sp.1* n. sp. was an adult female from the Filchner Trough area, sampled between 77° 21.42'S – 35° 21.64'W and 77° 21.47'S – 35° 21.90'W at a depth range of 654 – 656 m respectively; the paratype of *Notopais sp.2* n. sp. was a manca (stage III) sampled in the South Orkney Islands between 62° 09.61'S – 44° 58.92'W and 62° 09.45'S – 44° 59.00'W (561 – 524 m respectively). The sex of this latter paratype could not be determined since the pleotelson was missing.

DNA was extracted from the two paratypes using an adaptation of the protocol by Miller et al. (Miller et al. 1988) for high molecular weight DNA extraction. The DNA samples were used for short read Illumina genome sequencing. One library with and insert size of 350 basepairs (bp) was prepared per species and 150 bp paired-end reads were sequenced on the Illumina NovaSeq 6000 platform (San Diego, CA). The short read data from both samples was analyzed the same way. A k-mer profile was generated from the raw reads using Jellyfish 2.3.0 (Marçais and Kingsford 2011) and analyzed in the GenomeScope 1.0.0 (Vurture et al. 2017). Raw reads were trimmed for low quality regions and adapter sequences and filtered for possible contamination using Trimmomatic 0.39 (Bolger et al. 2014) and Kraken 2.0.9 (Wood et al. 2019) respectively. Optimal k-mer length for de novo genome assembly was estimated using KmerGenie 1.7051 (Chikhi and Medvedev 2014). Subsequently the unclassified paired and unpaired reads were assembled using Velvet 1.2.10 (Zerbino and Birney 2008). Basic assembly statistics were determined using Quast 5.0.2 (Gurevich et al. 2013). Backmapping (a procedure where the reads used for the assembly are mapped again to the assembly) was performed with backmap.pl 0.3 (https://github.com/schellt/backmap), which utilized bwa mem 0.7.17-r1188 (Li 2013), samtools 1.10 (Li et al. 2009), Qualimap 2.2.1 (Okonechnikov et al. 2016), bedtools 2.28.0 (Quinlan and Hall 2010), R 4.0.3 (R Core Team 2020) and MultiQC 1.9 (Ewels et al. 2016). Possible contamination was identified with Blobtools 1.1.1 (Laetsch and Blaxter 2017) and screening for single-copy orthologs with BUSCO 4.1.4 (Simão et al. 2015) using the arthropoda_odb10 data set. From the initial assembly contigs originating from contamination (either taxonomic assignment to bacteria, virus and/or coverage < 10 and GC>0.5) or the mitochondrial genome were filtered out. Afterwards, the quality checks (BUSCO, backmap, blobtools) were repeated as described above.

The mitochondrial genomes were assembled using first, MitoZ 2.3 om a 3 Gb subset of unclassified read pairs that stayed at 150 bp full length after trimming each. Since these assemblies were insufficient, the longest sequence of a protein coding gene from MitoZ was used as seed in NOVOPlasty 4.2 (Dierckxsens et al. 2017). Annotations of the mitochondrial genomes were manually merged and curated in Geneious Prime 2021.1.1 (https://www.geneious.com) using automated annotations from MITOS2 (Donath et al. 2019) and GeSeq (Tillich et al. 2017).

CO1 sequences of the two new *Notopais* species were compared to sequences of selected marine isopods of the same family (Munnopsidae) available in GenBank (Table 1). Sequences were aligned with MUSCLE (Edgar 2004) as implemented in the software AliView 1.26 (Larsson 2014) and manually inspected. A phylogenetic analysis was done using maximum likelihood (ML) using the CO1 sequence alignment with IQ-TREE 1.6.12 (http://www.iqtree.org/) (Minh et al. 2013; Nguyen et al. 2015; Trifinopoulos et al. 2016). Ultrafast bootstrap analysis was used to assess for node support (Minh et al. 2013; Hoang et al. 2018), this latter was tested using SH-aLRT branch test based on 1000 replicates. The phylogenetic tree was visualized using FigTree 1.4.4 (available at http://tree.bio.ed.ac.uk/software/figtree/).

3. Results

3.1. Taxonomy Munnopsidae Lilljeborg, 1864Ilyarachninae Hansen, 1916 *Notopais* Hodgson, 1910

Notopais Hodgson, 1910: 69.— Merrin, 2004: 3–4.— Merrin, 2007: 131–132. Type species *Notopais spicatus* Hodgson, 1910, by monotypy.

Diagnosis (updated from Merrin, 2004): Slender cephalon with frons, leading to an almost horizontal appearance of the maxillipeds *in situ* in lateral view. Anterior margins of pereonites 1-4 with spines or with robust setae; spines always tipped with robust (pedestal) setae, making them appear more pointed. Horn-like distinctive spine and a varying number of terminal robust setae on article 1 of antenna 2. Without mandible palp; large incisor processes, rounded; reduced or absent *lacinia mobilis.* Carpus and propodus of pereopods 5 and 6 flat, expanded, with plumose setae on the margins. Ambulatory pereopods 7 robust, with plumose setation similar to that of pereopod 5 and 6. Biramous uropods (Merrin, 2004).

Description of the genus: Body solid; frons of cephalon broad, oblong, ventrally flattened, leading to a nearly horizontal appearance of the maxillipeds in lateral view; pereonites 1–4 anterior margins usually with spines, if not, margins with short stiff setae; robust (pedestal) setae on top of every spine; natasome streamlined, not reduced; pleon without anterolateral spines. Antennae positioned closely together; Antenna 2 article 1 distolateral with at least one horn-like spine and a varying numberof terminal robust setae Mandible with or without spine row, calcareous; *Lacinia mobilis absent or reduced*; palp absent; large, curved incisor processes, without teeth.Non-enlarged ambulatory pereopod 2, prolonged ischium; pereopods 5 and 6 natatory, carpus paddle-shaped, flat; propodus expanded, flat; dactyli distally narrowing; ischium, carpus and propodus with large plumose setae; ambulatory pereopod 7, robust, long, similar plumose setation as in pereopod 5 and 6. Pleon vaulted, in dorsal view triangular. “Operculum vaulted” (Merrin 2007, p.62), bearing a distinctive medial keel. Exopod of pleopod 4 with one or more plumose setae. Uropods biramous (Merrin 2004, 2007).

Remarks: *Notopais* can be recognized by the mouthparts, which appear plane *in situ*, the anterior marginal spines or robust setae on pereonites 1-4, the long and plumose setation of pereopod 5-7, as well as the horn-like spine on article 1of antenna 2, which is distinct and unique for this genus, as well as the biramous uropods (Merrin 2004).

Notopais and *Echinozone* G. O. Sars, 1897 differ in body shape, which is more vaulted in *Echinozone* than in *Notopais*. Besides, *Notopais* can be distinguished from *Echinozone* by the cephalon (narrower in *Notopais*), the presence of pedestal setaeand the exclusive shape of the spine on antenna 2 article 1. This spine resembles a “bull´s horn” (Merrin 2004 p.4) and it is tipped with a robust seta, making it appear more pronounced (Merrin 2004).

Composition: *Notopais quadrispinosa* (Beddard, 1886); *Notopais spinosa* (Hodgson, 1902); *Notopais spicatus* Hodgson, 1910; *Notopais magnifica* (Vanhöffen, 1914); *Notopais minya* (Merrin, 2004); *Notopais zealandica* (Merrin, 2004); *Notopais* *beddardi* (Merrin, 2004); *Notopais echinatus* (Merrin and Bruce 2006); *Notopais euaxos* (Merrin and Bruce 2006).

The genus *Notopais* is restricted to the Southern Hemisphere, ranging from the SO to the South-eastern continental slope of Australia. It has been found at depths between 36 - 1640 m (Merrin 2007).

***Notopais sp.1* Di Franco, Krüger & Brandt, 202x (Figures 4-7)**

Diagnosis of the new species: Pereonites 1-3 with spines on the anterior margin. Pereonites 4-7 without anterior marginal spines, smooth. Pereonites 1-4 laterally with few small spines. Pereonite 4 dorsally with four tubercles, inner pair with two spines. Pereonite 6 with two tubercles. Cephalon with two large spines.

Material examined: *Holotype*: female (4.75 mm), Filchner Trough, Weddell Sea, Antarctica, 75°14.46'S – 27°51.72'W, 413 – 416 m, 4 March 2012, RRS *James ClarkRoss; allotype:* male (6.1 mm), Filchner Trough, Weddell Sea, Antarctica, 75°45.72'S –30°26.56'W, 428 – 440 m, 22 February 2012, RRS *James Clark Ross; paratype:* female (7.3 mm), same locality as holotype.

Description of the female

Body (Figure 4, A,B). Body length 4.75 mm; 2.3 as long as pereonite 3 (the widest pereonite, from spine to spine); highly setose.

Cephalon (Figure 4, A-E). Lightly setose, with two dorsal spines; anterolateral margins with two small spines; posterolateral margins rounded; ridge encompassing antennae, with no extension.

Pereonites (Figure 4, A, B). Pereonites 1 and 2 anterior margins each with four well developed spines; pereonite 3 with two well developed anterior marginal spines and one small spine; pereonite 4 anterior margin smooth with four dorsal tubercles, inner pair of tubercles with two small spines; pereonite 5 anterior margin smooth; pereonite 6 with two dorsal tubercles; pereonite 5-7 anterolateral margins pointing towards cephalon; pereonites 1 and 2 each with pair of widely spaced, small, dorsal spines near lateral margins; pereonites 3 and 4 each with one small, dorsal spine near lateral margin.

Antenna 1 (Figure 4, E). Antenna 1 of six articles, 3 penduncular, one small ring- like article and 2 flagellar ones; article 1 distally triangular, 2.3 times as long as wide, distal margin with one robust and one broom seta; article 2 0.3 times as long as article 1, 2.3 times as long as wide, distal margin with two robust seta and one broom seta; article 3 without setae; flagellar article 6 with one distal aesthetasc.

Antenna 2 (Figure 4, A-D). Article 1 and 2 of antenna 2 broken; article 1-3 more or less triangular, each wider than long; article 1, distolateral angle with three spines; article 2 0.7 times as long as article 1, distolateral angle with one spine; article 3 1.3 times as long as article 1, distolateral angle with one spine and two simple setae, distomedial margin with one short robust seta and seven long robust setae; article 4
1.7 times as long as article 1, distomedial margin with one simple seta.

Mandible (Figure 5, A, B). Left mandible slightly broader than the right mandible; mandible with four simple setae on mesial margin, spine row absent; molar small, terminated with six short simple setae.

Maxilla 1 (Figure 5, C). Lateral lobe 2.4 times as wide as medial lobe, lateral marginwith 13 fine simple setae, distal margin with four fine simple setae and 11 robust setae; mesial lobe with three fine simple setae on mesial margin, distal margin with two robust setae and 14 fine simple setae.

Maxilla 2 (Figure 5, D). Lateral lobe with ten fine simple setae, distally with two smaller and two long simple setae; middle lobe 0.7 times as wide as lateral lobe, distally with two long simple setae; mesial lobe 1.6 times as wide as lateral lobe, mesial margin with 13 fine simple setae, terminated with 13 long simple setae and three short simple setae.

Maxilliped (Figure 5, E). Coxa more or less rectangular, small, 0.4 times as long as wide, 0.2 times as long as basis (including endite); basis elongate, length including endite 2.6 times as long as wide; endite distally with six fan setae (five large, one small), and many fine simple setae; palp wider proximally, tapers distally, article 1 wide, rectangular, shortest, 0.2 times as long as basal endite, anteromesial marginwith one simple seta, article 2 5.1 times as long as, and 1.4 times as wide as article 1,
1.5 times as wide as basal endite; article 3 3.7 times as long as, and 0.9 times as wide as article 1article 4 almost rectangular, 2.5 times as long as, and 0.4 times as wide as article 1; article 5 small, narrowest of all articles, 1.1 times as long as, and 0.2 timesas wide as article 1; epipod elongate, 1.0 times as long as, and 1.9 times as wide as

basis length (including endite).

Pereopods (Figure 6, A, C, D). *Pereopod 1* basis 7.2 times as long as wide, ventral margin with 13 simple setae, dorsal margin with one simple seta; ischium 6.6 times as long as wide, dorsal margin with 11 simple setae; merus 1.4 times as long as wide, ventral margin with ten simple setae, distodorsal margin with one robust and one simple seta; carpus 4.8 times as long as wide, ventral margin with nine long simple setae; propodus 6.8 times as long as wide, ventral margin with nine simple setae, dorsal margin with five simple setae in distal corner; dactylus 5.7 times as long as medial width, distodorsal margin with one simple seta.

Pereopod 6 basis 3.1 times as long as wide, ventral margin with eight robust setae and seven simple setae, dorsal margin with nine simple setae; ischium 3.4 times as long as wide, ventral margin with seven sub-marginal simple setae, dorsal margin with 20 long plumose setae; merus 1.2 times as long as wide, ventral margin with five simple setae and three robust setae, dorsal margin with two simple setae in distal half; carpus 1.4 times as long as wide, ventral margin with 24 long plumose setae, dorsal margin with 42 long plumose setae; propodus slightly expanded, 4.9 times as long as wide, ventral margin with 20 long plumose setae, dorsal margin with 26 long plumose setae; dactylus 13 times as long as medial width, dorsal margin with four long simple setae.

Pereopod 7 basis 5.8 times as long as wide, ventral margin with seven simple setae and two sub marginal simple setae in distal half, dorsal margin with four simple setae; ischium 3.6 times as long as wide, distoventral margin with two simple setae, dorsal margin with two simple setae and one broom seta in proximal half; merus distodorsal margin cup-shaped, 2.2 times as long as wide; carpus 5.4 times as long as wide, ventral margin with three simple setae and at least ten long plumose setae, dorsal margin with 30 long plumose setae; propodus ventral margin with four simple setae in distal half, dorsal margin with three simple setae; dactylus with five simple setae on distal end.

Pleotelson (Figure 4, A, B). 0.7 times as long as proximal width, posterior tip rounded, with scattered simple setae.

Operculum (Figure 7, A). Large, 2.2 times as long as proximal width, distally with medial slit, median keel provided with three robust setae (broken), entire surface with scattered fine simple setae, lateral margins with numerous long plumose setae.

Pleopod 3 (Figure 7, D). Exopod narrowing, 1.0 times as long as endopod, with row of fine simple setae and distally with six long plumose setae; endopod 2.7 times as long as wide, with ten long plumose setae.

Pleopod 4 (Figure 7, E). Exopod slender, shorter than endopod, with its distal point at 0.6 times length of endopod, with five terminal long plumose setae; endopod oval, 1.5 times as long as wide.

Pleopod 5 (Figure 7, F). Oval, 1.9 times as long as wide.

Description of the male

Body. Body length 6.1 mm, widest at pereonite 3; similar to female in shape and setation.

Cephalon. Lightly setose, less bulk than in female, with two dorsal spines; anterolateral margins with one small spine; posterolateral margins rounded, similar tofemale.

Pereonites. Shape similar to female, but spines are smaller.

Antenna 1 (Figure 4, F). Broken at article 3, article 1 distal end triangular, 2.0 times as long as wide distal margin with one robust and one broom seta as in female; article 2 0.3 times as long as article 1, 2.0 times as long as wide, distal marginwith only one robust seta and one broom seta; article 3 rectangular, longer than article2.

Pereopod 1 (Figure 6, B). Basis 6.4 times as long as wide, ventral margin with 21 simple setae, dorsal margin with 11 simple setae; ischium 7.0 times as long as wide, dorsal margin with only eight simple setae (scattered), lateral surface with foursimple setae, distoventral margin with three simple setae; merus 1.5 times as long as wide, ventral margin with 11 simple setae (varying in length, scattered), distodorsal margin only with one robust seta; carpus 3.7 times as long as wide, ventral margin with only eight long simple setae in proximal half and one long simple seta on dorsal margin; propodus 7.2 times as long as wide, lateral surface with 17 long simple setae in distoventral half and five long simple setae in distodorsal half; dactylus 6.6 timesas long as medial width, distodorsal margin with three simple setae.

Pleopod 1 (Figure 7, B). 2.8 times as long as proximal width, lateral margins indent 0.2 from distal end, either side of centre margin with 27 simple setae (11+16) in proximal half, distally with pair of lobes which go over distolateral horns, with 27 simple setae (14+13).

Pleopod 2 (Figure 7, C). Sympod 3.6 times as long as wide, lateral margin with 28 long plumose setae (one broken), eight short simple setae in distolateral half; exopod elongate, length 0.1 times as long as sympod; stylet elongate 0.7 times as long as sympod, terminating to a point; sperm duct 0.4 times as long as stylet.

Remaining appendages: Same as in female.

Remarks: *N. sp.1* is the only described SO species of *Notopais* not having any dorsal spines on pereonite 4, except for the two small spines on top of the inner pair of the four tubercles. Together with the two tubercles on pereonite 6, these features are autapomorphic for the new species. *Notopais sp.1* shares some characters with *N. quadrispinosa* (Figure 4E, Figure 5E), the spines are also set on the edge of the anterior margins and are less acutely angled as in *N. spicatus* (Figure 4B, Figure 5B). However, it neither has any spines on the fifth pereonite which are similar to those of

N. beddardi (Merrin, 2004), nor a row of short stout setae, which are characteristic for this species. Moreover,

Distribution: Filchner Trough, south eastern Weddell Sea, Antarctica.

Etymology: The proposed name for *N. sp.1* (*Notopais criophyla*) is related to the ecology of this species, since it was mostly found at stations with cold ice-shelf water, therefore it may have a high affinity with very low temperatures. Cryo is the Latinized form of the Ancient Greek word *kryos* meaning “icy cold” and phila, derived from the Ancient Greek word *phileo* which stands for “having affection for”.

Notopais sp.2 Di Franco, Krüger & Brandt, 202x (Figures 8-11)

Diagnosis of the new species: Pereonites 1-5 with spines on the anterior margin. Pereonite 4 with large dorsal spines. Pereonites 6 and 7 without spines. Pereonites 1-4 each with one pair of small spines laterally. Pereonite 5 and 6 with two tubercles dorsally. Cephalon with two large spines and two small sub-marginal spines in anterolateral half.

Material examined: *Holotype*: female (4.9 mm), South Orkney Islands, Antarctica, 62°09.61'S – 44°58.92'W, 500 - 760 m, 6 March 2016, RRS *James Clark Ross;*
allotype: male (4.0 mm) and *paratype*: female (4.7 mm) both from same locality as holotype.

Description of the female

Body (Figure 8, A,B). Body length 4.90 mm; in total 2.1 times as longer as the greatest width (from spine to spine) of widest pereonite; widest at pereonite 4.

Cephalon (Figure 8, A-E, G). With two dorsal spines and one small sub marginal spine on each side in antero-marginal half; posterolateral margins rounded; ridge encompassing antennae, with no extension.

Pereonites (Figure 8, A, B). Pereonites 1-3 anterior margins with continuous row of spines; pereonite 4 with four small anterior marginal spines and six well developed anteriorly directed dorsal spines; pereonites 1-4 each with pair of widely spaced, small, dorsal spines near lateral margins; pereonite 5 with four spines on anterior margin; pereonite 5 and 6 dorsally with two tubercles; pereonite 5-7 anterolateral margins pointing towards cephalon.

Antenna 1 (Figure 8, E). Antenna 1 of 9 articles (number of articles, that were actually visible); article 1 1.7 times as long as wide, distal margin rectangular, with one robust and one broom seta; article 2 0.3 times as long as article 1, 1.6 times as long as wide, distal margin with one broom seta; article 4-8 each with one simple seta; article 9 distally with two fine simple setae and two aesthetascs.

Antenna 2 (Figure 8, A-D, G). Article 1 and 2 more or less triangular, both wider than long; article 3 pentagonal, longer than wide; article 1 lateral margin with three spines; article 2 0.6 times as long as article 1, distomedial margin with one broom seta; article 3 1.2 times as long as article 1; article 4 1.0 times as long as article 1;
article 5 3.6 times as long as article 1; article 6 8.0 times as long as article 1; flagellum of 56 articles, distalmost article with two aesthetascs.

Mandible (Figure 9, A, B). Left mandible slightly broader than the right mandible; mandible with four simple setae on mesial margin, spine row absent; molar small, terminated with six long simple setae.

Maxilla 1 (Figure 9, C). Lateral lobe 2.0 times as wide as medial lobe, distal margin with six fine simple setae, two robust dentate setae and eight robust setae; mesial lobe with three fine simple setae on mesial margin, distal margin with two robust setae and 13 fine simple setae.

Maxilla 2 (Figure 9, D). Lateral lobe with ten fine simple setae on lateral margin, distally with four long simple setae (same length); middle lobe 1.2 times as wide as lateral lobe, lateral margin with four simple setae, distally with two long simple setae (one shorter than the other); mesial lobe 3.0 times as wide as lateral lobe, mesial margin with 15 long, fine simple setae, lateral margin with ten short, fine simple setae, terminating with ten long simple setae and three short simple setae.

Maxilliped (Figure 9, E). Coxa rectangular, 1.2 times as long as wide, 0.4 times as long as basis (including endite); basis elongate, length including endite 3.1 times as long as wide, setae; endite with five coupling hooks on mesial margin, distally with four fan setae and many fine simple setae; palp wider proximally, tapers distally, article 1 wide, rectangular, shortest, 0.2 times as long as basal endite; article 2 5.3 times as long as, and 1.3 times as wide as article 1, 1.8 times as wide as basal endite; article 3 2.0 times as long as, and 0.9 times as wide as article 1; article 4 heart shaped,
2.2 times as long as, and 0.5 times as wide as article 1;article 5 rectangular, narrowest of all articles, 1.5 times as long as, and 0.2 times as wide as article 1; epipod elongate, 1.1 times as long as, and 1.5 times as wide as basis length (including endite).

Pereopods (Figure 10, A, C). *Pereopod 1* basis 8.5 times as long as wide, dorsal margin with three distal robust setae; ischium 6.5 times as long as wide, dorsal margin with two simple setae, ventral margin also with two simple setae; merus 1.4 times as long as wide, ventral margin with five simple setae, distodorsal margin with one simple seta, and distal margin with one robust seta; carpus 5.2 times as long as wide, ventral margin with seven long simple setae, two simple setae on dorsal margin, and one long simple seta on distodorsal margin; propodus 7.5 times as long as wide, ventral margin with 13 simple setae, dorsal margin with four simple setae in distal corner; dactylus 5.3 times as long as proximal width, distodorsal margin with one simple seta.

Pereopod 6 basis 2.8 times as long as wide, ventral margin with five robust setae, five simple setae and two fine simple setae, dorsal margin with four long simple setae; ischium 2.6 times as long as wide, ventral margin with four simple setae in distal half and three fine simple setae in proximal half, dorsal margin with 16 long plumose setae; merus 0.9 times as long as wide, ventral margin with six simple setae; carpus 1.1 times as long as wide, ventral margin with 20 long plumose setae; propodus elongated, 8.1 times as long as wide; dactylus six times as long as proximal width, lateral surface with two simple setae in distodorsal corner.

Pleotelson (Figure 8, A, B). 0.6 times as long as proximal width, posterior tip rounded, lateral margins with ventrally facing robust setae.

Operculum (Figure 11, A). Large, 2.2 times as long as proximal width, distally with medial slit, median keel provided with nine robust setae (five broken), lateral margins with numerous long plumose setae.

Pleopod 3 (Figure 11, D). Exopod narrowing, 1.2 times as long as endopod, distally with eight long plumose setae (varying in length); endopod 2.2 times as long as wide, with six long plumose setae.

Pleopod 4 (Figure 11, E). Exopod slender, shorter than endopod, with two terminal long plumose setae; endopod oval, 1.7 times as long as wide.

Pleopod 5 (Figure 11, F). Oval, 1.8 times as long as wide.

Description of the male

Body. Body length 4.0 mm, widest at pereonite 3; similar to female in shape, but smaller and narrower than in female.

Cephalon. With two dorsal spines; posterolateral margins rounded, similar to female.

Pereonites. Shape similar to female, but spines and tubercles are smaller.

Antenna 1 (Figure 8, F). Antenna 1 of 11 articles (number of articles that were actually visible); article 1 distal end more rounded than rectangular, 1.7 times as long as wide, distal margin with one robust and one small simple seta instead of onebroom seta as in female; article 2 0.3 times as long as article 1, 1.4 times as long as wide, distal margin with one robust seta instead of one broom seta; remaining articles rectangular, varying in length; last article with one aesthetasc on distal margin.

Pereopod 1 (Figure 10, B). Basis 5.2 times as long as wide, dorsal margin with only one distal robust seta; ischium 6.1 times as long as wide, dorsal margin without setae; merus 1.4 times as long as wide, ventral margin only with four simple setae, distodorsal margin with two simple setae, distal margin without robust setae; carpus 5.3 times as long as wide, ventral margin with only four long simple setae in proximal half, no simple setae on dorsal margin; propodus 5.6 times as long as wide, ventral margin with only 11 simple setae, dorsal margin without simple setae; dactylus 3.5 times as long as proximal width, distodorsal margin with four simple setae, distoventral margin with one simple seta and proximal end of ventral margin with one simple seta.

Pleopod 1 (Figure 11, B). 3.7 times as long as proximal width, either side of center margin with ten simple setae (5+5) in proximal half, distally with pair of lobes which go over distolateral horns, with four simple setae (2+2).

Pleopod 2 (Figure 11, C). Sympod 2.8 times as long as wide, lateral margin with 20 long plumose setae (nine broken), and distolateral margin with five fine simple setae; exopod elongate, length 0.1 times as long as sympod, with one plumose seta; stylet 0.3 times as long as sympod, terminating to a point; sperm duct 0.5 times as long as stylet.

Remaining appendages: Same as in female.

Remarks: *Notopais sp.2* shares some traits with *N. magnifica* (Figure 4A, Figure 5A), as it also has continuous rows of spines on the anterior margins of pereonites 1-3. Besides, *N. magnifica* shows anterior marginal spines and dorsal spines on pereonite 4, although these are only two instead of six. *N. quadrispinosa* (Figure 4E, Figure 5E) and *N. spinosa* (Figure 4D, Figure 5D) also show sub-marginal spines, however, both have only four of them. Moreover, *N. quadrispinosa* has no anterior marginal spines, while *N. spinosa* shows sub marginal spines only on the posterior margin. These spines in *N. sp.2* are situated more medial and much larger. Although *N. sp.2* bears four anterior marginal spines on pereonite 5 like *N. spicatus*, *N. spinosa* and *N. quadrispinosa* (Figure 4, Figure 5), the presence of two tubercles on its pereonite 5 is an unique feature. Besides, it presents two additional tubercles on pereonite 6 as solely seen in *N. sp.1*, which makes them the only described species of *Notopais* from the Southern Ocean with this feature.

Distribution: South Orkney Islands, Antarctica.

Etymology: *Notopais sp.2* has a large number of spines, a shape resembling a star. Derived from the Latin words *stella polaris*, meaning “pole star”, *N. polaris* sp. nov. is the proposed name for the species.

3.2. Genetic results

3.2.1. Whole genome sequencing and assembly

Illumina sequencing yielded 573,110,218 reads for *Notopais sp.1* and 624,723,258 reads for *Notopais sp.2*. K-mer analysis estimated the genome size of *Notopais sp.1* to 1.44 Gb and 2.59 Gb for *Notopais sp.2*. The genomic heterozygosity in *Notopais sp.1* was 1.52%, while in *Notopais sp.2* it was 0.70%.

The mitochondrial genomes were assembled into one linear sequence each as neither MitoZ nor NOVOPlasty were able to circularize them (21,955 bp *Notopais sp.1*; 19,878 bp *Notopais sp.2*). All expected 13 protein coding genes, 2 rRNAs could be annotated on each of the mitochondrial genome sequences. For *N. sp.1* all 20 different expected tRNAs could be annotated of which 8 were found more than once (37 in total). In *N. sp.2*´s mitochondiral genome one of the 20 expected tRNAs (Isoleucine) was not found and 4 tRNAs are annotated at least twice (27 in total).
The final nuclear *Notopais sp.1* genome assembly contained 544,079 contigs with a total length of 535,477,874 bp. The genome size was estimated to 1.12 Gb and heterozygosity to 1.53% based on k-mers. The back-mapping rate was as high as 98.54% and the genome sequence coverage of the holotype specimen was uniformly distributed at ca. 43X. The BUSCO search resulted in 43.3% present BUSCO loci (C:15.5%[S:15.4%,D:0.1%],F:27.8%,M:56.7%,n:1013).

The final nuclear *Notopais sp.2* genome assembly contained 448,606 contigs with a total length of 609,453,175 bp. The genome size was estimated to 2.08Gb and heterozygosity to 0.713% based on k-mers. The back-mapping rate was as high as 98.59% and the genome sequence coverage of the holotype specimen was uniformly distributed at ca. 25X. The BUSCO search resulted in 58.9% present BUSCO loci (C:21.7%[S:21.7%,D:0.0%],F:37.2%,M:41.1%,n:1013).
The Genbank accession numbers of the mitochondrial genomes are JAJNBS000000000 and JAJNBT000000000 for mitochondrial gene rearrangements of *Notopais sp.1* n.sp. and *N. sp.2* n. sp. respectively.

3.2.2. Phylogenetic results

The CO1 alignment of 20 species of Isopoda (Table 1) was 643 nt. ML analyses reconstructed a phylogeny where *Notopais sp.1* and *Notopais sp.2* are sibling species with 99.8/100% support (Figure 12). The internal nodes in the phylogeny received very low support values between 7.7-99.8% likely reflecting the deep evolutionary relationship between the species. Pairwise distance estimation using the K2P model calculated that the two new species of *Notopais* have 23.8% sequence distance. Thus, the phylogenetic analysis supports the morphological distinction between the two new *Notopais* species.

4. Discussion

The genus *Notopais* is exclusively distributed in the Southern Hemisphere (Merrin 2004), from New Zeland (*Notopais zealandica* Merrin, 2004, *Notopais euaxos* Merrin and Bruce, 2006) and the Eastern Australia (*Notopais echinatus* Merrin and Bruce, 2006, *Notopais minya*, Merrin 2004) to the South Indian Ocean (*Notopais beddardi*, Merrin 2004, *Notopais quadrispinosa* (Beddard, 1886), *Notopais spicatus* Hodgson, 1910) and the Southern Ocean (*Notopais magnifica* (Vanhöffen, 1914), *Notopais spinosa* (Hodgson, 1902), *Notopais quadrispinosa* (Beddard, 1886), *Notopais spicatus* Hodgson, 1910). SO *Notopais* species present a Circumpolar distribution (Brandt 1990), while the two new *Notopais* species described in the present study are only known from their type locality. Given the brooding nature of isopod crustaceans and thus their low dispersal ability, one of the possible explanation for the circumpolar distribution of this genus is the possible presence of a seaway that connected the Weddell Sea and the Ross Sea in the Late Quaternary (Barnes and Hillenbrand 2010; Pierrat et al. 2013).

Integrative taxonomy analysis provides evidence for two new *Notopais* species from the Southern Ocean based morphologic differences as well as molecular phylogenetics. The two species were subjected to a thorough morphological characterization as well as whole genome sequencing. The obtained sequence data is the first whole genome draft assemblies from the deep sea Munnopsidae as well asthe first mitochondrial sequences from the genus *Notopais*. Findings provide significant support that the two new *Notopais* should be considered species and are distantly related.

The reported threshold values to delineate intraspecific divergence for isopods are usually below 5%, while 5-10% indicate closely related species, and >18% should be considered distantly related species (Brix et al. 2011). Based on the COI mitochondrial gene, the two new *Notopais* species had a pairwise distance of 23%. The distinction between the two species was also confirmed by their different genome size of 1.44 Gb and 2.59 Gb as well as large differences in genomic heterozygosity (1.52%/0.70%). This indicates that the two *Notopais* species are significantly distinct on the molecular level and that the observed morphological differences are not due to phenotypic adaption.

So far no mitochondrial sequences have been published from the genus *Notopais*. Genetic analyses were previously performed on this genus in (Raupach et al. 2004, 2007, 2009), however no COI sequences were analyzed. We tried to obtain COI sequences from the two new *Notopais* species using protocol, universal primers and other COI primers as described in Riehl et al. (Riehl et al. 2014) without success. DNA barcoding and the use of the COI gene is a successful and widely used tool for the identification of many species in association with classical taxonomy (DeSalleand Goldstein 2019). But it has become evident that the identification of speciesbased on the COI can be problematic, the evolutionary rate of COI varies highly between taxa and for this reason this gene marker has failed for a wide range of marine invertebrates (Rach et al. 2017); frequently, the universal primers designed for the COI region by Folmer et al. (Folmer et al. 1994) are replaced with primers that are specific for a certain taxon (Rach et al. 2017). In genetic studies of isopods, universal primers are very often used in association with other COI primers (Brix et al. 2011, 2014; Riehl et al. 2014; Kaiser et al. 2018; Bober et al. 2019). It has been shown that in the Munnopsidae family the universal primers for COI can have a rate of success of about 50%, lower than that of the mitochondrial 16S rRNA gene (Riehl et al. 2014).

The use of next generation sequencing techniques can generate both complete genome and mitochondrial genome sequences. Such information can solve the issueof finding working primers for certain taxa and provides additional genetic information compared to those obtained from traditional mitochondrial barcoding markers such as COI or 16S. Due to this limitation, Köhler et al. proposed to add genome data for the genetic characterization of holotype specimens, suggesting to use a low-coverage short-read based genome sequence given that the costs for this analyses have significantly decreased (Köhler et al. 2021). Recent studies on the complete mitochondrial genomes revealed to be very promising and useful for the systematic and phylogenetic reconstruction of marine isopods (Kilpert and Podsiadlowski 2006; Shen et al. 2017; Yu et al. 2018). In line with the aforementioned authors, we suggest that whenever possible, the use of a complete mitochondrial genome, or a draft genome assembly, in association with the holotype species description should be considered for isopods. However, it is not always possible to obtain large amounts of DNA from tissue samples. Concerning deep-sea isopods, for example, it is difficult to obtain fresh material due to their remote habitat and issues on their DNA extraction and amplification were frequently reported,possibly due to active nucleases that quickly digest the DNA (Raupach et al. 2004; Raupach and Wägele 2006; Brix et al. 2011; Riehl et al. 2014). Although recent developments in next-generation technologies allow using a small amount of DNA, often it is necessary to destroy the whole specimen of small animals. However, given the taxonomic importance of holotype specimens, we suggest using paratype specimens whenever it is not possible to obtain sufficient amounts of DNA and to prevent the destruction of holotype material.

Our results provide the first nuclear and mitochondrial draft assemblies of isopods from the Southern Ocean. This represents the first step for a more comprehensive genetic characterization of holotype specimens that will facilitate researchers in obtaining systematic and phylogenetic information on Southern Ocean isopods.

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Figure 1. Map of *Notopais* species distribution in the Southern Ocean, based on Gbif and OBIS databases.

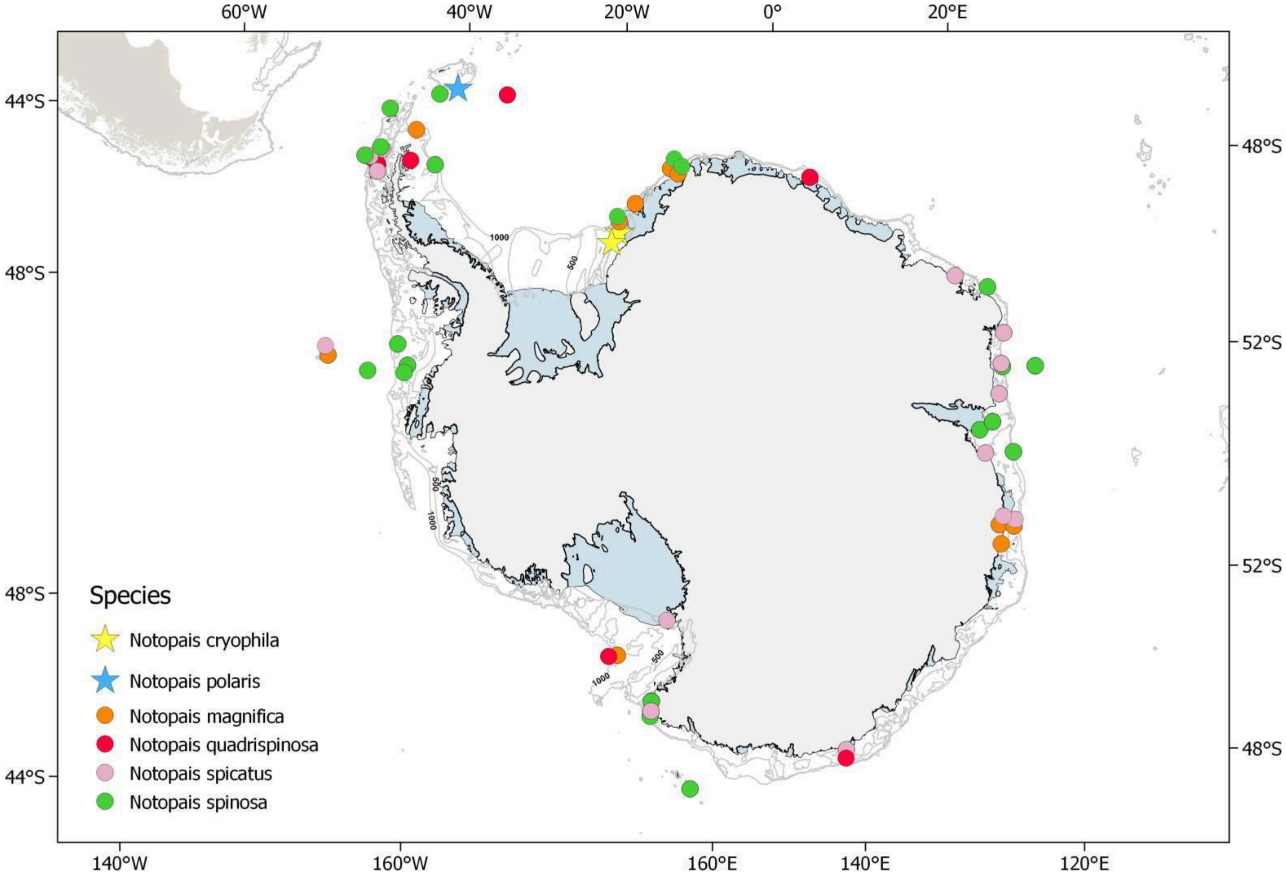

Figure 2. Southern Ocean species of *Notopais* Hodgson, 1910, dorsal view. A, *N. magnifica* (Vanhöffen, 1914); B, *N. spicatus* Hodgson, 1910; C, *N. sp.1*; D, *N. spinosa* (Hodgson, 1902); E, *N. quadrispinosa* (Beddard, 1886); F, *N. sp.2*. Scale bars: A, C-F = 3 mm; B = 2 mm.

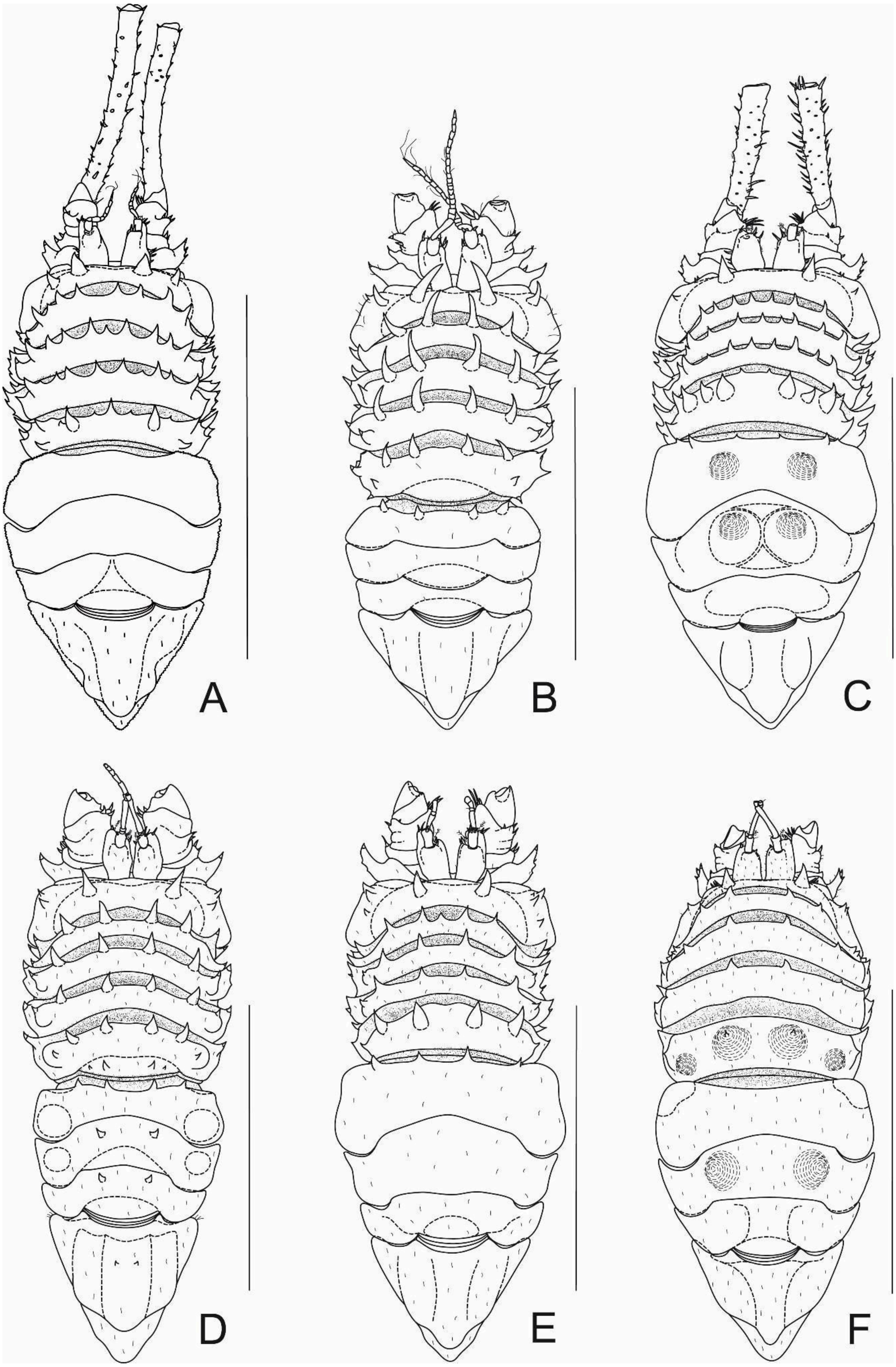

Figure 3. Southern Ocean species of *Notopais* Hodgson, 1910, lateral view. A, *N. magnifica* (Vanhöffen, 1914); B, *N. spicatus* Hodgson, 1910; C, *N. sp.1*; D, *N. spinosa* (Hodgson, 1902); E, *N. quadrispinosa* (Beddard, 1886); F, *N. sp.2*. Scale bars: A, B = 2 mm; C-F = 3 mm.

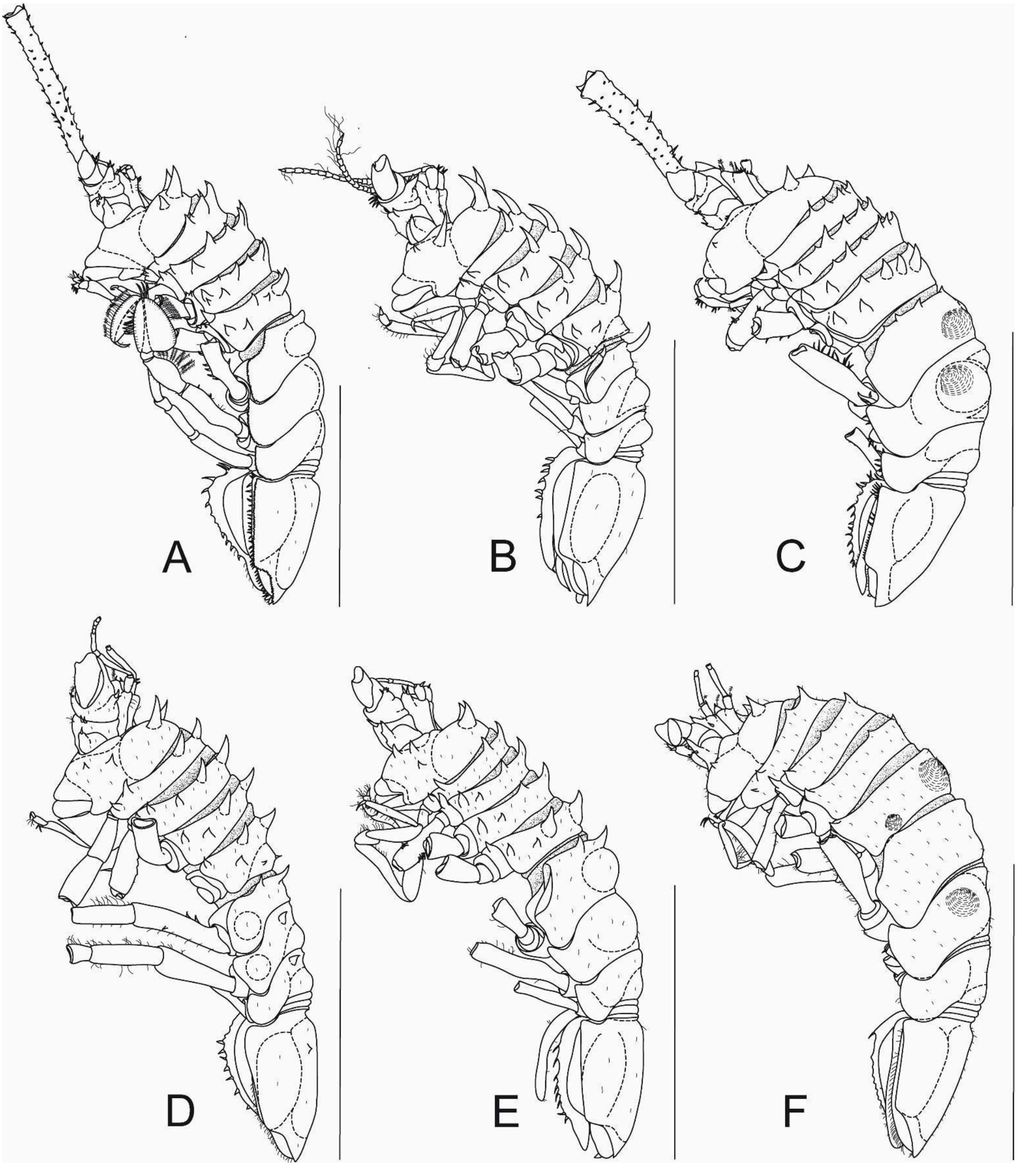

Figure 4. *Notopais sp.1*. A,B, female holotype, 4.75 mm; C-E, female paratype; F, male allotype. A, dorsal view; B, lateral view; C, right antenna 2 basis, dorsal view; D, right antenna 2 basis, ventral view; E, right antenna 1, dorsal view; F, right antenna 1, dorsal view. Scale bars: A, B = 3 mm; C-F = 0.5 mm.

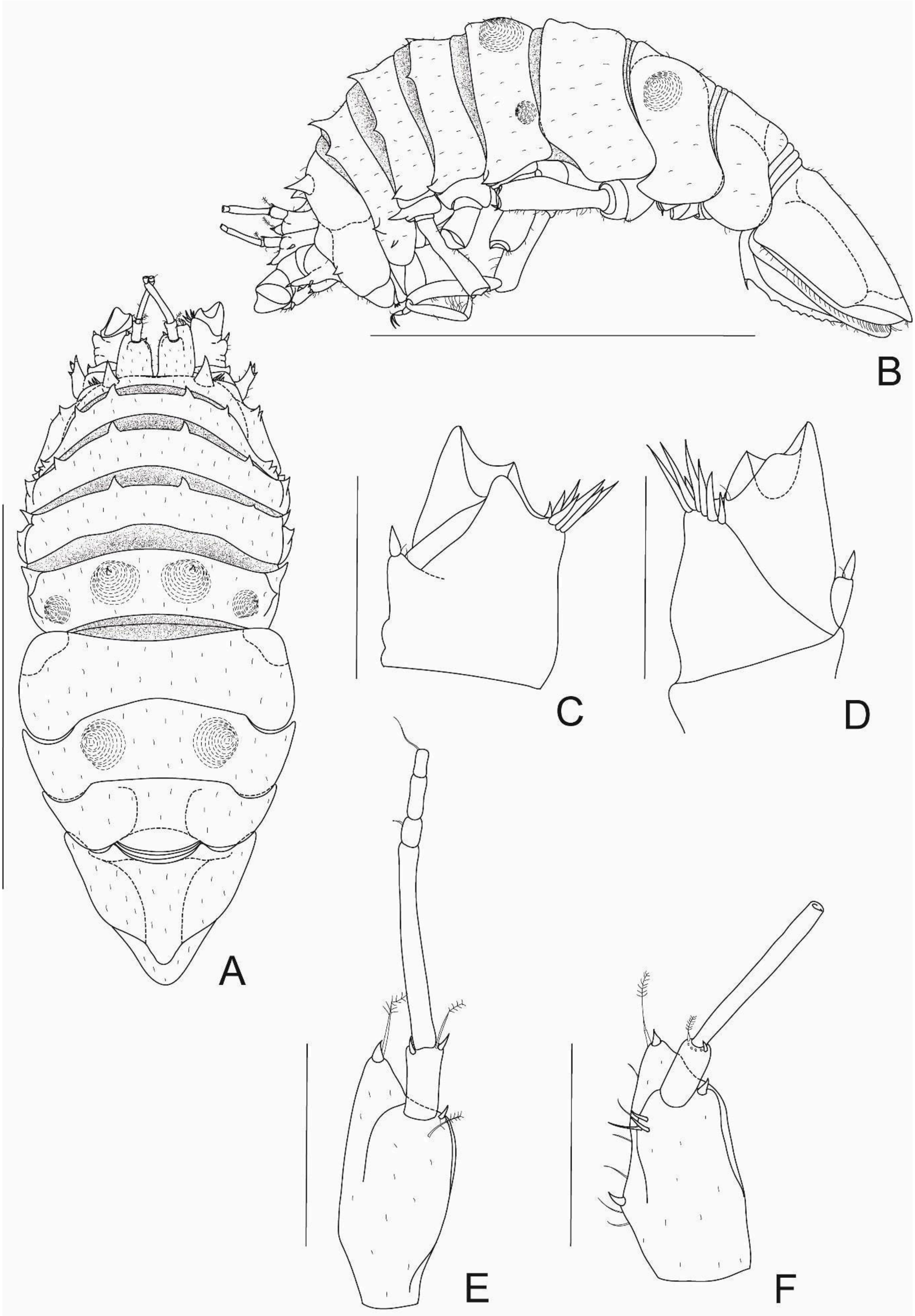

Figure 5. *Notopais sp.1*. All figures from female paratype. A, left mandible; B, left mandibular molar; C, left maxilla 1; D, left maxilla 2; E, left maxilliped. Scale bars A, C-E = 0.5 mm; B = 0.25 mm.

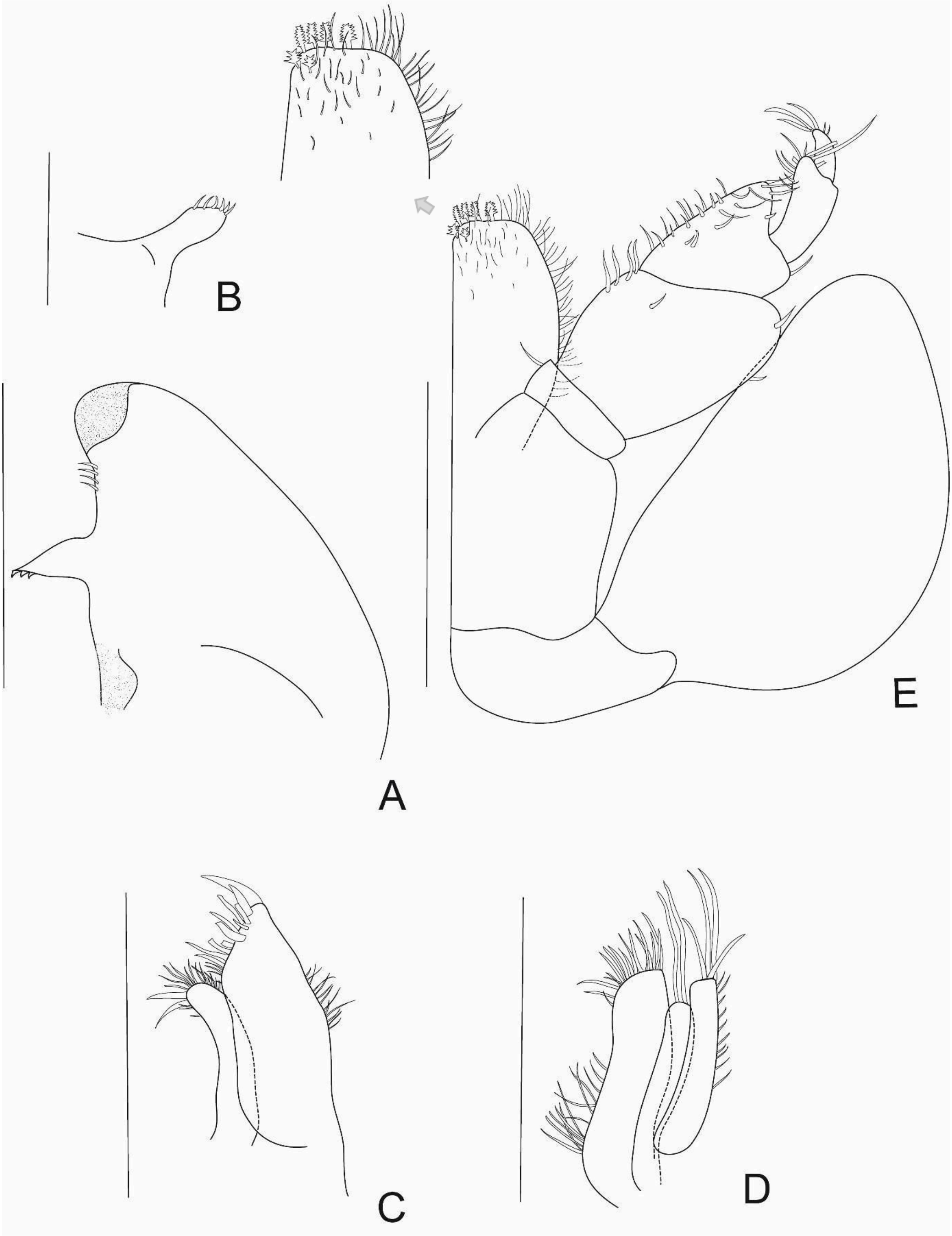

Figure 6. *Notopais sp.1*. A, C, D, female paratype; B, male allotype; A, left pereopod 1; B, left pereopod 1; C, left pereopod 7; D, right pereopod 6. Scale bars A-D = 0.5.mm.

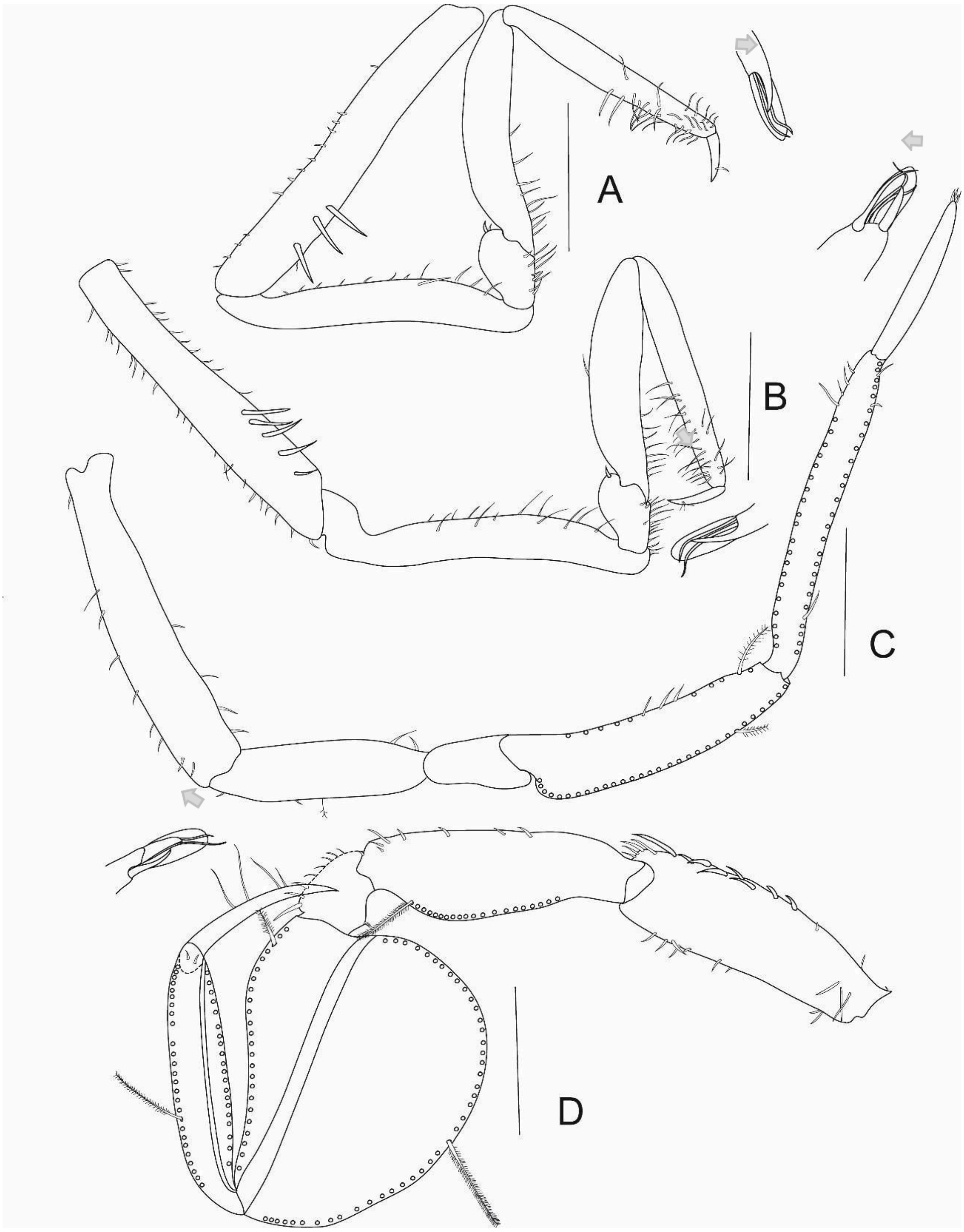

Figure 7. *Notopais sp.1*. A, D-F, female paratype; B,C, male allotype; A, operculum; B, pleopods 1; C, left pleopod 2; D, left pleopod 3; E, left pleopod 4; F, left pleopod 5. Scale bars A = 1 mm; B-F = 0.5 mm.

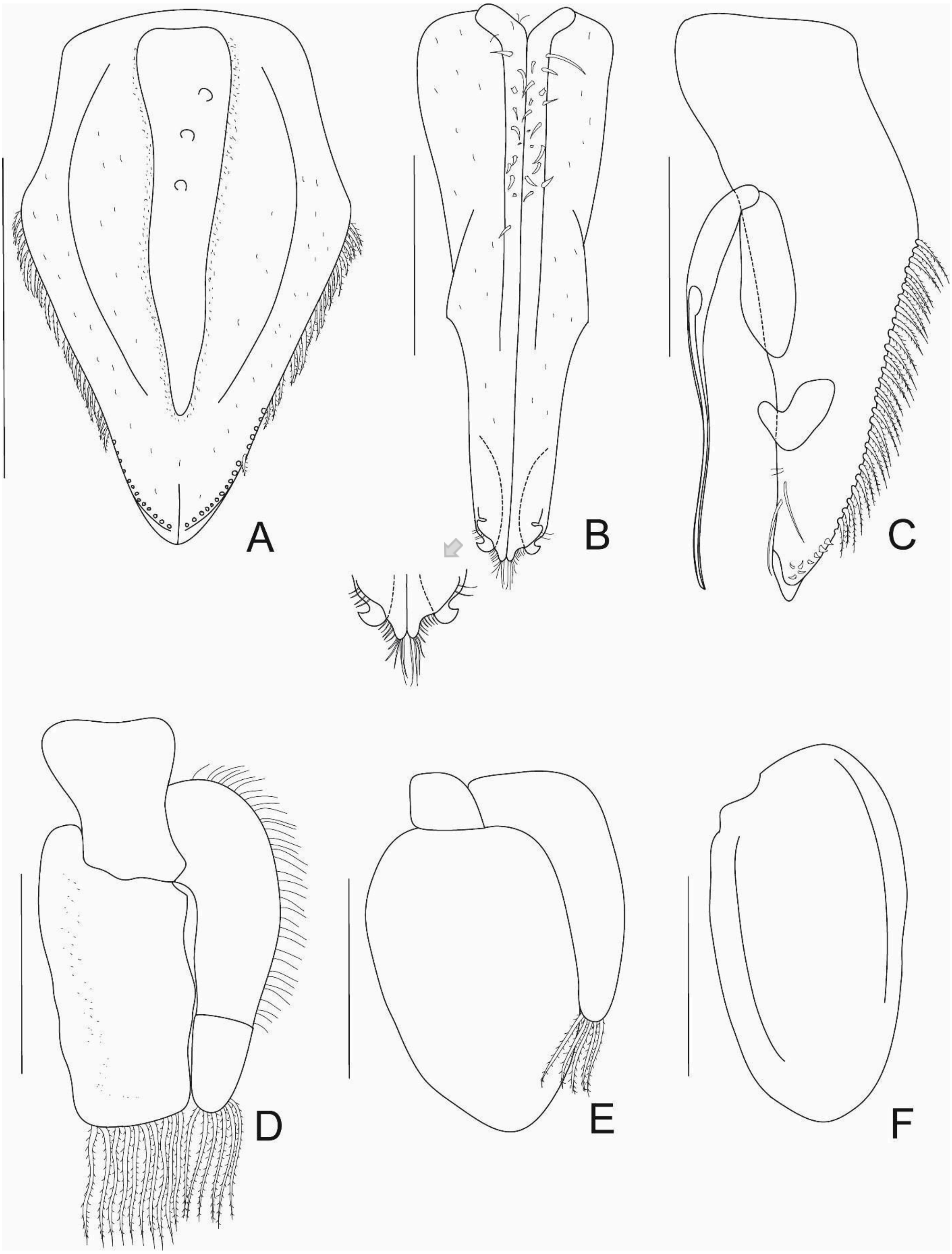

Figure 8. *Notopais sp.2*. A,B,G, female holotype, 4.90 mm; C-E, female paratype; F, male allotype. A, dorsal view; B, lateral view; C, right antenna 2, dorsal view; D, right antenna 2, ventral view; E, right antenna 1, dorsal view; F, right antenna 1, dorsal view; G, right A2, dorsal view. Scale bars: A, B, G = 3 mm; C-F = 0.5 mm.

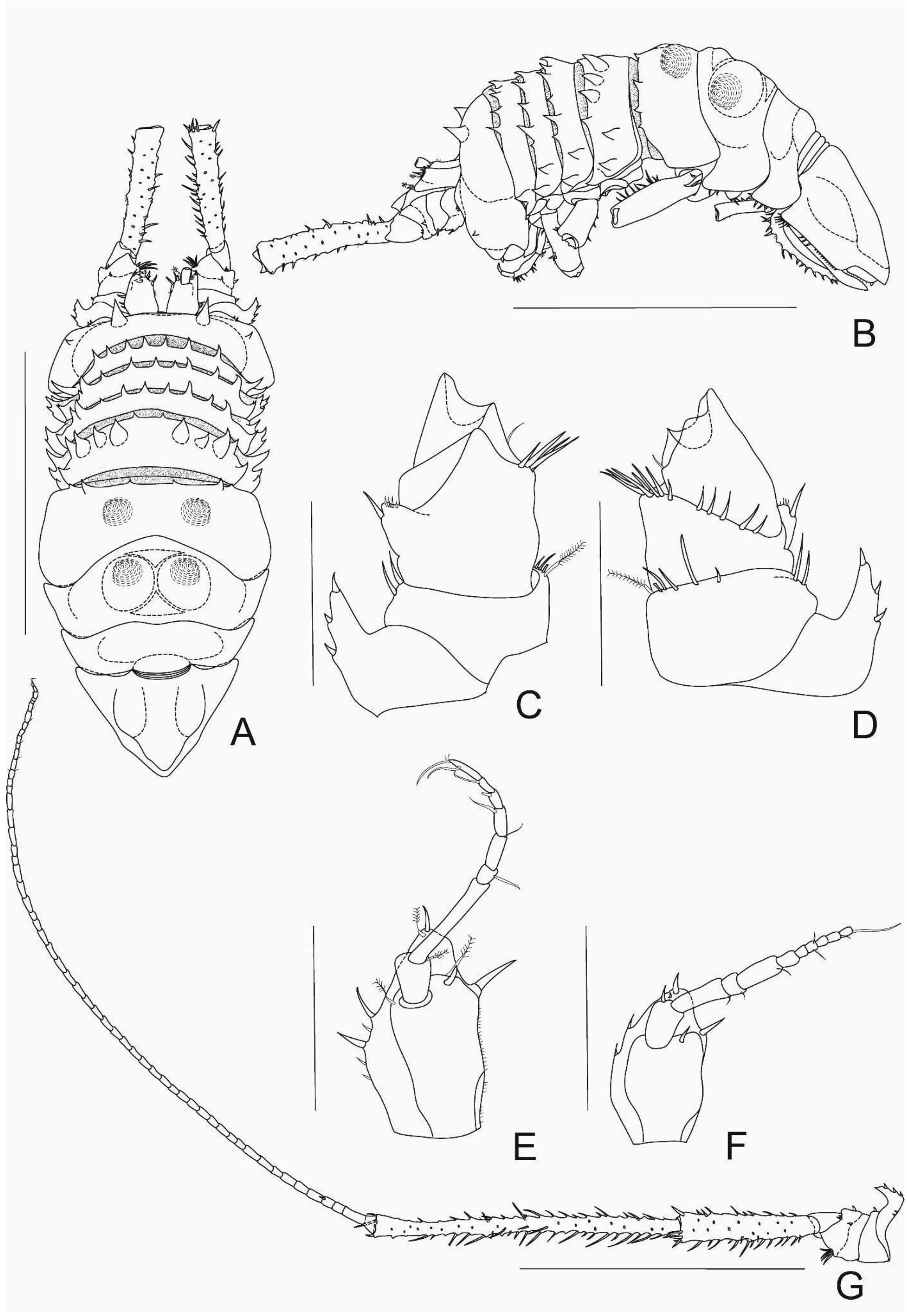

Figure 9. *Notopais sp.2*. All figures from female paratype. A, left mandible; B, left mandibular molar; C, left maxilla 1; D, left maxilla 2; E, left maxilliped. Scale bars A, C-E = 0.5 mm; B = 0.25 mm.

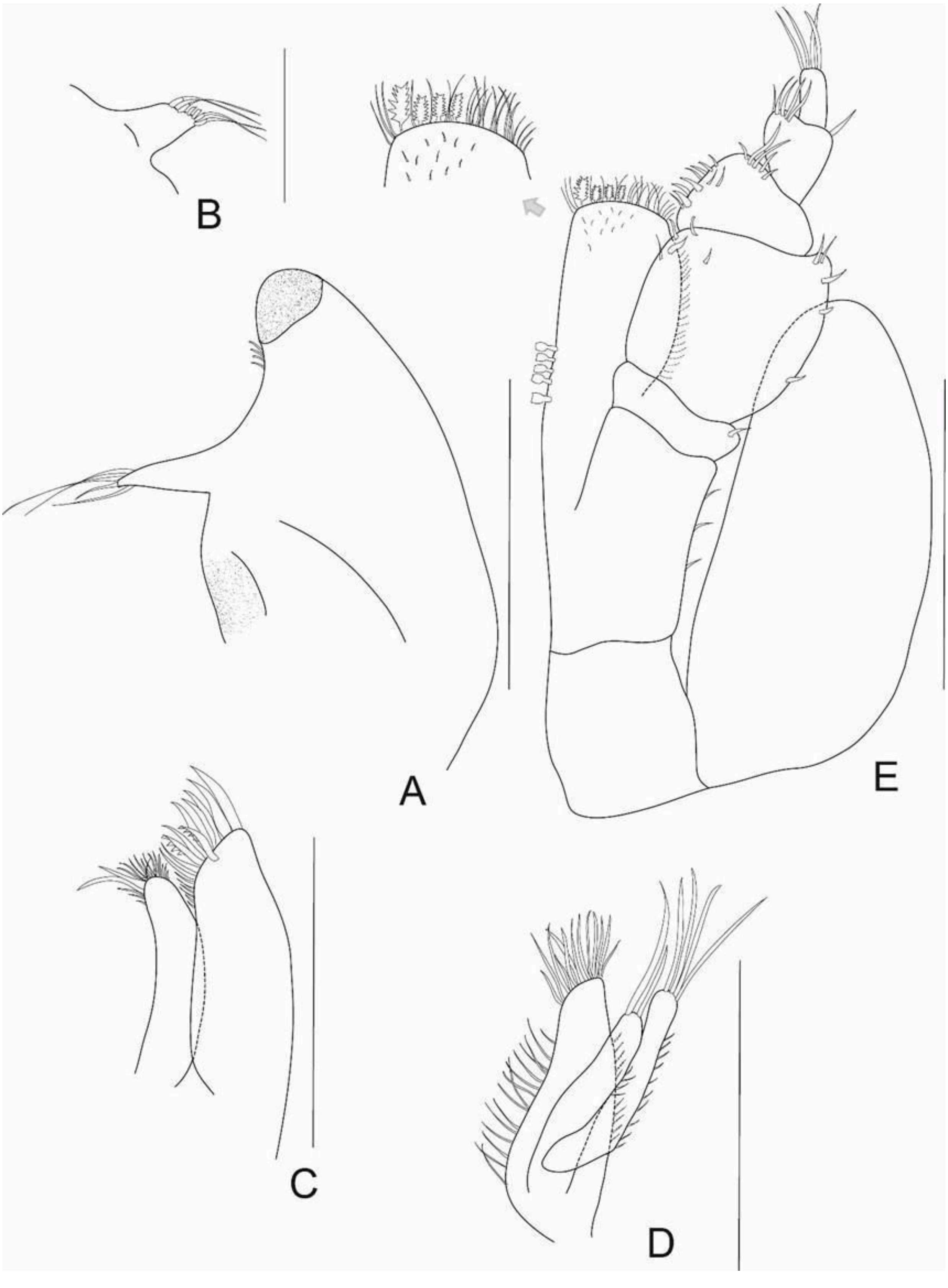

Figure 10. *Notopais sp.2*. A, C, female paratype; B, male allotype; A, left pereopod 1; B, left pereopod 1; C, right pereopod 6. Scale bars A-C = 0.5 mm.

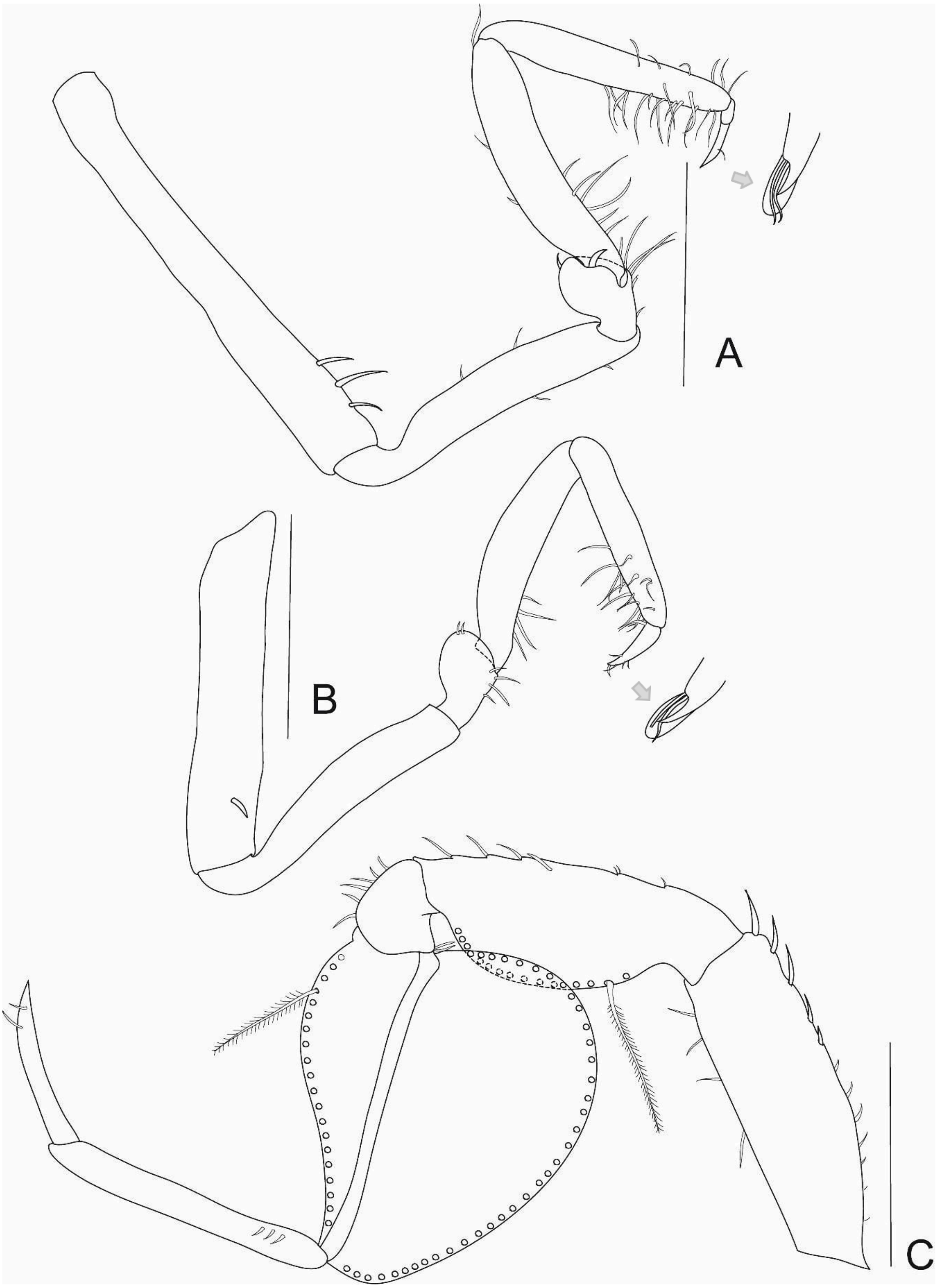

Figure 11. *Notopais sp.2*. A, D-F, female paratype; B,C, male allotype; A, operculum; B, pleopods 1; C, left pleopod 2; D, left pleopod 3; E, left pleopod 4; F, left pleopod 5. Scale bars A = 1 mm; B-F = 0.5 mm.

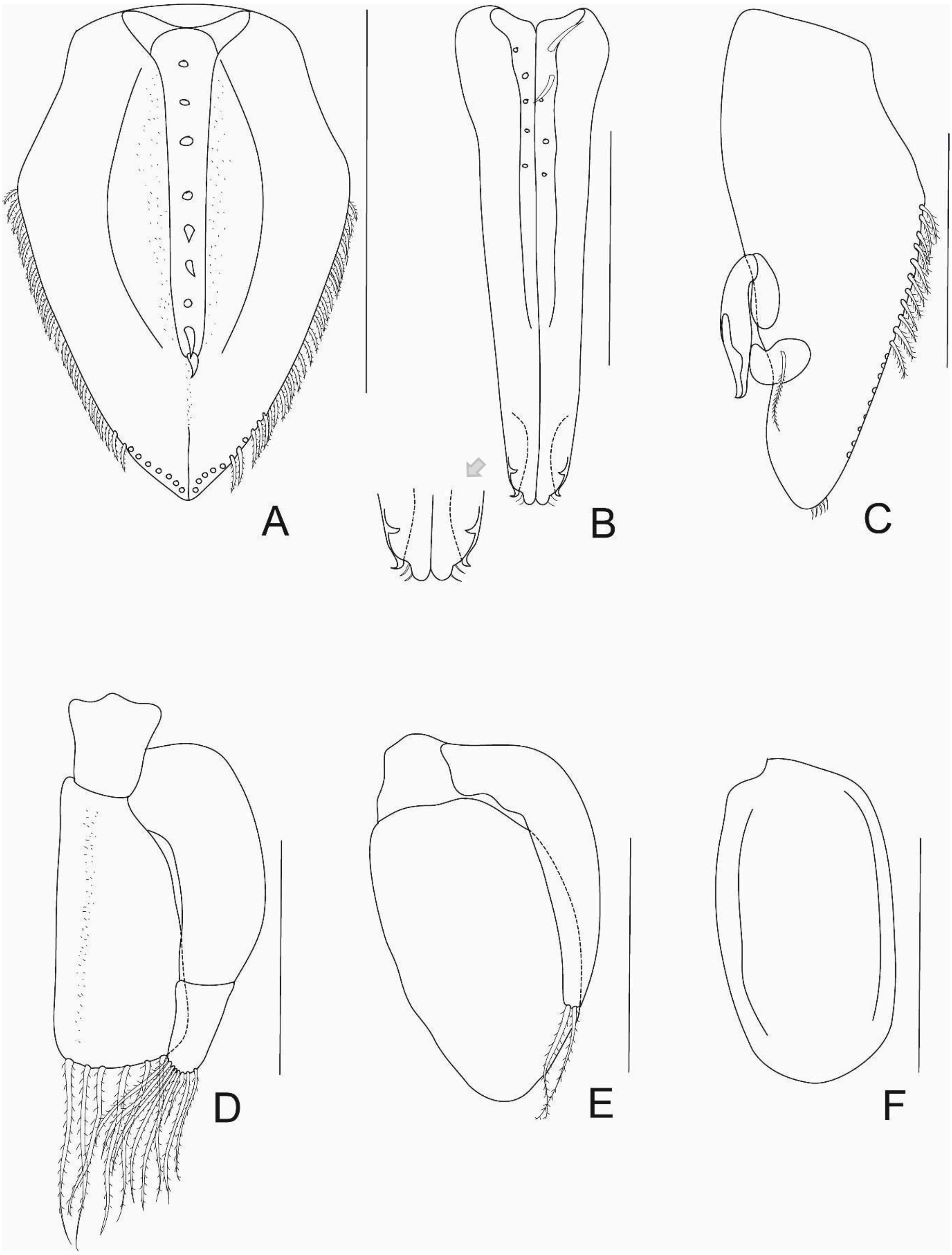

Figure 12. Phylogenetic tree based on COI sequences of 19 species of munnopsid isopods and one outgroup (*Santia sp.)*. The two new species of Notopais´ branch are highlighted in red. Node support values are expressed as SH-aLRT support (%) / ultrafast bootstrap support (%).

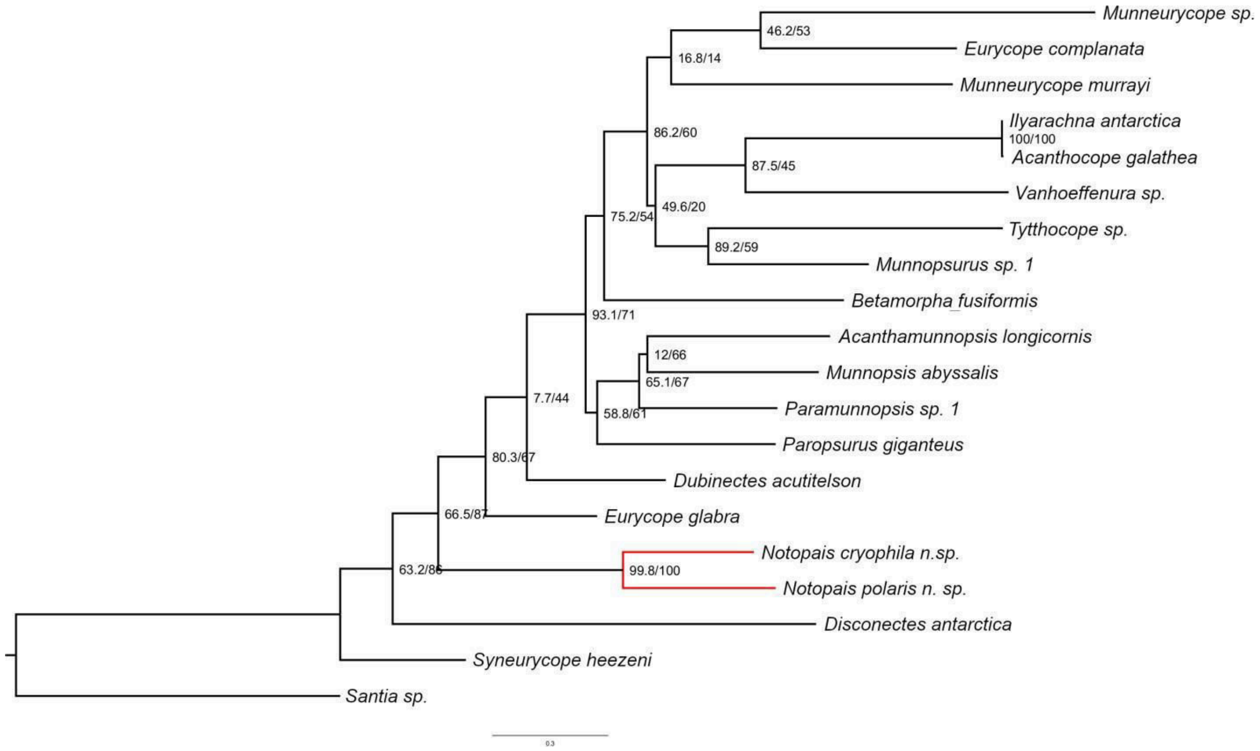

Table 1. Genbank Accession number and source of isopod species used for the phylogenetic analysis.

Species	**Genbank Accession no.**	**Source**
Acanthamunnopsis longicornis (Hansen, 1895)	EF682265	Osborn 2009
Munnopsis abyssalis Menzies & George, 1972	EF682273	Osborn 2009
Paramunnopsis sp. 1	EF682267	Osborn 2009
Eurycope glabra Kensley, 1978	EF682280	Osborn 2009
Eurycope complanata Bonnier, 1896	EF682281	Osborn 2009
Dubinectes acutitelson (Menzies, 1962)	EF682294	Osborn 2009
Disconectes antarcticus (Vanhöffen, 1914)	EF682293	Osborn 2009
Tytthocope sp. 3	EF682290	Osborn 2009
Munnopsurus sp. 1	EF682289	Osborn 2009
Munneurycope murrayi (Walker, 1903)	EF682275	Osborn 2009
Munneurycope sp.	EF682283	Osborn 2009
Paropsurus giganteus Wolff, 1962	EF682287	Osborn 2009
Betamorpha fusiformis (Barnard, 1920)	EF682291	Osborn 2009
Syneurycope heezeni Menzies, 1962	EF682295	Osborn 2009
Ilyarachna antarctica Vanhöffen, 1914	EF682299	Osborn 2009

Notopais sp.1	JAJNBS000000000	
Notopais sp.2	JAJNBT000000000	
Vanhoeffenura sp.	EF682284	Osborn 2009
Acanthocope galatheae Wolff, 1962	EF682285	Osborn 2009
Santia sp.	AY857831	Lindquist et al. 2005

Table S1. Specimens used for taxonomic illustrations shown in Figure 3-4.

Specimens	**Sex**	**Life Stage**	**Length**	**Treatment**
N. sp.1 (holotype)	female	adult	4.75 mm	habitus drawings of dorsal and lateral view
N. sp.1 (allotype)	male	adult	6.10 mm	dissected for appendage drawings (antenna 1, pereopod 1, pleopod 1, 2)
N. sp.1 (paratype)	female	adult	7.30 mm	dissected for appendage drawings (antenna 1, 2, maxilliped, maxilla 1, 2, mandible, pereopod 1, 6, 7, pleopod 3-5, operculum)
N. sp.2 (holotype)	female	adult	4.90 mm	habitus drawings of dorsal and lateral view, antenna 2
N. sp.2 (allotype)	male	adult	4.00 mm	dissected for appendage drawings (antenna 1, pereopod 1, pleopod 1, 2)
N. sp.2 (paratype)	female	adult	4.70 mm	dissected for appendage drawings (antenna 1, 2, maxilliped, maxilla 1, 2, mandible, pereopod 1, 6, pleopod 3-5, operculum)
N. magnifica (Vanhöffen, 1914)	female	adult	3.85 mm	habitus drawings of dorsal and lateral view
N. spicata (Hodgson, 1910)	male	adult	3.35 mm	habitus drawings of dorsal and lateral view
N. spinosa (Hodgson, 1902)	female	adult	5.15 mm	habitus drawings of dorsal and lateral view
N. quadrispinosa (Beddard, 1886)	male	adult	5.15 mm	habitus drawings of dorsal and lateral view

6.6. Chapter VI

Chapter VI

Chaetarcturus cervicornis sp. n., a new Ross-Sea isopod of the genus *Chaetarcturus* Brandt, 1990 (Crustacea, Malacostraca)

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Chaetarcturus cervicornis sp. n., a new Ross-Sea isopod of the genus *Chaetarcturus* Brandt, 1990 (Crustacea, Malacostraca)

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Abstract

Background

In the framework of the PNRA (Italian National Antarctic Research Program) project CARBONANT focusing on biogenic carbonates and held in January-February 2002, several Ross Sea banks were sampled to obtain samples of biogenic carbonates.

New information

In the Mawson Bank, species belonging to the isopod genus *Chaetarcturus* Brandt, 1990 were recorded, comprising a specimen that did not match any described species. In this paper we thus describe *Chaetarcturus cervicornis* n. sp., which is characterized by peculiar supraocular spines and two pairs of tubercle-like protrusions on the cephalothorax. The new species is very similar to *C. bovinus* (Brandt & Wägele, 1988) and *C. adareanus* (Hodgson, 1902), but has a clearly different spinel pattern. The study of the species of the genus *Chaetarcturus* in the Ross Sea contributes to increase our knowledge on the diversity of the Antarcturidae in the Southern Ocean.

Keywords

Ross Sea, morphology, distribution

Introduction

Our knowledge of Southern Ocean isopod taxa is still far from complete, with new species being described and new distributional data being added at each increment of the sampling efforts in a given area. Within the family Antarcturidae Poore, 2001, the discovery rate of new species was found to be strongly correlated to the scientific expeditions held in the Weddell Sea and the Antarctic Peninsula areas. In contrast, the Ross Sea seems comparatively poor in terms of new distributional records of known species as well as in terms of new species discovered. In the framework of the XVII Italian Expedition of the Italian National Antarctic Research Program (PNRA), a new antarcturid species belonging to the genus *Chaetarcturus* Brandt, 1990 was sampled.

The genus *Chaetarcturus* Brandt, 1990, according to the World Register of Marine Species (WoRMS http://marinespecies.org/index.php), numbers 23 species distributed in the north, equatorial and south Pacific Ocean, the south Atlantic Ocean and in the Southern Ocean. Some of these records of *Chaetarcturus* are very deep, for example those from the Kuril-Kamchatka area, in the Northwest Pacific, where *C. abyssalis* (Birstein, 1963) and *C. ultrabyssalis* (Birstein, 1963) were sampled at 5,680 and 7,280 metres depth, respectively (Birstein 1963).

According to the WoRMS Antarctica section RAMS (http://www.marinespecies.org/rams/index.php), to date only six species of *Chaetarcturus* occur in the Southern Ocean (Fig. 1): *C. acutispinis* (Kussakin, 1982), *C. adareanus* (Hodgson, 1902), *C. bovinus* (Brandt & Wägele, 1988), *C. brunneus* (Beddard, 1886), *C. franklini* (Hodgson, 1902) and *C. longispinosus* Brandt, 1990.

In this contribution, we describe a new antarcturid from the Ross Sea as *Chaetarcturus cervicornis* n. sp. . We decided to describe this new species due to its clearly distinct morphology and unique features that are not present in any previously described species of *Chaetarcturus*. Descriptions of peculiar new species based on the availability of a single specimen were already done in the past for another *Chaetarcturus* species, i.e . *C. cryophilus* (Hille et al. 2008).

Materials and methods

Taxon sampling

The single specimen available for the present study was collected in the Mawson Bank area (Ross Sea) during the XVII expedition of the Italian National Antarctic Program (PNRA) 2001/02, on board of the RV “Italica”, in the framework of the PNRA project CARBONANT (Processi genetici e significato paleoclimatico e paleoceanografico dei CARBONati marini biogenici in ANTartide; Genesis processes and paleoclimatic and paleoceanographic significance of marine Antarctic biogenic carbonates; PNRA project 4.7, PI Marco Taviani). The specimen was sampled using a dredge, at a depth of 389 m, (station Carb 34, 73°14.56’ S, 175°38.35’ E; Fig. 2). After the first sorting on board, the specimen was stored and fixed with 96% ethanol in order to preserve it for further genetic analysis.

Photography and laboratory analyses

Only one specimen was found during the campaign and it represents the holotype of the new species. The holotype was not dissected in order to preserve it for further observations and it was drawn in standard view (Wilson 2008). Drawings were performed using a camera lucida, followed by digital inking made by combining the stack photos and the scanned hand-made drawings as layers. The graphic software used was Autodesk SketchBook, digital inking was performed with a XP-PEN Deco 02 graphic tablet. Stacks were obtained by using a Canon EOS 600D and a Leica 125 C, mounting a Leica DMC 4500 camera. The use of stack photos as base layer of a digital-inking work is not new for crustacean illustrations (see for example the paper by Verheye and D’Udekem D’Acoz (2020)).

Additional distribution data

Additional *Chaetarcturus* distribution data (Bosman 2017, Bosman 2018, Arntz 2019, Birstein 1963, Choudhury and Brandt 2009, Data Manager 2019, Dmartin 2019, Grant 2019, Mackay 2018a, Mackay 2018b, Mackay 2019, Natural History Museum 2014, Norton 2017, Orrell and Informatics Office 2021, Registry-Migration.Gbif.Org 2015, Registry-Migration.Gbif.Org 2016, Registry-Migration.Gbif.Org 2019, Registry-Migration.Gbif.Org 2020a, Registry-Migration.Gbif.Org 2020b, Registry-Migration.Gbif.Org 2021a, Registry-Migration.Gbif.Org 2021b, Registry-Migration.Gbif.Org 2021c, Seid 2019, Telenius 2019) were provided through GBIF (Global Biodiversity Information Facility, available from https://www.gbif.org/) and OBIS (Ocean Biodiversity Information System https://obis.org/).

Quality check and data cleaning were performed using bibliographic research and rgbif package (https://CRAN.R-project.org/package=rgbif) in RStudio software.

Maps were drawn using QGIS (QGIS.org 2021) package QAntarctica (Matsuoka et al. 2018).

Morphological abbreviations

A = antenna

P = pereopod

PL = pleopod

UR = uropod

MNA = Italian National Antarctic Museum (Section of Genoa), Genoa

PNRA = Italian National Antarctic Research Program

Taxon treatment

Chaetarcturus cervicornis Noli, Brandt, Di Franco, Schiaparelli, sp. n.

Material

Holotype:

a. kingdom: Animalia; phylum: Arthropoda; class: Malacostraca; order: Isopoda; family: Antarcturidae; genus: *Chaetarcturus*; continent: Antarctica; locality: Mawson Bank; verbatimDepth: 389; decimalLatitude: -73.24266; decimalLongitude: 175.63916; eventID: Carb 34; samplingProtocol: bottom trawl; year: 2002; month: 1; day: 15; individualCount: 1; sex: male; lifeStage: adult; catalogNumber: MNA 10739; identifiedBy: Nicholas Noli; dateIdentified: 2019; type: PhysicalObject; basisOfRecord: PreservedSpecimen

Description

Measurements. BL = 20 mm.

Body. Body long and slender. The whole-body surface is covered by very small spines and tubercles, especially on the lateral and caudal margins of the somites (Fig. 3A, B, Fig. 5A, B).

Antennae. A1 is broken in the holotype; A2 is broken in holotype, remaining only the first and second peduncular articles. First peduncular article about half size of the second, with short, rounded spine on dorsal side, laterally directed; second peduncular article twice as long as the first one, laterally with four short spines (Fig. 5C).

Cephalothorax. With large laterally protruding eyes, slightly subtriangular, blunt supraocular spines, dorsally directed and frontally curved, not surpassing the eyes in dorsal view (Fig. 3B, Fig. 5A); in the middle of each supraocular spine, a particular spinal shorter process is evident. Cephalothorax with two lobes, that end with a short rounded tubercular spine each; dorsolaterally on pereonite 1, a pair of small blunt and rounded spines is present, about twice as long as the small tubercular spines of lobes and located medially on the first fused pereonite; another pair of minor spines are evident in the distal part of pereonite 1, and are also present in pereonite 2 (Fig. 5C).

Pereonites. Pereonite 1 fused with cephalothorax; pereonite 2 subequal in length to pereonite 3; pereonite 4 the longest; pereonite 5 subequal in length to pereonite 4; pereonites 6 and 7 the smallest. Tergites of pereonites 5-7 with concave posterior border into which the following segment fits when the animal bends dorsally (Fig. 3A, B, Fig. 5A, B). Pereonite 1 bears short lateral supracoxal spines.

Pleonites. All three anterior pleonites fused with pleotelson, but first three pleonites still present incisions; they are covered in small tubercles, and very tiny spines-like protrusions laterally, barely distinguishable (Fig. 3A, B, Fig. 5A, B).

Pleotelson. Pleotelson covered with spiny tubercles. Caudal part of pleotelson with two long and stout spines approximately one third and half the length of pleotelson, which surpass the uropods (Fig. 3A, B). Dorsal pleotelsonic surface covered with small spines (Fig. 3A).

Pereopods. P1 about half the length of P2, basis long, carpus trapezoidal, subchelate propodus broad-oval, dactylus shorter than propodus (dactylus roughly half size of propodus), with one long and one short distal claw. All articles densely setose. Dorsal side of propodus with few setae, mostly distally, on the mouthparts-directed lateral side long setulated setae, on outer-directed surface of propodus smaller and thin setae, densely setose ventrally (Fig. 4A, Fig. 5E). P2-3 similar. P2 shorter (0.9 length of P3), simple setae ventrally on ischium and merus, longest setae on carpus, slightly shorter on propodus and dactylus. Basis with posterodistal semi-circular group of setae (Fig. 4 B, C, Fig. 5D, F). P4 severely damaged in holotype (Fig. 4D), propodus and dactylus lacking. P5-7 shorter and stouter than P2-4 (0.7-0.8 of the length of P2-3), basis always the longest article (almost twice as long as ischium, roughly three times as long as merus and carpus, slightly longer than propodus and twice as long as dactylus), cuticle with several spines and tubercles on posterolateral surface. Ventral side of merus and carpus of P5-7 with two rows of strong spines, one single ventral row on propodus; dactylus terminally with two claws, ventral one shorter and less stout, one small seta between claws (Fig. 4E, F, G).

Pleopods. Plp1 with a row of nine teeth laterally of sympodite. Exopod of Plp1 with a medially protruding lateral lobe and a ridge from this edge diagonally to distolateral margin, where many simple setae insert; the diagonal ridge ends distally at the base of setulated setae. Endopod with many setulated setae on the apical side (Fig. 3D, Fig. 5 G).

Uropods. Uropods oval, elongated, dorsal surface covered with acute tubercles; caudal rami bearing short setae (Fig. 3C).

Diagnosis

The new species is characterized by the characteristic supraocular spines, consisting of a main spine, dorsolaterally directed, blunt and rounded. In the middle of the main spine is a distinct protrusion, forming a simple ramification, somewhat resembling the antlers of a deer. In addition, the spinal pattern in the cephalothorax presents a second pair of short tubercle-like blunt spines, caudally to the large supraocular spines; another pair of slightly bigger (roughly 1.5 times of the first pair of protrusions) tubercle-shaped elevations is present, caudally to the first pair of blunt spines (Fig. 5C).

Etymology

This species is characterized by its peculiar supraocular spines, somewhat resembling the antlers of a deer, hence the name *cervicornis*.

Distribution

Only known from type locality, the Mawson Bank, Ross Sea (Antarctica), found at 389 m.

Type species (by monotypy) and type locality

Chaetarcturus longispinosus in Brandt (1990)

Remarks

The genus *Chaetarcturus* Brandt, 1990 is clearly distinguishable from the close genus *Antarcturus* Zur Strassen, 1902 by the presence of long filter spines on the dactyli of pereopods 2-4; the genus *Mixarcturus* Brandt, 1990 also presents the same filter spines, but the lack of tergal spines and a flagellum which consists of no more than four articles make the genera clearly different (Brandt 1990, White 1992).

To date, six species belong to the genus *Chaetarcturus* (original names are given; the type species is marked with an asterisk) according Worms' section RAMS (Register of Antarctic Marine Species):

Chaetarcturus acutispinis - described in Kussakin 1979

Chaetarcturus adareanus - described in Hodgson (1902)

Chaetarcturus bovinus - described in Brandt and Wägele (1988)

Chaetarcturus brunneus - described in Beddard (1886)

Chaetarcturus franklini - described in Hodgson (1902)

**Chaetarcturus longispinosus* - described in Brandt (1990)

Chaetarcturus cervicornis sp. nov.

Differential diagnosis

Within the genus *Chaetarcturus*, *C. adareanus* (Hodgson, 1902) and *C. bovinus* (Brandt & Wägele, 1988) share with *C. cervicornis* n. sp. the cylindrical shape of the body and the terminal spines, slightly shorter in *C. adareanus*. Rounded, blunt and stout supraocular spines are present in the new species and in *C. bovinus*. However, the unique shape of the supraocular spines of *C. cervicornis*, with the two main spines bearing a second very short pair of spines transversally creating a sort of “deer horns” shape- is clearly distinguishable; another major difference between *C. bovinus* and *C. cervicornis* is the complete lack of the characteristic two pairs of longer spines on the pleotelson in *C. cervicornis*; the latter is characterized by a rough and spiny, but rather uniform pleotelsonic spine pattern. *Chaetarcturus adareanus* differs from *C. cervicornis* by having a second pair of shorter spines caudally on supraocular ones. The main supraocular spines in *C. cervicornis* presents the second pair of caudally directed protrusions as well; however, these are more tubercular-like than spines-like. Furthermore, a second pair of tubercles located in first-pereonite area, stronger than the other protrusions characterising the surface of the species, is evident.

Acknowledgements

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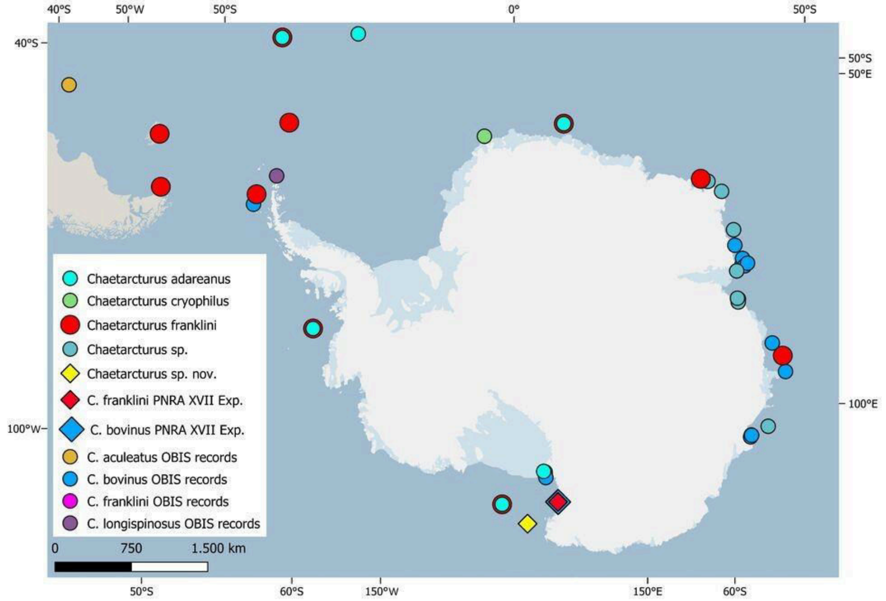


Figure 1.

Distribution records of *Chaetarcturus* Brandt, 1990 in Southern Ocean. GBIF and OBIS database data are represented by dots, squares stand for *Chaetarcturus* species recorded during the PNRA XVII Italian Expedition 2001/02, blue and red for *C. bovinus* (Brandt & Wägele, 1988) and *C. franklini* (Hodgson, 1902) respectively. Yellow square indicates record of *C. cervicornis* sp. n.

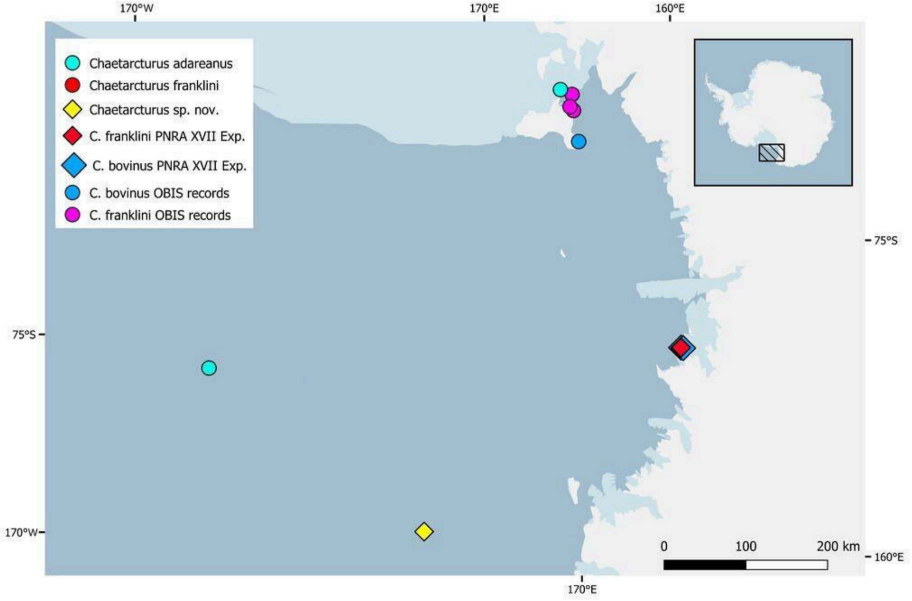


Figure 2.

Distribution records of *Chaetarcturus* species in Ross Sea. Circles stand for GBIF and OBIS records, squares represent PNRA XVII Italian Expedition 2001/02; yellow square indicates record of *Chaetarcturus cervicornis* sp. n..

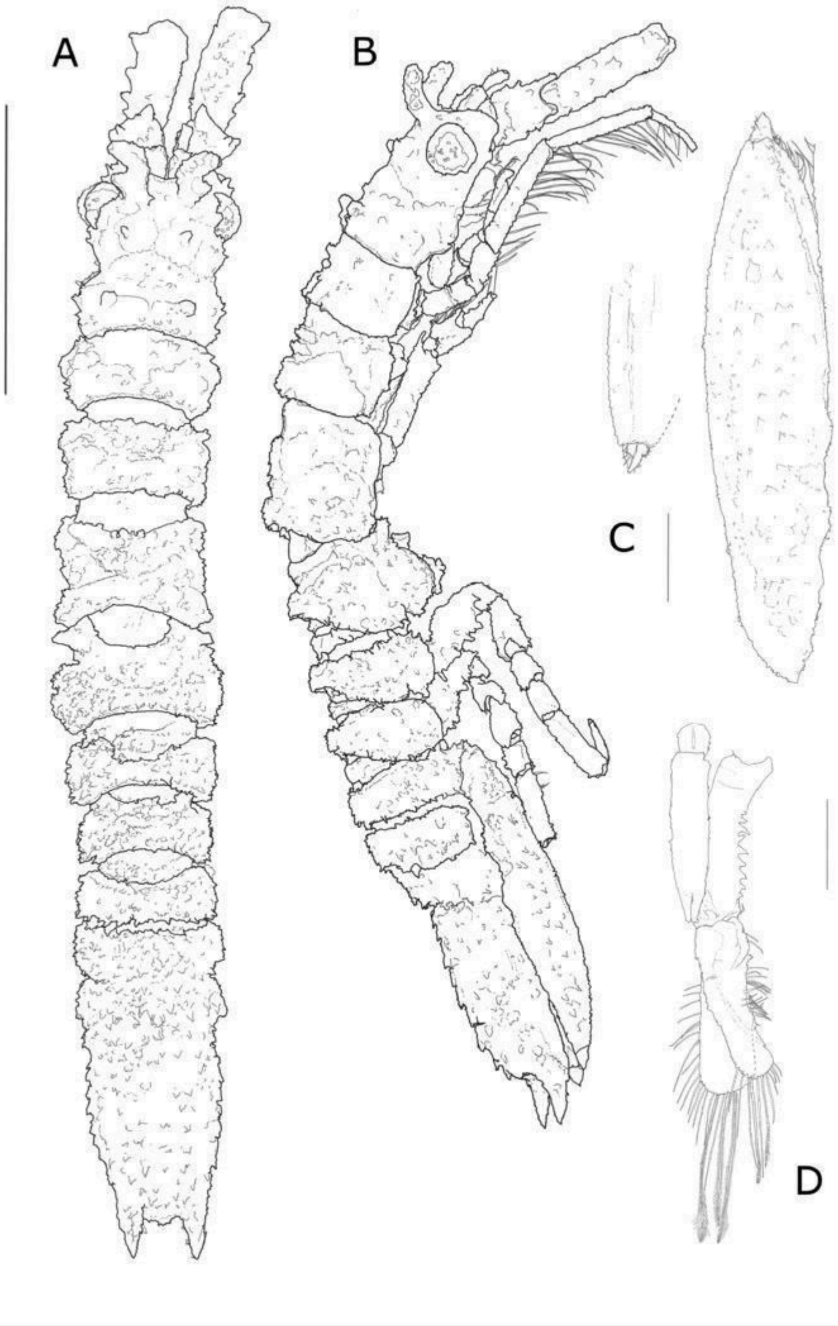
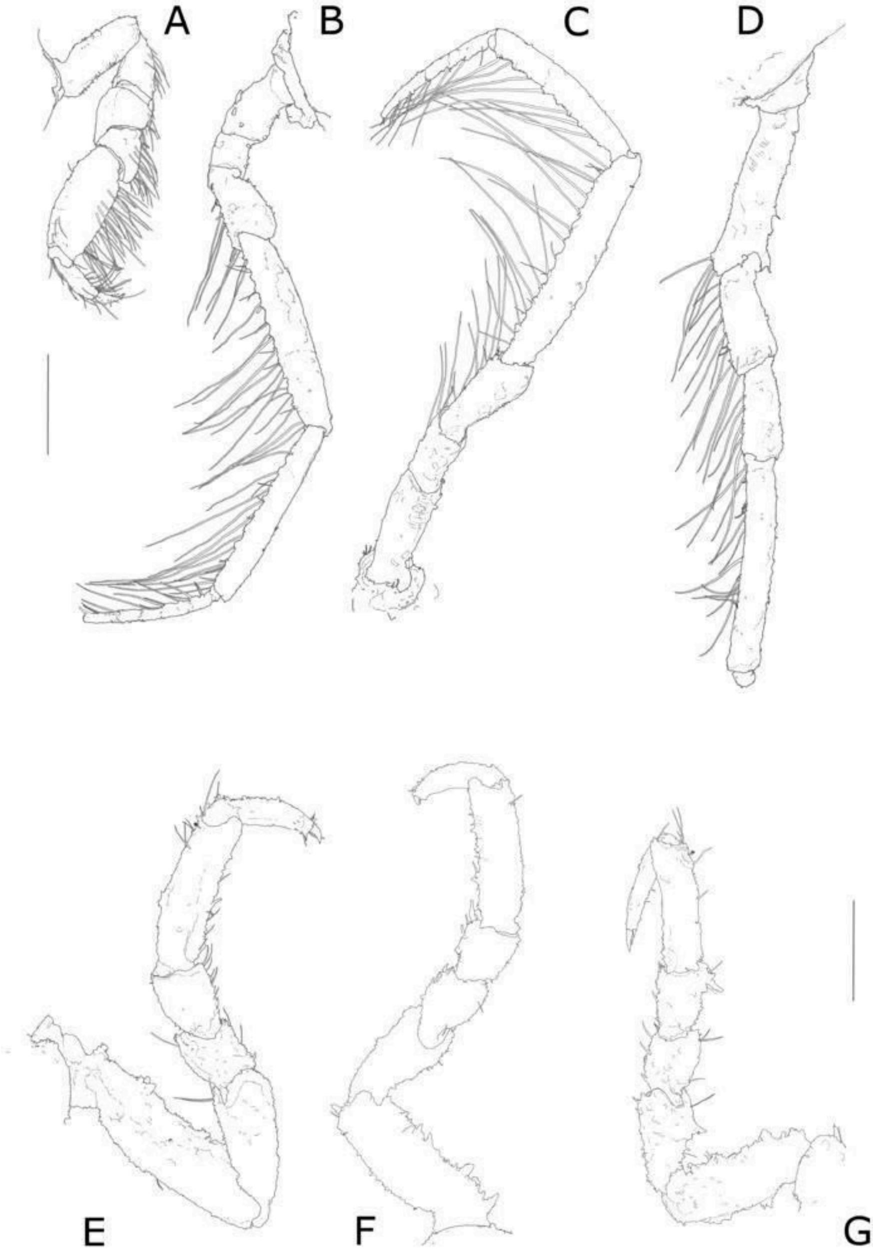


Figure 3.

Chaetarcturus cervicornis sp. n. male holotype (MNA 10739) **A** dorsal view, scale refers to 5 mm **B** lateral view, scale refers to 5 mm **C** right uropod, scale refers to 1 mm **D** penis and left first pleopod, scale refers to 1 mm.



Fi gure 4.

Chaetarcturus cervicornis sp. n., male holotype (MNA 10739) **A** left first pereopod **B** second pereopod **C** left third pereopod **D** left fourth pereopod (broken) **E** left fifth pereopod **F** right sixth pereopod **G** right seventh pereopod. All scale bars refer to 1 mm.

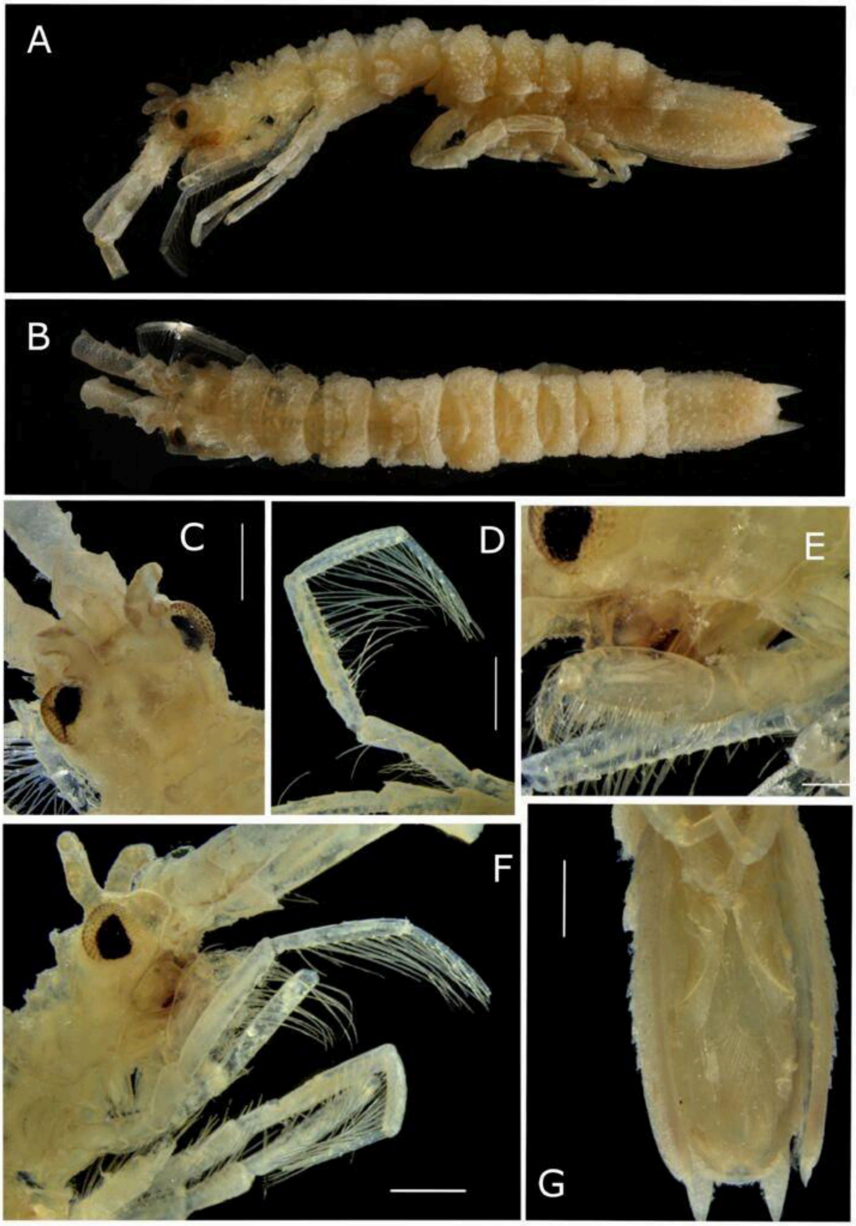


Figure 5.

Chaetarcturus cervicornis sp. n., male holotype (MNA 10739) stack photo **A** lateral view. **B** dorsal view **C** dorsal side of cephalothorax, where peculiar supraocular spines and the two pairs of blunt tubercle-like spines are evident **D** of third pereopod **E** of first pereopod **F** of the lateral side of cephalothorax, focus on second pereopod **G** of ventral side of the pleotelson, focus on pleopods.

6.7. Chapter VII

Chapter VII

Pseudidothea armata sp. n., a new isopod of the genus *Pseudidothea*(Crustacea, Malacostraca) from the Atlantic sector of the SO

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Pseudidothea armata sp. n., a new isopod of the genus *Pseudidothea*(Crustacea, Malacostraca, Isopoda) from the Atlantic sector of the Southern Ocean

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Abstract

Background

In the framework of the Brithish Antarctic Survey (BAS) Expedion JR 15005 SO-AntEco, held in February-March 2016, the South Orkney Islands seafloor was sampled in order to investigate the distribution and composition of benthic communities around the area.

New information

A new species of the genus *Pseudidothea* Ohlin, 1901 is described from the Burdwood Bank area (South Orkney Islands). It has been collected during the SO-AntEco JR15005 RRS James Clark Ross expedition under the lead of the British Antarctic Survey (BAS). The new species, *Pseudidothea armata* sp. n., is very similar to *P. scutata* (Stephensen, 1947), however, it is characterized by peculiar supraocular spines and a different tubercular pattern. The study of the species of the *Pseudidothea* helps to better understand the diversity of the Pseudidotheidae in the Southern Ocean.

Keywords

Southern Ocean, morphology, ecology, distribution

Introduction

The family Pseudidotheidae Ohlin, 1901 is monogeneric with the only genus *Pseudidothea* Ohlin, 1901, comprising four accepted species. The family was erected through the description of its type species *P. bonnieri* Ohlin, 1901, now accepted as *P. miersi* (Studer, 1884) and was recently redescribed by Poore and Bardsley (2004). According to the WoRMS (World Register of Marine Species) and RAMS (Register of Antarctic Marine Species), only *P. scutata* Stephensen, 1947 (Stephensen 1947) occurs in the Southern Ocean in the area of the Antarctic Peninsula, off the Elephant Island and the South Shetlands. However, undertemined records of the genus *Pseudidothea* were reported in several parts of the Antarctic Peninsula, and in the Mawson Bank area, Ross Sea (Mills 2020) (Fig. 1).

The biogeographic knowledge of this genus is as follows: in the Southern Hemisphere, most of the records are from Chile (*P. miersi* (Studer 1884, Scarabino et al. 2008)), South Australia (*P. hoplites* (Poore and Bardsley 2004)), and New Zealand (*P. richardsoni* Hurley, 1957 (Hurley 1957)); only one specimen was found in the Southern Ocean, in 1927 and has been described by Stephensen (1947) as *Microarcturus scutatus* (Stephensen, 1947). In 1990, it was redescribed and placed in the genus Pseudidothea as *P. scutata* by Brandt and Wägele (1990).

In order to improve the biogeographic knowledge of the species of the Southern Ocean, *P. armata* sp. n. is described herein. Though only one specimen is available and used for the description, clear characteristics provide sufficient evidence that the new species differs from the closest morphological (and geographical) species *P. scutata*.

Materials and methods

Taxon sampling

The specimen was collected at Burdwood Bank, during the British Antarctic Survey (BAS) Expedition JR 15005 (https://www.bodc.ac.uk/resources/inventories/cruise_inventory/reports/jr15005.pdf) on board of the RRS James Clark Ross, by means of a Rauschert dredge at a depth of 852 m (Station 143, 18 April 2016, 60°33.526' S, 41°5.306' W). After the first sorting on board, specimen was stored and fixed with 96% ethanol in order to preserve it for further genetic analysis.

Photography and laboratory analyses

Only one specimen, the holotype of the new species, was found during the campaign. The holotype was not dissected in order to preserve it for further studies, and it was drawn in dorsal and lateral views following standard descriptions (Wilson 2008). Drawings were performed using a camera lucida, followed by digital inking made by combining the stack photos and the scanned hand-made drawings as layers. The graphic software used was

Autodesk SketchBook, digital inking was performed with a XP-PEN Deco 02 graphic tablet. Stacks were obtained by using a Canon EOS 600D and a Leica 125 C equipped with a Leica DMC 4500 camera. The use of stack photos as base layer of a digital-inking work is not new for crustacean illustrations (see for example the paper by Verheye and D'Udekem D'Acoz (2020).

Additional distribution data

Additional distributional data of *Pseudidothea* (Appiah-Madson and Distel 2019, Data Manager 2019, Mackay 2018, Mackay 2019, Mackay 2021, Mills 2020, Orrell and Informatics Office 2021, Rdmpage 2016, Registry-Migration.Gbif.Org 2016, Registry-Migration.Gbif.Org 2020, Registry-Migration.Gbif.Org 2021, Tablado 2021) were provided through GBIF (Global Biodiversity Information Facility, available from https://www.gbif.org/) and OBIS (Ocean Biodiversity Information System https://obis.org/).

Quality check and data cleaning were performed using bibliographic research and rgbif package (https://CRAN.R-project.org/package=rgbif) in RStudio software.

Maps were drawn using QGIS (QGIS.org 2021) package QAntarctica (Matsuoka et al. 2018).

Morphological abbreviations

A = antenna;

P = pereopods;

PL = pleopod;

UR = uropod;

MNA = Italian National Antarctic Museum (Section of Genoa), Genoa;

PNRA = Italian National Antarctic Program;

BAS = British Antarctic Survey

Taxon treatment

Pseudidothea armata Noli, Di Franco, Schiaparelli, Brandt 2021, sp. n.

Material

Holotype:

a. kingdom: Animalia; phylum: Arthropoda; class: Malacostraca; order: Isopoda; family: Pseudidotheidae; genus: *Pseudidothea*; continent: Antarctica; locality: Burdwood Bank; verbatimDepth: 852; decimalLatitude: -60.55876; decimalLongitude: -41.08843; eventID: St143; samplingProtocol: bottom trawl; year: 2016; month: 3; day: 18; individualCount: 1;

sex: male; lifeStage: adult; catalogNumber: MNA 10749; identifiedBy: Nicholas Noli; dateIdentified: 2019; type: PhysicalObject; basisOfRecord: PreservedSpecimen

Description

Measurement. BL = 15mm; BW = 5 mm.

Body: Entire body surface rough and granular, covered with small hair-like setae (Fig. 2A, B, Fig. 3A, B).

CEPHALOTORAX. Head with two frontomedial lobes with many small tubercle-like protrusions. Cephalothorax with two big and stout spines, frontally directed (Fig. 2A, B, Fig. 3A, B, Suppl. materials 1, 2), covered with tubercles and with diffused short hair-like setae (not illustrated in drawings but visible in Fig. 3). Cephalotorax with two lateral eyes of medium size, more slightly subtriangular than oval (Fig. 2A, B, Fig. 3A, B, Suppl. material 1).

ANTENNA 1. First Antenna (A1) consisting of three peduncular and two flagellar articles. First peduncular article broadest, almost surpassing in width the length of the second peducular article, with one mediolateral simple bristle; second peduncular article long nearly 1.5 of the first, the third almost a third of the second, rounded distally. First flagellar article short, ring-like, barely distinguishable; last flagellar article is long as the length of all the other articles of the A1. Distoventrally on this article six pairs of aesthetascs, another single aesthetasc present in the tip of the A1 together with two simple setae (Fig. 2E, Fig. 3D).

ANTENNA 2. Second Antenna (A2) half as long as body, consisting of 5 peduncular and 3 flagellar articles. First peduncular article very small, second about double in length of the first; third peduncular article 3 times longer than second, with a two ventral rows of long simple setae, each group with one long and one short seta. Fourth and fifth peduncular articles longest, nearly subequal in length, with similar setae pattern of the third article. Last peduncular article with a distolateral small feather-like seta. First flagellar article about twice as long as second and third flagellar articles together, bearing short bristles and one longer apical simple seta. Second article smaller and narrower than first, with many simple short bristles. Last flagellar article smallest, claw-like. The whole antenna covered with lots of short and small hairs (Fig. 2D).

PEREONITES. Pereonite 1 fused with cephalotorax but separated by a ridge. Pereonite 2 only slightly shorther than pereonite 3; pereonite 4 longest. Pereonite 5 slightly shorter than pereonite 2, pereonite 6 and 7 smallest and shortest. Pereonite 1 with one pair of big dorsal spine-like tubercles, anteriorly directed. Pereonites 2-4 with two pairs of tubercles (one spine-like dorsal pair and one shield-like lateral pair). Dorsal pair of tubercles in pereonite 2-4 are big and high, apically flattened, covered with few hair-like small setae and small tubercle-like protrusions; in pereonites 5-7 these are smaller, more slender, apically acute but with blunt tip, and more laterally flattened. Lateral pair of tubercles are large in pereonites 2-4, smaller in pereonites 5-7. Evident elevations separated by deep grooves characterise the surface of pereonites 2-4, between the dorsal and lateral tubercles. Elevations are also present on pereonites 5-7. However, these are shallower, barely visible and uniformely covering the surface between the dorsal and lateral tubercles (Fig. 2A, B, Fig. 3A, B).

PLEOTELSON. All pleonites fused to pleotelson, frontolaterally of pleotelson two stout and slightly rounded protrusions, caudally directed (Fig. 2A, B, Fig. 3E). Pleotelson frontally broadest, narrowing caudally. Tip of telson acuminating, but with blunt tip, slightly rounded, slightly bent dorsally; subapical telsonic spines absent, but two pair of rounded big tubercles in two rows in the dorsal side of pleotelson; the pleotelson lacks in spines, but is covered entirely by medium-sized rounded protrusions, slightly smaller laterally (Fig. 2A, B, Fig. 3E).

PEREOPODS. P1 shorther than P2-7. Basis and propodus longest; basis with few distoventral and distolateral simple setae; a row of small protuberances on the lateral outer-directed side of the article. Carpus trapezoidal, ischium, merus and carpus densely covered with sensory spines, especially on ventral and lateral surfaces. Subchelate propodus broad, oval, dactylus shorter than propodus, with two short smooth claws (the ventral one shorter) and a small spine in between (Suppl. material 3). Ventral surface of propodus forming slightly concave "spoon", medial surface with few short simple bristles. Convex dorsolateral surface with long setulated setae, arranged in 6 transverse rows, the number of setae per row increasing distally (Fig. 2 C, Fig. 3C, Suppl. material 4). P2-4 similar, one strong spine dorsolaterally on basis of P2-P4, distodorsal margins of ischium, carpus and propodus without strong spines, but with rough cuticular surface; merus of P2-4 presents an evident protrusion on the dorsal surface of the distal part; important protrusion is also present dorsomedially on ischium of P2 and P4. Setation in P2-4 is similar, but most prominent in P2. Merus, carpus and propodus with groups of setae arranged in two ventral rows, each group consisting of one long seta and one short seta (Suppl. material 5). Small hairs present in all pereopods (Fig. 2F, G, H). P5-7 slightly shorter but subequal in length to P2-4. P5 with two long setae on basis, P6 and 7 without long setae. Basis of P5-7 presenting one stout rounded spine dorsolaterally, in addition to smaller spines;, stout spines are also present on carpus and merus (Fig. 2I, J, L, K). In P5-7 basis longest, ischium and propodus elongated compared to other articles; dactylus presenting a terminal claw with one simple seta in the terminal part. On propodus of P5-7 some feather-like bristles; all pereopods covered with small hairs (Fig. 2I, J, L).

UROPODS. Ventral surface of uropods covered with many simple hairs. Uropod elongated, both rami of uropods about subequal in length (Fig. 3E).

Diagnosis

The new species is characterized by one pair of large blunt anteriorly directed supraocular spines on the first pereonite. In dorsal view, these are long, divergent, forming a v-shape, reaching beyond the eyes. Pereonites 2-7 with only two pairs of tubercles: one dorsal pair of spine-like tubercles and one lateral pair of shield-like tubercles. Dorsal tubercles on pereonites 2-4 are big, apically flattened in lateral view, slightly anteriorly directed; on pereonites 5-7 these are smaller, slender, more pointed but apically blunt and upwards directed. Pleotelson with blunt, strong protrusions.

Etymology

The species is named *armata* for its long supraocular and the dorso-apical spine-like tubercles, not simple "shielded" tubercles like *Pseudidothea scutata*, but more like strong blunt "spines": as a contraposition to *P. scutata* meaning "that bears shield", *P. armata* sp. n. "bears weapons".

Distribution

Only known from type locality, the Burdwood Bank (Antarctica), found at 852 m.

Conservation

Specimen is stored and fixed with 96% ethanol in order to preserve it for further genetic analysis.

Remarks

Pseudidothea Ohlin, 1901 is clearly distinguishable from other genera by the oval shape of the body and peculiar conformation of pereonites and first pereopod. *P. bonnieri* was the type species representing the genus, it was described by Ohlin (1901) . Subsequently, it was synonymized with *P. miersi* (Studer 1884) because of the many similarities with the latter species. The genus is only known from the Southern Hemisphere and it is mostly known from the Antarctic Peninsula in the Southern Ocean. A record of *Pseudidothea* Ohlin, 1901 was also recorded in the Ross Sea (Fig. 1), although undetermined to species level (Mackay 2018). To date, four species belong to the genus *Pseudidothea* as referred to above (original names are presented; the type species is marked with an asterisk):

Pseudidothea hoplites - Poore and Bardsley (2004)

**Pseudidothea miersi* - Ohlin 1901

Pseudidothea richardsoni - Hurley 1957

Pseudidothea scutata - Stephensen 1947

Pseudidothea armata sp. n.

Differential diagnosis

Within the genus *Pseudidothea*, *P. scutata* (Stephensen 1947) is most similar to *P. armata* sp. n. in shape and spine pattern. The main differences are the large supraocular spines and general body armature, that significatively differs from the apically flattened tubercles in *P. scutata*; similar is also the position of the flattened tubercles dorsally located in every pereonites of *P. scutata*, however, all of these structures are more like blunt spines in *P. armata* sp. n. Another difference can be found in the extreme reduction of the elevations present in between lateral flattened tubercles and dorsal spine-like tubercles. Brandt and Wägele (Brandt and Wägele 1990) redescribed *P. scutata*, and illustrated flattened, irregular elevations on pereonites 5-7, while in *P. armata* sp. n. these are barely present. The pleotelson of *P. scutata* and *P. armata* sp. n. is similar in shape and tubercular pattern, however, it completely lacks pleotelsonic dorsal spines in *P. armata*, only rounded, short and strong tubercles are present in the latter species.

Supraocular spines of *P. armata* are long, dorsally pointed and anteriorly directed, reaching beyond the eyes in dorsal view. *P. scutata* presents supraocular tubercles that are shorter, dorsally flattened and do not reach the eyes on dorsal view. In addition, supraocular spines in *P. armata* are divergent, forming a v-shape in dorsal view, while in *P. scutata* the supraocular tubercles are aligned parallel. The body armature in the two species shows a different pattern of tubercles. In *P. armata*, dorsal tubercles are more similar to blunt spines, apically less flattened than those present in *P. scutata*. In particular, *P. armata*'s spine-like tubercles on pereonite 5-7 are not apically flattened at all but slender and pointed with a blunt apex, while in *P. armata* pereonite 5-7 have small apically flat tubercles. *Pseudidothea scutata* presents raised areas in lateral position, between the dorsal and lateral tubercles; these are marked on pereonites 5-7 and even described as distinct tubercles (Brandt and Wägele 1990, White 1992). *Pseudidothea armata* presents raised areas as well. However, elevations are more evident on pereonite 2-4, separated by deep grooves, making the surface between the dorsal and lateral tubercles look “wrinkly”, while elevations on pereonite 5-7 are less visible. Basis of P5 in *P. armata* has two long setae, only simple setae on P5 of *P. scutata*.

The pleotelson of *P. scutata* and *P. armata* is similar in shape and tubercular pattern, however, it completely lacks pleotelsonic dorsal spines in *P. armata*; only rounded, short and strong tubercles are present in the latter species.

Distribution

Only known from type locality.

Identification keys

***Pseudidothea* Ohlin, 1901**

This key to species is based to the *Pseudidothea* key persent in the work of Poore and Bardsley "Pseudidotheidae (Crustacea: Isopoda: Valvifera) reviewed with description of a new species, first from Australia" (Poore and Bardsley 2004).

1	Pereonites 2 and 3 with forked dorsolateral spines; all pereonites with lateral rows of blade-like ridges, each with anteriorly and posteriorly directed spines; tergites produced laterally over coxae to form a shield with 3 points	*Pseudidothea hoplites*
–	Pereonites with low or high flat tubercles; tergites produced laterally as large tubercles or rounded or flattened laterally	2
2	Pereon with large high flat tubercles; pereonite 1 with dorsal pair, pereonites 2–4 with dorsal and lateral pair and pereonites 5–7 with dorsal, dorsolateral and lateral pair; male pleopod 2 with appendix masculina twice as long as rami	*Pseudidothea scutata*
–	Pereonites with high tubercles, laterally flattened; rounded, short and strong tubercles	3
3	Pereonites with strong laterally flattened tubercles; supraocular spines dorsally pointed and anteriorly directed, reaching beyond the eyes, forming a "v" shape in dorsal view; pereonite 5-7 with small apically flat tubercles	*Pseudidothea armata* sp. n.
–	Pereon with low irregular tubercles; male pleopod 2 with appendix masculina and rami subequal	4
4	Uropodal exopod with a single strong setae, endopod with 3 pappose setae; antenna 2 peduncle with long fine setae on articles 3–5; pereopods without tubercles; male pleopod 1 endopod with 5 lateral spinules proximally, 5 apical plumose setae; exopod with 15 spinules on lateral margin, tapering distally to an obtuse apex	*Pseudidothea richardsoni*
–	Uropod rami each with single seta; antenna 2 peduncle with short setae on articles 3–5; pereopods with tubercles; male pleopod 1 endopod with plumose setae marginally; exopod with 16–17 spinules laterally, with acute apex bent outwards	*Pseudidothea miersii*

Acknowledgements

We are indebted with Dr. Huw Griffiths, PI of the Cruise JR15005, which part of the Biodiversity, Evolution and Adaptation team of the Environmental Change and Evolution Programme at the British Antarctic Survey (BAS). Thanks are due to Claudio Ghiglione for sorting and fixation of the Rauschert materials. Compelling and sincere are the thanks to the Senckenberg Institute Crustacea Section of the Marine Zoology department and to the Italian National Antarctic Museum (MNA, Section of Genoa) and their respective staffs for the continuous support and collaboration. This paper was written during the Erasmus+ experience of the first author.

1	Pereonites 2 and 3 with forked dorsolateral spines; all pereonites with lateral rows of blade-like ridges, each with anteriorly and posteriorly directed spines; tergites produced laterally over coxae to form a shield with 3 points	*Pseudidothea hoplites*
–	Pereonites with low or high flat tubercles; tergites produced laterally as large tubercles or rounded or flattened laterally	2
2	Pereon with large high flat tubercles; pereonite 1 with dorsal pair, pereonites 2–4 with dorsal and lateral pair and pereonites 5–7 with dorsal, dorsolateral and lateral pair; male pleopod 2 with appendix masculina twice as long as rami	*Pseudidothea scutata*
–	Pereonites with high tubercles, laterally flattened; rounded, short and strong tubercles	3
3	Pereonites with strong laterally flattened tubercles; supraocular spines dorsally pointed and anteriorly directed, reaching beyond the eyes, forming a "v" shape in dorsal view; pereonite 5-7 with small apically flat tubercles	*Pseudidothea armata* sp. n.
–	Pereon with low irregular tubercles; male pleopod 2 with appendix masculina and rami subequal	4
4	Uropodal exopod with a single strong setae, endopod with 3 pappose setae; antenna 2 peduncle with long fine setae on articles 3–5; pereopods without tubercles; male pleopod 1 endopod with 5 lateral spinules proximally, 5 apical plumose setae; exopod with 15 spinules on lateral margin, tapering distally to an obtuse apex	*Pseudidothea richardsoni*
–	Uropod rami each with single seta; antenna 2 peduncle with short setae on articles 3–5; pereopods with tubercles; male pleopod 1 endopod with plumose setae marginally; exopod with 16–17 spinules laterally, with acute apex bent outwards	*Pseudidothea miersii*

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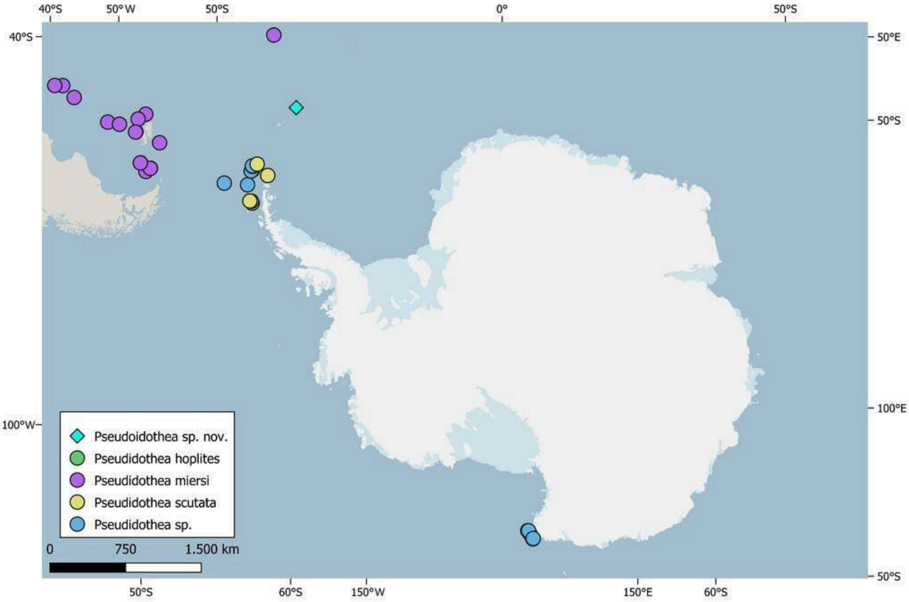

Figure 1.

Distribution records of *Pseudidothea* Ohlin, 1901 in Southern Ocean. Light blue square represents the location of *Pseudidothea armata* sp. n, recorded during the SO-AntEco JR15005 RRS James Clark Ross expedition, in Burdwood Bank area (South Orkneys) in the framework of the British Antarctic Survey (BAS), 2016.

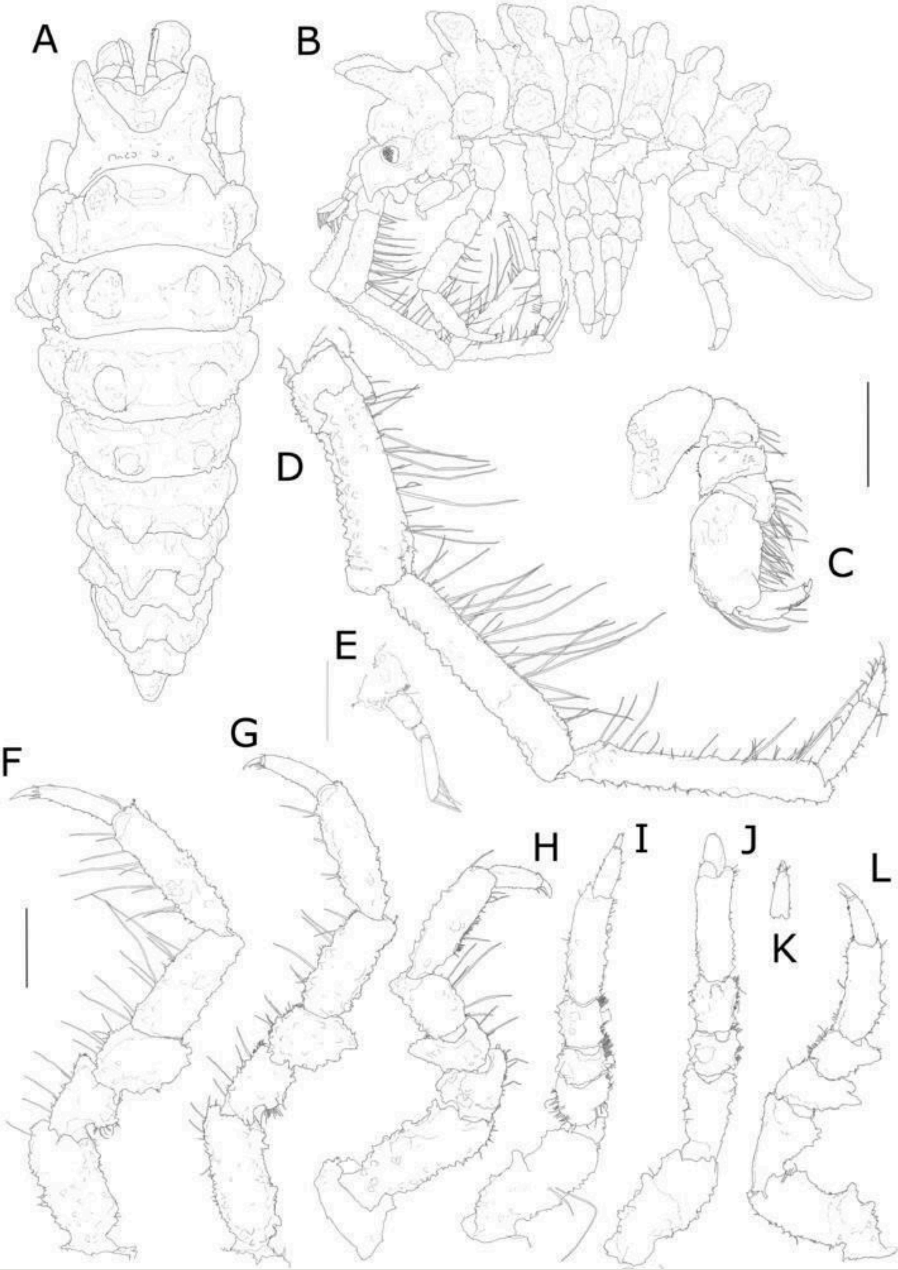

Figure 2.

Pseudidothea armata sp. n. male holotype (MNA 10749). **A** dorsal view **B** lateral view **C** P1 Scale refers to 0.5 mm length. **D** A2 **E** A1 **F** P2 **G** P3 **H** P4 **I** P5 **J** P6 **K** Dactylus of P6 **L** P7. Scale refers to 1 mm length for **D-L**.

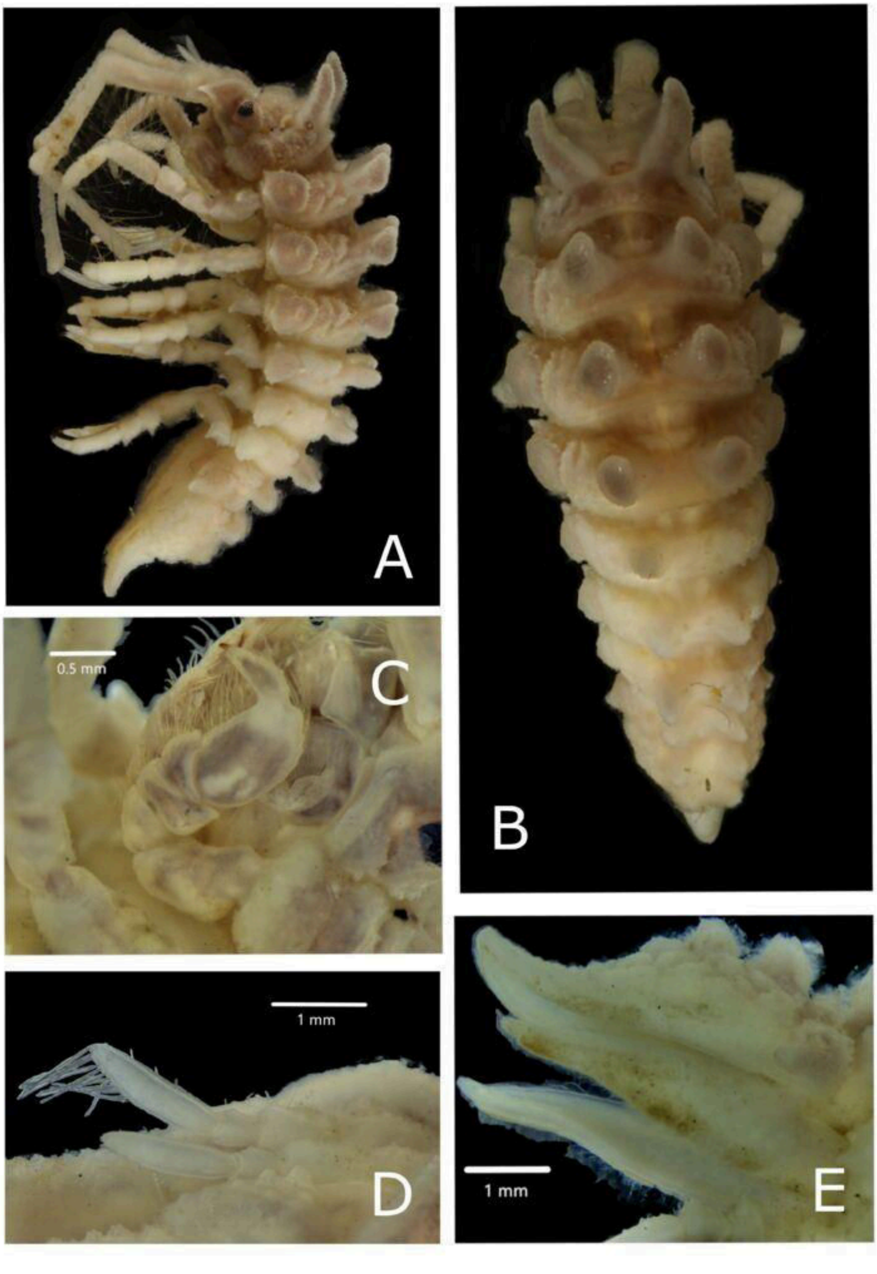

Figure 3.

Pseudidothea armata sp. n. male holotype (MNA 10749). **A** stack photo of lateral view **B** stack photo of dorsal view **C** stack photo of P1, scale bar represents 0.5 mm **D** stack photo of A1, scale bar represents 1 mm **E** stack photo of pleotelson. Scale bar represents 1 mm length.

7. General Discussion

In the present thesis, I investigated the distributional patterns, abundance and diversity of peracarid crustaceans collected using an epibenthic sledge (EBS) in three different areas from the Atlantic sector of the SO: the seasonally ice-covered Filchner Trough area, the ice free South Orkney Islands and the Prince Gustav Channel which has been partly covered by ice until the 1995, year in which the ice-shelf collapsed.

The overall abundance of peracarids was consistent with previous studies, in which amphipods dominated (Brökeland et al. 2007; Kaiser et al. 2008) (**Chapter I, II**). In this thesis, peracarid abundances varied between sampling locations and areas. The variability in peracarid abundances was previously shown in previous studies from the SO continental shelf, slope and deep sea (Linse et al. 2002; Lörz and Brandt 2003; Brökeland et al. 2007; Kaiser et al. 2008). The extreme variability in abundance recorded in peracarid crustaceans is probably driven by the different environmental conditions characterising the different areas and sampling locations (Kaiser et al. 2007; Meyer-Löbbecke et al. 2014; Brandt et al. 2016). It could be argued that sampling bias is causing these differences in abundance, because it is usual to perform one single replicate for each sampling location due to logistic reasons. However, in this thesis a few stations were sampled with two replicates and also in this case, abundances varied greatly between them. Furthermore, it was possible to identify a pattern in abundance between the areas investigated, abundances increased towards lower latitudes in the Filchner Trough area (**Chapter I**). In 2007, Brandt et al. described an increase in abundance and species richness from the Scotia Arc area towards the Southern Weddell Sea (2007c).

7.1. Influence of environmental variables on peracarids from the Atlantic sector of the SO

The Filchner Trough was not only the sampling location where the highest peracarid abundance was recorded but also the area where the highest number of isopod species was found (**Chapters I, IV**). It is possible that the higher isopod diversity in this location is related to the high rate of floating icebergs that characterise the Filchner Trough. A recent study showed that iceberg scouring may play an important role in maintaining high diversity levels in SO benthic communities (Robinson et al. 2021). As aforementioned in the introduction, iceberg scouring can enhance the heterogeneity of the habitat and increase benthic diversity through intermediate disturbance. However, further analyses performed at species level (**Chapter IV**) showed that sea-ice extent is the key environmental variable shaping abundance, composition and species richness of benthic peracarids. Results showed a strong significant correlation between peracarid abundance and isopod species richness, with these two latter increasing with increasing sea-ice concentrations.

At date, studies investigating the influence of environmental variables on peracarid crustaceans are not numerous. Sediment type and depth have been identified as important factors driving faunal abundance and composition patterns in SO peracarids (Brandt et al. 2007b; Rehm et al. 2007). Among other investigated environmental variables are salinity, temperature, oxygen, nitrate, silicate, longitude, latitude, surface chlorophyll-a (Brandt et al. 2005, 2007a, 2009, 2016; Brökeland et al. 2007; Meyer-Löbbecke et al. 2014). However, no studies investigating the influence of sea-ice coverage on SO benthic peracarids were performed, thus the present thesis represents the first study assessing this.

Interestingly, chlorophyll-a, primary productivity and iron were also identified as physical variables affecting peracarid assemblages (**Chapters I, IV**). This allowed me to better understand the mechanisms through which sea ice influences the benthos.

Sea ice hosts very large communities of sympagic algae and sympagic fauna (Lizotte 2001; Thomas and Dieckmann 2002), when sea ice melts, these communities are released in the water column. As a result, sea-ice algae trigger enormous phytoplankton blooms, increasing the productivity in the surrounding area thus increasing the availability of food particles available for the benthos (Jin et al. 2007; Gradinger 2009). In addition, SO phytoplankton is strongly limited by the availability of iron. This latter accumulates in large quantities in the thickness of sea-ice layers (Lannuzel et al. 2020). Thus, sea-ice dynamics and the consequent seasonal pulses of iron into the water column highly increase primary productivity. Moreover, sympagic fauna released increase the sinking organic matter available to the benthos through secondary production (e.g. when they die and sink to the seafloor or through the production of faecal pellets), as well as the organic products of sympagic microbial communities (Arrigo and Thomas 2004; Wing et al. 2018).

Previous studies investigated the effects of changing sea-ice concentrations on SO benthic biomass (Pineda-Metz et al. 2020) and SO planktonic diversity (Lin et al. 2021). However, while the first study focuses only on biomass of benthic fauna identified at a high taxonomic level, the second study does not go further than the genus level. As a result, these two studies are far from understanding the influence that changing sea-ice concentration can have on SO species diversity. Lin´s study investigates only seven different genera of phytoplanktonic diatoms from the Western Antarctic Peninsula. In addition, the pelagic ecosystem is highly affected by short-time environmental changes that cause shifts in community composition. In contrast, the benthos is less affected by short-term changes and it is more vulnerable to long-term ones. Thus, identifying negative consequences of environmental changes on the benthos is compelling. The present thesis identified a reduction of sea-ice coverage as a threat for benthic isopod biodiversity and peracarid assemblage structure and abundance. The climate-change driven sea-ice reduction will change peracarid composition and reduce the number of isopod species, with a major threat for those species that will not be able to adapt (Griffiths et al. 2017). This latter threat was highlighted in **Chapter IV**, where a higher number of rare species and specialist species were reported in sampling locations characterised by higher concentrations of sea ice. For example, four different species of the selective phytodetritivore family Macrostylidae Hansen, 1916 and seven selective deposit-feeding species belonging to the family Ischnomesidae Hansen, 1916 were found in stations present high sea-ice concentrations, while only one species of Ischnomesidae and no macrostylids were found at stations of lower sea-ice concentrations. The same pattern was observed in species belonging to the sponge-commensal family Dendrotionidae Vanhöffen, 1914. A previous study showed that sponge communities show a positive correlation with sea ice, therefore higher abundances of sponges might represent a favourable habitat for dendrotionid species. The climate-driven reduction of sea-ice extent will hamper dendrotionid communities as well as other specialist and rare species that are not able to quickly adapt to drastic changes in time.

This suggests that specialist and rare species are particularly vulnerable to climate change due to the increasing temperatures and the consequent reduction of sea-ice extent. However, all peracarids are ectotherm and stenothermal organisms (Young et al. 2006; Peck et al. 2010), thus particularly vulnerable to changing conditions and rising temperatures. Previous studies performed on amphipods showed that warmer temperatures can affect their respiration and growth rate, impacting their mobility and feeding habits (Auel and Ekau 2009; Ingels et al. 2012); warmer temperatures interfere with the transcription of muscle proteins altering the rate of protein synthesis. Changes in primary productivity and thus in the quantity and quality of food will have consequences for peracarid species. The quality and quantity of food can affect the egg development in SO isopods, these are larger than those of tropical and boreal isopods (Wägele 1987, 1988; Ingels et al. 2012). In addition, changes in primary productivity can cause shifts in foraminiferan abundance (Katz et al. 2010), this would affect those isopods that have made of foraminiferans one of their main food source, such as munnopsids and haploniscids (Svavarsson et al. 1993; Gudmundsson et al. 2000; Brökeland et al. 2010).

A reduction in peracarid diversity or abundance would have a strong impact the entire SO ecosystem. Among the reasons is that peracarid crustaceans play a key role in SO ecosystem, they process the organic matter and transfer it through the food web, up to the top predators. Recently, researchers found that sea-ice dynamics can strongly affect and alter the food-web structure, suggesting that these changes may affect benthic invertebrates' diets, especially in zoobenthos that lack dispersing larvae and/or are restricted in mobility (Michel et al. 2019). For example, the study showed that the diet of the echinoderms *Odontaster validus* Koehler, 1906 and *Sterechinus neumayeri* (Meissner, 1900) shifted towards a more sympagic-based diet due to variations in sea-ice seasonality. Similar results on *Sterechinus neumayeri* (Meissner, 1900) were reported by Rossi et al. in the Ross Sea (2019).

Wing et al. (2018) showed that the mollusc *Laternula elliptica* (P. P. King, 1832) from the Ross Sea increased the percentage of sympagic component in its diet in locations characterised by higher sea-ice extent. Another recent study found that sea-ice break-up and its associated input of sympagic algae alters the structure of the food-web, for example predator and scavenger species such as the soft coral *Alcyonium antarcticum* Wright & Studer, 1889 and the anemone *Urticinopsis antarctica* (Verrill, 1922) had a narrower range of resources in their diet (Caputi et al. 2020). In light of this latter study, the reduced abundance and diversity of peracarid crustaceans due to a decline in sea-ice concentration would thus probably threaten predator species along the food web, because for example, 60 million tons of amphipods are consumed every year within the Antarctic food web (Dauby et al. 2003).

This chapter of the thesis showed that - unfortunately - this threat is not limited to the continental shelf only but also extends to the deep sea. Analyses including deep-sea stations (up to ~4900 m), showed that a reduction in sea-ice concentration will yield lower diversity also in this remote environment. Deep-sea environments are stable and this stability was identified as one of the possible causes of their diversity (R. Hessler and L. Sanders 1967), however (surprisingly) climate-driven changes have started to be recorded also at exceptional depths. (Strass et al. 2020). This latter cited study showed that the mean heating rates below 2000 m in the deep Weddell Sea is five time that of the global ocean. This warming has been attributed to changes of the Weddell Gyre strength and its interaction with the ACC and to variations in sea-ice coverage which can modify the heat loss from ocean to atmosphere and alter radiative fluxes (Strass et al. 2020).

7.2. Influence of environmental variables on SO peracarid assemblages: perspective on a large geographic scale

Results of the present thesis discussed in the previous paragraphs were obtained performing analyses on peracarid samples from areas that are linked by the Weddell Gyre. The Weddell Gyre is one of the main currents of the SO, it branches off from the warmer and more saline ACC north of the Antarctic Peninsula extending 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).

When the influence of environmental variables on peracarid assemblages is investigated on a much larger scale and different water masses are included (e.g. sampling locations from the South Atlantic Ocean), results give us a different point of view with additional information. In this case, the main variable driving peracarid assemblage dissimilarities in abundance and peracarid composition is depth (Chapter III). In the introductive paragraph of this thesis, I mentioned that different peracarid crustacean orders show different composition and diversity patterns in relation to depth. This statement could be validated in Chapter III. Results showed that while isopod abundance is positively correlated with depth, the abundance of amphipods and mysidaceans is negatively correlated. Cumaceans and tanaidaceans did not show any correlation. An increase of isopod abundance towards the deep sea can be caused by the higher number of species that thrive in this environment compared to those inhabiting the shelf and compared to amphipod species that, in contrast, are more abundant on the shelf (De Broyer and Jazdzewska 2014; Kaiser 2014). In addition, it is possible to suggest that at a large geographical scale depth is the main physical driver due to the marked environmental differences between continental-shelf and deep-sea environments. In this regard, Chapter III showed a clear dissimilarity in abundance between peracarid assemblages from the continental-shelf and those from the deep sea. It was possible to identify the level of occurrence of continental-shelf peracarid fauna at up to 1500 m depth, while assemblages from the deep sea where identified at depth > 1500 m. This result provides evidence of the geomorphological history of the SO; the weight of ice masses suppressed the continent, increasing the depth of the shelf (Clarke et al. 2009), while scouring events caused the erosion of the continental shelf and formed local basins down to 1500 m depth (Clarke et al. 2009). The different results obtained when investigating peracarid abundances on a large geographic scale are the consequence of an assessment performed at a lower resolution. When large geographic scales are considered, analyses will include a high rate of environmental heterogeneity (e.g. water bodies, primary productivity rate, presence/absence of ice, current regimes) that might hamper the interpretation of the results. Kaiser et al. (2007) showed the importance of the different geographic scale when the distribution and abundance of benthic communities and assemblages are investigated, suggesting that smaller-scale analyses are more informative compared to large-scale ones: "our findings suggest that focus on what drives differences in abundance at local scale may ultimately advance our knowledge more." (Kaiser et al. 2007). Benthic patterns over a broad range of spatial scales are derived from a variety of physical, chemical, and biological factors; for example, factors like food supply and hydrodynamics can affect abundance and distribution at small scales, while others like biogeochemistry and disturbance can affect abundance and distribution at larger geographic scales (Thrush et al. 2005; Kaiser et al. 2007; Gutt et al. 2019). A recent study on nematodes from the SO showed that different environmental variables explained the nematode community structure on different spatial scale (Hauquier et al. 2018). The authors suggested that at a small spatial scale the level of heterogeneity is low and biotic interactions are probably the main drivers affecting nematode communities; at larger spatial scales they found a substantial increase in the environmental heterogeneity and identified hydrodynamic features such as the Weddell gyre and the circumpolar current, as possible driving forces.

7.3. New SO isopod species identification through integrative taxonomy

The fifth chapter of the thesis provides the description of two new SO species of the genus *Notopais*, belonging to the family Munnopsidae, the most dominant and species-rich group of deep-sea isopods. The genus *Notopais* is endemic of the Southern Hemisphere, it includes a total of nine species distributed exclusively in the Southern Hemisphere (Merrin 2004): *Notopais beddardi*, Merrin 2004, discovered off Cumberland Bay, Kerguelen Island, in the Southern Indian Ocean; *Notopais echinatus* Merrin and Bruce, 2006 from the continental slope of the Eastern Australia, Tasman Sea; *Notopais euaxos* Merrin and Bruce, 2006 from New Zeeland, South Island; *Notopais magnifica* (Vanhöffen, 1914) from the SO; *Notopais minya*, Merrin 2004 from the Eastern Australia; *Notopais quadrispinosa* (Beddard, 1886), largely distributed in the Southern Hemisphere, including the SO, South Atlantic Ocean and South Indian Ocean (Kerguelen Islands) (Brandt 1990; Merrin 2004); *Notopais spicatus* Hodgson, 1910 from the SO and Southern Indian Ocean (Crozet Islands) (Kensley 1980); *Notopais spinosa* (Hodgson, 1902) from the SO; *Notopais zealandica* Merrin, 2004 from the Chatham Rise, New Zeeland (Merrin 2004).

Species of this genus can be easily distinguished by the dorsal spine pattern of their pereonites and for the presence/absence of tubercles on these latter. *Notopais sp.1* n.sp. can be distinguished by the spine pattern on its pereonite 4. It is the only described SO species of

Notopais not having any dorsal spines on its dorsal surface, except for the two small spines on top of the inner pair of four tubercles. *Notopais sp.2* n. sp. can be distinguished by the presence of six dorsal spines on pereonite 4 and two tubercles on peronite 5, unique features characterising this species. *Notopais sp.1* n. sp. and *Notopais sp.2* n. sp. share a new autapomorphic feature, the presence of two tubercles on their pereonite 6 that are absent in all other SO *Notopais* species. The two new species, *Notopais sp.1* n. sp. and *Notopais sp.2* n. sp., were discovered in the Filchner Trough area and in the South Orkney Islands respectively and are only known from their type locality. However, all other SO *Notopais* species present a circumpolar distribution (Figure 1, Chapter V). Given the brooding nature of isopods and thus their reduced dispersal mobility, a possible explanation for their remarkable wide distribution can be given by the evolutionary history of the Antarctic continent. Previous studies showed an affinity between species from the Weddell Sea and those from the Ross Sea (Barnes and Hillenbrand 2010; Pierrat et al. 2013). They assumed that a possible collapse of the Western Antarctic Ice Sheet in the Late Quaternary determined the opening of a seaway in the West Antarctica, connecting the two aforementioned seas and thus their species communities.

The morphological distinction between the two new *Notopais* species was supported by COI barcoding. My thesis work provides the first COI sequences from *Notopais* species ever obtained. Previous attempts were tried by Osborn (personal communication) without success. The latter author recently published the most comprehensive genetic study performed on munnopsid isopods (Osborn 2009). In her study, Osborn investigated the phylogeny of munnopsid isopods using three different markers (18S, 28S and COI). However, the author provided the sequence of only one described *Notopais* species (18S sequence, the other two markers did not produce any valid results). Integrative taxonomy by means of COI barcoding has been successfully used to describe new isopod species from the SO (Riehl and Kaiser 2012), however studies using COI sequences from SO isopod crustaceans are still not numerous. One possible explanation is the higher efficiency of other genetic markers (e.g. the 16S subunit of the ribosomal RNA) as it was demonstrated in a recent study in which COI sequencing had only ~40% and ~50% rate of success in Macrostylidae and Munnopsidae isopods respectively (Riehl et al. 2014). Integrative taxonomy was successfully used also on other SO peracarid crustaceans such as Podosiridae and lysianassoid amphipods (Havermans et al. 2010, 2011; Ashford et al. 2020), Neotanaid tanaidaceans (Araújo-Silva et al. 2015) as well as on other SO taxa; for example, the family Pterasteridae (Asteroidea) (Jossart et al. 2021), the cephalopod *Asperoteuthis lui* Salcedo-Vargas, 1999 (Braid 2017), fishes of the genus *Macrourus* and other SO fishes (Smith et al. 2011, 2012). COI has been useful not only as a complementary tool to the identification of species, but also to study patterns of genetic connectivity and diversity among peracarid assemblages and other taxa inhabiting the SO. For example, several Circum-Antarctic species such as the pycnogonid *Colossendeis megalonyx* Hoek, 1881, the mollusc *Doris kerguelenensis* (Bergh, 1884) and amphipod species of the genus *Epimeria* revealed to include a series of putative species that may be sympatric (Krabbe et al. 2009; Wilson et al. 2009; Lörz et al. 2009). However, in some cases the real distribution ranges of the species studied have become unexpectedly large even for species with (potentially) limited dispersal abilities, as it was shown for example in the Circum-Antarctic sea spider *Nymphon australe* Hodgson, 1902 (Arango et al. 2011). In these cases, the so called stepping-stone models could be considered one of the possible alternative dispersal mechanisms maintaining the gene flow (Baird et al. 2012). A similar study was performed on the SO isopods of the genus *Glyptonotus*, however in this case a different genetic marker was used (the mithocondrial 16S ribosomal gene) (Held and Wägele 2005).

Recent studies showed that complete mitochondrial genomes are useful for the systematic and phylogenetic reconstruction of marine isopods (Kilpert and Podsiadlowski 2006; Shen et al. 2017; Yu et al. 2018) and these can be especially useful to obtain COI sequences when the primer efficiency and DNA quality are too low. Almost thirty years have passed since the first complete mitogenome from an arthropod was obtained (Clary and Wolstenholme 1985), while in 2017 Shen et al. reported that there have been 1,160 Arthropoda mitogenomes determined and only three complete mitogenomes available within the Isopoda order (2017). In the last three years more and more complete mitogenomes of terrestrial, marine and brakish-water isopod species have been sequenced: *Cymothoa indica* Schioedte & Meinert, 1884 (Zou et al. 2018), *Argeia pugettensis* Dana, 1853, *Tachaea chinensis* Thielemann, 1910, *Ichthyoxenos japonensis* Richardson, 1913, *Ligia oceanica* (Linnaeus, 1767), *Ligia (Megaligia) exotica* Roux, 182, *Mongoloniscus sinensis* (Dollfus, 1901) (Yang et al. 2021), *Sphaeroma terebrans* Bate, 1866 (Yang et al. 2019), *Gyge ovalis* (Shiino, 1939). Nevertheless, sequences of SO isopods were still unavailable before the present research thesis, while complete mitogenomes of SO taxa available were, for example, those from fishes such as *Bathyraja eatonii* (Günther, 1876) (Kim et al. 2021), *Trematomus loennbergii* Regan, 1913 (Choi et al. 2021), *Notothenia rossii* Richardson, 1844 (Jo et al. 2020) or birds such as the Antarctic *Pagodroma nivea* (Forster, 1777) (Kim and Kim 2020) and *Eudyptes chrysolophus* (Brandt, 1837) (Kim and Kim 2021), the annelid *Polyeunoa laevis* McIntosh, 1885 (Bogantes et al. 2020). The aforementioned studies showed that mitochondrial sequences can be very useful for phylogenetic analyses, they can also serve as models of gene rearrangement and genome evolution due to the difference in rates of evolutionary change in different segments of the mitogenome (Liebers et al. 2004; Helfenbein et al. 2004; Shen et al.

2017), the gene order (Roehrdanz et al. 2002; Shen et al. 2017), and the RNA secondary structure (Macey et al. 2000; Shen et al. 2017). For example, mitogenome analyses revealed to be very useful to study the evolution, phylogeny and gene structure of marine deep-sea and shallow-water isopods (Lloyd et al. 2015; Shen et al. 2017), as well as freshwater ones (Kilpert and Podsiadlowski 2006). In light of all this, in the present research thesis it is proposed to use the mitogenome (or whole genome when possible) to characterise new species holotypes, as phylogenetic and taxonomic studies will benefit from the availability of comparable and useful materials, even in those situations where previously designed primers cannot provide COI sequences.

8. Conclusions

The present thesis aimed to expand the knowledge on SO peracarid assemblage abundance patterns and diversity and to investigate the influence of environmental variables across different geographic scales. Results from the thesis confirmed the remarkable abundance and diversity of SO peracarids, and showed that benthic assemblages are governed by processes operating at different spatial scales. Sea ice was identified as the most significant environmental variable affecting peracarid abundance and composition, and isopod diversity at a small scale (Weddell Sea), while depth was the main factor shaping peracarid assemblage structure and composition on a larger scale (Weddell Sea and South Atlantic Ocean). These results provide valuable data that are useful to predict the consequences of the ongoing climate change on their abundance, diversity and composition. In light of the present thesis results, it is possible to conclude that a future climate-change driven reduction in sea-ice extent and changes in its dynamics (e.g. seasonality), would highly threaten benthic peracarid diversity and abundance, due to changes in the productivity in the water column and thus the availability of organic matter available for the benthos. As aforementioned in the previous paragraphs of this thesis, peracarids are brooders and ectothermic, thus particularly vulnerable to environmental changes; given the important role that they play in the ecosystem, changes in their diversity, composition and abundance will have consequences through the SO food-web. Also, regions that were characterised by higher sea-ice concentrations showed a high number of rare and specialist isopod species (species that present a limited/specific diet). Specialist species that rely on a specific food source and are not able to migrate elsewhere are likely to face extinction, while opportunistic species would probably dominate. Ultimately, during the thesis research a total of four new isopod species were discovered and described by classic taxonomy. Two of these new species were also identified by integrative taxonomy (COI barcoding) and new generation sequencing methods were used to provide their complete genomes and mitogenome. This is the first time that whole genome sequencing has been successfully performed on isopod species from the SO. These results (and those from previous studies are discussed in this thesis, e.g. ANDEEP expeditions), showed that the knowledge on SO benthic isopods is still far from being completed and their diversity is most probably still underestimated. Also, genetic whole genome and mitogenome analyses-successfully performed for the first time in SO isopods - revealed to be a successful tool for the extraction of COI sequence data from difficult samples. Thus, new generation sequencing can be very useful for the identification of species through integrative taxonomy.

9. Future perspectives

In light of all this it is possible to conclude that the present thesis represents a significant contribution to the Antarctic research, providing data on the vulnerability of the SO benthos to future climate change as well as valuable information about how to improve the efficiency of DNA barcoding in SO isopodcrustaceans with new generation sequencing methods.

It is of the outmost importance to expand analyses performed in this thesis on isopod species diversity to all other peracarid orders. This will give us important information to assess the response of different species to a changing environment. In addition, it would be as well important to extend these studies to different benthic taxa (e.g. different classes and phyla), single species may appear vulnerable to environmental changes, but communities and ecosystems may be more resilient (Clarke et al. 2007), further studies are thus needed. Expanding the investigation to a wider range of taxa will give us useful information on how the different species will respond to future environmental changes. While for some species climate change can be a threat (e.g. specialist species), other species can be advantaged by it (e.g. opportunistic species). Further analyses will help us understand these mechanisms and understand which SO taxa are more or less vulnerable to changes in sea-ice concentrations.

The subsequent closing of the seaway connecting the Ross Sea and the West Antarctica probably reduced the gene flow between these two areas (Pollard and DeConto 2009). This could slowly lead to speciation processes and genetic differentiation between assemblages from the two areas. In the Antarctic environment, molecular analyses have already been used to evaluate the distribution of diversity at specific levels or to test the role of physical barriers to the gene flow, such as the Polar Front. It would be extremely interesting to investigate such processes in the genus *Notopais* in the SO and assess the identity and genetic connectivity between samples from different areas, in particular those from the Ross Sea and the Weddell

Sea. During the PhD I had the opportunity to elaborate a research proposal aiming to investigate this and to assess the oceanographic features that shaped the present distribution of isopods in the SO. In addition, the proposal aims to investigate migration events around and in/out the SO using different genetic markers (including COI barcoding). The present thesis significantly increased our understanding of peracarid diversity and composition from different SO areas in relation to different environmental conditions, thus it represents an important starting point for future studies that aim to increase our knowledge on the past, present and future consequences of a changing environment on the SO benthos.

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