Endobenthic communities of the Antarctic Peninsula and the Weddell Sea shelf - their composition, diversity and functional traits in relation to environmental drivers

Kumulative Dissertation
zur
Erlangung des akademischen Grades
Doctor rerum naturalium (Dr. rer. nat.)
der Mathematisch-Naturwissenschaftlichen Fakultät
der Universität Rostock

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https://doi.org/10.18453/rosdok_id00004511

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Jahr der Einreichung: 2023

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Jahr der Einreichung: 2023

Verteidigung: 03.11.2023

Für meine Eltern – danke!

„Wessen wir im Leben am meisten bedürfen, ist jemand,
der uns dazu bringt, das zu tun wozu wir fähig sind.“

Ralph Waldo Emerson

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Abstract

The seafloor of the Southern Ocean (SO) holds a considerable level of biodiversity, partly due to a mix of exceptional environmental conditions. However, this unique Antarctic benthic biodiversity is under increasing pressure as changes in sea-ice cover in the SO have a major impact on sensitive benthic organisms which rely on food input from the surface to the seafloor. Still we know surprisingly little about the endobenthic diversity, including meio- and macrofauna organisms, in the SO, and how it is shaped, assembled and structured, so it is difficult to predict changes related with climate change.

This thesis aims to provide an understanding of the endobenthic biodiversity by linking taxonomic and functional aspects on species and community level with environmental drivers in the regions Antarctic Peninsula (AP) and southeastern Weddell Sea (WS). More specifically I study, which endobenthic organisms exist under different ice-cover regimes, how these are distributed across the study regions, and how seafloor food availability, sediment texture, sea-ice cover and water-column parameters influence the endobenthos. I used fauna and environmental sediment data (grain size, TOC: total organic carbon, total nitrogen, pigment content) and water-column data (temperature, salinity, chlorophyll *a*) that were collected from three expeditions with the RV *Polarstern* (PS81: chapter I, II, III; PS96: chapter I, II, III; PS118: chapter III). Sea-ice cover data were compiled from 2010–2019. Nine environmental parameters presented as raster grids were used for the bioregionalization approach in chapter III (e.g. TOC, current speed).

I provided the first integrated analysis of Antarctic meio-and macrofauna communities in relation to their environment and their responses under different ice-cover regimes in the AP and WS region (chapter I). Meiofauna communities differed significantly between almost all ice-cover regimes, whereas macrofauna or the combined meio- and macrofauna communities differed only between some regions. Environmental drivers differed for the two faunal size classes explaining > 66% of the variation among different meio- and macrofauna communities, but 1-year ice cover and chlorophyll *a* were most important drivers for both community compositions.

Further, this thesis contributed to the knowledge of endobenthic diversity in the AP and WS region on the species level by describing a new Ampharetidae (Polychaeta, Annelida) species and including an identification key for all known *Anobothrus* species (chapter II). By linking taxonomic, functional and environmental information, I showed that the hemi-sessile deposit feeder *Anobothrus konstantini* Säring & Bick, 2022, may favor constant ice-cover regimes with a low food availability at the seafloor. Such combinations provide an essential basis for modelling habitat and species distribution and an important tool for conservation management of the SO ecosystem.

Finally, I to improve knowledge of endobenthic spatial distribution patterns I investigated the biodiversity of polychaetes, a dominant group in soft-bottom ecosystems (chapter III). Results showed heterogeneous polychaete communities, namely 6 taxonomic and 5 functional community types. Ice-cover variation and TOC were major drivers, explaining > 39% of the community patterns with a stronger link to functional than taxonomic communities. While the bioregions based on environmental surrogates (*k*-means cluster algorithm) did not capture the complex faunal distribution patterns, I could identify areas within the survey regions with heterogenous community compositions, e.g. the Filchner Trough region, that are potentially vulnerable.

With this comprehensive study of endobenthic diversity, I highlighted that predicting their spatial distribution patterns was challenging, potentially due to its complex structure compared to epibenthos. I propose including meiofaunal data in future assessments, as these were strongly linked to ice-cover and food-related parameters, which could make climate change effects more noticeable. Further assessments of environmental change on the Antarctic benthic ecosystem should incorporate functional and taxonomic information along with several ice-cover and food-related parameters. The results underscore that filling spatial gaps in faunal and environmental data it is crucial to apply advanced models (e.g. Species Archetype Models) in order to establish reliable conservation strategies for vulnerable areas in the SO.

Zusammenfassung

Der Meeresboden des Südlichen Ozeans (SO) beherbergt eine beachtliche Artenvielfalt, was zum Teil auf eine Kombination von außergewöhnlichen Umweltbedingungen zurückzuführen ist. Diese einzigartige biologische Vielfalt des antarktischen Meeresbodens steht jedoch unter zunehmendem Druck, da Veränderungen der Meereisbedeckung im SO erhebliche Auswirkungen auf empfindliche benthische Organismen haben, die auf den Nahrungseintrag von der Oberfläche zum Meeresboden angewiesen sind. Noch immer ist erstaunlich wenig über die endobenthische Vielfalt im SO bekannt, einschließlich der Meio- und Makrofauna, und darüber, wie sie geformt, aufgebaut und strukturiert ist, sodass es schwierig ist, Veränderungen im Zusammenhang mit dem Klimawandel vorherzusagen.

Ziel dieser Arbeit ist es, die endobenthische Biodiversität zu verstehen, indem taxonomische und funktionale Aspekte auf Arten- und Gemeinschaftsebene mit Umweltfaktoren in den Regionen Antarktische Halbinsel (AP) und Südöstliches Weddellmeer (WS) verknüpft werden. Dabei untersuchte ich konkret, welche endobenthischen Organismen unter verschiedenen Eisbedeckungsregimen vorkommen, wie diese über die Untersuchungsregionen verteilt sind und wie die Nahrungsverfügbarkeit am Meeresboden, die Sedimentbeschaffenheit, die Meereisbedeckung und die Wassersäulenparameter das Endobenthos beeinflussen. Ich verwendete Daten zur Fauna und zur Sedimentumgebung (Korngröße, TOC: gesamter organischer Kohlenstoff, Gesamtstickstoff, Pigmentgehalt) sowie Daten zur Wassersäule (Temperatur, Salzgehalt, Chlorophyll *a*), die auf drei Expeditionen mit der RV Polarstern gesammelt wurden (PS81: Kapitel I, II, III; PS96: Kapitel I, II, III; PS118: Kapitel III). Die Daten zur Meereisbedeckung wurden von 2010 bis 2019 zusammengestellt. Neun als Raster dargestellte Umweltparameter wurden für den Bioregionalisierungsansatz in Kapitel III verwendet (z. B. TOC, Strömungsgeschwindigkeit).

Ich habe die erste integrierte Analyse der antarktischen Meio- und Makrofauna-Gemeinschaften in Bezug auf ihre Umwelt und ihre Reaktionen unter verschiedenen Eisbedeckungsregimen in der AP- und WS-Region durchgeführt (Kapitel I). Die Meiofauna-Gemeinschaften unterschieden sich signifikant zwischen fast allen Eisbedeckungsregimen, während sich die Makrofauna oder die kombinierten Meio- und Makrofauna-Gemeinschaften nur zwischen einigen Regionen unterschieden. Die Umweltfaktoren waren für die beiden Größenklassen der Fauna unterschiedlich und erklärten mehr als 66 % der Variation zwischen den verschiedenen Meio- und Makrofauna-Gemeinschaften, aber die einjährige Eisbedeckung und Chlorophyll *a* waren die wichtigsten Faktoren für die Zusammensetzung beider Gemeinschaften.

Darüber hinaus trug diese Arbeit zum Wissen über die endobenthische Vielfalt in der AP- und WS-Region auf Artniveau bei, indem eine neue Ampharetidae-Art (Polychaeta, Annelida) beschrieben und ein Bestimmungsschlüssel für alle bekannten Anobothrus-Arten erstellt wurde (Kapitel II). Durch die Verknüpfung von taxonomischen, funktionellen und umweltbezogenen Informationen konnte ich zeigen, dass der hemi-sessilen Ablagerungsfresser *Anobothrus konstantini* Säring & Bick, 2022, konstante Eisbedeckungsregime mit einer geringen Nahrungsverfügbarkeit am Meeresboden möglicherweise bevorzugt. Solche Kombinationen bilden eine wesentliche Grundlage für die Modellierung der Lebensraum- und Artenverteilung und ein wichtiges Instrument für das Schutzmanagement des SO-Ökosystems.

Schließlich untersuchte ich zur Verbesserung der Kenntnisse über die räumlichen Verteilungsmuster von Endobenthos die biologische Vielfalt von Polychaeten, einer dominanten Gruppe in Weichboden-Ökosystemen (Kapitel III). Die Ergebnisse zeigten heterogene Polychaetengemeinschaften, nämlich 6 taxonomische und 5 funktionale Gemeinschaftstypen. Eisbedeckungsvariationen und TOC waren die Hauptfaktoren, die mehr als 39 % der Gemeinschaftsmuster erklärten, wobei eine stärkere Verbindung zu funktionellen als zu taxonomischen Gemeinschaften bestand. Während die auf Umweltsurrogaten basierenden Bioregionen (*k*-means Cluster-Algorithmus) die komplexen Verteilungsmuster der Fauna nicht erfassten, konnte ich Gebiete innerhalb der Untersuchungsregion mit heterogenen Gemeinschaftszusammensetzungen identifizieren, z. B. die Region des Filchner-Trogs, die potenziell gefährdet sind.

Mit dieser umfassenden Studie zur endobenthischen Vielfalt habe ich deutlich gemacht, dass die Vorhersage ihrer räumlichen Verteilungsmuster womöglich aufgrund ihrer komplexen Struktur im Vergleich zum Epibenthos eine Herausforderung darstellt. Ich schlage vor, Meiofaunendaten in künftige Bewertungen einzubeziehen, da diese stark mit der Eisbedeckung und nahrungsbezogenen Parametern verknüpft sind, was die Auswirkungen des Klimawandels deutlicher machen könnte. Weitere Bewertungen der Umweltveränderungen im antarktischen benthischen Ökosystem sollten funktionale und taxonomische Informationen zusammen mit verschiedenen eisbedeckungs- und nahrungsbezogenen Parametern einbeziehen. Die Ergebnisse unterstreichen, dass die Anwendung fortschrittlicher Modelle (z. B. Species Archetype Models) zur Schließung räumlicher Lücken in den Faunen- und Umweltdaten von entscheidender Bedeutung ist, um zuverlässige Schutzstrategien für gefährdete Gebiete in den SO zu entwickeln.

Glossary

Abundance: The extent to which organisms are present within a sample unit, measured either as presence/ absence, count, biomass, % cover or a factor with ordered levels. Within this study I used count data, based on 10 or 100 cm^2.

Benthos: Organisms relating or living on or in the sediments of the seafloor.

Biodiversity: The variability and variety among living organisms from all origins including terrestrial, marine and aquatic ecosystems and the ecological complexes they belong to, including diversity within species, between species and ecosystems.

Bioregion: Relevant environmental characteristics existing within specific but dynamic spatial boundaries and differ to their adjacent regions.

Bioregionalization: Bioregionalization incorporates biological and/ or physical data into the analyses to define regions for management purposes. Classifying large areas according to their defined environmental characteristics and/ or unique species composition. Within this thesis the bioregionalization approach focus only on environmental properties.

Community: Ecological unit composed of different species occurring in the same geographical area.

Continental shelf: A submerged part of the continent in the ocean, e.g. Antarctic continental shelf part of the Antarctic continent, which underlies part of the Southern Ocean to a depth of about 800–1000 m.

Ecosystem: The dynamic complex composed of communities (e.g. flora and fauna) and their surrounding environmental conditions interacting as a functional unit.

Extended Weddell Sea: It comprises the region of the Antarctic Peninsula (Drake Passage, Bransfield Strait and northwestern Weddell Sea) and the southeastern Weddell Sea (Filchner Trough region) in this thesis.

Endobenthos: Within in this thesis endobenthos is defined as organisms living in and on the sediment.

Epibenthos/ epifauna: Benthic organisms living on the sediment.

Infauna: Benthic organisms living in the sediment.

Macrofauna: Benthic organisms with body size > 500 µm.

Marginal sea-ice zone: The transitional zone between open sea waters and dense drift ice. The marginal sea-ice zone can extent tens or hundreds of kilometers from the ice-edge and is usually a zone with high primary production.

Megafauna: Benthic organisms with a body size > 1 cm and large enough to be visible via seabed images mostly living on the sediment.

Meiofauna: Benthic organisms with body size 32–500 µm.

Surrogate: Using elements (e.g. species, environmental parameters) that stands or represents another aspect, as a substitute. For instance, environmental properties (e.g. sediment types) can used to identify bioregions instead of biological information.

Weddell Sea: within this thesis Weddell Sea is defined as a region extending the geographical ranges, including the southeastern Weddell Sea (Filchner Trough region) as well as the Antarctic Peninsula (Drake Passage, Bransfield Strait, northwestern Weddell Sea).

Abbreviations thesis

1-year-ice cover	ice-cover situation in the summer previous to the respective sampling campaign, daily mean summer (December–February) in percentage, sea-ice cover calculated for every year (%)
ACC	Antarctic Circumpolar Current
AP	Antarctic Peninsula
CCAMLR	Conservation of Antarctic Marine Living Resources
Chl*a*	Chlorophyll *a* content in the sediment [$\mu g\ g^{-1}$]
$Chla_{Cmax}$	Chlorophyll *a* content in the water-column at the chlorophyll a maximum [$\mu g\ l^{-1}$]
Coarse Sand	Coarse Sand content in the sediment > 1000 µm (%)
CPE	Sum of chlorophyll *a* and phaeopigment content in the sediment [$\mu g\ g^{-1}$]
C/N_{molar}	molar Carbon:nitrogen ratio
CSLM	Confocal laser scanning microscope
FT	Filchner Trough
GKG	Giant box corer
Micro-CT	Micro- computed tomography
MPA	Marine Protected Areas
MUC	Multicorer
Phaeo	Phaeopigment content
PS	Polarstern
RV	Research vessel
SAMs	Species Archetype Models
SD-10-year-ice	standard deviation of the daily mean values (%) of the sea-ice cover (December–February) between 2010–2019
SEM	Scanning electron microscope
Silt & Clay	Silt and clay content in the sediment, < 63 µm (%)
SO	Southern Ocean
St.	Station
TOC	Total organic carbon (%)
WS	Weddell Sea

General Introduction

Biodiversity – its magnitude and concepts

Robert May stated that, if aliens came to visit Earth, their first question would refer to the earth's biodiversity: '*How many distinct live forms – species does this planet have?*' (May 1992). However, he mentioned that unfortunately we could not give a precise answer for this question. Despite over 250 years of taxonomic research and the classification and description of over 1.2 million species, the knowledge of the biological diversity on earth is still incomplete and very patchy. Only a small proportion is well documented, mostly including larger organisms, such as mammals, birds, reptiles, amphibians, fish and higher plants. Mora et al. (2011) predict that 86% of the species on land and even 91% in the ocean remain unknown, for the most part consisting of invertebrates and microbes.

It was not until 1990 that the interests for biodiversity research increased significantly (Liu et al. 2011). The term biodiversity describes the natural variety and variability of all living organisms regarding biological organization. It includes a variety of aspects, such as intra-specific genetics, morphological and demographic diversity, species and community diversity including their biological interaction and ecosystem diversity (DeLong Jr 1996). Biodiversity is affected by different factors on various spatial and temporal scales. On larger spatial scales biotic variety patterns are influenced by climate, geology and physical geography. In local ecosystems these patterns are affected by direct environmental variations, such as temperature or nutrient fluctuation, and interactions among invasive and native organisms (Noss & Cooperrider 1994). In ecological research the available biotic and abiotic information are used to understand how communities or populations are structured and distributed. Further, predictions are made on how the ecosystem will change over space and/ or time in response to environmental conditions, e.g. via bioindicators that can be used as natural indicators for assessing water quality. However, to date the environmental key drivers as well as effects of the changing environment for species diversity are only known for a few taxa (e.g. nematodes & foraminiferans: Ingels et al. 2012, krill: Flores et al. 2012, ascidians: Segelken-Voigt et al. 2016, hexactinellid sponges and hydrocorals: Post et al. 2017).

Describing biodiversity by its ecologically relevant components

The detailed characterization of biodiversity provides insights into the different components and features of biodiversity. Redford & Richter (1999) present a modified matrix from Noss (1990), characterizing the three components of biological diversity (in the following levels): (i) *species/ population*, (ii) *community/ ecosystem* and (iii) *genetics*. Each level includes the three attributes: (a) composition (identity and variety), (b) structure (physical organization or pattern) and (c) function (ecological and evolutionary processes). As part of my thesis scope I will focus on the levels (i) species and (ii) community (Figure 1). *Species* diversity describes the variety of living organisms at local to global scales, whereas *community* diversity refers to a group of taxa that exist in the same region and interact with each other through trophic, spatial biotic and abiotic relationships.

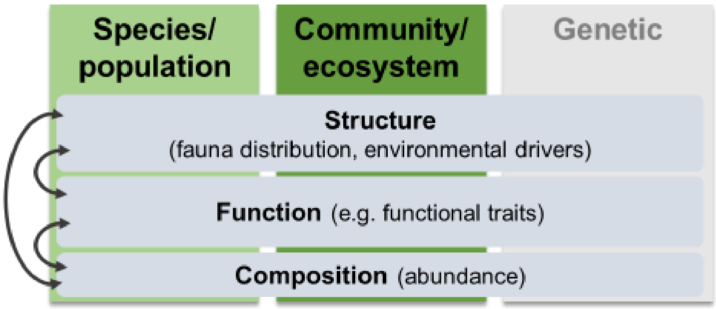

Figure 1: Concept of biodiversity: Represented are the components (*species/population, community/ecosystem, genetic)* and the attributes (*structure, function, composition*) of biodiversity. The components species/population and community/ecosystem with their three attributes were studied for this thesis. Arrows indicate link between attributes, as these depend and affect each other.

Species or community *composition* can be studied and measured for example through abundance measurements, as well as the analysis of (dis)similarity within and between populations or communities of sampling units. Species or community *structure* is determined by the distribution of fauna and environmental drivers and their relationships. *Functional trait* information (e.g. feeding type) can be achieved on e.g. species level and contribute to the understanding of biodiversity on the *community* level. An integration of the different components and attributes will provide a holistic picture of the biodiversity for the survey region.

Taxonomy: fundamental base for theoretical and applied biodiversity research

Taxonomy is the classification and description of organisms. Assigning organisms to hierarchical groups, that emphasize their phylogenetic (evolutionary) relationships, is essential for the survey and understanding of life on earth (Lincoln et al. 1988, Wägele 2005). It builds a baseline for biodiversity knowledge, necessary for theoretical and applied biology, such as ecology and agriculture (Kapoor 1998) and plays a major role in conservation management (McNeely 2002).

Classic taxonomical approaches use light microscopy, confocal laser scanning microscopy (CLSM), scanning electron microscopy (SEM), and/ or micro-computed tomography (micro-CT) to morphologically describe eukaryotes. SEM, CLSM and micro-CT are usually applied when the resolution of the light-microscopy is insufficient. Typically for small specimens or for taxa with complex features e.g. Ampharetidae (Polychaeta) which display a complex poorly resolved taxonomy with insufficient diagnoses (Reuscher et al. 2009), despite their species richness with more than 300 described species worldwide (World Register of Marine Species, http://www.marinespecies.org). For instance, CLSM and micro-CT scanners provide three-dimensional images, which can be used as a virtual representation of these types of materials and are necessary for detailed and sufficient species description and for identification keys for such taxa. Further, these tools may promote the development of digital species collections in the future (Faulwetter et al. 2013, Paterson et al. 2014).

Moreover, the use of molecular techniques in taxonomy has increased. However, in order to identify new or re-identify specimens through molecular analysis (taxonomic annotation), samples need to be related to existing species names in gene databases, which include taxonomic information (e.g. the Silva database https://www.arb-silva.de/). Without morphological information the results of molecular analyses are hard to interpret for most eukaryotes taxa (Ebach & Holdrege 2005, Meier et al. 2008). Despite this ongoing great demand for taxonomic information and its major role for biodiversity research, there is a lack of taxonomic expertise with a decreasing number of taxonomists especially for small taxa (Guerra-Garcia et al. 2008, Boero 2010). Between 1,300–1,500 marine species, including prokaryotes, algae, protozoa, fungi, and animals are described per year (Bouchet 2006), around 25 of them from the Southern Ocean (SO) (De Broyer et al. 2011, 2023). Hence the description of the existing biodiversity on *species* level is unrealistic and the majority of species will remain undescribed. Appeltans et al. (2012) suggested that about 50,000 free-living nematode species occur in the marine ecosystems worldwide, meaning that 90% of the nematode species are undescribed. Nearly 400 free-living nematode species are presently known for the SO but there could be around 2,000 (De Broyer et al. 2001). Thus, a higher taxonomic level (e.g. family, phylum) is commonly used for biodiversity research at the *community* level. Previous studies showed that only little information was lost and that community responses to changes are visible and easier to detect, if higher taxonomic levels are used (Olsgard et al. 1998, Olsgard & Somerfield 2000).

Recently more research questions combine evolutionary biology, ecology, conservation biology and biogeography. Therefore, multidisciplinary approaches are required for species delineation and description beyond morphology-based taxonomy. By including habitat and environmental information, new insights into the ecological niche of species and their role in the community can be provided (Dayrat 2005, Boero 2010).

Functional traits: improvement of knowledge on ecosystem functions

Investigations of functional traits open new possibilities to assess biodiversity with detailed insights in community structures, functions and responses to environmental conditions (Sunday et al. 2015), e.g. why certain organisms are abundant in specific habitats but absent in others. Taxa are grouped by their morphological, trophic, physiological, behavioral, biochemical characteristics or environmental responses using functional traits (Table 1), which are important for the function of interest (Petchey & Gaston 2006, Beauchard et al. 2017). For instance, in the SO, the functional traits *mobility* and *feeding type* have been reported to be key factors affecting species distribution across regions with different environmental conditions (e.g. Barry et al. 2003, Gutt et al. 2016, Jansen et al. 2018a).

Table 1: Trait-function relationships between organism and ecosystem for benthic invertebrates. The table presents examples modified after Degen et al. (2018).

Traits		**Ecosystem Functions**		
		Energy & nutrient cycling	**Heterogeneity**	**Stability & vulnerability**
Morphology	Body size	x	x	x
	Body form	x	x	x
Behavior	Motility/ movement	x	x	x
	Feeding type/ diet	x	x	x
	Living habit	x	x	x
	Sediment mixing (bioturbation)	x	x	x
Live history	Reproduction type			x
	Live span			x

Different species with similar functional traits and responses to the environment are classified in the same functional group. Functional biodiversity approaches can be time-saving and applied to a range of different systems (e.g. marine, limnic). They directly relate traits to environmental conditions and thereby improve a mechanistic prediction over environmental gradients (McGill et al. 2006, Webb et al. 2010). Mouillot et al. (2013) mentioned in a theoretical approach another advantage of trait-base approaches: early responses to environmental changes (e.g. early snowmelt) are more evident in functional community structures than in taxonomic ones. This improved understanding of ecosystem processes and functioning is important for future management and conservation planning, especially for regions that are threatened by climate change, as e.g. the SO (Degen et al. 2018).

Biodiversity of the benthic shelf in the Weddell Sea ecosystem

Environmental properties of the Southern Ocean: Seasonality and climate change affect sea-ice cover

The total area of the Antarctic continent and the SO is ~34.8 million km^2 and with ~4.6 million km^2 its continental shelf comprises approximately 15% of the continental shelves worldwide (Zwally 2002, Convey et al. 2009). Around one third of the Antarctic shelf is covered by floating ice shelves. Depending on the season, the remaining two thirds are more or less covered by sea ice. It ranges between a seasonal minimum in the austral summer with 3–4 x 10^6 km^2 in February to a maximum in winter with 1.8–2 x 10^7 km^2 (Gloersen et al. 1993). Seasonal variations of sea-ice cover and sea-surface temperatures lead to high productivity in austral spring/ summer and low productivity during autumn/ winter months in the marginal sea-ice zones (Arrigo et al. 2008, Isla 2016).

The Antarctic Circumpolar Current (ACC) is the largest and fastest ocean current worldwide. It is constantly circling and transporting cold water masses around the Antarctic continental shelf (Deacon 1984, Rintoul 2007) and affects the Antarctic benthic[1] ecosystem. The ACC and the shelf counter currents promote the circumpolar dispersal and transport of food particles and pelagic larval stages of benthic organisms (Arntz et al. 1994, Turner et al. 2009, Brasier et al. 2017). However, large-scale oceanographic and atmospheric conditions can also override spatial and physical proximities and inhibit the dispersal of the Antarctic benthos to lower latitudes. The Antarctic shelf benthos[2] is, therefore, characterized by long-lasting biogeographic isolation and high endemism (Arntz et al. 1994, Griffiths et al. 2009).

Further, the SO is characterized by constant bottom temperatures and salinities on one hand and extreme seasonality in light, primary production and food input to the seafloor on the other hand (Cook et al. 2005). Thus, the Antarctic benthos displays spatially and temporally patchy distribution patterns. It developed different strategies (e.g. feeding types) in response to regional differences and seasonality of abiotic and biotic factors (Gerdes et al. 1992, Arntz et al. 1994, Gutt 2000, Barnes & Conlan 2007).

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[1] Benthic: adjective of the benthos, living on the seafloor

[2] Benthos: organisms living on or closely related to bottom of body of water

However, variations in regional sea-ice patterns are also influenced by the effects of climate change (Vaughan et al. 2003, Gutt et al. 2015). The Weddell Sea [3](WS) is characterized by different and complex sea-ice cover situations over the past century. While sea-ice cover decreases, and sea-surface temperatures increase along the eastern shelf of the Antarctic Peninsula (AP) in the western WS, the opposite applies to the eastern WS shelf with only a few polynyas (open-water area surrounded by sea ice) towards the coast (Liu et al. 2004, Turner et al. 2016, Comiso et al. 2017). Even though sea-ice extent in the WS has increased in past decades with a record high in 2014, a precipitous decline was observed just three years later (Parkinson 2019). To date, it remains unclear, how trends will develop in the future, but there is evidence indicating a turning point (Ludescher et al. 2019). Future scenarios predict for both WS regions a decline of sea-ice cover and salinity as well as an increase of sea-surface and bottom temperatures in the next decades (Timmermann & Hellmer 2013, Hellmer et al. 2017). Due to these complex environmental conditions and the contradiction of instrumental records (Liu et al. 2004, Turner et al. 2016, Comiso et al. 2017) versus the predicted values in the WS (Timmermann & Hellmer 2013, Hellmer et al. 2017) it is an important and challenging key region to investigate the effects of climate change on the benthic ecosystem.

Tip of an iceberg: current knowledge on benthic biodiversity

Around 70% of the earth's surface is covered by oceans and their seafloors are mostly composed of soft sediments. Marine sediments are among the most species-rich habitats on the planet (Wilson 1990, NRC 1995, Snelgrove 1999). However, compared to terrestrial ecosystems, ocean seafloors are much less explored (Thrush & Dayton 2002, Hooper et al. 2005), due to the difficult access beyond a certain depth (Solan et al. 2003).

Organisms inhabiting marine sediments are called benthos (bottom-living), living in (infauna) and on the (epibenthos/ -fauna) the sediment (Figure 2).

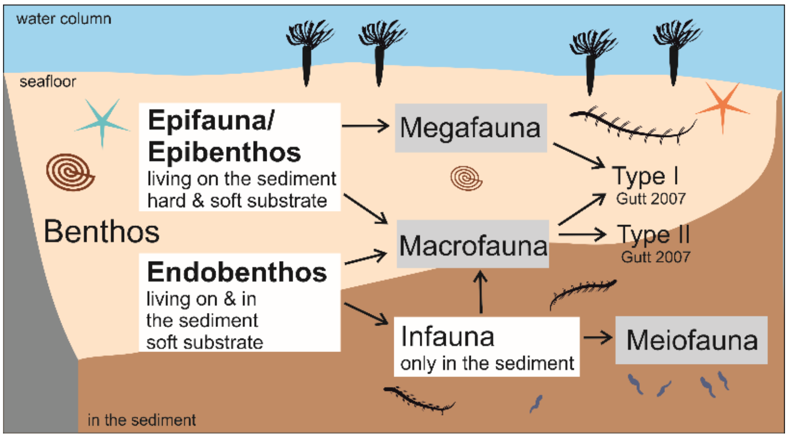

Figure 2: Overview benthos definition used in this study. Arrows refer to respective fauna type.

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[3] Weddell Sea: within this thesis Weddell Sea is defined as a region extending the geographical ranges, including the southeastern Weddell Sea (Filchner Trough region) as well as the Antarctic Peninsula (Drake Passage, Bransfield Strait, northwestern Weddell Sea)

Benthic organisms are important contributors to the global ocean ecosystem, e.g. by carbon and nitrogen cycles, and carbon storage in the sediment (Schratzberger & Ingels 2017).Most benthic species are invertebrates considered as macrofauna (body size > 500 µm, in- and epibenthos) and meiofauna (body size between 32–500 µm, mostly infauna). Despite its high abundances, wide distribution ranges, and the essential role the benthos plays for ecosystem functioning, the current knowledge about benthic species is sparse. Only a small fraction, approximately < 1%, of benthic species are known to date. Overall, of marine benthic species only 12% and even < 1% of macro- and meiofauna species, respectively, are known so far (Snelgrove 1999). Our biodiversity knowledge gaps are particularly evident for higher latitudes. The highest species diversity in polar regions was documented for the Antarctic benthos, referring to all organisms living on the continental shelves and slopes and adjacent islands in the SO (De Broyer et al. 2001, Gutt & Piepenburg 2003, Clarke & Johnston 2003). Nevertheless, in terms of species richness only the tip of the iceberg is known so far, including > 7,000 valid species in the Register of Antarctic Marine Species (De Broyer et al. 2023). Half of the known species from the Antarctic benthos have only been found once or twice (Clarke et al. 2007). An estimation based on the extrapolation of trawl-catch data from the WS assumes ~17,000 macrofauna species on the Antarctic shelf alone. These mainly comprise epibenthic species (Gutt et al. 2004), whereas even higher species numbers are expected for smaller-sized organisms (micro- and meiofauna), due to their higher abundance in the sediment and wider and distribution patterns there is higher probability of various and more species. However, several authors assumed that estimations for these organisms are rare (De Broyer et al. 2011, Kaiser et al. 2013). The unique benthic biodiversity was and will be threatened by direct and indirect effects of environmental and anthropogenic pressure, such as climate change, habitat devastation as well as ocean use (Vitousek 1994, Halpern et al. 2008, 2015, Poloczanska et al. 2016), which may lead to a species-mass extinction in the future (Thomas et al. 2004), especially in polar regions (Peck 2005, Griffiths et al. 2017). It is therefore likely that species will become extinct without us noticing. Therefore, an investigation and integration of different biodiversity levels (*species, community*) and attributes (e.g. functional traits, environmental parameters as surrogates) is relevant to obtain a detailed overview of the Antarctic biodiversity for conservation strategies (Figure 1).

Different benthic community types in the Weddell Sea

Till now, the majority of benthic community studies in the WS and around the AP focused on the diversity and distribution of epibenthos, including the size classes megafauna (body size > 1 cm, mostly living on the sediment) and macrofauna (Figure 2, Table S1).

Early studies suggested a classification of the Antarctic macro- and megafauna in soft and hard substrate communities (White 1984, Mühlenhardt-Siegel 1988, Voß 1988, Clarke 1990). However, this traditional division is more evident in shallower zones than in deeper shelf regions (Figure 1g & h in Gutt 2007). A more recent classification of the Antarctic macro- and megafauna by Gutt (2007) defines two major community types for shelf regions (Figure 2) based on their functional traits (feeding and mobility type).

The first community type is associated with poorly differentiated substrates and comprises a tridimensional community structure with stratified epifauna of sessile suspension feeders and colonial organisms dominated by sponges, bryozoans, ascidians, corals and certain echinoderms. This community type accounts for the largest proportion of biomass of the overall Antarctic benthos (Arntz et al. 1994, Gutt 2000, Orejas et al. 2000, Pineda-Metz et al. 2019). The second community type comprises the so-called mobile deposit feeders with burrowing or crawling life styles. These organisms prefer softer sediments and benefit from deposited phytodetritus. This community type includes the endobenthic communities of macrofauna in the SO, including filter feeding fauna, which are burrowing into the sediment, such as bivalves, nematodes and polychaetes. But it also contains vagrant deposit feeders, which are mostly crawling on the sediment, such as ophiuroids, holothurians, isopods, amphipods, or polychaetes (Gutt 2007). Endobenthos also includes meiofauna organisms which were not considered by Gutt (2007).

Meio- and macrofauna communities make up the largest part of the Antarctic endobenthos, living in the sediment and also on the sediment surface (Figure 2). Most endobenthic organisms with sediment-dwelling life styles are not detectable with epibenthic observation and sampling devices. Their investigation requires a sampling and analysis effort using grabs and coring devices and microscopy work. Hence, endobenthic communities, especially meiofauna, are rare in biodiversity studies in the SO (Table S1). Even though different endobenthic size classes occur within the same sediment substrate, previous studies on the SO shelf investigated either meiofauna (e.g. Herman & Dahms 1992, Rose et al. 2015, Veit-Köhler et al. 2018) or macrofauna (e.g. Gerdes et al. 1992, Gutt et al. 2016, Pineda-Metz et al. 2019) communities in relation to their environmental drivers.

Known patterns of meio- and macrofauna diversity in Southern Ocean

Within the endobenthic metazoans, meiofauna is the most abundant size class (32–500 µm). Fitting their body size and shape, the sediment-dwelling meiofauna conducts burrowing, interstitial and to a lesser extent epibenthic life styles. Due to their small body size, meiofauna taxa are dominating sediment samples in terms of individual numbers. These small organisms should be included in ecological studies, to include a wide range of taxa and understanding their role in the ecosystem. In the WS, most dominant meiofaunal metazoan taxa are nematodes, followed by harpacticoid copepods. Other taxa such as kinorhynchs, ostracods, and tardigrades represent a smaller proportion (Vanhove et al. 2000, De Skowronski & Corbisier 2002, Pasotti et al. 2014, Veit-Köhler et al. 2018). Contrary to the larger-sized macrofauna (> 500 µm), meiofauna species lack pelagic larval stages, do not actively shape their habitat and have higher turnover rates (Remane 1933). With their wide distribution ranges, their mostly interstitial life cycles, high biodiversity, and distinct ecological requirements, meiofauna organisms can respond earlier to various types of environmental changes (e.g. Frontalini et al. 2018, Appolloni et al. 2020).

The macrofauna dominates endobenthic soft-bottom assemblages in terms of biomass. Deposit feeders, make up the largest proportion of these macrofaunal communities consisting of infauna and mobile epifauna. In the WS, previous studies have demonstrated that polychaetes dominate macrofaunal endobenthic communities, followed by bivalves, echinoderms, amphipods and isopods in various order (Gerdes et al. 1992, Piepenburg et al. 2002, Hilbig et al. 2006, Pineda-Metz et al. 2019). To date 546 polychaeta species belonging to more than 50 families are known from more than 5,600 benthic records from the SO (Schüller & Ebbe 2014, De Broyer et al. 2023). More than 90% of all Antarctic polychaete species are recorded from the Atlantic sector of the SO (WS, AP, Scotia Arc) and around 45% are restricted to the shelf regions (Schüller & Ebbe 2014). Polychaetes were observed in higher abundances around the AP compared to regions in the southeastern WS (Gerdes et al. 1992, Piepenburg et al. 2002, Hilbig et al. 2006, Pineda-Metz et al. 2019).

Benthic diversity in relation to ice coverage and food availability in the Southern Ocean

The composition and distribution of Antarctic endobenthos is shaped by a wide range of factors on different spatial scales (Figure 3), such as hydrodynamics (Cummings et al. 2021), primary production in the water column (Arrigo et al. 1998) and transport of organic material from the pelagic to the benthic zone (Grebmeier & Barry 1991). Sea-ice cover directly affects the regulation of primary production and the particle flux from the upper water column (euphotic zone) to the seafloor. Thus, sea-ice dynamics not only have an impact on ice-dependent organisms but also on benthic species which depend on the quality and quantity of organic matter reaching the seafloor (Mincks et al. 2005, Mincks & Smith 2007, Glover et al. 2008, Ingels et al. 2012, Smith et al. 2012). For instance, previous studies showed a correlation between food availability and meiofauna abundances (Hauquier et al. 2015, Veit-Köhler et al. 2018).

The high but irregularly distributed primary production combined with variable vertical particle fluxes cause local and regional variabilities between and within the sites (e.g. organic material, substrate texture, Figure 3).

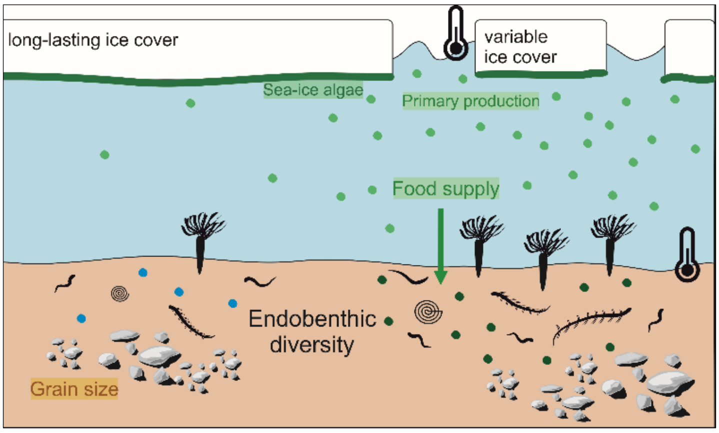

Figure 3: Schematic illustration of environmental properties affecting endobenthic biodiversity in the Antarctic. Regions with long-lasting ice cover (left) are characterized by lower food input to the sediment and fewer endobenthic organisms. Regions with variable sea-ice cover (right) have a high primary production firstly in the water column and secondly through released ice algae. This higher food supply at the seafloor leads to higher faunal abundances.

During the seasonal sea-ice melt in austral summer, meltwaters enable a stable stratification of the water column and the formation of regional phytoplankton blooms consisting primarily of diatoms (Kang et al. 2001, Lizotte 2001, Smith & Comiso 2008). Further, the release of sea-ice algae during the ice melt adds to the local and temporal enhancement of biogenic material in the water column (Lizotte 2001). Throughout the year, sea-ice algae make up to 25% of total primary production in ice covered regions (Arrigo & Thomas 2004). The produced phytodetritus is rapidly transported throughout the water column towards the seafloor, e.g. as fecal pellets from zooplanktonic grazers (Lizotte 2001), and causes a high seasonal particulate organic carbon flux to the sediment (Figure 3). However, cold bottom-water temperatures decelerate remineralization processes of the phytodetritus and lead to an accumulation of fresh organic matter at the seafloor, so-called *food banks* (Isla et al. 2002, Mincks et al. 2005). Hence, temperature and sea-ice cover play a crucial role for the food availability at the ocean floor. The regular opening and closing of the sea ice in the marginal sea-ice zones and temporary polynyas near the coast are an optimal motor for the primary production and food input to the seafloor (Sañé et al. 2012). Food banks were observed in the northwestern WS leading to a higher meiofauna and nematode abundance even in deeper sediment layers (Hauquier et al. 2015, Veit-Köhler et al. 2018). Nevertheless, it is known that several meiofauna taxa rely on different types and characteristics of food. Whereas the food quality plays a major role for nematode abundances, the food quantity is more important for copepodes (Veit-Köhler et al. 2018). It needs to be noted that these meiofaunal studies did not include any ice-cover parameters in their analyses.

The food-availability optimum at the Antarctic seafloor is accompanied by two productivity minima (Grebmeier & Barry 1991). One minimum exists in regions with a constant ice cover throughout the year. The thick sea-ice cover hampers the light penetration and the release of ice algae into the water column leading to lower primary production in the water column and less fresh organic material at the seafloor. These regions are mostly inhabited by deposit feeders (Gerdes et al. 1992, Pineda-Metz et al. 2019). Another minimum is present in open oceans. Wave action and missing sea ice result in less stratification of the water column. Warm nutrient-rich bottom water mixes with the upper water masses which results in phytoplankton blooms (Prézelin et al. 2004). Despite high primary production rates most of the phytodetritus is already recycled and consumed by zooplankton in the water column. Further, lateral advection and resuspension driven by bottom currents hampers the accumulation of fresh organic matter at the seafloor (Isla et al. 2004, Isla 2016).

Further, Gerdes et al. (1992) mentioned that sediment characteristics are crucial for explaining the benthic soft-bottom ecology in the SO. For instance, grain size for building tubes or burrow structures, chlorophyll *a* content and quantity of total organic matter as food supply play an important role for the endobenthos of marine environments (Rhoads 1974, Gray & Elliott 2009).

For the SO, most effects that alter ecosystem conditions are still poorly understood for wider regional scales (Gutt et al. 2015) and are only analyzed for epibenthic macro- and megafauna (e.g. (Gutt et al. 2016, Pineda-Metz et al. 2020) while investigations on their influence on endobenthic communities in the WS are still missing. To improve our current knowledge of the benthic ecosystem on the WS shelf and the AP and its development in the future it is important to investigate *which endobenthic organisms are present* and *what are the environmental drivers that structure their communities*.

Towards predicting spatial distribution patterns of the benthos on the Weddell Sea shelf and the Antarctic Peninsula via bioregionalization approaches

A key challenge in ecology is the prediction of how organisms respond to varying abiotic and biotic conditions. The stressed ocean recently became a major environmental concern and it is now a priority to improve the protection of endangered and unique ecosystems. For the SO, international agreements, particularly the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR), have been established to conserve the biodiversity and, among other aspects, to control the exploitation of marine living resources (Agnew 1997, Constable 2000, Kock 2007). CCAMLR has the primary responsibility to develop a representative network of Marine Protected Areas (MPAs) in the SO (SC-CAMLR 2009b a). MPAs define areas of oceans or coastal regions where human activities are restricted or prohibited, in order to protect, conserve or re-establish nature, its associated ecosystem services and cultural values (Day et al. 2012). The first Antarctic high-sea MPA on the southern shelf of the South Orkney Islands was established in 2009 (CCAMLR 2009, Trathan & Grant 2020). CCAMLR has been proposed MPAs for the AP (Sylvester & Brooks 2020), East Antarctica (CCAMLR 2020) and the WS (Teschke et al. 2021). To date, however, < 12% of the SO is under the protection of MPAs, with 4.6% representing no-take areas (Brooks et al. 2020).

An efficient and sustainable conservation management depends on providing policymakers and managers the best available scientific expertise and guidance. An essential step is to understand and predict the spatial distribution and extent, as well as assessing the status of endangered species (O'Hara et al. 2020). The identification and evaluation of the relationship between abiotic properties and biological communities, as outlined in section 2, can therefore be an essential instrument for mapping and understanding vulnerable marine habitats. A classification of regions including endobenthic diversity is needed to close the existing gaps of physical habitat properties and spatial distribution of endobenthic communities in order to provide valuable information for the establishment of MPAs.

Spatial patterns of distribution still patchy and limited for the Antarctic benthos

Major knowledge deficits exist regarding the spatial distribution for benthic organisms in the SO in terms of geographic, bathymetric, taxonomic and functional information (Gutt 2007, Barnes et al. 2009, Griffiths et al. 2011). To fill these gaps, first attempts have been undertaken to estimate species diversity at larger spatial scales for the Antarctic shelf regions (Clarke & Johnston 2003, Gutt et al. 2004) and for the deep sea (Brandt et al. 2007) by applying wide sampling ranges. However, spatial distribution patterns of the Antarctic endobenthos are hard to identify and to predict, even if sampling intensity and effort increased considerably during the last two decades (Griffiths et al. 2011, Kaiser et al. 2013, Convey et al. 2014), given a rapidly changing and harsh environment concerning weather, depth, currents and long-lasting ice conditions (see section 0).

Given the challenging environmental conditions, most sampling sites on the continental shelf are located close to routes that supply vessels use to travel to national research facilities. One fourth of benthic sampling sites lie in a radius of 50 km to a research base, 50% in a radius of 150 km. In addition, there are also regional differences in sampling frequency. For instance, the South Shetland Islands show the highest sampling-site density for benthic sampling sites followed by South Georgia, the eastern WS, the Ross Sea and Prydz Bay. Other regions remain mostly unexplored such as the ice-covered western WS and the Filchner Trough (FT) region, or the geographically isolated Amundsen Sea (Griffiths et al. 2011).

Taxonomic and functional surrogates for the investigation of the polychaete biodiversity

To simplify the understanding of ecological processes, *taxonomic* and *functional surrogates* are used for biodiversity analyses and assessments. Surrogates correlate with the abundance of other species within the area of interest but are easier to assess and evaluate (Williams et al. 1997, Gaston 2000).

Polychaetes were widely used as indicators and surrogates in different studies to predict potential biodiversity patterns of benthic organisms (e.g. Olsgard et al. 2003). They are an important component in ecosystem monitoring (e.g. Olsgard & Somerfield 2000) and conservation planning (e.g. Giangrande et al. 2005). Compared to other major taxonomic groups of the marine benthos such as molluscs, crustaceans and echinoderms, polychaetes most closely reflect similar abundance and distribution patterns of the benthic community (e.g. Olsgard & Somerfield 2000).

Their high abundance within a benthic community is, however, not necessarily the main reason for polychaetes to be a suitable indicator of invertebrate species richness and community patterns. Rather, this is more likely related to the high functional diversity of polychaetes, according to their morphological, feeding, motility and reproductive variations, which encompass various trophic levels of tube-building sessile but also sedentary mobile species (Fauchald & Jumars 1979, Jumars et al. 2015). This allows polychaetes to adapt to a wide range of different habitat and environmental conditions (Jumars et al. 2015) from the intertidal to abyssal depths (Schüller & Ebbe 2014) and from soft to hard substrates (Gambi et al. 1997). Further, given their wide diversity of feeding types, such as filter and deposit feeding, and their preferred habitat, surface or subsurface, as well as their strong influence on respiratory irrigation and burrowing activities, polychaetes in general enhance sedimentary processes (Fauchald & Jumars 1979, Hutchings 1998, Jumars et al. 2015).

Spatial information on the distribution of functional groups of polychaetes using bioregionalization approaches could provide different insights in contrast to the more traditional taxonomic groups and increase our knowledge of ecological benthic processes in the WS. This could help determine regions with similar functional services that may require similar conservation strategies.

Physical surrogates to improve spatial biodiversity knowledge

Compared to biological data multiple physical parameters can be measured relatively easily (e.g. satellite) and provide a better spatial and temporal coverage and greater data availability (e.g. bathymetry, sea-ice cover). Hence, they can be used for defining distinct habitats within bioregionalization approaches. Predictive methods and habitat suitability approaches, summarized as bioregionalization, became more important recently to overcome the fragmentary information on species and habitats (e.g. Grant et al. 2006, Douglass et al. 2014). These methods offer a wide range of applications, such as risk analysis, ecosystem modelling, or the prediction of the dispersal of invasive species (Grant et al. 2006). Thus, bioregionalization approaches play an important role for MPA planning.

The aim is to detect spatially distinct, contiguous, and recognizable biogeographic patterns by spatially partitioning a region into so-called distinct *bioregions* or *ecoregions* based on a variety of spatial physical or biological surrogates. The following sections focuses on *bioregions* that are based only on abiotic properties, whereas *ecoregions* are defined by abiotic and biological properties (e.g. Douglass et al. 2014). Each of the resulting *bioregions* has relatively homogeneous and predictable ecosystem features compared to adjacent regions (Figure 4, Leathwick et al. 2003, e.g. Spalding et al. 2007).

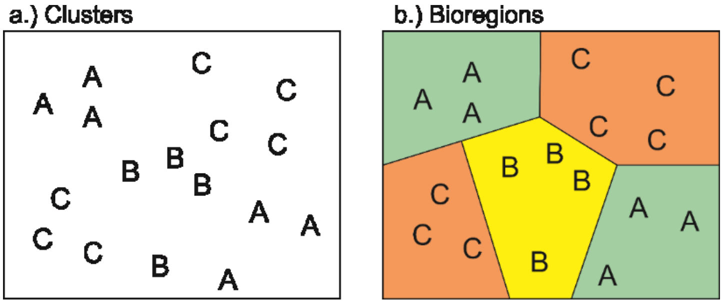

Figure 4: Schematic overview of a survey region, (a) shows the spatial distribution of sampling points each assigned to a cluster, (b) represents bioregions that form based on cluster and spatial information.

The outcome can suggest the potential occurrence for species or habitats in regions, with no or low sampling frequencies based on other (mostly environmental) available information, hence the term *physical surrogates*.

A key aspect of conducting an ecologically meaningful regionalization is to understand how relevant ecological processes correlate and respond to environmental conditions (physical and satellite-observed parameters) and if these parameters are suitable as proxies or surrogates. This may require environmental data that have the potential to provide insights into the environmental heterogeneity that determines the ecology of these bioregions.

Clustering approach to subdivide habitats

In order to understand how sites differ in species/ community abundance and/ or composition, or environmental properties, ecologists commonly follow two multivariate approaches, which provide a visualization of the data matrix structure: (i) unstrained ordination and (ii) cluster analysis. Generally, both approaches require a metric to characterize and evaluate the (dis)similarities between individuals and sampling sites but neither uses any information about the source or origin of each sample. Ordination approaches commonly attempt to create two-dimensional visual representations of the relationship between the samples based on their (dis)similarities. The relative distance between any sample pair represents their relative (dis)similarity. In contrast, the cluster analysis attempts to assign samples to clusters based on their similarities (Clarke & Green 1988), which makes them suitable for bioregionalization analysis.

Within the context of bioregionalization, cluster analyses use sites (or grid cells) from the raster grid which is a spatial digital data layer where each cell contains a value representing an information within the geographic space. The clustering algorithms used rely e.g. on dissimilarity metrics in order to evaluate the differences between two sites on the basis of their ecological characteristics. Sites (grid cell) are, therefore, grouped together in clusters (based only on environmental characteristics, ignoring any spatial information), if the intra-region dissimilarity of sites is low (sites within a bioregion share similar characteristics) compared to the inter-region dissimilarity. Clusters therefore include sites which can be spatially separated from each other. In order to identify the spatial coverage of the resulting bioregions, clusters or *environmental spaces* are re-projected onto geographic coordinates in the next step. A bioregion is formed by a cluster and is defined as a group of sites that share the same cluster but also constitute a spatially contiguous area. Bioregions are discrete in their environmental space but can have a scattered or fragmented distribution over a geographic space. Thus, multiple bioregions with similar properties are present in different geographic locations (Figure 4, Grant et al. 2006).

Clustering methods are divided into hierarchical or non-hierarchical clustering schemes (Table 2). A hierarchical and nested system has the advantage of allowing for multiscale analyses, where each level of the hierarchy is important for conservation planning spanning from global to local scales (Roff & Taylor 2000). Hierarchical classification systems can be used to define inter-environment relationships and the link between habitats and their biota. For instance, Douglass et al. (2014) used three classification levels to classify the Antarctic seafloor: benthic ecoregions were identified with primary environmental drivers that are relevant for distribution of the benthic biodiversity in the SO (level 1), bathomes (broad-scale depth classes) were nested within an ecoregion (level 2) and geomorphological properties within bathomes (level 3) (see Figure 1 in Douglass et al. 2014). However, data must be available in high resolution in order to classify hierarchical levels. One disadvantage is that the assignment of the hierarchical clustering is permanent and rigid, because objects assigned to a cluster in a classification level are unable to change to another cluster in the next level (Gordon 1987). Contrarily, the non-hierarchical clustering is more flexible. The goal of this technique is to identify a grouping of objects which minimizes or maximizes some evaluation criteria (Hartigan 1975, Kaufman & Rousseeuw 1990).

Table 2: Comparison of hierarchical and non-hierarchical clustering methods based on their main characteristics.

Hierarchical clustering	**Non-hierarchical clustering**
Relatively slower	Fast and preferable to use for larger data sets
Agglomerative clustering most used hierarchical algorithm	*k-means* popular and widely used non-hierarchical clustering algorithm
Based on distances to measure (dis)similarity	Based on the variance with the clusters as a measure of similarity
No decision about the number of clusters	Requires the number of optimal clusters as an input parameter to start
Objects assigned to cluster remain in this cluster; creating clusters in a predefined order	Objects can be reassigned to other clusters during clustering processes; no hierarchical order

Therefore, non-hierarchical clustering is a fast and simple (Table 2, Gulagiz & Suhap 2017) and an efficient method to reduce the large number of grid cells and can handle large data sets, so that a subsequent hierarchical clustering step would be manageable (e.g. Raymond 2011), which can only be applied and interpreted for a few hundred samples clustering (Murtagh & Contreras 2012).

Hence, multiple clustering approaches are compared for their consistency. The *k-means* clustering is the most commonly used algorithm for unsupervised machine learning subdividing or distributing data objects into clusters.

The basic idea of k-means

The principle idea of *k-means* is to define clusters in such a way that the total variation within a cluster (intra-cluster variation, here intra-region dissimilarity) is minimized. This algorithm requires the optimal cluster number as an input, followed by an iterative sequence of different steps until the most optimal classification is achieved (Figure 5, Greenacre & Primicerio 2014).

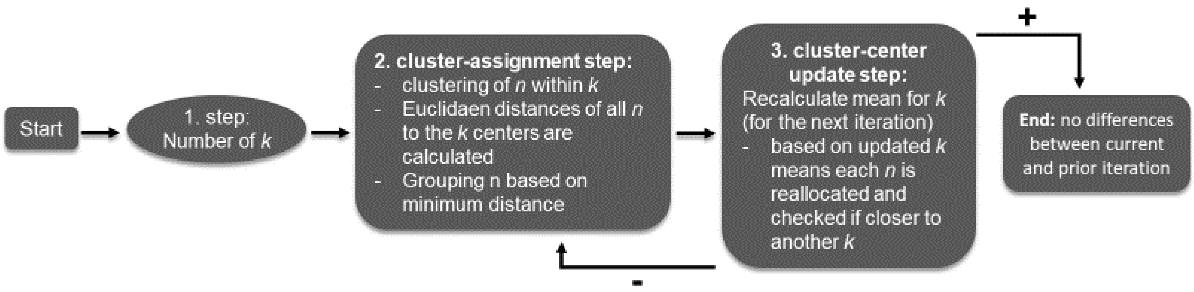

Figure 5: Flow chart of the *k-means* algorithm steps. *k*: clusters, *n*: data object. The assignment and center-update steps are repeated iteratively with another, random *k* starting cluster centers and its total variation is compared to that of the previous solutions. The process is repeated until there are differences between the current to the prior iteration (indicated by the plus, whereas minus indicated differences between iteration).

The optimal determination of k clusters is a balance between the maximum compression of the data obtained by assigning all samples to a single cluster and the maximum accuracy which is achieved by allocating all data points to their specific cluster (Kaufmann & Rousseeuw 1990, Greenacre & Primicerio 2014). There are more than 30 indices and methods described with which the optimal number of clusters for starting point for the *k-means* algorithm can be determined (Charrad et al. 2014), all lead to a different optimal number of clusters. The optimal number of clusters most frequently suggested across the different indices is often used for *k-means* clustering (e.g. Jerosch et al. 2018).

Bioregionalization approaches in the Southern Ocean on the basis of environmental properties

In the past, the SO has been partitioned into bioregions, commonly based on physical properties. Tréguer & Jacques (1992) classified five functional units south of the Polar Front related to ice and nutrient dynamics. Their study highlighted the impact of sea-ice dynamics in controlling phytoplankton initiation and growth, as well as the nutrient regimes that distinguished each of these units. Another investigation from Orsi et al. (1995) characterized large-scale frontal properties of the ACC using historical hydrographic data. Three main fronts within the ACC were identified based on gradients in sea surface characteristics, which separate water masses and current features. In a global ocean classification system based on a simple set of environmental parameters (surface temperature, mixed-layer depth, nutrient dynamics and circulation) combined with planktonic algal ecology, the SO comprises four provinces (Longhurst 1998).

More recent bioregionalization approaches on a global scale in the SO have integrated biological and environmental information within analyses. For instance, Douglass et al. (2014) used in hierarchical classification by (as described before) information about known relationships between environmental drivers (e.g. depth, seafloor temperature, sea-ice cover, geomorphology) and biogeographic patterns, and knowledge of dispersal barriers (e.g. distances, geomorphic barriers) of benthic organisms, and identified 562 unique environmental types for benthic ecosystem in the SO. More than 100 environmental types were identified as restricted ones, which contained rare environmental features. Most of these rare environmental types are not represented within MPAs yet.

A more regional (small-scaled) subdivision of the SO can more accurately reflect the spatial heterogeneity of ecosystems in the SO, than a large-scale classification. This is particularly relevant for ecosystems in the marginal ice zone, and slope and continental shelf regions, which are affected by variable conditions due to seasonality. These small-scale approaches are relevant for understanding ecosystem properties and functions and allow further ecosystem studies on the effect of environmental drivers of benthic community distribution related to local drivers (e.g. substrate type, organic matter and nutrient content, erosion and disposition of sediments). In the WS, some smaller-scale classification has been attempted for the bioregionalization on the basis of seabed properties, giving a detailed seafloor classification (Jerosch et al. 2016). The results are represented in maps and indicate a highly diverse environment in the WS. on small scales vulnerable or critical habitats may be identified and hence may be considered as MPAs, whereas they may not detectable in the larger-scale regionalization (Last et al. 2010, Roberson et al. 2017). The inclusion of biological data, such as abundance, biomass, or presence/ absence data, within a small-scale classification of bioregions in the WS may provide information necessary for the extrapolation of potential spatial distribution patterns. This could allow a more holistic view on this ecosystem and is relevant part for conservation management.

General objective

The goal of this thesis is to provide a baseline knowledge on endobenthic biodiversity and its drivers in the WS (AP and FT region) by using environmental conditions enabling the prediction of biodiversity patterns (Figure 6). For this my study aims firstly to investigate which endobenthic organisms are present and how these are distributed on the WS shelf and around the AP. Secondly, I determined how food availability, ice cover, and grain size among other environmental parameters influence endobenthic communities in the WS and under with different ice-cover regimes. Finally, I tested the representation of endobenthic distribution using bioregionalization approaches.

I combined the methods and approaches of different biological research fields (taxonomy, ecology, bioregionalization, Figure 6). I investigated the biodiversity, as described by Redford & Richter (1999), on different levels, including *species* (**chapter II**) and *community* (**chapter I, III**), with different attributes, such as *composition* (faunal abundance: **chapter I, II, III**), *structure* (environmental drivers, fauna distribution: **chapter I, II, III**) and *function* (functional traits: **chapter III**). Further, I attempt at the community level to predict the distribution of taxonomic and functional groups (*composition, structure, function*) based on physical surrogates (*structure*) using bioregionalization approaches (**chapter III**). Given the necessity to describe spatial variation and to present a holistic view of endobenthic biodiversity to estimate the effects of future changes in the WS, my general objective is addressed by three steps which are described in the following **chapters:**

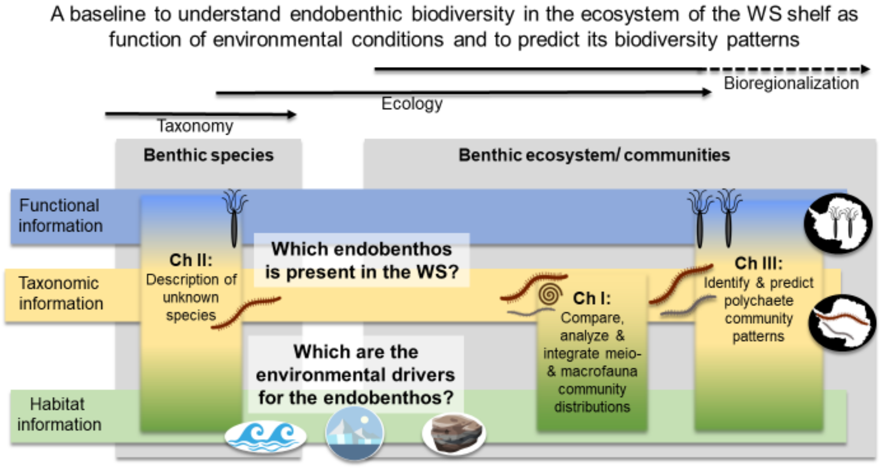

Figure 6: Overview of how the objectives of this thesis analyze the different aspects on the biodiversity of the benthic ecosystem (endobenthos). Grey boxes indicate the investigated biodiversity levels: species or ecosystem/ community level. Color of vertical boxes represent which part type of information is used int the respective chapter (Ch). Arrows represent the involved research fields for the analyses in respective chapter. Icons indicate the following within the chapters, single organisms: single species, multiple organisms: communities, crawling polychaete: taxonomic information, polychaete with tentacle crown: functional groups, Antarctic map: spatial information. Environmental information has been used in all chapters.

Chapter I: Meio-and macrofauna community composition in relation to environmental drivers

On the community level, the objective of **chapter I** is to understand how environmental drivers may differ for communities of different size classes, namely meio- and macrofauna in regions with different ice-cover regimes in the WS.

Specifically, I test for the following hypotheses:

(i) Primary production and the related food availability parameters at the seafloor differ according to sea-ice cover. The highest freshness and amount of food at the seafloor is found in regions with the most variable sea-ice cover: lowest values are expected for regions with a constant or absent ice-ice cover,

(ii) Faunal *community* composition (meiofauna, macrofauna, and combined meio- and macrofauna) follow the introduced classification of ice-cover regimes,

(iii) Meio- and macrofauna communities are structured by biotic and abiotic environmental parameters–to a different extent. Temporally stable descriptors (e.g. depth, grain size) are expected to be more important for macrofauna.

Chapter II: Description of a new Ampharetidae (Polychaeta) species linked to environmental information

The aim of **chapter II** is to contribute to the knowledge of biodiversity at the species level linked with ecological and functional information, by

(i) providing a detailed description of an unknown Ampharetidae (Polychaeta) species,
(ii) Including a new key to the Ampharetidae group, and
(iii) presenting key environmental factors that characterize its habitat by combining taxonomic and ecological information.
(iv)

Chapter III: Polychaete community (taxonomic and functional) distributions via bioregionalization and their relationship to environmental drivers

In **chapter III**, I used taxonomic (family level) and functional surrogates of the polychaete community data to improve the current knowledge on distribution patterns of the endobenthos. One aim of **chapter III** is to analyze the taxonomic and functional polychaete community composition in relationship with environmental conditions in different habitats. Further, I aim to test if regional spatial taxonomic and functional distribution patterns of the polychaete community can be identified based on environmental surrogates using bioregionalization approaches. The results contribute to further modelling approaches used as an important tool for management of the SO ecosystem and for species conservation.

I address the following questions:

(i) what are the patterns in polychaete community distribution in the WS,
(ii) which environmental parameters drive the taxonomic and functional polychaete community distribution in the WS,
(iii) based on the results, can potential habitats be identified for different polychaete communities by using bioregionalization approaches within the study area?

Sampling design

To observe and analyze the benthic biodiversity in regions with different ice-cover regimes in the extended region of the WS multiple samples were taken during three expeditions with the RV *Polarstern* from 2013 to2019. During PS81 (Jan 22–Mar 18, 2013, Gutt 2013) to the AP, PS96 to the FT region (Dec 06, 2015–Feb 02, 2016, Schröder 2016) and PS118 to the northwestern WS (Feb 02–Apr 10, 2019, (Dorschel 2019) sediment samples for the analysis of meio- and macrobenthic communities were obtained from 20 stations using the MUC or a GKG. For the major parameters describing the sediment (e.g. grain size, content of pigments and organic matter) 31 stations were sampled with the multicorer (MUC) or giant box corer (GKG). Water-column properties (e.g. temperature, salinity, pigment content) were collected with the CTD (conductivity temperature density) for each sampling location. St. 241 and 244 (both PS81) were counted and analyzed as one station. Further, st. 115 (PS96) was handled as a replicate of st. 190 (PS81) in terms of averaged benthic environmental data due to geographic proximity and lack of environmental data for st. 190. An overview of the original data is given in Figure 7 and Table *3*, more detailed information and precise methods are described in the respective chapters. All data have been deposited in the *PANGAEA* database (Veit-Köhler et al. 2017, Säring et al. 2021a, 2021b, 2021c, 2021d, 2021e, Vanreusel et al. 2021a, 2021b, Weith et al. in review a, review b, review c). The following samplings and analyses were performed for:

Chapter I – *Meio- and macrofauna communities in relationship with to environmental drivers*: Data from a total of 16 sites stations were sampled from the two expeditions PS81 and PS96 (meio- and macrofauna abundance, sediment pigment concentration, grain size, content of organic matter, water-column properties).

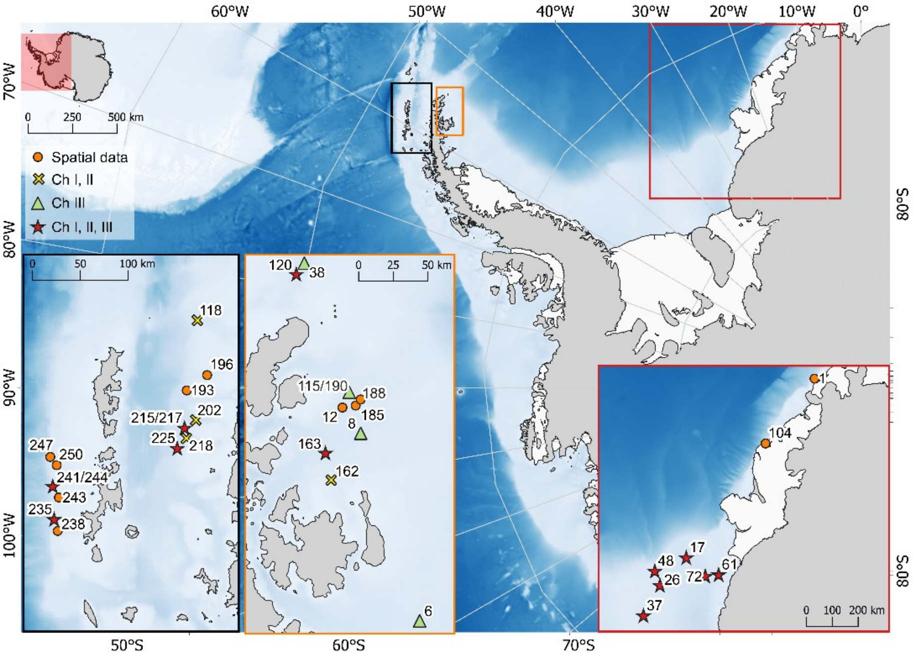

Figure 7: Station map of this thesis. Symbols represent different sampled data, for more information see Table 3. Black frame represents sampling sites located in the Drake Passage and Bransfield strait (PS81), orange frame represents sampling sites in the AP region (PS81, PS96, PS118), and red frame represents sampling sites in the southeastern WS (PS96). Red box indicates the chosen map section of the SO.

Chapter II – *Description of a new Ampharetidae (Polychaeta) species linked to environmental information:* A total of 16 sites of the two expeditions PS81 and PS96 was used (occurrence of new *Anobothrus* species, sediment pigment concentration, grain size, content of organic matter, water-column properties)

Chapter III – *Polychaete communities (taxonomic and functional) distribution via bioregionalization and their relationship to environmental drivers*: A total of 31 sites during the three expeditions PS81, PS96 and PS118 was used (descriptive analysis: 16 st. for polychaete biodiversity, 16 st. for water-column and for sediment properties; spatial data: 31 st. for grain size and content of organic matter). Further, spatial data for 9 parameters were compiled and produced (Table 3 in **chapter III**) for the bioregionalization approaches.

Table 3: Station list for data used in this thesis including sampling during RV *Polarstern* expeditions PS81 (Jan 22–Mar 18, 2013), PS96 (Dec 06, 2015–Feb 14, 2016) and PS118 (Feb 9 – April 10, 2019). Expedition number, region, station label, sampling date, geographic position, water-column depth (CTD Conductivity, Temperature, Depth at the Chl*a* maximum and bottom), depth of the benthic sampling gear, sampling gear, the according symbol in Figure 7, presentation of results in the following chapters (Ch) and the obtained data are presented. Multicorers (MUC6, MUC 10) and the giant box corer (GKG) were deployed for fauna community sampling and for sediment sampling of environmental parameters. Symbols indicate which data was used for which chapter within this thesis (see description below table). Samples for environmental characterization of the water column were collected with a CTD-Rosette equipped with Niskin bottles (Schröder et al. 2013, 2016, Janout et al. 2020). Geographic positions are shown for the CTD deployment for each station, except for st. 217, 244, 185 and 188, where the latitude and longitude data from st. 217-2 (MUC), 244-5 (MUC6), 185-2 (GKG) and 188-2 (GKG), respectively, are presented as no water-column samples were taken there. Obtained data: W = water-column data (temperature, salinity, Chla), G = grain size, P = pigment content in the sediment, O = organic material in the sediment, Meio = meiofauna, Macro = macrofauna, Poly = polychaetes. Data for spatial was used to update existing sediment texture (Jerosch et al. 2015) and TOC (Seiter et al. 2004) datasets in the WS. For more information, see station tables within each chapter.

Expedition & Region	**St.**	**Date**	**Latitude**	**Longitude**	**Sampling depth**		**Benthic sampling gear**	**Symbol**	**Ch I**	**Ch II**	**Ch III**		**Analyzed data**		**Pangaea reference**
					Water column Cmax/ bottom CTD [m]	**GKG/ MUC [m]**					**Descriptive part (fauna + env.)**	**Spatial data set**	**Env. data**	**Fauna data**	
PS 81 **Drake Passage**	235	2013-03-07	62'16.30'S	61'10.27'W	21/372	355	MUC6/ 10	★	x	x	x	x	WGPO	MeiMaPoly	1,2,3,4,11
	238	2013-03-08	62'20.73'S	61'20.15'W	20/454	464	MUC6	●				x	WGPO		1,2
	241	2013-03-09	62'06.63'S	60'36.52'W	20/396	400	GKG	★	x	x	x		W	MaPoly	1,4,11
	243	2013-03-10	62'12.27'S	60'44.42'W	20/486	497	MUC6	●				x	WGPO		1,2
	244	2013-03-10	62'06.64'S	60'36.53'W		398	MUC6	★	x	x	x	x	GPO	Mei	2,3
	247	2013-03-11	61'56.90'S	60'07.49'W	14/396	397	MUC6	●				x	WGPO		1,2
	250	2013-03-12	62'02.28'S	60'12.11'W	20/479	488	MUC6	●				x	WGPO		1,2
Bransfield Strait	118	2013-01-27	62'26.47'S	56'17.26'W	20/420	425	MUC6/ 10	✖	x			x	WGPO	MeiMa	1,2,3,4
	193	2013-02-23	62'43.01'S	57'34.16'W	20/562	577	MUC6	●				x	WGPO		1,2
	196	2013-02-24	62'48.01'S	57'4.97'W	20/543	567	MUC	●				x	WGPO		1,2
	202	2013-02-27	62'56.00'S	58'00.47'W	50/739	757	MUC6/ 10	✖	x	x		x	WGPO	MeiMa	1,2,3,4
	215	2013-03-01	62'53.57'S	58'14.66'W	40/518			★	x	x	x		W		1
	217	2013-03-02	62'53.31'S	58'14.17'W	40/519	529	MUC6/ 10	★	x	x	x	x	GPO	MeiMaPoly	2,3,4,11
	218	2013-03-02	62'56.93'S	58'25.66'W	20/672	689	MUC6/ 10	✖	x	x		x	WGPO	MeioMacro	1,2,3,4
	225	2013-04-02	62'56.07'S	58'40.62'W	20/525	543	MUC6/ 10	★	x	x	x	x	WGPO	MeiMaPoly	1,2,3,4,11
Northwestern WS	120	2013-01-28	63'04.62'S	54'33.11'W	20/511	494	MUC6/ 10	★	x	x	x	x	WGPO	MeiMaPoly	1,2,3,4,11
	162	2013-02-10	64'00.27'S	56'44.28'W	20/207	223	GKG/MUC6	✖	x	x		x	WGPO	MeioMacro	1,2,3,4
	163	2013-02-11	63'53.07'S	56'26.19'W	50/453	517	MUC6/ 10	★	x	x	x	x	WGPO	MeiMaPoly	1,2,3,4,11
	185	2013-02-19	63'52.20'S	55'36.67'W		232	GKG	●				x	GO		2
	188	2013-02-20	63'52.01'S	55'35.15'W		310	GKG	●				x	GPO		2

		190	2013-02-21	63'50.58'S	55'31.66'W	20/390	389	MUC10	△			x		W	Poly	1,11
PS 118		6	2019-03-05	64'58.81'S	57'46.56'W	7/418	423	MUC10	△			x	x	WGPO	Poly	9,10,11
		8	2019-03-11	63'59.83'S	55'54.37'W	3/404	414	MUC10	△			x	x	WGPO	Poly	9,10,11
		12	2019-03-14	63'48.39'S	55'44.66'W	21/449	454	MUC10	●				x	WGPO		9,10
		38	2019-03-22	63'04.35'S	54'21.43'W	51/438	414	MUC10	△			x	x	WGPO	Poly	9,10,11
		115	2016-02-08	63'50.71'S	55'31.16'W	50/397	400	MUC10	△			x	x	W**GPO		9,10
PS 96	**South Filchner**	37	2016-01-16	75'41.87'S	42'20.25'W	40/369	391	MUC10	★	x	x	x	x	WGPO	MeiMaPoly	5,6,7,8,11
		61	2016-01-21	76'05.86'S	30'18.66'W	46/446	467	MUC10	★	x	x	x	x	WGPO	MeiMaPoly	5,6,7,8,11
		72	2016-01-24	75'54.22'S	32'02.57'W	40/720	755	MUC10	★	x	x	x	x	WGPO	MeiMaPoly	5,6,7,8,11
	North Filchner	17	2016-01-04	75'00.85'S	32'53.48'W	50/581	608	GKG	★	x	x	x	x	WGPO	MeiMaPoly	5,6,7,8,11
		26	2016-01-08	75'15.97'S	37'55.17'W	35/393	415	MUC10	★	x	x	x	x	WGPO	MeiMaPoly	5,6,7,8,11
		48	2016-01-19	74'46.18'S	37'18.59'W	44/4670	482	MUC10	★	x	x	x	x	WGPO	MeiMaPoly	5,6,7,8,11
	North eastern	1*	2015-12-24	70'52.89'S	11'06.03'W	40/330	309	MUC10	●				x	WGPO		5,6,7***, 8***
		104*	2016-01-31	72'36.39'S	18'02.60'W	20/306	306	MUC10	●				x	WGPO		5,6

★ Ch I, II, III; ● data used to update existing spatial data sets (sediment texture: Jerosch et al. 2015, TOC: Seiter et al. 2004); ✕ Ch I, II; △ Ch III

* Data were used to update existing spatial data sets of TOC and sediment texture (see chapter III) but were not included within the analyses as they are located outside the FT survey region

** Water-column data was analyzed and published but not used for included into statistical analysis

*** Faunal data were published but not used for faunal analysis

1: Vanreusel et al. (2021b), **2:** Vanreusel et al. (2021a), **3:** Veit-Köhler et al. (2017), **4:** Säring et al. (2021c), **5:** Säring et al. (2021b), **6:** Säring et al. (2021e), **7:** Säring et al. (2021a), **8:** Säring et al. (2021d), **9:** Weith et al. (in review b), **10:** Weith et al. (in review c), **11:** Weith et al. (in review a)

General Discussion

The general objective of my thesis was to provide a baseline knowledge on Antarctic endobenthic biodiversity and its drivers by using environmental conditions enabling the prediction of biodiversity patterns. I integrated methods and approaches of different biological research fields (taxonomy, ecology, bioregionalization). The investigation meiofauna and macrofauna communities in relation to their environmental drivers demonstrated a stronger relationship with environmental parameters in meiofauna communities than in macrofauna communities (chapter I). Using the lowest taxonomic resolution possible, I identified and described a new *Anobothru*s species (Ampharetidae, Polychaeta) including a new identification key and habitat information, which is relevant for distribution modelling (chapter II). Using a bioregionalization approach I showed in chapter III that bioregions classified based on environmental parameters could only partially reflect the distribution patterns of taxonomic or functional polychaete community types in the WS. In the following, the findings are placed, integrated and discussed under the perspective of current knowledge and future directions. The gained knowledge from my thesis can be used for predictions and conservation.

New knowledge on endobenthic diversity in the Weddell Sea

This thesis allows for the first time to assess endobenthic biodiversity under different ice-cover regimes in the WS. The results of chapters I, II and III are important and necessary steps towards the understanding of endobenthic ecosystem processes and their functionality in the WS, which represents an important element of biodiversity in ecology surveys (Petchey & Gaston 2006).

In context to my objectives, I showed that within the endobenthos meiofauna has the highest abundances (excluding microorganisms here). Across the WS, nematodes were the dominant meiofauna taxon, whereas polychaetes dominated macrofauna communities (chapter I, III), which is similar to previous findings in this region (Gerdes et al. 1992, Herman & Dahms 1992, Piepenburg et al. 2002, Hilbig et al. 2006, Rose et al. 2015). However, nematode and polychaete abundances were considerably lower under high ice-cover regimes in the FT region than under regimes with seasonal ice-cover in the northwestern WS (chapter I, III), this pattern goes along with the overall endobenthic abundance across the survey region in the WS. This suggests, that these taxa may be less well adapted to high ice-cover conditions or it indicates the competition of space under high ice-cover conditions. The dominance of these taxa within the endobenthos could be an indication of their ecological importance for soft-bottom ecosystems and hence could be relevant to predict other endobenthic taxa.

Commonly, the Antarctic benthos has been classified as mobile deposit and sessile suspension feeders based on epifauna data (macro- and megafauna), which were recorded by seabed images (Barry et al. 2003, Gutt et al. 2016, Jansen et al. 2018a, Pineda-Metz et al. 2019). In contrast, I did not find such a division of endobenthic communities. Subsurface deposit feeders were the predominant feeding type (chapter III) in all five functional polychaete community types observed across the WS. In addition, the functional composition and structure of endobenthos differed to previous findings of epibenthos in the

WS (Gutt et al. 2016, Pineda-Metz et al. 2019). For instance, whereas in the northwestern WS sessile and sedentary suspension feeders filtering organic particles from the water column dominated macroepifauna communities (Gutt et al. 2016), the endobenthic polychaete community was dominated by mobile deposit feeders and predators (chapter III). This indicates that functional information of epibenthos are not applicable for endobenthos

I demonstrated, that some endobenthic taxa or functional groups displayed distinct distribution patterns in terms of their occurrence and abundance across the WS (chapter I, II, III). For instance, sessile suspension (sabellids) and surface deposit (ampharetids) feeders with a tentacle crown were more abundant in the Drake Passage, Bransfield Strait and FT region, however, these were less common in the northwestern WS (chapter II, III). Furthermore, comparing the results of the two community studies of this thesis demonstrates that despite the different taxonomic resolutions, polychaete and macrofauna communities had similar distribution patterns. Communities from Drake Passage and Bransfield Strait displayed a closer similarity to FT communities in their taxonomic and functional composition than to those in the northwestern WS (chapter I, III). Similarities in biodiversity between these regions could also be highlighted at the macrofaunal species level in this thesis. The holotype and paratypes of the new species, *Anobothrus konstantini* Säring & Bick, 2022, were found on the shelves of the FT region and the additional material originated from shelf regions in the Drake Passage and Bransfield Strait but no specimens were found in the northwestern WS (chapter II). In contrast to these similarities among regions with extreme ice-cover regimes, I demonstrated that the meiofauna community composition differed between almost all regions across the WS (chapter I). Most studies so far focused on macro- and/ or megafauna communities (Table S1) but my finding shows that meiofauna should be considered in future studies of the benthic ecosystem in the SO (chapter I, III), as the effects of climate change (e.g. differences in ice-cover) may be seen more clearly in communities of smaller benthic organisms. Data of larger epifauna (macro- and megafauna) has not been included in this thesis. An even more comprehensive precise picture of the whole benthic ecosystem could have been obtained if additional epifauna community data from seafloor images collected at the same sampling sites had been used. Such further extensions to investigate the different ecosystem processes and their functionalities as well interaction between epi- and endobenthos would be possible, for example, with the additional epifauna data from Pineda-Metz et al. (2019) and Gutt et al. (2016) for the FT and AP region, respectively.

Despite the (dis)-similarities of the community compositions and species occurrence between the AP and FT region (chapter I, II, III) and even if some polychaete families were observed exclusively only in one region (chapter III), I cannot draw any precise inferences about species dispersal or their dispersal barriers of endobenthos based on the geographic separations. Such conclusion require a more detailed taxonomic, morphological and genetic study approach at a lower taxonomic resolution, as species level (e.g. Brasier et al. 2017). For the polychaete dispersal at species level considering larval dispersal phase, Brasier et al. (2017) recorded for 12 out of 17 species broad distributions across the West Antarctic. The applied particle tracking model, which was used to detect dispersal ranges indicated larval dispersal among the different populations. However, it may be likely, that dispersal barriers have less impact on the functional similarity of organisms between regions as individuals are grouped by their functional traits rather than their taxonomic similarities.

In general, I can conclude, that most taxa and functional groups were not limited to one region, but their relative contributions varied among regions and can be related to the different environmental conditions prevailing there.

Environmental drivers for the benthos are parameters describing sea-ice cover and food availability at the seafloor

Finding the environmental drivers shaping the endobenthos community composition was a major aim of my thesis. I demonstrated that one parameter alone did not explain the community variation, indicating the interplay of several drivers. Biodiversity variations of endobenthic communities on different scales in the WS are shaped by a complex ensemble of several sediment (e.g. food-related parameters), water-column and ice-cover parameters (Figure 8) explaining > 39% of the variation among different communities (chapter I, III).

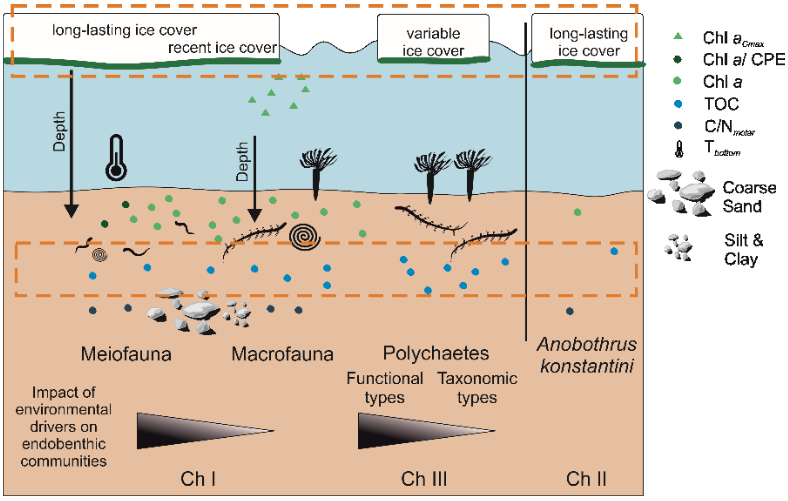

Figure 8: Schematic illustration of environmental properties affecting endobenthic biodiversity in the Southern Ocean. Orange boxes indicate most important parameters for endobenthic biodiversity throughout this thesis. Results for meio-macrofauna and polychaete communities are based on statistical analysis described in the respective chapter, whereas results for *A. konstantini* Säring & Bick, 2022, are based only on observations. Gray triangles indicate impact of environmental parameters to community type, wide end: high impact, pointed end: less impact.

The importance of ice-cover parameters for structuring the endobenthic community composition across different size classes and taxonomic resolutions (1-year ice cover: 35% meiofauna, 21% macrofauna, chapter I; SD-10-year-ice: 16% taxonomic polychaete community, chapter III) as well as for functional groups (SD-10-year-ice: 16% functional polychaete community, chapter III) confirmed that variations in community composition were, indeed, linked to sea-ice dynamics and were not an artefact of regional sampling. Similarly, environmental parameters reflecting sea-ice cover conditions (e.g. ice thickness, duration, snow cover) were important drivers for taxonomic and functional benthic communities also in other habitats such as shallow waters in the Ross Sea (Cummings et al. 2018). This underlines that sea-ice conditions are of paramount importance for the abundance, species richness, composition and function of benthic communities through their regulation of light availability, productivity, particle flux and food availability at the seafloor (chapter I, III, Thrush & Cummings 2011, Fountain et al. 2016, Gutt et al. 2016, Cummings et al. 2018, Pineda-Metz et al. 2019).

Furthermore, my findings (chapter I, I, III) underline that food supply at the seafloor is a key factor structuring marine benthic species and communities as stated by several authors (e.g. Pearson & Rosenberg 1978, Wieking & Kröncke 2005). Variable and seasonally changing environmental conditions (e.g. ice cover, seasonal food pulse) of organic-rich habitats, characterized by a food high quantity and quality, in the northwestern WS (Säring et al. 2021e, chapter I) seem to favor high standing stocks of endo- (chapter I, III) and epibenthos (Gutt et al. 2016) but have no positive effect on the biodiversity of polychaete communities (Shannon-Wiener index, species evenness and richness, chapter III). Contrarily, high or none ice-cover with organic-poor sediments, as in Drake Passage (category I: none), Bransfield Strait (category II: irregular) and FT (category IV, V: high & constant), may limit the endobenthic abundance throughout different size classes and taxonomic resolutions. However, rare taxa, such as tardigrades, loriciferans (meiofauna, chapter I), sabellids, syllids and ampharetids (polychaetes, chapter III), and in particular *A. konstantini* Säring & Bick, 2022 (chapter II), appear to favor such food conditions. Often these rare taxa are important to accentuate differences between ice-cover regimes (chapter I, II) or regions (chapter III).

Nevertheless, the effects of food availability on the endobenthic community structure are only partially consistent (Figure 8). Polychaetes depend less on quality and more on the quantity of food at the seafloor, which is supported by the high explanatory power of TOC (proxy for quantity of detritus at the seafloor, 23%, 26%, respectively, chapter III). Moreover, it seems that the quantity of organic matter has an impact on the functional composition of different benthic size classes. For instance, the vertical flux of phytodetritus in the northwestern WS presents favorable food conditions for mobile deposit-feeding and predatory polychaetes (Figure 2 in chapter III) but which were less abundant in other regions with lower food quantity. Similarly, in the Ross Sea Barry et al. (2003) suggested a relationship between carbon-rich sediments and a high abundance of epifaunal deposit feeders, such as holothurians and echiurans, even though these relationships were not significant. In an approach focused on food availability modelling, Jansen et al. (2018a) showed for epifauna, that the estimated availability of deposited food particles correlated with increasing abundance of deposit feeders and decreasing suspension feeder richness. Moreover, the quality proved to be a structuring factor for meio- and macrofauna community compositions, highlighted by the high explanatory power of Chl*a* (proxy for fresh detritus at the seafloor) for these communities (20%, 11%, respectively) versus TOC (5%, 11%, respectively, chapter I). These findings suggest, that the quantity is relevant for the consideration of size classes, as it affects the presences and abundance of different endobenthic taxa within the meio- and macrofauna community, whereas the quantity seems to be a more specific driver for polychaete communities.

Water depth is often considered as another important indicator for the quantity and quality of food supply in benthic ecosystems (e.g. Rex et al. 2006, McClain et al. 2006). More organic matter can be degraded during a longer vertical export in the water-column (Smith et al. 2006). However, ice-covered regions, such as the SO, may deviate from this pattern, because here the phytodetritus has faster sinking rates (Grebmeier & Barry 1991). Hence, the sea-ice cover and actual vertical transport are more relevant for the food situation at the seafloor than water depth in energy-limited ecosystems (Grebmeier & Barry 1991, Piepenburg 2005). Here, it was confirmed that meio- and macrofauna as well as the polychaete community compositions in the WS respond less to water depth than to ice-cover parameters and food availability at the seafloor (chapter I, III).

Further, I also considered other parameters that were suggested to be important for benthic communities in the SO, such as grain size (Piepenburg et al. 2002, Cummings et al. 2006, 2018). However, grain size had a minor effect on the examined endobenthos in the studied regions (chapter I, II, III). Thus, it is reasonable to expect that grain size parameters are less relevant for approaches focusing on smaller soft-bottom communities in shelf regions in the SO than for epifauna, e.g. megafauna.

The large number of abiotic and biotic parameters and interactions that contribute to the structure of benthic communities and the occurrence of species, illustrates the complexity of the processes occurring in the WS. My findings highlight, that the occurrence of single taxa (e.g. *A. konstantini* Säring & Bick, 2022) and the structure of endobenthic communities are affected by different environmental parameters (Figure 8, chapter I, II, III). For instance, eight environmental parameters explained the variation of the whole macrofauna composition (Depth, 1-year-ice cover, Chla_{Cmax}, Chl$a$, TOC, C/N$_{molar}$, Silt & Clay, Coarse Sand, Table 5 in chapter I), whereas the composition of the community of the dominant macrofauna taxon, the polychaetes, was explained by only two environmental drivers (TOC, SD-10-year-ice, chapter III). These findings suggest, that polychaetes could be more robust to changes of environmental parameters such as depth, granulometry, whereas the presence and abundance of other macrofauna taxa, such as molluscs, amphipods or echinoderms may be affected. Overall, the results (Figure 8) throughout my thesis show the predominant role of sea-ice cover and food-related parameters at the seafloor for the different endobenthic communities (chapter I, III) and a single species (chapter II), which should be included in future assessments focusing on endobenthic ecosystem in the SO.

Environmental parameters to consider in the future

As endobenthic communities depend on different ice-cover and food parameters, I suggest including parameters representing several ice-cover (e.g. 1-year-ice cover, SD-10-year-ice) and food properties (e.g. Chl$a$, TOC) to accurately assess the link about the link between organisms their environment for conservation strategies. Overall my findings suggest, that an indirect space-for-time substitution approach, including gradients for these drivers that are expected to change with ongoing warming, could be successfully implemented for the prediction of consequences for the ecosystem due to climate change under future scenarios. However, I anticipate these parameters only represent a subset and that additional drivers (e.g. water-mass parameters) may influence endobenthic community structure (chapter I, III).

The main missing ecologically relevant parameters consider pelagic-benthic coupling, such as the spatial distribution of surface-derived food on the seafloor (Jansen et al. 2018c) and high-resolution bathymetry

(Mayer et al. 2018), which could allow a more precise separation between habitats and be relevant for predicting faunal distribution patterns with changing environmental conditions. In addition to the seafloor and water-column pigment content presented in this thesis (chapter I, III) further measures are needed, e.g. particle flux and sedimentation flux. This will provide a more explicit way to relate the productivity sources derived from sea ice and the water column as well as their accumulation to the benthos and to model the food availability near the seafloor and estimate changes in the horizontal flux (Jansen et al. 2018c).

Further, the characterization of hydrodynamic regimes at different scales (site, location, bay; coastal-open ocean connectivity, water-mass circulations; e.g. Gutt et al. 2018) could be used to analyze potential food and larval sources, and ice-formation processes (e.g. Hauquier et al. 2015, Brasier et al. 2017). I assume that the structure of the macrofauna and polychaete communities could be linked to the influence of water-mass circulation (chapter I, III). For example, the functional heterogenous polychaete community $_{Func}$E occurs in two geographically separate regions (Figure 7 in chapter III), but both are shaped by water currents, the Drake Passage by the ACC (Hofmann et al. 1996), and the eastern and western FT shelf by the WS Gyre (Ryan et al. 2017).

Although according to recommendations of the CCAMLR Science Committee, benthic and pelagic environments should be handled separately in bioregionalization approaches (Penhale & Grant 2007, SC-CAMLR 2010), there is, however, increasing evidence of interactions between these two ecosystem compartments (Grebmeier & Barry 1991, Gili et al. 2006, Smith et al. 2006, Pineda-Metz et al. 2019). Additionally, I demonstrated that a combination of sediment, water-column and ice-cover parameters affects the endobenthic community composition in the WS together and not separately (chapter I, III). Thus, I recommend including parameters from multiple compartments and scales (e.g. local and regional), that are relevant for biological patterns within bioregionalization approaches (e.g. Douglass et al. 2014, chapter III).

Environmental drivers may change in future decades and could affect endobenthos in the Weddell Sea

The scientific community has identified major knowledge deficits related to the vulnerability of SO biota to anthropogenic effects and risks, particularly those caused by climate change (Flores et al. 2012, Vernet et al. 2019, Rogers et al. 2020, Gutt et al. 2021). The effects of climate change are anticipated to affect biological processes linked to sea-ice dynamics (e.g. food availability at the seafloor). Griffiths et al. (2017) demonstrated, that ~79% of the endemic species in the SO are projected to face a reduction in suitable habitats. It is possible that with strongly warming climate, not only epibenthic (Barnes 2015, Pineda-Metz et al. 2020) but also endobenthic organisms in the SO may experience a range shift, as endobenthos structured by environmental drivers that are expected to change in the future (chapter I, II, III). This may lead to dramatic changes of benthic ecosystems and biodiversity.

In general, Antarctic benthos are considered poorly adapted to warmer bottom temperatures (Somero 2010) and have limited potential to cope with a 1–3 °C temperature increase (Pörtner et al. 2007, Barnes

& Peck 2008, Doddridge & Marshall 2017). Nevertheless, such temperature ranges are often unknown for endobenthic organisms. Although temperature has none or minor impact on endobenthos organisms (chapter I, II, III), temperature changes could affect the endobenthic diversity, as such changes are closely linked to sea-ice cover and resulting seafloor food inputs. Thus, accurately separating the effects of individual environmental factors on communities is complex and nearly impossible.

For the western AP, studies stated an increase of ice-free days linked to an increase of primary production, which in turn had a positive effect on the abundance and biomass of epibenthic organisms and the quantity of benthic *'blue carbon'* (biological carbon), which is stored in the local benthos (Peck et al. 2010, Barnes 2015, Barnes et al. 2018). Based on a temporal data set over 26 years for epibenthos in the eastern WS Pineda-Metz et al. (2020) suggested an increase of biomass and abundance in response to the prediction of a decreasing sea-ice covers in the future (Timmermann & Hellmer 2013). I assume that it could be possible that such a predicted decline of sea-ice cover in the FT region may increase the diversity and abundance of the endobenthos, favoring endobenthic taxa from regions with seasonal ice-cover conditions (e.g. nematodes) without excluding taxa that can persist under long-lasting ice-cover conditions (e.g. tardigrades) and may manage certain environmental shifts (chapter I).

However, if environmental conditions change drastically these could pose a potential threat to organisms that seem to prefer long-lasting ice-cover conditions with low food supply and may lead to a decreasing biodiversity (Griffiths et al. 2017). For instance, heterogenous and less mobile polychaete communities, as well as rare meiofauna taxa (e.g. tardigrades, loriciferans) in the FT region (chapter I, III) may not be able to persist under changing conditions of decreasing sea-ice covers (e.g. higher quantity and quality of food availability at the seafloor). These assumptions apply as well for the new described *Anobothrus* species, as no individuals were found in the northwestern WS with its higher food availability (chapter II). Further, regions such as the northwestern WS could face a reduction of species richness and abundances, due to drastically warmer bottom temperatures and less or no sea-ice cover that could exclude taxa adapted to seasonal ice-cover conditions. Another potential threat for taxa adapted to long-lasting ice covers could be the dispersal of taxa from other WS regions. Distribution patterns of taxa and functional groups living under long-lasting ice-cover regimes may be affected by the competition for space. Heterogenous and less mobile polychaete communities, as well as tardigrades and loriciferans abounded in the FT region while other meiofauna taxa (e.g. nematodes) or mobile polychaetes which were abundant in e.g. the northwestern WS were scarce in the FT region (Hauquier et al. 2015, chapter I, III). Therefore, the migration of taxa from regions with seasonal or irregular ice-cover conditions to the FT region, could lead to a replacement of the current taxonomic and functional endobenthic communities consisting of rare taxa. However, to date most endobenthic taxa occurring in long-lasting ice-cover regions, are new to science (chapter II), poorly studied (e.g. tardigrades chapter I) or even completely unknown to us. We can only speculate how they may be influenced by future climate change. Although biological processes in the Antarctic benthos are considered to be slow, a 40-year study by Dayton et al. (2013) indicated that increase and decrease of a population may proceed over decades and not centuries. This highlights the need to re-assess the concepts of slow processes and stability on a time scale of centuries, as well as the benthic response to change. This is necessary to develop most accurate models and outputs to ensure efficient and early protection of ecosystems and areas in the SO.

From understanding endobenthic diversity in the Weddell Sea to prediction

Predicting distribution patterns for endobenthic organisms of the AP and WS shelf was a goal of applying my thesis outcomes. Bioregionalization approaches have been applied to understand spatial patterns of biodiversity in the SO before (Grant et al. 2006, Raymond 2011, Douglass et al. 2014). However, the relatively small sample size and sparse density compared to the large survey areas could be limiting factors to run reliable models in this thesis.

The open-access publication of all datasets used in this thesis according to the FAIR principles (Findable, Accessible, Interoperable, Reusable, Wilkinson et al. 2016) contributes to expand the current sparse spatial data situation of endobenthic information at different biodiversity levels, e.g. species level (*A. konstantini* Säring & Bick, 2022: AlphiaID 1561325, urn:lsid:zoobank.org:pub:BE630DB7-6B9F-47E3-8A63-54CDF6ABC413) and community level (meiofauna: Veit-Köhler et al. 2017, Säring et al. 2021a, macrofauna: Säring et al. 2021d, 2021c, polychaetes: Weith et al. in review a). Additionally, the coverage of environmental sediment (Säring et al. 2021e, Weith et al. in review c) and water-column data (Säring et al. 2021b, Weith et al. in review b) in the WS is enhanced. These records are easy to access via the global biogeographic databases and thus be used to assess distribution patterns in the WS, as broad spatial data coverage is essential for predicting and validating broad-scale distribution patterns and for monitoring shifts in the spatial distribution of biotic and abiotic properties.

Studies within the SO mostly focused on utilizing statistical clustering methods to highlight areas with relatively dissimilar properties on broader (e.g. Grant et al. 2006, Harris & Whiteway 2009) or regional scales (e.g. chapter III). This approach seems to be useful if synoptic data are present on abiotic parameters that are known to be common drivers or correlate with biological patterns, but only limited data exist on actual biological patterns (e.g. Clarke et al. 2009, chapter I, III). I demonstrated, chapter I, that the classification of ice-cover categories is a useful approach to define different benthic habitats and could be valuable surrogates for endobenthos of the AP and WS shelf, in particular for meiofauna. Although, in chapter III I used ice-cover parameters among other spatially available parameters, which have been identified as important environmental drivers, such as organic content at the seafloor (e.g. chapter I, III), geomorphological features (e.g. Barry et al. 2003, Veit-Köhler et al. 2018) and temperature (e.g. Gutt et al. 2016) for the none-hierarchical clustering to map habitats, it was not possible to predict spatial distribution patterns of the endobenthos. The classified environmental bioregions only partially correspond to the distribution patterns of the taxonomic and functional polychaete community types in the WS (chapter III), potentially due to a more complex structure and ecology of endobenthos compared to epibenthos. The applied bioregionalization approach on a small scale could be a more promising and efficient tool to predict the distribution of other benthic communities, e.g. epibenthos:

Comparing FT bioregions (${}_{4}$B2, ${}_{4}$B3, ${}_{4}$B4) defined in chapter III with macrobenthic community types described by Pineda-Metz et al. (2019), indicated that these bioregions could reflect epifauna distribution patterns more accurately than for endobenthos. It should be noted that this comparison is restricted to the locations used in both studies and does not refer to the complete data set from Pineda-Metz et al. (2019).

Linking taxonomic studies with the quantitative description of habitat and functional information (chapter II) can improve the understanding of species distribution by providing a basis for species distribution models (e.g. Gutt et al. 2012, Pierrat et al. 2012, Meißner et al. 2014). Such models allow mapping of spatial distribution patterns of the organism due to its response to a set of environmental properties. So far, most climate change impact studies in the SO focusing on single species distributions are based on presence data (Gutt et al. 2012). While such studies give valuable insight regarding habitat preferences of single species, these cannot be used to draw conclusions about where and how biodiversity patterns are distributed. Modelling the distribution of multiple species individually is not feasible, as many marine taxa are rare (e.g. chapter I, II, III). Where the data permits, community-based analyses based on abundance or presence data in combination with environmental properties can offer insight on the biodiversity distribution through analyzing dissimilarities between sites. For instance, a hierarchical classification was used to identify distinct environmental types of a certain region based on known and probable relationships between environmental drivers, biogeographic patterns and ecology of taxa (e.g. dispersal, life history) for coastal shelf areas worldwide (Spalding et al. 2007) and the seafloor of SO (Douglass et al. 2014).

However, the majority of methods used so far, the taxa composition of assemblages in classified bio-or ecoregions is challenging to dissect as derived values which represent the community structure are modelled rather than the responses of individual taxa.

Relative novel statistical methods for analyzing ecological community data modify models to fit the data properties (Warton et al. 2015), and directly focus on observed data instead of randomly transformed or otherwise derived metrics. Such approaches include combining species specific models within a single hierarchical model (Ovaskainen & Soininen 2011), grouping taxa with similar responses to environmental properties together into *species archetypes* (Species Archetype Models SAMs, Dunstan et al. 2011, 2013), or sites with similar properties into *regions of common profile* (Foster et al. 2013). Considerable progress had been achieved using SAMs and food availability models in understanding and mapping the distribution of epibenthos in shelf regions in the SO. It was possible to estimate the horizontal flux of food after a glacier calving event with the food availability model (Jansen et al. 2018c) and then to predict the post-calving multispecies distribution patterns of suspension feeders using the SAMs (Jansen et al. 2018a). With a higher sample density and a smaller survey region SAMs can be useful to predict variation of endobenthic distribution, by using meiofauna community data, in relationship with changing sea-ice cover due as an effect of climate change.

Such valuable spatial information can be used for conservation planning, as the lack of information on marine biodiversity over the past 20 years has led to a shift away from conservation of species (e.g. keystone species) to conservation of spaces (e.g. Roff & Evans 2002). However, no single analysis strategy will be capable of resolving all current and future research questions and related issues. It is important to ensure that the methods used are suitable for the data and the ecological questions of interest: are the assumptions and structure made by the model appropriate?

Remaining challenges for predicting spatial distribution patterns of the endobenthic biodiversity in the SO

It appears that the small sample size and density of 16 benthic sampling sites compared to the large survey area complicated and even prevented the prediction of polychaete distribution patterns across the WS, particularly for the FT region with only six benthic sampling sites (chapter III). Thus, it was not feasible to run reliable models to interpolate the polychaete distribution and integrate these with environmental covariates for the SAMs or a joint clustering approach. With a higher sample density across the survey regions it could work (e.g. Galanidi et al. 2016, Jansen et al. 2018a).

Instead we focused on the physical data to apply the bioregionalization approach to characterize environmental habitats by using physical data as environmental surrogates (chapter III). It needs to be noted that using solely environmental data introduces the risk of overprediction, as without the knowledge of the species and community biology, major environmental covariables could be missing within the analysis (Anderson et al. 2016). Although I identified key drivers for structuring endobenthic community composition in the WS (chapter I, III) it seems that these were possibly not important parameters for classifying bioregions as these parameters did not significantly differ between all four bioregions and may cause the inconsistencies between bioregions and endobenthic distribution patterns. Further, it is often not feasible to predict whether biological communities are actually different within or across bioregions, as biological variables are commonly not incorporated in the classification process, unless the bioregionalization has been indirectly validated through testing models against the direct observations. Results based on environmental data alone should be, therefore, interpreted with caution. Previous studies have shown there is less partitioning of the geographic space when biological data has been included (e.g. Woolley et al. 2013) suggesting that species can survive in broader ranges of environmental variation than in the variation range inferred from using physical information alone. The clustering process forces boundaries to be drawn, e.g. between the four different bioregions in chapter III, where in reality variations in environmental characteristics and faunal distribution tend to appear on a spatial gradient. Those artificial boundaries should be handled and considered to be part of a gradient, instead of a strict barrier across faunal and environmental features (Post 2008). For example, it cannot be excluded that stations within one bioregion represents an outliner due to its proximity to another adjacent bioregion presents an outliner. Further, due to the low sampling density in some bioregions it is possible that community types may not represent the entire community as each is represented by only a single sampling site (chapter III).

Nowadays, there is still a large number of potentially relevant ecologically environmental parameters that are not consistently available for biodiversity approaches. These area-wide lacking data can reduce the ability to model familiar regional biodiversity hotspots (e.g. AP, FT region chapter III). Further, this can lead to residual spatial autocorrelation in statistical analyses that goes counter to the assumptions of multiple models. It can cause overly reliable predictions and estimations of the environmental variable relevance (Dormann et al. 2007) which is particularly an issue if poor models are subsequently applied to guide management planning or to predict future changes. Meiofauna could be a promising endobenthic group for prediction approaches predicting ecologically relevant endobenthic taxa in the WS due to its strong link to environmental data. Testing could be done in smaller survey regions with a higher sampling density.

Which is the most valuable way to investigate endobenthic biodiversity?

Aside from how biological data are physically collected, the way how biological data are recorded and assembled unintentionally affects what kind of biodiversity patterns can be predicted out of them. Are organisms recorded on *species level*, higher taxonomic resolution, a common *functional trait* or are they investigated on the *community level*? In my thesis on the Antarctic endobenthos, I have used the different *levels* and *attributes* of biodiversity (Figure 1), which raises the question '*which is the most valuable one*?'. To get to the bottom of this question, the different research fields and methods of this thesis are highlighted below regarding their benefits and weaknesses for biodiversity research.

The evaluation of biodiversity and functional ecology is built on the fundamental knowledge of reliable taxonomic data (Cousins 1994). Each year since the introduction of the Linnaean nomenclature in 1758, more than thousand species have been described and named (Zhang 2008). This progress has been accelerated by new discovery tools, virtual access to museums collections (Knapp 2008), high throughput sequencing (Vogler & Monaghan 2007), geographic information systems (Graham et al. 2004), and computed tomography (chapter II, Parapar et al. 2018). Nevertheless, several authors stated that the research field taxonomy is in a crisis (e.g. Linse 2008, Boero 2010) leading to less accurate taxonomic identifications and to a considerable underestimated richness of multiple groups (Giangrande 2003), such as for invertebrates in the SO (e.g. Gutt et al. 2004, De Broyer et al. 2011). To describe the various facets of biodiversity within an ecosystem taxonomic information on species level alone are not sufficient. Previous polychaete species descriptions from the SO only mentioned the geographic location, depth and temperature (e.g. Schüller 2008, Schüller & Jirkov 2013) but did not include other relevant habitat information to understand species occurrence and distribution, e.g. food-related parameters or grain size. By describing a new species, I was not only able to fill a small gap of the unknown polychaete species on this planet, but with the ecological information about the species occurrence, I could also point out a potential future threat to *A. konstantini* Säring & Bick, 2022 (chapter II).

But as ecosystems or geographic regions are inhabited by multiple species, single species approaches only represent a small fraction of the ecosystem biodiversity (Ferrier & Guisan 2006, Warton et al.

2015). Benthic biodiversity surveys on *community level* combine data from multiple community types e.g. taxa (chapter I, III) or functional groups (chapter III) to generate information on the biodiversity. Higher taxonomic resolutions than species or genus level are usually applied for large biodiversity-community studies, as in this thesis where I grouped organisms by their phylum, class, order (chapter I: 589,799 individuals, 39 higher taxa) or family (chapter III: 1,605 individuals, 34 families). Further, community studies can provide significant application benefits when addressing a larger number of species, especially if many of these have been recorded irregularly and infrequently (e.g. tardigrades and loriciferans in chapter I). In addition, multiple species approaches showed a higher probability of containing a greater diversity of phenotypic traits (Loreau et al. 2001).

Biodiversity on the *community level* is often associated and described with biodiversity indices e.g. alpha biodiversity (total diversity of several samples within a habitat, local scale) including species richness and/ or evenness (e.g. Piepenburg et al. 2002, Schüller et al. 2009) whereas other components related with biodiversity have been less well studied, such as environmental interaction and effects. It seems that regions with extreme ice-cover conditions favor heterogenous communities, as biodiversity indices were higher compared to regions with a seasonal ice-cover (chapter III). Such surveys on the community level, include a broad range of biodiversity including different taxa and can be useful to assess the link between biota and environmental conditions. Thus, they are important to maintain information on the ecosystem function and integrity, which have been noted as key objectives of the ecosystem management (Haynes et al. 1996). By incorporating environmental and endobenthic community data, I recommend including ice-cover classifications and meiofauna communities in future assessments and modelling approaches concerning the impact of environmental changes on SO ecosystems, given the stronger relationship of sea-ice cover and meiofauna communities compared to other endobenthos communities (chapter I, III). Further, even though endobenthic communities are affected by sea-ice cover and benthic food parameters, taxa grouped by a higher taxonomic resolution respond to different types of these environmental parameters (as discussed before, chapter I, III). Therefore, I suggest that polychaete communities should only be partially considered as *zoom in* or proxy for macrofauna communities, even though they showed similar partitioning between regions regarding their community composition (chapter I, III) and have been used as surrogates in different studies to predict potential biodiversity patterns of benthic organisms (e.g. Olsgard et al. 2003). It is possible that any taxonomic rank higher than species could behave similarly to a random group of species that yields no ecologically useful information. But inconsistencies may not be variable based on the habitat and trophic level (Sutcliffe et al. 2012). Thus, it appears reasonable to investigate different endobenthic communities together assess differences and to obtain a comprehensive picture of the Antarctic benthic ecology.

Inferences between organisms and the environment are difficult to reach if the community is examined only in terms of taxonomic information. For instance, a hint of bioturbation in the northwestern WS can be given due to the high Chl*a* and CPE content even in deeper sediment layers (Veit-Köhler et al. 2018). In addition, given the information from the functional groups regarding the organisms-environment linkage, it is possible to presume which environmental conditions prevail independent of additional environmental assessments. For instance, the occurrence of suspension and surface deposit feeders with a tentacle crown within the community types $_{Func}$C, $_{Func}$D and $_{Func}$E in the respective regions (chapter III) could indicate a higher energy flow from the pelagic to the benthic system there. Such functional biodiversity patterns could, therefore, be valuable for a better understanding and accurate predictions of climate change impacts on endobenthos and its ecosystem in the WS.

I highlighted that functional groups may approximate the biodiversity patterns of taxonomic community types, as the differences in the community composition between bioregions were almost similar (Figure 7 in chapter III) and the community variation has been explained by the same environmental parameters for the taxonomic and functional community types (Figures 8, 9 in chapter III). Similarly, previous studies in the Arctic have shown that taxonomic and functional macroepibenthic communities are influenced by similar environmental drivers (Cochrane et al. 2012, Lin et al. 2018, Liu et al. 2019). Further, my results support the assumption, that in contrast to taxonomic biodiversity, functional diversity is thought to be related directly to environmental structuring mechanisms (Usseglio-Polatera et al. 2000), as grouping by functional traits showed a stronger link to the prevailing environmental key driver compared to the taxonomic community composition: TOC and SD-10-year-ice explained 45% and 40% of the total functional and taxonomic community variation, respectively (chapter III). Cochrane et al. (2012) also mentioned a stronger impact of depth on the functional than on the taxonomic macroepibenthic community in the Artic.

However, the analysis of functional traits, should not stand alone as an alternative to the traditional community analysis, as this method poses some difficulties that need to be considered. Functional traits may have limited value if higher taxa are *lumped together* (Cochrane et al. 2012). The taxonomic level to record traits can vary among taxonomic groups e.g. some genera include species with different traits, whereas in others the entire family displays similar traits. It is likely that functional groups may not sufficiently resolve assemblage structures for every data type (e.g. Jansen et al. 2018b).

Non-standardized, heterogenous, even conflicting trait terminology and the few existing guidelines in the literature on how and what scale taxa should be grouped, leads to a variety of approaches depending on individual researchers, which limits the objectivity (Violle et al. 2007, Costello et al. 2015, Kremer et al. 2017). Further, due to large knowledge gaps of functional and ecological traits, functional-biodiversity approaches are not suitable for all taxa (Beauchard et al. 2017), especially for smaller-sized organisms. There are a few exceptions e.g. for nematodes: Wieser (1953) or polychaetes: Fauchald & Jumars (1979), Jumars et al. (2015), PolytraitsTeam (2023). Although the mentioned sources were used in chapter II, III, most of them are not based on polar records. It is possible that functional traits of polychaetes in polar regions may differ from those in lower latitude regions due to the extreme environmental conditions.

It can be concluded that as there is no “right” way to describe and study the biodiversity of an ecosystem, so that no valid and definitive answer can be given to the question: *which is the most valuable way?* But, I highlighted that it is important to include many different aspects of the biodiversity and to combine and integrate these in order to achieve the most comprehensive realistic picture of the ecosystem. This can lead to greater confidence in management decisions for the mutual of the marine ecosystems and humans. Depending on the research question or taxa, it is possible and important to choose a valuable level and attribute of biodiversity that will provide the most meaningful outcome. As biodiversity predictions are fundamental to many types of spatial management, these require an understanding of the ecological structure and functioning of a region. Predicting biodiversity such that the results are easy to interpret, and key statements are well presented helps to enhance the decision cycle and conservation outcomes, which is a top priority given the current biodiversity loss. In order to obtain conclusions and predictions about the distribution of a single species (*species level*), it is necessary to link taxonomic and functional information with prevailing environmental conditions (chapter II). It is crucial to focus on more than one taxon to get a holistic picture of the ecosystem, as taxon distributions, community differences and their relationships to environmental drivers can vary among taxa of soft bottom communities (chapter I, III). Thus, I suggest using *community level* with the focus on composition and distribution patterns linked to environmental properties for large comprehensive benthic surveys, especially in the context of prevailing and changing environments. Further, it appears that functional groups could reflect taxonomic community patterns and display a stronger link to environmental drivers (chapter III). It is important to generate functional and environmental information on the basis of the lowest taxonomic resolution possible. As the taxonomic resolution an organism is grouped in affects the results of the biodiversity approach, caution is needed when using a-priori groupings of organisms to give inferences concerning the distribution of biodiversity.

Conclusion

The contribution of this thesis to the scientific field can be described as follows (Figure 9): It can be concluded that predicting spatial distribution patterns of endobenthos was not possible, as the structure of endobenthic biodiversity and its ecology could be more complex compared to epibenthos. Bioregionalization approaches to predict endobenthos across the WS shelf, still need to be improved, due to descriptive inconsistencies of distribution patterns between community types and bioregions (chapter III). However, the outcome and data of this thesis can provide a potential ecological basis for future investigations on endobenthic distribution patters and may complement establishing MPAs in the WS (e.g. Teschke et al. 2021), as I identified areas where endobenthic communities or species occurrence are likely to differ across extended WS. I suggest, given my results and potential future changes of the endobenthic biodiversity, that particularly areas with long-lasting ice-cover regimes (e.g. FT region) should be subject of protection and integrated in MPAs. To improve conservation strategies for the WS I recommend, that future ecological surveys focusing on spatial distribution patterns of benthos in the context of current and changing environmental situations should include abundance data of operational taxonomic information of meiofauna. Effects of climate change may be seen more clearly in communities of smaller benthic organisms, as meiofauna communities showed the strongest relationship to ice-cover regimes compared to other endobenthic assemblages. Ice-cover classification can be useful to predict meiofauna composition and the distribution of ecologically relevant taxa e.g. nematodes (chapter I).

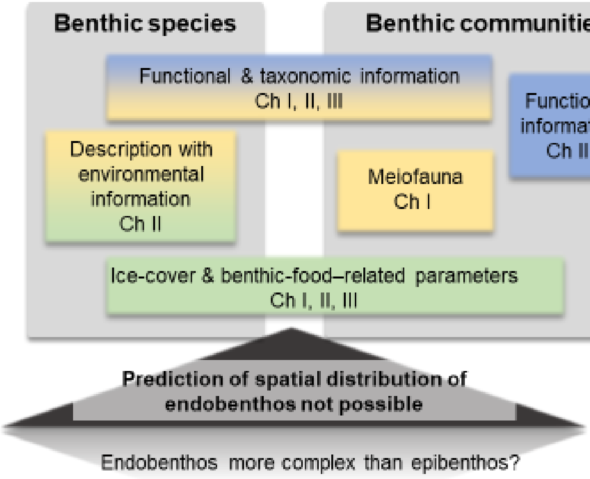

Figure 9: Overview of the conclusions from the different chapters (Ch) of this thesis and their link to the overall conclusion.

Further, functional information should be included in benthic ecological issues to improve understanding of endobenthic distribution patterns in the context of ecosystem conditions (chapter III), especially if taxonomic information is lacking. Moreover, as different sea-ice cover and benthic-food–related parameters may affect the occurrence of a single polychaete species (chapter II) and were most reliable for explaining endobenthic community patterns (chapter I, III), multiple parameters representing different aspects of sea-ice cover and benthic food supply should be in the set of analyzed parameters as environmental surrogates in future analysis of endobenthic distribution patterns. In addition, future ground-truthing with sea-surface data (Chl*a* in the water column) could improve the predictions of endobenthic community distribution patterns in the face of environmental changes.

Overall, I highlighted the relevance to integrate information of a single species (chapter II) and different communities (chapter I, III) with their functional traits and environmental drivers. Thus, I recommend a multidisciplinary approach linking taxonomic and functional information as well as an extensive analysis of pelagic–benthic coupling for better understanding of how the distribution of endobenthos is affected by its environment and respond to the effects of climate change.

Future directions

Although my thesis answers many questions on the endobenthic biodiversity of the SO, there are many more aspects that still need to be studied, as it opens directions for additional investigations on endobenthic biodiversity.

One aspect that could not be investigated in this study is the genetic biodiversity and connectivity of communities between regions. In the future some samples could be stored e.g. in ethanol so genetic analyses would be easier to conduct. However, at the same time, storage of specimen material in formol is necessary to identify morphological structures, as these could change in ethanol (e.g. appendages became brittle). Additionally, high concentrated ethanol is very expensive. Nevertheless, genetic investigations could be useful to investigate, if specimens of polychaete species that were found in the AP and FT region, such as *A. konstantini* Säring & Bick, 2022, are genetically distinct. A genetic homogeneity between samples from both sites could be evidence for a widespread distribution, maybe due to pelagic larval dispersal. Such dispersal information is useful for understanding the species distribution ranges and patterns in the past and present as well as integrated this in prediction approaches to investigate the endobenthic distribution in response to the effects of climate change in the future. Thus, if possible this information should be added to taxa descriptions.

A temporally and spatially verified description of endobenthic biodiversity in the WS including its ecological adaptation and distribution patterns under prevailing and predicted changing environmental conditions could provide a precise idea, how sensible benthic organisms and functions in the SO. Additionally, it could reveal how relevant their carbon storage could be as negative feedback to climate change for the world oceans. A first step towards such large-scale biodiversity comparisons is surely to compare the endobenthic biodiversity and its function of the Antarctic and Arctic. Both regions are considered highly dynamic and altered by ongoing climate changes. In fact, monitoring the temporal and spatial stability of described potentially endangered areas in the Antarctic (northwestern WS, FT region) vs. the Arctic could help to yield valuable insights about the impacts and their pace at which climate change is affecting our marine ecosystems.

It would be useful to create a measure like *biodiversity distinctness* within the bioregionalization approaches based on biological data, indicating the uniqueness of taxonomic and functional biodiversity of regions. This could help to underline the importance and the protection of regions with a unique biodiversity rather than only regions that are known as biodiversity hotspots. Further, highlighting changing and endangered areas could be done by indicator taxa such as polychaetes, because of their direct contact with the water column (e.g. suspension feeding) and sediment (e.g. burrowing). Syllids have been mentioned with lower abundances or completely disappear under different adverse impacts e.g. high sedimentation rates or pollution (Giangrande et al. 2005). Identifying such taxa for the SO could be useful in studies monitoring marine environmental quality as health indicator for habitats and other taxa prevailing there.

A standardized catalog or atlas for taxonomic and functional identification with labelling of Antarctic taxa is needed, to avoid classification uncertainties using references from none Antarctic regions. As this is not possible for all taxa in the SO, I suggest focusing on main taxa, such as polychaetes, nematodes, amphipods and copepods. Further, future research should test if other functional traits (e.g. body shape and length), which were not used here, may be more suitable to predict abundance patterns of endobenthos. Moreover, the taxonomic identification process of endobenthic fauna could be improved by deep-learning detection of images from the samples under the microscope. Such methods have just recently provided promising results already for the identification of foraminiferans from light microscopy images (Plavetić 2023).

Another aspect that should be considered in future investigations, are temporal scales. Data and the assumptions about potential changes within this thesis only represent a snapshot in time of different endobenthic communities at each study site. The variation in environmental drivers over time (seasonal, annual, multiyear scales), as for the ice-cover variability (chapter III) or the variation in productivity and food supply could be anticipated and may show a strong impact on the benthic communities (Thrush & Cummings 2011). Therefore, temporal and spatial aspects (repeated and consistent sampling of sites e.g. seasonal or annual) should be incorporated into study approaches and models in the future and cannot be overestimated. This type of information including dynamic processes on temporal and spatial scales is urgently required to generate high-confidence projections of ecosystem changes in the future (Meredith et al. 2019, IPCC 2022) and to support targeted action to alleviate or avoid such changes, as also recently indicated in the Southern Ocean Action Plan to promote the UN Decade of Ocean Science for Sustainable Development (Jansen et al. 2022).

To increase our knowledge in terms of endobenthic biodiversity with benthic ecosystem processes as well as to understand climate-related ecological change in the WS it would be beneficial to link the results of this thesis with benthic boundary fluxes of nutrients (e.g. ammonium, nitrate, phosphate, silicate). For example, the Canadian Artic macrofauna community composition have been shown to have a relevant role in regulating benthic carbon and nutrient remineralization fluxes (Link et al. 2013). It would be interesting, if SAMs can be applied to meiofauna. I suggest testing SAMs for meiofauna abundances on a spatially smaller region e.g. Potter Cove. It is possible that valuable regions and habitats and changes of habitats and biodiversity may be detectable early and easily by including meiofauna data within models. To validate present uncertainties and potential outlines, a greater spatial coverage of endobenthic and environmental data (e.g. benthic Chl*a*, TOC content) is needed, especially in the FT region, which should be considered in planning processes of future expeditions.

Future biodiversity approaches focusing on endobenthos should consider a combination of statistical and dynamic process models within integrated approaches, e.g. for epibenthos (Jansen et al. 2020). These provide a more comprehensive view on how the ecosystem structure and functioning is influenced by its spatial, temporal and ecological interactions and feedbacks. With the increasing computing power and technical progress environmental parameters that are relevant for modelling species distribution patterns can be predicted at higher temporal and spatial resolution than ever before. This enables the development of ocean models with high temporal and spatial resolution including simulations of ocean-ice-shelf interactions, tidal movements, and stokes drift (e.g. Stewart et al. 2018) and could be helpful for the investigation of endobenthic dispersal patterns.

Further, species interactions, which are known to regulate ecosystem processes (e.g. Cardinale et al. 2002) along with other factors, were usually not incorporated into distribution models but should be considered in the future. The development of collaborative frameworks that combine the benefits of each method will be challenging but would allow us to address new and more complex ecological research questions in less and well-studied areas, e.g.: (i) *where*, *when* and *how* endobenthos will restructure under the effects of climate change, and (ii) *where*, *when* and *how* this will eventually influence endobenthic biodiversity and key-ecosystem services.

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Publication

Chapter I

Declaration of author contributions:

Sea-ice–related environmental drivers affect meiofauna and macrofauna communities differently at large scales (Southern Ocean, Antarctic)

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This chapter was published in the journal *Marine Ecology Progress Series* Progress as:

Säring F., Veit-Köhler G., Seifert D., Liskow I., Link H. (2022): Sea-ice–related environmental drivers affect meiofauna and macrofauna communities differently at large scales (Southern Ocean, Antarctic). *Marine Ecology Progress Series* 700: 13-37. https://doi.org/10.3354/meps14188

Friederike Weith performed the laboratory work for analyzing meio- and macrofauna samples from PS 96 and was supported by Stephan Durst and Jan Schuckenbrock for analyzing fauna samples as well as by the Marine Biology Research Group Ghent University for analyzing environmental data from PS 81. Friederike Weith processed and analyzed the data.

Gritta Veit-Köhler conceived and designed the study, collected the samples, helped with the identification of meiofauna specimens.

Heike Link conceived and designed the study, collected the samples, helped with the identification of macrofauna specimens and pigment analysis.

Derya Seifert collected the samples during PS96 and helped with the identification of macrofauna specimens.

Iris Liskow performed the nitrogen and carbon analysis of sediment and water samples and contributed to the manuscript.

Heike Link and Gritta Veit-Köhler reviewed the statistical analysis and results.

Friederike Weith drafted the manuscript, Heike Link and Gritta Veit-Köhler critically commented on the manuscript and redrafted parts of it.

Friederike Weith's contribution to the written manuscript was ~ 85%.

Vol. 700: 13–37, 2022
https://doi.org/10.3354/meps14188

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published November 10

Sea-ice–related environmental drivers affect meiofauna and macrofauna communities differently at large scales (Southern Ocean, Antarctic)

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ABSTRACT: The structure and drivers of Southern Ocean meiofauna and macrofauna were investigated together in one extensive study. From the tip of the Antarctic Peninsula to the southeastern Weddell Sea, we classified the investigated stations into 5 categories according to their summer sea-ice cover: (I) none (Drake Passage), (II) irregular (Bransfield Strait), (III) seasonal (northwestern Weddell Sea), (IV) high (South Filchner Trough), and (V) constant (North Filchner Trough). The categories differed significantly in primary-production–related characteristics in the water column and food availability at the seafloor. Almost all ice-cover categories differed significantly in meiofauna communities (32–500 µm, 20 taxa, 585 825 individuals). Fewer regions differed significantly in macrofauna (>500 µm, 19 taxa, 3974 individuals) or the combined meiofauna and macrofauna communities. Environmental drivers explained >66% of the variation among different communities and differed for the faunal size classes: for meiofauna (84.2%), sea-ice cover (1 yr) and availability of fresh food (chlorophyll *a* [chl *a*]) were most important, whereas 1 yr ice cover, chl *a*, and total organic carbon were decisive drivers for macrofauna (66.6%). Grain size, water depth, water-column chl *a*, long-term ice cover, seafloor temperature, and the carbon/nitrogen ratio influenced communities to a lesser extent. We demonstrated a stronger relationship with sea-ice cover in meiofauna communities than in macrofauna communities, and we recommend including meiofauna in future assessments of the influence of environmental changes on Southern Ocean ecosystems.

KEY WORDS: Benthos · Meiofauna · Macrofauna · Food availability · Sea-ice cover · Weddell Sea · Antarctic Peninsula · Community composition

1. INTRODUCTION

Benthic ecosystems of the Southern Ocean shelf are typically characterized by stable temperatures and salinities on the one hand, and seasonally varying environmental drivers such as sea-ice cover, primary production, and food input on the other (Cook et al. 2005). Variations in regional sea-ice patterns are influenced by seasonality (Gloersen et al. 1993) and climate change (Vaughan et al. 2003). Because sea-ice cover directly affects the regulation of primary production and the particle flux from the upper water column (euphotic zone) to the seafloor (Sañé et al. 2012, Arrigo et al. 2015, Isla 2016), changes in sea-

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ice cover strongly affect sensitive benthic communities, their composition, and their abundance (Ingels et al. 2012). Food input to the seafloor shows a maximum in marginal sea-ice zones, because of the regular opening and closing of the sea-ice cover. Melting sea ice releases ice algae, which contribute significantly to benthic food supply, and it stabilizes the water column, encouraging phytoplankton blooms, as recorded for the western Antarctic Peninsula (Smith et al. 2006, Mincks & Smith 2007) and the Arctic Ocean (Carmack & Wassmann 2006). This maximum is flanked by 2 productivity minima. One is present in open oceans, where wave action and lack of sea-ice cover lead to a less stratified water column. Although these so-called oceanic productions can be characterized by high primary production rates, less fresh material reaches the seafloor, because most phytodetritus is consumed in the water column, as observed for the Drake Passage (Grebmeier & Barry 1991) and the Atlantic sector of the Southern Ocean (Lochte et al. 1997). Another minimum occurs in regions with year-round ice cover, e.g. the water adjacent to the Ross Ice Shelf and Rønne Ice Shelf. Here, constant ice cover limits light penetration and inhibits the release of ice algae into the water column. As a result, little fresh material is deposited at the seafloor (Grebmeier & Barry 1991).

The Weddell Sea encompasses different sea-ice cover regimes, from nearly constant and high ice cover in the southeast due to low sea-surface temperatures (Comiso et al. 2017) to seasonally varying ice cover in the northwest. The neighboring Drake Passage shows higher and variable sea-surface temperatures, which do not facilitate sea-ice cover in the summer months (Gutt et al. 2015, Turner et al. 2016). We expect correspondingly different food regimes: higher amounts of fresh material under variable ice-cover conditions and less fresh material under constant ice cover and in open waters, albeit this pattern not been shown for the Weddell Sea. Water depth is often considered as a good proxy for food supply at the seafloor, because more organic matter is degraded during longer vertical export in the water column. However, this pattern differs for ice-covered regions, because the phytodetritus can sink rapidly to the seafloor (Grebmeier & Barry 1991). Therefore, ice cover and vertical transport are known to be more relevant than water depth for food situation at the seafloor in energy-limited systems (Grebmeier & Barry 1991, Piepenburg 2005). We expect analogous results for shelf areas in the Weddell Sea.

Changes in sea-ice dynamics have a major effect on benthic communities that rely on algal blooms for food (Mincks et al. 2005, Mincks & Smith 2007, Glover et al. 2008, Ingels et al. 2012, Smith et al. 2012).

The composition of benthic communities should reflect such productivity and food-availability regimes. Macrofauna (organisms with a body size >500 µm) and their ecological functions depend strongly on the quantity and quality of organic matter reaching the seafloor (Link et al. 2011). Pineda-Metz et al. (2020) showed that in regions in the southeastern Weddell Sea with changing sea-ice cover, lower primary production due to higher ice cover leads to lower macrofaunal abundance and biomass. Polychaetes, bivalves, ophiuroids, and amphipods are the numerically dominant taxa of macrofauna in the Southern Ocean; polychaetes show high abundances in different habitats (Pineda-Metz et al. 2019). Polychaetes, isopods, and amphipods are especially speciose (Gerdes et al. 1992), and sessile suspension feeders and colonial organisms (poriferans, bryozoans, ascidians) make up the largest proportion of the Antarctic benthos in terms of biomass (Griffiths 2010, Pineda-Metz et al. 2019).

A previous study around the Antarctic Peninsula showed that the abundance and community composition of the smaller size class meiofauna (organisms with body sizes between 32 and 500 µm) is strongly affected by the amount and the freshness of deposited primary production (Veit-Köhler et al. 2018), but that investigation did not include sea-ice cover as an environmental parameter. Unlike macrofauna, organisms in the meiofauna do not actively shape their habitat and lack pelagic larval stages, so they are more restricted in spatial distribution. These sediment-dwelling organisms lead burrowing, interstitial, or epibenthic lives depending on their body sizes and shapes (Remane 1933). Nematodes are the dominant metazoan taxon, followed by harpacticoid copepods and other taxa such as kinorhynchs, ostracods, and tardigrades.

To date, all studies in the Weddell Sea investigated the communities of either meiofauna (e.g. Herman & Dahms 1992, Rose et al. 2015, Veit-Köhler et al. 2018) or macrofauna (e.g. Gerdes et al. 1992, Brey & Gerdes 1998, Gutt et al. 2016, Pineda-Metz et al. 2019) and their responses to environmental drivers separately. Environmental conditions are predicted to change, and their effects have so far been evaluated mostly for macrofauna and megafauna (Gutt et al. 2015, Pineda-Metz et al. 2020). A holistic view of how they may affect the benthic fauna of all size classes can only be achieved if all size classes are directly integrated into quantitative analyses. Therefore, the overarching objective of our study was to investigate the community compositions of meiofauna and macrofauna individually and combined in regions with different ice-cover regimes. We aimed to test their relationships including the most complete set of environmental drivers possible. We addressed the following hypotheses.

Hypothesis 1: Primary production and the related food-availability parameters at the seafloor differ according to the sea-ice cover. The highest freshness and amount of food at the seafloor is found in regions with the most variable sea-ice cover; lower values are expected for regions with a constant or absent sea-ice cover.

Hypothesis 2: Faunal community compositions (meiofauna, macrofauna, and combined meiofauna and macrofauna) follow the classification of the ice-cover categories. The combined community composition is distinguished best among ice-cover categories.

Hypothesis 3: Meiofauna and macrofauna communities are structured by biotic and abiotic environmental parameters (food parameters, ice cover, water temperature, grain size, depth) to a different extent. Temporally stable descriptors (e.g. depth, grain size) are expected to be more important for macrofauna.

We focused on 5 geographically and environmentally different regions, which were sampled during 2 expeditions with the RV 'Polarstern': PS 81 to Drake Passage, Bransfield Strait, and the northwestern Weddell Sea, and PS 96 to the southeastern Weddell Sea, including the North and South Filchner Trough areas (Fig. 1).

Our study provides the first integrated analysis of the meiofaunal and macrofaunal size class in relation to their environment and their different responses in the Southern Ocean. It therefore contributes to the overall assessment of the effects of climate change on Antarctic marine ecosystems in the Weddell Sea and around the Antarctic Peninsula.

2. MATERIALS AND METHODS

2.1. Study areas

Sediment and water-column samples from 16 stations were collected during 2 expeditions with the RV 'Polarstern'. The tip of the Antarctic Peninsula (Drake Passage, Bransfield Strait, northwestern Weddell Sea) was the target of expedition PS 81 (22 January to 18 March 2013), whereas PS 96 (6 December 2015 to 14 February 2016) explored the Filchner Trough area in the southeastern Weddell Sea (Fig. 1; Gutt 2013, Schröder 2016). Water depth at the sampled stations ranged from 222 to 757 m (Table 1). The regions will hereafter be referred to by their initials.

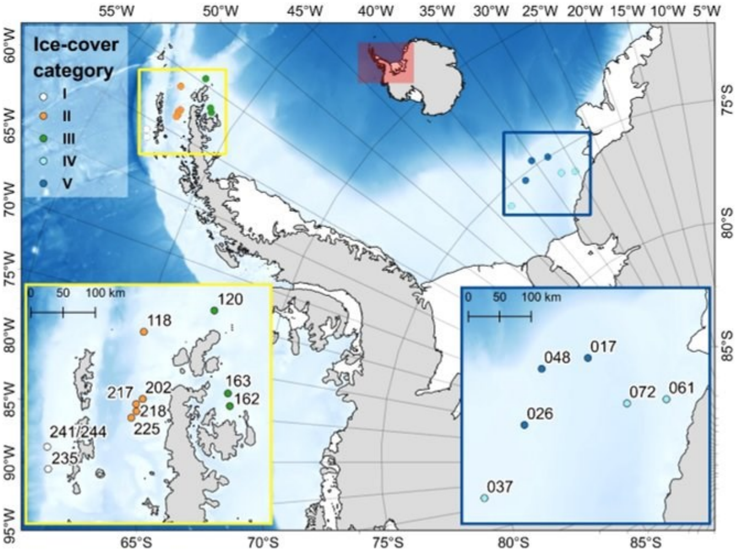

Fig. 1. Sampling stations for meiofauna and macrofauna communities and environmental parameters in the vicinity of the Antarctic Peninsula during RV 'Polarstern' expedition PS 81 (yellow frame) and southeastern Weddell Sea during expedition PS 96 (blue frame). The red box represents the chosen map section of Antarctica. Explanation and definition for ice-cover categories and sampled stations given in Tables 1 & 2

Table 1. Station list and sampling during RV 'Polarstern' expeditions PS 81 (22 January–18 March 2013) and PS 96 (6 December 2015–14 February 2016). Multicorers (MUC6, MUC10) and the giant box corer (GKG) were deployed for meiofauna and macrofauna community sampling and for sediment sampling for environmental parameters. Only successful MUC and GKG deployments are listed. For community analyses of PS 81, 1 MUC6 core for meiofauna and 3 MUC10 cores for macrofauna were usually used per respective deployment. For PS 96, 3 MUC10 cores from each deployment were used for both meiofauna and macrofauna community analyses. Samples for environmental characterization of the water column (CTD conductivity, temperature, chl *a* at the maximum and near-bottom) were collected with a CTD rosette equipped with Niskin bottles. For CTD deployments, chl *a* maximum and near-bottom sampling depths as well as salinity (Sal_{bottom}) and temperature (T_{bottom}) are given (from Schröder et al. 2013b, 2016b)

Expedition	Region	Stn	Date (d.m.yr)	Latitude	Longitude	Depth (m)	Gear	Fauna	Sal_{bottom}	T_{bottom}
PS 81 Antarctic Peninsula	Drake Passage (DP)	235-1	07.03.2013	62°16.30'S	61°10.27'W	21/372	CTD		34.50	0.43
		235-2	07.03.2013	62°16.35'S	61°10.23'W	355	MUC10	Macro		
		235-4	07.03.2013	62°16.29'S	61°10.24'W	373	MUC6	Meio		
		235-5	07.03.2013	62°16.31'S	61°10.24'W	363	MUC6	Meio		
		235-6	07.03.2013	62°16.35'S	61°10.25'W	350	MUC6	Meio		
		241-1	09.03.2013	62°6.63'S	60°36.52'W	20/396	CTD		34.54	0.65
		241-2[a]	09.03.2013	62°6.59'S	60°36.47'W	400	GKG	Macro		
		241-3[a]	09.03.2013	62°6.60'S	60°36.51'W	403	GKG	Macro		
		241-4[a]	09.03.2013	62°6.59'S	60°36.50'W	403	GKG	Macro		
		241-5[a]	09.03.2013	62°6.60'S	60°36.50'W	403	GKG	Macro		
		244-5	10.03.2013	62°6.64'S	60°36.53'W	398	MUC6	Meio		
		244-6	10.03.2013	62°6.62'S	60°36.50'W	400	MUC6	Meio		
		244-7	10.03.2013	62°6.65'S	60°36.54'W	396	MUC6	Meio		
	Bransfield Strait (BS)	118-1	27.01.2013	62°26.47'S	56°17.26'W	20/420.1	CTD		34.53	−1.14
		118-5[a]	27.01.2013	62°26.93'S	56°17.05'W	425.2	MUC10	Macro		
		118-7	27.01.2013	62°27.00'S	56°16.96'W	422.4	GKG	Macro		
		118-9	27.01.2013	62°26.95'S	56°17.14'W	423.3	MUC6	Meio		
		118-10[b]	27.01.2013	62°26.90'S	56°17.19'W	427	MUC6	Meio		
		118-11	27.01.2013	62°26.89'S	56°17.22'W	427	MUC6	Meio		
		202-1	27.02.2013	62°56.00'S	58°0.47'W	50/739	CTD		34.55	−0.72
		202-2	27.02.2013	62°56.00'S	58°0.55'W	757	MUC10	Macro		
		202-3	27.02.2013	62°56.00'S	58°0.49'W	756	MUC6	Meio		
		202-4	27.02.2013	62°56.01'S	58°0.52'W	756	MUC6	Meio		
		202-5	27.02.2013	62°55.99'S	58°0.61'W	757	MUC6	Meio		
		215-1	01.03.2013	62°53.57'S	58°14.66'W	40/519	CTD		34.52	−0.95
		217-2[c]	02.03.2013	62°53.31'S	58°14.17'W	529	MUC6	Meio		
		217-3	02.03.2013	62°53.31'S	58°14.12'W	527	MUC6	Meio		
		217-5	02.03.2013	62°53.25'S	58°14.13'W	532	MUC10	Macro		
		218-1	02.03.2013	62°56.93'S	58°25.66'W	20/672	CTD		34.54	−0.80
		218-2	02.03.2013	62°56.94'S	58°25.73'W	688	MUC10	Macro		
		218-4	02.03.2013	62°56.95'S	58°25.81'W	689	MUC6	Meio		
		218-5	02.03.2013	62°56.95'S	58°25.84'W	689	MUC6	Meio		
		218-6	02.03.2013	62°56.93'S	58°25.81'W	689	MUC6	Meio		
		225-1	04.03.2013	62°56.07'S	58°40.62'W	20/525	CTD		34.54	−0.85
		225-2	04.03.2013	62°56.08'S	58°40.76'W	543	MUC10	Macro		
		225-3	04.03.2013	62°56.04'S	58°40.73'W	545	MUC6	Meio		
		225-4	04.03.2013	62°56.06'S	58°40.76'W	544	MUC6	Meio		
		225-5[b]	04.03.2013	62°56.05'S	58°40.77'W	546	MUC6	Meio		
	Northwestern Weddell Sea (NW-WS)	120-1	28.01.2013	63°4.62'S	54°33.11'W	20/511	CTD		34.49	−1.81
		120-4	28.01.2013	63°4.78'S	54°31.45'W	493.8	MUC10	Macro		
		120-5	28.01.2013	63°4.58'S	54°31.00'W	503.6	MUC6	Meio		
		120-6	28.01.2013	63°4.10'S	54°30.86'W	484.8	MUC6	Meio		
		120-7	28.01.2013	63°3.72'S	54°30.87'W	436.8	MUC6	Meio		
		162-1	10.02.2013	64°0.27'S	56°44.28'W	20/207	CTD		34.45	−1.86
		162-2	10.02.2013	64°0.11'S	56°44.43'W	222.9	GKG	Macro		
		162-3	10.02.2013	64°0.11'S	56°44.28'W	222.1	MUC6	Meio		
		162-4	10.02.2013	64°0.07'S	56°44.20'W	223.4	MUC6	Meio		

(*Table 1 continued on next page*)

Table 1 (continued)

Expedition	Region	Stn	Date (d.m.yr)	Latitude	Longitude	Depth (m)	Gear	Fauna	Sal_{bottom}	T_{bottom}
		162-5	10.02.2013	64°0.14'S	56°44.33'W	221.9	MUC6	Meio		
		162-6[b]	10.02.2013	64°0.12'S	56°44.12'W	223.8	MUC10	Macro		
		163-1	10.02.2013	63°53.07'S	56°26.19'W	50/453	CTD		34.50	−1.77
		163-3	11.02.2013	63°50.97'S	56°25.24'W	517	MUC10	Macro		
		163-4	11.02.2013	63°50.95'S	56°24.43'W	517.6	MUC6	Meio		
		163-5	11.02.2013	63°51.01'S	56°23.97'W	516.6	MUC6	Meio		
		163-6	11.02.2013	63°51.03'S	56°23.68'W	517.1	MUC6	Meio		
PS 96 Southeastern Weddell Sea	North Filchner Trough (N-FT)	017-1	08.01.2016	75°00.63'S	32°53.48'W	50/581.1	CTD		34.67	−1.91
		017-3	04.01.2016	75°00.85'S	32°52.51'W	608.2	GKG	Meio/Macro		
		026-13	08.01.2016	75°15.97'S	37°55.17'W	35/393.3	CTD		34.66	−1.92
		026-7[a]	08.01.2016	75°16.19'S	37°54.96'W	416.1	MUC10	Meio/Macro		
		026-8[b]	08.01.2016	75°16.10'S	37°54.85'W	415.2	MUC10	Meio/Macro		
		026-11[a]	08.01.2016	75°15.65'S	37°54.44'W	413.6	MUC10	Meio/Macro		
		048-1	18.01.2016	74°46.18'S	35°18.59'W	44/469.9	CTD		34.66	−1.92
		048-7	19.01.2016	74°45.52'S	35°20.91'W	481.9	MUC10	Meio/Macro		
		048-8	19.01.2016	74°45.52'S	35°20.91'W	481.8	MUC10	Meio/Macro		
	South Filchner Trough (S-FT)	037-2	16.01.2016	75°41.87'S	42°20.25'W	40/369.3	CTD		34.67	−1.91
		037-8	16.01.2016	75°43.30'S	42°27.71'W	390.6	MUC10	Meio/Macro		
		037-9[b]	17.01.2016	75°43.29'S	42°27.66'W	390.5	MUC10	Meio/Macro		
		061-2	21.01.2016	76°05.86'S	30°18.66'W	46/445.7	CTD		34.58	−1.90
		061-5[b]	21.01.2016	76°05.93'S	30°18.23'W	467.6	MUC10	Meio/Macro		
		061-6[b]	22.01.2016	76°05.89'S	30°18.38'W	466.6	MUC10	Meio/Macro		
		072-2	23.01.2016	75°51.37'S	32°25.27'W	40/719.9	CTD		34.66	−1.90
		072-9	24.01.2016	75°50.85'S	32°17.44'W	755.1	MUC10	Meio/Macro		

[a]One MUC core from this deployment was used for community analyses; [b]Two MUC cores from this deployment were used for community analyses; [c]Core could only be sliced down to 4 cm sediment depth

The Antarctic Peninsula (AP) regions included Drake Passage (DP; Stns 235, 241/244), Bransfield Strait (BS; Stns 118, 202, 217, 218, 225), and the northwestern Weddell Sea (NW-WS; Stns 120, 162, 163). The southeastern Weddell Sea (SE-WS) regions included North Filchner Trough (N-FT; Stns 017, 026, 048) and South Filchner Trough (S-FT; Stns 037, 061, 072). Further station information and abbreviations are listed in Table 1.

2.2. Sea-ice data and ice-cover categories

Our sampling covered stations with differing sea-ice cover. The ice-cover data we used are daily satellite measurements of sea-ice cover in percentages and are provided by the 'Meereisportal', University of Bremen (https://www.meereisportal.de; Grosfeld et al. 2016). Data stem from remote sensing conducted with Advanced Microwave Scanning Radiometer-EOS (AMSR-E 89) with a resolution of 3.125 km (Spreen et al. 2008). For each station, data were obtained for 9 yr before the sampling event. We assigned the stations visually to 5 ice-cover categories taking into account the amount, duration, and fluctuation of summer and early autumn sea-ice cover (December to April; Fig. 2, Table 2).

For each station, mean summer (December–February) sea-ice cover values were calculated for every year. These data were used to express 3 values (percentage) for each station: the situation in the summer previous to the respective sampling campaign (1-yr ice cover), over the 3 yr before sampling (3-yr ice cover), and over the last 9 yr (9-yr ice cover) before sampling.

2.3. Sampling procedure

2.3.1. Sediment sampling

Sampling sites representative of each area were determined on the basis of bathymetry and Ocean Floor Observation System surveys before multicorer (MUC) deployments. Where possible, we carried out 3 to 5 MUC deployments in order to collect true replicates (Table 1). In DP, BS, and NW-WS (PS 81), sediment samples for meiofauna counts and environmental parameters were collected with a MUC6 equipped with 12 plexiglass core liners (inner diameter 57 mm, surface area 25.5 cm^2; Hauquier & Veit-Köhler 2013). Macrofauna samples were collected with a MUC10 equipped with 8 plexiglass core liners (inner diameter 94 mm, surface area 69.4 cm^2; Link & Piepenburg 2013). In the SE-WS (PS 96), meiofauna and macrofauna as well as sediment samples for environmental analyses were collected from the same MUC10 (inner core diameter 94 mm, surface area 69.4 cm^2; Link et al. 2016). Because of ship constraints, the giant box corer (GKG) was used at 2 stations for PS 81 and one for PS 96 to obtain a sufficient number of cores. Heavy sea ice at Stn 017 minimalized ship movements. Visual inspection of all GKG samples confirmed clear overlying water and an intact sediment surface with light epifauna (such as isopods) present and no sign of sloshing. Bow-wave or sloshing effects can therefore be neglected. Moreover, ANOSIM on a data subset for site samples with GKG and MUC confirmed that macrofauna or meiofauna communities in samples obtained by GKG and MUC did not differ (global R = 0.01, p = 0.3; global R = 0.24, p = 0.05, respectively). The GKG was subsampled by insertion of MUC10 core liners (Table 1). During PS 81, meiofauna samples were sliced into 1 cm layers down to 5 cm depth (data published by Veit-Köhler et al. 2017). Macrofauna cores were sieved whole through a 500 µm mesh. During PS 96, meiofauna and macrofauna were retrieved from the same cores, which were sliced into 1 cm layers down to 5 cm depth. The remainders (5 cm–bottom) were sieved through a

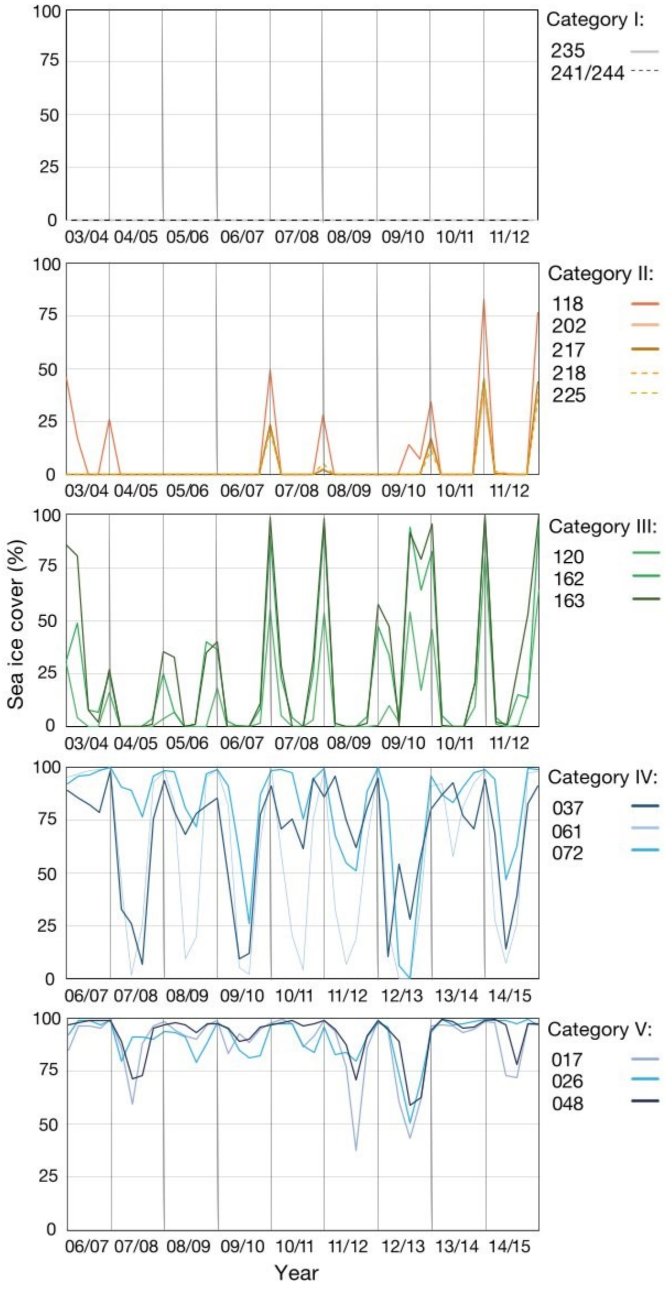

Fig. 2. Percentage of sea-ice cover at stations sampled during the RV 'Polarstern' expeditions PS 81 and PS 96. Data from the austral summer (December to April; April depicted as vertical grid line) of 9 yr before the sampling events are shown. Stations are grouped and categorized according to their ice-cover regime. PS 81, category I: Drake Passage (235, 241/244); II: Bransfield Strait (118, 202, 217, 218, 225); III: northwestern Weddell Sea (120, 162, 163); PS 96, category IV: South Filchner Trough (037, 061, 072), V: North Filchner Trough (017, 026, 048). Data were extracted from the 'Meereisportal' of the University of Bremen (https://www.meereisportal.de)

Table 2. Ice-cover categories classified according to ice-cover situation in the different regions (see Table 1 for abbreviations) and stations investigated during RV 'Polarstern' expeditions PS 81 and PS 96 (based on visual inspection of Fig. 2). Definitions for the interpretation of the results (descriptors) and median depth per category are given. Chl *a*/CPE (chloroplastic pigment equivalents) ratios (mean ± SD of the integrated 0–5 cm of sediment), an indicator of freshness of the sediment organic matter derived from primary production, are given to illustrate differences in food input in regions of different ice cover (see Section 3.1)

Category	Description/Definition	Stns	Region	Depth median (m)	Chl *a*/CPE
I	None: no sea-ice cover during summer months	235, 241/244	DP	380	0.08 ± 0.01
II	Irregular: ice-free December to March; mostly below 40 % in March, sea-ice formation in April (irregular, not every year)	118, 202, 217, 218, 225	BS	545	0.21 ± 0.03
III	Seasonal: mostly ice-free January and February; ice cover in April mostly above 50 %	120, 162, 163	NW-WS	478	0.72 ± 0.04
IV	High: sea-ice cover throughout the year; in March mostly above 75 %	037, 061, 072	S-FT	467	0.07 ± 0.01
V	Constant: sea-ice cover throughout the year; in summer mostly 75 % or above	017, 026, 048	N-FT	482	0.06 ± 0.01

500 µm mesh. All fauna samples were preserved in a 4 % formaldehyde–seawater solution (borax-buffered). The overlying water was sieved through a 32 µm sieve and the retained organisms were added to the sample of the upper sediment layer. No statistical differences were found between macrofauna communities obtained from different sieving procedures.

Sediment cores were subsampled for environmental parameters. Depending on expedition and type of core, cut-off 10 or 60 ml syringes were pushed 5 cm deep into the sediment. Subsamples for the analyses of total organic carbon (TOC), total nitrogen (TN), and grain size were stored at −20°C, samples for pigments were stored at −80°C. All cores that were used for macrofaunal analyses had undergone noninvasive incubations for a maximum of 4 d before sample preservation. In these cases, pigment subsamples were taken after the incubation. Incubations were run from 100 % to a minimum of 70 % oxygen saturation, so that oxygen supply was sufficient for benthic organisms over the whole incubation period. The overlying water was constantly stirred to prevent stratification. No evidence indicated macrofaunal stress or emergence.

2.3.2. Water-column sampling

Oceanographic measurements and water-column sampling were carried out at all investigated stations by means of a conductivity, temperature, and depth profiler rosette (Table 1) (Schröder et al. 2013a, 2016a). Water-mass parameters were measured at the chlorophyll maximum (C_{max}, at approximately 20–50 m, defined by looking at *in situ* fluorescence profiles) and close to the sea bottom (207–753 m). Temperature and salinity were determined *in situ*, and water samples for measurements of the chlorophyll content were taken with Niskin bottles mounted on the conductivity, temperature, and depth profiler rosette (Schröder et al. 2013b, 2016b). Seawater was first poured through a 100 µm sieve, which removed larger particles, and then filtered through glass fiber filters (at approximately 250 mbar so that wells would not be ruptured). For each filtration, 2 to 5 l were used; the coloring of the filters determined the amount of seawater used. Filters were stored at −80°C.

2.4. Fauna sample processing and identification

Sediment samples were sieved with filtered tap water and organisms separated by size. For PS 81, meiofauna cores were passed through a 32 µm sieve (0–5 cm depth, Veit-Köhler et al. 2018) and macrofauna cores were passed through a 500 µm sieve (Link & Piepenburg 2013). For PS 96, mesh sizes of 32 µm (only for 0–5 cm layers), 500 µm, and 1000 µm were used. In our study, organisms of the 500 and 1000 µm fractions were pooled and included as macrofauna. Meiofauna was extracted from the sediment by centrifugation in a flotation medium (Levasil® Colloidal Silica CS40-316P 200 m^2 g^{-1} 40 %). Kaolin was added to prevent sediment particles from contaminating the sample during decantation (Sommerfield & Warwick 2013). The centrifugation was repeated 3 times for 6 min each at 4000 rpm. The floating matter was decanted through a 32 µm mesh sieve and rinsed with tap water after each centrifugation step. The supernatant generally includes the whole organic material and animals present in the sample. Meiofauna were counted and classified to higher taxon level by means of stereo microscopes Leica Mz 12.5 and Mz 125 and the keys given by Higgins & Thiel (1988) and Giere (2009). Copepod nauplii were counted separately because of ecologically relevant differences in size and diet from adults and copepodids (Decho & Fleeger 1988). Counts of unidentified larvae and other organisms were unified as 'others'. Macrofauna were sorted with stereo microscopes Leica Mz 12.5 and Carl Zeiss Stemi 2000 and classified to family level or the lowest taxonomic resolution possible according to identification guides by Hartman (1964, 1996), Fauchald (1977), Pettibone (1982), Sieg & Wägele (1990), Branch et al. (1991), Hartmann-Schröder (1996), Brandt et al. (1999), Martin & Davis (2001), Brökeland (2005), Chapman (2007), and Hayward & Ryland (2017).

For statistical analyses, we calculated the total number of individuals per identified taxon per 10 cm^2 from the top to the bottom of the core for macrofauna and from the top 5 cm for meiofauna. Faunal data produced from this study has been published as Säring et al. (2021c–e)

2.5. Environmental parameters and sample processing

2.5.1. Water-column pigments

Methods and data for PS 81 have been published elsewhere (Veit-Köhler et al. 2018, Vanreusel et al. 2021a). During PS 96, chlorophyll *a* (chl *a*) in the water column (chl $a_{C\max}$ at the chlorophyll maximum, chl a_{bottom} near the sea bottom) was extracted from the glass fiber filters with 10 ml acetone (90%) and kept for 24 h at 4°C in the dark. Pigment content was measured with a fluorometer (Turner Designs, TD-700) and reported in µg l^{-1} (equivalent to mg m^{-3}) according to the method of Arar & Collins (1997). Data from PS 96 were published by Säring et al. (2021a).

2.5.2. Sediment pigments

Syringe sediment cores from PS 96 were divided into 1 cm layers down to 5 cm depth. Pigments were extracted from the resulting 2 ml wet sediment with 10 ml acetone (90%) and analyzed with a fluorometer (Turner Designs, TD-700) according to the protocol of Riaux-Gobin & Klein (1993). Chl *a* and its degradation products, phaeopigments (Phaeo), were determined for each 1 cm layer, expressed in µg g^{-1}, and published by Säring et al. (2021b). Methods and data for PS 81 have been published (Veit-Köhler et al. 2018, Vanreusel et al. 2021b). In deeper sediment layers, these measurements may include artefacts resulting from other pigments that fluoresce at the same wavelength as chl *a* and its degradations products (Mincks et al. 2005). Because our samples were from shallower sediment depths, we did not expect a major influence. From these data, another parameter was derived: CPE (chloroplastic pigment equivalents), the sum of chl *a* and Phaeo, which is a proxy for the quantity of deposited microalgae. The ratio chl *a*/CPE was used as a standardized proxy for the food quality at the seafloor (indicator for freshness of deposited microalgal remnants; Pantó et al. 2021).

2.5.3. Grain size

Sediment grain size from wet sediments was measured with a Malvern Mastersizer 2000 (PS 81; Veit-Köhler et al. 2018, Vanreusel et al. 2021b) and a Malvern Mastersizer 3000 (PS 96; Säring et al. 2021b) with a particle size range 0.002–2000 µm. Results were expressed as percentages of different size fractions according to Wentworth (1922). Usually, 1/4 of the 1 cm sediment layers from the syringes (0–5 cm) was analyzed. For better data handling, results of grain size fractions were summed to reduce the number of classes to 3: silt and clay (< 63 µm), sand (63–500 µm), and coarse sand (sand fraction > 500 µm).

2.5.4. Organic matter

Before analysis, 1 cm sediment slices from the syringes were freeze-dried. Percentages of TOC and TN were determined with a Flash EA 1112+ MAS 200 elemental analyzer for PS 81 (Veit-Köhler et al. 2018, Vanreusel et al. 2021b) and flash combustion in a Flash 2000 (Thermo) elemental analyzer at 1020°C coupled via a ConFlo IV (Thermo) interface to a Delta V advantage (Thermo) isotope ratio mass spectrometer for PS 96 (Säring et al. 2021b). For TOC measurements, inorganic carbon was removed by addition of 2% HCl until fizzing stopped, and samples were dried before combustion. As an indicator of the degradation state of organic matter, the C/N_{molar} ratio was calculated as TOC/TN × 14/12.

For a detailed overview of definitions of environmental variables and the interpretation of the results, see Table 2 of Veit-Köhler et al. (2018).

2.6. Statistical analyses

Environmental data included in statistical analyses are 1-yr, 3-yr, and 9-yr ice cover; water depth, salinity, and temperature at the bottom; and the biological water-column measurements chl $a_{C\max}$ and chl a_{bottom}, at the chlorophyll maximum and from bottom water, respectively. Sediment parameters were silt and clay, sand, coarse sand, TOC, TN, C/N_{molar}, chl *a*, Phaeo, CPE, and chl *a*/CPE. For statistical analyses, data from 0–5 cm depth were averaged.

We tested for significant differences between the 5 ice-cover categories (Hypothesis 1) on the basis of major food-availability parameters for each (chl *a*, Phaeo, chl *a*/CPE, TOC, C/N_{molar}, chl $a_{C\max}$, chl a_{bottom}). Because of multiple testing, a Bonferroni correction ($p < 0.05/n$, n = number of parameters) was carried out, and a threshold alpha of $p < 0.007$ was applied for the main tests. We used one-way ANOVA (factor 'ice-cover category,' 5 levels) and Tukey's post hoc test when assumptions of normality and homogeneity of variance were met (parameters C/N_{molar}, chl $a_{C\max}$). If data failed to meet these assumptions even after transformation, we applied the Kruskal-Wallis test on ranks and the pairwise multiple comparison procedures of Dunn's method (chl *a*, Phaeo, chl *a*/CPE, TOC, chl a_{bottom}). Box plots were used to visualize sediment parameters in each ice-cover category. Because replicates of water-column measurements per station were not usually available, water-column data were depicted as scatter plots. Univariate statistics were run with SigmaPlot 11. We used principal components analysis (PCA) to analyze the importance of environmental parameters related to primary production and food availability at the seafloor (chl *a*, Phaeo, CPE, chl *a*/Phaeo, chl *a*/CPE, TOC, TN, C/N_{molar}, chl $a_{C\max}$, chl a_{bottom}). Before analysis, Draftsman plots were created. In cases where strong correlations ($R > 0.76$) between variables were observed, one of the related variables was left out. Remaining variables included in the final dataset were normalized. We ran a one-way analysis of similarities (ANOSIM; 9999 permutations, food-availability parameters as variables, factor 'ice-cover category') on the similarity matrix to test for significant differences among the 5 ice-cover categories. The resemblance matrix for environmental data was based on Euclidean distance.

Differences in faunal communities (variables: meiofauna taxon abundances, macrofauna taxon abundances, and combined meiofauna and macrofauna taxon abundances) among the 5 ice-cover categories (Hypothesis 2) were analyzed by one-way ANOSIM (9999 permutations). Meiofauna data were square-root transformed; macrofauna data were not. The combined table of meiofauna and macrofauna was merged from the respective raw data and square-root transformed. Bray-Curtis similarity was applied as a resemblance measure for all matrices. Non-metric multidimensional scaling (nMDS) was used to visualize similarities among replicate cores for the separate meiofauna and macrofauna communities. For the combined meiofauna and macrofauna communities, the average per station was calculated, because meiofauna and macrofauna were not sampled from the same cores during expedition PS 81. Abundance was calculated as individuals per 10 cm^2; individual numbers per 100 cm^2 were used only for the visualization of macrofauna abundances with bubble plots.

We used distance-based linear models (DistLM) to test for the influence of environmental parameters on meiofauna and macrofauna communities (Hypothesis 3). For faunal communities, the similarity matrices described above were used. Before analysis, we checked for autocorrelation among the environmental variables. If strong correlations ($R > 0.83$) between variables were detected, one variable was left out (for details, Section 3.3). The remaining data were normalized before DistLM. The best solution model for predicting variables was chosen on the basis of the AIC_C criterion, which is particularly well suited when the number of samples (N) is small compared to the number of predictors (n; $N/v < 40$, v = number of parameters in the model) (Anderson et al. 2008). For the best model specified by this procedure, we ran sequential tests based on adjusted R^2 to determine the amount of variation explained by the retained environmental variables. The best models for meiofauna and macrofauna communities were visualized by distance-based redundancy analysis (dbRDA graphs). All multivariate analyses were run with PRIMER v7 and the PERMANOVA$^+$ add-on package (Anderson et al. 2008, Clarke et al. 2014).

3. RESULTS

3.1. Food production and availability in regions with differing ice cover

The sampled regions were classified into 5 categories of ice cover (see Section 2.2; Fig. 2, Table 2): I = none (DP), II = irregular (BS), III = seasonal (NW-WS), IV = high (S-FT), and V = constant (N-FT). We found significant differences among the ice-cover categories for all primary-production and food-availability proxies (Fig. 3, Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m700p013_supp.pdf). For chl *a*, categories III and V differed

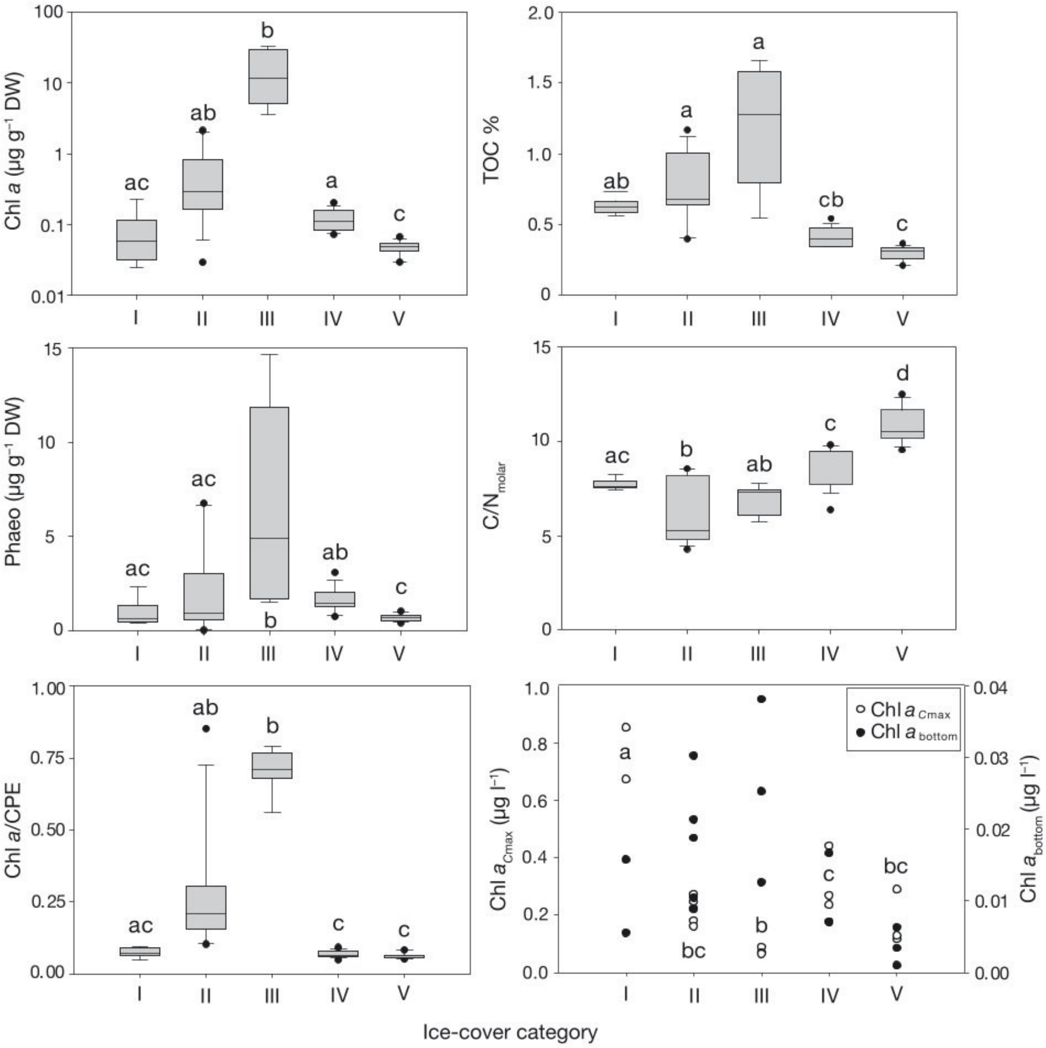

Fig. 3. Primary-production–related sediment (chl *a*, TOC, Phaeo, C/N_{molar}, chl *a*/CPE [chloroplastic pigment equivalents]) and water-column parameters sampled during RV 'Polarstern' expeditions PS 81 (22 January–18 March 2013) and PS 96 (6 December 2015–14 February 2016). Average station data grouped according to ice-cover categories I–V (see Table 2). Box plots indicate median (bar within box), 25th and 75th percentiles (upper and lower boundaries of box), 10th and 90th percentiles (whiskers), and outlying maximum and minimum values (dots) per category. Different lowercase letters indicate significant differences ($p < 0.5$) among groups detected by one-way ANOVA and Tukey's post hoc test (C/N_{molar}, chl a_{Cmax}) or Kruskal-Wallis test on ranks and Dunn's method (chl *a*/CPE, chl *a*, TOC, Phaeo). Note the logarithmic scale for chl *a*

from almost all other categories ($p < 0.05$), except for II and I, respectively. For TOC, significant differences ($p < 0.05$) were detected between category V and all other categories except IV. Significant differences in C/N_{molar} were detected between category V and all other categories ($p < 0.05$). For parameters chl *a*, Phaeo, and chl *a*/CPE, no significant differences were detected between the 2 most different ice-cover categories, I and V. Significant differences in chl $a_{C\mathrm{max}}$ were found between category I and all other categories and between categories III and IV ($p < 0.05$). Differences between categories could not be tested for chl a_{bottom} because of the low number of replicates.

Category III showed the highest mean values for sediment chl *a* (17.09 µg g^{-1}), Phaeo (6.94 µg g^{-1}), TOC (1.20 %), chl *a*/CPE (0.72), and the water-column parameter chl a_{bottom} (0.03 µg l^{-1}). Category III showed high variability in TOC and Phaeo (Fig. 3, Table 3). In contrast, categories IV and V in SE-WS displayed the lowest stocks of organic material (TOC: 0.41 and 0.30 %, respectively), low freshness values (chl *a*/CPE: 0.07 and 0.06), and the highest degradation state of the organic material (C/N_{molar}: 8.68 and 10.82). Categories I and II were characterized by intermediate values of TOC but clearly differed in their amounts of chl *a* (I: 0.08 µg g^{-1}; II: 0.53 µg g^{-1}) and Phaeo (I: 0.93 µg g^{-1}; II: 1.88 µg g^{-1}). In chl *a*/CPE, category I (0.08) was similar to categories IV and V. Overall, low pigment contents and freshness values were observed in the sediments of categories I, IV, and V, indicating high degradation rates and/or low food availability in the respective areas. In contrast, category III revealed a higher amount of fresh material and high food availability.

Table 3. Environmental characteristics of sediment (sampled with MUC; our data) and water column (sampled with CTD conductivity, temperature, and depth profiler equipped with Niskin bottles; chl *a*: our data; temperature and salinity data: Schröder et al. 2013a, 2016a) gathered during RV 'Polarstern' expeditions PS 81 (22 January–18 March 2013) and PS 96 (6 December 2015–14 February 2016). Sediment parameters were averaged from 0 to 5 cm depth. Mean ± SD of environmental parameters given per ice-cover category (I: Drake Passage; II: Bransfield Strait; III northwestern Weddell Sea; IV: South Filchner Trough; V: North Filchner Trough). Ice-cover parameters: 1-yr ice cover: mean Dec–Feb ice cover of the year before the sampling campaign; 9-yr ice cover: mean Dec–Feb ice covers of 9 years before the sampling campaign. Water-column parameters — $_{C\mathrm{max}}$: measurement at the chlorophyll maximum; $_{\mathrm{bottom}}$: measurement close to the seafloor; chl *a*: chlorophyll *a* content in the water column; *T*: temperature; Sal: salinity. Sediment parameters — silt and clay : grain size fraction <63 µm; sand %: grain size fraction >63 and <500 µm; coarse sand %: >500 µm; TN%: total nitrogen; TOC%: total organic carbon; C/N_{molar}: molar carbon:nitrogen ratio; Phaeo: content of phaeopigments; CPE: sum of chl *a* and Phaeo; chl *a*/CPE: ratio of chl *a* and CPE. Data are published in Säring et al. (2021a,b) and Vanreusel et al. (2021a,b)

Water-column parameters									
Region	Ice-cover category	1-yr ice cover (%)	9-yr ice cover (%)	$T_{C\mathrm{max}}$ (°C)	T_{bottom} (°C)	$Sal_{C\mathrm{max}}$	Sal_{bottom}	Chl $a_{C\mathrm{max}}$ (µg l^{-1})	Chl a_{bottom} (µg l^{-1})
DP	I	0	0	1.19	0.54	34.17	34.52	0.76	0.01
		± 0	± 0	± 0.07	± 0.11	± 0.03	± 0.02	± 0.09	± 0.005
BS	II	0.28	0.65	−0.85	−0.89	34.22	34.54	0.22	0.02
		± 0.27	± 1.16	± 0.37	± 0.15	± 0.15	± 0.009	± 0.04	± 0.008
NW-WS	III	5.71	9.87	−1.69	−1.82	34.35	34.47	0.07	0.03
		± 4.03	± 4.47	± 0.15	± 0.04	± 0.03	± 0.02	± 0.01	± 0.004
S-FT	IV	40.79	54.51	−1.74	−1.90	34.36	34.64	0.36	0.01
		± 18.07	± 13.38	± 0.02	± 0.007	± 0.08	± 0.04	± 0.10	± 0.004
N-FT	V	93.28	89.00	−1.80	−1.92	34.32	34.66	0.15	0.003
		± 4.06	± 2.62	± 0.04	± 0.005	± 0.03	± 0.004	± 0.06	± 0.002

Sediment parameters											
Region	Ice-cover category	Chl *a* (µg g^{-1})	Phaeo (µg g^{-1})	CPE (µg g^{-1})	Chl *a*/ CPE	TOC%	TN%	C/N_{molar}	Silt and clay (%)	Sand (%)	Coarse sand (%)
DP	I	0.08	0.93	1.01	0.08	0.63	0.09	7.70	92.12	7.11	0.77
		± 0.02	± 0.22	± 0.24	± 0.01	± 0.04	± 0.004	± 0.25	± 0.26	± 0.28	± 0.54
BS	II	0.53	1.88	2.41	0.21	0.79	0.17	6.03	67.89	25.58	6.53
		± 0.56	± 1.77	± 2.33	± 0.03	± 0.24	± 0.06	± 1.58	± 17.10	± 10.96	± 6.18
NW-WS	III	17.09	6.94	24.03	0.72	1.20	0.20	6.87	80.26	19.55	0.19
		± 10.46	± 3.99	± 14.32	± 0.04	± 0.41	± 0.04	± 0.69	± 13.15	± 12.98	± 0.17
S-FT	IV	0.11	1.42	1.54	0.07	0.41	0.06	8.68	82.68	15.36	0.70
		± 0.04	± 0.41	± 0.45	± 0.01	± 0.06	± 0.01	± 1.05	± 5.79	± 4.06	± 0.47
N-FT	V	0.05	0.79	0.84	0.06	0.30	0.03	10.82	64.33	33.19	2.48
		± 0.01	± 0.37	± 0.40	± 0.01	± 0.05	± 0.003	± 0.88	± 6.84	± 6.14	± 0.72

Water-column measurements represent a snapshot in time. Categories I–IV showed up to 10 times higher chl a_{bottom} values (0.01–0.03 µg l^{-1}) than category V. An ongoing phytoplankton bloom was detected for category I, which had 10 times higher chl $a_{C\mathrm{max}}$ values (0.76 µg l^{-1}) than category III (Fig. 3, Table 3).

The PCA was carried out on the basis of 6 environmental parameters representing the food situation (Fig. 4): chl $a_{C\mathrm{max}}$, chl a_{bottom}, chl *a*, chl *a*/CPE, TOC, C/N_{molar} (data were normalized before analysis). The variables Phaeo, chl *a*/Phaeo, CPE, and TN were left out because of their correlations with other variables (Phaeo and CPE: R = 0.95; chl *a*/Phaeo and chl *a*/CPE: R = 0.93; CPE and chl *a*: R = 0.99, TN and TOC: R = 0.91). Samples belonging to different ice-cover categories formed distinguishable clusters. The first 3 PC axes described 87.9 % of the detected variation. Along PC1, structuring parameters were chl *a*/CPE and TOC (coefficients 0.506 and 0.486, respectively). Along PC2, chl $a_{C\mathrm{max}}$ and C/N_{molar} were most important (0.627 and −0.562, respectively). Chl $a_{C\mathrm{max}}$ and chl *a* were the structuring parameters for PC3 (−0.645 and −0.532, respectively). The PCA separated category III from the other categories mainly by the food parameters chl *a*/CPE and TOC followed by chl *a* and chl $a_{C\mathrm{max}}$, whereas samples from the other categories were separated from each other by C/N_{molar} and chl a_{bottom} (Fig. 4).

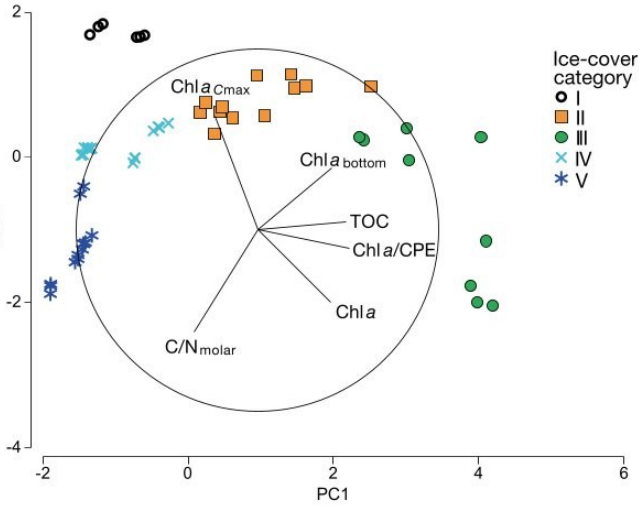

Fig. 4. Principal components analysis of the food-related parameters measured in the 5 ice-cover categories (I–V) during RV 'Polarstern' expeditions PS 81 and PS 96. Sediment (0–5 cm): chl *a*: chlorophyll *a*; Phaeo: phaeopigments; chl *a*/CPE: ratio of chl *a* and CPE (chloroplastic equivalents = sum of chl *a* and Phaeo); TOC: % total organic carbon; C/N_{molar}: molar carbon:nitrogen ratio. Water-column: chl $a_{C\mathrm{max}}$: chl *a* at the chlorophyll maximum in the water column; chl a_{bottom}: chl *a* close to/at the seafloor in the water column (see Table 3 for absolute values)

Hypothesis 1 was statistically confirmed by one-way ANOSIM of the environmental food parameters (chl $a_{C\mathrm{max}}$, chl a_{bottom}, chl *a*, chl *a*/CPE, TOC, C/N_{molar}; factor 'ice-cover category'; global R = 0.79, p = 0.0001; for nMDS, see Fig. S1). Pairwise tests showed that all 5 ice-cover categories differed significantly from each other. The lowest R-value of 0.66 (p = 0.0001) was that between categories II and III. Among all other categories, differences were greater ($R \geq 0.76$, $p \leq 0.0002$), with $R > 0.92$ in 5 out of 10 pairwise tests. The highest value (R = 1) was that between categories I and V.

3.2. Meiofauna and macrofauna community composition in regions with differing ice cover

The sediment samples collected for fauna community analyses contained 589 799 individuals, of which 585 825 belonged to meiofauna and 3974 to macrofauna (data available from PANGAEA: Veit-Köhler et al. 2017, Säring et al. 2021c–e). The taxa listed show the taxonomic resolution of identification for meiofauna and macrofauna. Meiofauna included 20 higher taxa and copepod nauplii (603 individuals remained undetermined). Nematodes dominated in all samples at all stations, followed by copepod nauplii and copepods. The other meiofauna groups were, in descending order of abundance: kinorhynchs, annelids, ostracods, tardigrades, bivalves, priapulids, gastrotrichs, loriciferans, coelenterates, tanaids, acari, rotifers, isopods, cumaceans, amphipods, cladocerans, ophiurids, and gastropods. For macrofauna, 19 different major groups were identified, of which annelids were the dominant group with 2194 individuals (2167 polychaetes, 27 oligochaetes). The macrofaunal groups were, in descending order of abundance: polychaetes, bivalves, nematodes, amphipods, echinoderms, ostracods, tanaids, isopods, cumaceans, copepods, oligochaetes, mysids, gastropods, chordates, acari, sipunculids, cnidarians, pantopods, and kinorhynchs. Ascidians, bryozoans, poriferans, and foraminifers were not sufficiently abundant or conserved and were therefore excluded from the analyses.

3.2.1. Meiofauna communities

In general, meiofauna communities followed the classification of regions into ice-cover categories (Hypothesis 2). One-way ANOSIM based on Bray-Curtis similarity of the meiofauna communities revealed significant differences among ice-cover categories (global R = 0.76, p = 0.0001, visualized by nMDS; Fig. 5). Pairwise tests detected the greatest differences between II and III; IV and II, III; and V and I, II, III ($R > 0.81$, $p < 0.0002$). Further significant differences were detected between categories I and II, III, and IV ($0.56 < R < 0.8$, $p < 0.0002$). Meiofauna communities of categories IV and V did not differ from each other (R = 0.19, p = 0.012).

The meiofauna nMDS (Fig. 5) shows the close connection between ice-cover categories IV and V and one sample from Stn 217 (category II). Superimposed bubble plots depict the abundances of the important taxa nematodes, copepods, kinorhynchs, ostracods, and tardigrades. Nematodes were the overall structuring taxon, with the highest numbers in category III (mean 5848.3 ind. 10 cm^{-2}) and the lowest in category V (mean 904 ind. 10 cm^{-2}). Copepods, kinorhynchs, and ostracods had highest abundances in category III (444, 64.7, and 65.7 ind. 10 cm^{-2}, respectively), which therefore differed from all other categories. Copepods and kinorhynchs showed a depth-related opposite abundance pattern for sampling sites in category III (Fig. 5). Tardigrades and loriciferans showed a distribution pattern the opposite of that of most of the other taxa.

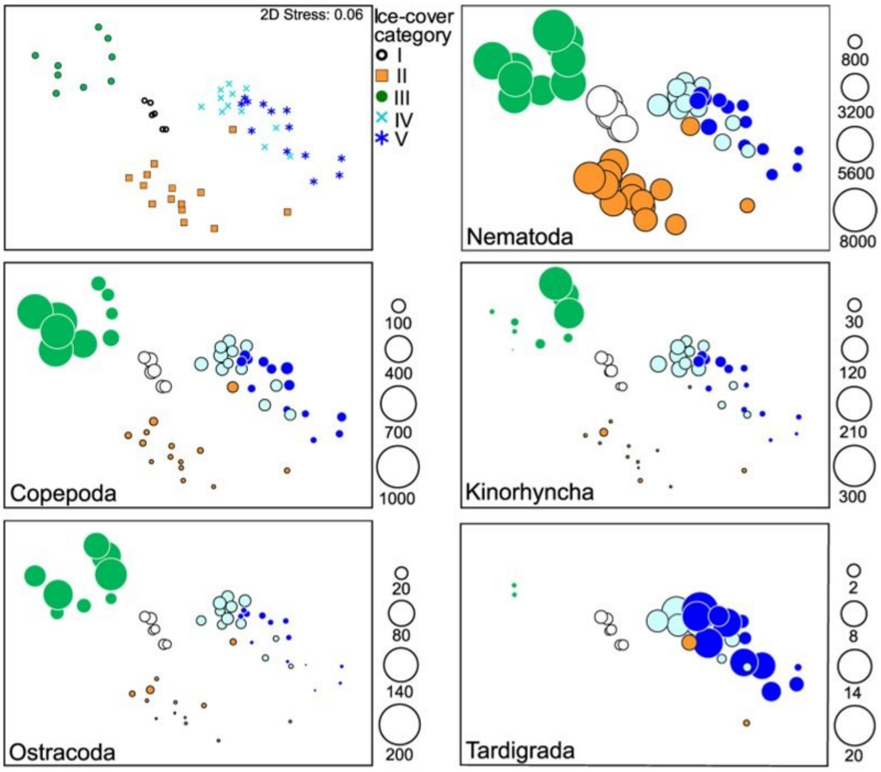

Fig. 5. Similarity of meiofauna communities: non-metric multidimensional scaling (nMDS) of the Bray-Curtis similarity of square-root-transformed fauna abundance data of single cores (0–5 cm) collected in regions in different ice-cover categories during RV 'Polarstern' expeditions PS 81 and PS 96. Bubble plots show the individual numbers of selected taxa per 10 cm^2

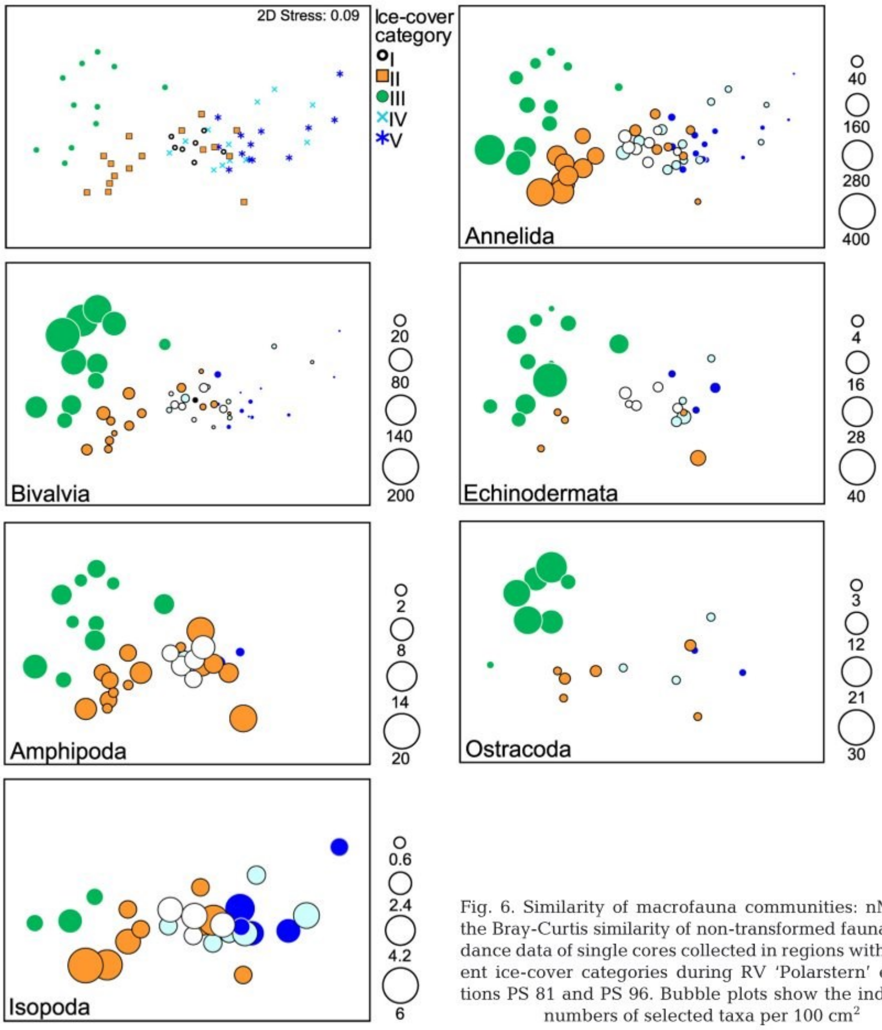

Fig. 6. Similarity of macrofauna communities: nMDS of the Bray-Curtis similarity of non-transformed fauna abundance data of single cores collected in regions with different ice-cover categories during RV 'Polarstern' expeditions PS 81 and PS 96. Bubble plots show the individual numbers of selected taxa per 100 cm^2

3.2.2. Macrofauna communities

One-way ANOSIM of the macrofauna community samples revealed significant differences among ice-cover categories (global R = 0.44, p = 0.0001, sample distribution depicted as nMDS; Fig. 6). Pairwise tests showed that ice-cover category III (NW-WS) differed from all other categories ($0.49 < R < 0.97$, $p < 0.0002$). Further significant differences in macrofauna communities were only detected between categories II and V (R = 0.46, p = 0.0001). Regarding Hypothesis 2, differences between macrofauna communities of different ice-cover categories were not as pronounced as those of meiofauna.

The nMDS shows the similarities between macrofauna communities of categories I, IV, and V (Fig. 6). Superimposed bubble plots depict the abundances of the most abundant macrofauna taxa: annelids, bivalves, echinoderms, amphipods, ostracods, and isopods. Annelids were most abundant in categories II and III (mean 85.1 and 100.2 ind. 100 cm^{-2}, respectively). Category III also displayed the highest abundances of bivalves (mean 93.9 ind. 100 cm^{-2}), ostracods (mean 9 ind. 100 cm^{-2}), and echinoderms (mean 10.9 ind. 100 cm^{-2}). Within this category, annelids showed a depth-related abundance pattern opposed to those of bivalves and ostracods (Fig. 6). Isopods showed highest abundances in categories I and II (mean 1.5–1.6 ind. 100 cm^{2}) and lower abundances across the other regions. Amphipods had similar abundances in categories I, II, and III (around 4.6 ind. 100 cm^{-2}) but were nearly absent in categories IV and V, as were echinoderms and ostracods. Ostracods were absent from category I.

3.2.3. Combined meiofauna and macrofauna communities

ANOSIM of the combined communities (average of each taxon per station) indicated significant differences between ice-cover categories (global R = 0.74, p = 0.0001). Pairwise tests were limited because of the low number of replicates and possible permutations (10–56). Significant differences were only detected between categories II and III, IV, and V (R > 0.72, p = 0.02), but the nMDS shows close connections between communities of categories IV and V and the separation of the remaining categories (Fig. 7). Hypothesis 2, to a certain degree, is still true for the combined analysis of meiofauna and macrofauna communities.

3.3. Relationship of meiofauna and macrofauna communities to environmental parameters

Environmental variables were tested for autocorrelation before DistLM analyses. The following variables were omitted from further analyses: Phaeo, correlation with chl *a* (R = 0.93) and CPE (R = 0.96); CPE, with chl *a* (R = 0.99); chl *a*/Phaeo, with chl *a*/CPE (R = 0.97); TN, with TOC (R = 0.91); and sand, with silt and clay (R = –0.98). Further correlations were found among the parameters 1-, 3-, and 9-yr ice cover, but each time span represents a distinct parameter for ecological interpretation. We therefore included the shortest and the longest time span (1- and 9-yr ice cover) and omitted 3-yr ice cover from further analyses to avoid an overrepresentation of the parameter 'ice cover'. Although $\mathrm{Sal}_{\mathrm{bottom}}$ was correlated with both remaining ice-cover variables, $T_{C\mathrm{max}}$ (correlation with T_{bottom}) and $\mathrm{Sal}_{C\mathrm{max}}$ were left out because they did not play a role in the study of the benthos.

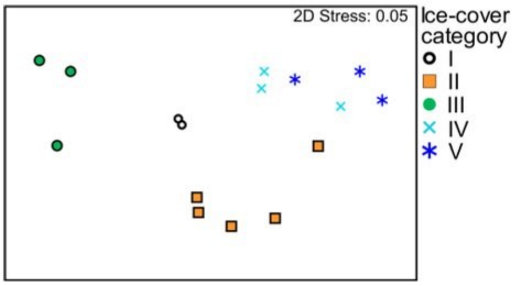

Fig. 7. Similarity of combined meiofauna and macrofauna communities: nMDS of the Bray-Curtis similarity of square-root–transformed fauna abundance data of single cores collected in regions in different ice-cover categories during RV 'Polarstern' expeditions PS 81 and PS 96

Predicting variables for the models were the 12 environmental parameters depth, 1-yr ice cover, 9-yr ice cover, T_{bottom}, chl $a_{C\mathrm{max}}$, chl a_{bottom}, chl *a*, chl *a*/CPE, TOC, $\mathrm{C/N}_{\mathrm{molar}}$, silt and clay, and coarse sand.

3.3.1. Meiofauna and the environment

The best model explaining variation in meiofauna communities included 11 out of the 12 variables (DistLM BEST procedure with $\mathrm{AIC}_{\mathrm{C}}$ selection criterion; Table S3): depth, 1-yr ice cover, 9-yr ice cover, T_{bottom}, chl $a_{C\mathrm{max}}$, chl a_{bottom}, chl *a*, chl *a*/CPE, TOC, $\mathrm{C/N}_{\mathrm{molar}}$, and coarse sand. The first 2 axes together explained 78.4% of the total variation and 89.5% in the fitted model (Fig. 8, Table 4). In the sequential tests, 1-yr ice cover contributed most to the explained total variation (34.7%, p = 0.0001), followed by chl *a* (20.2%, p = 0.0001), depth (9.7%, p = 0.003), and TOC (5.0%, p = 0.0001). The contributions of chl $a_{C\mathrm{max}}$ and chl a_{bottom} were not statistically significant (Table 4). The overall model explained 84% of the variation (adj. R^2, Table 4).

Variation on the first axis (dbRDA) mainly separated the meiofauna communities of ice-cover category III from those of all other categories (total variation 57.4%; Fig. 8). Chl *a*/CPE, TOC, 1-yr ice cover, and chl *a* (in that order) contributed most to dbRDA1 on the basis of the coefficients of the dbRDA. Meiofauna communities of ice-cover category II were separated from those of the other categories by the variation along dbRDA2 (20.9% of total variation; Fig. 8). The parameters 9-yr ice cover, depth, TOC, and coarse sand (in that order) contributed most to this axis. Along dbRDA3 (5.7%), chl *a* and 1-yr ice cover were the most important parameters. Overall, 1-yr ice cover, 9-yr ice cover, and $\mathrm{C/N}_{\mathrm{molar}}$ were the major parameters distinguishing meiofauna communities of ice-cover categories I, IV, and V.

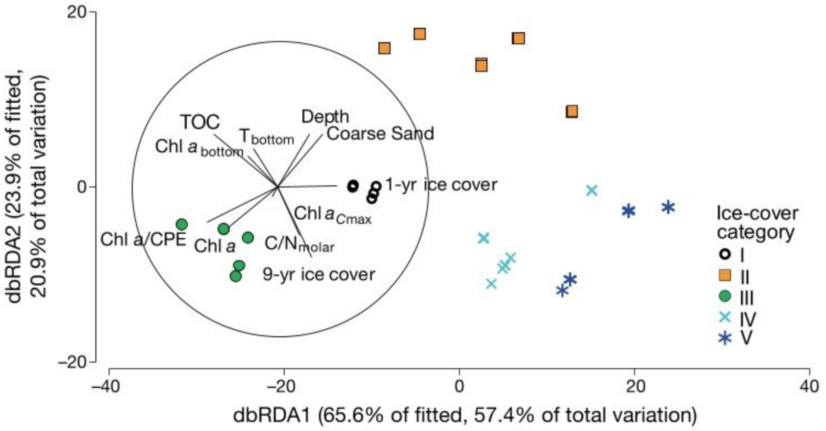

Fig. 8. Environmental drivers for meiofauna community composition: distance-based redundancy analysis (dbRDA) of environmental parameters explaining the multivariate fauna community of single cores from different ice-cover categories (I–V) sampled during RV 'Polarstern' expeditions PS 81 and PS 96 (see Table 1). Sediment parameters — coarse sand: % grain size fraction >500 µm; TOC: % total organic carbon; chl *a*: content of chl *a*; chl *a*/CPE: ratio of chl *a* and CPE. Water-column parameters — chl a_{Cmax}: chl *a* in the water column measured at the chlorophyll maximum; chl a_{bottom}: chl *a* in the water column measured at the bottom; T_{bottom}: temperature measured at the bottom. 1-yr ice cover: mean of the daily values (%) of Antarctic summer sea-ice cover (Dec–Feb) 1 yr before sampling; 9-yr ice cover: mean of the daily values (%) of Antarctic summer sea-ice cover (Dec–Feb) of the 9 yr before sampling

Table 4. Meiofauna communities explained by environmental parameters: results of sequential tests on the best distance-based linear model (DistLM) based on the AIC_C (Table S3) and variation explained along each axis of the best DistLM. The procedure included the 11 predictor variables to explain the variation in meiofauna community composition (Bray-Curtis resemblance matrix). p-values of significant predictor variables are in **bold**. Depth: mean MUC sampling depth per station. Abbreviations as in Table 3

Sequential tests	Adj. R^2	SS (trace)	Pseudo-*F*	p	Probability	Cumulative probability	Residual df
Depth	0.0801	2298.0	5.61	**0.0029**	0.0974	0.0974	52
1-yr ice cover	0.4224	8178.0	31.81	**0.0001**	0.3467	0.4442	51
9-yr ice cover	0.4575	1039.8	4.31	**0.0128**	0.0441	0.4882	50
T_{bottom}	0.4907	963.9	4.25	**0.0184**	0.0409	0.5291	49
Chl a_{Cmax}	0.4893	198.5	0.87	0.4013	0.0084	0.5375	48
Chl a_{bottom}	0.4976	400.9	1.79	0.1543	0.0170	0.5545	47
Chl *a*	0.7191	4756.6	38.05	**0.0001**	0.2017	0.7562	46
TOC	0.7722	1188.6	11.72	**0.0001**	0.0504	0.8066	45
C/N_{molar}	0.7818	290.6	2.99	**0.0274**	0.0123	0.8189	44
Coarse sand	0.7969	384.9	4.26	**0.0041**	0.0163	0.8352	43
Chl *a*/CPE	0.8423	940.1	13.40	**0.0001**	0.0399	0.8751	42

Percentage of variation explained by individual axes

Axis	Fitted model		Total variation	
	Individual	Cumulative	Individual	Cumulative
1	65.61	65.61	57.41	57.41
2	23.92	89.53	20.93	78.35
3	6.53	96.06	5.72	84.06
4	3.17	99.24	2.77	86.84
5	1.46	100.70	1.28	88.12

Best solution: adj. $R^2 = 0.842$; $R^2 = 0.875$; RSS = 2947; 11 variables

3.3.2. Macrofauna and the environment

On the basis of the selection criterion AIC_C, 9 out of 12 environmental variables were selected for the best DistLM model (Table S4) explaining the variation in macrofauna community composition (Table 5): depth, 1-yr ice cover, chl $a_{C\max}$, chl a_{bottom}, chl *a*, TOC, C/N_{molar}, silt and clay, and coarse sand. The first 2 axes together explained 56.7 % of the variation in the total model and 78.9 % in the fitted model (Table 5, Fig. 9). In the sequential tests, 1-yr ice cover contributed most to the explained total variation (21.0 %, p = 0.0001), followed by chl *a* (10.9 %, p = 0.0001), TOC (10.9 %, p = 0.0001), chl $a_{C\max}$ (10.6 %, p = 0.0001), and C/N_{molar} (8.4 %, p = 0.0001). The contribution of chl a_{bottom} was not significant (Table 5). The overall model explained 66 % of the variation (adj. R^2; Table 5).

Variation on the first axis (dbRDA) mainly separated the macrofauna communities of category III and parts of category II from those of the other categories (Fig. 9). TOC followed by C/N_{molar} and 1-yr ice cover contributed most to dbRDA1, explaining 42.4 % of total macrofauna community variation. Macrofauna communities of category III, and one station each from categories IV and V, were separated from the other categories by the variation along dbRDA2 (14.3 % of total variation; Fig. 9). The parameters chl *a* and 1-yr ice cover correlated most with the second dbRDA axis. Along the dbRDA3 (8.3 %), chl *a*, C/N_{molar}, and silt and clay (in that order) were the most important parameters.

The results tend to support our Hypothesis 3. Although 1-yr sea-ice cover and chl *a* were the parameters explaining most of the variation in both meiofaunal and macrofaunal community composition, chl $a_{C\max}$, C/N_{molar}, and TOC were more important for macrofauna. Depth and grain size were less important.

4. DISCUSSION

For the first time, we demonstrate the relationship between sea-ice cover regime, food input, and the composition of meiofauna and macrofauna communities. We assigned ice-cover categories that proved to be related to benthic conditions.

4.1. Regions with distinct ice-cover regimes represent different food situations at the seafloor

Climate change is altering sea-ice distribution and duration in the Southern Ocean. Increasing sea-

Table 5. Macrofauna communities explained by environmental parameters: results of sequential tests on the best distance-based linear model (DistLM) based on the AIC_C (Table S4) and variation explained along each axis of the best DistLM. The procedure included the 9 predictor variables to explain the variation in macrofauna community composition (Bray-Curtis resemblance matrix). p-values of significant predictor variables are in **bold**. Depth: mean MUC sampling depth per station. Abbreviations as in Table 3

Sequential tests	Adj. R^2	SS (trace)	Pseudo-*F*	p	Probability	Cumulative probability	Residual df
Depth	0.0266	4633.1	2.59	**0.0429**	0.0434	0.0434	57
1-yr ice cover	0.2263	22374.0	15.71	**0.0001**	0.2096	0.2530	56
Chl $a_{C\max}$	0.3236	11272.0	9.05	**0.0001**	0.1056	0.3585	55
Chl a_{bottom}	0.3300	1888.4	1.53	0.1609	0.0177	0.3762	54
Chl *a*	0.4371	11682.0	11.28	**0.0001**	0.1094	0.4857	53
TOC	0.5475	11601.0	13.93	**0.0001**	0.1087	0.5943	52
C/N_{molar}	0.6336	8917.0	13.22	**0.0001**	0.0835	0.6778	51
Silt & clay	0.6431	1548.6	2.36	**0.0261**	0.0145	0.6923	50
Coarse sand	0.6663	2746.2	4.47	**0.0009**	0.0257	0.7181	49

Percentage of variation explained by individual axes

Axis	Fitted model		Total variation	
	Individual	Cumulative	Individual	Cumulative
1	59.04	59.04	42.4	42.40
2	19.88	78.92	14.27	56.67
3	11.58	90.50	8.31	64.98
4	4.07	94.57	2.92	67.90
5	2.50	97.07	1.8	69.70

Best solution. adj. R^2 = 0.666; R^2 = 0.718; RSS = 30101; 9 variables

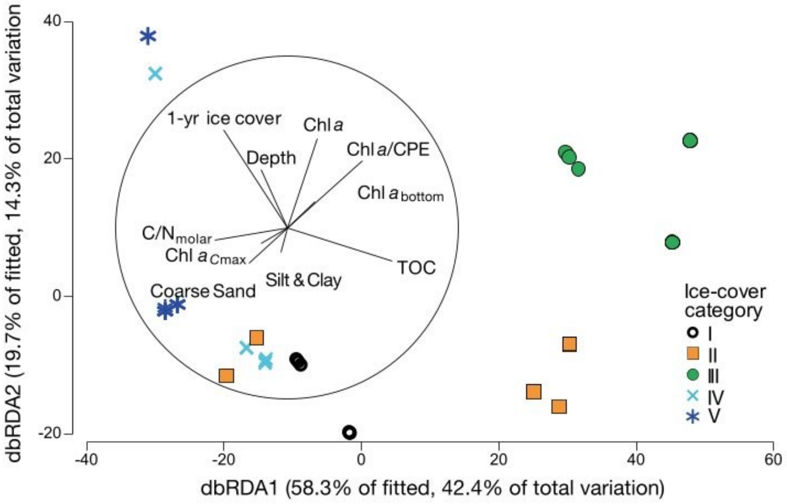

Fig. 9. Environmental drivers for macrofauna community composition. Distance-based redundancy analysis of environmental parameters and the multivariate fauna communities of single cores from regions in different ice-cover categories (I–V) sampled during RV 'Polarstern' expeditions PS 81 and PS 96 (see Table 1). Sediment parameters — silt and clay: % grain size fraction <63 µm; coarse sand: % grain size fraction >500 µm; TOC: % total organic carbon; C/N$_{\text{molar}}$: molar carbon:nitrogen ratio; chl *a*: content of chlorophyll *a*. Water-column parameters — chl a_{Cmax}: chl *a* in the water column measured at the chlorophyll maximum; chl a_{bottom}: chl *a* in the water column close to the seafloor. 1-yr ice cover: mean of the daily values (%) of Antarctic summer sea-ice cover (Dec–Feb) 1 yr before sampling

surface temperatures lead to decreasing sea-ice cover, as known from regions around the AP, whereas the opposite is known from the SE-WS (Turner et al. 2016, Comiso et al. 2017). Sea-ice cover and oceanographic conditions structure environmental conditions and influence habitats at the seafloor in the Southern Ocean (Gutt & Piepenburg 2003, Isla 2016). In the marginal sea-ice zones and temporary polynyas near the coast, a constant opening and closing of the sea ice encourages the release of ice algae and the stability of the water-column stratification, which support regional phytoplankton blooms (Grebmeier & Barry 1991, Kang et al. 2001, Lizotte 2001). The presence of food banks, as mentioned for the NW-WS (Veit-Köhler et al. 2018), is based on low bottom-water temperatures, which decelerate the remineralization of the phytodetritus (Isla et al. 2002, Mincks et al. 2005). A high chl *a*/CPE ratio as in category III is found when a very high input of fresh primary production occurs on a regular basis. The high input is counterbalanced by a continuous process of consumption by the (numerous) benthic organisms. This process leads to a Phaeo content that is lower than that of the freshly arrived chl *a*, which is not a contradiction of the presence of food banks. The chl *a*/CPE ratio used underlines the role of food freshness in the classification into ice-cover categories, because it describes a standardized proxy for food quality related to total available food at the seafloor. Categories also differed in measures of fresh primary production (chl *a*), degraded material (Phaeo, C/N$_{\text{molar}}$), and organic material as such TOC, but not as consistently. Chl *a*/CPE helps to unravel the relationships between the categories of these measures and proves to be a valuable proxy for them.

In our study, the highest pigment content, even in deeper sediment layers (0–5 cm depth: mean chl *a* 17.09 µg g^{-1}, Phaeo 6.94 µg g^{-1}), was found in category III, seasonal ice-cover (NW-WS). Comparable values in the Southern Ocean have been reported only from sediment surface layers in shallow Antarctic bays (Vanhove et al. 1998, de Skowronski & Corbisier 2002, Veit-Köhler 2005, Pasotti et al. 2014). Despite the high pigment values in the sediment, the chl *a* value in the water column was low compared to that of other regions with seasonal ice-cover regimes (Moore & Abbott 2000). An opposite pattern, highest primary production in the water column and low sediment pigment values, was observed for category I, with no ice cover (DP). Because relatively warm bottom water mixes with upper water layers in ice-free zones, the nutrient concentration increases in the upper water column and supports phytoplankton accumulation (mostly diatoms). Thus, a chl *a* maximum is established above the pycnocline (Prézelin et al. 2004). The deep vertical mixing of the surface waters encourages most of the phytodetritus recycling and consumption by zooplankton and microbiological degradation already in the water column (Grebmeier & Barry 1991, Lochte et al. 1997). Low carbon fluxes to the seafloor are the consequence (Zhou et al. 2010, Watson et al. 2013).

In regions with constant sea-ice cover, primary production and the release of ice algae is impeded, and less fresh material is deposited at the seafloor. Such areas show lower chl *a*/CPE values (IV, V) and host poorer benthic communities that are limited in individual numbers. In relation to the low amount of chl *a* exported, a higher relative amount of Phaeo can accumulate over a longer time under high and constant ice-cover situations (in combination with low temperatures).

Concerning categories IV and V (S-FT and N-FT), the organic content (~0.35%) in the sediments is lower than in other high Antarctic regions, such as the Ross Sea, with a more seasonal ice-cover (1.2%; DeMaster et al. 1991), but similar organic carbon contents were measured in the eastern Weddell Sea near Austasen (~0.39%; Isla et al. 2011) and in Halley Bay (0.29%; Herman & Dahms 1992).

These findings tend to support our Hypothesis 1. We demonstrated strong evidence for differences in environmental parameters related to primary production and food supply (sediment: chl *a*, Phaeo, chl *a*/CPE, TOC, C/N_{molar}; water column: chl $a_{C\max}$, chl a_{bottom}) among the 5 ice-cover categories. The main ecological drivers (PCA, Fig. 4) are benthic indicators for food freshness and availability (chl *a*, chl *a*/CPE, TOC) as well as the degradation state of the deposited detritus (C/N_{molar}). Further, we detected the highest chl *a* content in the upper water column in an ice-free area, decoupled from food availability at the seafloor. We suggest that water-column parameters alone are not as suitable for the description of ice-cover categories for benthos because they only show a snapshot in time and cannot include processes in the water column. We conclude, and agree with previous studies, that sediment parameters integrate availability, storage, and history of the deposited material (Isla et al. 2006, Peck et al. 2006, Veit-Köhler et al. 2018) and can therefore better reflect multiyear ice-cover dynamics.

Previous studies suggested a distinction between the regions east of Filchner Trough, with a seasonal ice cover in a polynya, and west of Filchner Trough, with a constant ice cover (Knust & Schröder 2014, Schröder 2016). Unexpectedly, we could not visually match the ice-cover graphs of our stations (Fig. 2) according to the suggested geographical arrangement. In contrast, grouping the stations in a 'South Filchner Trough' area (S-FT, category IV, high ice cover) and a 'North Filchner Trough' area (N-FT, category V, constant ice cover) produced a much better visual matching of variations in summer sea-ice cover over almost a decade.

Each single ice-cover category represents a geographic region with additional particular environmental conditions such as currents or the influence of islands or the mainland (Text S1). Influences of these parameters were not tested or considered in our study, but the ice-cover categories did prove useful as an approach to benthic habitat characterization for ecologically important parameters with focus on food availability at the seafloor.

4.2. Meiofauna communities reflect ice-cover categories better than macrofauna

Our approach extended current knowledge of the structure of benthic communities in the Southern Ocean by including and analyzing the 2 size classes meiofauna and macrofauna separately and combined. The 5 ice-cover categories, characterized by different patterns in primary production and food availability, clearly showed differences for all 3 faunal community compositions. Most taxa were not restricted to one of the ice-cover categories, but their relative contributions differed among the ice-cover categories and could be related to the different environmental conditions prevailing there.

A closer look at the taxa involved showed that nematodes were, as expected, the dominant taxon of meiofauna in all 5 ice-cover categories. Previous studies in the same areas showed similarly high abundances; nematodes followed by copepods and the frequently found taxa ostracods, kinorhynchs, and tardigrades (Herman & Dahms 1992, Rose et al. 2015). Certain nematode genera were differently represented at stations of category I than at stations of category III (Hauquier et al. 2015). This finding confirmed, at a lower taxonomic level, the differences in meiofauna communities between these categories. Rare taxa, such as tardigrades and loriciferans, showed high abundances only in high Antarctic regions with the longest-lasting ice cover (categories IV and V) and further accentuated the differences among the 5 ice-cover categories. Not much is known about the ecology and distribution of these taxa in the Southern Ocean, but they may not depend on regular food input and may favor conditions of extremely low availability of highly degraded food. In addition, their distribution pattern may be induced by competition for space: the high food availability in category III favored high numbers of nematodes (Hauquier et al. 2015), ostracods, and kinorhynchs, and exceptionally high numbers of copepods (Veit-Köhler et al. 2018). Even in categories I and II (low food availability), nematode numbers were high, but tardigrades and loriciferans abounded where nematode numbers were low (Fig. 5).

Macrofauna assemblages of the investigated soft sediments were dominated by polychaetes. This finding matches well with those of previous studies from Southern Ocean shelf areas (Arntz et al. 1994, Gutt 2007, Glover et al. 2008, Pineda-Metz & Gerdes 2018). On the basis of our findings, we assumed that the limited input and availability of fresh material and the amount of organic matter at the seafloor were limiting factors for macrofauna abundances. The environmental conditions of variable ice-cover regimes (e.g. regular food input, discussed in Section 4.1) favor higher abundances of annelids, bivalves, echinoderms, and ostracods. Low total abundances were clearly linked to extremes of ice cover (I: none; IV: high; V: constant). Contrarily, isopods showed a reverse pattern and may favor food conditions as described for categories I, IV, and V (Text S1).

From the distinct environmental conditions of the ice-cover categories (see Section 4.1, Hypothesis 1), we cannot reject our second hypothesis, that differences in community composition match the ice-cover classification. We showed evidence that community differences were most pronounced in meiofauna, followed by the combined meiofauna and macrofauna, and conclude that meiofauna strongly affects the combined community analysis and should not be neglected in future studies. Although we did not test the response of benthic communities to environmental change over time, the wide range of ice-cover categories and their related environmental characteristics allows us to support the results of Zeppilli et al. (2015): they demonstrated the importance of meiofauna as a proxy for responses of benthic communities to global environmental changes.

Because of our approach, functional variation and specialized groups within macrofaunal taxa may remain undiscovered. In contrast, for meiofauna, the chosen taxon level may represent a higher heterogeneity among groups and distinguish better between functional groups. Their burrowing, interstitial, or epibenthic lifestyles without pelagic stages may be linked to a limited large-scale distribution with less homogeneity among regions. Further analyses of polychaete data may show that a taxonomic resolution at the family level and/or including feeding mode could provide better separations between ice-cover categories than the determination of macrofauna at a higher taxon level (F. S. Säring et al. unpubl.). Combining habitat categories of ice cover with functional community data could greatly enhance our ability to predict faunal distribution in the Southern Ocean from regionally reported benthic communities (Gutt et al. 2013, Pineda-Metz et al. 2019).

The MUC is a useful sampling gear for soft sediments, but using it might underestimate large and comparatively rare benthic macrofauna because of the small sampling area of the cores. These problems might be mitigated by higher deployment numbers, analysis of more cores, or use in combination with other sampling gear (Piepenburg & von Juterzenka 1994, Pineda-Metz & Gerdes 2018). Note that we used cores with different sampling surfaces (MUC6: 25.5 cm^2; MUC10: 69.4 cm^2; see Table 1 for stations). Leduc et al. (2015) reported differences in nematode diversity due to different core surfaces, but the effects they found on genus diversity and community structure of nematodes were related to extremely large differences in core surface (6.6 versus 66.4 cm^2), which are not comparable to the core-size differences in our study.

Overall, we suggest the introduction of ice-cover categories to classify different regions in the Southern Ocean as habitats for large-scale comparisons of benthic communities and their ecology. The use of such categories in combination with other spatial data, such as sea-surface data (e.g. chl *a* in the water column) and water-mass circulation patterns (e.g. speed), could facilitate the description of benthic–pelagic processes and thus the prediction of small benthic organisms on a larger spatial scale. Further, these prediction results could be used for conservation management plans to protect regions with rare taxa.

4.3. Ice cover and fresh food are the major environmental drivers for faunal community composition

Benthic organisms can be influenced by various environmental drivers at a range of spatial scales around the AP and in the SE-WS (Gerdes et al. 1992, Moens et al. 2007, Hauquier et al. 2015, Gutt et al. 2016, Veit-Köhler et al. 2018, Pineda-Metz et al.

2019). We have shown that meiofauna communities were partly affected by environmental parameters different from those affecting macrofauna, as hypothesized (Hypothesis 3), but the main drivers, ice cover and fresh food, are important for both size classes. The roles of C/N_{molar} and TOC for structuring macrofauna and meiofauna indicated that the smaller size class communities reacted less to long-term food supply. As assumed for polar shelf regions (Piepenburg 2005, Cummings et al. 2010), depth only had a minor impact on macrofauna communities, and we found a small impact on meiofauna communities. The importance of the continuous parameter '1-yr sea-ice cover' for structuring the benthic meiofauna and macrofauna communities confirmed that variations in community composition (discussed in Section 4.2) were, indeed, linked to the sea-ice dynamics and not an artefact of regional sampling.

The influence of recent sea-ice cover has so far only been quantified as minor for epibenthic communities (AP, Gutt et al. 2016), whereas long-term changes in sea ice have a major impact on megabenthic and macrobenthic communities (Kapp Norvegia, Pineda-Metz et al. 2020). Unexpectedly, the longer-term sea-ice dynamics showed a minor or no importance to the mostly sediment-bound meiofauna and macrofauna in our study, but in our study, 9-yr ice cover and 1-yr ice cover were correlated, and the more recent impact of sea ice on the availability of fresh food at the seafloor may influence the abundance of the small taxa on this time scale and thus be more relevant overall.

This conclusion is supported by the high explanatory power of chl *a*, the proxy for fresh detritus at the seafloor (Tables 4 & 5). We came to these results by investigating primary-production–related pigments in the sediment, as is common for meiofauna studies in the Southern Ocean (e.g. Lins et al. 2014, Veit-Köhler et al. 2018) and macrofauna studies in the Arctic (e.g. Link et al. 2013). Previous macrofauna studies from our study area based their analyses on a different set of environmental parameters. Parameters that in our study proved important for the separation of benthic communities (food availability and food quality at the seafloor) were not tested (see e.g. Gutt et al. 2016, Pineda-Metz et al. 2019). For example, Pineda-Metz et al. (2019) concluded that the use of water-mass characteristics (e.g. productivity regimes) might have better explained the benthic spatial distribution patterns they found in the SE-WS, but productivity regimes usually describe primary production in the open water. Disintegrating sea-ice releases ice algae, which are rapidly deposited to the seafloor (phytodetritus aggregate sinking rates: 100–150 m d^{-1}; Gooday 1993). Their contribution to the food of benthic communities may be severely underestimated from water-column chl *a* concentration derived from satellite images as a proxy for benthic food supply (Lins et al. 2014). First, chl *a* satellite measurements are not available during long-term ice cover situations. Second, sea-ice algal productivity may account for up to 25% of total primary production (Arrigo & Thomas 2004). These circumstances may explain why authors who used chl *a* measures derived from satellite images did not find them relevant for the interpretation of their faunal distribution data (expedition PS 81; Gutt et al. 2016, Segelken-Voigt et al. 2016). Without a direct measure of phytopigments from sediment samples, features such as food banks (Mincks et al. 2005) may not be detected or their importance may be underestimated, as by Gutt et al. (2016). Food banks were in fact discovered in the NW-WS, as discussed in the literature (Hauquier et al. 2015, Veit-Köhler et al. 2018), and chl *a*/CPE proved to be an important driver in separating Weddell Sea meiofauna communities from those of BS and DP.

Although sediment structure only had a marginal influence on fauna structures, we assume that the highest proportion of coarse sand in category II is related to high macrofauna abundance but relatively lower meiofauna abundance for this category. Further, water depth was particularly relevant for the composition of meiofauna there. Possibly, the habitat was more suitable for borrowing polychaetes or predatory isopods, reducing the abundance of meiofauna.

We showed that Antarctic meiofauna and macrofauna communities are mostly structured by the recent sea-ice cover and fresh food availability at the seafloor. The latter factor depends strongly on sea-ice cover, its duration, and the regularity of melting and freezing cycles. In the perspective of climate change, the interaction between benthic communities and changing sea-ice cover might be studied in more depth through addition focusing on functional groups to clarify the importance of size in sensitivity to sea-ice changes.

5. CONCLUSIONS

This correlative study addressing Antarctic meiofauna and macrofauna communities in combination across 5 regions with different annual sea-ice cover and environmental parameters suggested that meiofauna are more responsive than macrofauna to differences in sea-ice cover. These findings should be considered in future studies of the Antarctic benthos that aim at a general understanding of the influence of sea ice on, and the consequences of, climate change for the ecosystem. Differentiation of meiofauna communities (mostly phylum level) under different ice-cover regimes allow use of such sea-ice cover classification in the future to forecast meiofauna distribution for the ecologically relevant taxa. Although most of the variation in meiofauna and macrofauna community patterns can be explained by the environmental parameters considered here, our results suggest additional drivers such as currents are lacking (especially for macrofauna). Besides the recent sea-ice cover, though, the amount of available fresh food (chl *a*) in the sediment is most reliable for explaining benthic community patterns and should always be included in the set of directly measured benthic parameters. Future ground-truthing with sea-surface data (sea-ice cover, chl *a* in the water column) could improve the large-scale predictions of benthic communities in the face of environmental changes. We therefore recommend a multidisciplinary approach that should include an extensive analysis of pelagic–benthic coupling for better understanding of how benthic communities are affected by their environment.

Acknowledgements. Marco Bruhn, Annika Hellmann, Stephan Durst, Jan Schuckenbrock, and Leon Hoffman (Senckenberg am Meer Wilhelmshaven); Freija Hauquier and Laura Durán Suja (Ghent University, Belgium); and Andreas Bick (University of Rostock) are thanked for helping with classification of meiofauna and macrofauna. We thank Ben Behrend (University of Rostock) for contributing to environmental data analyses. We gratefully acknowledge Fynn Warnke (Alfred-Wegener-Institute for Polar and Marine Research, [AWI], Germany) for providing the ice-cover data (1 December 2003 to 1 April 2016) from Meereisportal www.meereisportal.de (grant: REK-LIM-2013-04) and for a briefing on QGIS. Thanks are also due to the crew of RV 'Polarstern' and chief scientists Julian Gutt (PS 81) and Michael Schröder (PS 96, both AWI) for allowing sample collection on board. The members of the OFOS Team Dieter Piepenburg (Kiel University, Germany) and Alexandra Segelken-Voigt (University of Oldenburg, Germany) are thanked for information by video survey on board. Michael Schröder and his team (AWI) are thanked for water-column samplings. Yasemin Bodur (Senckenberg am Meer), Freija Hauquier, Dieter Piepenburg, and Enrique Isla (Institut de Ciències del Mar, Barcelona, Spain) helped with logistics and sampling during the cruises. The present study was funded by the Deutsche Forschungsgemeinschaft (DFG) SPP 1158 Antarctic Research (LI 2313/3-1, LI 2313/6-1 and VE 260/10-1). Support was given by the AWI (Grants AWI_PS81_03, AWI_PS96_02). We also thank Anne Thistle for editing and language correction, which improved this manuscript.

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Editorial responsibility: Jeroen Ingels,
St. Teresa, Florida, USA
Reviewed by: H. J. Griffiths and 1 anonymous referee

Submitted: November 26, 2021
Accepted: September 26, 2022
Proofs received from author(s): November 7, 2022

Chapter II

Declaration of author contributions:

A new species of *Anobothrus* (Polychaeta, Ampharetidae) from the Weddell Sea (Antarctica), with notes on habitat characteristics and an updated key to the genus

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This chapter was published in the journal *European Journal of Taxonomy* as:

Säring F., Bick A., Link H. (2022): A new species of *Anobothrus* (Polychaeta, Ampharetidae) from the Weddell Sea (Antarctica), with notes on habitat characteristics and an updated key to the genus. *European Journal of Taxonomy* 789: 139–152. https://doi.org/10.5852/ejt.2022.789.1637

Friederike Weith (née Säring) performed the laboratory work for the identification and description of a new species, analyzed grain size and pigment samples.

Andreas Bick provided literature and helped with the identification of the new species.

Heike Link collected samples and supervised the analysis of environmental data.

Friederike Weith (née Säring), Andreas Bick and Heike Link conceived and designed the study.

Friederike Weith, Andreas Bick and Heike Link discussed the results.

Friederike Weith drafted the manuscript, Andreas Bick and Heike Link critically commented on the manuscript.

Friederike Weith’s contribution in writing the manuscript was ~ 90%.

European Journal of Taxonomy 789: 130–152
https://doi.org/10.5852/ejt.2022.789.1637
ISSN 2118-9773
www.europeanjournaloftaxonomy.eu
2022 · Säring F. *et al.*

Research article

urn:lsid:zoobank.org:pub:BE630DB7-6B9F-47E3-8A63-54CDF6ABC413

A new species of *Anobothrus* (Polychaeta, Ampharetidae) from the Weddell Sea (Antarctica), with notes on habitat characteristics and an updated key to the genus

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Abstract. Benthic samples were collected during two expeditions near the Antarctic Peninsula and in the South-Eastern Weddell Sea. During these studies, a new species of Ampharetidae Malmgren, 1867, *Anobothrus konstantini* Säring & Bick sp. nov., was found. Here we present a detailed description of this species. We used the traditional light microscope and scanning electron microscope (SEM) to identify and describe the diagnostic characters: a circular glandular band on segment 6; an elongate ridge between the notopodia on segment 12 and modified notochaetae on this segment; 16 thoracic, two intermediate and ten abdominal segments. For the first time, micro-computed tomography (micro-CT) was used for a species description of *Anobothrus*. Micro-CT provided information on the shape of the prostomium (*Ampharete*-type) and the arrangement of branchiae (four pairs in two rows, without a gap). In addition, we provide quantitative information on the environmental niche based on sediment parameters (chlorophyll *a* content, organic matter content, chloroplast equivalent, grain size) for the new *Anobothrus* species, relevant for, e.g., species distribution modelling. Finally, an identification key for all *Anobothrus* species is provided.

Keywords. *Anobothrus konstantini* Säring & Bick sp. nov., Antarctic Peninsula, ecology, Filchner Trough, micro-CT analysis, SEM.

Säring F., Bick A. & Link H. 2022. A new species of *Anobothrus* (Polychaeta, Ampharetidae) from the Weddell Sea (Antarctica), with notes on habitat characteristics and an updated key to the genus. *European Journal of Taxonomy* 789: 130–152. https://doi.org/10.5852/ejt.2022.789.1637

Introduction

Polychaetes are one of the most speciose and dominant macrofaunal group of the Southern Ocean benthos (Clarke & Johnston 2003), and they are distributed in all substrates ranging from intertidal to abyssal depths (Schüller & Ebbe 2014). Despite comprehensive recent efforts, many species remain unknown. Many of the most abundant species in the Southern Ocean region belong to the hemi-sessile and tube-dwelling Ampharetidae (Schüller & Ebbe 2007, 2014). This family is one of the most abundant and species-rich among polychaetes, including so far more than 300 described species worldwide (Jirkov 2011; Bonifácio *et al.* 2015; Alalykina & Polyakova 2020; World Register of Marine Species, http://www.marinespecies.org). The taxonomy of Ampharetidae is complex and poorly resolved, with insufficient diagnoses. Major difficulties and confusion refer to different terminology and counting of segments and chaetigers following the prostomium. A conflict concerns the chaetae (paleae) of segment 2, which are excluded in the counts of chaetigers by some authors but included by others (Reuscher *et al.* 2009). The mode of counting needs to be defined to avoid uncertainties of the different counting expressions and misinterpretations. The terminology used in this work for counting segments, chaetigers, and uncinigers is shown schematically for a specimen of *Anobothrus* (Fig. 1).

Within the Ampharetidae Malmgren, 1867, *Anobothrus* Levinsen, 1884 is one of the most species-rich and diverse genera (Schüller & Jirkov 2013; Bonifácio *et al.* 2015). *Anobothrus* is characterized by modifications of the fourth-, fifth- or sixth-to-last thoracic unciniger with dorsally elevated notopodia and / or modified notochaetae and / or a transverse dorsal ridge between the elevated notopodia. In this genus, 22 species are currently considered valid, three of them having been described recently (Alalykina & Polyakova 2020). Species of the genus *Anobothrus* show a worldwide distribution (Alalykina & Polyakova 2020: table 3). Fourteen *Anobothrus* species have been described from the Pacific (Malmgren 1866; Hartmann-Schröder 1965; Fauchald 1972; Hilbig *et al.* 2000; Jirkov 2009; Reuscher *et al.* 2009; Imajima *et al.* 2013; Alalykina & Polyakova 2020), while only 5 species are reported from polar latitudes: *A. laubieri* (Desbruyères, 1979) from the Arctic Ocean and *A. antarctica* Monro, 1939, *A. paleaodiscus* Schüller & Jirkov, 2013, *A. pseudoampharete* Schüller, 2008 and *A. wilhelmi* Schüller & Jirkov, 2013 from the Southern Ocean.

Non-biological (seasonality of sea-ice extent, low bottom temperatures, currents, wind) and biological (seasonal primary production and nutrient pulses) parameters typical for polar systems shape the complexity of the benthic ecosystem in the Southern Ocean (Gutt *et al.* 2018). This study presents a

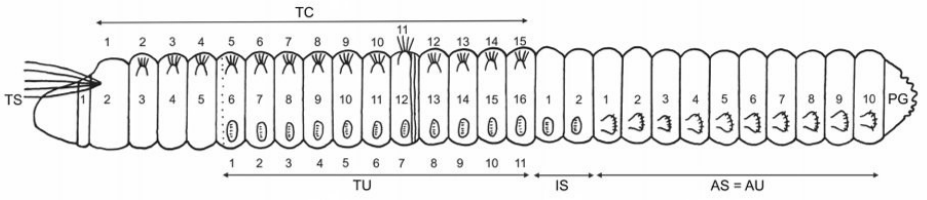

Fig. 1. Schematic lateral view of *Anobothrus konstantini* Säring & Bick sp. nov. Abbreviations: see Material and methods. Vertical dotted line in TS6 represents circular glandular band. Vertical lines in TS12 represent elongated ridge between notopodia.

detailed description of the abiotic parameters encountered at sites sampled for polychaetes to characterize the ecological niche, which builds a baseline for potential habitat modelling (Jansen *et al.* 2018) and species distribution modelling (Meißner *et al.* 2014) for the new species of *Anobothrus*.

The aim of this paper is to describe a new species of *Anobothrus* discovered during ecological studies in the Antarctic Peninsula area and in the Weddell Sea (Säring *et al.* submitted) including a revised key for all species of *Anobothrus* described worldwide. We show how the micro-CT method can help to describe diagnostic features that are otherwise difficult to recognize in poorly preserved individuals. We finally present the key environmental factors that characterize the habitat of this species.

Material & Methods

Study area and sample collection

Twelve specimens of *Anobothrus* were collected from 8 of 16 sampled stations during two expeditions with the RV *Polarstern.* The tip of the Antarctic Peninsula (Drake Passage, Bransfield Strait, North-Western Weddell Sea) was explored during expedition PS 81 (22 Jan.–18 Mar. 2013, Gutt *et al.* 2013), while the Filchner Trough area in the South-Eastern Weddell Sea was investigated during PS 96 (6 Dec. 2015–14 Feb. 2016, Schröder *et al.* 2016) (Table 1, Fig. 2; Säring *et al.* submitted). Water depth at the sampled stations ranged from 355 to 755 m.

Samples were collected with a MUC10 equipped with eight plexiglass core liners (inner diameter 94 mm, surface area 69.4 cm^2; Säring *et al.* submitted). For macrofaunal samples, sediments were sieved over a 500-µm mesh and fixed in a 4% formaldehyde-seawater solution (borax-buffered). More details on sediment core handling can be found in Säring *et al.* (submitted). For the comparison of spatial distribution, we calculated the total number of individuals per identified taxon per m^2 from the top until the bottom of the core.

For later morphological analyses, faunal samples were preserved in 70% ethanol. Environmental data from sediments (TOC = total organic carbon; Chl*a* = chlorophyll *a* content; CPE = chloroplastic equivalent, grain size) were obtained from additional samples up to 5 cm depth within the same or additional MUC cores and have been published elsewhere (Veit-Köhler *et al.* 2018; Säring *et al.* 2021a, b; Vanreusel *et al.* 2021a, b). Here, we used the sediment layer 0–1 cm for the comparison of the environmental parameters associated with the new species. Data for salinity and temperature of bottom water were obtained from data collected by the CTD at the same stations (Schröder *et al.* 2013, 2016). Among the different regions, salinity varied from 34.45 psu in the North-Western Weddell Sea (station PS81-162-2) to 34.67 psu in the North Filchner Trough region (station PS96-017-3). The bottom temperature ranged from the lowest, -1.9°C, in the North-Western and South-Eastern Weddell Seas to 0.7°C in the Drake Passage.

Morphology

Specimens were examined using an Olympus SZH10 stereo microscope and an Olympus BH2 light microscope. Photographs were taken with an Olympus SZX10 stereo microscope, an Olympus BX51 microscope and an Olympus UC30 camera. Specimens were stained with methyl blue and ShirlastainA to visualize specific body regions and structures. The staining fades completely when the specimens are returned to ethanol. Three specimens were transferred through a graded ethanol series in acetone and critical point dried with a Leica EM CPD300. Two of them were attached to a stub and covered with gold palladium and used for scanning electron microscopy (SEM). Scanning electron microscopy was carried out using a Zeiss DSM 960A microscope. The anterior end of the third specimen was used for the analysis with the micro-CT machine (Xradia 410 Versa, X-ray Microscope). The newly collected

Table 1. Station list and sampling during RV *Polarstern* expeditions PS 81 (22 Jan.–18 Mar. 2013) around the Antarctic Peninsula (Drake Passage, Bransfield Strait, North-Western Weddell Sea) and PS 96 (6 Dec. 2015–4 Feb. 2016) to the South-Eastern Weddell Sea (South-Filchner Trough, North-Filchner Trough) with the abundance of *Anobothrus konstantini* Säring & Bick sp. nov. (No. of ind.) for each station. Sediment samples for environmental characterization were collected with the multicorer at the same stations (Säring *et al.* 2021a; Vanreusel *et al.* 2021a). Mean and standard deviation of environmental parameters are given for each station. Sediment parameters: Chl*a* = content of chlorophyll *a*; CPE = sum of chlorophyll *a* and phaeopigments; TOC% = total organic carbon; Silt & Clay % = grain size fraction < 63 µm; Sand % = grain size fraction > 63 and < 500 µm; Coarse Sand% = grain size fraction > 500 µm.

Region	Station no.	Date	Latitude Longitude	No. of ind.	Depth [m]	Chl*a* [µg g^{-1}]	CPE [µg g^{-1}]	TOC%	Silt & Clay%	Sand%	Coarse Sand%
Drake Passage	PS81-235	7 Mar. 2013	62°16.35′ S 61°10.23′ W	1	355	0.17 ± 0.15	2.08 ± 1.3	0.6 ± 0.0	90.3 ± 0.4	9.2 ± 0.4	0.4 ± 0.1
	PS81-241	9 Mar. 2013	62°6.60′ S 60°36.50′ W	1	403	0.16 ± 0.06	0.28 ± 0.1	0.8 ± 0.0	89.0 ± 3.5	7.0 ± 1.3	4.0 ± 4.9
Bransfield Strait	PS81-118	27 Jan. 2013	62°26.93′ S 56°17.05′ W	0	425	0.48 ± 0.00	1.74 ± 0.2	0.7 ± 0.0	57.8 ± 10.0	31.2 ± 2.1	11.0 ± 7.9
	PS81-202	27 Feb. 2013	62°56.00′ S 58°0.55′ W	0	757	0.92 ± 0.00	5.33 ± 1.7	1.1 ± 0.0	85.7 ± 0.3	14.0 ± 0.5	0.2 ± 0.3
	PS81-217	2 Mar. 2013	62°53.25′ S 58°14.13′ W	2	532	0.31 ± 0.13	1.42 ± 1.1	0.4 ± 0.0	38.2 ± 3.3	43.1 ± 0.8	18.7 ± 2.5
	PS81-218	2 Mar. 2013	62°56.94′ S 58°25.73′ W	0	688	0.74 ± 0.00	2.63 ± 2.0	1.1 ± 0.0	79.6 ± 4.3	18.1 ± 2.3	2.3 ± 2.1
	PS81-225	4 Mar. 2013	62°56.08′ S 58°40.76′ W	1	543	0.13 ± 0.11	0.90 ± 0.9	0.7 ± 0.0	68.2 ± 3.0	24.0 ± 0.7	7.8 ± 2.3
North-Western Weddell Sea	PS81-120	28 Jan. 2013	63°4.78′ S 54°31.45′ W	0	494	9.31 ± 0.00	18.27 ± 11.3	1.1 ± 0.0	84.0 ± 3.1	15.8 ± 3.1	0.3 ± 0.4
	PS81-162	10 Feb. 2013	64°0.11′ S 56°44.43′ W	0	223	5.85 ± 0.00	8.58 ± 2.8	2.4 ± 0.0	57.4 ± 1.3	42.6 ± 1.3	0.0 ± 0.0
	PS81-163	11 Feb. 2013	63°50.97′ S 56°25.24′ W	0	517	25.20 ± 0.00	38.12 ± 4.2	1.6 ± 0.0	91.9 ± 0.5	8.1 ± 0.5	0.0 ± 0.0
South Filchner Trough	PS96-037	16 Jan. 2016	75°43.30′ S 42°27.71′ W	0	391	0.33 ± 0.11	4.41 ± 0.8	0.4 ± 0.0	77.7 ± 4.3	20.1 ± 1.6	2.2 ± 0.8
	PS96-061	21 Jan. 2016	76°05.93′ S 30°18.23′ W	1	468	0.13 ± 0.03	1.49 ± 0.1	0.5 ± 0.1	90.9 ± 2.1	9.1 ± 2.1	0.0 ± 0.0
	PS96-072	24 Jan. 2016	75°51.37′ S 32°17.44′ W	1	755	0.19 ± 0.04	2.88 ± 0.6	0.5 ± 0.0	79.7 ± 0.8	19.1 ± 1.0	1.2 ± 0.5
North Filchner Trough	PS96-017	4 Jan. 2016	75°00.85′ S 32°52.51′ W	4	608	0.06 ± 0.01	0.83 ± 0.03	0.2 ± 0.0	43.4 ± 6.1	49.1 ± 4.1	7.5 ± 2.0
	PS96-026	8 Jan. 2016	75°15.10′ S 37°54.85′ W	1	415	0.08 ± 0.06	1.49 ± 1.1	0.2 ± 0.1	63.2 ± 19.2	33.7 ± 16.3	3.0 ± 2.9
	PS96-048	18 Jan. 2016	74°46.18′ S 35°20.91′ W	0	482	0.15 ± 0.05	2.14 ± 0.5	0.3 ± 0.0	66.8 ± 2.2	30.3 ± 2.4	2.9 ± 1.1

Anobothrus material was deposited in the Zoologische Sammlung, Universität Rostock (ZSRO, Zoological collection of Rostock University). The catalogue numbers are given below.

There is continuing confusion about the numbering anterior to the paleal segment (Day 1964; Parapar *et al.* 2012). We follow the opinion that the second segment is considered as the paleal segment; therefore, uncini begin on segment 6 = thoracic chaetiger 5 (Annenkova 1930; Eliason 1955; Uschakov 1965; Cazaux 1982; Orrhage 2001; Reuscher *et al.* 2009). Here we include the paleal chaetiger in our counts of thoracic chaetigers (thoracic chaetiger 1), as described by Reuscher *et al.* (2009). Furthermore, we use the term "intermediate segments", as introduced by Imajima *et al.* (2012), for segments with neuropodia formed as tori (similar to those in thoracic uncinigers) but lacking notopodia and notochaetae. Therefore, these segments were excluded from the abdominal segment count. Fig. 1 shows a schematic overview of the terminology used and the counting of segments, chaetigers and uncinigers.

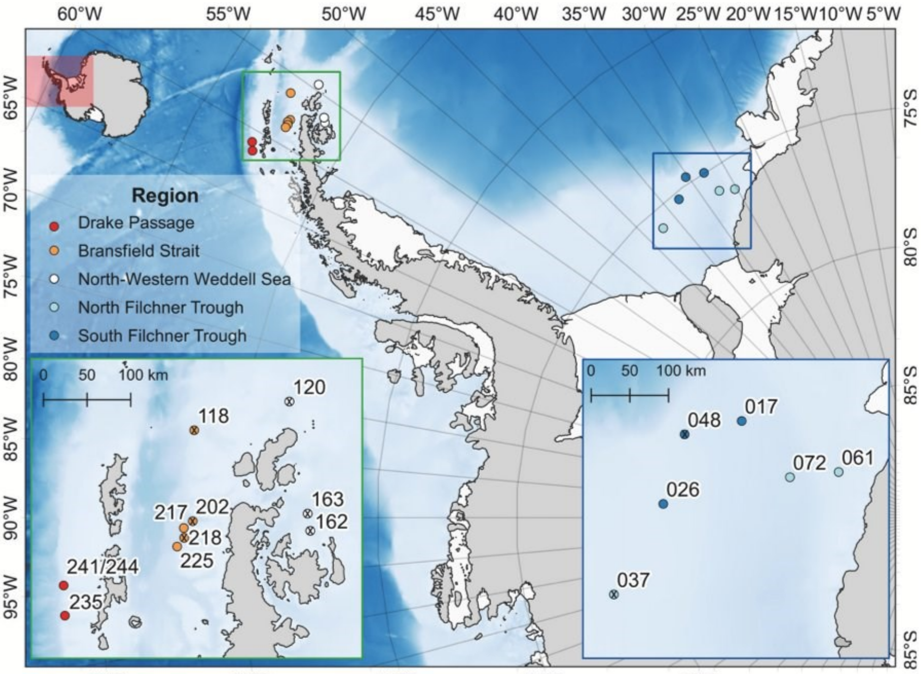

Fig. 2. Sampling stations in the vicinity of the Antarctic Peninsula during RV *Polarstern* expedition PS 81 (Drake Passage, Bransfield Strait, North-Western Weddell Sea, green frame) and the South-Eastern Weddell Sea during PS 96 (North Filchner Trough, South Filchner Trough, blue frame). Stations without *Anobothrus konstantini* Säring & Bick sp. nov. labeled with a cross. Information about sampled stations and number of individuals of *A. konstantini* Säring & Bick sp. nov. are given in Table 1.

Abbreviations used in the text, tables and figures

AS/AU = abdominal segment/abdominal unciniger
Chl*a* = content of chlorophyll *a*
Coarse Sand% = grain size fraction > 500 µm
CPE = sum of chlorophyll *a* and phaeopigments
IS = intermediate segment
PG = pygidium
Sand % = grain size fraction > 63 and < 500 µm
Silt & Clay % = grain size fraction < 63 µm
$_{bottom}T$ = bottom temperature (°C)
TC = thoracic chaetiger (including paleal segment)
TOC% = total organic carbon
TS = thoracic segment (including peristomium and paleal segment)
TU = thoracic unciniger

Results

Class Polychaeta Grube, 1850
Order Terebelliformia Levinsen, 1883
Ampharetidae Malmgren, 1866
Family Ampharetinae Chamberlin, 1919

Genus ***Anobothrus*** Levinsen, 1844

Sosanides Hartmann-Schröder, 1965: 243–246.
Anobothrella Hartman, 1967: 155–156.
Melythasides Desbruyères, 1978: 232–246.

Type species

Ampharete gracilis Malmgren, 1866.

Generic diagnosis (after Alalykina & Polyakova (2020), Bonifácio *et al.* (2015), Imajima *et al.* (2013), Jirkov (2009) and Reuscher *et al.* (2009))

Prostomium trilobed, *Ampharete*-type (Jirkov 2009), without glandular ridges. Buccal tentacles smooth or papillose. Segments 2 and 3 can be fused; notochaetae on either segment 2 or 3 reduced, or developed in both segments. Three or four pairs of smooth or papillose branchiae; three pairs arising from segments 2–4 arranged in a transverse row, with or without a gap; fourth pair, if present, behind this row and originating from segment 5. A pair of median nephridial papillae, if present, behind branchiae. Chaetae on segment 2 present and developed as paleae, or absent. Notopodia and notochaetae on segment 3 may be reduced or present. 16–17 thoracic segments, 14–16 thoracic chaetigers, and 11 or 12 thoracic uncinigers starting at segment 6. Notopodial cirri present or absent. Circular glandular band on thoracic unciniger 1, 2 or 3. Fourth-, fifth- or sixth-to-last thoracic unciniger with one, two or three modifications: elevated notopodia, a more or less pronounced glandular ridge between notopodia, and modified notochaetae. Subsequent thoracic uncinigers without modification but prolongated. One or two intermediate segments. Abdominal rudimentary notopodia absent. Pygidium with anus terminal, with or without numerous papillae, or with or without anal cirri.

Remarks

This generic diagnosis combines diagnoses proposed by Alalykina & Polyakova (2020), Bonifácio *et al.* (2015), Imajima *et al.* (2013), Jirkov (2009) and Reuscher *et al.* (2009), and follows the terminology of counts used by Imajima *et al.* (2012, 2013) and Reuscher *et al.* (2009). Ampharetidae are usually known for a constant number of thoracic chaetigers and uncinigers for adult individuals (Reuscher *et al.* 2009; Stiller *et al.* 2020 for exclusion of Melinnidae).

Anobothrus konstantini Säring & Bick sp. nov.

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Figs 3–6

Diagnosis

Four pairs of branchiae; three pairs in anterior transverse row with a small gap, and fourth pair posteriorly shifted, directly between innermost and middle branchiae of anterior row. Segment 6 (thoracic chaetiger 5, thoracic unciniger 1) with circular glandular band. Segment 12 (thoracic chaetiger 11, thoracic unciniger 7) with elongated ridge between notopodia; modified notochaetae present. Segment 2 (thoracic chaetiger 1) with long and thin paleae, about 12–14 on each side. Sixteen thoracic segments (15 thoracic chaetigers, 11 thoracic uncinigers); 2 intermediate and 10 abdominal segments.

Etymology

This species is dedicated to the brother of the first author (FS), Konstantin Zülske, who will be always a special part of her life.

Type Material

Holotype

SOUTH-EASTERN WEDDELL SEA • body length 9.3 mm; North Filchner Trough, PS96 exp., station 017-3; 75°00.85′ S, 32°52.51′ W; depth 608.2 m; 4 Jan. 2016; H. Link and G. Veit-Köhler leg.; multicorer; ZSRO-P2655.

Paratypes

SOUTH-EASTERN WEDDELL SEA • 1 spec.; South Filchner Trough, PS96 exp., station 061-5; 76°05.93′ S, 30°18.23′ W; depth 467.6 m; 21 Jan. 2016; same collector and sampling as for holotype; ZSRO-P2660 • 1 spec.; South Filchner Trough, PS96 exp., station 072-9; 75°51.37′ S, 32°17.44′ W; depth 755.1 m; 24 Jan. 2016; same collector and sampling as for preceding; used for SEM; ZSRO-P2661 • 3 specs; North Filchner Trough, PS96 exp., station 017-3; 75°00.85′ S, 32°52.51′ W; depth 608.2 m; 4 Jan. 2016; same collector and sampling as for preceding; ZSRO-P2662 • 1 spec.; North Filchner Trough, PS96 exp., station 026-8; 75°15.10′ S, 37°54.85′ W; depth 481.9 m; 8 Jan. 2016; same collector and sampling as for preceding; used for SEM; ZSRO-P2663.

Additional Material

ANTARCTIC PENINSULA • 1 spec.; Drake Passage, PS81 exp., station 235-2; 62°6.60′ S, 60°36.50’ W; depth 355m; 7 Mar. 2013; H. Link leg; multicorer; ZSRO-P2656 • 1 spec.; Drake Passage, PS81 exp., station 241-5; 62°6.60′ S, 60°36.50′ W; depth 403 m; 9 Mar. 2013; same collector and sampling as for preceding; ZSRO-P2657 • 2 specs; Bransfield Strait, PS 81 exp., station 217-5; 62°53.25′ S, 58°14.13′ W; depth 532 m; 2 Mar. 2013; same collector and sampling as for preceding; one specimen used for micro-CT; ZSRO-P2658 • 1 spec.; Bransfield Strait, PS81 exp., station 225-2; 62°56.08′ S, 58°40.76′ W; depth 543 m; 4 Mar. 2013; same collector and sampling as for preceding; ZSRO-P2659.

Description

Complete specimens 7–13 mm long (holotype 9.3 mm), and 0.5–0.8 mm wide (holotype 0.5 mm) on thorax (Fig. 3D, compare Fig. 3A).

16 thoracic segments (15 thoracic chaetigers, 11 thoracic uncinigers) (Fig. 1). Thorax wider and longer than abdomen, abdomen tapering posteriorly (compare Figs 3A, 4A). Continuous ventral shields on segments 2–12 (thoracic chaetigers 1–11). Median ventral groove from segment 13 (thoracic chaetiger 12) to pygidium**.**

Prostomium trilobed, anteriorly rounded, *Ampharete*-type (Jirkov 2009), without eye spots (compare Fig. 5B–C). Nuchal organs not observed. Buccal tentacles apparently smooth, observed for one specimen (ZSRO-P2662: paratype).

Four pairs of branchiophores; between two groups a small gap half as wide as branchiophores. Branchiae were lost on almost all specimens (11), one specimen with one outer gradually tapering papillose branchia (compare Figs 3A, 4A). First three pairs of branchiophores arranged in anterior transversal row (inner, middle and outer pairs), forming a high fold, originating from segments 2–4 (thoracic chaetigers 1–3), fourth pair of branchiae posteriorly shifted between innermost and middle branchiae of anterior row (Fig. 4F, compare Fig. 5A–B). Anterior end of branchiophores apparently fused together (Fig. 3D, compare Fig. 5A). Origin of branchiae not visible; nephridial papillae not visible.

Segment 2 (thoracic chaetiger 1) with 12–14 long, thin and slender paleae on each side, gradually tapering (holotype: left, 12 paleae plus a single small palea; right, 12 paleae plus a single small palea). Paleae protruding clearly beyond the prostomium (Fig. 3F, compare Fig. 4A), semicircularly arranged, with a small thin palea at the dorsal outer margin (compare Fig. 5B).

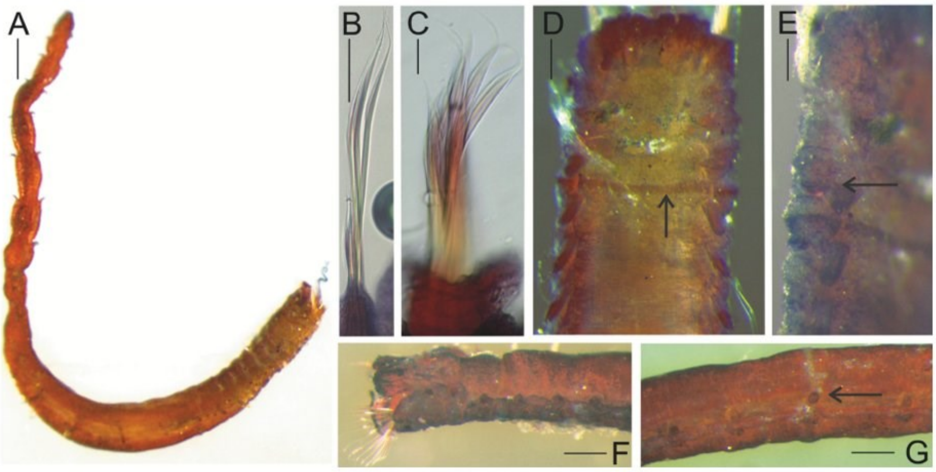

Fig. 3. *Anobothrus konstantini* Säring & Bick sp. nov. Micrographs of ShirlastainA staining pattern. **A**. Complete specimen, lateral view with one outermost branchia, additional material (ZSRO-P2657). **B**. Notochaetae on segment 11 (TC 10), paratype (ZSRO-P2662). **C**. Modified notochaetae on segment 12 (TC 11, TC 7), paratype (ZSRO-P2660). **D**. Dorsal view of anterior end, arrow: glandular circular band on segment 6 (TC 5, TU 1), paratype (ZSRO-P2662). **E**. Lateral view, arrow: reduced neuropodium on segment 5 (TC 4), without uncini, paratype (ZSRO-P2662). **F**. Lateral view of anterior end, paratype (ZSRO-P2662). **G**. Lateral view of three thoracic segments, arrow: modified notopodium with dorsal ridge on segment 12 (TC 11, TU 7), paratype (ZSRO-P2662). Scale bars: A = 500 µm; B = 50 µm, C = 20 µm; D–E = 100 µm; F–G = 200 µm.

Notopodia from segment 3 (thoracic chaetiger 2), well developed with a simple elongated lobe, and with some capillary chaetae; first notopodium smaller than subsequent notopodia and slightly shifted dorsally (Figs 4F, 6A); notopodia without cirri or papillae. Eleven thoracic uncinigers, from segment 6 (thoracic chaetiger 5) to segment 16 (thoracic chaetiger 15) (Fig. 1, compare Fig. 4A).

Segment 6 (thoracic chaetiger 5, thoracic unciniger 1) with circular glandular band (Figs 3D, 4F, 6A–B). Notopodia of segment 12 (thoracic chaetiger 11, thoracic unciniger 7) elevated and connected by a pronounced dorsal ridge (Figs 3G, 6A, compare Fig. 4K), with ciliated band (Fig. 6C).

Two intermediate segments; notopodia absent but neuropodia of thoracic type present (Figs 4L, 6E). Abdomen with 10 segments (10 uncinigers); notopodia and -chaetae absent. Abdominal neuropodia as elongated pinnules without dorsal cirri (Fig. 6D).

Thoracic notochaetae bilimbate capillaries, tapering to slender tips (Figs 3B, 6F–H, compare Fig. 4B–C); segment 3 (thoracic chaetiger 2) with 3–4 short notochaetae in a tuft; notochaetae of subsequent chaetigers arranged in two rows (Fig. 6F), anterior row with 3 shorter (compare Fig. 4C) and posterior row with 4 longer chaetae (compare Fig. 4B). Notochaetae of modified segment 12 (thoracic chaetiger 11, thoracic unciniger 7) tapered more abruptly toward the tip than regular notochaetae (Figs 3C, 6I, compare Fig 4D–E). Thoracic neuropodia with 17–21 uncini (holotype: thoracic segment 5 with 20 uncini, thoracic segments 10 and 16 with 17 uncini each) in one row. Thoracic uncini about 16 µm long, pectinated, with 6–7 teeth in lateral view, above rostral tooth 3–4 teeth in a row, and about 6 teeth in apical row (compare Fig. 4G–H). Neuropodia of intermediate segments with 15–22 uncini (holotype: intermediate segment 2 with 16 uncini), and abdominal neuropodia with 16–19 uncini (holotype: abdominal segments 1, 3 and 5 with 16 uncini each) in marginal position of pinnules. Abdominal uncini about 8 µm long, pectinated, with 5–6 teeth in lateral view, above rostral tooth 7–8 teeth in a row, about 2 teeth in apical row (Fig. 6J–K, compare Fig. 4I–J). Number of uncini declines towards pygidium.

Pygidium with terminal anus, without cirri but papillose folds present (Fig. 6D).

METHYL BLUE STAINING PATTERN. Intensive staining of bases of noto- and neuropodia. Body uniformly spotted blue, without distinct pattern, but a circular glandular band on segment 6 (thoracic chaetiger 5, thoracic unciniger 1) becomes visible.

SHIRLASTAINA STAINING PATTERN. Staining pattern similar to methyl blue staining pattern (Fig. 3B–G, compare Fig. 3A), but additional structures are visible: the circular glandular band on segment 6 (thoracic chaetiger 5, thoracic unciniger 1) (Fig. 3D) and an elevated dorsal ridge on segment 12 (thoracic chaetiger 11, thoracic unciniger 7) (Fig. 3G).

Biology

Male gametes, about 9–10 µm in diameter, were observed in segments 4–11 (thoracic chaetigers 3–10) in one specimen, collected in January in the North Filchner Trough.

Remarks

The branchiae were lost in almost all specimens, branchiophores are apparently fused together and are not separated (compare Fig. 5B–D). Due to poor conservation, the segmental origin of branchiae could not be described in more detail. We suggest the following arrangement of branchiae of the anterior row: segment 2, branchiae in the middle position, segment 3, branchiae of outermost position, segment 4, innermost position, segment 5, branchiae in posterior position between innermost and middle branchiae of anterior transverse row.

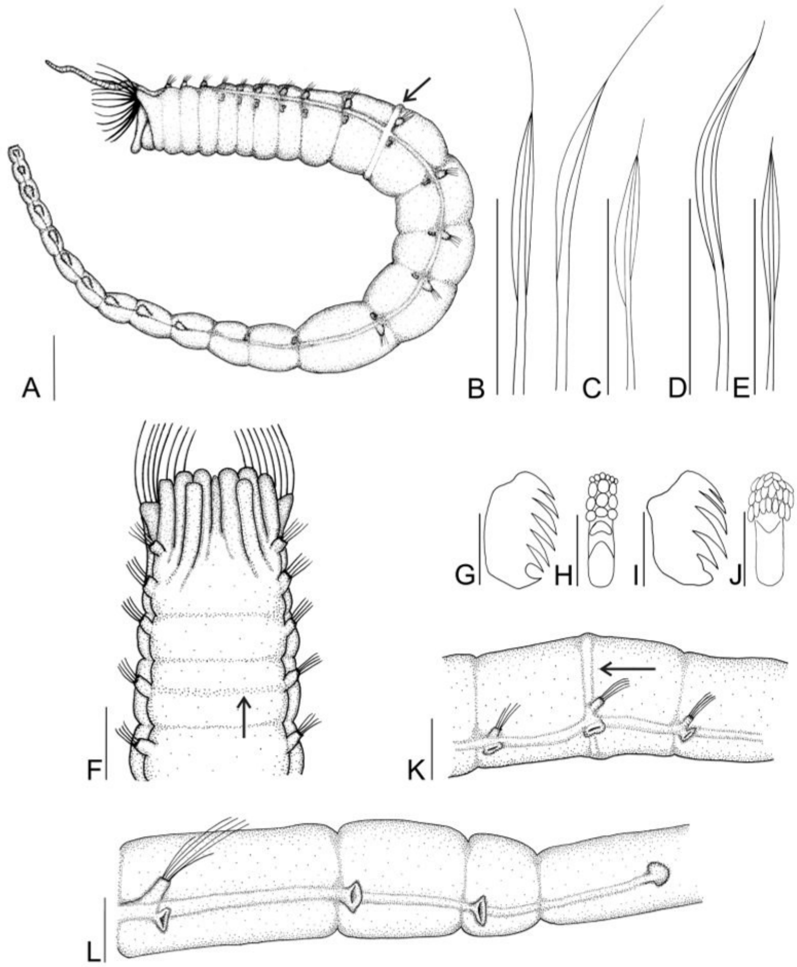

Fig. 4. *Anobothrus konstantini* Säring & Bick sp. nov. **A**. Complete specimen with one outermost branchia, lateral view, arrow: dorsal ridge on segment 12 (TC 11, TU 7), additional material (ZSRO-P2657). **B**. Long thoracic notochaeta, additional material (ZSRO-P2658). **C**. Short thoracic notochaeta, additional material (ZSRO-P2658). **D**. Long notochaeta of the modified segment 12 (TC 11, TU 7), additional material (ZSRO-P2658). **E**. Short notochaeta of the modified segment 12 (TC 11, TU 7), additional material (ZSRO-P2658). **F**. Dorsal view of the anterior end, paratype (ZSRO-P2662). **G**. Lateral view of thoracic uncinus, additional material (ZSRO-P2658). **H**. Frontal view of thoracic uncinus, additional material (ZSRO-P2658). **I**. Lateral view of abdominal uncinus, additional material (ZSRO-P2658). **J**. Frontal view of abdominal uncinus, additional material (ZSRO-P2658). **K**. Lateral view of three thoracic segments, arrow: dorsal ridge on segment 12 (TC 11, TU 7) with slightly elevated notopodia, additional material (ZSRO-P2656). **L**. Lateral view of last thoracic, two intermediate and first abdominal segments, paratype (ZSRO-P2663). Scale bars: A = 500 µm; B–E = 100 µm; F, K = 200 µm; G–H = 10 µm; I–J = 5 µm; L = 50 µm.

The holotype and paratypes from the South-Eastern Weddell Sea did not show any significant differences in diagnostic characteristics. Specimens of the additional material showed only minor differences to the diagnosis of the holotype and paratypes. Therefore, the additional material was used for the light microscopy (Fig. 3A), drawing (Fig. 4A–E, G–K) and the micro-CT (Fig. 5). However, we found one modification of one specimen from the additional material (ZSRO-P2658) when analysing the images from the micro-CT: one pair of small and fine paleae next to the regular large and thin paleae (Fig. 5B, D). The small paleae are placed where newly formed chaetae are expected and may be a growing state (Tilic *et al.* 2015). However, the shape and form is different compared to the other paleae. The purpose of these paleae was not clearly clarified.

The presence of a reduced neuropodium on segment 5 (thoracic chaetiger 4) was presumed on one specimen using ShirlastainA because at the position of the thoracic neuropodia and of the same size as these, the same staining pattern was visible on this segment (Fig. 3E). However, uncini were not observed.

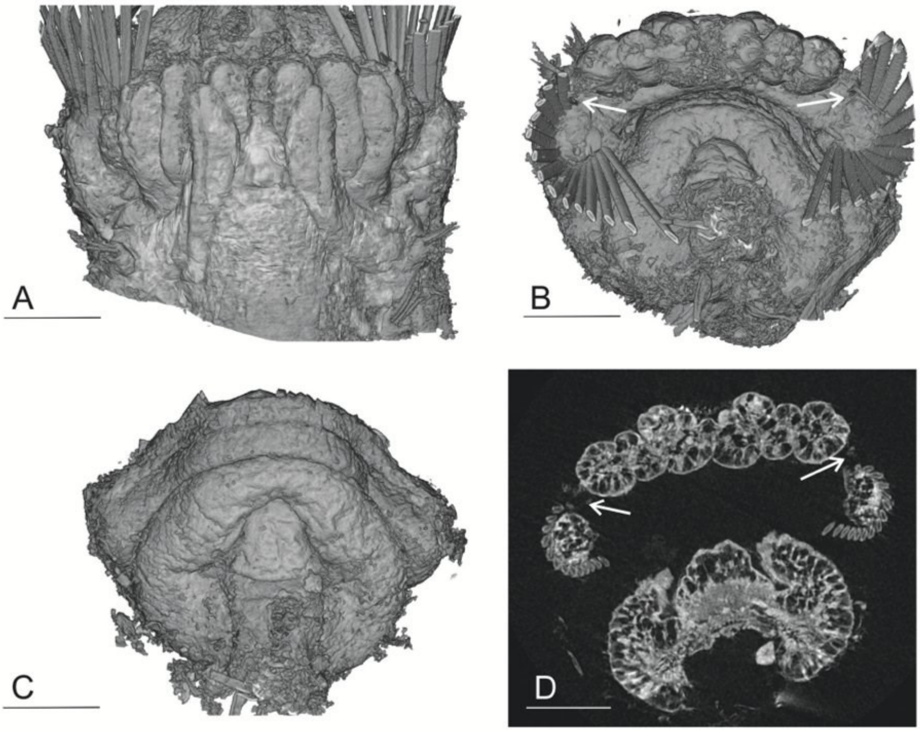

Fig. 5. *Anobothrus konstantini* Säring & Bick sp. nov., additional material (ZSRO-P2658). Micro-CT graphs, additional material. **A**. Anterior end with arrangement of branchiae, dorsal view. **B**. Anterior end with arrangement of branchiae, frontal view (note semicircular arrangement of paleae; arrows: small paleae on each side). **C**. Frontal view of anterior end, without branchiae or paleae (note: *Ampharete*-type prostomium). **D**. Anterior end, transverse section of branchiae, paleae and prostomium (note arrows: small paleae on each side). Scale bars: A–D = 100 µm.

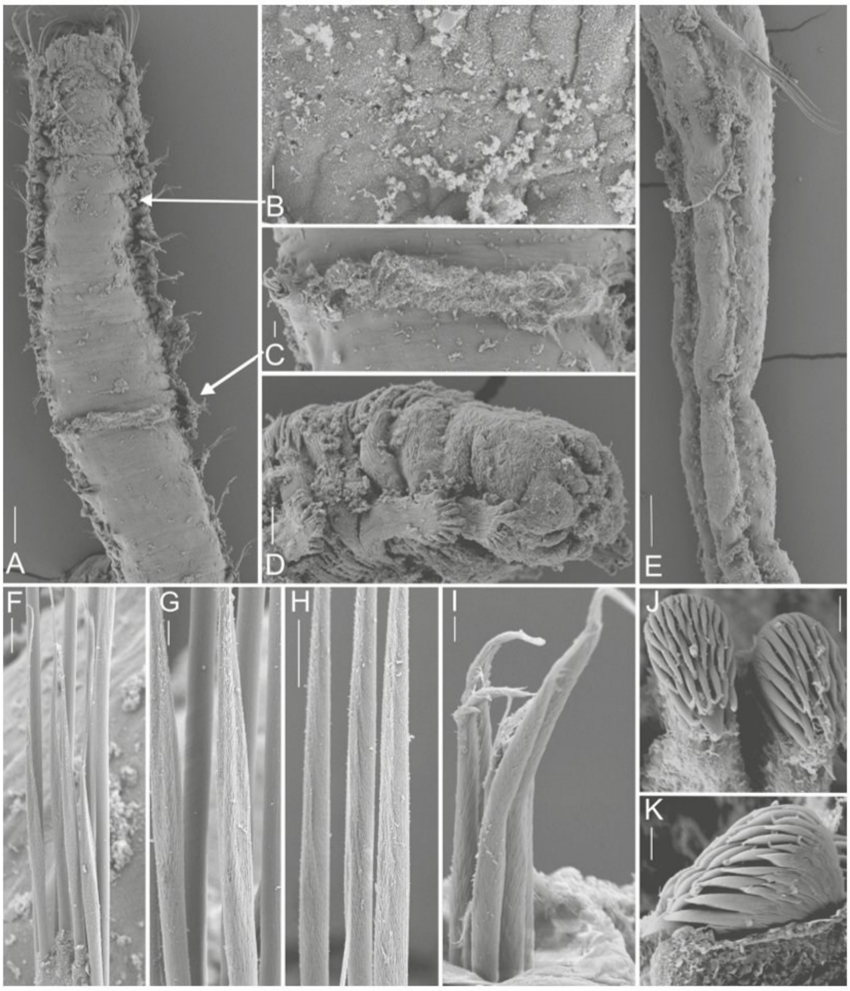

Fig. 6. *Anobothrus konstantini* Säring & Bick sp. nov. SEM micrographs. **A**. Anterior end and thorax, dorsal view, arrows: segment 6 (thoracic chaetiger 5, thoracic unciniger 1) and segment 12 (TC 11, TU 7), paratype (ZSRO-P2661). **B**. Pores in glandular band on segment 6 (TC 5, TU 1), dorsal view, paratype (ZSRO-P2661). **C**. Elevated ridge with cilia on segment 12 (TC 11, TU 7), dorsal view, paratype (ZSRO-P2661). **D**. Posterior end with papillose pygidium, lateral view, paratype (ZSRO-P2663). **E**. Last thoracic, two intermediate and first abdominal segments, lateral view, paratype (ZSRO-P2663). **F**. 4 longer and 3 shorter notochaetae of notopodium on segment 15 (TC 14, TU 10), paratype (ZSRO-P2661). **G**. Margin of short notochaetae on segment 15 (TC 14, TU 10), paratype (ZSRO-P2661). **H**. Margin of long notochaetae on segment 15 (TC 14, TU 10), paratype (ZSRO-P2661). **I**. Modified notochaetae on segment 12 (TC 11, TU 7), paratype (ZSRO-P2661). **J**. Abdominal uncini on abdominal segment 8, frontal view, paratype (ZSRO-P2663). **K**. Abdominal uncinus on abdominal segment 8, lateral view, paratype (ZSRO-P2663). Scale bars: A, E = 100 µm; B, I = 2 µm; C, D = 20 µm; F, H = 10 µm; G = 3 µm, J–K = 1 µm.

Uncini of the thoracic and intermediate neuropodia are about twice the size of uncini of the abdomen. A variation in size or shape of uncini along their row on a single neuropodium was not found.

Due to the fixation in 4 % formaldehyde solution and the subsequent preservation in a 70% ethanol solution, no statement can be made about the pigmentation of fresh material.

Anobothrus konstantini Säring & Bick sp. nov., *A. bimaculatus* Fauchald, 1972 and *A. mancus* Fauchald, 1972 differ from the other *Anobothrus* species with four pairs of branchiae and the presence of paleae, *A. amourouxi* Bonifácio, Lavesque, Bachelet & Parapar, 2015*, A. anatarctica* Monro 1939*, A. glandularis* (Hartmann-Schröder, 1965)*, A. gracilis* (Malmgren, 1866)*, A. mironovi* Jirkov, 2009*, A. paleatus* Hilbig, 2000*, A. paleaodiscus* Schüller & Jirkov, 2013*, A. patagonicus* (Kinberg, 1867)*, A. patersoni* Jirkov, 2009*, A. pseudoampharete* Schüller, 2008*, A. rubropaleatus* Schüller & Jirkov, 2013 and *A. wilhelmi* Schüller & Jirkov, 2013*,* in having 11 instead of 12 thoracic uncinigers. Within this group, only *A. paleatus* has a glandular band with an elevated ridge on the fourth-to-last thoracic segment (thoracic segment 14, thoracic unciniger 9) the remaining eleven *Anobothrus* species, as well as *A. konstantini* Säring & Bick sp. nov., show a modification of the fifth-to-last thoracic segment. However, due to the difference in the number of segments (12 thoracic uncinigers vs. 11 thoracic uncinigers), *A. konstantini* Säring & Bick sp. nov. posseses this character on segment 12, whereas it is present on segment 13 in the previously mentioned species. In addition, the first transverse band on the anterior part of the thorax is not mentioned for *A. pseudoampharete*.

Anobothrus amourouxi, *A. anatarctica*, *A. glandularis*, *A. gracilis*, *A. mironovi*, *A. paleatus*, *A. paleaodiscus* and *A. patersoni* have a transversal band on segment 8, while *A. rubropaleatus* and *A. wilhelmi* have it on segment 7. Only one species, *A. patagonicus*, possesses a transversal band on segment 6, as described for *A. konstantini* Säring & Bick sp. nov. However, *A. patagonicus* differs from *A. konstantini* Säring & Bick sp. nov. by the larger body length of about 19 mm and up to 30 uncini on neuropodia of segment 6, while the body length *A. konstantini* Säring & Bick sp. nov. ranges between 7 and 13 mm, with about 16–19 thoracic uncini on the neuropodia of segment 6.

The only two species with paleae on segment 2, four pairs of branchiae and 11 thoracic uncinigers are *A. bimaculatus* and *A. mancus*. However, *A. bimaculatus* is significantly larger (65 mm), has eyespots and has modified notopodia on segment 11, instead of on segment 12 as in *Anobothrus konstantini* Säring & Bick sp. nov. *Anobothrus mancus* is the only species with modified notopodia on segment 12, but segments 3 and 4 are fused, and notopodia are absent on segment 3. Furthermore, *A. mancus* is missing the circular glandular band on segment 6.

Distribution

The holotype and paratypes of *Anobothrus konstantini* Säring & Bick sp. nov. were found in shelf regions in the South-Eastern Weddell Sea (North Filchner Trough and South Filchner Trough). The additional material was sampled from shelf regions of the Antarctic Peninsula, in the Drake Passage and Bransfield Strait (Fig. 2, Table 1).

Ecology

The type material of *Anobothrus konstantini* Säring & Bick sp. nov. (1 holotype, 6 paratypes) was collected from soft sediments at water depths between 415 and 755 m from the South-Eastern Weddell Sea. This region is characterized by a high to constant ice cover and low $_{bottom}$T (around -1.9°C, Säring *et al.* submitted: table 2; Schröder *et al.* 2016). The highest abundance was detected at one sampling site in the North Filchner Trough region (4 individuals per station), with low organic (TOC 0.2% ± 0.0) and the least fresh (Chl*a* = 0.06 µg g^{-1} ± 0.01) material on the seafloor. This sampling site is described by a low amount of silt & clay (43.4%) compared to the higher amount of sand (49.1%). The remaining material (3 paratypes) was found at sites with higher silt & clay (> 63.2%) and lower sand (< 33.7%) content, and low Chl*a* concentrations (< 0.19 µg g^{-1}). *Anobothrus konstantini* Säring & Bick sp. nov. occurs in a high variety of sediments, from fine mud to coarser sandy substrates in regions with low amount of fresh material on the seafloor.

The localities for the additional material sampled adjacent to the Antarctic Peninsula, Drake Passage (2 specimens) and Bransfield Strait (3 specimens), are known for no or a variable ice-cover and $_{bottom}T$ up to 0.5°C (Säring *et al.* submitted: table 2; Schröder *et al.* 2013). Nevertheless, these localities for the additional material show similar environmental conditions as the sampling sites of the type material: low Chl*a* concentrations (< 0.31 µg g^{-1}) and TOC content (< 0.7%), and highly variable sediment substrates (Table 1).

Following the classification of functional traits by Jumars *et al.* (2015), *A. konstantini* Säring & Bick sp. nov. is a hemi-sessile, tube-dwelling, subsurface deposit feeder.

Key to all species of **Anobothrus** *Levinsen, 1844*

The key accounts for the 23 species of *Anobothrus* Levinsen, 1844 considered valid, including the new species proposed here. It is modified after Bonifácio *et al.* (2015) and Alalykina & Polyakova (2020).

1. Paleae absent 2
– Paleae present 3

2. Notochaetae always without hirsute tips; with circular band on thoracic unciniger 2 .... ***A. apaleatus*** Hilbig, 2000
– Notochaetae of modified notopodia with hirsute tips; without circular band on thoracic unciniger 2 .... ***A. fimbriatus*** Imajima, Reuscher & Fiege, 2013

3. 3 pairs of branchiae in a transversal row, with or without gap 4
– 4 pairs of branchiae, one transversal row or anterior and posterior rows, with or without gap 9

4. Branchiae with wide median gap .... ***A. dayi*** Imajima, Reuscher & Fiege, 2013
– Branchiae without median gap 5

5. Segment 14 (thoracic unciniger 9) with elevated notopodia and notochaetae with hirsute tips .... ***A. flabelligerulus*** Imajima, Reuscher & Fiege, 2013
– Segment 13 (thoracic unciniger 8) with elevated notopodia and notochaetae without modification 6

6. Two intermediate segments; segment 6 (thoracic unciniger 1) with circular band .... ***A. auriculatus*** Alalykina & Polyakova, 2020
– One intermediate segment, segment 7 or 8 (thoracic unciniger 2 or 3) with circular band 7

7. Segment 8 (thoracic unciniger 3) with circular band .... ***A. jirkovi*** Alalykina & Polyakova, 2020
– Segment 7 (thoracic unciniger 2) with circular band 8

8. Segments 2 and 3 (thoracic chaetigers 1 and 2) fused; without ventral fold; notopodia on segment 3 present; segment 5 (thoracic chaetiger 4) with one nephridial papilla dorsally .... ***A. laubieri*** (Desbruyères, 1979)
– Segments 2 and 3 (thoracic chaetigers 1 and 2) fused; ventral fold with 8–12 rounded papillae; notopodia on segment 3 absent .... ***A. sonne*** Alalykina & Polyakova, 2020

9. 11 thoracic uncinigers 10
– 12 thoracic uncinigers 12

10. Segment 11 (thoracic unciniger 6) with modified notopodia; with eye spots ....
....***A. bimaculatus*** Fauchald, 1972
– Segment 12 (thoracic unciniger 7) with modified notopodia; without eye spots 11

11. Segment 6 (thoracic unciniger 1) with circular glandular band; notopodia with notochaetae present from segment 3 .... ***A. konstantini*** Säring & Bick sp. nov.
– Segment 6 (thoracic unciniger 1) without circular glandular band; segments 3 and 4 fused; notopodia and notochaetae on segment 3 absent ....***A. mancus*** Fauchald, 1972

12. Modified notopodia on segment 14 (thoracic unciniger 9, fourth-to-last thoracic segment) ....
....***A. paleatus*** Hilbig, 2000
– Modified notopodia on segment 13 (thoracic unciniger 8, fifth-to-last thoracic segment) 13

13. Segment 6, 7 or 8 (thoracic unciniger 1, 2 or 3) without circular band; presumably dorsally shifted notopodia on segment 8 (thoracic unciniger 3); paleae abruptly to delicate tapering ....
.... ***A. pseudoampherete*** Schüller, 2008
– Segment 6, 7 or 8 (thoracic unciniger 1, 2 or 3) with circular band 14

14. Segment 6 (thoracic unciniger 1) with circular band ....***A. patagonicus*** (Kinberg, 1867)
– Segment 7 or 8 (thoracic unciniger 2 or 3) with circular band 15

15. Segment 7 (thoracic unciniger 2) with circular band 16
– Segment 8 (thoracic unciniger 3) with circular band 17

16. Branchiae arranged in transversal row; two outermost branchial pairs reduced in diameter compared to inner branchial pairs and positioned close to each other; paleae colorless, fine and more slender than notochaetae ....***A. wilhelmi*** Schüller & Jirkov, 2013
– First three pairs of branchiae arranged in anterior transversal row, fourth pair of branchiae posteriorly shifted between the two outermost branchiae of the anterior row; all branchiae with the same diameter; paleae stout, reddish, wider than notochaetae ....
....***A. rubropaleatus*** Schüller & Jirkov, 2013

17. All notochaetae with hirsute tips ....***A. gracilis*** (Malmgren, 1866)
– Most notochaetae without hirsute tips; notochaetae of modified notopodia with or without hirsute tips 18

18. Modified notochaetae with hirsute tips 19
– Modified notochaetae without hirsute tips 21

19. 8–9 teeth on thoracic uncini in lateral view; diameter of all branchiophores almost same; paleae conspicuous, stout and long, originating from a prominent disc-like epidermal structure ....
....***A. paleaodiscus*** Schüller & Jirkov, 2013
– 5 teeth on thoracic uncini in lateral view; inner and middle or posteriorly shifted pair of branchiophores half as thick and / or shorter than others; without prominent disc-like epidermal structure 20

20. First three pairs of branchiae arranged in anterior transversal row, fourth pair of branchiae posteriorly shifted between innermost and middle branchiae of the anterior row, fourth pair of

branchiophores smaller and thinner than others and their branchiostyles several times shorter than others .... ***A. patersoni*** Jirkov, 2009

– First three pairs of branchiae arranged in anterior transversal row, fourth pair of branchiae posteriorly shifted between innermost and middle branchiae of the anterior row, inner and middle pairs of branchiophores ⅔ as long as and more slender than others ....***A. mironovi*** Jirkov, 2009

21. Segment 3 with notopodia and notochaetae; 16 thoracic chaetigers; surface of branchiostyles papillated; 4–5 teeth on thoracic uncini in lateral view ....***A. antarctica*** Monro, 1939

– Segment 3 without or with reduced notopodia and without notochaetae; 15 thoracic chaetigers; more than 6 teeth on thoracic uncini in lateral view 22

22. Segment 3 (thoracic chaetiger 2) without notopodia; surface of branchiostyle smooth; 6 teeth on thoracic uncini in lateral view .... ***A. glandularis*** (Hartmann-Schröder, 1965)

– Segment 3 (thoracic chaetiger 2) with reduced notopodia, without notochaetae; surface of inner branchiostyle with transversal ciliated ridges; 6–7 teeth on thoracic uncini in lateral view ....***A. amourouxi*** Bonifácio, Lavesque, Bachelet & Parapar, 2015

Discussion

Taxonomy

All specimens of *A. konstantini* Säring & Bick sp. nov. have 11 thoracic uncinigers starting at segment 6, two intermediate, and 10 abdominal segments. Only one individual has been observed with a neuropodium-like structure on segment 5 but without uncini (Fig. 3E). The reduced neuropodium was detected on both sides of this segment. All other characters were identical to the remaining eleven specimens. It is possible that these reduced neuropodia were an artefact, or that they were not visible in the other specimens due to poor conditions.

Additionally, three specimens with similar body shape and characters but with 12, instead of 11, thoracic uncinigers were found in the material studied but excluded here. These individuals have elevated notopodia with a dorsal ridge on the fifth-to last thoracic segment (thoracic unciniger 8) as it is described for *A. patagonicus*, but differ in the number of thoracic uncini: *Anobothrus patatgonicus* possesses up to 30 (Jirkov 2009) and the unidentified specimens 17–21. Due to poor conditions and damage to the anterior region we could neither verify a correct counting of segments nor a presence of a glandular band, or a fusion of segments 2 and 3. These specimens can be described elsewhere when more individuals in better quality are available.

Species of *Anobothrus* have one or several modifications on the fourth-, fifth-, or sixth-to-last thoracic chaetigers: elevated notopodia and / or glandular ridge between notopodia and / or modified notochaetae. *Anobothrus konstantini* Säring & Bick sp. nov. possesses these three characters on the fifth-to-last thoracic segment (segment 12, thoracic chaetiger 11, thoracic unciniger 7). Additionally, another glandular band was observed on segment 6 (thoracic chaetiger 5, thoracic unciniger 1) using ShirlastanA staining (Fig. 3D). This complete circular band on the anterior thorax of *Anobothrus* species is often not clearly visible (Jirkov 2009). Within *Anobothrus* this character is described as absent for *A. fimbriatus* Imajima, Reuscher & Fiege, 2013 and *A. dayi* Imajima, Reuscher & Fiege, 2013, and is not mentioned in the description for *A. mancus* and *A. pseudoampherete*. However, based on the illustration in Schüller (2008), a modification of the notopodia on segment 8 (thoracic unciniger 3) may be assumed for the latter species and possibly be a hint of a circular band. In the literature, this band was compared with those from *Melinnampharete*, *Eusamythella* and *Neosamytha* (Desbruyeres 1979; Holthe 1986). However, the band is developed as a dorsal ridge in *Melinnampharete*, *Eusamythella* and *Neosamytha*, while in *Anobothrus* it is completely circular (Jirkov 2009). Glandular pores of this band were found on the dorsal side using a scanning electron microscope (Fig. 6B).

SEM micrographs are important and commonly used to detect not only epidermal structures, like pores, but also other hard-to-see characters. It is especially useful for small specimens and individuals in poor condition. Only using SEM, two rows of notochaetae were found on all thoracic chaetigers except for segment 3 (thoracic chaetiger 2), an anterior row with 3 shorter and a posterior row with 4 longer chaetae. A similar arrangement of notochaetae has been described for other *Anobothrus* species, e.g., *A. amourouxi* and *A. wilhelmi* (Schüller & Jirkov 2013; Bonifácio *et al.* 2015).

A micro-computed tomography (micro-CT) scanner can also be a useful tool for studying morphological characters (Faulwetter *et al.* 2013); three-dimensional imaging could give a boost to the development of virtual specimen collections, allowing rapid and simultaneous access to accurate virtual representations of type material. This paper explores the potential of micro-computed tomography (X-ray micro-tomography). In contrast to SEM, the advantage of micro-CT is that the examination of material is fast and gentle, the samples remain undamaged and are available for further investigations (Paterson *et al.* 2014). Micro-CT scanning is becoming a more widely used technique for the identification of new species, e.g., within the Trichobranchidae (Parapar & Hutchings 2015; Parapar *et al.* 2016a, b), and Cossuridae (Parapar *et al.* 2018b). Within the Ampharetidae this technique has only been utilized to examine the internal anatomy of *Ampharete santillani* (Parapar *et al.* 2018a). We used micro-CT scanning to obtain a closer insight of the anterior end, and were able to describe the prostomium and the arrangement of the branchiae (compare Fig. 5A–D). These characters were not visible using SEM or light microscopy, due to the bad condition of the specimens. Furthermore, we observed small paleae on the outer edge of the semicircular arrangement of the paleae (compare Fig. 5B). We could not clarify the purpose of these small paleae, which differed in shape and size to the remaining paleae. One assumption may be a growing state, based on the place where new paleae are expected (Tilic *et al.* 2015). To increase the image quality and reduce the examination time we freeze-dried our sample and cut off the posterior part. Due to the low number of individuals and poor condition, we did not consider a second micro-CT scan for this study.

Terebelliformia, including Ampharetidae, is one of the most species-rich groups in Polychaeta, with around 1100 described species and a notable ecological and morphological diversity (Reuscher *et al.* 2012; Eilertsen *et al.* 2017; Horton *et al.* 2021).

In addition, currently generic relationships within the Ampharetidae and the relationships of species within a genus, such as in *Anobothrus*, have not yet been clarified (Reuscher *et al.* 2009). The morphological descriptions of *Anobothrus* species are challenging, due to the high variation of modifications and the presence of many morphologically similar, small-sized species. In recent years, genetic analysis has been a useful tool to identify many cryptic and pseudocryptic polychaete species and record a higher diversity than described by morphology alone (Nygren *et al.* 2018). In this study, we could not perform genetic analyses due to preservation in 4% formaldehyde solution. To still achieve a detailed and unambiguous description for quantitative aspects of this new species, we carried out a multidisciplinary approach: traditional light microscopy with methylene blue and ShirlastanA staining to identify macro-morphology (e.g., appendages, glands, ciliary bands), SEM to detect micro-morphology (e.g., gland pores, structure of chaetae and uncini), and micro-CT for internal structures and external characters (e.g., paleae, branchial arrangement).

Distribution and ecology

A total of twelve individuals was found from the sampled shelf regions (355–755 m depth), whereas seven belong to the type material of *Anobothrus konstantini* Säring & Bick sp. nov., from the South-

Eastern Weddell Sea (415–755 m depth). This region is known as a high Antarctic region with a high and constant ice cover, low $_{bottom}$T and low input of fresh material. The remaining 5 specimens (additional material) are reported from the shelf regions around the Antarctic Peninsula (Drake Passage, Bransfield Strait, 355–543 m depth), with none or variable ice-cover and higher $_{bottom}$T. However, the specimens from sampling sites around the Antarctic Peninsula and South-Eastern Weddell Sea showed only minor morphological differences. Based on current knowledge, most *Anobothrus* species are reported from the Pacific Ocean (14 species), six of which are known only from bathyal to hadal depths (Alalykina & Polyakova 2020; Imajima *et al.* 2013; Jirkov 2009). The most common and widespread species, *A. gracilis*, as well as *A. dayi*, *A. glandularis*, *A. flabelligerulus* Imajima, Reuscher & Fiege, 2013, *A. mancus* and *A. paleatus,* are found in shelf waters in the Pacific (Fauchald 1972; Hilbig *et al.* 2000; Jirkov 2009; Imajima *et al.* 2013), whereas *A. amourouxi* was described from the North Eastern Atlantic (Bonifácio *et al.* 2015). A total of five species of *Anobothrus*, including *A. konstantini* Säring & Bick sp. nov., are known from the Southern Ocean. *Anobothrus paleaodiscus* from East Antarctica, as well as *A. pseudoampharete* and *A. wilhelmi* from the Weddell Sea, seem to be distributed in bathyal-abyssal depths (1047–4720 m) (Schüller 2008; Schüller & Jirkov 2013), while *A. antarctica* is known from the circumantarctic water bodies (175–2060 m) (Jirkov 2009), and *A. konstantini* Säring & Bick sp. nov. so far only from the shelf region.

However, nothing is known about the habitat of the species of *Anobothrus* in terms of grain size or food availability parameters so far. We found no specimens of *A. konstantini* Säring & Bick sp. nov. at sites with higher fresh food input (Chl*a*) and organic carbon (TOC), such as in the northwestern Weddell Sea, or in predominantly silty sediments (Table 1). Only general functional traits of Ampharetidae are known from the literature (Jumars *et al.* 2015: supplemental table A). According to this information, all genera within the Ampharetidae are characterized as discretely motile, tube-dwelling, surface-deposit feeders that use their tentacles to feed on microorganisms and particles. Combined with information on its general functional traits, we can assume that *A. konstantini* Säring & Bick sp. nov. has a preferred habitat with lower silt and higher sand content in the sediment and a lower content of fresh detritus on the surface of the sediment in the Southern Ocean.

This study is part of a larger ecological study (Säring *et al.* submitted) with a set of different environmental parameters, in which 857 polychaetes from 31 families were collected. Thirty-nine specimens were identified as Ampharetidae (4.5%), twelve of which belong to *Anobothrus konstantini* Säring & Bick sp. nov. It seems that the Ampharetidae have a somewhat opposite distribution to that of other deposit feeders, such as Maldanidae and Paraonidae, which are mostly subsurface feeders and are very abundant in the North-Western Weddell Sea, whereas they are less abundant in the other four regions (Säring *et al.* in prep.).

Combining taxonomic studies with the quantitative description of environmental parameters and/or functional traits can contribute to a better understanding of species distribution and provide the basis for species distribution modeling (e.g., Meißner *et al.* 2014). Most species descriptions, especially for small invertebrates, only include information on depth range and geographic distribution. Describing a new species including quantitative information about its habitat, as we do here, allows quantitative relationship analysis and can be used to predict species distributions in hard-to-reach regions or for changing habitats such as those expected in the Southern Ocean (Jansen *et al.* 2018).

Acknowledgments

We acknowledge the crew of FS Polarstern and the lead scientists Julian Gutt (PS 81) and Michael Schröder (PS 96, both AWI) for the opportunity to take samples on board. Yasemin Bodur, Gritta Veit-Köhler (Senckenberg am Meer) and Dieter Piepenburg helped with logistics and sampling during the cruises. We thank Derya Seifert for sorting the samples. We are grateful to Stefan Scholz (Department of Zoology, Rostock University), who prepared the specimens for SEM and took the micrographs on the micro-CT. Frank Springer (Electron Microscopic Centre of the Medical Faculty, Rostock University) is thanked for assisting with the SEM. We thank Anna Dietrich (Institute for Applied Ecosytem Research, Broderstorf) for helping with the microscope photographs. Igor Jirkov (Lomonosov Moscow State University), Julio Parapar (University A Coruña, Spain) and Michael Reuscher (EcoAnalysts, Inc., Moscow, ID, USA) kindly helped with uncertainties about the genera. Also, comments by two anonymous reviewers and editing by the editors of the European Journal of Taxonomy improved this manuscript. The micro-CT machine (DFG INST 264/130-1 FUGG) was jointly sponsored by the German Research Foundation (DFG) and the Land Mecklenburg-Vorpommern. This present work was funded by DFG SPP 1158 Antarctic Research Grants (LI 2313/6-1 and VE 260/10-1). Support was given by the Alfred Wegener Institute, Helmholtz-Centre for Polar and Marine Research (Polarstern cruise grants AWI_PS81_03, AWI_PS96_02).

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WoRMS Editorial Board 2021. World Register of Marine Species. https://doi.org/10.14284/170

Manuscript received: 16 August 2021
Manuscript accepted: 29 November 2021
Published on: 1 February 2022
Topic editor: Tony Robillard
Desk editor: Eva-Maria Levermann

Chapter III

Declaration of author contributions:

Bioregions cannot reflect polychaete community distribution (taxonomic and functional groups) on the Weddell Sea Shelf (Southern Ocean, Antarctic)

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This chapter was submitted to the journal *Progress in Oceanography's* special issue *Negative Results in Oceanography* as:

Weith F., Jerosch K., Pehlke H., Bick A., Behrend B., Veit-Köhler G., Link H. (submitted): Bioregions cannot reflect polychaete community distribution (taxonomic and functional groups) on the Weddell Sea Shelf (Southern Ocean, Antarctic). *Progress in Oceanography*.

Friederike Weith conceived the study, collected samples and performed laboratory work for analyzing polychaetes, sediment and water column samples. Friederike Weith processed and analyzed the data.

Kerstin Jerosch co-conceived the study, supervised the initial bioinformatic analysis, came up with essential ideas regarding the analysis of bioregionalization approaches.

Heike Link co-conceived the study, acquired and provided funding, collected samples and helped with the identification of polychaetes and pigment analysis and reviewed the statistical results.

Hendrik Pehlke supported the initial bioinformatic analysis and provided statistical and general coding support, performed the code review, and drafted parts of the manuscript.

Andreas Bick supported and guided the identification of polychaetes.

Ben Behrend collected samples, supported the polychaete identification and pigment analysis for four sites (PS118).

Gritta Veit-Köhler collected samples, acquired and provided funding.

Friederike Weith, Kerstin Jerosch, Hendrik Pehlke, Heike Link discussed the data and results.

Friederike Weith drafted the manuscript, Kerstin Jerosch, Hendrik Pehlke and Heike Link critically commented on the manuscript and redrafted parts of it. All other authors commented critically on the manuscript.

Friederike Weith's contribution to the written manuscript was ~80%.

ABSTRACT

The environment at the Antarctic Peninsula (AP) and the Weddell Sea (WS) is increasingly affected by climate change. To establish conservation strategies and forecast benthic communities under changing environmental conditions for these regions, it is essential to understand the benthic community composition and distribution and their relationships to abiotic drivers. In such remote biological data are limited due to accessibility constraints. Therefore, the use of environmental surrogates to forecast faunal distribution is an attractive tool. An important and dominant group in soft-bottom ecosystems are polychaetes with their high diversity of functional groups. However, knowledge about their distribution patterns and ecological drivers in the Southern Ocean is scarce. In this study, we linked polychaete communities (taxonomic and functional groups) in the extended region of the WS (AP: Drake Passage, Bransfield Strait, northwestern WS; eastern WS: Filchner Trough region, depth ~500 m) at 16 sampling sites to ice-cover regimes and benthic food situation. We considered data of fauna and sediment samples (grain size, total organic carbon (TOC), total nitrogen, pigment content) from three expeditions with the RV *Polarstern* (PS81, PS118: AP; PS96: FT), water-column data (temperature, salinity, chlorophyll a) from water samples and CTD recordings, as well as sea-ice cover data (2010–2019) extracted from remote sensing data. We further attempted to predict polychaete communities and functional group distribution based on bioregionalization using 9 environmental spatial surrogates (depth, distance to coast, broad-scale bathymetric position index, temperature, speed, median and standard deviation of the 10-year ice cover, TOC, sand). Using the cluster analysis (group average) based on relative abundance we found 6 taxonomic and 5 functional polychaete community types composed of a total of 34 families and 14 functional groups, respectively. Ice-cover variation and TOC were best suitable to explain the variation of the community composition by > 39%, with a stronger relationship to functional than to taxonomic communities. Although the four bioregions defined by *k*-means cluster algorithm reflected neither the complex distribution patterns of the taxonomic nor of the functional communities, we could highlight potentially vulnerable areas throughout the extended WS such as the FT region with heterogenous community compositions. Low fauna-sample densities compared to vast survey areas were limiting factors to run reliable models combining biological and physical information. Our findings underscore the relevance of filling spatial gaps of infauna sampling and environmental data to apply advanced models (e.g. Species Archetype Models), in order to specify reliable conservation strategies for vulnerable areas.

1. INTRODUCTION

Although infauna (organisms living inside soft sediments) play an essential role for carbon and nutrient cycling at the seafloor (Bouchet 2006, Schratzberger & Ingels 2017), for the Southern Ocean (SO) only a few studies focused on these highly abundant organisms (Hauquier et al. 2015, Säring et al. 2022). Highly variable seasonal sea-ice cover, primary production, sedimentation processes, trophic factors and hydrodynamics (Cook et al. 2005) lead to a significant spatial heterogeneity of habitats with adapted benthic communities in the SO (Clarke & Crame 1992). For the Weddell Sea (WS, extending geographic ranges including AP: Drake Passage, Bransfield Strait, northwestern WS, and FT region), so far it is only known that sea-ice cover along with food availability at the seafloor are important environmental drivers for structuring infauna shelf communities (Säring et al. 2022). Over the years, considerable progress has been made in understanding the distribution and ecological role of epifauna in coastal shallow waters and shelf regions of the SO (WS: Gutt et al. 2019, 2016; Pineda-Metz et al. 2019; East Antarctic: Post et al. 2011, 2017, Cummings et al. 2018, Jansen et al. 2018a, 2018b), whereas the distribution of smaller-bodied infauna communities is less explored in the WS with a few exceptions (e.g. Säring et al. 2022, Veit-Köhler et al. 2018).

Benthic communities of macrofauna (> 500 µm) living in the sediment show a variety of life strategies and distributions (Ingels et al. 2012) and could be sensitive to environmental changes (Peck et al. 2010, Griffiths et al. 2017). The need for sustainable conservation strategies to preserve the vulnerable and unique ecosystem has been reinforced, as the biodiversity of the SO is under increasing pressure due to the direct and indirect effects of climate change, human activities and altering habitat conditions (Peck 2005, Peck et al. 2010, Constable et al. 2014, 2017, Griffiths et al. 2017, Meredith et al. 2019, IPCC 2022). In order to provide scientific guidance for protecting the infaunal biodiversity and managing the living components in this dynamic and sensitive benthic ecosystem, it is essential to understand and assess the spatial distribution patterns of infauna species, communities, and their functions in relation to their variable environmental situations. Indeed, this aim requires investigations on larger spatial and temporal scales as suggested for the Antarctic benthic biodiversity (e.g. Gutt et al. 2012, Cummings et al. 2018).

Across geographic latitudes and longitudes, the climatic, topographic and physical conditions shape different habitat types, which are favored by different organisms. Therefore, bioregionalization approaches can characterize the distribution of communities (Jansen et al. 2018a) or ecosystems in a broader spatial context. For instance, Spalding et al. (2007) provided a comprehensive regionalization of the world's ocean shelves with 232 ecoregions, based on known and probable relationships among environmental drivers, biogeographic patterns and ecology of taxa (e.g. dispersal strategy, life history). Further, bioregionalization has been applied to map the distribution of myctophid fish in the Indian Sector of the SO (Koubbi et al. 2011). Geographic regions are divided into smaller and distinct so-called "bioregions" by integrating a variety of abiotic information, such as physical (e.g. temperature, salinity, sea-ice cover) and geomorphological (e.g. sediment structure), which are related to biotic (e.g. faunal occurrence) information. Each bioregion exhibits a homogeneous and predictable set of ecosystem properties reflecting the natural clustering of biotic and abiotic conditions (Leathwick et al. 2003). Habitat suitability approaches and predictive methods, as part of bioregionalization, have become increasingly useful over the last years to overcome the patchiness of information on species distribution, complex communities, and specific habitats. This is particularly relevant for hard-to-reach regions as the SO shelves, where long-term monitoring is often impeded by extreme and variable environmental conditions, such as weather, currents and sea-ice cover (Griffiths et al. 2011). Using environmental surrogates for potential species occurrence is attractive because physical data, measured by remote sensing (e.g. satellite sea-ice coverage) or modeled raster data (e.g. Broad benthic terrain index or speed), may be available or can be obtained at low costs (Grant et al. 2006, Harris & Whiteway 2009, Post et al. 2011). Clustering algorithms have been determined as a suitable tool for the analysis of bioregions, because they are feasible to use a large number of variables to subdivide a region into subsets based on dissimilarity metrics. Previous studies subdivided the SO into 5 and 3 subregions based on ice and nutrient dynamics (Tréguer & Jacques 1992) and large-scale frontal properties of the Antarctic circumpolar current (ACC) (Orsi et al. 1995), respectively. More recently, Douglass et al. (2014) integrated information about the environment (depth, seafloor temperature, sea-ice cover, productivity, ocean currents, geomorphology) and biographic patterns of benthic organisms (e.g. dispersal barriers, distribution with depth) in their analysis and identified 562 distinct environmental types in the SO. Jerosch et al. (2016) showed a highly diverse environment for a smaller geographic scale in the WS using seafloor characteristics. Nevertheless, none of these studies included any infauna data. The first study classifying habitats of infauna communities in the WS was presented by Säring et al. (2022). And they were the first to use sea-ice data as ecological classification measure for infauna showing that differences in community composition matched the ice-cover classification of five different regions.

Within the infauna, polychaetes represent a specious and the numerically dominant macrofauna taxon, occurring even in habitats in the WS, where other infauna taxa are sparse (Gerdes et al. 1992, Piepenburg et al. 2002, Hilbig et al. 2006, Säring et al. 2022). Hence, they likely reflect the abundance and distribution patterns of infauna communities more closely than other major macrofauna taxa such as molluscs or crustaceans (e.g. Olsgard & Somerfield 2000). Polychaetes cover a variety of different functional traits, including different trophic levels and feeding types (e.g. filter and deposit feeders) with sedentary mobile as well as tube-building sessile species (Fauchald & Jumars 1979, Jumars et al. 2015b, PolytraitsTeam 2023). However, our current knowledge on interactions between polychaete communities and their environment in the SO is poor. This information is needed to improve our understanding on the distribution patterns of polychaete communities in the extended WS region.

The use of meaningful surrogates that provide detailed information to predict distribution patterns and potential biodiversity of benthic fauna (Olsgard et al. 2003, Chaabani et al. 2019) has become a central part in ecosystem monitoring (Olsgard & Somerfield 2000) and conservation planning (Giangrande et al. 2005), even in the absence of detailed faunal sampling and analysis. In this study, we used the higher taxonomic level family and functional groups (feeding, motility, movement type) to describe polychaete communities. Grouping organisms by their functional traits is time-saving and opens possibilities to assess biodiversity in different aspects, including community structure, function and response to environmental change (Sunday et al. 2015). Functional groups provide information according to the ecological role of the organisms, including morphological, behavioral and reproductive characteristics as well as life history traits (Beauchard et al. 2017; for polychaetes see PolytraitsTeam 2023). Different taxa can have identical functional traits with similar responses to the environment (Usseglio-Polatera et al. 2000) and are therefore assigned to the same functional group. In the SO, functional traits associated with motility and feeding strategies were mentioned as main factors determining distribution of epibenthic organisms. In previous studies the Antarctic benthos has been classified as sessile suspension feeders and mobile deposit feeders (Gutt et al. 2016, Jansen et al. 2018b). These functional groups, however, were classified quite generally, focusing on epifauna rather than on infauna. A higher resolution of functional traits focusing on infauna could provide details on the relationship between sediment-dwelling communities and their environment in the SO. Although the integrated analysis of taxonomic and functional information contributes to a holistic understanding of the infauna biodiversity, this approach has not been applied for infauna communities (e.g. polychaetes) in the WS. Therefore, the overarching aim is to provide the first study using taxonomic and functional surrogates to understand the relationship between polychaete communities and their environmental drivers in the extended WS including the attempt to predict community distribution based on bioregionalization. This study addresses the following questions in two main regions of the WS (extended geographic ranges), the Antarctic Peninsula (AP) and the Filchner Trough (FT):

1.) What are patterns in polychaete community distribution in Weddell Sea?
2.) Which environmental parameters drive the taxonomic and functional polychaete community distribution in the Weddell Sea?
3.) Can we identify the potential habitats for the different polychaete communities by using bioregionalization approaches in the study area?

2. MATERIAL AND METHODS

2.1 Study Area

Sediment and water-column samples from 29 stations (st.) were collected during three expeditions with RV *Polarstern*: PS81, PS96, PS118 (summer seasons 2013, 2016, 2019) to the tip of the AP (Drake Passage, Bransfield Strait, northwestern WS) and the FT region in the southeastern WS (Figures 1, 2, Table 1; Gutt 2013, Schröder 2016, Dorschel 2019). Water depth at the sampled stations ranged from 350 to 755 m. Polychaete fauna was analyzed for 16 of the above stations (Table 1). In the following, the regions will be abbreviated by using their initials [Antarctic Peninsula (AP) including DP = Drake Passage (st. 235, 241), BS = Bransfield Strait (st. 217, 225), NW-WS = northwestern Weddell Sea (st. 6, 8, 38, 120, 163, 190); Filchner Trough region = FT (st. 17, 26, 37, 48, 61, 72)]. Sediment and water-column samples of the remaining 13 st. were used for the bioregionalization approach (Table S1).

For the bioregionalization, we defined the AP study area with an extent from 52° to 63° W and from 60° to 65° S, and the FT study area with an extent from 25° to 45° W and from 73° to 78° S. Both study areas are located on the continental shelf with an average water depth of ~500 m. Areas were chosen related to the availability of environmental data (grain size, total organic carbon).

2.2 Sampling procedure during the expeditions

Water-column samples for pigment analysis and oceanographic measurements (conductivity, temperature, and depth) were done at all investigated stations from PS81, PS96 and PS118 by using the seabird (SeaBird SBE19 plus) rosette (Table 1, Schröder et al. 2013a, 2016a, Janout et al. 2020). Sediment sampling sites representative for each area were determined on the basis of Ocean Floor Observation System survey and bathymetry prior to the multicorer (MUC) deployments. One to five MUC deployments were carried out at each station (Table 1). Data on sediment (pigment content, organic matter, grain size) and water-column ($_{Cmax}$Chl*a* at the chlorophyll a maximum, $_{bottom}$Chl*a* near the sea bottom) parameters and the respective sampling procedures for PS81 and PS96 have been published by Veit-Köhler et al. (2018) and Säring et al. (2022), respectively. Data for PS118 is published here, and was obtained following the same protocol as mentioned for PS96 (Säring et al. 2022). St. 115 (PS96, Säring et al. 2021b) is regarded as a replicate of st. 190 (PS81) due to geographic proximity. Therefore, averaged sediment data (pigments, organic matter, grain size) of st. 115 could be used for st. 190 (where these data were lacking) whereas fauna and water-column data were collected from st. 190 directly (PS81, Vanreusel et al. 2021b, Weith et al. in review b).

2.3 Polychaeta sample processing and identification

Sediment samples from 16 sampling sites of PS81, PS96 and PS118 that were used for faunal analysis were processed as described by Säring et al. (2022). Polychaetes (> 500 µm) were sorted with stereo microscopes Leica Mz 12.5 and Carl Zeiss Stemi 2000, and classified to family level using several identification keys: six identification guides: Hartman (1964, 1976, 1994), Fauchald and Jumars (1979), Pettibone (1982), Hartmann-Schröder (1996) and Hayward & Ryland (2017). Polychaete families were assigned to functional groups distinguishing between feeding type (F = suspension feeder, S = surface deposit feeder, Sb = subsurface deposit feeder, P = predator, O = omnivore), motility (S = sessile or none, D = discretely motile, M = motile), and movement (Se = sessile, B = burrowing, C = crawling) according to (Fauchald & Jumars 1979, Jumars et al. 2015, PolytraitsTeam 2023). For detailed information see the supplement (Table S1). We counted the total number of individuals per identified taxon from the top to the bottom of each core (mean: 0.23 m).

2.4 Environmental point data: origin, sampling and measurements

Fifteen parameters analyzed from the expeditions and two ice-cover parameters (Table 2) were used for testing the relationship of polychaete community distribution to environmental patterns. Total organic carbon (TOC) and percent of sand in the sediment were used to update the corresponding environmental spatial raster data (see below). For details on sediment and water-column measurement methods and data see Table 2. For PS118, parameters were measured as described for PS96 (Säring et al. 2022). Abbreviations of environmental parameters are listed in Table 2.

2.5 Spatial environmental parameters and data

We compiled and produced spatial data for 9 parameters listed in Table 3. These raster data were later used for bioregionalization attempts. Parameters derived for bioregionalization (raster data) carry the suffix "_s" (e.g. Depth_s) throughout the manuscript.

The spatial data used on sediment texture Sand_s and TOC_s were processed in this study by updating existing data sets (Table 3) of first sediment layers of the core data (Sand: 0–1 cm, TOC: 0–1 cm) and carried out with the Geostatistical Analyst of ArcGIS (10.7.1) (ESRI). We supplemented the TOC data set (Seiter et al. 2004b) published by Seiter et al. (2004b) and the data set for sediment texture (Jerosch et al. 2015) published by Jerosch et al. (2016) with recently measured data from the st. listed in Tables 1 and S1 (Säring et al. 2021b, Vanreusel et al. 2021, Weith et al. in review c) in the AP and FT regions. Both, AP and FT, are located in soft bottom areas (Jerosch et al. 2016). Since the sediment texture "Sand" negatively correlates with "Silt and Clay", we only included one of the two spatial layers, namely Sand_s in the bioregionalization analysis.

For the AP region, we applied inverse distance squared weighted method (IDW) to interpolate the sand sample data, giving greater weight to points closest to the prediction location (10 max., 5 min. neighbors with a minimized root mean square prediction error (RMSPE) of 22.89). For the FT region, the method Bayesian Kriging (BK) provided the best results (15 max., 10 min. neighbors, RMS: 20.61, standardized RMS of 0.99). BK is a geostatistical interpolation method automatically accounting for the error introduced by estimating the underlying semivariogram (Krivoruchko 2012). The interpolations were calculated with data projected in UTM21 and UTM26 coordinates, for AP and FT, respectively.

Due to the data distribution, we kept all data in one data set and applied Bayesian Kriging for an area that included AP and FT (with 15 max., 10 min. neighbors resulting in a RMS: 0.45 and a standardized RMS of 0.94. The areas of FT and AP were cut by masks in a last step. The maps are visualized in Polar Stereographic WGS84 projection (Figure S1).

2.5.1 Sea-ice data

The information on sea-ice concentration that we use is calculated from daily sea-ice concentration data provided by the University of Bremen: https://www.meereisportal.de (Grosfeld et al. 2016).

The University of Bremen retrieves the sea-ice cover data with the ARTIST Sea Ice (ASI) algorithm (Spreen et al. 2008) which is applied to microwave radiometer data of the sensors AMSR-E 89 (Advanced Microwave Scanning Radiometer for EOS) on the National Aeronautics and Space Administration (NASA) satellite Aqua from 2002 to 2011, and AMSR2-GCOM_W1 (Advanced Microwave Scanning Radiometer 2) on the Japan Aerospace Exploration Agency (JAXA) satellite GCOM-W1 (Melsheimer 2019) since 2012 (data available as of 2013).

The sea-ice cover data of one calendar day are resampled (gridded) into 6.25 km x 6.25 km and 3.125 km x 3.125 km grid spacing using the NSIDC Sea Ice Polar Stereographic South projection (EPSG:3412) for the Antarctic grid (Spreen et al. 2008, Ludwig et al. 2019, Melsheimer 2019).

We downloaded the geoTiff format and used these data to express two sea-ice cover values (%) for each station (median for 10 years: Median-10-year-ice, standard deviation for 10 years: SD-10-year-ice) and each region (median for 10 years: Median-10-year-ice_s, standard deviation for 10 years: SD-10-year-ice_s). The data download and processing was applied in R version 4.1.1 (full list of packages used and scripts are listed in the Table S10, S11).

2.6 Statistical analysis

Oceanographic, biological water-column, sediment and sea-ice point data (Table 2) were considered to analyze the relation between the distribution of polychaete communities and environmental parameters using statistical tests (abbreviations in Table 2). Sediment data from 0–1 cm sediment depth were used for pigments, TOC and total nitrogen (TN), and were averaged from 0–5 cm sediment depth for C/N_{molar} and grain size parameters. The data were normalized and visualized as Draftsman plots. Phaeo, CPE, Chl*a*/Phaeo, TN, Silt & Clay, $_{bottom}T$ were left out due to their correlation (Spearman correlation $R > 0.8$) with other parameters (CPE and Chl*a*: $R = 0.88$, Chl*a*/CPE and Chl*a*: $R = 0.91$, Phaeo and Chl*a*: $R = 0.82$, Chl*a*/Phaeo and Chl*a*/CPE: $R = 0.99$: Sand and Silt & Clay: $R = -0.99$, TN and TOC: $R = 0.96$, and $_{bottom}T$ and Median-10-year-ice: $R = 0.81$). Remaining parameters (Chl*a*, Chl*a*/CPE, TOC, C/N_{molar}, $_{Cmax}$Chl*a*, $_{bottom}$Chl*a*, Depth, Sand, Coarse Sand, Median-10-year-ice, SD-10-year-ice) were included in the final point data set. The resemblance matrix for the environmental data set was based on Euclidean distances.

We used average abundances for each (a) taxonomic (family level) or (b) functional group per station for the analysis. Abundance was calculated as individuals per 100 cm^2. Biodiversity indexes (species richness *S*, Shannon-Wiener index *H'*, species evenness *J'*, Simpson index λ) were calculated in PRIMER v7 (Clarke et al. 2014).

Bray-Curtis similarity of polychaete community data was applied as resemblance measure for all matrices. Similarities between communities (taxonomic and functional groups) were visualized with non-metric multidimensional scaling (nMDS) (Question 1). A hierarchical cluster analysis (average-group, similarity 50%) was chosen to differentiate the (a) taxonomic and (b) functional communities and define groups of stations with the same community type. We used SIMPER analysis to determine the mean similarity within-group clusters, to calculate the dissimilarity between-group clusters, and to identify which (a) taxonomic or (b) functional groups contribute most to them.

We tested the influence of environmental parameters on the polychaete community distribution (Question 2) by distance-based linear models (DistLM). For the determination of faunal communities, the similarity matrices described above were applied for (a) taxonomic and (b) functional groups. The environmental data were normalized. On the basis of the AIC_C criterion which performs particularly well with small numbers of samples (*N*) compared with the number of predictors (*n*; $N/v < 40$, v = number of parameters in the model), together with the highest R^2 value, the best model solution for the prediction parameters was selected (Anderson et al. 2008). For the best model determined by this procedure, we conducted sequential tests based on adj. R^2 to identify the amount of variation explained by the retained environmental parameters. The best models for (a) taxonomic and (b) functional groups of the polychaete communities were visualized by distance-based redundancy analysis (dbRDA graphs). All multivariate analyses were carried out with PRIMER v7 and the PERMANOVA$^+$ add-on package (Anderson et al. 2008, Clarke et al. 2014).

2.7 Bioregionalization

2.7.1 Model parameter selection

In total 9 environmental parameters from different sources presented as raster grids were compiled for the bioregionalization approach (Table 3). The data were standardized (variance from 0 to 1). To eliminate irrelevant and redundant input data, a stepwise pre-selection was done on the basis of different statistical and variable selection algorithms. The pre-processing improves the model performance by only including effective parameters, leading to a faster performance and to a more comprehensible model. No parameter was detected with a zero variance and near zero variance. No collinearity between the 9 environmental parameters was observed using the Spearman rank correlation ($R > 0.8$) and the variance inflation factor ($VIF > 10$) (Akinwande et al. 2015), hence all 9 parameters were included within the bioregionalization approach.

2.7.2 Clustering

Given the large number of values to be clustered (9 raster datasets per study area AP and FT consisting of 17850 and 17969 cells, respectively), the non-hierarchical clustering method *k*-means was applied with *k*-means of R version 4.1.1 (R Core Team 2022). The complete list of packages used in R and their associated sources can be found in Table S10, S11. In the present work, the *k*-means function of the R package stats version 4.3.0 (R Core Team 2022) was applied. The clustering was calculated with the algorithm of Hartigan and Wong (1979). This *k*-means function requires the optimal number of clusters (k) as an input. This minimizes the multivariate intra-cluster dissimilarity and optimizes the internal homogeneity and must be detected in advance of the clustering. The R package *NbClus*t version 3.0.1 (Charrad et al. 2014) was applied for 21 different indices to determine the best *k*-means clustering scheme from different results for the study area. The *k*-means algorithm sorts all objects to one of the cluster centers (centroids, cluster means), by either randomly selecting or specifying the first set of centers. The goal is to minimize the multivariate intra-cluster dissimilarity, here the intra-region dissimilarity. Then the means of the resulting clusters are calculated and the clusters are recalculated with the same settings. An iterative process achieves the settings for *k*, when preferably no further differences between the cluster centers exist and the *convergence* is reached (Kaufman & Rousseeuw 2009, Greenacre & Primicerio 2014). The identification of the optimal *k* thus is the balance between the maximum of the compressed data provided by a single cluster and the maximum precision given by having all data points assigned their own cluster. The resulting cluster id numbers were assigned to the raster cells and the raster data sets projected (Polar Stereographic WGS84).

We tested for significant differences between the bioregions on the basis of spatial environmental parameters for each (Depth_s, BPI_s, Dist_coast_s, Median-10-year-ice_s, SD-10-year-ice_s, $_{bottom}$T_s, Speed_s, TOC_s, Sand_s). Because of the multiple testing, a Bonferroni correction (Holm 1979) (p-value $< 0.05/n$, n = number of parameters) was carried out, hence a threshold alpha of $p < 0.006$ was applied for main tests. We used the the R package *rstatix* version 4.1.1 (Kassambara 2022) to apply the Kruskal-Wallis test on ranks and the pairwise multiple comparison procedure of Dunn's method for all parameters, as the data failed to meet the assumptions of normality and homogeneity of variance for the one-way analysis of variance (ANOVA, factor "bioregions", 2 or 4 levels). Box plots were used to visualize the spatial environmental parameters in each bioregion.

Differences in polychaete communities (variable: abundance of the taxonomic or functional groups) among the different habitat clusters provided by bioregionalization were analyzed using one-way ANOSIM (9999 permutations) to test if the visual comparison of the spatial distribution of bioregions and fauna clusters can be statistically represented.

3. RESULTS

3.1 Environmental conditions in the study area

Our study area (extended Weddell Sea) comprises the shelf areas around the tip of the Antarctic Peninsula (AP) and the southeastern Weddell Sea (FT) with different environmental conditions (Figures 3, 4). Based on the environmental point data cited in the methods, AP was previously distinguished into three regions (DP, BS, NW-WS) and FT in a further two regions based mainly on their ice-cover patterns. These five regions differed in the environmental parameters at the seafloor, with, e.g. highest pigment content in the NW-WS and lowest in the two FT regions (Säring et al. 2022). Compared to Säring et al. (2022), we included additional sampling sites (PS81, 2013, st.: 190; PS96, 2016, st.: 115; PS118, 2019, st.: 6, 8, 38) located in the NW-WS in this study (Figures 1, 2). As described in the material and methods section, st. 115 (PS96, Säring et al. 2021b) is treated as a replicate of st. 190 (PS81), in terms of sediment data. According to the duration and fluctuation of the sea-ice cover from December to February between 2010–2019 st. 8 and 38 showed similar seasonal ice-cover patterns as the other stations in the NW-WS (120, 163), whereas st. 6 experienced a constant sea-ice cover similar to stations in the FT region (Säring et al. 2022). These four additional stations were observed with a lower Chl*a* content, but with a similar Phaeo content compared to the remaining stations in the NW-WS, indicating high degradation rates of the fresh material. Stations 6, 8 and 38 (PS118) revealed high TOC values similar to the remaining NW-WS stations, whereas st. 115 (PS96) was described with a lower TOC content at the seafloor which was similar to sites in the FT region (Säring et al. 2021b, Weith et al. in review c).

3.2 Identification of bioregions in the Weddell Sea

At least 2 clusters are needed to describe environmental bioregions (B) based on the nine spatial parameters for the survey areas (Figure S4, Table S6), represented as the 2-bioregion option (${}_{2}$B). A more precise picture is presented with 4 clusters, as the 4-bioregion option (${}_{4}$B). The optimal number of clusters relies on the methods for identifying similarities and on the parameters for cluster partitioning, when using the function KMEANS in the R package *fdm2id* version 0.9.8 (Blansché 2022) for the *k*-means clustering. It is therefore necessary to validate clusters regarding to the overall research aim, as in our case here: "how to best cluster regions to possibly reflect the polychaete distribution patterns?". The visual inspection of the ${}_{2}$B and ${}_{4}$B options (Figures 7, S5) displayed spatial differences between the AP and FT regions, but no difference between ${}_{2}$B1 and ${}_{4}$B3 in the AP region. ${}_{2}$B1 and ${}_{4}$B2–${}_{4}$B3 cover almost the same area in the AP and FT region, whereas ${}_{2}$B2 covers the areas as ${}_{4}$B1 and ${}_{4}$B4 (Figures 7, S5). The ${}_{4}$B- option was chosen as the optimum number of clusters to reflect distribution patterns of the polychaete community in the AP and FT region as it represents more distinct habitats without showing a patchy pattern. For further information of the ${}_{2}$B- option, refer to the electronic supplement (Figures S5, S6, S8, Table S2).

Applying 4 clusters, only bioregions ${}_{4}$B3 and ${}_{4}$B4 were observed in both regions, whereas bioregion ${}_{4}$B1 and ${}_{4}$B2 only occurred in AP and FT, respectively (neglecting the minor contribution of ${}_{4}$B1 in the FT region). The spatial delineation of the bioregions ${}_{4}$B1–4 is reflected by the spatial ice-cover parameters Median-10-year-ice_s, SD-10-year-ice_s (Figure 7). Among ${}_{4}$B1–4, significant differences were found for Depth_s, ${}_{bottom}$T_s, Median-10-year-ice_s, Sand_s, and Speed_s (Figure S7, Table S3).

3.3 Taxonomic and functional polychaeta community compositions in different regions in the Weddell Sea

3.3.1 Recorded taxa and functional groups

A total of 1,605 polychaetes belonging to 34 families were counted in the sediment samples for fauna analysis (data available from PANGAEA: Weith et al. in review c). Paraonidae were the dominant family over all samples (9.1 ind. per 100 cm^2), followed by Cirratulidae (8.4 ind. per 100 cm^2), Hesionidae (5.2 ind. per 100 cm^2), Opheliidae (3.9 ind. per 100 cm^2) and Maldanidae (2.4 ind. per 100 cm^2). Other polychaete families found are listed in descending order of abundance: Lumbrineridae, Spionidae, Syllidae, Ampharetidae, Onuphidae, Glyceridae, Dorvilleidae, Sternaspidae, Sabellidae, Scalibregmatidae, Nephtyidae, Sphaerodoridae, Orbiniidae, Polynoidae, Terebellidae, Phyllodocidae, Flabelligeridae, Amphinomidae, Acrocirridae, Oweniidae, Capitellidae, Trichobranchidae, Nereididae, Chaetopteridae, Pisionidae, Pilargidae, Oenonidae, Nerillidae and Pectinariidae

Furthermore, the families were classified into 14 functional groups based on their feeding, motility and movement type (Table S1, Box 1). The dominant functional group over all samples was motile borrowing subsurface deposit feeding (SbMB; 14.6 ind. per 100 cm^2), followed by motile burrowing surface deposit feeding SMB (8.7 ind. per 100 cm^2), crawling motile predators PMC (6.1 ind. per 100 cm^2), burrowing discretely motile subsurface deposit feeding (SbDB) and crawling motile omnivore OMC (both 2.4 ind. per 100 cm^2). The other functional groups are listed in descending order: PMB, SDB, SDSe, ODC, PDB, FNSe, SbDC, SbMC, and SMC. The functional groups SbMB and PMC included the highest number of families (5, SbMB: paraonids, opheliids, orbiniids, sternaspids, scalibregmatids; PMC: hesonids, nephtyids, phyllodocids, polynoids, oenonids), followed by OMC and PMB including four and three families, respectively.

3.3.2 Regional polychaete community composition

The highest polychaete abundances occurred in the NW-WS: st. 8 showed the highest abundances (160.6 ind. per 100 cm^2), followed by st. 38, 190 and 163 (125.4, 86.5 and 61.5 ind. per 100 cm^2, respectively). The lowest polychaete abundances were observed for the two deepest (608.2–755.1 m) sampling sites located in the FT region (st. 17, 72 both with 11.5 ind. per 100 cm^2).

Cirratulids were dominant in the southern sampling sites in the NW-WS (st. 6 and 8 with 16 and 43.1 ind. per 100 cm^2, respectively), whereas paraonids showed an opposite pattern with higher abundance in the northern sampling sites (st. 120, 38 and 190 with 18.7, 39.1 and 32.2 ind. per 100 cm^2, respectively; Figure 1). Stations 38, 8, 120 and 6 were observed with the highest opheliid abundance (21.1, 19.1, 12 and 7.6 ind. per 100 cm^2, respectively) over all sampling sites (Figure 1). Stations. 6 and 120 differ from the previously described NW-WS sites with lower abundances (38 ind. per 100 cm^2 and 46.6 ind. per 100 cm^2, respectively) and less taxonomic groups of polychaetes (9 and 7, respectively). In the BS, ampharetids showed the highest abundance (st. 217 and 225 with 4.8 and 3.4 ind. per 100 cm^2, respectively) across all sampling sites. Sternaspids and onuphids were dominant groups in the BS st. 225 (4.8 and 3.8 ind. per 100 cm^2, respectively) and the DP st. 235 (4.3 and 3.8 ind. per 100 cm^2, respectively) but showed low abundances in the NW-WS and were not observed in the FT region. The taxonomic polychaete community composition for st. 241 was dominated by cirratulids (7 ind. per 100 cm^2), paraonids (5.4 ind. per 100 cm^2), onuphids (2.7 ind. per 100 cm^2), syllids and sabellids (both with 3.5 ind. per 100 cm^2). Sabellids were only found in the DP, BS and some sampling sites in the FT region (st. 37, 17, 26), but were not detected in the NW-WS. DP st. showed high taxonomic diversity in the area (235: 16 families, 241: 18 families).

The cluster analysis of the polychaete communities on the basis of taxonomic groups revealed six clusters ($_{Tax}$A–$_{Tax}$F) at a similarity of 50% (Figures 5, S2). In the SIMPER analysis, within-group similarity ranged from 50.1–63.3%, whereas the between-group dissimilarity ranged from 53.2–87.9% (Table 4). $_{Tax}$B (st. 163) consists of only one station, no within-group similarity was calculated. Three families (paraonids, opheliids, hesionids) contributed to the within-group similarity of TaxA (st. 6, 120) with over 90%, whereas the within-group similarities of the remaining clusters were influenced by more polychaete families. In most cases the abundance of paraonids, cirratulids, hesionids and opheliids contributed most to the between-group dissimilarity. The abundance of onuphids in $_{Tax}$F (st. 217, 225, 235, 241) contributed over 12% to the between-group dissimilarity with other clusters, except for the dissimilarity between $_{Tax}$F & $_{Tax}$C and $_{Tax}$F & $_{Tax}$B with a contribution less than 5%. Although dorvilleids and scalibregmatids did not contribute to any within-group similarity, they contributed to all between-group dissimilarities of $_{Tax}$C and $_{Tax}$B.

The functional polychaete community composition in the NW-WS was dominated by SbMB, except for st. 163, where PMC was most abundant. SMB increased in abundance from north to south in NW-WS and dominated at st. 6 (Figure 2). The lowest number of functional groups in the NW-WS was observed for st. 6 (7) and 120 (6). Contrarily, the DP showed a high functional diversity (235: 12 groups, 241: 11 groups). Here, communities were dominated by SbMB and surface deposit feeders (SMB, SDSe, SDB). Furthermore, st. 241 revealed the highest abundance of FNSe (3.5 ind. per 100 cm^2) across all sampling sites. As for the taxonomic community composition, st. 225 (BS) and 235 (DP) also showed a similar functional community-composition pattern: SbMB (10.1 and 9.1 ind. per 100 cm^2, respectively) being the dominant group followed by SDSe (3.4 and 4.8 ind. per 100 cm^2, respectively), ODC (both 3.8 ind. per 100 cm^2) and SMB (3.8 and 3.4 ind. per 100 cm^2, respectively). ODC were not observed for the FT region and only for two NW-WS stations. SDSe (5.3 ind. per 100 cm^2) was most abundant at st. 217, but not found at sites in the NW-WS, except for st. 163. The functional polychaete communities in the BS and DP revealed low proportions of the feeding type "predator", and a higher proportion of "sessile" forms.

The polychaete communities for deeper trough st., 17 and 72 in the FT region, showed low numbers of functional groups (17: 7, 72: 8). Both stations were dominated by surface and subsurface deposit feeders, including SDB, SbMB, SMB and SDSe. Contrary to these stations, PDB showed higher abundances in functional community composition for remaining stations in the FT region. At st. 37 and 26 predators (PMC, PMB, PDB) made up one third of the functional groups within the community (Figure 2).

The cluster analysis of the polychaete communities on the basis of functional groups revealed five clusters ($_{Func}$A–$_{Func}$E) at a similarity of 50% (Figures 6, S3). St. 241 located in the DP together with stations from the FT region (26, 37, 48, 61) forms one cluster ($_{Func}$E). SIMPER analysis showed that within-group similarity ranged from 57.1–77.3%, whereas the between-group dissimilarity ranged from 52.3–83% (Table 5). $_{Func}$A (st. 6) consists of only one station, no within-group similarity was calculated. Communities of st. 225 and 235 show the overall highest similarity and form Cluster $_{Func}$D with st. 217. SbMB contributed most to the within-group similarity with over 24% across all clusters. In most cases the abundance of SbMB, SMB, OMC and PMC contributed most to the between-group dissimilarity. The abundance of SDSe in $_{Func}$D (st. 217, 225, 235) with a contribution of 23.3% on its within-group similarity also had an important impact on its between-group dissimilarity.

3.4 Comparison of polychaete community distribution patterns and bioregions

Visualization of the environmental bioregions with the polychaete community types showed no clear pattern, neither for clusters $_2$B nor for $_4$B with the $_{tax}$onomic or functional polychaete community types (Question 3, Figure 7, S5). $_4$B4 included four taxonomic community types, three occurring in the AP region ($_{Tax}$A, $_{Tax}$B, $_{Tax}$C) and one in the FT region ($_{Tax}$E). However, two functional clusters were observed for the $_4$B4, one in the AP ($_{Func}$B) and one in the FT ($_{Func}$E) region. $_4$B3 contained three different taxonomic ($_{Tax}$A, $_{Tax}$D, $_{Tax}$E) and functional ($_{Func}$A, $_{Func}$C, $_{Func}$E) community types in the spatially separated areas. $_4$B2 included the same taxonomic and functional community types as $_4$B3 in the FT region. ${}_{4}$B1 (only occurring in the AP region) included all DP and BS stations and hosts one taxonomic (${}_{Tax}$F) but two functional (${}_{Func}$D, ${}_{Func}$E) community types. Functional community type E was found in all bioregions, and taxonomic community type E in 3 bioregions, while ${}_{Tax}$A, ${}_{Tax}$D were present in 2 bioregions.

3.5 Relation of taxonomic and functional polychaete communities to environmental parameters

The best models explaining variation in the polychaete communities for (a) taxonomic and (b) functional groups included the same 3 out of 11 variables (DistLM BEST procedure with AIC_C selection criterion at highest R^2, Tables S7, S8): TOC, SD-10-year-ice, depth. For the polychaete community described by the taxonomic groups, the first two axes together explained 45.3% of the total variation and 88.5% in the fitted model (Figure 8, Table 6), whereas for the functional groups the first two axes together explained 49.8% of the variation in the total model and 89% in the fitted model (Figure 9, Table 7). For both community types TOC contributed most to the explained variation in the sequential test (taxonomic: 22.6%, $P = 0.09\%$; functional: 26.1%, $P = 0.1\%$), followed by the SD-10-year-ice (taxonomic: 16.3%, $P = 0.2\%$; functional: 15.7%, $P = 0.2\%$). The contribution of depth was statistically not significant in either analysis (Table 6, 7). The overall model explained 38.9% of the variation for the taxonomic community analysis (adj. R^2, Table 6), whereas for the functional community analysis the overall model explained 44.9% (adj. R^2, Table 7). Variation on the first axis (dbRDA) mainly separated the polychaete community (taxonomic and functional groups) of taxonomic and functional clusters in the geographic regions NW-WS (${}_{Tax}$A–${}_{Tax}$C, ${}_{Func}$A & ${}_{Func}$B) and two stations in the FT region (37, 61: ${}_{Tax}$E, ${}_{Func}$E) from the remaining stations and clusters (Figures 8, 9). TOC and SD-10-yer-ice (in that order) contributed most to dbRDA1 on the basis of the coefficient of the dbRDA. The taxonomic and functional groups of the polychaete community (${}_{Tax}$F, ${}_{Func}$D) of the DP and BS were separated from those of all other locations by the variation along dbRDA2 (taxonomic: 9.6% of total variation, Figure 8; functional: 8.5% of total variation, Figure 9). The parameter SD-10-year-ice contributed most to this axis. Along the dbRDA3 (taxonomic: 5.9% of total variation, Table 6; functional: 6.1% of the total variation, Table 7) TOC was the most important parameter.

4. DISCUSSION

We provide distribution and composition patterns of polychaete communities that are different from the overall epibenthic communities in the two regions FT and AP. We incorporate for the first time to our knowledge taxonomic and functional information about polychaete communities and their relationship with ice-cover regime and food situation at the seafloor. Patterns of taxonomic and functional community types only differed in the AP region. TOC and ice-cover variation were more relevant for the structure of functional communities than for taxonomic communities. Further, we tested bioregionalization approaches as a predictor for the spatial distribution of infauna communities. The four bioregions including TOC and SD-10-year-ice as predictor variables reflect the polychaete distribution patterns only to a limited extent but provide a descriptive interpretation of environmental bioregions and the distribution patterns of polychaete communities.

4.1 Differences using the taxonomic and functional diversity approach for polychaete composition across the Antarctic Peninsula and Filchner Trough region

We identified 6 and 5 distinct taxonomic and functional community types, respectively (Question 1). Most of the taxonomic and functional groups were present in several geographic regions, but their relative contribution varied among the locations. In a study from Hilbig et al. (2006) cirratulid and maldanid species (identified to genera or species) dominated around the AP and spionid and syllid species in the southeastern part of the WS. In our study however, high abundances of paraonids and cirratulids were characteristic elements for community composition across the WS. Additionally, hesionids, opheliids, and maldanids were commonin the AP region, whereas syllids, glycerids, lumbrinerids, spionids, and ampharetids abundant the FT region. These differences could be related to different sampling depths: The shelf regions investigated by Hilbig et al. (2006) were often either shallower (< 300 m) or deeper (> 700 m) than our stations (400–700 m). In addition, the study area in the southeastern WS presented by Hilbig et al. (2006) was located further north than our FT region. Paraonids, spionids and cirratulids (as in the FT region, this study), together with dorvilleids have previously been reported to show highest abundances in deep-sea polychaete communities of the northwestern Atlantic and northeastern Pacific (Hilbig 1994, Hilbig & Blake 2000).

The functional polychaete assemblages of soft sediments were mostly dominated by mobile burrowing subsurface deposit feeders, which matches previous findings for macrofauna communities (Gutt 2007). We demonstrated that the classification of polychaete communities based on taxonomic and functional types was the same for the FT region but not for the AP region. The similarities in the FT region may indicate specialized taxa here have specific functional adaptations and traits to their respective habitat conditions (e.g. high or constant sea-ice cover). In contrast, the classification of taxonomic and functional community types differs in the NW-WS with its seasonal ice conditions. Despite the taxonomic differences (${}_{Tax}$A, ${}_{Tax}$B, ${}_{Tax}$C) in the NW-WS, communities showed the same ecological functions adapted to the ecosystem properties, as almost all NW-WS sites clustered in ${}_{Func}$B. We assume that these ${}_{Func}$B-communities (Table S8) with their high standing stocks and a low functional biodiversity prefer variable and seasonally changing conditions (e.g. seasonal food pulses) in the organic-rich habitats of the NW-WS. The organisms forming ${}_{Func}$B communities may also compete in space, which could explain the different taxonomic but same functional types that were detected. Previous studies also revealed high abundances of infauna (Veit-Köhler et al. 2018, Säring et al. 2022) and epifauna organisms (Gutt et al. 2016) in the NW-WS. The functional composition and structure of epibenthos, however, differed in these studies: Whereas sessile and sedentary suspension feeders filtering organic particles from the water column dominated macroepifauna communities (Gutt et al. 2016), the infauna polychaete community type ${}_{Func}$B was dominated by mobile deposit feeders and predators and not by suspension feeders. The motility of the burrowing and crawling polychaetes influences bioturbation processes and stratification of the sediments in the NW-WS which fits observations of high Chl*a* and CPE content even in deeper sediment layers (Veit-Köhler et al. 2018).

The functional biodiversity distribution patterns of polychaetes in the DP and BS only partially match the description for the macroepifauna from Gutt et al. (2016), where both regions were dominated by suspension feeders. Although we observed in both regions the same taxonomic (${}_{Tax}$F) community type we found two functional community types ${}_{Func}$D (in BS and DP) and ${}_{Func}$E (in DP). The more common ${}_{Func}$D was, composed of omnivores (onuphids, syllids) and deposit feeders (sternaspids) as well as polychaetes with a tentacle crown such as sessile suspension (sabellids) and deposit feeders (ampharetids). Notably, the latter 2 groups were less common in other communities across this study area. The taxonomic and functional community types from DP and BS showed closer similarities to the FT communities than to those in the NW-WS (Figures 5, 6, S2, S3). We assume that ${}_{Func}$E, a heterogeneous functional community dominated by deposit feeders, predators and omnivores found in DP and FT, is adapted to different harsh environments. Due to the high variety of functional traits represented by the organisms grouped in ${}_{Func}$E this community can persist even under extreme ice-cover conditions (DP: none, FT: high & constant) with low food availability (Säring et al. 2022). This finding is noteworthy because there are clear taxonomic differences between the AP and the FT region and a geographic separation of 1321 km between st. 6 and 37.

We differentiated two functional and two taxonomic polychaete communities in the FT region. The communities ${}_{Tax}$D and ${}_{Func}$C were defined as poor and mixed communities with low numbers of individuals, families or functional groups, and with less mobile but rather sessile deposit feeders (e.g. ampharetids). The structure and distribution of these polychaete communities only partially correspond to the macrofauna "Ice/ Ice Shelf-Water related community" distribution described by Pineda-Metz et al. (2019). Contrary to them, we only observed ${}_{Tax}$D and ${}_{Func}$C at the inner slope of the central part of the FT (around 700 m depth) and not in proximity to the iceberg A23-A (st. 37, Figure 7). The second community types in the FT region ${}_{Tax}$E, and ${}_{Func}$E showed a similarly wide distribution pattern as the macrofauna "Eastern Shelf community" established by Pineda-Metz et al. (2019). The community compositions, however, clearly differed. Whereas the polychaete infauna was dominated by mobile species and different feeding types with a heterogenous taxonomic and functional composition (${}_{Tax}$E, ${}_{Func}$E), the "Eastern Shelf community" (including all macrofauna for this region, excluding st. 37) was dominated by the presence of suspension feeders (Pineda-Metz et al. 2019). However, Pineda-Metz et al. (2019) included 29 stations in their study while we had only 6 sites sampled in the FT region. Thus, it is possible that sampling effects occur. We may have had too few samples to find suspension feeders in the FT region. Similar macrofauna community types between eastern and western shelves and northern continental slope, as mentioned in previous studies (Pineda-Metz et al. 2019) and extended distribution ranges of eastern shelf macro-and megaepifauna communities (Gerdes et al. 1992, Gutt &

Starmans 1998), could indicate a connection between the western and eastern FT shelf (Pineda-Metz et al. 2019). Future studies may want to verify if polychaete communities of the northern continental slope are similar to those of the eastern and western shelves in the FT region.

Some polychaete families were found exclusively in one region, e.g. trichobranchids and nerillids in the FT region, or sternaspids and onuphids in the AP region which have mostly a short or no pelagic larval phase and thus low dispersal ranges. However, no conclusions on dispersal barriers due to geographic separations can be derived for polychaetes in the WS, as this would require a more detailed taxonomic and genetic study approach at species level (e.g. Brasier et al. 2017).

4.2 Linking infauna community structure and patterns to environmental drivers

4.2.1 Environmental drivers explaining the polychaete distribution in the Weddell Sea

The infauna biodiversity in the SO is affected by various environmental drivers on different spatial scales. Most commonly a combination of environmental drivers including ice-cover parameters or grain size, depth or bottom water temperature (Pineda-Metz et al. 2019), food availability (Veit-Köhler et al. 2018, Säring et al. 2022) or oceanographic regimes (Hauquier et al. 2015) have an impact on the community structure of different infaunal size classes on the shelf.

We have shown that taxonomic and functional community distribution patterns were affected by the same environmental parameters (SD-10-year-ice, TOC) (Question 2, Figures 8, 9; Tables 6, 7). As environmental parameters explained functional communities to a higher extent functional groups may be useful for approaches predicting infauna biodiversity.

Our results also provide evidence that polychaete communities could be affected by changing ice-cover conditions in the future as has been highlighted for mega-and macrobenthic communities in the WS (Pineda-Metz et al. 2020). This is in contrast to the results from (Säring et al. 2022), where long-term ice-cover (as opposed to ice cover in the sampling season) only showed a minor or no impact on mixed infaunal communities (meio- and macrofauna) in the WS.

Further, the longer-term impact of sea ice on the quantity of organic material at the seafloor affects the abundance and compositions of polychaetes, supported by the high explanatory power of TOC. Food supply is a key factor structuring marine benthic communities (Pearson & Rosenberg 1978, 1987, Wieking & Kröncke 2005). It appears that organic-poor sediments, such as those in the DP, BS and FT region, limited the polychaete abundance which exhibited more similarities in their taxonomic (${}_{Tax}$D, ${}_{Tax}$E, ${}_{Tax}$F) and functional (${}_{Func}$C, ${}_{Func}$D, ${}_{Func}$E) composition compared to those found at sites with greater quantities of deposited organic material in the NW-WS (${}_{Tax}$A, ${}_{Tax}$B, ${}_{Tax}$C, ${}_{Func}$A, ${}_{Func}$B). Although polychaetes were the dominant taxon in the macrofauna communities, the impact of food availability on polychaete communities only corresponded partially to overall macrofauna where also Chl*a* at the seafloor proved to be an important driver (Säring et al. 2022). Also, polychaete diversity patterns on the Arctic shelf were affected by both, benthic pigments and TOC (Ambrose, Jr. & Renaud 1995, Piepenburg & Schmid 1997), as well as sediment characteristics (Ambrose, Jr. et al. 2009). The results of a correlation analysis from Kröger & Rowden (2008) indicate that a combination of four parameters (including sediment Chl*a*, sorting coefficient, sponge spicule content, distance to nearest iceberg scour, but not including organic matter) was relevant for the composition of polychaete communities on the northwestern Ross Sea shelf. In the WS, polychaete communities depend less on the quality of food, but rather on its quantity.

As mentioned for infauna of polar shelf regions (Arctic: Piepenburg 2005, Antarctic: Säring et al. 2022), depth had no impact on the taxonomic or functional polychaete community.

Although the parameter grain size had a minor impact on shaping the mixed infauna communities in the WS (Säring et al. 2022) and was relevant for benthic community structure (e.g. Cummings et al. 2018) and species diversity (Shannon-Wiener and Simpson´s Reciprocal Index) of polychaetes in the Arctic (Ambrose, Jr. et al. 2009), it surprisingly did not influence sediment-bound polychaete community composition in our study. Despite the strong evidence for differences in the sediment structure between the ${}_{4}$B bioregions, different taxonomic and functional communities usually occur within a bioregion (e.g. ${}_{4}$B4: ${}_{Tax}$A, ${}_{Tax}$B, ${}_{Tax}$C; ${}_{4}$B1: ${}_{Func}$D, ${}_{Func}$E). Differences in silt and clay content in the FT region (Säring et al. 2021b) affected the polychaete communities neither, as the same taxonomic (${}_{Tax}$E) and functional (${}_{Func}$E) community types were observed in several bioregions (${}_{4}$B2, ${}_{4}$B3, ${}_{4}$B4) with different grain sizes at the sampling sites (Säring et al. 2021b). A minor importance of grain size has previously been reported from the southeastern Gulf of California (Mexico), where the percentage of mud played a minor role for the distribution of deep-sea polychaetes (Méndez 2007), and from the North Atlantic, the eastern Pacific and the Indian Ocean, where sand and clay contents were found to be non-significant determinants influencing macrofaunal distribution (Levin & Gage 1998).

Our results highlight that the impact of food quantity and ice-cover variation could be more important for polychaete communities than other parameters, such as grain size. We propose that further research should focus on the evaluation of more complex ecological scales (e.g. food availability model by Jansen et al. 2018b) in order to understand the overall impact of organic matter and food input on the biodiversity of polychaetes.

4.2.2 Bioregions can only partially reflect polychaete distribution patterns

To assess the various habitats in the WS, we used spatially available parameters for the bioregionalization, including TOC and sea-ice parameters, which have previously been identified as important environmental drivers. Our classified environmental bioregions, however, only partially reflected the taxonomic and functional distribution patterns of the polychaete communities in the AP and FT region (Question 3, Figure 7, S5). The ${}_{4}$B differed between 5 out of 9 environmental parameters of the spatial data set: Depth, ${}_{bottom}$T, Median-10-year-ice, Sand, Speed (Figure S7, Table S3). Out of those 5 parameters, the DistLM model incorporated, among others, point data of the parameters Depth, ${}_{bottom}$T, Median-10-year-ice and Sand, and interestingly none of them was found to explain the impact on the taxonomic or functional polychaete community composition. The results from previous studies based on shallow-water polychaete communities on the northern Atlantic shelves indicate the relevance of sediment characteristics for the occurrence of polychaetes, as spionids, syllids, and orbiniids dominated in sandy sediments as the sediment structure in bioregion 2 of the 4-cluster-option (${}_{4}$B2), whereas capitellids, scalibregmatids, and cirratulids are abundant when the sediment is composed of silt and clay as in ${}_{4}$B1 and ${}_{4}$B3 (Hilbig & Blake 2000: Massachusetts Bay, U.S. Atlantic; Maurer & Leathem 1980: Georges Bank and other sites in the U.S. Atlantic; Santos & Simon 1974: Tampa Bay, Florida, U.S. Atlantic). However, our classification of the taxonomic and functional polychaete community types could not be explained by grain size. It seems that the main key drivers (SD-10-year ice cover, TOC) for structuring the polychaete communities in the AP and FT region were possibly not important parameters for classifying bioregions, as these two parameters did not significantly differ between all ${}_{4}$Bs and may cause the inconsistencies between bioregions and polychaete distribution patterns. We presented a newly generated TOC projection for the AP and FT region, which is currently based on a sparse data basis. This can lead to irregularities such as the observed "bulls eye" of high TOC content in Figure 3H. More data on benthic organic matter is necessary to avoid such interpolation uncertainties and provide a better basis for predicting polychaete distribution.

On the basis of our findings, that different taxonomic and functional community types occurred in the same bioregion, various community types seemingly adapt to similar environmental conditions. For example, the following three taxonomic and functional community types from distinct sites appear to prefer high but variable ice-cover conditions and low ${}_{bottom}$T observed in ${}_{4}$B3 (Figure 4, 7, S5): a deposit feeder dominated community on the inner slope of the Filchner Trough at 700 m depth (${}_{Tax}$D, ${}_{Func}$C), a heterogeneous community near the large iceberg A23-A on the western shelf in FT region at 380 m depth (${}_{Tax}$E, ${}_{Func}$E), and a mobile deposit feeder and predator community (${}_{Tax}$A, ${}_{Func}$A) near Larsen C in the AP region at 425 m depth. In contrast, it seems that environmental conditions reflect epifauna distribution patterns more accurately than for infauna, as Pineda-Metz et al. (2019) observed the same macroepifauna community type for the two ${}_{4}$B3 FT sites. Furthermore, inconsistencies become apparent as the same communities inhabit bioregions with different habitat properties, as observed for ${}_{4}$B2 and ${}_{4}$B3 in the FT region which contain the same taxonomic (${}_{Tax}$D, ${}_{Tax}$E) and functional (${}_{Func}$C, ${}_{Func}$E) community types (Figure 7). Possibly, our bioregionalization approach was lacking a parameter important for polychaete communities. We assume that local conditions not measured here, played an important role for differentiating community types in FT even though sampling sites were less than 11 km apart from each other. A similar level of patchiness has been reported for macroepibenthic communities in the AP, where the Joinville North community in the BS was more similar to those in the DP than to adjacent communities in the BS and NW-WS (Gutt et al. 2016).

In DP and BS, however, the bioregions based on 9 environmental parameters represented the taxonomic community patterns. The impact of ice-free areas, warmer ${}_{bottom}$T and water currents, as in the ACC where nutrients and pelagic larvae are transported to the continental slope (Arntz et al. 1994, Turner et al. 2009), may favor the dispersal and settlement of different taxa and may explain the occurrence of the taxonomically heterogenous community ${}_{Tax}$F (see subsection 4.1), with higher abundances of polychaetes with tentacle crowns that filter particles from the water column (Fauchald 1977) and less mobile deposit feeders in ${}_{4}$B1.

The use of functional groups is valuable to understand the ecology of communities, even though less differences in the community composition may be displayed. Thus, ${}_{4}$B4 in the AP region did not reflect the taxonomic pattern, but functional polychaete distribution patterns. Albeit, this was not the case for ${}_{4}$B4 in the FT region with a distance of approx. 1641 km to AP.

It is possible that a combination of sea-ice cover (e.g. polynya) and water-mass circulation is responsible for regulating the quantity of organic matter at the seafloor. This has been previously mentioned for other regions in the SO (Grebmeier & Cooper, 1995, Isla et al. 2006, Jansen et al. 2018b, 2018c). In the FT region the main polynya is formed on the eastern shelf (Fetterer et al. 2018), where warm deep-water masses from the WS Gyre enter and flow south to the Filchner Ice Shelf (Ryan et al. 2017). The warmer water masses and the enhanced primary production of the polynya region, classified here as ${}_{4}$B4, favored the occurrence of a heterogeneous mobile polychaete community with different diet types (${}_{Tax}$E, ${}_{Func}$E). However, the same polychaete community types occurred on the western FT shelf (${}_{4}$B2: st. 26, 48; ${}_{4}$B3: st. 37), supporting the assumption of a connectivity between the eastern and western shelves due to the circulation of warm deep waters along the continental slope of the FT region. Such a connection was mentioned for macrofauna communities by Pineda-Metz et al. (2019). But this possible connection cannot be picked up by the different habitat conditions (3 bioregions). Only a few taxonomic and functional polychaete groups (${}_{Tax}$D, ${}_{Func}$C), such as the sessile deposit feeders (e.g. ampharetids) can persist the outflow of the Ice Shelf Waters in the inner Filchner Trough, which should transport less dissolved organic matter (Ryan et al. 2017, Pineda-Metz et al. 2019). Similar patterns were mentioned for the macrofauna community, dominated by deposit feeders and with a concurrent absence of suspension feeders (Pineda-Metz et al. 2019). However, on the basis of our bioregionalization results, the two FT stations belong to different bioregions (st. 17: ${}_{4}$B2, st. 72: ${}_{4}$B3), but represent the same taxonomic and functional type (${}_{Tax}$D, ${}_{Func}$C). It is possible that st. 17 is an outlier of ${}_{4}$B2 due to its proximity to the adjacent bioregion ${}_{4}$B3, however, we cannot exclude such uncertainties here, due to the low number of stations.

However, it could be possible that a prediction on species-level would have yield a better prediction. Only species may occupy an ecological niche as adaptations differ to the species level. If such characteristics are known, it could be possible to better specify, i.e. accurately explain, distribution patterns. Unfortunately, for Antarctic polychaetes, less is known about corresponding species niches.

4.2.3 Future directions to consider for benthic biodiversity research in the Southern Ocean

We recommend including sea-ice parameters in future models predicting benthic distribution patterns, as, in addition to their ecological importance for mixed infauna (Säring et al. 2022), epifauna (Gutt et al. 2016) and polychaete communities in the SO, sea-ice data are freely available from satellite measurements over a large spatial coverage in the SO. Additional parameters, such as food availability or water mass parameters (flow direction, water mass transport) in future bioregionalization approaches could allow a more accurate separation between bioregions and representation of the polychaete community distribution patterns. So far only a few bioregionalization approaches include parameters providing information about the food input at the seafloor (e.g. Jansen et al. 2018a) due to the sparse data coverage of benthic pigment data. The identification of relevant environmental surrogates for biological biodiversity can enable rapid assessment of marine ecosystems and contributes to the monitoring and identification of Marine Protected Areas (MPAs) worldwide (e.g. Harris et al. 2008).

The relatively novel approach Species Archetype Models (SAMs, Dunstan et al. 2011, 2013) can play an important role for future conservation planning. Multispecies archetypes share similar responses to environmental predictors, therefore they may necessitate similar management strategies. Previous studies have already shown promising results for mapping the distribution of fauna and habitats using the SAM (Jansen et al. 2018a, O'Hara et al. 2020). We tried the SAMs, R package *ecomix* version 1.0.0 (Woolley et al. 2021) to determine taxonomic and functional groups based on their similar responses to environmental parameters in the WS. The sampled area was applied as an offset in the model formula on log-scale. The count data per station with the setting negative binomial was used and only included taxonomic or functional groups that occurred in at least 10 samples. First, we defined the optimal number of archetypes for both data sets (taxonomic and functional groups) by comparing models (em.fit = 1–5, em.step =1–5) with different numbers of archetypes (2–10) based on the model maximum likelihood using the Bayesian Information Criterion (BIC) (Dunstan et al. 2011, Leaper et al. 2014). In a second step, we selected the covariates (linear and quadratic) to consider in the SAM. The best variable selection was based on the BIC by comparing models with different covariable combinations (em.fit = 1–5, em.step =1–5). The model with the lowest BIC was used to predict the occurrence of taxonomic and functional archetypes throughout the survey area, including areas where only environmental data were available. SAMs, however, could not be applied to our input data as no prediction could be run, despite the intensive efforts to adjust the current code by the SAM authors (Skipton Woolley and Jan Jansen, pers. communication) and ourselves. Valle et al. (2021) have also mentioned problems using the SAMs, indicating that the algorithm failed to find a suitable solution leading to numerical problems for estimating the uncertainty of the regression coefficients, as some archetypes were empty (without species). The relatively small sample size and density compared to the large survey areas could be limiting factors to run reliable models, interpolate the polychaete distribution and integrate these with environmental covariates for a joint clustering approach or the SAMs. Thus, there is an urgent need to revisit possible problems in SAM and to improve the spatial coverage of infauna abundance data and food-related parameters (Chl*a*, TOC) for regions with long-lasting ice-cover regimes (e.g. FT region), as this may allow the SAMs to be applied for Antarctic infauna communities in the future and increase their role for conservation planning processes.

5. CONCLUSION

Our approach allowed a comprehensive polychaete community description by including taxonomic and functional information in combination with different environmental parameters across the two survey areas in the extended WS (AP, FT). We observed the polychaete communities to be heterogenous and composed of 6 taxonomic and 5 functional community clusters/ groups. Even though the variation of the sea-ice cover and the content of organic carbon at the seafloor are the most reliable parameters for explaining the taxonomic and functional polychaete community pattern, we demonstrated a stronger relationship with these two parameters in functional than in taxonomic communities. We recommend implementing these environmental drivers and functional information into future studies of the Antarctic infauna to improve our understanding of the effects of environmental change for the marine ecosystem in the SO. Our findings reveal that further drivers for the polychaete community structure such as planktonic community abundance and composition as well as particle flux are lacking. The bioregionalization based on 9 environmental surrogates was not suitable to describe the distribution pattern of either the taxonomic or functional polychaete community. We therefore highlight potential vulnerable sampling sites e.g. in the Filchner Trough for future expeditions where additional sampling would be necessary to explain outliers and specify and apply (advanced) models, such as SAM which include fauna and environmental data simultaneously. More biological and environmental data would therefore improve the prediction of the current and future distribution of polychaete communities facing environmental changes. We finally recommend that existing data should be published with open access and thus contribute to a better science on the infauna biodiversity in the SO.

6. HIGHLIGHTS

(1) Comprehensive polychaete community descriptions need taxonomic & functional traits

(2) Heterogenous polychaete communities with 5 taxonomic and 5 functional types

(3) Weddell Sea regions with no or constant ice cover show high polychaete diversity

(4) Sea-ice cover and TOC most important drivers for polychaete community composition

(5) Bioregions did not reflect taxonomic/ functional distribution of community types

ACKNOWLEDGMENT

Derya Seifert (Kiel University, GER) is thanked for helping with the classification of polychaetes and other macrofauna. We thank Iris Liskow and Maren Voß (Institute of Baltic Research Warnemünde, GER) for contributing to environmental data analysis (TOC, TN). We appreciate Jan Jansen (University of Tansmania, Australia) and Skipton Woolley (Commonwealth Scientific and Industrial Research Organization, Australia) for their assistance and guidance in applying the code for the R packages

SpeciesMix and ecomix to our data. We are also grateful to the crew and chief scientists Julian Gutt (PS81), Michael Schröder (PS96) and Boris Dorschel (PS118, all Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, AWI GER) on RV *Polarstern* for providing the possibility of sample collection on board. The members of the OFOS Team Dieter Piepenburg (Kiel University), Alexandra Segelken-Voigt (University of Oldenburg, GER) and Autun Purser (AWI) are thanked for information by video survey on board. Michael Schröder and Markus Janout and their teams (both AWI) are thanked for water-column samplings. Yasemin Bodur (Senckenberg am Meer), Freija Hauquier (Ghent University, Belgium), Dieter Piepenburg, Enrique Isla (Institut de Ciències del Mar, Barcelona, Spain), Michael Schreck (University of Tromsø, Norway), Ursula Witte and Kirsten Macsween (both University of Aberdeen, United Kingdom) helped with logistics and sampling during the cruises. The present work was funded by the Deutsche Forschungsgemeinschaft (DFG) in the framework of the priority program SPP 1158 "Antarctic Research with comparative investigations in Arctic ice areas" (Grants LI 2313/3-1, LI 2313/6-1 and VE 260/10-1). Support was given by the Alfred Wegener Institute, Helmholtz-Centre for Polar and Marine Research (Grants AWI_PS81_03, AWI_PS96_02, AWI_PS118). We also thank XXX for editing and language correction, which improved this manuscript.

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TABLES & BOXES

Box1: Abbreviation for functional traits and groups. Functional traits for polychaetes according to Fauchald & Jumars (1979), Jumars et al. (2015), PolytraitsTeam (2023). Functional groups derived from specific combinations of functional traits.

Behavioral attribute	**Functional trait**	**Abbreviation**
Feeding type	Surface deposit feeder	S
	Subsurface deposit feeder	Sb
	Predator	P
	Omnivore	O
	Suspension feeder	F
Motility	Motile	M
	discretely motile	DM
	no motility	N
Movement	Crawling	C
	Burrowing	B
	Sessile	Se
Acronym	**Functional group**	
SbMB	Motile burrowing subsurface deposit feeder	
SbMC	Motile crawling subsurface deposit feeder	
SbDB	Discretely motile burrowing subsurface deposit feeder	
SbDC	Discretely motile crawling subsurface deposit feeder	
SMB	Motile burrowing surface deposit feeder	
SMC	Motile crawling surface deposit feeder	
SDB	Discretely motile burrowing surface deposit feeder	
SDSe	Discretely motile sessile surface deposit feeder	
PMB	Motile burrowing predator	
PMC	Motile crawling predator	
PDB	Discretely motile burrowing predator	
OMC	Motile crawling omnivore	
ODC	Discretely motile crawling omnivore	
FNSe	No motile sessile suspension feeder	

Table 1. Station list and sampling during RV *Polarstern* expeditions PS81 (January 22–March 18, 2013), PS96 (December 06, 2015–February 14, 2016) and PS118 (February 9 – April 10, 2019). Multicorers (MUC) and the giant box corer (GKG) were deployed for polychaete community sampling and for sediment sampling of environmental parameters. Samples for environmental characterization of the water column (CTD Conductivity, Temperature, Chl*a* at the maximum and near-bottom) were collected with a CTD-Rosette equipped with Niskin bottles. For CTD deployments chlorophyll*a*-maximum and near-bottom sampling depths as well as salinity and temperature are given (Janout et al. 2019; Schröder et al. 2016b, 2013a). Only successful MUC and GKG deployments are listed, which were used for faunal analysis. Additional stations for sediment sampling of environmental parameters that were used to update existing data sets (total organic carbon: Seiter et al. 2004, sediment texture: Jerosch et al. 2016) for the bioregionalization analysis are listed in Table S1.

Expedition & Region		St.	no. of env. cores	no. of fauna cores	Date	Latitude	Longitude	Depth [m]	Gear	T_{bottom}	Sal_{bottom}
PS81 Antarctic Peninsula (AP) (PS81)	Drake Passage (DP)	235-1			2013-03-07	62'16.30'S	61'10.27'W	21/372	CTD	0.43	34.50
		235-2		3	2013-03-07	62'16.35'S	61'10.23'W	355	MUC		
		235-4	2		2013-03-07	62'16.29'S	61'10.24'W	373	MUC		
		235-5	2		2013-03-07	62'16.31'S	61'10.24'W	363	MUC		
		235-6	2		2013-03-07	62'16.35'S	61'10.25'W	350	MUC		
		241-1			2013-03-09	62'06.63'S	60'36.52'W	20/396	CTD	0.65	34.54
		241-2		1	2013-03-09	62'06.59'S	60'36.47'W	400	GKG		
		241-5		1	2013-03-09	62'06.60'S	60'36.50'W	403	GKG		
		241-4		1	2013-03-09	62'06.59'S	60'36.50'W	403	GKG		
		241-3		1	2013-03-09	62'06.60'S	60'36.51'W	403	GKG		
		244-5	2		2013-03-10	62'06.64'S	60'36.53'W	398	MUC		
		244-6	2		2013-03-10	62'06.62'S	60'36.50'W	400	MUC		
		244-7	2		2013-03-10	62'06.65'S	60'36.54'W	396	MUC		
	Bransfield Strait (BS)	215-1			2013-03-01	62'53.57'S	58'14.66'W	40/519	CTD	-0.95	34.52
		217-3	2		2013-03-02	62'53.31'S	58'14.12'W	527	MUC		
		217-5		2	2013-03-02	62'53.25'S	58'14.13'W	532	MUC		
		225-1			2013-02-04	62'56.07'S	58'40.62'W	20/525	CTD	-0.85	34.54
		225-2		3	2013-02-04	62'56.08'S	58'40.76'W	543	MUC		
		225-3	2		2013-02-04	62'56.04'S	58'40.73'W	545	MUC		
		225-4	2		2013-02-04	62'56.06'S	58'40.76'W	544	MUC		
		225-5	1		2013-02-04	62'56.05'S	58'40.77'W	546	MUC		
	Northwestern Weddell Sea (NW-WS)	120-1			2013-01-28	63'04.62'S	54'33.11'W	20/511	CTD	-1.81	34.49
		120-4		3	2013-01-28	63'04.78'S	54'31.45'W	494	MUC		
		120-5	2		2013-01-28	63'04.58'S	54'31.00'W	504	MUC		
		120-6	2		2013-01-28	63'04.10'S	54'30.86'W	485	MUC		
		120-7	2		2013-01-28	63'03.72'S	54'30.87'W	437	MUC		
		163-1			2013-02-10	63'53.07'S	56'26.19'W	50/453	CTD	-1.77	34.50
		163-3		3	2013-02-11	63'50.97'S	56'25.24'W	517	MUC		
		163-4	2		2013-02-11	63'50.95'S	56'24.43'W	518	MUC		
		163-5	2		2013-02-11	63'51.01'S	56'23.97'W	517	MUC		
		163-6	2		2013-02-11	63'51.03'S	56'23.68'W	517	MUC		
		190-1			2013-02-20	63'50.50'S	55'33.65'W	20/390	CTD	-1.43	34.52
		190-6		3	2013-02-21	63'50.58'S	55'31.66'W	389	MUC		
P S9		115-1			2016-02-08	63'50.71'S	55'31.16'W	50/377	CTD		
		115-2	3		2016-02-08	63'50.56'S	55'31.72'W	400	MUC		
PS96 Southeastern WS	Filchner Trough (FT) region	17-1			2016-01-04	75'00.63'S	32'53.48'W	50/581	CTD	-1.91	34.67
		17-3	2	3	2016-01-04	75'00.85'S	32'52.51'W	608	GKG		
		26-13			2016-01-08	75'15.97'S	37'55.17'W	35/393	CTD	-1.92	34.66
		26-7	1	1	2016-01-08	75'16.19'S	37'54.96'W	416	MUC		
		26-8	1	2	2016-01-08	75'16.10'S	37'54.85'W	415	MUC		
		26-10	1	1	2016-01-08	75'15.80'S	37'54.87'W	414	MUC		
		26-11	1	1	2016-01-08	75'15.65'S	37'54.87'W	414	MUC		
		48-1			2016-01-18	74'46.18'S	35'18.59'W	44/470	CTD	-1.92	34.66
		48-7	1	3	2016-01-19	74'45.52'S	35'20.91'W	482	MUC		
		48-8	2	3	2016-01-19	74'45.52'S	35'20.91'W	482	MUC		
		37-2			2016-01-16	75'41.87'S	42'20.25'W	40/370	CTD	-1.91	34.67
		37-8	2	3	2016-01-16	75'43.30'S	42'27.71'W	391	MUC		
		37-9	2	2	2016-01-17	75'43.29'S	42'27.66'W	391	MUC		
		61-2			2016-01-21	76'05.86'S	30'18.66'W	46/446	CTD	-1.90	34.58
		61-5	2	1	2016-01-21	76'05.93'S	30'18.23'W	468	MUC		
		61-6	2	3	2016-01-22	76'05.89'S	30'18.38'W	467	MUC		
		72-2			2016-01-23	75'51.37'S	32'25.27'W	40/720	CTD	-1.90	34.66
		72-8	2		2016-01-23	75'50.92'S	32'18.42'W	753	MUC		

	72-9	1	3	24.01.2016	75'50.85'S	32'17.44'W	755	MUC
	72-10	1		24.01.2016	75'50.94'S	32'21.42'W	749	MUC

Table 2: Summary of environmental parameters (point data) with reference and sampling method, taken on board RV *Polarstern* at each station and sea-ice data (median and standard deviation of daily mean values Dec-Feb from 2009–2019). Time periods of the sampling: PS81 Feb–March 2013, PS96 Dec 2015–Jan 2016, PS118 Feb–March 2019.

Parameters of point data	Description	Unit	Source	Method	Descrip. analysis
Water column parameters					
$_{Cmax}$Chl*a*	Chlorophyll *a* content at the chlorophyll maximum	µg l^{-1}	PANGAEA: Säring et al. (2021a), Vanreusel et al. (2021a), Weith et al. in (in review b)	fluorometer: Turner designs, TD-700 (Veit-Köhler et al. 2018, Säring et al. 2022)	x
$_{bottom}$Chl*a*	Chlorophyll *a* content near the sea bottom	µg l^{-1}			x
$_{bottom}$T	Temperature near the sea bottom	° C	PANGAEA: Schröder et al. (2013b, 2016a), Janout et al. (2020)	measured with CTD (Janout et al. 2019, Schröder et al. 2013a, 2016b)	
Depth	Depth of sampling location	m			x
Sediment parameters					
Silt & Clay	Silt & Clay (< 63 µm) content in the 0–5 cm sediment layer from the sediment cores	%	PANGAEA: Säring et al. (2021b), Vanreusel et al. (2021b), Weith et al. in (in review c)	PS81: Malvern Mastersizer 2000 (Veit-Köhler et al. 2018); PS96, PS118: Malvern Mastersizer 3000 (Säring et al. 2022)	
Sand	Sand (63–500) content in the 0–5 cm sediment layer from the sediment cores	%			x
Coarse Sand	Coarse Sand (> 500 µm) content in the 0–5 cm sediment layer from the sediment cores	%			x
Chl*a*	Chlorophyll *a* content in the 0–1 cm sediment layer from the sediment cores	%	PANGAEA: Säring et al. (2021b), Vanreusel et al. (2021b), Weith et al. in (in review c)	PS81: High Performance Liquid Chromatography (HPLC) and fluorescence dector (Veit-Köhler et al. 2018); PS96, PS118: fluorometer Turner desings, TD-700 (Säring et al. 2022)	x
Phaeo	Phaeopigment content in the 0–1 cm sediment layer from the sediment cores	%			
CPE	CPE in the 0–1 cm sediment layer from the sediment cores	%	calculated from: Säring et al. (2021b), Vanreusel et al. (2021b), Weith et al. in (in review c)	calculated as Chla + Phaeo	
Chl*a*/Phaeo	Chl*a*/Phaeo in the 0–1 cm sediment layer from the sediment cores			calculated as Chl*a*/Phaeo	x
Chl*a*/CPE	Chl*a*/CPE in the 0–1 cm sediment layer from the sediment cores	%		calculated as Chl*a*/CPE	
TOC	Total organic carbon in the 0–1 cm sediment layer from the sediment cores	%	PANGAEA: Säring et al. (2021b), Vanreusel et al. (2021b), Weith et al. in (in review c)	PS81: Flash EA 1121+ MAS 200 elemental analyzer (Veit-Köhler et al. 2018); PS96, PS118: flash combustion in a Flash 2000 (Thermo) elemental analyzer (Säring et al. 2022)	x
TN	Total nitrogen in the 0–1 cm sediment layer from the sediment cores	%			
C/N$_{molar}$	carbon:nitrogen ratio in the sediment, was averaged from 0–5 cm sediment depth	%	calculated from: Säring et al. (2021b), Vanreusel et al. (2021b), Weith et al. in (in review c)	calculated as TOC/TN*14/12 from the sediment 0–5 cm	x
Median-10-year-ice	Median of the daily mean values (%) of the Antarctic summer sea-ice cover (Dec–Feb) between 2010–2019	%	https://www.meereisportal.de (Grosfeld et al. 2016) [remote sensing]	R Script (Pehlke in prep.)	x
SD-10-year-ice	standard deviation of the daily mean values (%) of the Antarctic sea-ice cover (Dec–Feb) between 2010–2019	%		DOI R Script (Pehlke in prep.)	x

Table 3: Summary of modeled spatial environmental parameters (raster data) with references. Processed raster data of environmental parameters are presented in the electronic supplement Figure S1.

Spatial parameters	**Description**	**Unit**	**Data source**	**Data processing this study**
$_{bottom}$T_s	Temperature near the sea bottom	° C	FESOM, (Wang et al. 2014) [modeled]	
Median-10-year-ice_s	Median of the daily mean values (%) of the Antarctic summer sea-ice cover (Dec–Feb) between 2010–2019	%	https://www.meereisportal.de (Grosfeld et al. 2016) [remote sensing]	R Script (Pehlke in prep.)
SD-10-year-ice_s	standard deviation of the daily mean values (%) of the Antarctic sea-ice cover (Dec–Feb) between 2010–2019	%		R Script (Pehlke in prep.)
Depth_s	Seafloor depth (Bathymetry)	m	IBSCO: www.ibsco.org/	
Sand_s	Sand (> 63 µm) content of the seafloor	%	combined from: Jerosch et al. (2015), Säring et al. (2021b), Vanreusel et al. (2021b), Weith et al. (in review c)	IDW & BK interpolation
TOC_s	Bottom total organic carbon	%	combined from: Säring et al. (2021b), Seiter et al. (2004a), Vanreusel et al. (2021b), Weith et al. (in review c)	IDW & BK interpolation
Dist_coast_s	Distance to coast	m	IBSCO, Chaabani et al. (2019)	
BPI_s	Broad benthic positioning index	no unit		
Speed_s	Bottom current speed	m s^{-1}	FESOM, (Wang et al. 2014) [modeled]	

Table 4: Taxonomic polychaete community: Results of the SIMPER analysis representing within-group similarities, between-group dissimilarities (**bold**), and taxonomic unit contribution (%, cut off for low contribution: 90%) of the benthic stations groups (A–F).

	A (6, 120)	**B (163)**	**C (8, 038, 190)**	**D (17, 72)**	**E (26, 37, 48, 61)**	**F (217, 225, 235, 241)**
within-group similarity (%)	**50.15%;** Paraonidae (35.8%), Opheliidae (35.8%), Hesionidae (21.6%)		**63.3%;** Paraonidae (36%), Cirratulidae (24.9%), Opheliidae (11%), Hesionidae (9.7%), Maldanidae (6.3%), Spionidae (4%),	**54.55%;** Ampharetidae (16.7%), Cirratulidae (16.7%), Paraonidae (16.7%), Spionidae (16.7%), Hesionidae (8.3%), Maldanidae (8.3%), Oweniidae (8.3%)	**57.5%;** Paraonidae (23%), Cirratulidae (19.5%), Syllidae (17.3%), Glyceridae (16.6%), Spionidae (3.8%), Ampharetidae (3.3%), Phyllodocidae (3.2%), Lumbrineridae (3.1%), Maldanidae (2.9%)	**55.7%;** Onuphidae (21.2%), Cirratulidae (15.8%), Paraonidae (15.4%), Ampharetidae (10.4%), Sternaspidae (8.3%), Maldanidae (7.4%), Syllidae (6%)
Between-group similarity (%)						
A						
B	**55.7%;** Hesionidae (32%), Cirratulidae (12.7%), Opheliidae (12.2%), Maldanidae (12.2%), Paraonidae (9%), Lumbrineridae (5%), Scalibregmidae (4.85), Polynoidae (2.4%)					
C	**54.5%;** Cirratulidae (23.3%), Paraonidae (22.3%), Hesionidae (16.7%), Opheliidae (9.5%), Maldanidae (6.2%), Dorvilleidae (5.3%), Lumbrineridae (4%), Spionidae (3.8%)	**53.2%;** Cirratulidae (27.3%), Paraonidae (24.3%), Hesionidae (13%), Opheliidae (11.8%), Dorvilleidae (4.3%), Spionidae (3.2%), Scalibregmidae (2.3%), Maldanidae (2.2%), Lumbrineridae (2.2%)				
D	**81.9%;** Paraonidae (24.9%), Opheliidae (20.8%), Cirratulidae (18.3%), Hesionidae (11%), Ampharetidae (4.8%), Maldanidae	**81%;** Hesionidae (40.6%), Maldanidae (14.1%), Paraonidae (12.3%), Lumbrineridae (7.2%), Scalibregmidae (4.9%), Opheliidae (3.2%), Polynoidae (2.4%), Cirratulidae (2.3%),	**87.8%;** Paraonidae (27.2%), Cirratulidae (24.3%), Hesionidae (13.8%), Opheliidae (11.3%), Maldanidae (5.6%), Dorvilleidae (4%),			

	A (6, 120)	B (163)	C (8, 038, 190)	D (17, 72)	E (26, 37, 48, 61)	F (217, 225, 235, 241)
	(4.2%), Lumbrineridae (4.1%), Spionidae (3.1%)	Ampharetidae (1.9%), Spionidae (1.8%)	Lumbrineridae (3.7%), Ampharetidae (1.9%)			
E	**72.2%;** Opheliidae (20.5%), Paraonidae (20.4%), Cirratulidae (17.2%), Hesionidae (10.9%), Syllidae (5.5%), Lumbrineridae (5.1%), Glyceridae (4.5%), Maldanidae (4%), Nephtyidae (1.6%), Spionidae (1.5%)	**73.9%;** Hesionidae (39.7%), Maldanidae (14%), Paraonidae (9.2%), Lumbrineridae (5.8%), Cirratulidae (4.3%), Scalibregmidae (4.1%), Syllidae (4%), Glyceridae (3.7%), Opheliidae (3.3%), Polynoidae (2.2%)	**81.6%;** Paraonidae (25.7%), Cirratulidae (21.5%), Hesionidae (14%), Opheliidae (11.5%), Maldanidae (5.6%), Dorvilleidae (4%), Lumbrineridae (3.3%), Spionidae (2.4%), Gylceridae (1.8%), Syllidae (1.8%)	**62%;** Cirratulidae (15.2%), Syllidae (13%), Glyceridae (10.2%), Paraonidae (9.3%), Ampharetidae (8%), Lumbrineridae (7.6%), Spionidae (4.4%), Nephtyidae (3.7%), Opheliidae (3.9%), Flabelligeridae (2.7%), Sphaerodoridae (2.7%), Phyllodocidae (2.6%), Maldanidae (2.5%), Oweniidae (2.4%), Sabellidae (2.3%), Amphinomidae (2.2%)		
F	**76.6%;** Paraonidae (18.2%), Opheliidae (17.3%), Cirratulidae (14.5%), Hesionidae (9.7%), Onuphidae (5.8%), Ampharetidae (5.3%), Sternaspidae (5.1%), Maldanidae (3.6%), Lumbrineridae (3.5%), Sabellidae (3.4%), Syllidae (3.2%), Spionidae (2.3%)	**77.1%;** Hesionidae (35.7%), Maldanidae (11.4%), Paraonidae (8.6%), Lumbrineridae (6.8%), Onuphidae (5.1%), Scalibregmidae (4.1%), Sternaspidae (4%), Cirratulidae (2.8%), Ampharetidae (2.7%), Opheliidae (2.6%), Sabellidae (2.6%), Syllidae (2.5%), Spionidae (2%)	**82.5%;** Paraonidae (24.5%), Cirratulidae (20.7%), Hesionidae (13.5%), Opheliidae (10.7%), Maldanidae (4.7%), Dorvilleidae (3.9%), Lumbrineridae (3.8%), Spionidae (2.6%), Onuphidae (2.3%), Ampharetidae (2.2%), Sternaspidae (2%)	**65.3%;** Onuphidae (14.2%), Sternaspidae (10.5%), Cirratulidae (10.3%), Spionidae (8%), Ampharetidae (7%), Paraonidae (6.9%), Syllidae (6.8%), Sabellidae (5.8%), Terebellidae (4.7%), Maldanidae (2.4%), Polynoidae (2.3%), Hesionidae (2.2%), Flabelligeridae (2.2%), Opheliidae (2.2%), Lumbrineridae (2.2%), Sphaerodoridae (2.2%)	**59.4%;** Onuphidae (12.6%), Sternaspidae e (9.5%), Cirratulidae (9.3%), Ampharetidae (8.4%), Glyceridae (7.7%), Lumbrineridae (5.8%), Spionidae (5.5%), Paraonidae (5.4%), Sabellidae (5.2%), Syllidae (4.6%), Terebellidae (4.2%), Maldanidae (2.6%), Nephtyidae (2.6%), Opheliidae (1.9%), Polynoidae (1.9%), Hesionidae (1.9%), Amphinomidae (1.7%)	

Table 5: Functional polychaete community: Results of the SIMPER analysis representing within-group similarities, between-group dissimilarities (**bold**), and functional unit contribution (%, cut off for low contribution: 90%) of the benthic stations groups (A–E).

	A (6)	**B (8, 38, 120, 163, 190)**	**C (17, 72)**	**D (217, 225, 235)**	**E (26, 37, 48, 61, 241)**
within-group similarity %		**57.10%;** SbMB (51.1%), PMC (17.5%), SMB (11.5%), SbDB (9.7%), PMB (6.8%)	**77.30%;** SbMB (29.4%), SDB (29.4%), SMB (17.7%), SDSe, (11.8%), PMC (5.9%)	**69.20%;** SbMB (24.1%), SDSe (23.3%), ODC (21.2%), SMB (12%), SbDB (6.6%), FNSe (5.8%)	**60.20%;** SbMB (25.5%), SMB (20.3%), OMC (17.5%), PMC (11.4%), PDB (9.5%), SDB (5.5%), SDSe (3.1%)
between-group dissimilarity					
A					
B	**52.70%;** SbMB (31.6%), SMB (22.4%), PMC (19.4%), SbDB (10.5%), PMB (6.5%)				
C	**78%;** SMB (37.4%), SbMB (32.6%), PMC (11.5%), SDB (5.8%), SDSe (5.4%)	**83%;** SbMB (41.7%), PMC (20.1%), SMB (16.3%), SbDB (7.4%), PMB (5.2%)			
D	**63%;** SMB (34%), SbMB (21.8%), SDSe (11.6%), PMC (10.8%), ODC (7.5%), SbDB (3.6%), OMC (3.5%)	**75.40%;** SbMB (35.2%), PMC (19.2%), SMB (16.1%), SbDB (6.6%), PMB (5.5%), SDSe (5.3%), ODC (4.2%)	**53.90%;** SbMB (23.6%), ODC (19.4%), SDSe (13.1%), SDB (12.5%), OMC (7.5%), SMB (6.7%), FNSe (5.2%), SbDB (3.4%)		
E	**59%;** SMB (31.7%), SbMB (28.6%), OMC (8.7%), PMC (8.5%), PDB (4.5%), SDB (3.8%), PMB (3.6%), ODC (2.7%)	**72.70%;** SbMB (39.1%), PMC (18.5%), SMB (17.1%), SbDB (7.7%), PMB (4.8%), OMC (4.2%)	**54.70%;** SMB (17%), OMC (16.9%), SbMB (12%), SDB (9.7%), PDB (9.4%), SDSe (8%), PMB (7.3%), PMC (7.4%), FNSe (4.8%)	**52.30%;** SbMB (16.7%), SDSe (15.7%), ODC (13.4%), SMB (11%), OMC (7.5%), PDB (7.5%), SDB (6.3%), MB (5.8%), FNSe (5%), PMC (4.8%)	

Table 6: Taxonomic polychaete communities explained by environmental parameters: results of sequential tests on the best distance-based linear model (DistLM) based on the AIC$_C$ (Table S4) and variation explained along each axis of the best DistLM. The procedure included the 11 predictor variables to explain the variation in polychaete community composition on the basis of taxonomic groups (Bray-Curtis resemblance matrix). *P* values of significant predictor variables in boldface type. SD-10-year-ice = standard deviation of the daily mean values (%) of the Antarctic summer sea-ice cover (Dec–Feb) between 2010–2019, Depth = mean MUC sampling depth per station, Prop = probability, Cumul = cumulative probability, res.df = residual degrees of freedom.

Sequential Tests

	Adj. R^2	**SS (trace)**	**Pseudo-*F***	***P***	**Prop.**	**Cumul.**	**res.df**
Depth	0.059	4367.2	1.94	0.074	0.122	0.122	14
TOC	0.248	8111.3	4.52	**0.001**	**0.226**	0.348	13
SD-10-year-ice	0.389	5844.2	4.01	**0.001**	**0.163**	0.512	12

Percentage of variation explained by individual axes

	% explained variation out of fitted model		% explained variation out of total variation	
Axis	Individual	Cumulative	Individual	Cumulative
1	69.6	69.6	35.6	35.6
2	18.8	88.5	9.6	45.3
3	11.5	100.0	5.9	51.2

Best solution: Adj. $R^2 = 0.389$; $R^2 = 0.512$; RSS = 17496; 3 variables

Table 7: Functional polychaete communities explained by environmental parameters: results of sequential tests on the best distance-based linear model (DistLM) based on the AIC_C (Table S5) and variation explained along each axis of the best DistLM. The procedure included the 11 predictor variables to explain the variation in polychaete community composition on the basis of functional groups (Bray-Curtis resemblance matrix). P values of significant predictor variables in boldface type. SD-10-year-ice = standard deviation of the daily mean values (%) of the Antarctic summer sea-ice cover (Dec–Feb) between 2010–2019, Depth = mean MUC sampling depth per station, Prop = probability, Cumul = cumulative probability, res.df = residual degrees of freedom.

Sequential Tests							
	Adj. R^2	SS (trace)	**Pseudo-*F***	***P***	Prop.	Cumul.	res.df
Depth	0.080	4217.1	2.31	0.054	0.142	0.142	14
TOC	0.311	7769.2	5.68	**0.001**	**0.261**	0.403	13
SD-10-year-ice	0.449	4671.2	4.27	**0.002**	**0.157**	0.560	12

Percentage of variation explained by individual axes				
	% explained variation out of fitted model		% explained variation out of total variation	
Axis	Individual	Cumulative	Individual	Cumulative
1	73.8	73.8	41.3	41.3
2	15.2	89.0	8.5	49.8
3	11.0	100	6.1	56.0
Best solution: Adj. R^2 = 0.449; R^2 = 0.560; RSS = 13115, 3 variables				

FIGURES

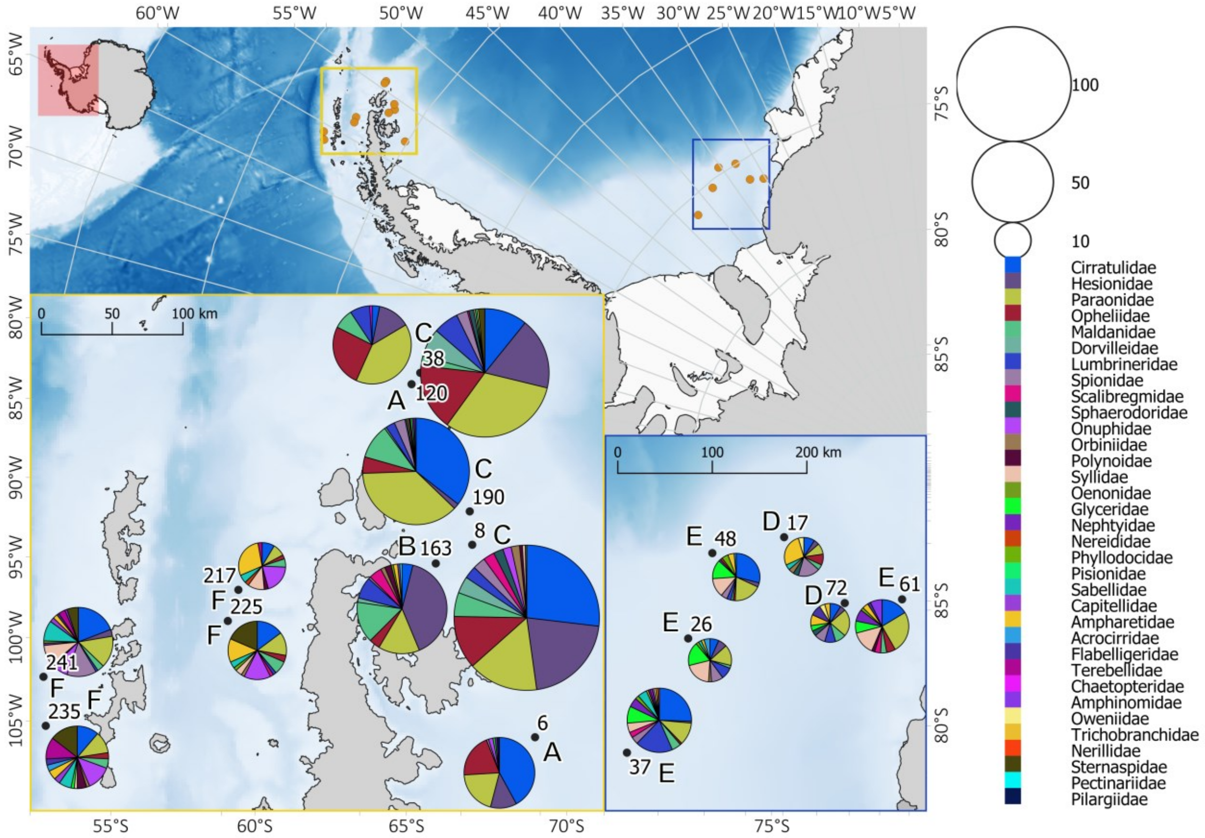

Figure 1: Taxonomic polychaete community composition at family level: fauna abundance from single core data averaged per station during RV *Polarstern* expedition PS81, PS118 around the Antarctic Peninsula (10 stations, yellow frame) and PS96 to the Filchner Trough region (6 stations, blue frame). Black dots with small numbers indicate sampling stations. Size of bubbles shows the abundance of polychaetes per 100 cm^2. Red box represents the chosen map section of the SO. Letters represent clusters (A–F) of the taxonomic polychaete community.

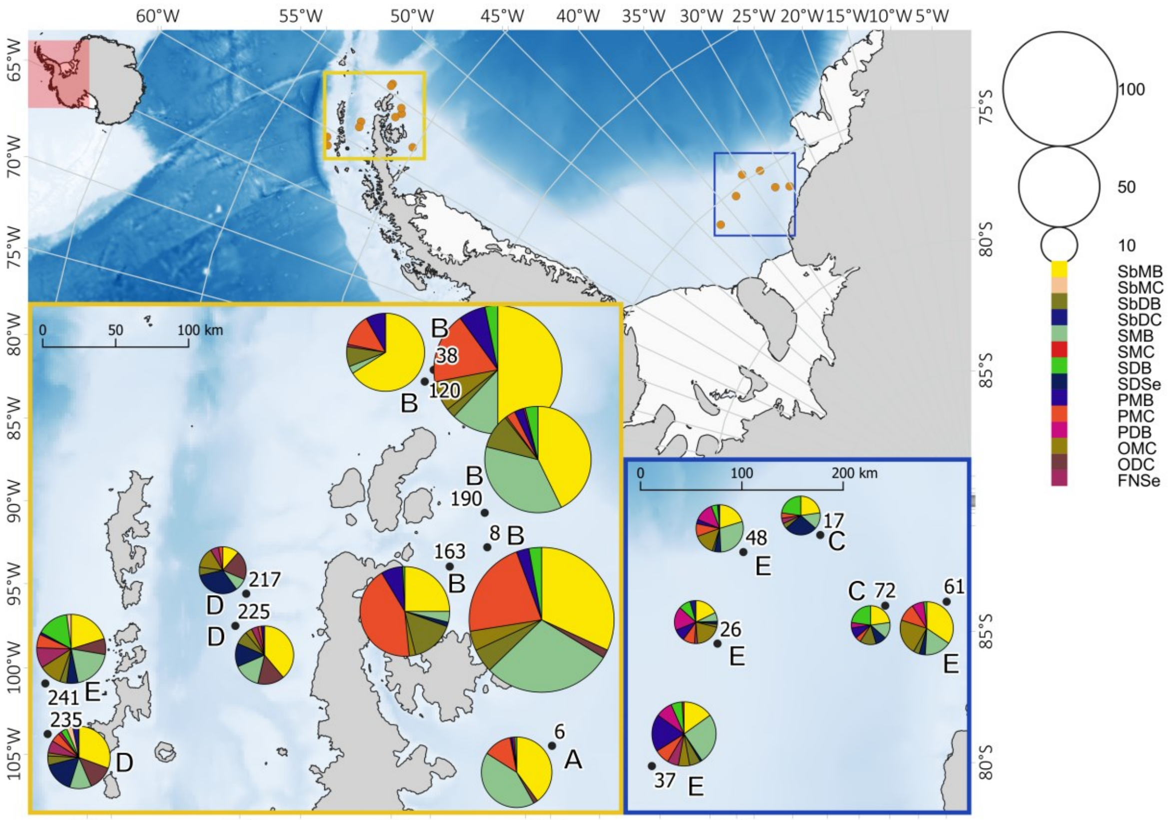

Figure 2: Functional polychaete community composition based on feeding, motility and mobility type: fauna abundance from single core data averaged per station during RV *Polarstern* expeditions PS81 and PS118 around the Antarctic Peninsula (10 stations, yellow frame) and PS96 to the Filchner Trough region (6 stations, blue frame). Black dots with small numbers indicate sampling stations. Size of bubbles shows the abundance of polychaetes per 100 cm^2 (same as Figure 1). Feeding types: Sb = subsurface deposit feeder, S = surface deposit feeder, O = omnivore, P = predator, F = suspension/filter feeder; Motility: M = motile, D = discretely motile, N = none; Mobility: B = burrowing, C = crawling, Se = sessile. Red box represents the chosen map section of the SO. Letters represent clusters (A–E) of the functional polychaete community.

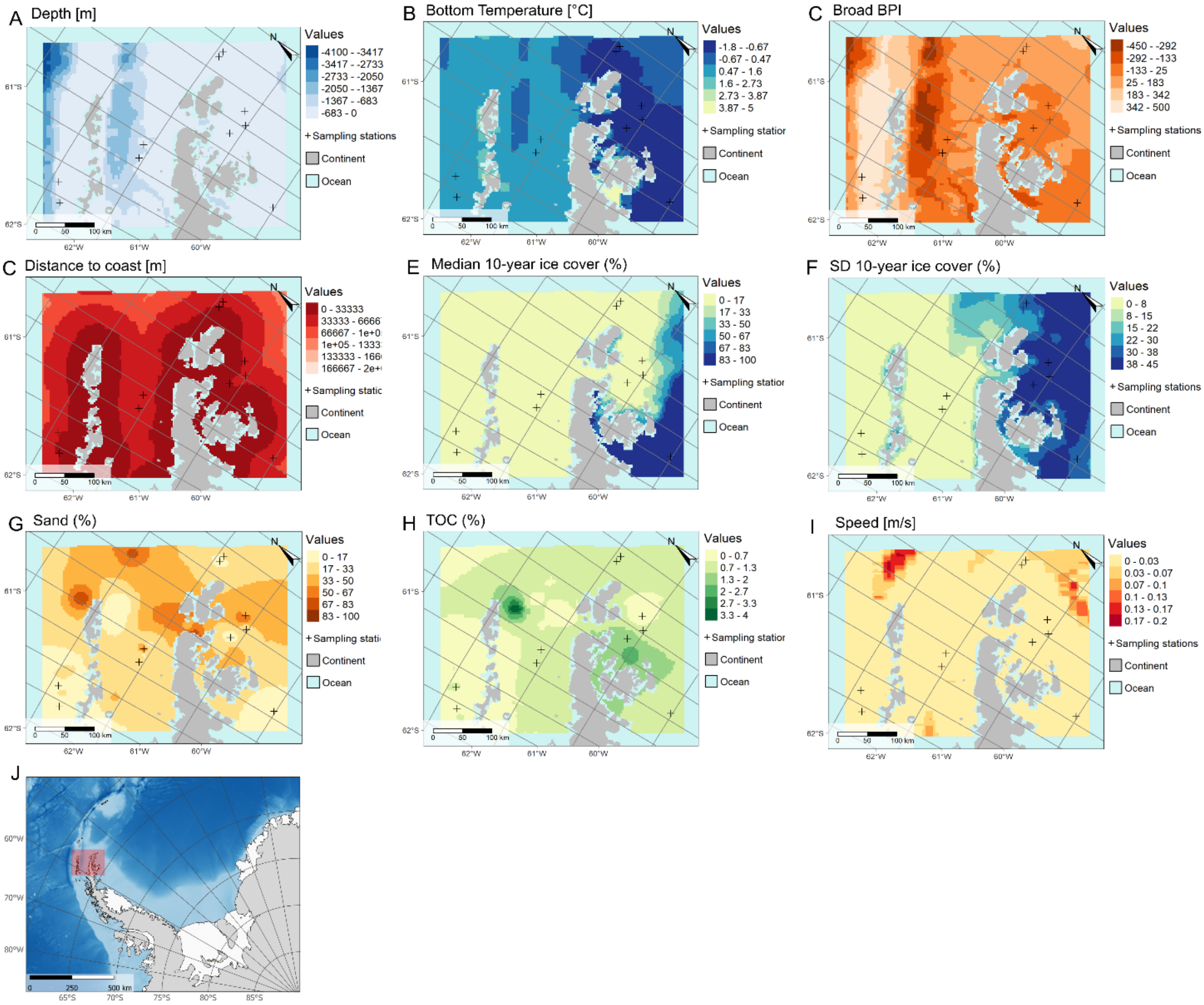

Figure 3: Environmental input data for the k mean clustering algorithm in the AP region, small crosses numbers indicate sampling sites: (A) Depth [m], (B) Bottom Temperature [°C], (C) Broad BPI, (D) Distance to coast [m], (E) Median 10-year ice cover of the daily mean values (%) of the Antarctic summer sea-ice cover (Dec–Feb) between 2010–2019, (F) Standard deviation of the daily mean values (%) of the Antarctic summer sea-ice cover (Dec–Feb) between 2010–2019, (G) Sand (%), (H) Total organic carbon in the sediment (%), (I) Speed [m/s], (J) overview and red box represents the chosen map section of the SO for input data.

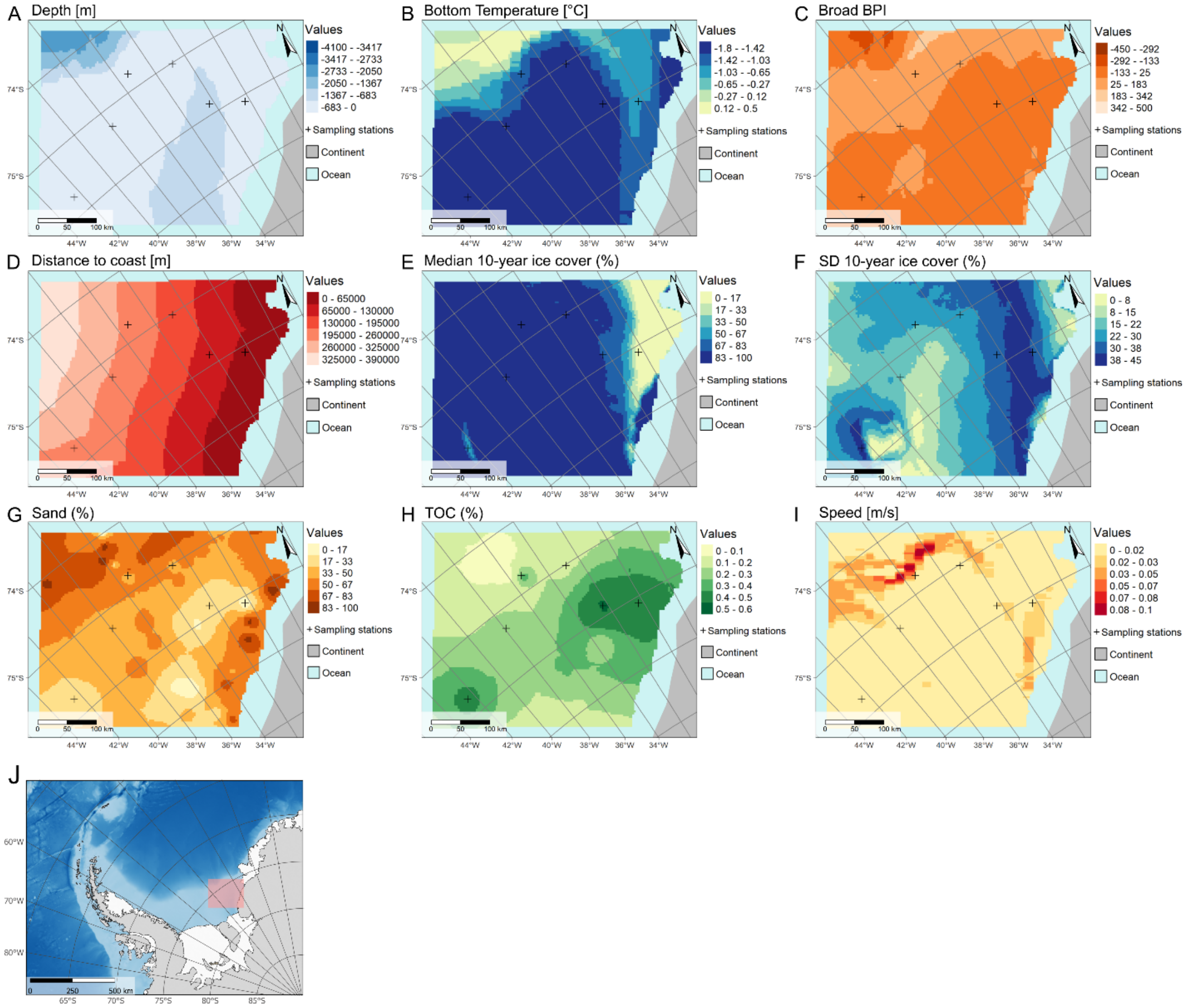

Figure 4: Environmental input data for the k mean clustering algorithm in the FT region, small crosses numbers indicate sampling sites: (A) Depth [m], (B) Bottom Temperature [°C], (C) Broad BPI, (D) Distance to coast [m], (E) Median 10-year ice cover of the daily mean values (%) of the Antarctic summer sea-ice cover (Dec–Feb) between 2010–2019, (F) Standard deviation of the daily mean values (%) of the Antarctic summer sea-ice cover (Dec–Feb) between 2010–2019, (G) Sand (%), (H) Total organic carbon in the sediment (%), (I) Speed [m/s], (J) overview and red box represents the chosen map section of the SO for input data.

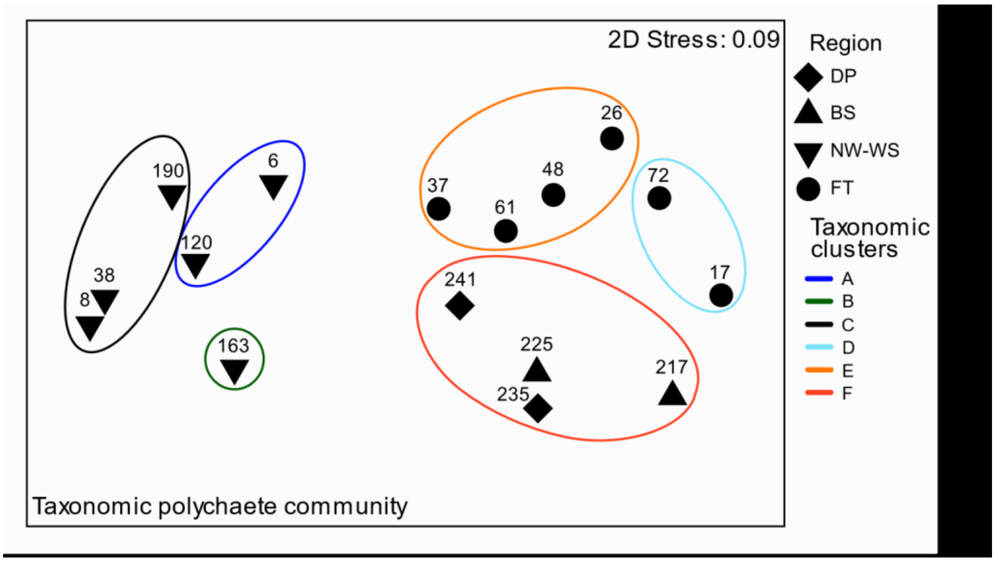

Figure 5: Similarity of the taxonomic polychaete community (at family level): non-metric multidimensional scaling (nMDS) of the Bray-Curtis similarity of non-transformed fauna abundance data of stations sampled in different regions (see map Figure 1) during PS81, PS96 and PS118. Ellipses represent taxonomic clusters (A–F) of the polychaete community (see Figure S2).

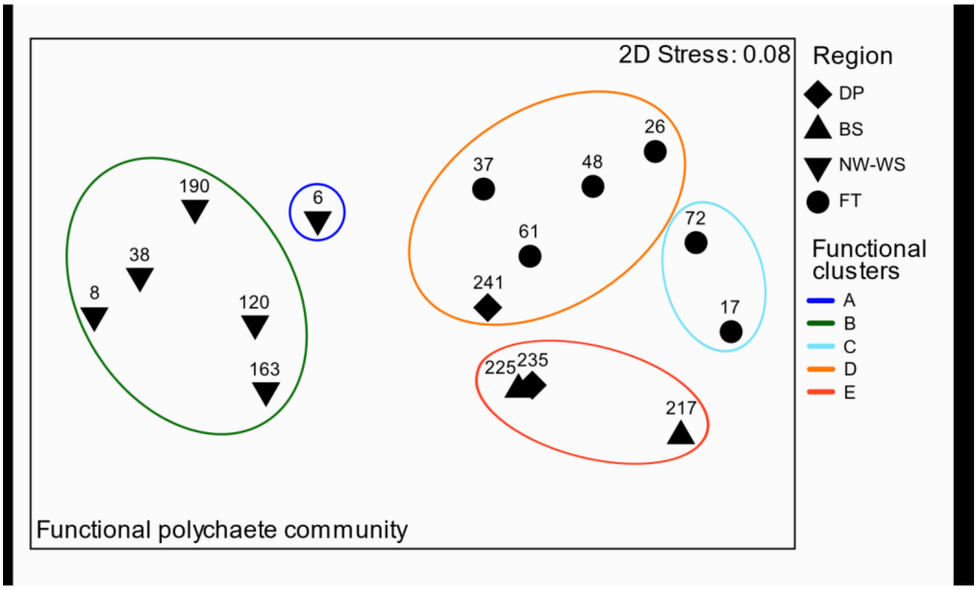

Figure 6: Similarity of the functional polychaete community: non-metric multidimensional scaling (nMDS) of the Bray-Curtis similarity of non-transformed fauna abundance data of stations sampled in different regions (see map Figure 2) during PS81, PS96 and PS118. Ellipses represent functional clusters (A–E) of the polychaete community (see Figure S3)

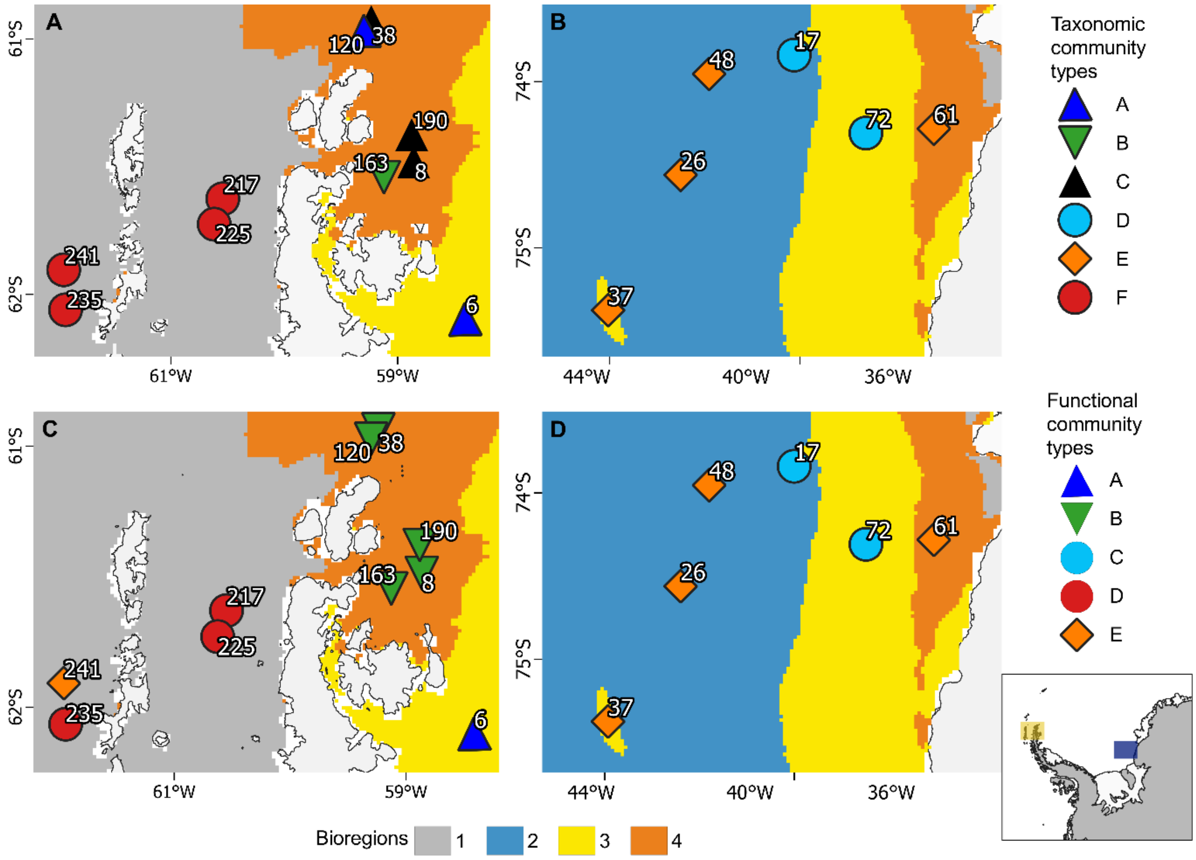

Figure 7: Bioregion (${}_4$B1–${}_4$B4) and taxonomic (${}_{Tax}$A–${}_{Tax}$F) and functional (${}_{Func}$A–${}_{Func}$E) community type distribution in AP (**A, C**) and FT (**B, D**): Bioregion resulting from *k*-means clustering analysis of 9 environmental variables (Depth_s, BPI_s, Dist_coast_s, Median-10-year-ice_s, SD-10-year-ice_s, ${}_{bottom}$T_s, Speed_s, TOC_s, Sand_s). **A**: AP region with taxonomic community types, **B**: FT region with taxonomic community types, **C**: AP region with taxonomic community types, **D**: FT region with functional community types. The yellow and blue box represent the chosen AP and FT map sections, respectively, of Antarctica.

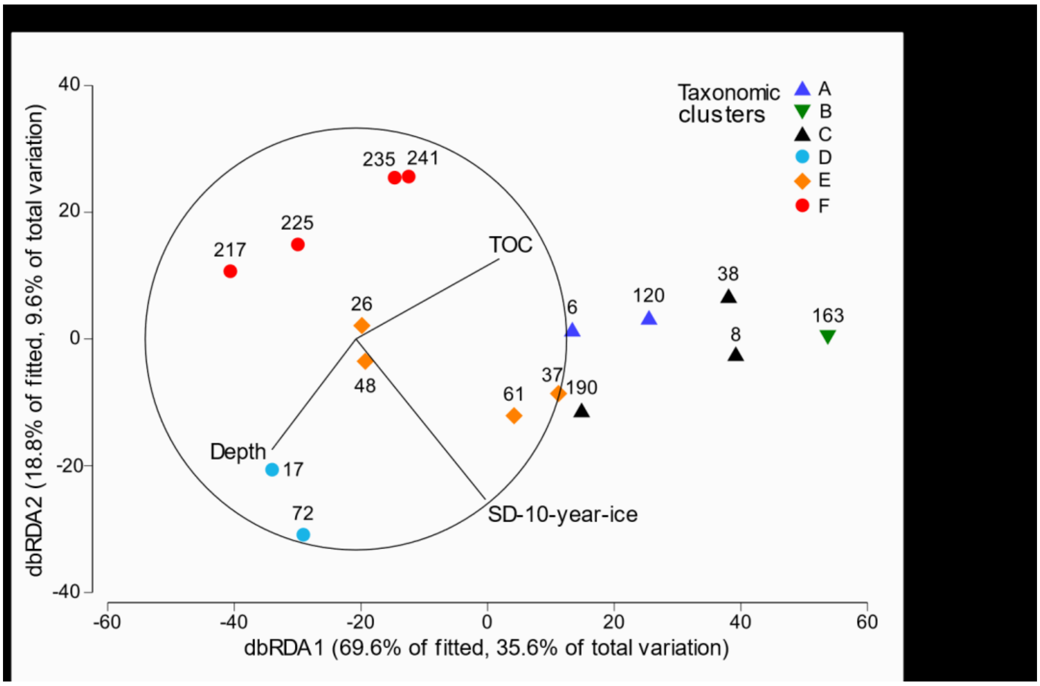

Figure 8: Environmental drivers for the taxonomic polychaete community composition: distance-based redundancy analysis (dbRDA) of environmental parameters explaining the multivariate fauna community of stations from different taxonomic clusters (A–F) sampled from different regions during PS81, PS96 and PS118 (see map Figure 1 and Table 1). Parameters: (Depth = sampling depth measured from the sampling device, TOC = % total organic carbon, SD-10-year-ice: standard deviation of the daily mean values (%) of the Antarctic summer sea-ice cover (Dec–Feb) between 2010–2019.

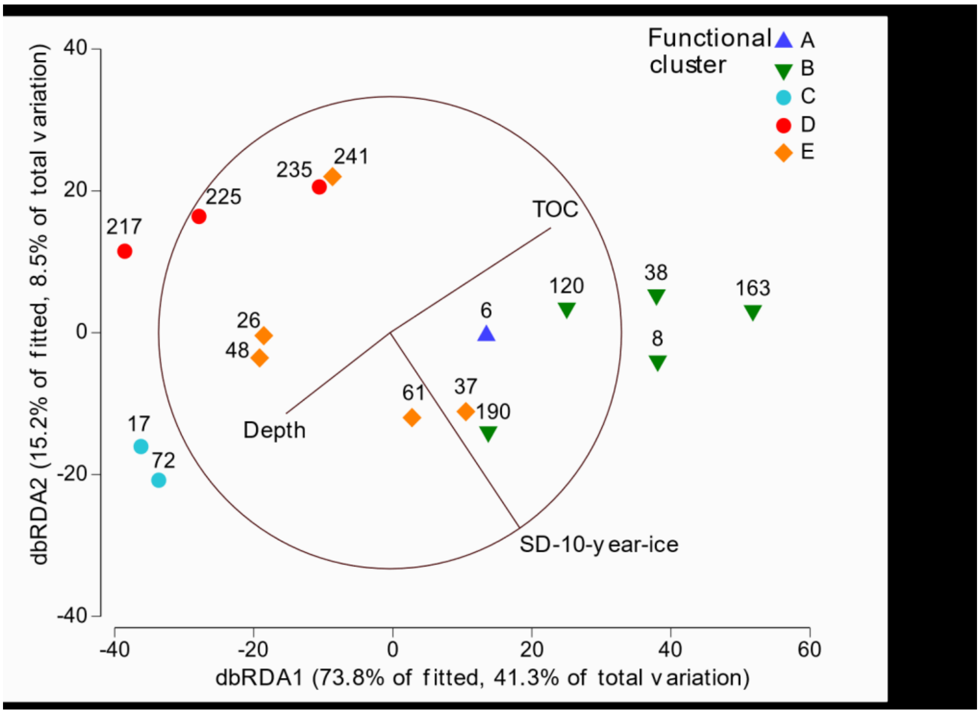

Figure 9: Environmental drivers for the functional polychaete community composition: distance-based redundancy analysis (dbRDA) of environmental parameters explaining the multivariate fauna community of stations from different functional clusters (A–E) sampled from different regions during PS81, PS96 and PS118 (see map Figure 2 and Table 1). Parameters: (Depth = sampling depth measured from the sampling device, TOC = % total organic carbon, SD-10-year-ice: standard deviation of the daily mean values (%) of the Antarctic summer sea-ice cover (Dec–Feb) between 2010–2019.

Supplementary material

Supplementary material thesis

Table S1: Benthic community studies in the extended Weddell Sea (WS) including the Antarctic Peninsula (AP) and southeastern WS, using different sampling advices: multicorer (MUC), agassiz trawl (AGT), giant box corer (GBC), van Veen grab and via sea-bed imaging (SBI). Table does not include shallow-water studies. The following abbreviation were used in this table: FT: Filchner Trough, T_{bottom}: water temperature near the seafloor, Sal_{bottom}: water salinity near the seafloor, C/N_{molar}: molar carbon:nitrogen ratio, Chl$a$: content of chlorophyll a. For more information on the respective studies, please refer to the given references.

Region	Subregion	Fauna	Dominant group	Substrat information	Described and measured environmental parameters	Depth [m]	Sampling method	Reference
Southeastern WS & Lazarev Sea	Halley Bay & Kapp Norvegia	epifauna	megafauna: porifera, ascidiacea, bryozoa	soft bottom	distance to coast, characterization of sediment and cover of phytodetritus, water depth	99–1243	SBI	Gutt & Starmans (1998)
Southeastern WS & Lazarev Sea	Halley Bay & Kapp Norvegia	in- & epifauna	macrofauna: poriferans, echinoderms, polychaetes,	soft bottom	$_{bottom}T$, water depth	132–4293	MUC	Brey & Gerdes (1998)
Southeastern WS	Halley Bay	infauna	meiofauna: nematodes, copepods, bivalves, polychaetes	soft sediments (Silt)	grain size, organic carbon content, C/N_{molar}, porosity, water depth	500–2000	MUC	Herman & Dahms (1992)
Southeastern WS	FT region	infauna	polychaetes, bivalves, ophiuroids, clitellate worms, amphipods (deposit feeders)	soft sediment (Silt&Clay, Sand)	T_{bottom}, Sal_{bottom}, sea-cover, grain size, organic carbon content, water depth	243–1217	MUC	Pineda-Metz et al. (2019)
		epifauna	ophiuroids, polychaetes, holothurians, tunicates (suspension feeders)				SBI	
Southeastern WS	FT region	**infauna & some epifauna**	**meiofauna:** nematodes, copepods, kinorhynchs, tardigrades	soft sediments	water depth, grain size, organic carbon content, C/N_{molar}, benthic pigment content, water-column pigments (Chla_{Cmax}, Chla_{bottom}), T_{bottom}, Sal_{bottom}, T_{Cmax}, Sal_{Cmax}, **ice-cover parameters**	416–755	MUC, GKG	**chapter I**
			macrofauna: polychaetes, echinoderms, isopoda					
		polychaetes (taxonomic and functional groups)	cirratulids, paraonids, syllids, lumbrinerids, ampharetids, glycerids, spionides					**chapter III**
Southeastern WS	Eastern shelf region	epifauna	sponges and bryozoans (suspension feeders)	sand, stones (rarely soft bottom)	sediment characterization, water depth	204–445	AGT	Voß (1988)
	Southern shelf region		bryozoans (suspension feeders)	sand, some soft bottom with		220–531		

Region	Subregion	Fauna	Dominant group	Substrat information	Described and measured environmental parameters	Depth [m]	Sampling method	Reference
				stones				
	Southern trough region		holothurians (deposit feeders)	soft bottom with stones		622–1176		
Southeastern WS		in-& epifauna	sponges, holothurians, asteroids, polychaetes	soft bottom with mud, sand gravel, boulders	sediment characterization, water depth	170–2037	MUC	Gerdes et al. (1992)
Southeastern WS		epifauna	macrofauna: sessile suspension feeder		water depth	100–283	SBI	Gutt & Piepenburg (2003)
Eastern WS		in-& epifauna	polychaetes, amphipods, echinoderms (mobile forms)	soft bottom	sediment characterization, water depth	225–360	MUC, SBI	Gerdes et al. (2003)
Southeastern WS		in-& epifauna	polychaetes, bivalves, ophiuroids	soft bottom (high Sand)	water depth	311–489	MUC	Sañé et al. (2012)
Northwestern WS			Polychaetes, bivalves, gastropods, ophiuroids	soft bottom (high Silt&Clay)	lipid, protein & carbohydrate concentration, grain size, water depth	239–446		
Northwestern WS	Larsen A/B region	infauna	meiofauna: nematodes, copepods	soft bottom	grain size, benthic pigment content, characterization of anoxia, water depth	242–4068	MUC	Rose et al. (2014)
Northwestern WS	Larsen A/B region	infauna	meiofauna: nematodes, copepods, copepod nauplii	soft bottom > 400m	T_{bottom}, Sal_{bottom}, sediment characterization	146–446	MUC	Gutt et al. (2011)
			macrofauna: actinians, polychaetes				AGT	
		epifauna	macro- &megafauna: sponges, ascidians, hydrocorals	hard bottom < 300m			SBI	
Northwestern WS	Larsen A	epifauna	macro- & megafauna focusing on ascidians, ophiuroids	hard bottom (cobble)	T_{bottom}, Sal_{bottom}, bathymetry, sea-ice cover	~200	SBI	Gutt et al. (2013)
	Larsen B			soft sediment				
South Shetland Island	King George Island	in-& epifauna	polychaetes, bivalves, echinoderms, crustaceans	soft bottom	sediment characterization, water depth	15–250	van Veen grab	Jażdżeski et al. (1986)
South Shetland Island	King George Island	infauna	macrofauna: polychaetes, bivalves, crustaceans ophiuroids	soft sediment	T_{bottom}, Sal_{bottom}, grain size, water depth	120–2000	MUC	Piepenburg et al. (2002)
		epifauna	megafauna: ophiuroids, pycnogonids, sponges, hydrozoa			120–930	SBI	

Region	Subregion	Fauna	Dominant group	Substrat information	Described and measured environmental parameters	Depth [m]	Sampling method	Reference
South Shetland Island	Elephant Island	in- & epifauna	macrofauna: polychaetes, molluscs, crustaceans, echinoderms	soft sediments	water depth	60–850	GBC, van Veen grab	Mühlenhardt-Siegel (1988)
AP	Drake Passage	infauna	meiofauna: nematodes, copepods, kinorhynchs, ostracods, tardigrades	soft sediments	water depth, grain size, organic carbon content, C/N_{molar}, benthic pigment content, water-column pigments ($\mathrm{Chl}a_{Cmax}$, $\mathrm{Chl}a_{bottom}$), T_{bottom}, Sal_{bottom}, T_{Cmax}, Sal_{Cmax}	220–758	MUC, GKG	Veit-Köhler et al. (2018)
	Bransfield Strait							
	Northwestern WS							
AP	Drake Passage	**infauna & some epifauna** **integrate meiofauna data** (Veit-Köhler et al. 2018) with **macrofauna data**	polychaetes, amphipods, isopoda	soft sediments	water depth, grain size, organic carbon content, C/N_{molar}, benthic pigment content, water-column pigments ($\mathrm{Chl}a_{Cmax}$, $\mathrm{Chl}a_{bottom}$), T_{bottom}, Sal_{bottom}, T_{Cmax}, Sal_{Cmax}, **ice-cover parameters**	222–757	MUC, GKG	**chapter I**
	Bransfield Strait		polychaetes, amphipods, isopoda					
	Northwestern WS		polychaetes, bivalves, echinoderms, ostracods					
AP	Drake Passage	**polychaetes (taxonomic and functional groups)**	paraonids, cirratulids, spinodes, syllids, sabellids	soft sediments	water depth, grain size, organic carbon content, C/N_{molar}, benthic pigment content, water-column pigments ($\mathrm{Chl}a_{Cmax}$, $\mathrm{Chl}a_{bottom}$), T_{bottom}, Sal_{bottom}, T_{Cmax}, Sal_{Cmax}, **ice-cover parameters**	222–757	MUC, GKG	**chapter III**
	Bransfield Strait		onuphids, sternaspids, ampharetids, paraonids					
	Northwestern WS		paraonids, cirratulids, opheliids, hesionids					
AP	Drake Passage	epifauna	macrofauna: hexactinellids, ascidians, holothurians	soft sediments	T_{bottom}, Sal_{bottom}, $oxygen_{bottom}$, surface Chl*a* & sea-ice cover (satellite data), seafloor ruggedness & seabed slope, water depth	20–780	AGT	Gutt et al. (2016)
	Bransfield Strait		macrofauna: demosponges, ophiuroids, echinoids (sessile suspension feeders)					
	Northwestern WS		macrofauna: ascidians, demosponges, epifaunal polychaetes (sessile suspension feeders)					
AP	Drake Passage	epifauna	megafauna: echinoids, crinoids, ophiuroids, anthozoans, bryozoans	soft bottom	T_{bottom}, Sal_{bottom}, $oxygen_{bottom}$, surface Chl*a* & sea-ice cover (satellite data), seafloor ruggedness & seabed slope, visual classification of hard substrate, water depth	32–786	SBI	Gutt et al. (2019)
	Bransfield Strait		megafauna: solitary and colonial ascidians, asteroids, gorgonians, bryozoans	hard bottom				

Region	**Subregion**	**Fauna**	**Dominant group**	**Substrat information**	**Described and measured environmental parameters**	**Depth [m]**	**Sampling method**	**Reference**
	Northwestern WS		megafauna: ophiuroids, gorgonians, demosponges	mix soft and hard bottom				
West AP		in- & epifauna	macrofauna: polychaetes, bivalves, crustaceans	soft bottom (high Silt&Clay)	water depth	550–625	MUC, GBC	Glover et al. (2008)
West AP		epifauna	megafauna: holothurians, cnidarians	soft bottom (high Silt&Clay)	pigment content (phytodetritus), water depth	526–641	SBI	Sumida et al. (2008)

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Supplementary material chapter I

Table S1. Results of the one-way analysis of variance (ANOVA) with the factor “ice-cover category,” 5 levels, and the Tukey’s post-hoc test for the parameters C/N$_{molar}$ and Chl$a_{C\mathrm{max}}$. Abbreviations: df = degrees of freedom, SS = sum of square, MS = mean square, np = not possible.

ANOVA—Tukey test								
Environmental parameters	**Normality test *P***	**Equal variance Test *P***	**Source of variation**	**df**	**SS**	**MS**	**Pseudo-*F***	***P***
C/N$_{molar}$	0.094	0.135	ice cover category	4	171.991	42.997	34.457	< 0.001
			Residuals	52	64.890	1.248		
			Total	56	236.881			
Chl$a_{C\mathrm{max}}$	0.299	0.463	ice cover category	4	0.649	0.162	26.308	< 0.001
			Residuals	11	0.068	0.006		
			Total	15	0.716			

All pairwise multiple comparison procedure				
C/N$_{molar}$			**Chl$a_{C\mathrm{max}}$**	
Comparison	**Difference of means**	***P***	**Difference of means**	***P***
I and II	**1.678**	**0.029**	**0.547**	**<0.001**
I and III	**0.832**	**0.622**	**0.690**	**<0.001**
I and IV	**0.973**	**0.374**	**0.449**	**<0.001**
I and V	**3.121**	**<0.001**	**0.585**	**<0.001**
II and. III	0.846	0.416	0.143	0.163
II and IV	2.651	<0.001	0.099	np
II and V	4.799	<0.001	0.038	np
III and IV	**1.805**	**0.003**	**0.241**	**0.021**
III and V	3.953	<0.001	0.105	np
IV and V	2.149	<0.001	0.136	0.275

Table S2. Results of the Kruskal-Wallis test on ranks and the pairwise multiple comparison procedures of Dunn's Method per ice-cover category for the parameters Chl*a*, Phaeo, Chl*a*/CPE, TOC, and Chla_{bottom}. Abbreviations: df = degrees of freedom, H = test value of the Kurstkal Wallis test, np = not possible.

Kruskal-Wallis			
Environmental parameters	**df**	**H**	***P*-values**
Chl*a*	4	42.058	< 0.001
Phaeo	4	26.603	< 0.001
Chl*a* /CPE	4	41.216	< 0.001
TOC	4	46.830	< 0.001
Chla_{bottom}	4	9.639	< 0.001

Dunn's test								
	Chl*a*		**Phaeo**		**Chl*a*/CPE**		**TOC**	
Comparison	**Diff. of ranks**	***P***	**Diff. of ranks**	***P***	**Diff. of ranks**	***P***	**Diff. of ranks**	***P***
I and II	21.500	> 0.05	10.750	np	19.250	> 0.05	3.872	np
I and III	36.000	**< 0.05**	31.056	**< 0.05**	28.000	**< 0.05**	11.222	> 0.05
I and IV	12.000	np	17.750	> 0.05	4.375	np	15.792	> 0.05
I and V	5.692	> 0.05	1.577	np	8.077	> 0.05	30.205	**< 0.05**
II and III	14.500	> 0.05	20.306	**< 0.05**	8.750	> 0.05	7.350	np
II and IV	9.500	np	7.000	np	23.625	**< 0.05**	19.663	**< 0.05**
II and V	27.192	**< 0.05**	12.327	> 0.05	27.327	**< 0.05**	34.077	**< 0.05**
III and IV	24.000	**< 0.05**	13.306	> 0.05	32.375	**< 0.05**	27.014	**< 0.05**
III and V	41.692	**< 0.05**	32.632	**< 0.05**	36.077	**< 0.05**	41.427	**< 0.05**
IV and V	17.692	**< 0.05**	19.327	**< 0.05**	3.702	np	14.413	> 0.05

Table S3. Meiofauna communities: selection of best model by distance based linear modeling for meiofauna community composition (Bray-Curtis resemblance matrix) and number of chosen variables based on the AIC$_{C}$ (boldface type). Selection among 11 possible environmental predictors for the variables 1-year ice-cover, 9-year-ice cover, T_{bottom}, Chl$a_{C\mathrm{max}}$, Chla_{bottom}, Chl*a*, Chl*a*/CPE, TOC, C/N$_{molar}$, silt & clay, and coarse sand. The R^2 and AIC$_c$ for the 10 best models are shown.

Selection criterion: AIC$_C$			
Selection procedure: BEST			
Overall best solution			
AIC$_C$	**R^2**	RSS	No. variables
247.59	**0.8751**	**2947**	**11**
248.82	0.8641	3206.3	10
248.89	0.8800	2830.3	12
249.1	0.8715	3030.6	11
249.99	0.8694	3081	11
250.24	0.8604	3292.1	10
250.72	0.8676	3123.2	11
250.91	0.8587	3333.2	10
251.07	0.8583	3343.1	10
251.23	0.8578	3353.1	10

Table S4: Macrofauna communities: selection of best model by distance based linear modeling for macrofauna community composition (Bray-Curtis resemblance matrix) and number of chosen variables based on the AIC$_C$ (boldface type). Selection among 11 possible environmental predictors for the variables: 1-year-ice cover, 9-year-ice cover, T_{bottom}, Chla_{Cmax}, Chla_{bottom}, Chl*a*, Chl*a*/CPE, TOC, C/N$_{molar}$, silt & clay, and coarse sand. The R^2 and AIC$_C$ for the 10 best models are shown.

Selection criterion: AIC$_C$			
Selection procedure: BEST			
Overall best solution			
AIC$_C$	**R^2**	**RSS**	**No. variables**
392.44	0.7181	30101	9
392.96	0.7011	31907	8
392.98	0.7154	30382	9
393.28	0.7140	30537	9
393.58	0.7269	29155	10
393.61	0.6979	32257	8
393.72	0.7119	30763	9
393.86	0.7111	30839	9
393.96	0.7252	29343	10
394.05	0.7102	30936	9

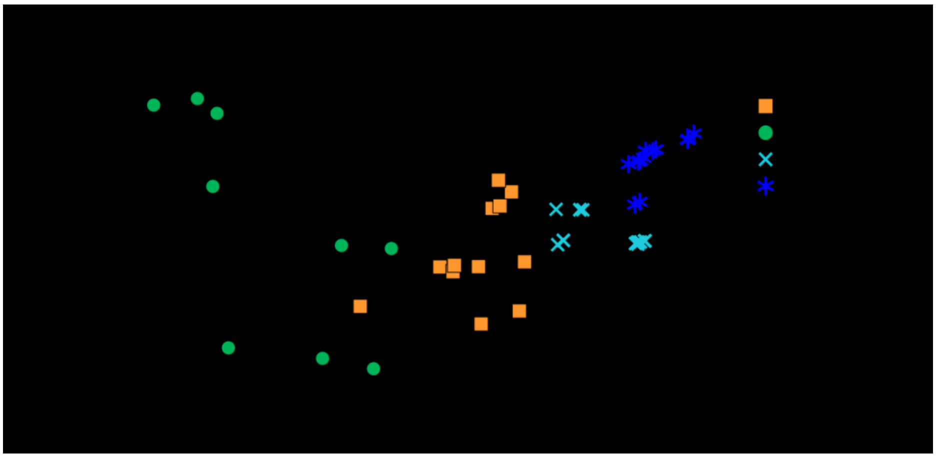

Fig. S1: Food related parameters: nonmetric multidimensional scaling of the Euclidean distance of nontransformed environmental data (Chl*a*, Chl*a*/CPE, TOC, C/N$_{molar}$, Chla_{Cmax}, Chla_{bottom}) of single cores collected in regions in different ice-cover categories during PS 81 and PS 96.

Text S1: Habitat Summaries: characteristics of ice-cover categories and their significance for faunal community compositions

Ice-cover category I

Ice-cover category I is found in Drake Passage. The region is influenced by Circumpolar Deep Water of the Antarctic Circumpolar Current (Hofmann et al. 1996). High water temperatures, in this study T_{bottom} 0.42–0.65°C and T_{Cmax} 1.12–1.26°C, inhibit the development of sea ice throughout the year. Nutrient-rich water masses affect primary production in the water column (Hofmann et al. 1996). Although the highest Chla_{Cmax} was found in the water column at the sampling dates, category I shows very low Chl*a* and CPE contents and intermediate concentrations of organic matter in the sediment. This discrepancy may result from lateral advection of primary production to other regions (Yoon et al. 1992, Palanques et al. 2002, Isla et al. 2004). Compared to the other categories, the region is characterized by low abundances of macroepibenthos (Gutt et al. 2016), low macrofauna, and intermediate abundances of meiofauna (our study, Veit-Köhler et al. 2018). The high content of silt & clay in the sediments of category I may represent unfavorable conditions for macro(in)fauna, which showed the lowest number of taxa in the complete study.

Ice-cover category II

This category was found in Bransfield Strait. It shows a wide range of water temperatures (T_{bottom}: −1.1 to –0.7°C), induced by different water inflows: warm water masses from the Antarctic Circumpolar Current and cold water from the Weddell Sea. Ice cover therefore does not usually exist in March and forms on an irregular basis in April at the earliest. Despite slightly better food availability and quality than in category I the lowest copepod abundances were found in category II. Strong currents and complex water inflow may explain the high amounts of sand (grain size 63–500 µm) and coarse sand (> 500 µm), representing optimal conditions for burrowing annelids (mostly polychaetes). Annelids, amphipods, and isopods are the characteristic groups of the macrofauna and are a structuring and dominating faunal compartment in category II.

Ice-cover category III

Seasonal ice cover characterizes category III in the northwestern Weddell Sea. This region is dominated by low water temperatures close to the freezing point of seawater. Because of its geographic position close to the boundary of the Antarctic Circumpolar Current (Orsi et al. 1995, Sokolov & Rintoul 2009) and climate change–induced decline of ice cover and thickness (Cook et al. 2005, Turner et al. 2009), it is a more variable region than the high Antarctic. The seasonal ice cover leads to the highest input of fresh organic material to the seafloor (Chl*a* = 17.1 µg g^{-1}, TOC = 1.2%) that was observed in our study. Regular cycles of formation and melting of sea ice lead to the deposition of ice algae and stabilize the water-column, facilitating phytoplankton blooms (Smith et al. 2006, Mincks & Smith 2007, Saba et al. 2014). The highly seasonal input of fresh organic material, combined with the low water temperatures, leads to the creation of food banks in the sediment (Isla et al. 2002, Mincks et al. 2005). The highest CPE values are reported even from deeper sediment layers (3–4 cm up to 102.5 µg g^{-1}), an indicator of bioturbation (Mermillod-Blondin & Rosenberg 2006). Polychaetes, bivalves, and echinoderms are characterized by their burrowing activities and show the highest standing stocks in category III. The high food availability and freshness is also linked to the highest meiofaunal abundance, e.g. nematodes (5848.3 ind. 10 cm^2) and copepods (444.4 ind. 10 cm^2).

Ice-cover categories IV and V

Category IV with high and category V with constant ice cover are assigned to the South and North Filchner Trough regions, respectively. Despite clear differences in summer ice cover, the two regions show similar environmental conditions. Their benthic ecosystems are characterized by the lowest sediment organic contents (TOC) recorded in our study (IV = 0.41%, V = 0.3%). The low water temperatures T_{bottom} (IV: –1.90° C, V: –1.92° C) may decelerate remineralization processes at the seafloor (Isla et al. 2002, Mincks et al. 2005), leading to highly degraded material (C/N_{molar}). Especially category V is characterized by highly polar and extreme environmental settings: constant ice-cover, lowest T_{bottom} and $T_{C\mathrm{max}}$, and the lowest food availability (Chl*a*, TOC) at the seafloor lead to the lowest meio- and macrofauna abundances observed. Tardigrades and loriciferans, however, show abundance patterns opposite to those of the other meiofauna taxa. Tardigrades and loriciferans may prefer the constant but adverse environmental conditions caused by extreme sea-ice cover.

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Supplementary material chapter III

Table S1: Station list and sampling during RV *Polarstern* expeditions PS81 (January 22–March 18, 2013), PS96 (December 06, 2015–February 14, 2016) and PS118 (February 9 – April 10, 2019) of additional stations for sediment sampling of environmental parameters that were used to update existing data sets (total organic carbon: Seiter et al. (2004), Säring et al. (2021), sediment texture: Jerosch et al. (2015), Säring et al. (2021) for the bioregionalization analysis. Multicorers (MUC) and the giant box corer (GKG) were deployed for sediment sampling of environmental parameters. Only successful MUC and GKG deployments are listed. Samples for environmental characterization of the water column (CTD Conductivity. temperature. Chl*a* at the maximum and near-bottom) were collected with a CTD-Rosette equipped with Niskin bottles. For CTD deployments chlorophyll*a*-maximum and near-bottom sampling depths as well as salinity and temperature are given (Schröder et al. 2013, 2016, Janout et al. 2020).

Expedition & Region		**Sts**	**No. of env cores**	**Date**	**Latitude**	**Longitude**	**Depth [m]**	**Gear**	**T_{bottom}**	**Sal$_{bottom}$**
PS81 Antarctic Peninsula (AP)	**Drake Passage (DP)**	238-2		2013-03-08	62'20.73'S	61'20.15'W	20/454	CTD	0.74	34.56
		238-4	1	2013-03-08	62'20.82'S	61'20.01'W	460	MUC		
		238-5	2	2013-03-08	62'20.78'S	61'20.10'W	464	MUC		
		238-6	2	2013-03-08	62'20.80'S	61'20.06'W	467	MUC		
		243-1		2013-03-10	62'12.27'S	60'44.42'W	20/486	CTD	0.99	34.61
		243-3	2	2013-03-10	62'12.32'S	60'44.47'W	498	MUC		
		243-5	2	2013-03-10	62'12.31'S	60'44.54'W	495	MUC		
		247-2		2013-03-11	61'56.90'S	60'07.49'W	15/396	CTD	0.65	34.54
		247-4	2	2013-03-11	61'56.93'S	60'07.48'W	396	MUC		
		247-7	3	2013-03-11	61'56.91'S	60'07.47'W	400	MUC		
		250-1		2013-03-12	62'02.28'S	60'12.11'W	20/479	CTD	0.57	34.57
		250-3	2	2013-03-12	62'02.22'S	60'12.01'W	489	MUC		
		250-4	2	2013-03-12	62'02.24'S	60'12.06'W	488	MUC		
		250-5	2	2013-03-12	62'02.24'S	60'12.03'W	488	MUC		
	Bransfield Strait (BS)	118-1		2013-01-27	62'26.47'S	56'17.26'W	20/420	CTD	-1.14	34.53
		118-9	1	2013-01-27	62'26.95'S	56'17.14'W	423	MUC		
		118-10	1	2013-01-27	62'26.90'S	56'17.19'W	427	MUC		
		193-1		2013-02-23	62'43.01'S	57'34.16'W	20/562	CTD	-0.95	34.52
		193-4	2	2013-02-23	62'43.03'S	57'34.23'W	577	MUC		
		193-5	2	2013-02-23	62'43.03'S	57'34.24'W	579	MUC		
		193-6	2	2013-02-23	62'43.03'S	57'34.25'W	578	MUC		
		196-1		2013-02-24	62'48.01'S	57'04.97'W	20/543	CTD	-1.31	34.48
		196-5	1	2013-02-24	62'48.03'S	57'04.97'W	567	MUC		
		196-6	1	2013-02-24	62'48.04'S	57'05.00'W	574	MUC		
		196-7	1	2013-02-24	62'48.00'S	57'04.99'W	559	MUC		
		202-1		2013-02-27	62'56.00'S	58'00.47'W	50/739	CTD	-0.72	34.55
		202-3	1	2013-02-27	62'56.00'S	58'00.49'W	756	MUC		
		202-4	2	2013-02-27	62'56.01'S	58'00.52'W	756	MUC		
		202-5	2	2013-02-27	62'55.99'S	58'00.61'W	757	MUC		
		218-1		2013-03-02	62'56.93'S	58'25.66'W	20/672	CTD	-0.80	34.54
		218-4	2	2013-03-02	62'56.95'S	58'25.81'W	689	MUC		
		218-5	2	2013-03-02	62'56.95'S	58'25.84'W	689	MUC		
		218-6	2	2013-03-02	62'56.93'S	58'25.81'W	689	MUC		
	Northwestern Weddell Sea	162-1		2013-02-10	64'00.27'S	56'44.28'W	20/207	CTD	-1.86	34.45
		162-3	1	2013-02-10	64'00.11'S	56'44.28'W	222	MUC		
		162-4	1	2013-02-10	64'00.07'S	56'44.20'W	223	MUC		
		162-5	2	2013-02-10	64'00.14'S	56'44.33'W	222	MUC		
		185-2	1	2013-02-19	63'52.20'S	55'36.67'W	232	GKG		
		188-3	1	2013-02-20	63'52.01'S	55'35.15'W	310	GKG		
PS118 AP		012-1		2019-03-14	63'48.39'S	55'44.66'W	20.5/449	CTD	-1.21	34.55
		012-6	3	2019-03-14	63'48.99'S	55'42.26'W	455	MUC		
		012-5	2	2019-03-14	63'48.83'S	55'42.70'W	454	MUC		
		012-3	1	2019-03-14	63'48.75'S	55'43.67'W	453	MUC		

Table S2: Detailed list showing the assignment of the polychaete families into the particular functional groups (feeding type: F = filter/ suspension feeder, O = omnivore, P = predator, S = surface deposit feeder, Sb = subsurface deposit feeder; motility: M = motile, D = discretely motile, N = no motility; movement: C = crawling, B = burrowing, Se = sessile; feeding) and the corresponding reference. In cases of uncertainties or ambiguous assignments, comments have been added to underline the classification/assignment.

Family	Feeding type	Reference	Comment	Mobility	Reference	Comment	Movement	Reference
Acrocirridae	Sb	Jumars et al. (2015)		D	Jumars et al. (2015)		C	Jumars et al. (2015)
Ampharetidae	S	Jumars et al. (2015)		D	Jumars et al. (2015)	Jumars et al. (2015): can extent tubes and build new ones	Se	Polytraits Team (2023), Jumars et al. (2015)
Amphinomidae	O	Jumars et al. (2015)		M	Jumars et al. (2015)		C	Polytraits Team (2023), Jumars et al. (2015)
Capitellidae	Sb	Jumars et al. (2015)		M	Jumars et al. (2015)	Jumars et al. (2015): mostly tube builder	Se	Jumars et al. (2015)
Chaetopteridae	F	Jumars et al. (2015)		N	Jumars et al. (2015)	Jumars et al. (2015): tube dwelling	Se	Jumars et al. (2015)
Cirratulidae	S	Polytraits Team (2023), Jumars et al. (2015)		M	Jumars et al. (2015)	Jumars et al. (2015): can be tube dwelling, but here no tube dwellings forms were observed	B	Polytraits Team (2023), Jumars et al. (2015)
Dorvilleidae	O	Jumars et al. (2015)	Jumars et al. (2015): carnivore/scavenger, feed on diatoms, macroalgae, bacterial mats, detritus material	M	Jumars et al. (2015)	Jumars et al. (2015): mostly crawling	C	Jumars et al. (2015)
Flabelligeridae	S	Polytraits Team (2023), Jumars et al. (2015)		D	Jumars et al. (2015)	Jumars et al. (2015): most burrowing, many burrow in sand or mud	B	Jumars et al. (2015)
Glyceridae	P	Polytraits Team (2023), Jumars et al. (2015)		D	Jumars et al. (2015)	Jumars et al. (2015): burrowing, sitting and waiting predator	B	Jumars et al. (2015)
Hesionidae	P	Polytraits Team (2023), Jumars et al. (2015)	Jumars et al. (2015): many carnivores	M	Jumars et al. (2015)	Jumars et al. (2015): some crawl or construct burrow galleries, mostly unknown, personal observation: bodies formed like crawling and motile organisms	C	Jumars et al. (2015)
Lumbrineridae	P	Polytraits Team (2023), Jumars et al. (2015)	individuals had visible jaw	M	Jumars et al. (2015)		B	Jumars et al. (2015)
Maldanidae	Sb	Polytraits Team (2023), Jumars et		D	Jumars et al. (2015)	Jumars et al. (2015): more active, can extent tubes, tube	B	Jumars et al. (2015)

Family	Feeding type	Reference	Comment	Mobility	Reference	Comment	Movement	Reference
		al. (2015)				builder; burrowing in sand and mud		
Nephtyidae	P	Polytraits Team (2023), Jumars et al. (2015)		M	Jumars et al. (2015)	Jumars et al. (2015): burrowing and crawling, but personal observation: body form preferred for crawling movement	C	Jumars et al. (2015)
Nereididae	O	Polytraits Team (2023), Jumars et al. (2015)		M	Jumars et al. (2015)	Jumars et al. (2015): burrowing and crawling, but personal observation: body form preferred for crawling movement	C	Jumars et al. (2015)
Nerillidae	S	Jumars et al. (2015)		M	Jumars et al. (2015)		C	Jumars et al. (2015)
Oenonidae	P	Polytraits Team (2023), Jumars et al. (2015)		M	Jumars et al. (2015)	Jumars et al. (2015): burrowing and crawling, but personal observation: body form preferred for crawling movement	C	Jumars et al. (2015)
Onuphidae	O	Jumars et al. (2015)		D	Jumars et al. (2015)	Jumars et al. (2015): mostly tubicolous, often in soft sediments, but are motile, carry their tubes with them in clearly discrete motility	C	Jumars et al. (2015)
Opheliidae	Sb	Jumars et al. (2015)		M	Jumars et al. (2015)		B	Polytraits Team (2023), Jumars et al. (2015)
Orbiniidae	Sb	Polytraits Team (2023), Jumars et al. (2015)		M	Jumars et al. (2015)		B	Polytraits Team (2023), Jumars et al. (2015)
Paraonidae	Sb	Polytraits Team (2023), Jumars et al. (2015)		M	Jumars et al. (2015)		B	Polytraits Team (2023), Jumars et al. (2015)
Pectinariidae	Sb	Polytraits Team (2023), Jumars et al. (2015)		D	Jumars et al. (2015)		B	Jumars et al. (2015)
Phyllodocidae	P	Polytraits Team (2023), Jumars et al. (2015)		M	Jumars et al. (2015)	Jumars et al. (2015): actively burrowing and crawling	C	Polytraits Team (2023), Jumars et al. (2015)
Pilargiidae	P	Jumars et al. (2015)		M	Jumars et al. (2015)		B	Jumars et al. (2015)
Sigalionidae	P	Jumars et al.		M	Jumars et al. (2015)	Jumars et al. (2015): larger	B	Jumars et al. (2015)

Family	Feeding type	Reference	Comment	Mobility	Reference	Comment	Movement	Reference
		(2015)				morphotype is well suited to burrowing in mud, crawls interstitially		
Polynoidae	P	Polytraits Team (2023), Jumars et al. (2015)		M	Jumars et al. (2015)		C	Polytraits Team (2023), Jumars et al. (2015)
Oweniidae	S	Polytraits Team (2023), Jumars et al. (2015)		D	Jumars et al. (2015)	Jumars et al. (2015): tubicolous, but can move tubes, burrowing in muddy sediment	B	Polytraits Team (2023), Jumars et al. (2015)
Sabellidae	F	Polytraits Team (2023), Jumars et al. (2015)		N	Jumars et al. (2015)		Se	Polytraits Team (2023), Jumars et al. (2015)
Scalibregmatidae	Sb	Jumars et al. (2015)		M	Jumars et al. (2015)		B	Polytraits Team (2023), Jumars et al. (2015)
Sphaerodoridae	S	Jumars et al. (2015)	no jaw was observed, really small individuals	M	Jumars et al. (2015)	but poorly understood, body shape not build for fast crawling	B	Polytraits Team (2023), Jumars et al. (2015)
Spionidae	S	Polytraits Team (2023), Jumars et al. (2015)		D	Jumars et al. (2015)	Jumars et al. (2015): most discretely motile in tubes; a few are more motile; boring species are unlikely to create new tube	B	Jumars et al. (2015)
Sternaspidae	Sb	Jumars et al. (2015)		M	Jumars et al. (2015)		B	Jumars et al. (2015)
Syllidae	O	Jumars et al. (2015)		M	Jumars et al. (2015)		C	Polytraits Team (2023), Jumars et al. (2015)
Terebellidae	S	Polytraits Team (2023), Jumars et al. (2015)		D	Jumars et al. (2015)	Jumars et al. (2015): mostly tube-dwelling, Polytraits: crawling, but here from personal perspective body form was looked like a sessile movement type	Se	Jumars et al. (2015)
Trichobranchidae	Sb	Jumars et al. (2015)		D	Jumars et al. (2015)		B	Jumars et al. (2015)

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Table S3: Results of the Kruskal-Wallis test on ranks and the pairwise multiple comparison procedures of Dunn's Method per bioregion of the $_2$B option for the parameters BPI, Depth, Dist_coast, Speed, $_{bottom}$T, Median-10-year-ice, SD-10-year-ice, Sand and TOC. Abbreviations: df = degrees of freedom, H = test value of the Kruskal-Wallis test.

Kruskal-Wallis			
Environmental parameters	**df**	**H**	***P*-values**
BPI	1	534.17	< 0.001
Depth	1	1112.99	< 0.001
Dist_coast	1	11383.68	< 0.001
Speed	1	3739.49	< 0.001
$_{bottom}$T	1	2662.70	< 0.001
Median-10-year-ice	1	19061.14	< 0.001
SD-10-year-ice	1	5066.94	< 0.001
Sand	1	2662.70	< 0.001
TOC	1	10355.91	< 0.001
Dunn's Test		Comparison	
		$_2$B1 vs. $_2$B2	
		Diff of Ranks	***P***
BPI		2127.22	**< 0.05**
Depth		3070.56	**< 0.05**
Dist_coast		9820.05	**< 0.05**
Speed		5623.17	**< 0.05**
$_{bottom}$T		4749.34	**< 0.05**
Median-10-year-ice		12448.09	**< 0.05**
SD-10-year-ice		6547.78	**< 0.05**
Sand		4749.34	**< 0.05**
TOC		9366.26	**< 0.05**

Table S4: Results of the Kruskal-Wallis test on ranks and the pairwise multiple comparison procedures of Dunn's Method per bioregion of the $_4$B option for the parameters BPI, Depth, Dist_coast, Speed, $_{bottom}$T, Median-10-year-ice, SD-10-year-ice, Sand and TOC. Abbreviations: df = degrees of freedom, H = test value of the Kruskal-Wallis test, np = not possible.

Kruskal-Wallis			
Environmental Parameters	**df**	**H**	***P*- values**
BPI	3	2359.13	< 0.001
Depth	3	3307.36	< 0.001
Dist_coast	3	17,544.59	< 0.001
Speed	3	5,347.89	< 0.001
$_{bottom}$T	3	15,236.93	< 0.001
Median-10-year-ice	3	20,531.64	< 0.001
SD-10-year-ice	3	18,806.66	< 0.001
Sand	3	6,021.45	< 0.001
TOC	3	14,477.09	< 0.001

Dunn's Test	Comparison											
	$_4$B1 vs. $_4$B2		**$_4$B1 vs. $_4$B3**		**$_4$B1 vs. $_4$B4**		**$_4$B2 vs. $_4$B3**		**$_4$B2 vs. $_4$B4**		**$_4$B3 vs. $_4$B4**	
	Diff. of ranks	**P**	**Diff. of ranks**	**P**	**Diff. of ranks**	**P**	**Diff. of ranks**	**P**	**Diff. of ranks**	**P**	**Diff. of ranks**	**P**
BPI	252.94	np	5,418.76	**< 0.05**	25.37	np	5,165.82	**< 0.05**	278.30	> 0.05	5,444.13	**< 0.05**
Depth	727.79	**< 0.05**	1,925.19	**< 0.05**	6,032.29	**< 0.05**	1,197.39	**< 0.05**	6,760.09	**< 0.05**	7,957.48	**< 0.05**
Dist_coast	13,803.30	**< 0.05**	4,337.99	**< 0.05**	7.30	> 0.05	9,465.31	**< 0.05**	13,796.00	**< 0.05**	4,330.70	**< 0.05**
Speed	72.25	**< 0.05**	5,143.19	**< 0.05**	5,754.02	**< 0.05**	3,275.22	**< 0.05**	2,664.39	**< 0.05**	610.83	**< 0.05**
$_{bottom}$T	13,210.81	**< 0.05**	12,492.35	**< 0.05**	7,961.69	**< 0.05**	718.46	**< 0.05**	5,249.12	**< 0.05**	4,530.66	**< 0.05**
Median-10-year-ice	14942.35	**< 0.05**	11820.48	**< 0.05**	3372.06	**< 0.05**	3121.87	**< 0.05**	11570.29	**< 0.05**	8448.42	**< 0.05**
SD-10-year-ice	8229.76	**< 0.05**	15278.06	**< 0.05**	15457.51	**< 0.05**	7048.30	**< 0.05**	7227.75	**< 0.05**	179.45	> 0.05
Sand	8640.64	**< 0.05**	2004.16	**< 0.05**	3929.68	**< 0.05**	6636.48	**< 0.05**	4710.96	**< 0.05**	1925.52	**< 0.05**
TOC	12437.23	**< 0.05**	5036.50	**< 0.05**	431.64	**< 0.05**	7400.73	**< 0.05**	12868.87	**< 0.05**	5468.14	**< 0.05**

Table S5: Biodiversity indexes for the taxonomic polychaete community composition.

Region	Subregion	St.	Total species number *S*	Average ind. number per st. *N*	Species richness (Margalef) *d*	Evenness (Pielou) *J'*	Shannon-Wiener *H'*	Simpson *λ*
Antarctic Peninsula (AP)	Drake Passage (DP)	235	16	29.78	4.42	0.92	2.54	0.09
		241	18	36.44	4.73	0.85	2.46	0.11
	Bransfield Strait (BS)	217	11	16.81	3.54	0.87	2.08	0.16
		225	13	25.94	3.69	0.88	2.26	0.12
	Northwestern Weddell Sea (NW-WS)	6	9	38.04	2.20	0.69	1.52	0.27
		8	15	160.55	2.76	0.78	2.11	0.16
		38	14	125.43	2.69	0.75	1.97	0.18
		120	7	46.59	1.56	0.80	1.55	0.26
		163	15	61.48	3.40	0.73	1.96	0.22
		190	14	86.46	2.92	0.61	1.61	0.28
Filchner Trough (FT)		17	11	11.52	4.09	0.90	2.16	0.14
		26	13	14.13	4.53	0.89	2.27	0.12
		37	20	31.45	5.51	0.80	2.39	0.13
		48	14	17.06	4.58	0.81	2.13	0.16
		61	13	21.59	3.91	0.87	2.24	0.14
		72	12	11.52	4.50	0.94	2.35	0.11

Table S6: Biodiversity indexes for the functional polychaete community composition.

Region	Subregion	St.	Total number of functional groups *S*	Average ind. number per st. *N*	Species richness (Margalef) *d*	Evenness (Pielou) *J'*	Shannon-Wiener *H'*	Simpson *λ*
Antarctic Peninsula (AP)	Drake Passage (DP)	235	12	29.78	3.24	0.85	2.10	0.16
		241	11	36.44	2.78	0.90	2.15	0.13
	Bransfield Strait (BS)	217	8	16.81	2.48	0.89	1.85	0.19
		225	9	25.94	2.46	0.81	1.78	0.22
	Northwestern Weddell Sea (NW-WS)	6	7	38.04	1.65	0.62	1.21	0.35
		8	8	160.55	1.38	0.78	1.62	0.24
		38	7	125.43	1.24	0.76	1.49	0.31
		120	6	46.59	1.30	0.62	1.11	0.47
		163	8	61.48	1.70	0.73	1.52	0.28
		190	8	86.46	1.57	0.65	1.35	0.33
Filchner Trough (FT)		17	8	21.59	2.28	0.84	1.74	0.21
		26	10	17.06	3.17	0.84	1.94	0.18
		37	8	11.52	2.86	0.93	1.93	0.16
		48	11	31.45	2.90	0.87	2.09	0.15
		61	8	21.59	2.28	0.84	1.74	0.21
		72	7	11.52	2.46	0.88	1.72	0.20

Table S7: Taxonomic groups: selection of best model by distance based linear modeling for polychaete community composition (Bray-Curtis resemblance matrix) and number of chosen variables based on the AICc (boldface type). Selection among 11 possible environmental predictors for the variables depth, C/N$_{molar}$, $_{Cmax}$Chl*a*, $_{bottom}$Chl*a*, Chl*a*, TOC, Sand, Coarse Sand, Median-10-year-ice, SD-10-year-ice and Chl*a*/CPE. The R^2 and AIC$_c$ for the 10 best models are shown.

Selection criterion: AICc			
Selection procedure: BEST			
Overall best solution			
AICc	**R^2**	RSS	No. variables
123.22	0.4009	21457	2
123.30	0.3980	21562	2
123.59	**0.5115**	**17496**	**3**
123.73	0.3817	22148	2
123.82	0.2461	27003	1
123.86	0.2444	27066	1
123.93	0.3737	22434	2
123.99	0.3712	22522	2
124.11	0.4955	18072	3
124.23	0.4917	18205	3

Table S8: Functional groups: selection of best model by distance based linear modeling for polychaete community composition (Bray-Curtis resemblance matrix) and number of chosen variables based on the AICc (boldface type). Selection among 11 possible environmental predictors for the variables depth, C/N$_{molar}$, $_{Cmax}$Chl*a*, $_{bottom}$Chl*a*, Chl*a*, TOC, Sand, Coarse Sand, Median-10-year-ice, SD-10-year-ice and Chl*a*/CPE. The R^2 and AIC$_c$ for the 10 best models are shown.

Selection criterion: AICc			
Selection procedure: BEST			
Overall best solution			
AICc	**R^2**	RSS	No. variables
118.98	**0.5595**	**13115**	**3**
119.43	0.4311	16936	2
119.56	0.4267	17070	2
119.61	0.4248	17125	2
119.65	0.4234	17168	2
119.70	0.5392	13718	3
119.74	0.5379	13757	3
119.94	0.2882	21193	1
119.98	0.2868	21234	1
119.99	0.5308	13969	3

Table S9: Indexes and their optimal number of clusters for the examination of the optimal number for the *k*-means Clustering. The following settings were chosen for this investigation with the function NbClust (R-package NbClust: Charrad et al. 2014): distance = euclidean, minimum number of clusters = 2, maximum number of clusters = 15 and method = *k*-means.

Indices	**Optimal number of cluster**
ch	2
db	2
silhouette	2
duda	2
pseudot2	2
beale	2
dunn	2
sdindex	2
trcovw	3
ratkowsky	3
ball	3
hartigan	4
scott	4
marriot	4
tracew	4
kl	11
rubin	11
friedman	14
ccc	15
cindex	15
sdbw	15

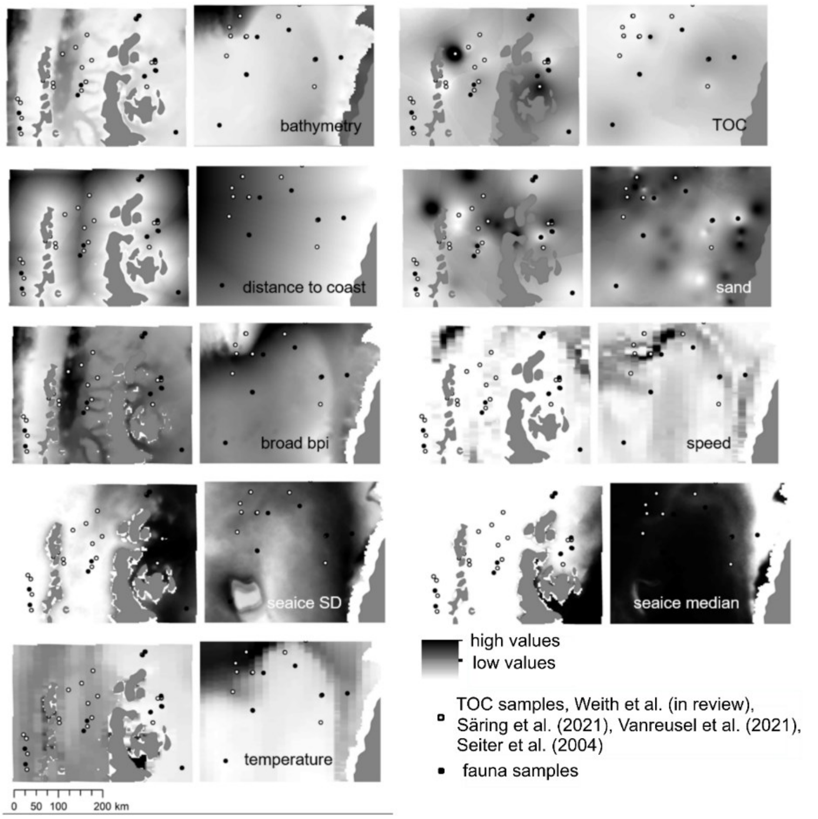

Figure S1: Environmental data in the AP and FT region, small black dots indicate fauna and enviromental samples, small white dotes indicate sediment samples TOC measurements and interpolation (Säring et al. 2021, Vanreusel 2021, Weith et al. in review, Seiter et al 2004).

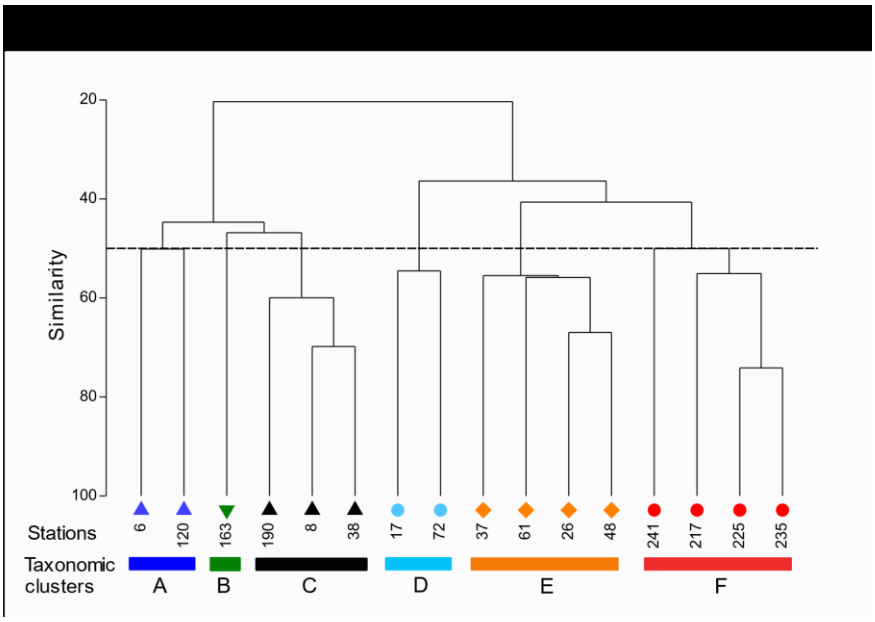

Figure S2: Dendrogram of taxonomic polychaete communities based on cluster analysis (group average) with similarity at 50% as cut off (dashed line), used to differentiate stations groups. Dashed line shows used Color bars represent taxonomic cluster (A–F) to which stations were assigned.

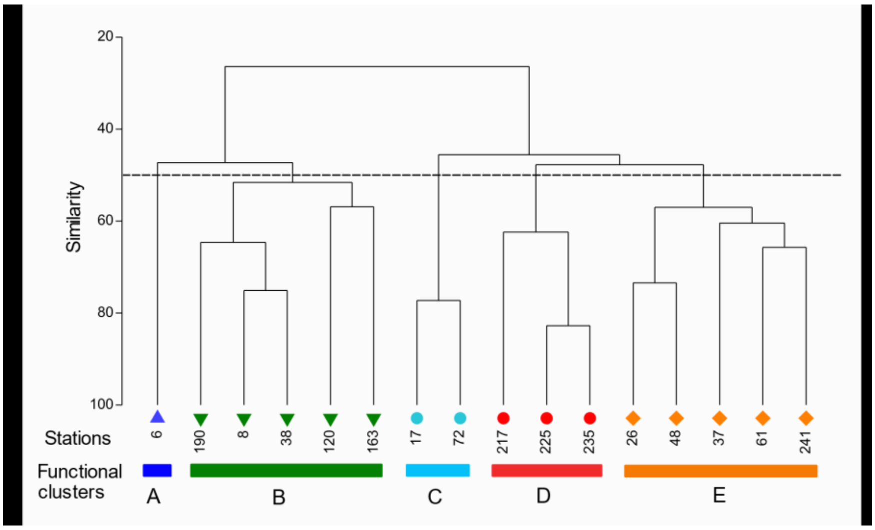

Figure S3: Dendrogram of functional polychaete communities based on cluster analysis (group average) with similarity at 50% as cut off (dashed line), used to differentiate stations groups. Color bars represent functional cluster (A–E) to which stations were assigned.

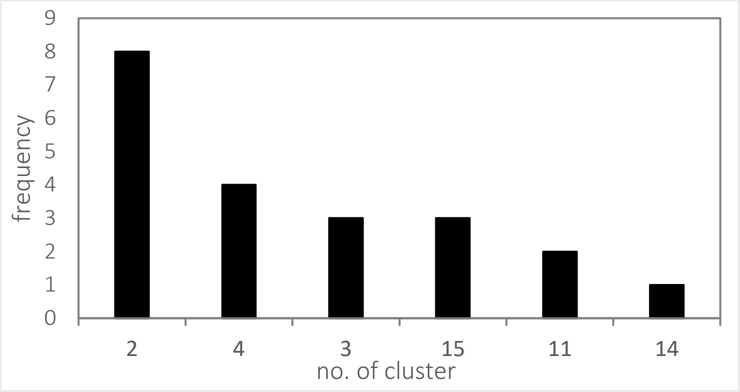

Figure S4: Investigation of the optimal cluster numbers for the application of *k-mans* clustering. The R package *NbClust* (Charrad et al. 2014) was used to apply 21 indices and propose the best clustering scheme from the different results.

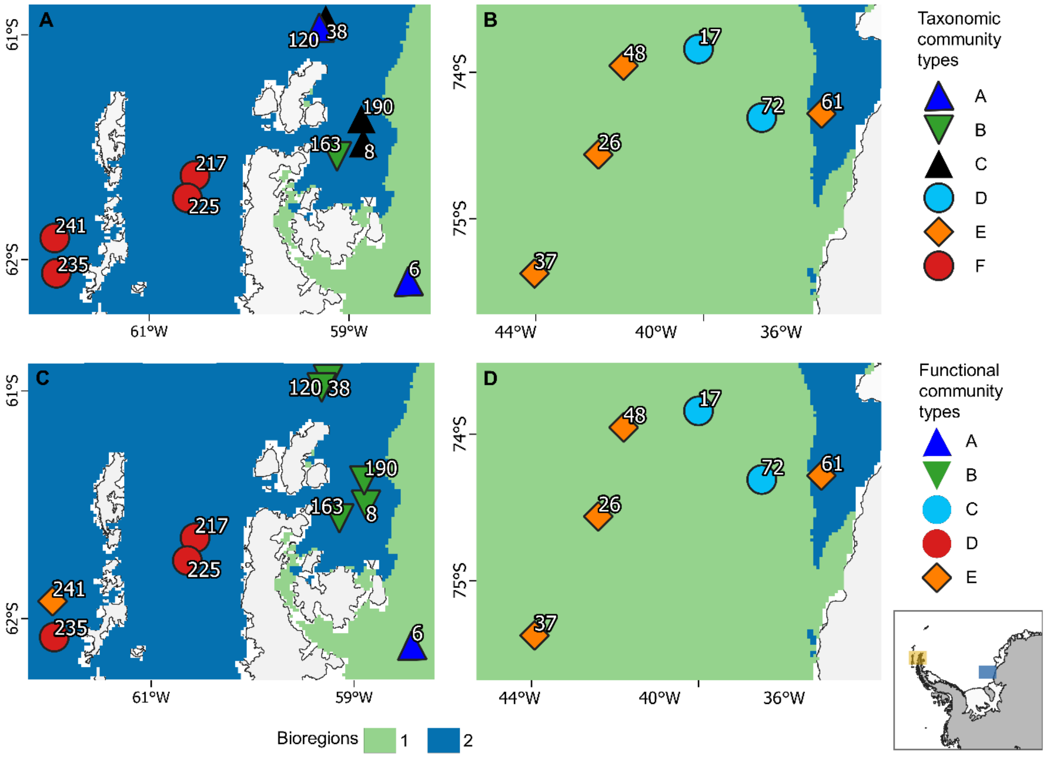

Figure S5: Bioregion ($_2$B1, $_2$B2) and taxonomic ($_{Tax}$A–$_{Tax}$F) and functional ($_{Func}$A–$_{Func}$E) community type distribution in AP (**A, C**) and FT (**B, D**): Bioregion resulting from *k*-means clustering analysis of 9 environmental variables (Depth_s, BPI_s, Dist_coast_s, Median-10-year-ice_s, SD-10-year-ice_s, $_{bottom}$T_s, Speed_s, TOC_s, Sand_s). **A**: AP region with taxonomic community types, **B**: FT region with taxonomic community types, **C**: AP region with taxonomic community types, **D**: FT region with functional community types.

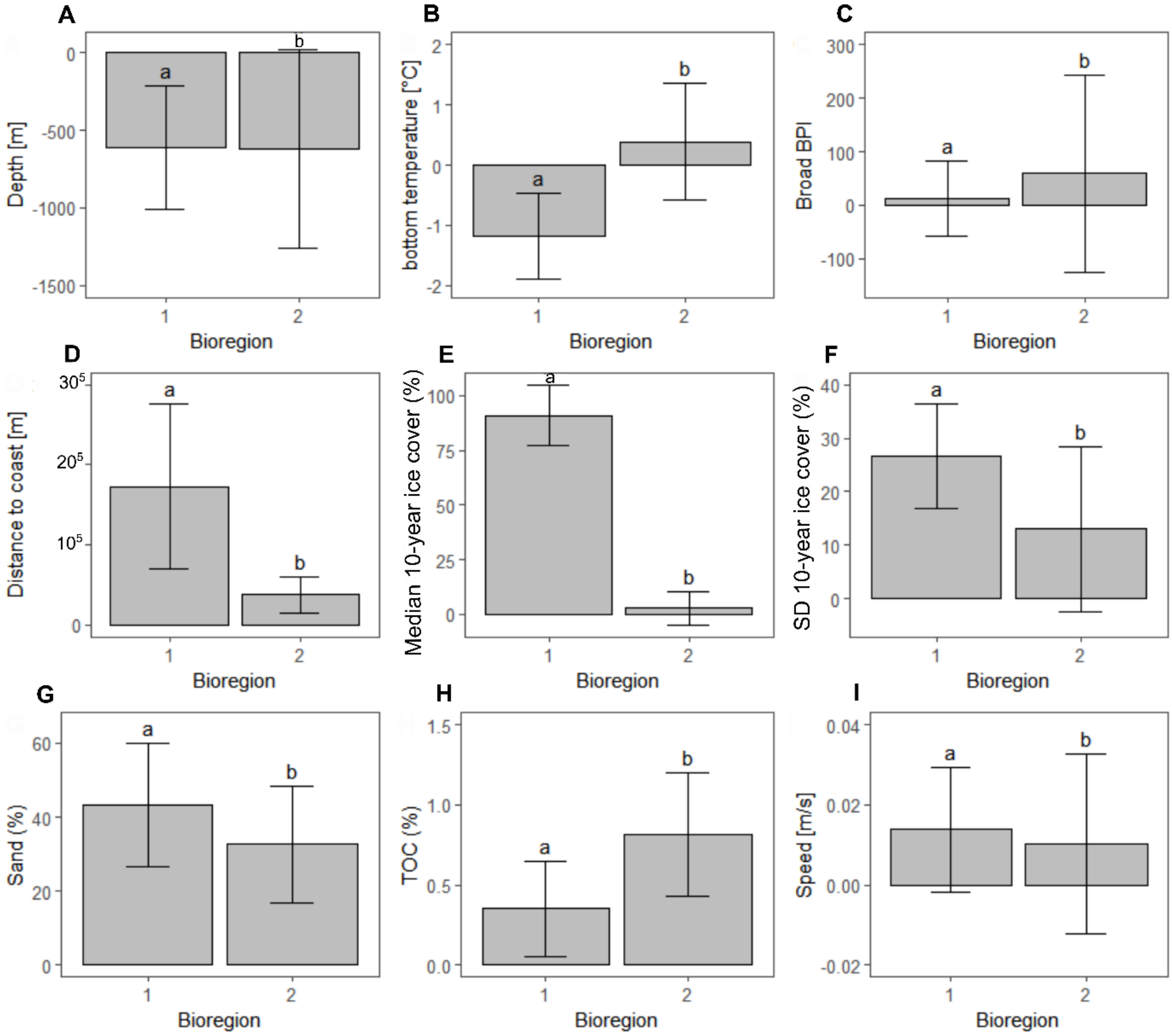

Figure S6: Barplots of $_2$B cluster option representing the data distribution (spread and standard deviation) of the 9 selected variables (Depth, $_{bottom}$T, BPI, Dist_coast, Median-10-year-ice, SD-10-year-ice, Sand, TOC, Speed) within the survey areas. Bioregions assigned with different letters show strong evidence to differ significantly. For the location of $_2$B1 and $_2$B2 refer to Figure S5 in the supplements.

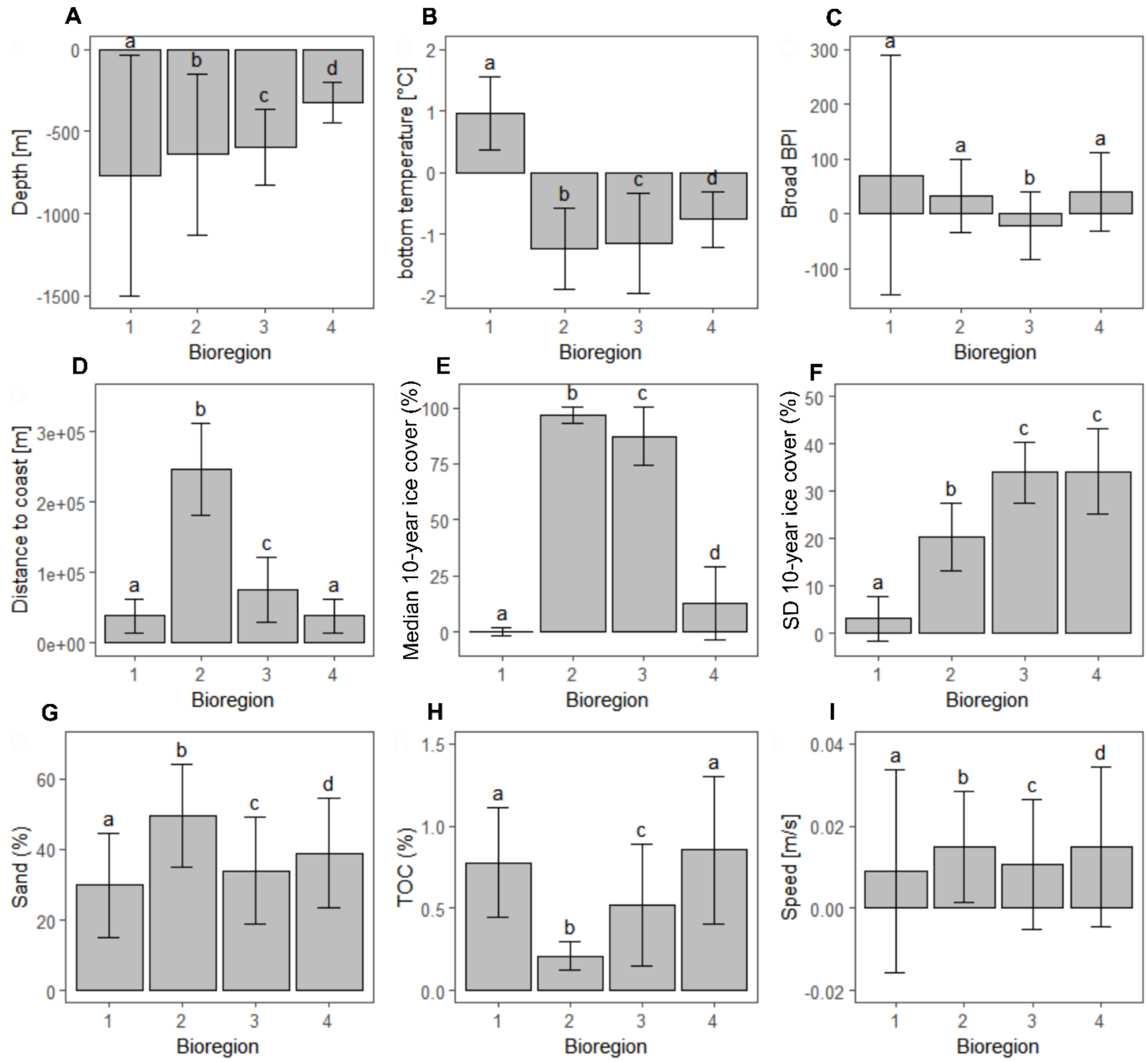

Figure S7: Barplots of $_4$B cluster option representing the data distribution (spread and standard deviation) of the 9 selected variables (Depth, $_{bottom}$T, BPI, Dist_coast, Median-10-year-ice, SD-10-year-ice, Sand, TOC, Speed) within the survey areas. Bioregions assigned with different letters show strong evidence to differ significantly. For the location of $_4$B1, $_4$B2, $_4$B3 and $_4$B4 refer to Figure 7 in the main manuscript.

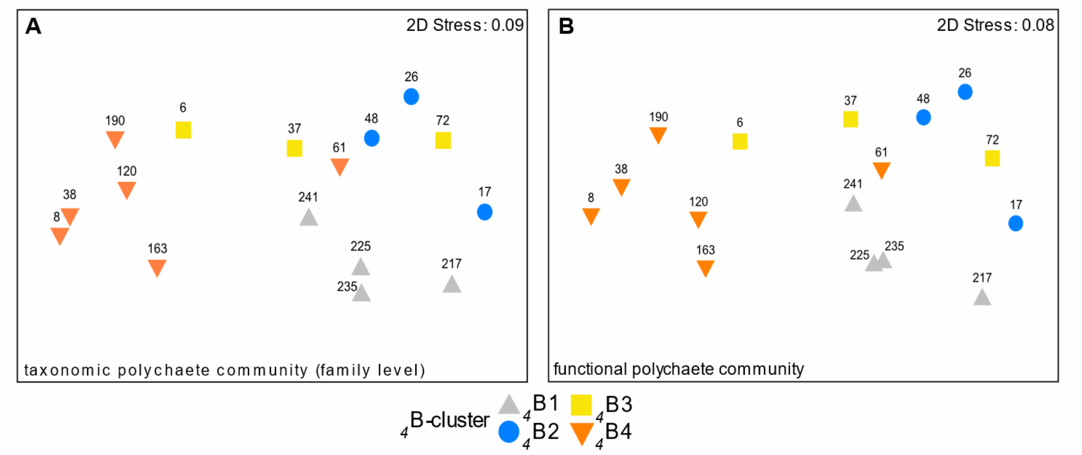

Figure S8: Similarity of **A:** taxonomic and **B:** functional polychaete community according to the $_{4}$B clusters: non-metric multidimensional scaling (nMDS) of the Bray-Curtis similarity of non-transformed fauna abundance date of stations collected during PS81, PS96 and PS118.

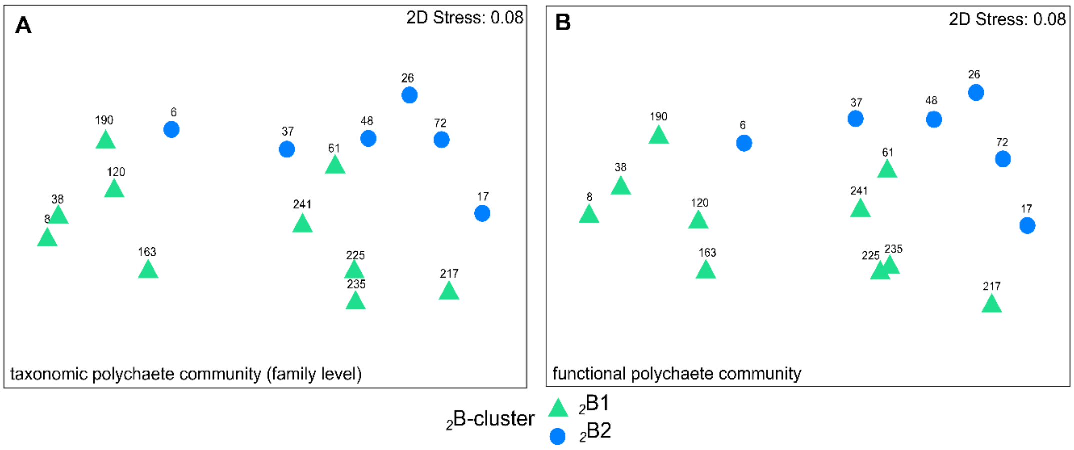

Figure S9: Similarity of **A:** taxonomic and **B:** functional polychaete community according to the $_{2}$B clusters: non-metric multidimensional scaling (nMDS) of the Bray-Curtis similarity of non-transformed fauna abundance date of stations collected during PS81, PS96 and PS118.

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References for R applications

The extraction of the sea-ice cover data, the non-hierarchical clustering method *k-means* and the archetype classification were applied in R version 4.1.3 (R Core Team, 2022). Due to the large number of R packages that were necessary for the analyses a complete list is provided in the following below:

Table S10: R base packages.

Package	Content	Citation
basic	contains the basic functions: arithmetic, input/output, basic programming support, etc	R Core Team (2022)
graphics 4.3.0	The R graphic package	R Core Team (2022)
stats 4.3.0	The R Stats Package	R Core Team (2022)
tcltk 3.6.2	Interface and language bindings to Tcl/Tk GUI elements	R Core Team (2022)
tools 3.6.2	Tools for package development, administration and documentation	R Core Team (2022)
utils	R utility functions	R Core Team (2022)

Supplementary table S11: Other packages.

Package	Content	Citation
car 3.1-1	car: Companion to Applied Regression	Fox & Weisberg (2019)
caret 6.0-93	Misc functions for training and plotting classification and regression models	Kuhn (2022)
cartography 3.0.1	Create and integrate maps in your R workflow, helps to design cartographic representations such as proportional symbols, choropleth, typology, flows or discontinuities maps.	Giraud & Lambert (2016)
cluster 2.1.4	Methods for Cluster analysis	Maechler et al. (2022)
corrplot 0.92	providing visual exploratory tool on correlation matrix that supports automatic variable reordering to help detect hidden patterns among variables	Wei & Simko (2021)
dplyr 1.0.10	A Grammar of Data Manipulation: fast, consistent tool for working with data frame like objects, both in memory and out of memory	Wickham (2022)
ecomix 1.0.0	ecomix is a package to implement model based species level (Species Archetype Models) or site level (Regions of Common Profile) grouping of community data.	Wolley et al. (2021)
factoextra 1.0.7	Provides some easy-to-use functions to extract and visualize the output of multivariate data analyses.	Kassambara (2020)
fdm2id 0.9.8	Contains functions to simplify the use of data mining methods (classification, regression, clustering, etc.).	Blansché (2022)
fmsb 0.7.4	functions for Medical Statistics Book with some Demographic Data	Nakazawa (2022)
FSA 0.9.3	A variety of simple fish stock assessment methods.	Ogle (2022)
gdalUtils 1.2.2	Wrappers for 'GDAL' Utilities Executables	O'Brien (2022)
ggplot2 3.4.0	ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics	Wickham (2016)
ggpubr 0.5.0	provides some easy-to-use functions for creating and customizing 'ggplot2'- based publication ready plots	Kassambara (2022)

Package	**Content**	**Citation**
ggthemes 4.2.4	ggthemes: Extra Themes, Scales and Geoms for 'ggplot2'	Arnold (2021)
glmmTMB 1.1.5	Fit linear and generalized linear mixed models with various extensions, including zero-inflation.	Brooks et al. (2017)
here 1.0.1	file referencing by using the top-level directory of a file project to easily build file paths	Müller & Bryan (2020):
httr 1.4.4	Useful tools for working with HTTP organised by HTTP verbs (GET(), POST(), etc).	Wickham (2022)
lattice	Trellis Graphics for R, a high-level data visualization system	Sarkar (2008)
maptools 1.1-5	Set of tools for manipulating and reading geographic data, in particular 'ESRI Shapefiles'	Bivand & Koh (2022)
mapview 2.11.0	Quickly and conveniently create interactive visualisations of spatial data with or without background maps.	Appelhans et al. (2022)
multcompView 0.1-8	Visualizations of Paired Comparisons. Designed for use in conjunction with the output of functions like TukeyHSD, dist{stats} etc.	Graves et al. (2019)
NbClust 3.0.1	Determining the Best Number of Clusters in a Data Set. It provides 30 indexes for determining the optimal number of clusters.	Charrad et al. (2014)
openxlsx 4.2.5.1	Simplifies the creation of Excel .xlsx files by providing a high-level interface to writing, styling and editing worksheets.	Schauberger & Walker (2022)
pacman	Package Management Tool. Tools to more conveniently perform tasks associated with add-on packages	Rinker & Kurkiewicz (2018)
performance 0.10.1	Utilities for computing measures to assess model quality, which are not directly provided by R's 'base' or 'stats' package	Lüdecke et al. (2021)
plyr 1.8.8	A set of tools that solves a common set of problems (e.g.breaking a big problem down into manageable pieces).	Wickham (2011)
psych 2.2.9	functions are primarily for multivariate analysis and scale construction using factor analysis, principal component analysis, cluster analysis and reliability analysis, although others provide basic descriptive statistics.	Revelle (2022)
raster 3.6-11	raster: Geographic Data Analysis and Modeling	Hijmans (2022)
RColorBrewer 1.1-3	ColorBrewer Palettes. Provides color schemes for maps and other graphics.	Neuwirth (2022)
rcompanion 2.4.18	functions and datasets to support "Summary and Analysis of Extension Program Evaluation in R" and "An R Companion for the Handbook of Biological Statistics"	Mangiafico (2022)
Rcurl 1.98-1.9	General Network (HTTP/FTP/...) Client Interface for R	Lang (2022)
readr 2.1.3	Read Rectangular Text Data, provides a fast and friendly way to read rectangular data (like 'csv', 'tsv', and 'fwf')	Wickham et al. (2022)
readxl 1.4.1	Import excel files into R	Wickham & Bryan (2022)
rgdal	Provides bindings to the 'Geospatial' Data Abstraction Library ('GDAL') and access to projection/transformation operations.	Bivand et al. (2022)
rstatix 0.7.1	Provides a simple and intuitive pipe-friendly framework, for performing basic statistical tests, including t-test, Wilcoxon test, ANOVA, Kruskal-Wallis and correlation analyses.	Kassambara (2022)
sf 1.0-9	Support for simple features, a standardized way to encode spatial vector data.	Pebesma (2018)
sp 1.5-1	Classes and methods for spatial data; the classes document where the spatial location information resides, for 2D or 3D data. Utility functions are provided, e.g. for plotting data as maps, spatial selection, as well as methods for retrieving coordinates, for subsetting, print, summary, etc.	Pebesma & Bivand (2005)
SpeciesMix 0.3.4	itting Mixtures to Species distributions using BFGS and analytical derivatives	Dunstan et al. (2016)
stringr 1.5.0	Consistent, simple and easy to use set of wrappers around the fantastic 'stringi' package.	Wickham (2022)
svDialogs 1.1.0	SciViews GUI API - Dialog boxes. Rapidly construct dialog boxes for your GUI, including an automatic function assistant	Grosjean (2022)
tcltk2 1.2-11	A series of additional Tcl commands and Tk widgets with style and various functions (under Windows: DDE exchange, access to the registry and icon manipulation) to supplement the tcltk package	Grosjean (2022)
terra 1.6-47	terra: Spatial Data Analysis	Hijmans (2022)
tidyverse 1.3.2	tidyverse: Easily Install and Load the 'Tidyverse'	Wickham et al. (2019)

Package	Content	Citation
tmap 3.3-3	Thematic maps are geographical maps in which spatial data distributions are visualized, offers a flexible, layer-based, and easy to use approach to create thematic maps.	Tennekes (2018)

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Acknowledgment

Während der letzten Woche vor der Abgabe habe ich realisiert, es ist nun vorbei, zudem habe ich mich erinnert, was alles auf dem Weg zum Fertigstellen dieser Arbeit passiert ist und wer mich dabei alles unterstützt begleitet hat. Diese Arbeit wäre nicht möglich gewesen ohne die Unterstützung vieler toller Menschen, wie Betreuerinnen, Kollegen, Freunde und Familie.

Natürlich möchte ich mich bei meinen beiden Betreuerinnen Heike und Gritta bedanken.

Heike, vielen Dank für deine Unterstützung, das Vertrauen in mich und mein Können. Ich bin dir sehr dankbar, dass du mich gefördert und gefordert hast und besonders, dass du mich ermutigt hast, meine eigenen Wege zu gehen. Du hast mir den Rückhalt gegeben, wenn ich Fragen oder Probleme hatte und mir gleichzeitig den Freiraum gelassen, Dinge selbst zu erarbeiten und meinen Interessen nachzugehen. Danke, dass du bei mir die „richtigen Knöpfe" gedrückt für den letzten Endspurt. Du hast einen sehr großen Teil dazu beigetragen, dass ich in den letzten Jahren nochmal viel über mich gelernt habe und gewachsen bin, aber Kopfrechnen wird nie meine Stärke werden. Danke für deine dein offenes Ohr auch in schwierigen Zeiten, in denen du oft sehr genau erkannt hast, was los war. Ich bin dir auch dankbar, dass du geschaut hast, wie ich eine Finanzierung bekomme, was die Dinge im Kopf schon oft entspannter macht. Zudem wird mir nie mehr der Satz aus dem Kopf gehen: „Friederike, was ist nochmal deine Fragestellung?". Danke für alles was ich von dir lernen und mit dir erfahren konnte. Ich hoffe sehr, dass wir auch irgendwann nochmal zusammen an Board der Polarstern forschen werden.

Gritta, ohne dich und Willi Xylander wäre ich nie zur Antarktisforschung gekommen. Vielen Dank, dass du mir die Welt der kleinen Tiere so schmackhaft gemacht hast und ich nach unzähligen Stunden vor dem Bino mit dem zählen der Meiofauna während der Masterarbeit, Lust hatte weiter zu machen. Ich dachte mir schon während des ersten Telefonats: „Wow, das ist eine sehr kommunikative, aufgeschlossene und hilfsbereite Frau". Dies hat sich komplett bestätigt. Danke für deine Herzlichkeit und Gastfreundschaft! Es sind schon viele komische und lustige Dinge sowie schöne Momente während der PS118 Ausfahrt, in unserer gemeinsamen „Corona-Lockdown-WG" oder während anderen Besuchen passiert, die wir miteinander teilen können. Danke, dass ich bei dir und Leon so lange bleiben konnte und ihr mich natürlich nicht nur wissenschaftlich, sondern auch sportlich unterstützt habt. Ich denke gerne so oft an unsere gemeinsame Zeit mit viel Rohkost zurück. Ich bin dir sehr dankbar für das stets flotte Korrekturlesen meiner Texte natürlich immer mit dem Gritta-Adlerauge und dass du dir dafür immer Zeit freigeschaufelt hast (besonders jetzt in den letzten Wochen).

Ich möchte mich auch bei der Arbeitsgruppe Meeresbiologie der Universität Rostock bedanken, für eure Hilfsbereitschaft und Ratschläge. Ein besonderer Dank gilt dabei an Inna Sokolova und Stefan Forster für eure fachlichen Tipps bezüglich meiner Arbeit der letzten Jahre, sowie Elke Meier und Holger Pielenz für eure Unterstützung im Labor.

Ich danke auch ganz herzlich Herrn Bick, der in mir die Begeisterung für Polychaeten weckte und dafür verantwortlich ist, dass ich jetzt unter meinen Freunden „Wurm-Profi" genannt werde. Danke, dass Sie sich die Zeit genommen haben, um mit mir zum zehnten Mal die Hakenleisten zu zählen und mit mir stundenlag hinter dem Bino und/ oder Mikroskop zu sitzen, um die kleinen, und wunderschönen Würmer zu bestimmen. Es war für mich eine sehr schöne und lehrreiche Zeit mit Ihnen an die ich sehr gern zurückdenke. Danke, dass ich an Ihrem gefühlt unendlichen Wissen über Poylchaeten teilhaben konnte. Ich denke und hoffe, dass mich die Polychaeten noch weiterhin begleiten werden.

Auch Kerstin Jerosch möchte ich an dieser Stelle danken, für die schöne sowie verrückte Schiffszeit während PS118 und dass wir uns danach nicht aus den Augen verloren haben, sondern wir weiterhin Freundinnen sind und sogar zusammengearbeitet haben. Danke, dass ich immer bei dir schlafen konnte,

wenn ich am AWI war verbunden mit langen Gesprächen, die mir geholfen haben für mich zu planen und herauszufinden was ich will. Ich bewundere dich, wie du immer alles unter einen Hut bekommst und freu mich schon, wenn wir endlich mal wieder zusammen die Laufschuhe schnüren können.
Bei Hendrik Pehlke möchte ich mich bedanken, dass du mir meine Programmierfähigkeiten weitervorangetrieben hast, und mir die Skripte und die Schritte mir immer wieder erklärt hast.

Danke auch an alle meine Co-Authoren der einzelnen Kapitel dieser Arbeit für eure Unterstützung, Zuarbeit, Analysen, konstruktive Kommentare und die Überarbeitung der Manuskripte.

Danke auch an meine LAV Trainingsgruppe für die unzähligen tollen und witzigen Trainingsstunden, die manchmal auch von fiesem Muskelkater gefolgt waren, sodass ich an manchen Tagen sehr viel auf meinem Bürostühl gerollt bin, um so wenig wie möglich zu gehen. Danke, für den Ausgleich und die Ablenkung in unserer bunten Gruppe. Ein besonderer Dank an Lea und Christian mit denen ich auch ein ganzes Training so durchquatschen könnte, was Gabi natürlich nicht immer duldet.

Zudem möchte ich mich auch bei meinen laufbegeisterten Mitmenschen bedanken, die mit mir immer eine Runde gedreht haben, damit ich mich genug Auslauf habe und meine überschüssige Energie los werden kann. Besonders danke ich Geppi, Simon und Sigmar für die unzähligen Laufkilometer, die wir gemeinsam verbracht haben. Es waren meist schöne Runden (wenn wir nicht gerade Intervalle gemacht haben, und es nicht gerade -15° im Schneesturm bei der Groß Stove Runde waren) bei denen wir uns immer austauschen konnten und ihr immer ein offenes Ohr hattet.
Geppi und Sylvi möchte ich danken, dass sie auch teilweise meine Doktorarbeit gegengelesen haben. Zudem danke Sylvi, dass du mir einen tollen Büroplatz mit einem Thron für meine Leipzig Home-office Zeit zu Verfügung gestellt hast, ich konnte dort immer super arbeiten.

Alice, danke für die vielen schönen und bunten Momente. Ich bin sehr froh dich in der Zoologiezeit kennengelernt zu haben. Mit dir kann man schon echt witzige Sachen erleben aber gleichzeitig konnten wir uns auch über die Zeit als Doktorandinen austauschen und miteinander mitfühlen.

Kati, danke für deine Offenheit und Hilfsbereitschaft. Oft wusstest du schnell Rat und hast mir immer zugehört. Danke, dass ich bei dir mein „Corona-Home-Office Lager“ aufschlagen konnte, nachdem mir zu Hause die Decke auf den Kopf gefallen ist.

I would like to thank Werna, my office colleague, even though we didn't see each other that often in the office but rather in the Lindenpark, I am glad that we could always exchange thoughts honestly, whether privately or professionally. Thank you for your honesty and openness. Besides that, I learned a lot about Indonesian culture.

Ich danke der Deutschen Forschungsgemeinschaft für die Finanzierung des Projekts worin meine Arbeit einen Teil darstellt.

Ich möchte mich bei meiner ersten Rostocker WG bedanken, Dafür, dass ihr mir alles in und rund um Rostock gezeigt habt und mich am Anfang einfach überall mit hingenommen habt, damit ich schnell Anschluss finde. Danke für diese weiterhin bestehende Freundschaft. Besonders möchte ich nochmal René danken, für die schöne und verrückte gemeinsame Zeit, die uns auch manchmal an unsere Grenze gebracht hat. Danke, dass du da bist, mich ermutigt hast weiterzumachen, wenn gefühlt zum 100x etwas nicht funktioniert hat aber mir auch gesagt hat: „Fritzi mach mal eine Pause“. Danke für die schöne Zeit hier in Rostock und die langen Telefonate seit du nicht mehr hier wohnst. Ein großes Dankeschön für deine Hilfe beim Programmieren und besonders beim Korrekturlesen. Ich verspreche dir, dieses Jahr komme ich endlich mal nach Innsbruck.

Maxi auch bei dir möchte ich mich bedanken, dass du mich besonders jetzt, kurz vor der Abgabe nochmal mit so viel guter Laune überschüttet hast. Dein Besuch hat mir ganz viel Kraft gegeben. Danke! Und ich hoffe, dass nächste Wiedersehen lässt nicht so lang auf sich warten und wir können wieder unsere Laufrunden zusammendrehen, in die Warnow oder die Ostsee springen und danach Perlenkettchen fädeln.

Bei meiner jetzigen WG mit Antonia, Nina und Katha möchte ich mich bedanken für die wunderschöne Zeit mit euch. Danke für die vielen gemeinsamen Ausflüge mit dem ein oder anderen kühlen Getränk, Spieleabend, tanzende Stunden oder gemeinsame Spaziergänge. Ich bin froh mit euch zusammen zu wohnen und dass ihr es in meiner stressigen Zeit mit mir ausgehalten habt. Danke, dass ich immer zu euch kommen konnte! Das Zusammenleben, die bunte und aufregende Zeit mit euch wird mir fehlen.

Thank you Richard Wellman for proof reading this thesis.

Alex Kaminski, danke für deine Musik die mich bei vielen Stunden des Schreibens begleitet hat.

Ich möchte mich ich auch bei meinen ganzen Leipzigern Freunden bedanken, die mich immer mit offenen Armen empfangen, wenn ich mal wieder zu Besuch da bin! Ich bin immer froh immer wieder Leipziger Luft zu schnuppern und freue mich über zukünftige gemeinsame Urlaube, am liebsten natürlich zum Skifahren. Besonders danke ich Marina, die immer ein offenes Ohr hat und das du immer so mitfühlend bist.

Bei meinen beiden ältesten Freundinnen Lotte und Sophie möchte ich mich bedanken, dass ihr immer so viel Verständnis und Interesse für meine Arbeit gezeigt habt. Ich bin froh, dass wir es immer wieder schaffen uns zusammenzufinden obwohl es durch die Entfernung nicht immer ganz so leicht ist. Danke für die vielen schönen Telefonate und der wunderschöne Trip nach Prag, der mir nochmal sehr viel Kraft und Freunde gebracht hat. Ich habe euch lieb!

Danke Basti und Magdalena, dass ihr mich bei euch in der WG in Greifswald während Corona mit aufgenommen habt. Es war eine unglaublich schöne Zeit mit euch auch wenn wir nicht viel machen konnten, hatte ich das Gefühl, dass wir viel erlebt haben.

Ich möchte meiner Familie bedanken, die mich immer unterstützt haben und bestärkt haben in dem was ich mache beziehungsweise vorhabe. Ohne euch wäre ich jetzt nicht hier. Danke, dass ihr meine Ausbildung unterstützt habt und, dass ihr interveniert habt bei meinem einen Kipppunkt im Studium, als ich mein Studium gegen eine Bäckerinnenlehre eintauschen wollte. Ich bin euch dankbar, dass ihr euch meine Sorgen angehört habt und mich hier in Rostock besucht habt. Ich habe euch sehr lieb.

Danke Till für deine unendliche Unterstützung, besonders in den Momenten, die schwierig für mich waren oder etwas nicht funktioniert hat. Danke, dass ich einfach immer zu dir kommen konnte und dass du mir den Freiraum gibst. um meine Dinge durchzuziehen. Ich bin dankbar für all die schönen Momenten in den letzten Jahren und ich freu mich auf die noch kommen werden. Ich bin so froh dich an meiner Seite zu haben.

Declaration of authencity

Ich versichere hiermit an Eides statt, dass ich die vorliegende Arbeit selbständig angefertigt habe und ohne fremde Hilfe verfasst habe, keine der außer von mir angegebenen Hilfsmittel und Quellen dazu verwendet habe und die in benutzten Werken inhaltlich und wörtlich entnommenen Stellen als solche kenntlich gemacht habe. Mir sind die Vorschriften der Universität über Plagiate bekannt, einschließlich der Vorschriften über disziplinarische Maßnahmen, die sich aus Plagiaten ergeben können.

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Friederike Weith

Rostock den, 26.07.2023