BENTHIC COMMUNITIES OF THE WEDDELL SEA: PAST, PRESENT AND FUTURE

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BODENTIERGEMEINSCHAFTEN IM WEDDELL MEER: VERGANGENHEIT; GEGENWART UND ZUKUNFT

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ABSTRACT

Benthos is the term used to refer to all organisms living on, within or in tight relation with the bottom of any water body. In this particular case, it is used to refer to fauna inhabiting the shelf of the Weddell Sea.

The study of benthos in the Southern Ocean has over 100 years of history, with its first important milestone being the *Challenger* expedition. From then onwards, benthic research has been marked by “periods” with various focus: the “taxonomical period” with focus on species descriptions; the “ecology focused period” started with technological advances which allowed for SCUBA diving, settling of Antarctic research bases, and the development of icebreakers; followed by the “ecophysiological and experimental period” with focus on animal physiology and *in-situ* experiments ; and the recent “functional ecology and physiology period” focusing on how benthos might react to ongoing and predicted climate change.

Collective knowledge obtained through the research history of Antarctic benthos has helped to understand how seabed living organisms have evolved and adapted to its extreme environment. Glaciations in the Oligocene (~35 mya) caused the loss of top predators such as large lithodid crabs and sharks. The formation of the circumpolar current, isolation of the Antarctic continent (Pliocene 5.3-1.6 mya), and further glacial/interglacial periods (Pleistocene 1.6-0.01 mya) resulted in the high endemism of Antarctic benthos and radiation of groups such as pycnogonids and peracarid crustaceans. More recently (in a geological time-scale), the last glacial maxima is pointed out as key in the evolution of cryptic species, the similarity of Antarctic and deep-sea benthos, and the circumpolar distribution of many groups and species.

Benthos has been shaped by its isolation and evolution pressure of glaciations, and the additional effect of low but stable temperatures, and highly variable input of primary produced organic matter, and iceberg scours. “Present day” benthos is characterized by its capacity to live in temperatures well below 0°C, being stenotherm and eurybathic, distribute patchily, being dominated by suspension feeders and gigantisms, among others. These characteristics allow Antarctic benthos to develop dense and highly diverse communities, which can be richer than sub-tropical environments. To date, more than 7,200 benthic species have been described. However, based on estimations, the total number should lie well above 17,000, meaning we are still far from a complete inventory. The infauna fraction of Antarctic benthos is mainly composed by burrowing worms, bivalves and small crustaceans, and the epifauna fraction varies according to local pelagic environmental regimes. Examples of this are the sponge dominated communities of the Ross Sea and Weddell Sea, and the motile holothurian deposit feeder community of the West Antarctic Peninsula shelf. This bentho-pelagic coupling with its local and regional variations resulted in benthic communities and assemblages to be also diverse. However, our knowledge on benthic communities, its distribution and relation with the abiotic environment, still has many gaps, especially in areas with heavy sea-ice conditions which are hard to reach.

Recent awareness on climate change prompted Antarctic scientists to focus on how the Antarctic climate has changed during the instrumental period, and how it might change under different IPCC scenarios. The amounted knowledge shows general trends of increased sea-ice cover and decreased temperatures in the eastern Weddell Sea. However, other regions such as the Antarctic Peninsula and Bellingshausen Sea evidence an opposite trend (i.e. less sea-ice and higher temperatures). Recent studies in the Antarctic Peninsula have shown the decrease of sea-ice cover to increase primary productivity, which in turn increased the amount of carbon produced and fixed by benthic organisms.

The present thesis tackles different aspects of the past, present and future of high Antarctic benthic communities of the Weddell Sea. Four manuscripts are included:

- Manuscript 1 tackles methodological approaches used to sample benthos. This manuscript shows the complementary nature of sediment cores and seabed images, proving data of two compartments of benthos, the infauna and epifauna. This approach combining both methods is a practical and efficient method to study benthic fauna.
- Manuscript 2 reviews knowledge on bentho-pelagic coupling on Antarctic shelves in order to put together the puzzle of how the coupling works. It is shown that bentho-pelagic coupling in the Weddell Sea differs considerably from coupling processes in waters of the West Antarctic Peninsula.
- Manuscript 3 builds up on the methodological knowledge of Manuscript 1 and uses it to describe benthic communities in the hard to access Filchner Region (southern Weddell Sea). In this area, which is predicted to suffer near-seabed temperature increases with serious implications for the global water mass circulation, benthos was studied intensively after a first attempt with trawls > 30 years ago. This manuscript shows changes in benthic community distribution and describes two “novel” benthic communities inhabiting the Filchner Region.
- Manuscript 4 is a long-term study which considers a unique 26-year time series of benthic data obtained on the southeastern Weddell Sea shelf off Austasen. Based on these data, the benthos communities appear severely affected by a decrease of productivity due to increased sea-ice cover, and increase of scouring potential due to higher iceberg frequency and area after 2000.

The answers provided by the manuscripts of this thesis bring with them a whole new set of questions. However, to answer these new questions (and those which are not or partially answered), we need to include additional benthos data. In the context of this thesis, such benthic metadata include e.g. physiological concepts and experiments, local particle flux and productivity regimes, sediment geomorphology and chemistry, water currents and water mass characteristics. Additionally to these metadata, modern mathematical and statistical approaches should be considered over classical ones, to include qualitative and categorical data which are usually not included in e.g. linear algebra. In conclusion, a key concept to answer unresolved and new question is “multidisciplinary work”, which would help to connect Antarctic benthic fauna with other biotic and abiotic characteristics, and to draw lines between benthic and pelagic realms. By doing this we will be able to put together the benthic puzzle piece by piece, and understand how benthos has been, and will be, affected by an everchanging environment.

ZUSAMMENFASSUNG

Der Begriff “Benthos” umfasst alle Organismen, die auf oder im Sediment oder in enger Beziehung mit dem Sediment in Gewässern jeglicher Art leben. In der vorliegenden Arbeit bezeichnet dieser Begriff die Makrofauna des Weddell Meer Schelfs.

Untersuchungen des Benthos im Südpolarmeer haben auf eine über 100-jährige Geschichte, die ihren Anfang mit der „Challenger Expedition“ nahm. Nachfolgende Untersuchungen des Benthos lassen sich in Zeiträume mit unterschiedlichen Schwerpunkten einteilen. In einer „taxonomischen Phase“ stand zunächst die Beschreibung der Arten im Mittelpunkt. Die anschließende „ökologisch ausgerichtete Phase“ begann mit zunehmender Technologisierung der Forschung; insbesondere das Gerätetauchen, die Errichtung von Forschungsstationen in der Antarktis und die Entwicklung leistungsstarker Forschungseisbrecher waren wichtig für die Forschung in dieser Phase. Danach folgte eine „ökophysiologische und experimentelle Phase“ mit Fokus auf die Tierphysiologie und in situ Experimenten. Im Moment durchlaufen wir eine “funktionelle und physiologische Phase“ mit einem Schwerpunkt auf Studien, die sich mit der zukünftigen Entwicklung von Benthos vor dem Hintergrund prognostizierter Klimaveränderungen befassen.

Das im Verlauf der bisherigen Untersuchungen des Benthos erlangte Wissen erlaubt uns Einblicke, wie Benthosorganismen sich unter den rauen Bedingungen des Südpolarmeeres entwickelt und angepasst haben. Die Vereisung im Oligozän (~35 mya) führte zum Aussterben von Räubern wie lithodiden Krebsen und Haien in diesen Gewässern. Die Ausbildung des Zirkumpolarstroms (Pliozän~5,3 bis 1,6 mya) isolierte den Antarktischen Kontinent. Weitere glaziale-interglaziale Perioden während des Pleistozäns (~ 1,6 bis 0,1 mya) resultierten dann in einem hohen Endemismus der benthischen Fauna mit Ausbreitung von Gruppen wie z.B. Pycnogoniden und peracariden Krebsen. Ein zentrales Ereignis in jüngerer Zeit war die letzte glaziale Periode, die dazu führte, dass sich kryptische Arten ausbilden konnten und, zu einer Ähnlichkeit von Tiefsee- und antarktischem Benthos führte sowie zu einer zirkumpolaren Verbreitung vieler Gruppen und Arten.

Isolation und Evolutionsdruck durch Vereisung haben das Benthos geprägt sowie, zusätzliche Effekte wie z.B. niedrige aber stabile Wassertemperaturen, sehr variable Verfügbarkeit von organischem Material und Störung durch gestrandete Eisberge. Heutzutage ist das Benthos charakterisiert durch seine Fähigkeit, in Wassertemperaturen < 0°C zu leben, die Tiere sind stenotherm und eurybath, unregelmäßig verbreitet, sie sind dominiert von Suspensionsfiltrierern, und Gigantismus ist häufig. Aufgrund dieser Eigenschaften ist das antarktische Benthos in der Lage, dichte Gemeinschaften mit hoher Diversität zu entwickeln, die artenreicher und diverser als sub-tropische Gemein-schaften sein können. Bis heute sind > 7200 benthische Tierarten beschrieben worden. Allerdings haben Berechnungen ergeben, dass die tatsächliche Artenzahl mit > 17000 erheblich höher liegen dürfte, das heißt wir sind im Moment weit davon entfernt, die komplette Artenvielfalt der Antarktis zu kennen. Die Endofauna des antarktischen Benthos besteht im Wesentlichen aus bohrenden Würmern, Muscheln und kleinen Krebsen, wohingegen die Zusammensetzung der Epifauna variiert und stark von lokalen Parametern im Pelagial geprägt wird. Beispiele hierfür sind die Schwamm-dominierten Gemeinschaften im Ross und Weddell-Meer und die von freibeweglichen

Holothurien dominierten Gemeinschaften von Sustratfressern auf dem westlichen Schelf der Antarktischen Halbinsel. Dieses bentho-pelagische Zusammenspiel mit seinen lokalen und regionalen Charakteristiken fördert die hohe Diversität der benthischen Gemeinschaften. Leider haben wir aber immer noch erhebliche Wissenslücken hinsichtlich der Verteilung der benthischen Gemeinschaften und ihrer Interaktion mit abiotischen Umweltparametern; dieses gilt insbesondere für Gebiete, die wegen permanenter und starker Eisbedeckung auch heute nur schwer zugänglich sind.

Die aktuelle Diskussion über Klimaveränderungen richtet die Aufmerksamkeit der Antarktisforscher auf die Fragen aus, wie das antarktische Klima sich im Verlauf des instrumentellen Zeitalters verändert hat und wie es sich unter Berücksichtigung verschiedener IPCC-Szenarien künftig verändern wird. Unser bisheriges Wissen lässt vermuten, dass die Meereisbedeckung im östlichen Weddell Meer zunehmen wird und die Wassertemperaturen dort sinken werden. Andere Regionen wie z.B. die Bellingshausen See und die Gewässer an der Antarktischen Halbinselzeigen allerdings einen gegenläufigen Trend mit weniger Meereisbedeckung und steigenden Wassertemperaturen. Neuere Untersuchungen an der Antarktischen Halbinsel zeigen, dass steigende Temperaturen und abnehmende Meereisbedeckung zu einer erhölten Primärproduktion führen und somit auch zu steigender Kohlenstoffproduktion und durch Benthosorganismen vermehrt gebundenen Kohlenstoffs.

Diese Doktorarbeit befasst sich mit verschiedenen Aspekten der Vergangenheit, der Gegenwart und der zukünftigen Entwicklung der benthischen Gemeinschaften im hochantarktischen Weddell-Meer. Vier Veröffentlichungen sind eingebunden:

- Manuskript 1 befasst sich mit verschiedenen Methoden, die verwendet werden um Benthos zu sammeln und zu beschreiben. Bei den Methoden handelt es sich um quantitatives Sammeln mit Bodengreifern insbesondere der Endofauna und um das Fotographieren der Bodenfauna mit UW-Kameras, wobei diese Methode besser die Epifauna erfasst. Die Ausrüstung eines Bodengreifers mit einer UW-Kamera erlaubt eine sehr effiziente Beprobung und Darstellung der Fauna am Meeresboden.
- Das zweite Manuskript ist ein Review, in dem Prozesse der bentho-pelagischen Kopplung auf dem Antarktischen Schelf und deren Funktionsweise, anschaulich dargestellt werden. Es wird gezeigt, dass sich die bentho-pelagische Kopplung im Weddell-Meer erheblich anders darstellt als in den Gewässern westlich der Antarktischen Halbinsel.
- Das dritte Manuskript beschreibt, aufbauend auf den im ersten Manuskript dargestellten Methoden, die Benthosgemeinschaften der schwer zugänglichen Filchner-Region im südlichen Weddell Meer. In diesem Gebiet, für das eine Zunahme der bodennahen Wassertemperaturen prognostiziert wird, mit drastischen Folgen auch für die globale Wassermassenzirkulation, wurde das Benthos erstmals nach > 30 Jahren intensiv untersucht. In diesem Manuskript werden Veränderungen in der Verbreitung der benthischen Gemeinschaften in dieser Region beschrieben und es werden zwei für die Filchner-Region neue Gemeinschaften vorgestellt.
- Manuskript 4 ist eine Langzeitstudie. In ihr wird eine einzigartige 26-jährige Beprobung des Benthos auf dem südöstlichen Schelf des Weddell-Meeres vor Austasen vorgestellt. Das Benthos in diesem Gebiet scheint erheblich unter einer

Abnahme der Primärproduktion zu leiden, die auf eine Zunahme der Meereisbedeckung zurückgeführt wird und auf ein erhöhtes Störpotential aufgrund des zunehmenden Auftretens von großen Eisbergen ab dem Jahr 2000.

Die Antworten auf viele der Fragen, die in dieser Doktorarbeit und den Manuskripten gegeben werden, werfen gleichzeitig eine Vielzahl von neuen Fragen auf. Die Antworten auf diese Fragen, auch auf Fragen, die im Rahmen dieser Arbeit nur teilweise beantwortet werden konnten, erfordern weitere Untersuchungen des Benthos. Im Kontext dieser Arbeit sollten diese weiteren Untersuchungen auf physiologische Konzepte und Experimente, auf lokal unterschiedliche Partikelflüsse und Produktionsregime ausgedehnt werden, und die Geomorphologie und Chemie des Meeresbodens müssten berücksichtigt werden, ebenso wie Strömungssysteme und unterschiedliche Wassermassen mit ihren Charakteristiken. Erforderlich ist weiterhin die Einbindung moderner mathematischer und statistischer Methoden, um auch qualitative und kategorische Daten einarbeiten zu können, die normalerweise in z.B. linearer Algebra nicht berücksichtigt werden. Zusammenfassend kann man sagen, dass der Schlüssel zu Antworten auf ungelöste und auch neue Fragen ein zukünftiger multidisziplinärer Forschungsansatz ist, in dem Fragen zum Benthos eng verknüpft werden mit anderen biotischen und abiotischen Fragen und Prozessen, die dann das Pelagial und Benthal verbinden. Wenn wir das verwirklichen, werden wir in der Lage sein, dass "benthische Puzzle" Stück für Stück zusammen zu setzen, und werden verstehen, wie das Benthos sich entwickelt hat und wie es sich in einer dynamischen Umwelt weiterhin entwickeln wird.

GLOSSARY

- **Community:** Ecological unit composed of populations of different species, co-occurring in the same environment.
- **Assemblage:** Sub-unit of a community.
- **Diachronous:** Feature or phenomenon occurring in different geological periods.
- **Cryptic species:** One of two or more morphologically indistinguishable species which are genetically different.
- **Infaunal benthos:** Fraction of seabed biota living burrowed in the sediment.
- **Epifaunal benthos:** Fraction of seabed biota living on the sediment.
- **Macrobenthos:** Benthic organisms with body size > 0.5 mm.
- **Megabenthos:** Benthic organisms with body sizes > 1 cm. Large enough to be observed in seabed images and videos.
- **Ice Shelf Water:** Water mass generated by the interaction of ice shelves and High Salinity Shelf Water, one of the precursors of Weddell Sea Bottom Water and Antarctic Bottom Water, drivers of the global thermohaline circulation.
- **Bentho-pelagic coupling:** Term used to refer to the interconnectivity between benthic and pelagic systems, with a focus on benthic processes affecting and modifying pelagic abiotic/biotic factors.
- **Pelago-benthic coupling:** Term used to refer to the interconnectivity between benthic and pelagic systems, with a focus on benthic processes affecting and modifying benthic abiotic/biotic factors.

GENERAL INTRODUCTION

General remarks

The study of benthos has a long tradition, even in the Southern Ocean (Clarke 2008, Griffiths et al. 2018). As stated by Arntz et al. (1999), *"already at first glance, the marine benthos reveals a number of properties which render its study not only exciting, but also particularly rewarding for the solution of ecological questions"*, this needs to be even more emphasized in view of ecological questions regarding Antarctic cold water systems, which are forming the focus of this thesis. Anrtz' statement is particularly true if we consider that benthic habitats are extremely diverse, including soft and hard bottoms, shallow shelf and deep sea regimes, reefs, estuaries and hydrothermal vents. Antarctic benthic biota have been proposed as "canaries" of global climate change (Barnes and Clarke 2011), since they are profoundly and quickly affected by climate-driven ice and temperature regimes. Hence, in the context of the uneven impact of climate change in Antarctica with sea-ice gains and sea-surface temperature drops in the eastern Weddell Sea, and opposite trends in the western Weddell Sea (e.g. Liu et al. 2004, Turner et al. 2014, 2016), studies of the "Antarctic benthos" can provide valuable information on how different Antarctic systems might react.

Research history

"Antarctic benthos" is the term used in literature to refer to benthos inhabiting the shelves slopes and deep waters around the Antarctic continent and adjacent islands (Gutt 2007). The history of its scientific exploration is over a century long (Clarke 2008). While Antarctic exploratory expeditions started in the late 18th century (Griffiths et al. 2018), the first substantial benthic samples were taken during the *Challenger* expedition in the late 19th century (Arntz et al. 1994, Griffiths et al. 2009). Until the first half of the 20th century, most subsequent benthic studies aimed at species descriptions and faunal inventories (De Broyer et al. 2010).

After this "taxonomical period", in the second half of the 20th century an "ecology focused period" commenced, hand-in-hand with the establishment of research bases and the development of SCUBA gear for divers, allowing for the early description of benthos living within diving reach, such as the sponge dominated community in the McMurdo Sound in the Ross Sea (Dayton et al. 1974). Another technological breakthrough was the use of icebreaking research vessels, such as *Polarstern*, *Nathaniel B. Palmer,* and *James Clarke Ross*. In the Weddell Sea, the expeditions of RV *Polarstern* started in the early 1980s. Based on bottom and Agassiz trawls deployed during the first *Polarstern* expeditions, Voß (1988) described for the first time benthic community types inhabiting the southern and eastern Weddell Sea shelves. This description was further developed by the studies of Gerdes et al. (1992) and Gutt and Starmans (1998), which were based on different quantitative approaches.

During the last decades technological advances led to the onset of an "ecophysiological and experimental period" that has been characterized by more complex experimental works, and molecular techniques used for taxonomic and physiological studies (see e.g. Pörtner et al. 2007, De Broyer et al. 2010, Peck et al. 2014). However, field ecological research is also continuing, benefiting from taxonomic and physiological advances, as well as from modern research facilities in Antarctic stations (e.g. *Rothera* and *Carlini* Stations) which allowed for performing *in situ* studies of benthic physiology. Recently, our awareness of climate change resulted in a focus shift to functional ecology and physiological studies in a pursuit of understanding how the unique and rich Antarctic benthos is able to cope with its extreme environment, and how it will respond to future climate scenarios.

Despite the technological advances of the past decades, for instance regarding image resolution and computational power, many approaches to sample benthos in ecological studies remained almost unchanged, thus, the statement made by Arntz et al. (1994) still holds true: *"Benthologists are comparatively conservative in their methods"*. The use of grabs, corers, trawls, dredges and seabed imaging gear, while fine-tuned, is relatively the same as when they were introduced. Some gears such as the Agassiz trawl, Petersen grab, and Reineck box corer were introduced to scientific field research 130, 107 and 55 years ago, respectively (Agassiz 1888, Petersen and Boysen Jensen 1911, Reineck 1963). This long history has allowed comparisons between studies over a long period of time. One example is the BENthic Disturbance EXperiment (BENDEX), in the course of which an artificially disturbed seabed area in the eastern Weddell Sea was re-sampled with a camera-guided coring device four times, in order to follow the recolonization process (Gerdes et al. 2008, Knust and Schröder 2014).

In general, the use of different sampling approaches impedes comparative across-study analyses. Therefore, large-scale studies on the benthos in different Antarctic regions are notoriously difficult (Arntz et al. 1994). This holds particularly true when quantitative data of different benthic compartments, such as, e.g. epifauna (based on seabed imagery) are compared with quantitative data on infauna (based on box corer samples). A way of homogenizing or combining spatial data from different gears, and its transformation for sound comparisons is still lacking. The same holds true for dedicated sampling strategies in order to study different benthic compartments in parallel and in a quantitative way.

Evolutionary history of Antarctic benthos

Antarctic benthic biota has been shaped to current state after millions of years of isolation and adaptation, making them a unique example of environment driven evolution (Rogers 2012). This process occurred in an environment with low but stable temperatures, low terrestrial inputs, a highly variable sea-ice cover, anchor ice, iceberg scours, and long-term/large-scale modifications of circulation patterns and ice shelf extensions and collapses (Arntz et al. 1994, Convey et al. 2009, Turner et al. 2009, 2014, Constable et al. 2014).

The long evolutionary history of Antarctic cold-water benthos was markedly impacted in the Oligocene ~35 million years ago (mya). Sediment records give evidence of glaciation events and decrease of temperatures, which led to a loss of diversity due to physiological constraints, especially of top predators such as sharks and crabs (Brandt 2005, Thatje et al. 2005, Rogers 2012). The further development of the Antarctic ecosystems towards their current state was influenced by the formation of the circumpolar current system and the isolation of the Antarctic continent during the Pliocene (5.3-1.6 mya). For the benthos the recurrent glaciation/deglaciation events during the Pleistocene (1.6-0.01 mya) played a particularly important evolutionary role (Arntz et al. 1994, Thatje et al. 2005, Barnes and Clarke 2011).

These glaciation events and the biogeographic isolation of the Antarctic continent led to the generally high endemism and pronounced radiation of benthic species in Antarctic waters (Thatje et al. 2005, Barnes and Kuklinsiki 2010). First estimates of the endemism of Antarctic benthos resulted in values as high as ~70% (Arntz et al. 1997). Later estimates, however, suggest a lower level of ~50% (Griffiths et al. 2009). The level of radiation of some groups, such as pycnogonids and peracarid crustaceans, has been regarded to be similar to the one of marsupials in Australia (Brandt 2005), which radiated due to absence of placental mammals (Clemens 1968). Likewise, Antarctic pycnogonids and peracarid crustaceans are thought to have radiated due to the absence of top predators, such as large lithodid crabs, after the cooling of the Southern Ocean.

Another key event for the Antarctic benthos occurred during the last glaciation maximum. During this period, the Antarctic ice shelves reached their maximum extension 15kya, and almost completely coved the Southern Ocean shelves. The diachronous extension of the ice shelves during Pleistocene glacial periods is hypothesized to explain not only the circumpolar distribution of many Antarctic benthic organisms, but also the high amount of Antarctic cryptic species (Thatje et al. 2005). On the one side, benthos is thought to have "escaped" shelf-ice advances by migrating to the deep sea. After the shelf ice retreated during warmer interglacial periods, benthic organisms started to recolonize the Antarctic shelves, leading to the current circumpolar distribution (Brey et al. 1996). On the other side, some benthic organisms could have migrated from one shelf refuge to the next, before the ice shelf fully developed, thus recolonizing adjacent shelves (Thatje et al. 2005, Barnes and Kuklinski 2010). Surviving by migrating among shelf refugia would have allowed for evolution of cryptic species (Thatje et al. 2005). Both strategies are reflected in the eurybathy of present-day Antarctic benthic organisms (Brey et al. 1996). Some benthic taxa inhabiting Antarctic shelves still share similarities with deep-sea organisms (Barnes and Clarke 2011), and the different geological, geographical and climatic histories are now reflected in regional faunistic differences and in the high amount of cryptic species (Rogers 2012).

Characteristics of modern Antarctic benthos

Antarctic benthos has been shaped by its long-lasting biogeographic isolation and the evolutionary pressure exerted by recurrent glaciations. Other drivers are low but stable temperatures, a highly variable input of primary produced organic matter, and iceberg scouring. The combined effect of this environmental setting and the geological history have given Antarctic benthos the following general characteristics (Clarke 1988, Gerdes et al. 1992, Brey and Clarke 1993, Arntz et al. 1994, 1999, Cattaneo-Vietti et al. 1999, Orejas et al. 2001, Brandt 2005, Thatje et al. 2005, Griffiths et al. 2009, Barnes and Clarke 2011, Rogers 2012, Peck et al. 2014):

A. Adaptation to low ambient temperatures
B. Stenothermia, with loss of resistance to high temperatures (often less than a few degrees above 0°C)

C. Patchy abundance, biomass and diversity
D. Eurybathy (wide depth ranges) of many species
E. Dominance of sessile suspension feeders
F. Brooding as main reproductive strategy
G. Long generation time and late maturity age
H. Gigantism
I. Paucity of exotherm top predators (e.g. lack of large decapod crustaceans and sharks)
J. Capacity to maintain metabolic activity during periods with low available food

In the following, further details will be given on the biodiversity, abundance, biomass, and adaptations of benthic organisms, as well as some features of benthic communities and their distribution patterns.

Biodiversity, abundance, and biomass

Clarke (1996) mentioned that *"for many people, reference to the polar regions conjures pictures of vast bleak wasteland populated by those few hardy species able to maintain a precarious existence in the face of extremely harsh physical conditions".* While this notion is partly true for Antarctic land ecosystems, is far away from the reality of Antarctic benthic ecosystems. High-Antarctic benthic biodiversity is generally on an intermediate level and can be higher than that of some sub-Antarctic ecosystems (Gutt et al. 2004, Griffiths et al. 2009). Therefore, the notion of a latitudinal cline described by Thorson (1957) and Stehli et al. (1967), with diversity decreasing from low to high latitudes, applies only for the northern hemisphere (Clarke 1996, Gray 2001, Clarke and Johnston 2003, Gutt et al. 2004, Griffiths et al. 2009).

More than 7,200 benthic species have been described for Southern Ocean shelves(De Broyer et al. 2010), most of which can be found in the taxonomic repository "Register of Antarctic Marine Species" (RAMS; DeBroyer et al 2018). Many species have a circum-Antarctic distribution (Arntz et al. 1994, Clarke and Johnston 2003, Thatje et al. 2005), which suggests the Antarctic shelf to be a single biogeographic unit (Griffiths et al. 2009). While records on the inventory of benthic species have been dutifully, albeit slowly, added since the 19th century, and more with a recently renewed effort after the signature of the Rio Convention in 1992 (De Broyer et al. 2010), we are still far from a complete inventory of benthic species. However, the question "how incomplete is the benthic species inventory?" is still hard to answer. Estimates on how many benthic species inhabit Antarctic waters are rare. Gutt et al. (2004) estimated a total of ~17,000 benthic species to inhabit the Antarctic shelf, by extrapolating trawl catch data from the Weddell Sea. However, due to the common existence of cryptic species (Brandt 2005, Rogers 2012) it is quite likely that a new estimation of the total number of benthic species will give a higher value.

Not only is the diversity of Antarctic benthos higher than expected, but also its abundance and biomass. While abundance values are in the same order of magnitude as those found in temperate and subtropical shelves (Arntz et al. 1997), average biomass values of Antarctic benthos can be even higher (Brey and Clarke 1993).

Antarctic infaunal benthos is mainly composed of burrowing worms (especially polychaetes), bivalves, and small crustaceans (mostly amphipods and tanaids; Gerdes et al. 1992, Sañé et al. 2012). However, composition and density of epifaunal benthos varies regionally due to differences in local food regimes and characteristics of bentho-pelagic processes. Areas with high local primary production and input of carbon such as the Ross Sea and Weddell Sea, and islands in the vicinity of the Antarctic Peninsula are mainly dominated by suspension feeders, such as sponges, ascidians and bryozoans (Dayton et al. 1974, Barnes 1995, Gerdes et al. 1992, Gutt and Starmans 1998). In contrast, areas where local carbon production is masked by inputs from adjacent shelves, such as the West Antarctic Peninsula shelf (Smith et al. 2006) are mainly dominated by motile deposit feeders (e.g. Sumida et al. 2008, 2014).

Adaptations

Antarctic benthos is well adapted to low temperatures close to the water freezing point (Peck 2005) and seasonal variability of food input (Clarke 1988). Considering this specialization and the physiological importance of these two factors, I will mainly focus on adaptations related to seasonality of food input and temperature.

The markedly seasonal input of food, with pronounced differences between light and dark periods, have been proposed to directly regulate benthic processes, such as sexual development, reproduction, recruitment of juveniles, growth, and feeding activity (e.g. Clarke 1988). However, there is evidence that Antarctic benthos is well adapted to this food shortage and has developed various strategies to meet biological requirements also during winter months (McClintic et al. 2008, Sumida et al. 2008, Souster et al. 2018). Some of these strategies include the use of energetic reserves produced during summer periods (e.g. Brockington et al. 2001, Peck 2005), change of feeding habits, e.g., polychaetes shift from suspension feeding to deposit feeding, cnidarians change their prey between seasons (e.g. Cattaneo-Vietti et al. 1999, Orejas et al. 2001), and deposit feeders make use of locally formed “food banks” and laterally transported resuspended material (Smith et al. 2006, McClintic et al. 2008, Sumida et al. 2008, 2014). Examples of processes performed during winter season, outside the high food input season, include feeding activity (Barnes and Clarke 1995), growth (Peck 2002, Pörtner et al. 2007), recruitment (Bowden 2005, Galley et al. 2005), larval release (Stanwell-Smith et al. 1999), and sexual development (Brockington et al. 2001).

At temperatures close to the water freezing point, organisms, do not only need to deal with reduced metabolic rates and their implication on molecular and individual level (e.g. Peck 2016), but also with the risk of freezing and intra-cellular ice formation, causing lethal dehydration and ion concentration, which damage cellular membranes and protein structures (Ramlov 2000). To deal with ice formation, organisms either avoid freezing or tolerate it by using cryoprotecting substances that regulate ice formation, the growth, recrystallization and melting point of ice crystals, and supercooling point of body fluids (Johnston 1990, Ramlov 2000). Two families of cryoprotecting compounds have been described, small cryoprotective substances, and large protein like cryoprotective substances (Ramlov 2000). Most of these compounds have been found in Antarctic fish and in few investigated invertebrates, e.g. intertidal limpets (Johnston 1990). Other adaptations to prevent freezing are higher unsaturated fatty acids in cellular membranes and increased concentration of solutes (e.g. sodium chloride) to lower the freezing point of body fluids (Johnston 1990).

Temperatures directly affect the speed at which biological processes occur. Due to the extremely low water temperatures in the Southern Ocean, growth, development and maturation rates, swimming, burrowing, and assimilation of food occur at lower speed in Antarctic invertebrates than in invertebrates elsewhere (Peck 2002, 2005, 2016, Pörtner et al. 2007, Peck et al. 2014). To compensate these temperature effects, organisms show four adaptations: no compensation; full compensation; partial compensation; and overcompensation. In most cases, Antarctic benthos only partially compensates for the effect of low temperature over several biological processes (Peck 2002). There are other processes such as swimming (for fish) and burrowing (e.g. in the bivalve *Laternula elliptica*), which are fully compensated. To achieve this compensation, fish have an increased number of mitochondria in their red muscle cells to increase metabolic activity (Peck 2005, Pörtner et al. 2007), whereas in *L. elliptica* the muscle involved in burrowing is larger than that of temperate species (Peck 2016). However, the case of *L. elliptica* is an exception, since most processes requiring muscular activity are not or only poorly compensated in Antarctic invertebrates, such as, e.g., the sticking capacity of limpets and burrowing speed of anemones (Peck 2002). The fact that processes such as growth and development rates, as well as assimilation of food, are not fully compensated has been taken as evidence of Antarctic benthos to be only partially adapted to its environment (Pörtner et al. 2007, Peck 2016).

The cold resistance of Antarctic benthos has been proposed to come with a reduced temperature range, i.e., the organisms tend to be stenothermic, to live in a rather narrow thermic window of 6-7°C (Peck 2002), and show poor acclimation capacity (Peck et al. 2009). Peck (2002, 2005) and Pörtner et al. (2007) reviewed experimental results on Antarctic invertebrate and fish physiology, and found that temperature increases of only a few degrees above 0°C could already result in critical failure of biological functions in Antarctic organisms. Peck et al. (2009, 2010b) and Richard et al. (2012) proposed Antarctic benthos to have poor acclimation capacities, and that temperature ranges ~3°C above present day temperatures could already be harmful (Richard et al. 2012).

Communities

Antarctic benthic communities are patchily distributed, mainly due to differences in local food input, and/or magnitude and periodicity of physical disturbances (see e.g. Gerdes et al. 1992, Arntz et al. 1997, Gutt 2000, 2001, Barnes and Conlan 2007).

Gutt (2007) defined two community types for shelves unaffected by anchor ice: a suspension-feeder community and a mobile deposit-feeder and infaunal community. A third community, the so-called “physically controlled” community, was defined for shelves heavily affected by anchor ice (a misnomer, as all communities are controlled by both biotic and abiotic, including physical factors). Furthermore, Gutt (2007) included the divisions: zero abundance within trophic guilds; extremely low abundances; and monospecific. While the first two divisions apply to the suspension-feeders community and the mobile deposit-feeder and infaunal community, the monospecific division consisted in a mix of the three major communities.

The classification of Gutt (2007) was updated by Turner et al. (2009) by including a fourth major unit, “mixed assemblage”, which includes overlaps between suspension-feeder and mobile deposit-feeder and infaunal community *sensu* Gutt (2007). Further groups included were “Seep” and “Vent” assemblages. According to the updated classification system of Turner et al. (2009), Antarctic benthos can be classified into three major community types and 5 distinct assemblages:

A. Communities:
  A. Sessile Suspension Feeders with Associated fauna (SSFA)
  B. MObile deposit feeders, INfauna and grazers (MOIN)
  C. Physically controlled (mainly by anchor ice)
B. Assemblages:
  A. MIXed (MIX)
  B. Seep
  C. Vent
  D. Monospecific
  E. Very low biomass or absence of trophic guilds

This classification was used by Gutt et al. (2013b) to describe the spatial distribution of benthic communities using samples obtained via different sampling gears and strategies around Antarctic shelves. They grouped point data within 3° latitude x 3° longitude cells, to describe regional patterns and found an almost equal amount of cells to be dominated by SSFA and MOIN communities, and MIX assemblage, a finding that was in contrast to the common notion that Antarctic benthic communities are mainly dominated by sponges. Furthermore, Gutt et al. (2013b) found cells on the eastern and southern Weddell Sea, eastern Ross Sea shelves, as well as off Adélie Land, South Shetland Islands, and South Orkney Islands, to have between 5 and 9 community sub-types per cell, strongly indicating the pronounced local patchiness of Antarctic benthos.

The classification of Gutt (2007) and Turner et al. (2009) is general and broad, making it applicable for circumpolar studies. However, on a regional level, benthic communities for some Antarctic regions are defined based on local characteristics of benthic abundance, biomass and diversity. For the Weddell Sea, there are three major community types that have been originally described by Voß (1988), and later validated by Gerdes et al. (1992) and Gutt and Starmans (1998): a) a Eastern Shelf community, with high diversity, abundance and biomass, dominated by sessile suspension feeders, predominantly sponges; b) a Southern Shelf community, with intermediate diversity, abundance and biomass, also dominated by suspension feeders, but predominantly bryozoans; and c) a Southern Trench community, with low diversity, high abundance, intermediate biomass values, and dominated by holothurians.

Recent studies described benthic communities on the eastern Weddell Sea shelf to resemble the Eastern Shelf community *sensu* Voß (1988) on seabed sections unaffected by iceberg scours (Gutt and Starmans 2001, Gerdes et al. 2008, Sañé et al. 2012). The benthos in the adjacent Filchner Region in the southern Weddell Sea has been regarded as particularly heterogeneous and diverse (Voß 1988, Gerdes et al. 1992, Gutt and Starmans 1998). This high-Antarctic region is characterized by heterogeneous topography, hydrography and sea-ice conditions. Furthermore, this part of the Weddell Sea is an important study region to understand how the Filchner Ice Shelf, which is key for the generation of Ice Shelf Water (ISW), a precursor of deep-water, thus, a driver of the global water mass circulation, will be affected by climate change (Hellmer et al. 2012). Considering that the last description of the benthos of the Filchner Region had been conducted almost 30 years ago, an update on the benthic status-quo is needed to understand how observed sea-ice and temperature variations in the last decades (Turner et al. 2016, Comiso et al. 2017), and predicted climate change (Hellmer et al. 2012, Timmerman and Hellmer 2013) have affected - and will affect - benthic communities.

Bentho-pelagic coupling

Antarctic benthos lives in connection with the pelagic realm via biological and environmental processes. This interconnectivity is marked by the downward flux of matter, especially carbon, from the upper water layer to the seabed (Hargrave 1973). This pelago-benthic coupling or bentho-pelagic coupling is regulated by processes that directly modulate the flux of carbon, such as water depth, seafloor topography, benthic and pelagic community structure, water circulation, wind, as well as ice in any of its forms (e.g. Smith et al. 2006, Raffaelli et al. 2003). Therefore, local differences of those processes can result in local differences in benthic community characteristics such as abundance, biomass, diversity and composition.

How benthos affects water column and planktonic biological characteristics is quite an open question. To date, the few known examples include regulation of resuspension and deposition of particles (Graf and Rosenberg 1997, Mercuri et al. 2008, Tatián et al. 2008), and modification of planktonic communities via predation or release of meroplanktonic larvae (Bowden 2005, Schnack-Schiel and Isla 2005). Any fraction of the benthos (e.g. macro- or megabenthos) directly affects sediment erosion and regulates the sediment-mixing regime (Orvain et al. 2012, Queirós et al. 2015). A typical Antarctic example is observed in sponge-dominated communities where vast spicule mats are found. These biogenic silica mats entrap and consolidate sediment, and work as silicate traps. Furthermore, both sponges and spicule mats provide substrate and refuge for other invertebrates and fish (Barthel 1992, Barthel and Gutt 1992, Gutt et al. 2013a). This enhanced biodiversity in sponge dominated communities affects water column particulate matter content, due to how filter feeders feed by collecting suspended particles from the water column, thus enhancing downward flux of particles and biodeposition (Barthel 1992, Mercuri et al. 2008, Tatián et al. 2008). Similar examples of enhanced biodeposition can be found locally in seabed patches with high abundance of tube-forming polychaetes which generate a local effect similar to that of sediments traps, enhancing downward flux of suspended particles (Frithsen and Doering 1989).

The term bentho-pelagic coupling implies a two-way relationship. Pelagic biotic and abiotic processes play a key role for benthos, since the main carbon (food) input comes from local pelagic primary production. Due to the seasonality of sea ice with high sea-ice cover during winter and low sea-ice cover during summer, primary production is also seasonal, with high productivity during spring/summer and low during autumn/winter seasons (Clarke 1988). Pelagic primary productivity is higher close to the sea-ice edge where melting of ice stabilizes the water column, and nutrients and entrapped algae, are released, seeding subsequent phytoplankton blooms (Scharek et al. 1994, Sedwick and DiTullio 1997, Sedwick et al. 2000, Arrigo et al. 2008, Bertolin and Schloss 2009, Isla 2016). Another factor regulating not only phytoplankton blooms, but also downward particle flux, is zooplanktonic activity. Zooplankton consumes primary-production carbon (Flores et al. 2014), resulting in enhanced pellet production which largely contributes and regulates particle flux characteristics (Bathmann et al. 1991, Palanques et al. 2002, Schnack-Schiel and Isla 2005, Isla et al. 2009, Rossi et al. 2013, Isla 2016). This particle flux can provide the benthos with an amount of carbon equal to <1 to 18% of the local annual production (Bathmann et al. 1991, Palanques et al. 2002, Isla et al. 2006, 2009), which is sufficient to support benthic communities with high biomass (Gutt et al. 1998) and form “food banks” on the sediment surface (Smith et al. 2006).

Climate change and the Antarctic continent

Since the onset of industrialization, the natural variability of the composition of the atmosphere has been modified by anthropogenic inputs, resulting in an increase of greenhouse gases and local depletion of the stratospheric ozone (Constable et al. 2014, Turner et al. 2014, Gutt et al. 2015). During the 2000s and 2010s, the Scientific Committee on Antarctic Research (SCAR) and its members published a set of reviews which spanned climatic and biological changes occurring on geological and instrumental (i.e. since the 20th century) time scales, also including predicted changes based on several climate change scenarios published by the International Panel on Climate Change (IPCC; e.g. Convey et al. 2009, Turner et al. 2009, 2011, 2014, Constable et al. 2014, Gutt et al. 2015). The general observations that can be drawn from their extensive work are: Antarctica has been affected by climate change at an exceedingly fast rate; general trends suggest, Antarctic sea-surface temperatures have decreased, while sea-ice cover and duration of sea-ice have increased; on a regional scale, however, some sectors of the Southern Ocean have shown an increase of sea-surface temperatures and decrease of sea-ice covered (e.g. Antarctic Peninsula and Bellingshausen Sea), whereas other sectors exhibited trends in sea-surface temperature and ice cover similar to those for the entire Antarctic continent, i.e., decreasing sea-surface temperatures and increasing sea-ice cover (e.g., Ross Sea and eastern Weddell Sea).

Sea-ice and sea-surface temperature variations are influenced by the variation of the westerly wind regime, which is regulated by the Southern Ocean Annular Mode (SAM; Liu et al. 2004, Convey et al. 2009, Turner et al. 2009, 2014, 2016, Constable et al. 2014, Comiso et al. 2017, Kostov et al. 2017). The term SAM refers to an alteration of atmospheric mass between mid-latitude surface pressure and high latitude surface pressure (Gong and Wang 1999), which has positive and negative phases. During negative SAM phases westerly winds are weakened, causing the Antarctic Coastal Current to migrate northwards, whereas a strengthening of the SAM during positive phases generates a strengthening of westerly winds. This strengthening causes a southward migration of the Antarctic Coastal Current, resulting in higher sea temperatures in the West Antarctic Peninsula region, and Bellingshausen and Amundsen Seas. A positive SAM also implies a deepening of the low-pressure cell located at the Amundsen

Sea, which causes sea-ice losses in the Amundsen Sea, but the opposite effect in the Ross Sea and eastern Weddell Sea (Liu et al. 2004, Turner et al. 2016).

The most affected area by increase of temperatures is the West Antarctic Peninsula, its adjacent islands and the sub-Antarctic Islands, where in some sectors the temperature of the upper 150m of the water column has increased >2.3°C over the last 8 decades (Convey et al. 2009). This region as well as the Amundsen Sea and Bellingshausen Sea, are the areas where the highest sea-ice losses were recorded since the start of satellite measurements in 1979, with losses of $51 \text{x} 10^3$ km^2 decade^{-1} (Turner et al. 2016, Comiso et al. 2017). Furthermore, these regions have also shown the biggest ice-shelf losses and glacier retreats of the whole Antarctic continent (see e.g. Cook et al. 2005). Opposite trends were recorded, especially, in the Ross Sea. This region has experienced the largest increase of sea-ice cover (119 $\text{x}10^3$ km^2 dec^{-1}), double than that observed in the Weddell Sea (48 $\text{x}10^3$ km^2 dec^{-1}), and the Indian (56 $\text{x}10^3$ km^2 dec^{-1}) and western Pacific (23 $\text{x}10^3$ km^2 dec^{-1}) sectors of the Southern Ocean (Turner et al. 2016). Comiso et al. (2017) related sea-ice cover trends to sea-surface temperature trends, and considering data from the period 1981-2015, estimated decreases of up to 0.5 °C decade^{-1} for all areas where sea-ice cover has increased.

As the East Antarctic Peninsula is part of the Weddell Sea, the situation is more complex than mentioned above. The average trends for the whole Weddell Sea sector show an increase of sea-ice cover and a decrease of sea-surface temperature (Turner et al. 2016, Comiso et al. 2017). However, this situation only applies to the eastern Weddell Sea shelf, whereas on the western Weddell Sea, especially for waters surrounding the Antarctic Peninsula, sea-ice cover has decreased, and sea-surface temperatures increased in the last decades (Liu et al. 2004, Gutt et al. 2015, Turner et al. 2016). While the instrumental records of the last five decades show contrasts between eastern and western Weddell Sea sub-regions, models based on different IPCC future scenarios predict sea-ice cover and salinity to decrease, and sea-surface and near-seabed temperature to increase (Timmerman and Hellmer 2013, Hellmer et al. 2017).

Sea-ice cover and sea-surface temperature directly affect the pelagic primary production. While a decrease of sea-ice (enlarging of polynyas) as well as an increase of temperatures would enhance pelagic primary production, an increase of sea-ice cover and decrease of temperatures would have the opposite effect (Arrigo et al. 2008, 2015). Recently, Peck et al. (2010a), Barnes (2015), and Barnes et al. (2016, 2018) have studied how the observed increase of open water in the West Antarctic Peninsula, and consequent increased pelagic primary production, have affected benthic organisms and the amount of biological carbon ("blue carbon") stored in the local benthic communities. They found the increase of open water to enhance benthic "blue carbon" production and carbon fixation, thus functioning as a negative feedback to climate change. In a similar study, Fillinger et al. (2013) analyzed the situation of the area formerly covered by the Larsen A ice shelf; they found benthic abundance and biomass tripled and doubled, respectively, in a four-year period parallel with a shift to a system with higher pelagic primary production (Bertolin and Schloss 2009). An increase of ice shelf basal melting due to temperature raises, also resulted in an increased number of icebergs, which translated into an increased susceptibility of benthos to calving events (Barnes 2017, Barnes et al. 2018, Budge and Long 2018). An increase of calving events could eliminate portions of the benthos, thus reducing the amount of fixed "blue carbon" (Gutt 2000, Barnes and Souster 2011, Barnes 2017).

Research questions

This section includes short rationales of open questions found throughout the "General Introduction" (and the open questions themselves). The manuscripts of this thesis aim to address these questions, in order to shed new light on the past, present and future of benthic communities inhabiting the Weddell Sea shelf.

Manuscript 1

Benthologists are creatures of habit and tend to use a single methodology, which have not changed except for some minor technical updates. This approach facilitates performing temporal comparisons, but may be problematic with regard to spatial comparisons with other regions, or studies where a different methodology was used. By doing this, we end up with different "truths", one for each benthic compartment studied. The use of imaging approaches is ideal to investigate the epifaunal benthos, whereas the use of coring devices is most appropriate for infaunal benthos, which burrows in the sediment. While complementary, both techniques are seldom used together, although both can be combined in a time-constrained sampling campaign by using camera-equipped corers. This brings the question: is there an advantage in using both methods and what would this advantage be?

Manuscript 2

Benthos is not independent from the pelagos, neither spatially nor temporally. The coupling between realms is known as bentho-pelagic coupling, a concept critical to understand how benthos is shaped by its surrounding abiotic and biotic environment. While extensive data exist on bentho-pelagic processes, just few attempts tried to combine them in a comprehensive and "easy-to-read" way. Recent focus on the bentho-pelagic coupling on West Antarctic Peninsula (WAP) shelves provided a description on how the coupling in this region works (e.g. Smith et al. 2006, McClintic et al, 2008, Sumida et al. 2008). However, despite having all the "dots" for the Weddell Sea, few attempts exist to link them as Smith et al. (2006) showed for the WAP. I investigate whether the bentho-pelagic coupling works in the same way in both regions or not, and how local characteristics of both regions make this coupling different.

Manuscript 3

The last benthic sampling in the high-Antarctic Filchner region before RV *Polarstern* cruise PS82 (Knust and Schröder 2014) was conducted almost 30 years ago. Even the study of Voß (1988), one of the spatially broadest benthic studies, failed to sample the central and northern parts of the shelf west of the Filchner Trough due to heavy sea-ice conditions. Consequently, this area is still under-studied.

Recently, the Filchner Region, key for the formation of deep-water (the latter being an important driver of the global water mass circulation), has been predicted to suffer drastic changes which could have global implications (Hellmer et al. 2012). These predictions have made the region a focal point for oceanographic studies aiming to understand how the complex hydrography of the Filchner Region works. Additionally, since the last benthic samplings, the region suffered changes in its hydrography due to the calving and grounding of iceberg A23-A (Grosfeld et al. 2001). Furtheron, sea-ice trends in the region provide evidence for an increase of sea-ice cover during the 1979-2013 period (Turner et al. 2016), which could potentially cause a decrease of locally produced food input to the benthos.

We know from previous studies in the region that the benthos has a heterogeneous distribution and is composed of (at least) three different communities (Voß 1988, Gerdes et al. 1992, Gutt and Starmans 1998, Gutt et al. 2013b). Furthermore, considering observed environmental changes in the region, e.g. the sea-ice cover increments with likely primary productivity losses, we need to query whether the benthic communities previously described in the Filchner Region changed or not, and if so, how. Another point to consider is the role of the present spatial environmental heterogeneity in the region, and if the benthic spatial distribution in the Filchner Region is affected by it and how. Answers to these questions can give hints on how benthos might change under the predictions made by Hellmer et al. (2012).

Manuscript 4

The situation in the western Weddell Sea appears favourable for benthic growth due to enhanced pelagic primary production (Peck et al. 2010a, Fillinger et al. 2013, Barnes 2015, 2017, Barnes et al. 2016, 2018). In comparison, the situation of the benthos in the eastern Weddell Sea is far from being clear. Barnes (2015) described an increase of benthic blue carbon in the eastern Weddell Sea. However, this was done considering only one sampling campaign in 2012. Another fact which might prove wrong the observation of Barnes (2015) is the observed trend of increased sea-ice cover (Turner et al. 2016), which implies a reduction of pelagic primary production. This contradiction raises, at least, three questions: 1) What is the actual situation of the benthos in the eastern Weddell Sea? 2) How has the benthic community of this high-Antarctic region been affected by the observed increased sea-ice cover and iceberg numbers? 3) What would be expected to happen to the eastern Weddell Sea benthos under scenarios where the environmental context is predicted to be quite different to the present one (i.e. less sea-ice and higher temperatures)?

Manuscripts within the context of the research questions

This section describes how the four manuscripts of this thesis will address the questions mentioned in the previous section.

Manuscript 1

This manuscript addresses methodological approaches used to study benthos in the past, and how two classic sampling techniques can be used in combination. The main aim of this manuscript is to compare two sampling methodologies, sediment cores and seabed images. In order to do this comparison, a set of 16 stations with concomitantly taken corer samples and seabed images during RV *Polarstern* cruise PS82 (ANT XXIX/9) in the austral summer 2013/14 were used to compare benthic composition and abundance data obtained by both approaches. These data further allowed insights into benthic community patterns of the formerly understudied Filchner Region in the southern Weddell Sea.

Manuscript 2

Manuscript 2 reviews the knowledge on the bentho-pelagic coupling. The manuscript describes benthic and pelagic processes which regulate transfer of carbon between compartments, also considering local differences. "How are benthic communities shaped by such processes?" Within this context, examples of environmental and biological factors and processes regulating the strength and characteristics of bentho-pelagic coupling are explained to give, even non-experts, a clear view of how this coupling works in different Antarctic shelf areas. To further explain how shifts in local pelagic characteristics affect and modify the benthos, I compare the shelves west of the Antarctic Peninsula as well as the area formerly covered by the Larsen Ice Shelf, with the shelf in the eastern Weddell Sea.

Manuscript 3

This manuscript addresses questions regarding the little studied benthic communities of the Filchner Region in the southern Weddell Sea by combining data from analyses of multibox corer samples and seabed images. This comprehensive data set was then used to describe benthic communities in the Filchner Region (southern Weddell Sea) including both infaunal- and epifaunal benthos. Furthermore, past (Voß 1988, Gerdes et al. 1992, Gutt and Starmans 1998) and present benthic community spatial patterns in the Filchner Region are compared. Additionally, the described benthic fauna is correlated with a set of geological, oceanographic, and sea-ice-related variables, to get hints on how the environmental heterogeneity of the Filchner Region affects the spatial distribution patterns of benthos.

Manuscript 4

Manuscript 4 describes the benthic community living on the shelf off Austasen, eastern Weddell Sea, and how this community changed over the last decades. This manuscript relates to Manuscript 2 by including concepts and components of the bentho-pelagic coupling, which are key to understand the present status of the benthos and how it future could be. Thus, Manuscript 4 mainly aims to describe the actual situation of the benthos in the eastern Weddell Sea shelf. To achieve this, the manuscript includes data from eight sampling campaigns performed in the period 1988-2014, and describes how different benthic taxa, their abundance and biomass, have changed during a 26-year time series, and which environmental factors drive these changes.

Addressing these topics might give hints on how the future of a typical Weddell Sea benthic community might look like under climate scenarios where the environmental context is predicted to be quite different to the present one, i.e. with less sea-ice and higher temperatures.

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MANUSCRIPTS

MANUSCRIPT 1: Seabed images versus corer sampling: a comparison of two quantitative approaches for the analysis of marine benthic communities in the southern Weddell Sea (Southern Ocean)

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Seabed images versus corer sampling: a comparison of two quantitative approaches for the analysis of marine benthic communities in the southern Weddell Sea (Southern Ocean)

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ABSTRACT

Corer sampling and seabed imaging are two quantitative approaches used to investigate benthic fauna. Despite the complementary nature of these methods, very few studies have been done using both in parallel. Here, we compare benthic composition and abundance data derived from the quantitative faunistic analysis of both multibox corer samples (MBC) and seabed images (SBI) taken concomitantly at 16 stations in the Filchner-Ronne region of the southern Weddell Sea (Southern Ocean) during R/V *Polarstern* cruise PS82 (ANT-XXIX/9) in 2013/14. A total of 43 benthic taxa were found, 34 in MBC and 29 in SBI samples. Mean benthic abundance derived from MBC was twenty times higher than the SBI abundance (1,708 vs. 71 ind m^{-2}) – best explained by SBI being a method focusing on the epifauna alone whereas MBC also captures the more abundant infauna. Differences in taxa caught by both gears demonstrated that MBC alone was not sufficient for a comprehensive representation of the entire benthic fauna. The among-station similarity patterns derived from both methods correlated significantly; a different combination of taxa best explained the specific distribution patterns. Overall, our results demonstrate similar and comparable spatial distribution patterns in the benthic communities by both methods. We therefore highly recommend the use of both, MBC and SBI in combination.

Keywords: in- and epifauna, Filchner region, zoobenthic distribution patterns, quantitative sampling

INTRODUCTION

In general, benthic marine macrofauna can be divided into three habitat-related compartments: a) infauna living in the sediment; b) epifauna comprising vagile and sessile organisms living on the sea floor and c) suprabenthic fauna living above the sea floor but remaining connected to the benthic habitat (Dauvin and Vallet 2006).

Specific collection gear has been designed to adequately sample each of these benthic compartments. While trawled gear provide qualitative estimates of species numbers and richness (Clark et al. 2016), corers are used to quantitatively determine abundance and biomass of the different benthic taxa by providing precise numeric data that allow for inferences on the general ecology of Antarctic benthos. However, quantitative abundance data for Southern Ocean macroinvertebrates are still comparatively scarce (Clarke 2008). In the present study, we compare the performance of two sampling gears by assessing the quantitative data obtained by a) multibox corer samples and b) seabed images.

Corers have been extensively used in marine ecology and are mainly used for sampling soft-bottom benthic fauna across multiple size ranges. One commonly used corer is the giant box corer, which covers a seabed area of 0.25 m^2 (AWI 2006) and can catch organisms > 20 mm. Another example of coring device is the multibox corer (MBC; Gerdes 1990). While single corers provide information of large macrobenthos, they are inefficient as many deployments are required to build up a statistically robust picture of the nature of macrobenthic distribution patterns. In comparison, each box of a MBC is inefficient to sample large macrobenthos (each box covers an area of 0.024 m^2). However, the circular area subsampled per deployment of a MBC is ~2.3 m^2, this allows to “better” represent patchily distributed macrobenthos, while being able to treat each of the 9 cores as a replicate (Gerdes 1990).

Corers often provide relatively undisturbed samples of both infaunal- and epifaunal benthos, although they are better suited to study the infaunal compartment (Eleftheriou and McIntyre 2005; Lozach et al. 2011). The problems of sampling epifaunal benthos with corers are: a) the scattered abundance of large epifauna (*e.g.* hexactinellid sponges); b) patchily distributed organisms (*e.g.* ophiuroids; Syvitski et al. 1989) are underestimated; c) motile organisms tend to avoid being caught by corers (*e.g.* Thurston et al. 1994); and d) the approaching gear may generate a bow-wave effect that flushes away smaller organisms. For further discussion about corers and other soft-bottom sampling gear, we refer to Blomqvist (1991) or Eleftheriou and McIntyre (2005), and further literature cited therein.

The disadvantages of corers for the investigation of epibenthos have led to the implementation of seabed imaging methods to overcome these constraints (Rumohr 1995; Solan et al. 2003). Since its first use over a century ago in the 1890s, seabed imaging transformed from a qualitative technique to a quantitative one and has been recognized as a valuable complement to traditional benthos sampling approaches involving trawls or corers. A wide range of information can be obtained from seabed images, as they provide an in-situ view of epibenthic habitats and communities. If spatially calibrated with scales (e.g. by laser pointers), and corrected for optical distortion, quantitative data on epibenthic abundance and, to some extent, biomass estimations can be derived by this approach (Rumohr 1995). However, there are some constraints limiting the use of seabed images (Rumohr 1995): a) the light backscattering under turbid conditions can result in poor image quality; b) highly mobile, cryptic, and small-sized organisms are not well recorded; and c) high costs for acquisition and maintenance of seabed imaging equipment may be prohibitive.

In the Weddell Sea and off the Antarctic Peninsula, benthic communities have been studied by means of both corers (e.g. Gerdes et al. 1992, 2003, 2008; Sañé et al. 2012) and seabed imaging (e.g. Fillinger et al. 2013; Gutt and Piepenburg 2003; Gutt et al. 2011, 2013). Despite the fact that these methods complement each other, studies using both approaches in a comparative manner are scarce. This scarcity of information leaves open questions such as: a) how different are the infaunal- and epifaunal benthos sampled by both gears in parallel? or b) are benthic distribution patterns resulting from quantitative corer sampling and obtained from a parallel seabed imaging survey correlated? Piepenburg et al. (2002) conducted such a study off King George Island, using a combination of multibox corer (Gerdes 1990) and a still camera system (Piepenburg and Juterzenka 1994) to comparatively analyze the spatial distribution of infaunal- and epifaunal benthos with a special focus on assemblage description. In our study we aim to make a comprehensive comparison between both MBC and SBI to illustrate the differences in results obtained by these methodologies. Furthermore we analyzed the resemblance of the distribution patterns of infaunal- and epifaunal benthos.

MATERIAL AND METHODS

Fieldwork was performed during the R/V *Polarstern* PS82 (ANT-XXIX/9) expedition in the Weddell Sea from December 2013 to March 2014 (Knust and Schröder 2014). A total of 16 stations were investigated with a MBC (Table 1). The stations were distributed across three sub-regions of the Filchner-Ronne Outflow System (FROS): a) the eastern and b) western flanks of the Filchner Trough, and c) the trough itself (Fig. 1).

The MBC used to sample infaunal benthos covers a circular area of ~2.3 m^2 and provides a maximum of 9 cores, each core covering 0.024 m^2. Prior to core sampling, seabed images were taken with an underwater camera (Canon EOS D100) installed in a pressure housing attached to the MBC. Images were taken every 15 seconds for 15 minutes resulting in a mean of 55 images per deployment. The high-definition photographs were taken from 1-2 m above the seabed.

Sediment cores obtained with the MBC were sieved on deck over a 500-µm mesh size sieve. The sieve residues were stored in 5-L containers and fixed in a 5% sea water-formaldehyde solution buffered with borax. Overall, 101 corer samples were taken at 16 stations. These samples represented an average of 0.15 m^2 seabed per station. Benthic organisms were sorted from these samples, identified to the lowest possible taxon via a stereomicroscope and classified into 34 major taxonomic groups (Table 2). Abundance values (ind m^{-2}) were determined for each taxon and station. For colonial (e.g. bryozoans and hydrozoans) and large macrobenthic organisms (e.g. glass sponges) only presence was recorded.

A total of 279 seabed images (SBI) obtained at the 16 stations were analyzed. At three stations (033, 040 and 206), all images obtained were analysed in order to calculate the number of images per station sufficient to cover all taxonomic groups differentiated. The taxon accumulation curves at these three stations clearly indicated that the analysis of 15 images is sufficient for this purpose. For this reason, at all other stations a randomly selected image subset of 15 SBI was used for the description of the epifaunal community. The average seabed area analyzed per SBI station was 14.6 m^2, and an overall seabed area of 233.2 m^2 was investigated at the 16 stations considered in this study.

The optical axis of the camera attached to the MBC had an inclination of 45º in relation to the seabed. To compensate for the distortion of the area pictured, the images were edited prior to analysis with the Camera Distortion Correction tool of the software Adobe Elements v5.0. The size of the seabed area in each image, determined by means of two laser-pointer dots with a distance of 4.5 cm from each other, ranged from 0.38 to 2.86 m^2, depending on the distance of the camera from the seafloor. In the laboratory, all organisms visible in the SBIs were counted, identified to the lowest possible taxon, and classified into 29 taxonomic groups (Table 2). Organism counts were standardized to abundance figures (ind m^{-2}). The abundance of colonial organisms was calculated as area (in m^2) covered by the colonies. To make results and units between SBI and MBC data comparable, these abundance values were not used for statistical analysis.

Multivariate statistics were applied to perform benthic community analyses of abundance data obtained from both MBC and SBI by means of the software package PRIMERv6 with its PERMANOVA+ add-on (Clarke and Gorley 2006; Anderson et al. 2008). A similarity matrix was calculated by means of Euclidean distances. This similarity matrix was used in a PERMANOVA analysis to test for interactions between sampling method and sampled stations. For the design of the PERMANOVA, two factors were considered: a) sampling gear (MBC and SBI) as a fixed factor, and b) station (16 levels) as a random factor. The Monte Carlo option of the PERMANOVA routine was used to ensure 9999 permutations. In case of a significant interaction between the two factors, pairwise tests were performed to examine differences between methods and across stations. Abundance values per taxon and core/image were 4th-root transformed to reduce the effect of high variation among taxa. These transformed values were used in a two way SIMPER test (Clarke and Warwick 1994) to establish the percent dissimilarity between MBC and SBI across stations, and which taxa were the primary contributors to these differences.

Mean abundance values for each MBC and SBI station were calculated. These data were arranged in two matrices featuring the mean abundances per taxon and station (excluding colonial organisms). Abundance figures were 4th-root transformed to reduce the effect of high variation among taxa. Between-station similarities were calculated using the Bray-Curtis Index (Bray and Curtis 1957). The resemblance pattern in the similarity matrices was visualized using 2-d multidimensional scaling (MDS) plots. The stations were grouped based on a cluster and SIMPROF analysis (Clarke and Gorley 2006). To recognize the taxa that primarily explain these station groups, principal component analyses (PCA) of the weighted variables were performed. MDS and PCA results were compared to evaluate differences between distribution patterns of the two benthic community fractions represented in the MBC and SBI data (infauna vs. epifauna).

A RELATE test (Clarke and Warwick 1994) was performed to test for a correlation between the two similarity matrices based on MBC and SBI data, to check the resemblances between infaunal and epifaunal distribution patterns. In case a significant correlation was observed with the RELATE test, BEST tests (Clarke and Gorley 2008) were performed as well. BEST tests, as RELATE and Mantel tests (Mantel 1967), correlate two similarity matrices. One matrix is considered as the "explained" or dependent matrix and the other as the "explanatory" or independent matrix. As such, the test examines the variables from the "explanatory" matrix one at a time, then pairs of variables, triplets, and so on (Clarke et al. 2008). The BEST procedure then selects the variables that "best explain" the pattern of the "explained" matrix.

RESULTS

Combining all SBI and MBC data, a total of 43 benthic taxa were found (Table 2). Eight taxa were exclusively found in SBI (gorgonians, actinarians, scleractinians, nudibranchs, cephalopods, mysids, serolids, and decapods), and 13 taxa were exclusively found in MBC samples (sipunculids, flatworms, nemerteans, priapulids, aplacophors, clitellate worms, echiurids, cumaceans, harpacticoid copepods, cirripeds, tanaidaceans, and ostracods; Table 2).

The mean total benthic abundances of the MBC stations varied from 104 to 4,543 ind m^{-2}, with an overall mean of 1,708 ind m^{-2} and an overall median of 1,325 ind m^{-2}. Dominant taxa (*i.e.*, those that contributed at least 75% to the mean abundance at the stations) were polychaetes, amphipods, clitellate worms, ophiuroids and bivalves (Fig. 2 and 3). The mean total epibenthic abundances of the SBI stations ranged from 16 to 170 ind m^{-2}, with an overall mean of 71 ind m^{-2} and an overall median of 64 ind m^{-2}. Following the criteria given above, ophiuroids, holothurians, polychaetes, tunicates and unidentified organisms were identified as dominant taxa in the SBI (Fig. 2 and 4).

Two-way PERMANOVA analysis showed significant variability in the structure of the benthic assemblages (Table 3) both, between methods (MBC, SBI) and among stations. Furthermore, there was also a significant between-factor interaction (Table 3), indicating that the effect of the MBC and SBI was not the same across all stations. Pairwise comparisons showed, however, significant differences between MBC and SBI at each station, albeit to a different degree (*p* values ranged from <0.01 to 0.03). A complimentary SIMPER test established 80.1 % dissimilarity between MBC and SBI abundance values across all stations. The taxa that contributed ~50 % to this difference were polychaetes, ophiuroids, bivalves, amphipods, holothurians and clitellate worms (Table 4).

Cluster and SIMPROF analysis distinguished five groups of MBC stations, and three groups SBI stations (Fig. 5). A PCA of the weighted variables showed the grouping of MBC stations was caused almost exclusively by polychaetes, and the SBI station grouping to be mainly affected by the abundances of ophiuroids and holothurians (Table 5; Fig. 6 and 7).

MBC stations were divided into five groups (Fig. 5). Both MBC groups "a" and "b" were comprised by just one single station situated in the Filchner Trough at 684 (st 033) and 1111m depth (st 066). MBC group "c" was comprised of two stations located in the shallow area of the western flank of the trough (st 242, 436 m depth), and the deep trough (st 116, 1060 m depth). MBC group "d" was also comprised by two stations, both located on the western flank of the trough between 798 (st 236) and 1140 m water depth (st 206). MBC group "e" was the largest group with 10 stations, distributed across the entire FROS in a wide depth range (254 to 1217 m depth). In terms of abundance, all MBC groups were dominated by polychaetes. However, the second dominant taxon varied across station groups. For groups “a”, “b” and “c”, bivalves followed polychaetes, in group “a” they were almost as abundant as polychaetes, in groups “b” and “c” clearly less abundant (Fig. 3). The second dominant taxon in group “d” were ophiuroids and in group “e”, amphipods (Fig. 3). The highest abundance values were found at stations in group “e”, followed in descending order by stations of groups “d”, “c”, “b”, and “a”.

SBI stations were divided into groups “a”, “b” and “c” (Fig. 5). SBI group “a” included stations 066 and 116, which are located in the deep Filchner Trough. SBI group “b” included 4 stations (033, 040, 098 and 242) located in all three FROS sub-regions in water depths of 436 to 684 m. The remaining stations grouped in group “c”, were distributed across the entire FROS region and a wide depth range of 254 to 1217 m. The SBI group “c” stations showed the highest mean abundances, group “b” the lowest, and SBI group “a” contained just 2 stations with a max. abundance at st. 066 and a very low abundance at st. 116 (Fig. 4). SBI group “a” was dominated by holothurians, group “b” by ophiuroids and, group “c” was dominated by ophiuroids and polychaetes (Fig. 4).

Despite the differences in MBC and SBI station groupings, a RELATE test showed that the among-station resemblance pattern in MBC data was significantly correlated with the pattern found in SBI (Spearman rank correlation; $\rho = 0.395$, $p = 0.01$). A first BEST test using MBC resemblances as “explanatory” matrix suggested that flatworms, priapulids, amphipods, cirripeds, and holothurians were the taxa “best explaining” the similarity pattern among SBI stations (Spearman rank correlation; $\rho = 0.604$; $p = 0.04$). A vice-versa BEST test with SBI resemblances as “explanatory” matrix showed brachiopods, pycnogonids, isopods, unidentified crustaceans, echinoids, asteroids, and ophiuroids to be the taxa “best explaining” the similarity pattern among MBC stations (Spearman rank correlation; $\rho = 0.693$; $p = 0.02$).

DISCUSSION

The total area covered by SBI during our study was two orders of magnitude larger than that covered by MBC samples. Rumohr (1995) described special features of different seabed imaging techniques; seabed still images cover a range of square centimeters up to square meters. Although seabed images cover larger areas of seafloor, this method is limited by the resolution of the images (Rumohr 1995). This lack of high image resolution means that small organisms tend to be ignored and their importance for the community thus remains underestimated (Sloan et al. 2003). Examples of such taxa are crustaceans, especially amphipods, tanaidaceans, small isopods and ostracods, which occur regularly in high Antarctic shelf communities (Gerdes et al. 1992). On the other hand, the MBC with its small coring areas will underrepresent larger benthic organisms such as e.g. glass sponges. A way to overcome this problem is the use of giant box corers, which provide just one corer but of a larger area (0.25 m^2; AWI 2006).

All data presented and discussed in this paper rely on organism numbers and neglect biomass estimates, because at the moment we do not have the proxies to calculate biomass from density and organism size measures from SBI. PERMANOVA results showed significant differences of abundance values between sampling methods across stations (Table 3). Mean abundance values obtained from MBC stations were orders of magnitude larger than those obtained from SBI, although the SBI recordings considered two orders of magnitude more sea floor area. The maximum abundance value derived from the images was 170 ind m^{-2}, whereas comparable low abundance values in quantitative corer samples (237, 104 and 334 ind.m^{-2}) were found only at three deep stations in the Filchner Trough (st 033, 066 and 116, respectively). The mean abundance per station derived from MBC samples (1,708 ind m^{-2}) was more than 20 times higher than that obtained from SBI (71 ind m^{-2}).

There were distinct differences in the dominant taxa. Polychaetes were the most dominant taxon in the MBC samples, but ranked 3rd in SBI. In contrast, ophiuroids were the most dominant taxon in SBI, but ranked 4th in the MBC dominant taxa list (Fig. 2). With the exception of sedentary polychaetes, the dominant taxa in SBI include groups with medium mobility (e.g. ophiuroids and holothurians), organisms that are hard to capture with corers due to their size or patchy distribution (e.g. tunicates), and those that could not be identified. Unidentified organisms were found in 15 of the SBI stations and only at three MBC stations. The higher frequency of unidentified organisms found in SBI stations is not surprising when taking into account how organisms were identified. In SBI stations, organisms were identified directly from each image, which makes it difficult to distinguish small structures needed to properly identify individuals. Furthermore, in cases where images are out of focus or suspended particles are present, the task of identifying organisms is even harder. However, for MBC stations, organisms are identified in the laboratory by means of a stereomicroscope, making the identification task easier. MBC dominant taxa included organisms that either live in the substrate or are smaller than 1cm in size. The SIMPER comparison between methods across stations showed a mix between SBI and MBC dominant taxa to be main contributors to differences between methods (Table 4).

Piepenburg et al. (2002) documented enormous differences in abundance and composition between quantitative data derived from MBC and SBI. These differences can be explained by the suitability of a gear for catching specific benthic components. As already mentioned in the ´Introduction´, corers are effective for collecting infaunal benthos, whereas seabed photography is better suited to map epifaunal benthos > 1 cm in size. Solan et al. (2003) explained the advantages of seabed images for observing epibenthic patterns pointing out that a fundamental problem remains, because a big part of the soft-bottom benthos is living burrowed in the sediment and can thus not be detected. In our study area despite the presence of drop stones or gravel, the dominant sediment type at all stations was soft-sediment, which can be regarded as normal for the high Antarctic Weddell Sea shelf (Diekmann and Kuhn 1999b).

Combining both methods, we found a total of 43 taxa. Those taxa found exclusively in MBC samples include organisms living burrowed in the sediment or rather small organisms that are difficult to identify in images. Taxa exclusively found in SBI were either highly mobile, e.g. cephalopods and mysids, or they occurred in low abundances as e.g. nudibranchs (only one individual was found). A fact that stands out is the complementarity of the results obtained with both methods, i.e. taxa not or poorly represented in corer samples are better represented in images, and vice versa. This complementarity of both methods has been pointed out before (e.g. Rumohr 1995; Solan et al. 2003) and it is therefore surprising that both methods in combination are not used more often, since they can be treated as “the two sides of the same coin”.

A combination of cluster, SIMPROF and MDS (Fig. 5) showed differences between station groups obtained from MBC and SBI data. Furthermore, the PCA results clearly showed that the driving factors for grouping were different, mainly polychaetes in the case of MBC, and the combination of ophiuroids and holothurians for SBI (Table 5, Fig. 6 and 7). Despite these differences, the RELATE test showed that there is a statistically significant similarity between the distribution patterns of infaunal and epifaunal communities (Spearman rank correlation; $\rho = 0.395$; $p < 0.01$). This suggests a coupling between both benthic fractions. Such a match of distribution patterns resulting from both methods is a rather surprising result for two reasons: a) our study region in the FROS is characterized by a heterogeneous topography inhabited by very different benthic community types (Voß 1988; Pineda-Metz et al. in prep). How infaunal- and epifaunal benthos is affected by environmental gradients and how they respond to these gradients differs; thus, differences between benthic components are to be expected; and, b) a similar approach (Piepenburg et al. 2002) of comparing benthic compartments with these two methods did not reveal such a match between distribution patterns of infaunal- and epifaunal benthos (RELATE test; $\rho = 0.286$; $p = 0.081$). Based on these facts and considering the methods to better describe either infaunal or epifaunal benthic fractions, a mismatch between patterns would have been, *a priori*, a logical conclusion.

The match found with the RELATE test generated the question: which taxa might play a key role? In our study we tried to answer this by comparing both MBC and SBI data by means of a BEST test. When using MBC data as an “explanatory” matrix for the pattern found in the SBIs, a combination of five taxa (flatworms, priapulids, amphipods, cirripeds and holothurians) “best explains” the epifaunal pattern. Vice versa, when using SBI data as an “explanatory” matrix for the pattern found in MBC data, a combination of seven taxa (brachiopods, pycnogonids, isopods, unidentified crustaceans, echinoids, asteroids and ophiuroids) “best explains” the infaunal benthos distribution pattern. The variables “best explaining” the patterns of infaunal- and epifaunal benthic distribution could be used to optimize mathematical models (*e.g.* linear multiple regression, maximum entropy models).

Our study compares quantitative results from MBC and SBI samples. Although inherently different, they complement each other and future sampling strategies with deployment of both methods in parallel should be encouraged. Although traditional sampling with corers or towed gears resulted in robust descriptions of benthic communities with more focus on quantitative aspects (e.g. abundances/biomasses) or taxonomical composition, the combination of quantitative work with corers and seabed imaging methods increases the breadth of the community elements that can be described at each sampling site. Infaunal and epifaunal benthos fractions and thus the benthos as a whole can be described in more detail. Despite considering the benthic fractions in different resolution, both methods resulted in similar distribution patterns. Finally, it is worth mentioning that the combined use of both methods in the same gear, as the multibox corer in our study, is practicable, minimizing required ship time, and optimizing station grid and expedition planning.

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Tables and corresponding legends

TABLE 1: Benthic stations investigated during RV *Polarstern* cruise PS82 (ANT-XXIX/9) 2013/14. Data on fine (clay and silt) and coarse (gravel and sand) sediments from Diekmann and Kuhn (1999a). Near-bottom water densities (kg m^{-3}) from Schröder and Wisotzki (2014).

PS82 St. No.	**Latitude (S)**	**Longitude (W)**	**Water Depth (m)**	**Sub-region**	**Coarse sediment (%)**	**Fine sediment (%)**	**Sea water density (sigma-theta)**
033	75°56.83'	31°40.57'	684	Filchner Trough	55.95	44.05	27.92
040	76°03.96'	30°16.83'	472	Eastern flank	77.82	22.18	27.77
066	77°06.09'	36°34.39'	1111	Filchner Trough	34.34	65.66	27.93
089	76°59.02'	32°51.05'	254	Eastern flank	66.18	33.82	27.69
098	77°42.76'	35°55.73'	585	Filchner Trough	58.76	41.24	27.89
116	77°36.77'	38°56.70'	1060	Filchner Trough	28.69	71.31	27.90
125	75°29.48'	27°24.60'	286	Eastern flank	86.94	13.06	27.69
154	74°36.53'	28°28.72'	1217	Eastern flank	20.78	79.22	27.78
163	74°39.94'	28°40.16'	696	Eastern flank	27.22	72.78	27.76
164	74°53.67'	26°42.48'	290	Eastern flank	60.63	39.37	27.68
200	74°34.73'	36°23.70'	426	Western flank	85.43	14.57	27.83
206	74°26.09'	35°43.48'	1140	Western flank	83.78	16.22	27.88
226	74°21.12'	37°36.14'	554	Western flank	84.29	15.71	27.82
236	74°13.23'	37°39.67'	798	Western flank	83.87	16.13	27.84
242	74°40.84'	39°04.03'	436	Western flank	65.39	34.61	27.82
325	74°42.28'	29°48.41'	427	Eastern flank	46.04	53.96	27.75

TABLE 2: Occurrence of benthic taxa in seabed images (x) and multibox corer samples (o) collected at 16 stations during RV *Polarstern* cruise PS82 (ANT-XXIX/9) 2013/14.

TAXA / Stations	033	040	066	089	098	116	125	154	163	164	200	206	226	236	242	325
Porifera	x	o		xo	o	o	xo	xo	xo	xo	o	xo	xo	xo	x	xo
Stauromedusae										x						
Hydrozoa		o		ox		o	x	x	xo	xo	xo	xo	xo	x	o	xo
Alcyonacea				x	x		x	x	x	x	x	x	x	x	x	x
Actinaria			x	x		x	x	x	x	x	x		x			x
Scleractinia						x			x	x						x
Anthozoa[1]		o		o	o		o		o	o	o	o	o	o	o	o
Bryozoa		xo		xo		o	xo	xo	xo	xo	xo	xo	xo	xo	xo	xo
Brachiopoda										o	o	xo	o	o		
Sipuncula		o		o	o			o	o	o				o		o
Platyhelminthes			o	o												
Nemertina	o	o		o	o		o	o	o	o	o	o	o	o		o
Priapulida		o														o
Polyplacophora								o	xo							
Solenogastres				o	o			o	o	o	o		o			o
Bivalvia	o	o	o	o	o	o	o	o	o	xo	o	o	o	o	o	o
Nudibranchia												x				
Gastropoda	o	o		o	o		xo	xo	o	o	xo	o	o			xo
Scaphopoda		o					o		o	o						
Cephalopoda											x					x
Polychaeta	xo	xo	xo	xo	xo	xo	xo	xo	xo	xo	xo	xo	xo	xo	xo	xo
Clitellata	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o	o
Echiurida										o						
Pantopoda		xo		xo	x		x	xo	o	xo	xo	o	xo	x	x	xo
Mysida	x				x		x	x		x			x	x	x	x
Amphipoda	x	xo	x	o	o		o	xo	o	xo	xo	o	o	xo	xo	xo
Cumacea	o	o		o		o	o	o	o	o		o			o	o
Harpacticoida		o		o	o		o		o	o	o	o	o			
Cirripedia											o					
Serolidae	x	x	x			x		x			x			x		x
Isopoda	o	o		o	o	x	o		o	xo	o	o	o	o	o	o
Tanaidacea		o		o	o	o	o	o	o	o	o		o		o	o
Ostracoda	o	o			o		o	o		o		o			o	
Decapoda	x	x					x	x		x	x				x	x
Crustacea[1]	x	x			x	x		x	o	x	xo		o	x	x	x
Echinoidea	x	x	x	xo	x	x	x	x	xo	x	xo	x	x	x	x	x
Holothuroidea	x	x	x	xo	xo	x	xo	xo	xo	xo	x	x	x	x	x	xo
Asteroidea				xo	x	x	x	x	xo	x	xo	x	xo	x		x
Ophiuroidea	x	xo	x	xo	xo	xo	xo	xo	xo	xo	xo	xo	xo	xo	xo	xo
Crinoidea	o		x	xo	x		x	xo	xo	xo	x		x	x	x	x
Hemichordata							xo		xo			x				
Tunicata	x	o	x	x		xo	xo	x	xo	xo	o	x	x	xo	xo	x
Unidentified	xo		xo	x	x	x	x	xo	x	x	x	x	x	x	x	x

[1] = unidentified

TABLE 3: Results of two-way PERMANOVA test of significant differences in the structure of benthic assemblages investigated at 16 stations during RV *Polarstern* cruise PS82 (ANT-XXIX/9) 2013/14, with sampling gear - multibox corer samples (MBC) and seabed images (SBI) - as fixed factor and stations as random factor. *Significant at $p < 0.01$.

FACTOR	*PSEUDO-F*
Fixed: Sampling Gear (MBC, SBI)	30.7^*
Random: Station (16 levels)	57.8^*
Factor interaction	55.6^*

TABLE 4: Results of SIMPER analysis of the composition of benthic fauna identified in multibox corer samples (MBC) and seabed images (SBI) taken at 16 stations during RV *Polarstern* cruise PS82 (ANT-XXIX/9) 2013/14.

Groups	MBC	SBI
Average within-group similarity	Overall: 54.29 % Polychaeta: 37.83 % Bivalvia: 11.47 % Ophiuroidea: 11.05 %	Overall: 66.17 % Ophiuroidea: 35.24 % Polychaeta: 14.72 % Holothuroidea: 9.96 %
Average between-group dissimilarity	MBC vs. SBI	
	Overall: 80.14 % Polychaeta: 17.52 % Ophiuroidea: 8.07 % Bivalvia: 7.78 % Amphipoda: 6.96 % Holothuroidea: 6.67 % Clitellata: 5.38 %	

TABLE 5: Results of Principal Component Analysis (PCA) of the weighted abundances of benthic fauna identified in multibox corer samples (MBC) and seabed images (SBI) collected at 16 stations during R/V *Polarstern* cruise PS82 (ANT-XXIX/9) 2013/14.

Sampling Gear	Principal Component	% Variation	Linear coefficient	Taxa
MBC	PC1	99.5	-0.999	Polychaeta
	PC2	0.2	-0.776	Clitellata
SBI	PC1	84.3	-0.988	Ophiuroidea
	PC2	12.4	-0.988	Holothuroidea

Figures and corresponding captions

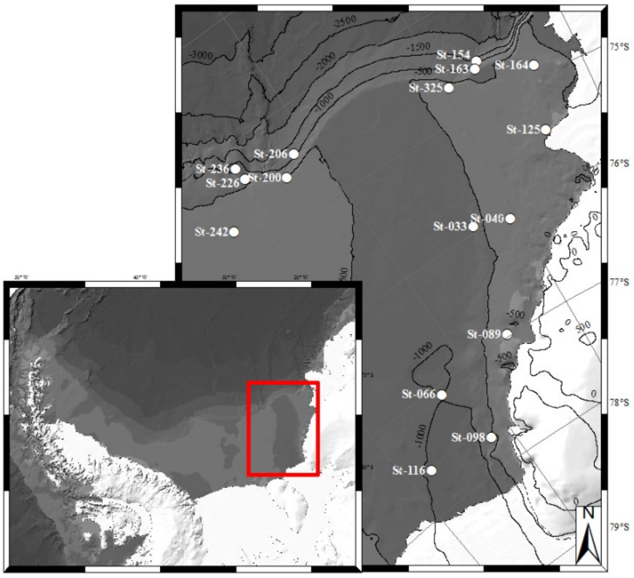

Fig. 1: Locations of benthos stations in the Filchner-Ronne Outflow System (FROS) region in the southern Weddell Sea visited during R/V *Polarstern* cruise PS82 (ANT-XXIX/9) 2013/14. Bathymetric data from IBCSO (Arndt et al. 2013)

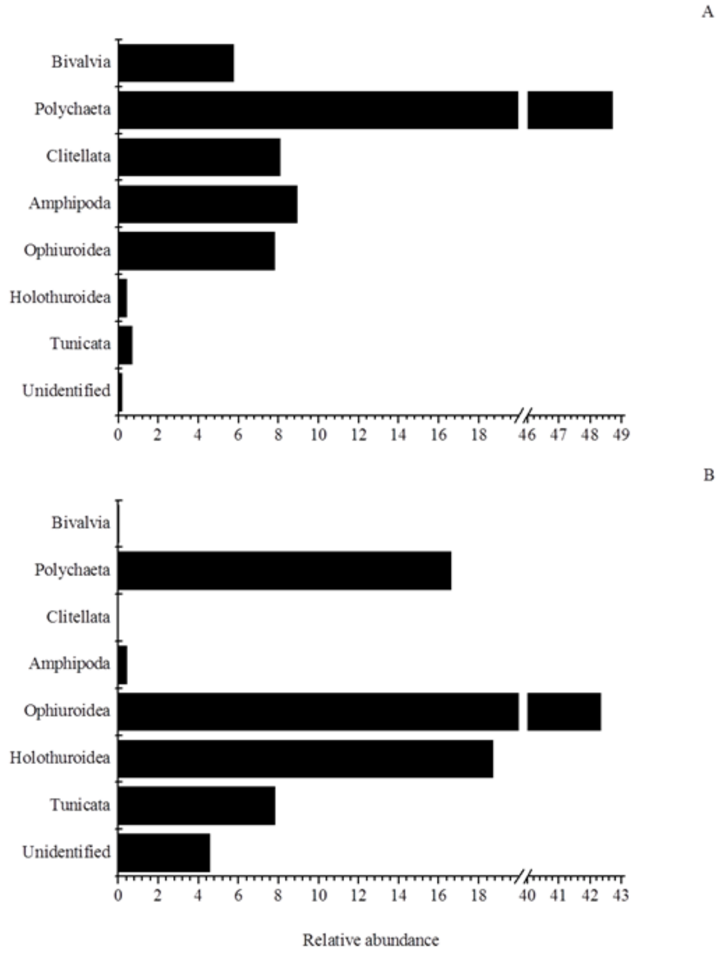

Fig. 2: Relative abundances (%) of dominant benthic taxa identified in a) multibox corer samples and b) seabed images collected during R/V *Polarstern* cruise PS82 (ANT-XXIX/9) 2013/14.

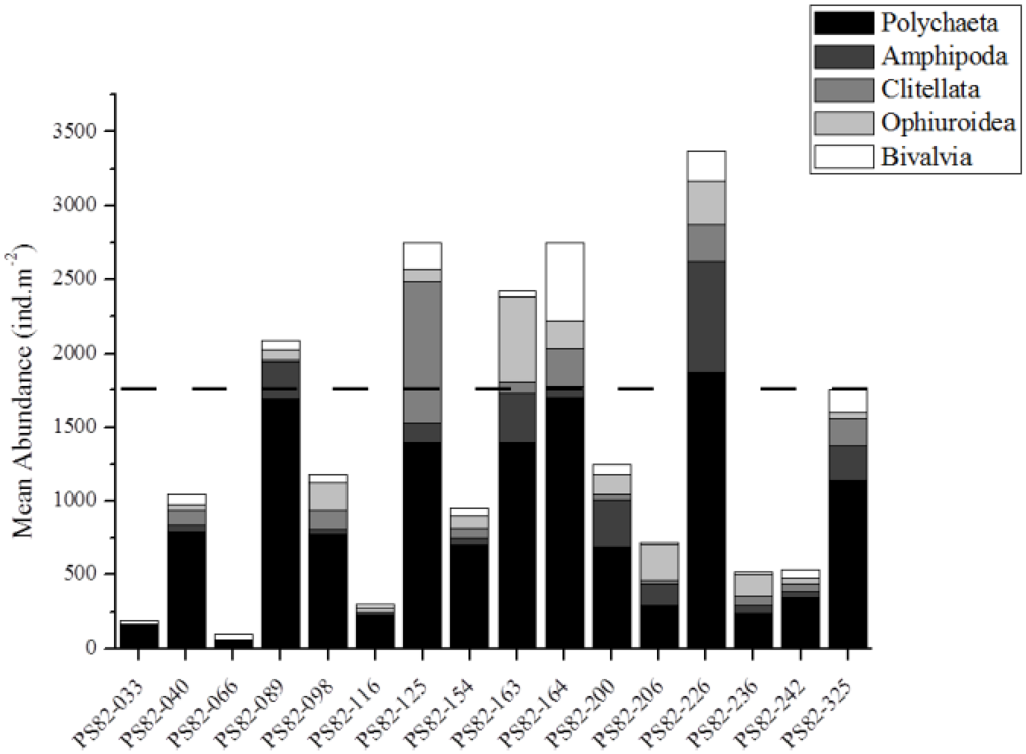

Fig. 3: Mean abundance values (ind m^{-2}) of dominant benthic taxa found in multibox corer samples collected during R/V *Polarstern* cruise PS82 (ANT-XXIX/9) 2013/14. Dashed line represents the overall mean abundance.

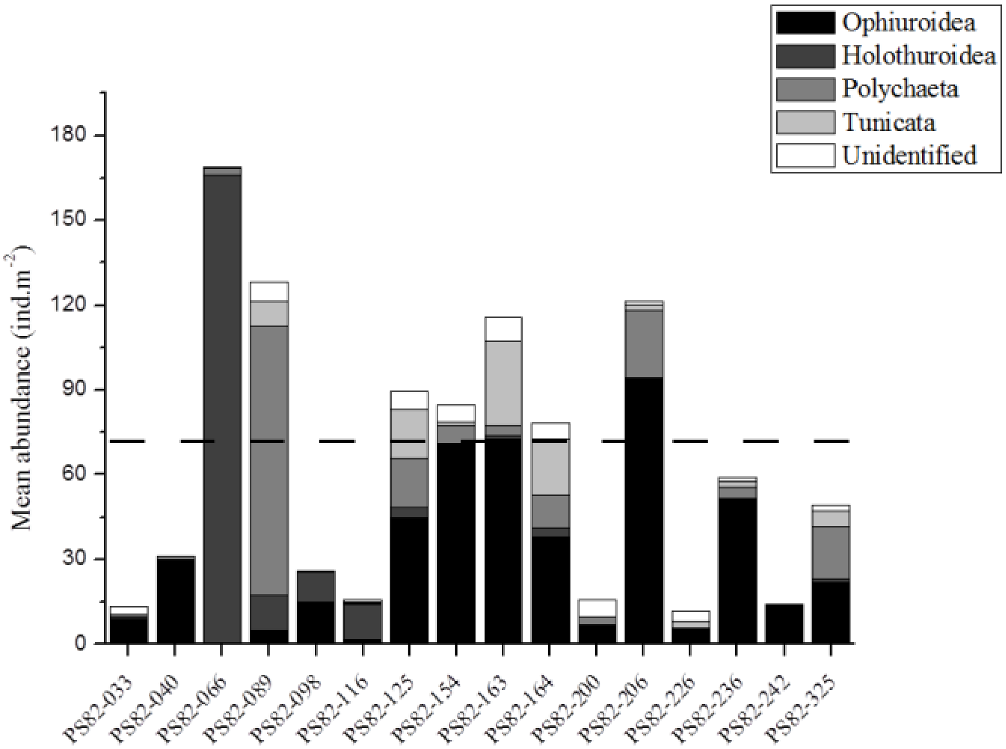

Fig. 4: Mean abundance values (ind m^{-2}) of dominant benthic taxa identified in seabed images collected during R/V *Polarstern* cruise PS82 (ANT-XXIX/9) 2013/14. Dashed line represents the overall mean abundance.

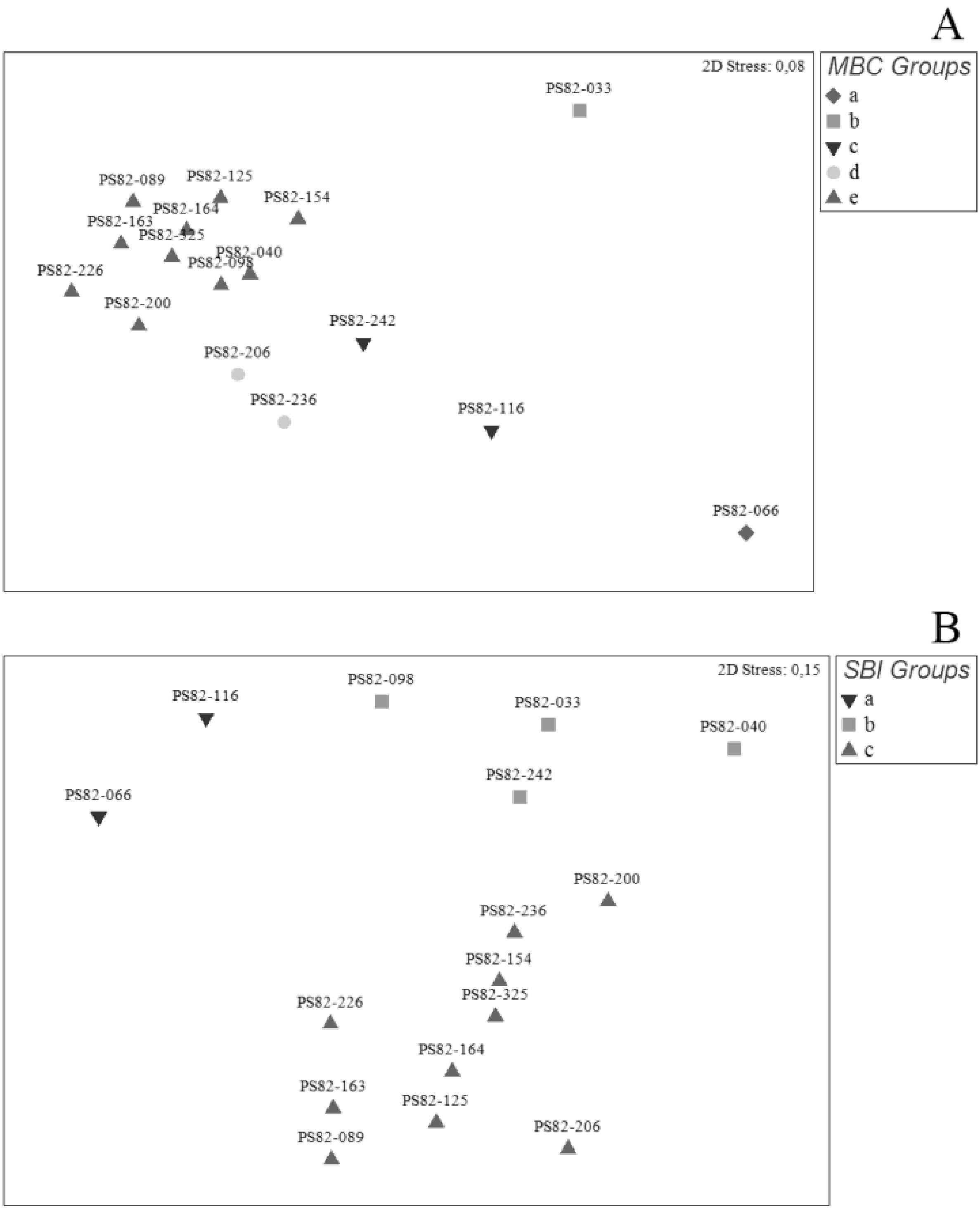

Fig. 5: Two-dimensional MDS (multi-dimensional scaling) plots visualizing the among-station resemblance pattern of benthic fauna identified in A) multibox corer samples (MBC) and B) seabed images (SBI) collected during R/V *Polarstern* cruise PS82 (ANT-XXIX/9) 2013/14. The pattern is based on between-station Bray-Curtis similarities calculated from abundance (ind m^{-2}) data. Grouping obtained from cluster and SIMPROF analysis is shown.

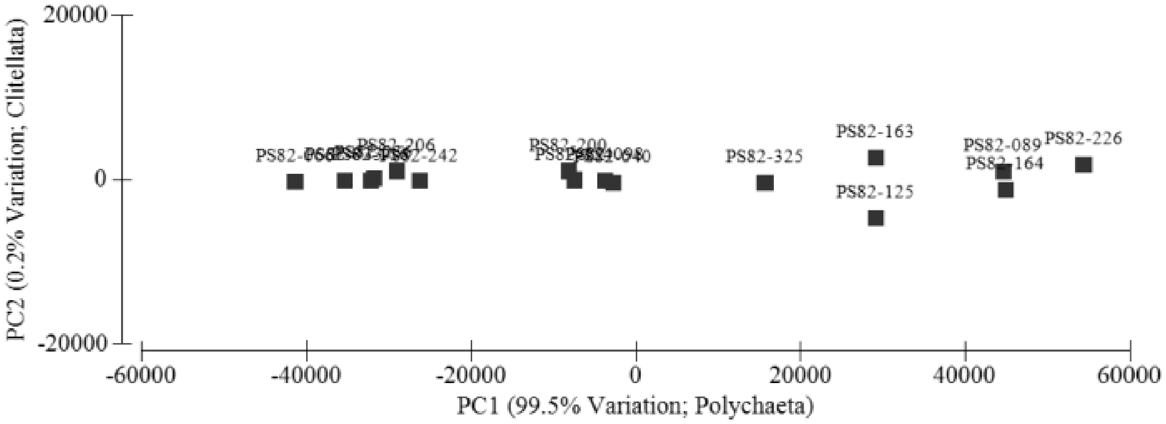

Fig. 6: Principal Component Analysis (PCA) of the weighted abundances of benthic taxa identified in multibox corer samples collected during R/V *Polarstern* cruise PS82 (ANT-XXIX/9) 2013/14. The first two axes (PC1 and PC2) explained 99.5 % and 0.2 %, respectively, of the total variance.

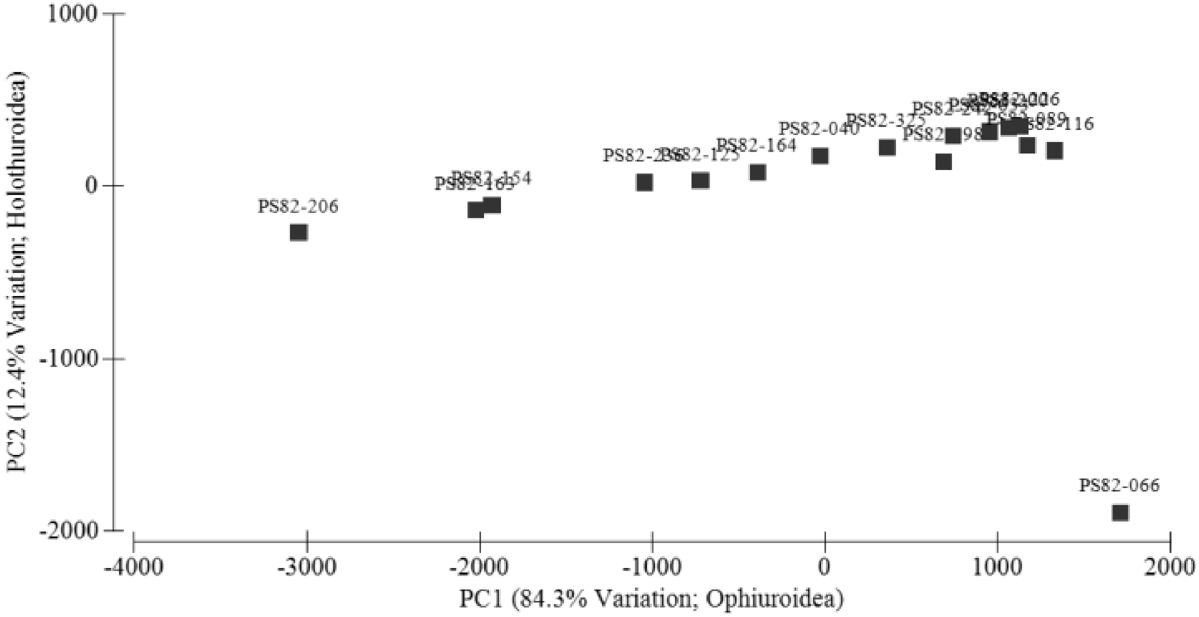

Fig. 7: Principal Component Analysis (PCA) of the weighted abundances of benthic taxa identified in seabed images collected during R/V *Polarstern* cruise PS82 (ANT-XXIX/9) 2013/14. The first two axes (PC1 and PC2) explained 84.3 % and 12.4 %, respectively, of the total variance.

MANUSCRIPT 2: Benthos-Pelagos Interconnectivity: Antarctic Shelf Examples

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Benthos-Pelagos Interconnectivity: Antarctic Shelf Examples

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Abstract This review focuses on studies dealing with the coupling between the benthic and pelagic realms on Antarctic shelves and on factors that regulate these processes. Such studies in Antarctic water are scarce, especially on the shelves, where flux studies via moorings are highly endangered by drifting icebergs. Nevertheless such studies are essential to understand these processes and functioning of the cold water ecosystem and how energy is transported through its different compartments. Different abiotic (currents, sea-ice, water depth, topography of the seafloor, seasonality) and biotic (composition and structure of the benthic and pelagic flora and fauna, primary production, vertical migrations) factors are presented as parameters regulating the coupling between benthos and pelagos, here defined as benthos-pelagos interconnectivity. Regional variability in these parameters may result in delayed or even different coupling and/or decoupling of these realms. This is exemplarily discussed comparing the west Antarctic Peninsula (WAP) and Eastern Weddell Sea Shelf (EWSS). While in the WAP both compartments appear decoupled, on the EWSS both compartments appear tightly connected. The development of the benthos in the Larsen embayments after the shelf ice disintegration is described as an example how changes in the pelagic realm affect and modify also the benthic realm.

Keywords: Bentho-pelagic coupling, Pelago-benthic coupling, Carbon flux, Weddell Sea shelf, Antarctic Peninsula shelf

1 Bentho-pelagic or Pelago-benthic Coupling? A short Introduction

When thinking of biotic (e.g., diversity, abundance, biomass) and abiotic (e.g., particle concentration, sediment grain size) parameters of both, benthic and pelagic realms, we start noticing lines or processes connecting them. One of the first studies on this connectivity was that of Hargrave (1973). He pointed out that both realms are connected by the flow of matter, especially that of carbon. Since that study, this interconnection between benthos and pelagos has been referred to as bentho-pelagic or pelago-benthic coupling. While the terms bentho-pelagic and pelago-benthic appear exchangeable, each one alludes to the predominant or driving component and direction in the coupling (Renaud et al. 2008). In bentho-pelagic coupling, it is the benthos which modifies or influences the pelagos. Contrastingly, in pelago-benthic coupling it is the pelagos which influences or modifies the benthos. In some literature bentho-pelagic coupling is referred to as “upward” coupling, while pelago-benthic coupling is referred to as “downward” coupling (e.g., Smith et al. 2006).

With this review I aim to exemplify in a concise and simple way how benthos-pelagos interconnectivity, i.e., upward and downward coupling, works in the Southern Ocean with special focus on Antarctic shelf ecosystems (Fig. 1). My second aim is to enable non-experts to get a rough picture of the Antarctic benthos-pelagos interconnectivity.

1.1 Pelago-benthic Coupling

The first approaches used to describe the coupling between pelagos and benthos included measurements of carbon input from the water column to calculate how much of this carbon was assimilated in the sediment (Hargrave 1973). Currently, studies of downward mass flux are still the most common type of coupling studies (e.g., Cattaneo-Vietti et al. 1999; Smith et al. 2006, 2008; Isla et al. 2006a, b, 2011). Other approaches to study pelago-benthic coupling include recruitment of benthic organisms via meroplanktonic larvae (Bowden 2005), change of sediment characteristics (Collier et al. 2000; Hauck et al. 2012; Isla 2016b), pelagic characteristics and seasonal patterns and how these affect benthic processes such as feeding activity (Barnes and Clarke 1995; McClintic et al. 2008; Souster et al. 2018), reproduction (Pearse et al. 1991; Stanwell-Smith et al. 1999; Brockington et al. 2001; Galley et al. 2005), growth rates and carbon fixed by benthos (Dayton 1989; Brey and Clarke 1993; Clarke 2003; Barnes et al. 2006, 2016, 2018; Barnes 2015), and benthic distribution patterns (Barry 1988; Barry and Dayton 1988; Graf 1989; Bathmann et al. 1991; Gutt et al. 1998; Sumida et al. 2008; Segelken-Voigt et al. 2016; Jansen et al. 2018).

1.2 Bentho-pelagic Coupling

Less common than pelago-benthic coupling studies are studies that show an effect from the benthos to the pelagos, i.e., a bentho-pelagic coupling. One clear example of this “upward” coupling is the regulation of particulate matter flow in the benthic boundary layer by means of benthic structures (Graf and Rosenberg 1997; Mercuri et al. 2008; Tatián et al. 2008), another example for this processes is the increase of abundance and diversity of plankton by the release of meroplanktonic larvae from benthic organisms into the water (Bowden 2005; Schnack-Schiel and Isla 2005). Benthic processes also create feeding grounds for birds, seals, and zooplankton (Arntz 1994; Ligowski 2000; Schmidt et al. 2011), they enhance primary production through export of micronutrients from remineralization and consumption/excretion processes of pelagic communities (Doering 1989; Smith et al. 2006; Schmidt et al. 2011), and can regulate the chemical characteristics of the water column (Doering 1989; Sedwick et al. 2000; Tatián et al. 2008).

2 Regulating Factors of Benthic and Pelagic Processes

In general terms, the interconnectivity between benthos and pelagos could be regarded as "weak" or "strong". This alludes to how directly changes in pelagos are reflected in benthos and vice-versa. When seen as a correlation, it would be how strong the correlation between compartments is. The strength of the coupling between benthos and pelagos depends on seasonality in both compartments, the ecology and structure of benthic and pelagic communities, water depth, seafloor topography, water circulation (e.g., tides, currents), and wind, all affecting the transport of particles and thus carbon flux from one compartment to the other. Around the Antarctic continent, another factor playing a major role for the regulation of this coupling between benthos and pelagos is the influence of ice in any of its forms (e.g., sea-ice and disintegrated shelf ice, i.e., icebergs).

2.1 Sea Ice

The Southern Ocean is characterized by its large extension of sea-ice, which covers up to 20 x 10^6 km^2 during Austral winter, and 4 x 10^6 km^2 during summer (Fig. 2), making sea-ice associated ecosystems one of the most dynamic and largest ecosystems on Earth (Arrigo et al. 1997; Thomas and Dieckmann 2002; Michels et al. 2008). The retreat of sea-ice during summer increases the water column stability, seeds summer phytoplankton blooms, and works as a source for micronutrients such as iron (as well as other particles), favouring phytoplankton blooms and explaining the higher productivity near sea-ice edges as compared to open waters (Clarke 1988; Sedwick and DiTullio 1997; Sedwick et al. 2000; Kang et al. 2001; Donnelly et al. 2006). It has been shown that reduction of the sea-ice duration contributes also to an increase of carbon drawdown by benthic organisms (Barnes 2015).

Sea-ice starts growing during March to its enormous extension in Austral winter. The high coverage of sea-ice and snow during winter time diminishes the light entering the water column, thus causing a drastic decrease in local productivity and particle flux (Scharek et al. 1994; Isla et al. 2006a). However, autotrophic plankton entrapped by sea-ice during its formation (along with nutrients and consumers) continues primary production in winter time, which can be 4 to 5 times higher than water column production (Garrison and Close 1993). While lower than summer production, sea-ice primary production has been pointed out to serve as a possible food source for meroplanktonic larvae (Bowden 2005) and various krill life stages (Nicol 2006; Kohlbach et al. 2017; Schaafsma et al. 2017). These few examples show how the sea-ice summer/winter cycle regulates primary and secondary production in the water column and the particle flux, thus directly influencing the benthos-pelagos interconnectivity.

2.2 Depth, Topography, Currents, and Wind

One conspicuous aspect of the Antarctic shelf is its depth. While other shelf ecosystems in the world are shallower (down to around 200 m depth), the isostatic pressure generated by the ice cap on the Antarctic continent deepens the surrounding shelf down to 400 – 600 m and even down to 800 – 1000 m in some regions (Gallardo 1987; Smith et al. 2006; Sumida et al. 2008). Smith et al. (2006) pointed out that the increased depth of the Antarctic shelf with its complex topography and current systems may reduce the strength of the coupling by increasing the time particles spend in the water column, allowing local characteristics of the benthic habitat to mask the pelagic signals on the seafloor. However, the effect of depth on particle receding time in the water column will depend on the nature of the particles, e.g., on their flocculation ability and other environmental factors such as, e.g., wind forcing, which regulates deposition or advection of particles (biological factors are treated later). For the Eastern Weddell Sea Shelf (EWSS; Fig. 1A) it has been described that particle flux is rather fast. Total mass fluxes measured at mid-water and near the seafloor with sediment traps appeared to be similar, and it has been noted that particles can reach the seafloor within days despite the long 400 – 600 m depth trip from the euphotic zone to the seafloor (Bathmann et al. 1991; Isla et al. 2006a, 2009). For the Ross Sea, while Dunbar et al. (1998) recorded mean settling velocities of 176 - 245 m d^{-1} for different types of faecal pellets, DiTullio et al. (2000) found aggregates of *Phaeocystis antarctica* to sink at speeds >200 m d^{-1}, i.e., it could take one to three days for pellets or *Phaeocystis* aggregates to reach the seafloor.

The topography of the shelf influences the benthos-pelagos interconnectivity as well. Topography affects benthic distribution patterns and the transport and deposition of particles suspended in the water column alike. Dorschel et al. (2014) pointed out that topographic features such as range hills, mounds, and seamounts modify water current pathways and their strength. Their study of the benthos at Nachtigaller Hill (Fig. 1B) at the tip of the Antarctic Peninsula described depth as one main factor explaining benthic distribution patterns. They related this to food availability for the benthos, which could have been enhanced by the topography of Nachtigaller hill. Another topographic feature affecting water currents is the width of the shelf. Along wider shelves the currents tend to be weaker, stronger currents are more usual when the shelf is narrow. Gutt et al. (1998) found relatively weaker current regimes on wider shelves of the EWSS to be beneficial for particle settling, which in turn benefits deposit feeding organisms. Conversely, the narrower areas off Austasen and Kapp Norvegia (Fig. 1A) on the EWSS generate relatively stronger currents promoting resuspension of particles and thus being favourable for suspension feeder dominated community types (Gutt et al. 1998).

Currents, tides, and advection of water parcels on the shelf also play a role in the benthos-pelagos interconnectivity. In some cases they weaken, in others they mask coupling processes between the compartments. An example can be drawn from the study of Isla et al. (2006b) at Johnston's Dock (Fig. 1B), where water current induced transport and advection of particles from shallower shelf areas enhance particle flux to deeper parts (Fig. 3). Other studies conducted in waters of the West Antarctic Peninsula (WAP) found particle flux on the deeper shelf to be enhanced by advected material originating from shallower shelves. This allochthonous input weakens the connection between benthic distribution patterns and metabolism of benthic organisms with primary production and local input of particles (McClintic et al. 2008; Sumida et al. 2008). Another clear example of the role of currents in the benthos-pelagos interconnectivity can be found in McMurdo Sound (Fig. 1C). Barry

(1988) and Barry and Dayton (1988) found benthic distribution patterns to be coupled with primary production regimes and water circulation patterns. Circulation on the eastern side of McMurdo has a southward direction towards the Ross Ice Shelf and transports productive waters, which fuel rich benthic communities, whereas on the western side of the Sound, where less productive waters arrive from the ice shelf, a poorer benthic community is found.

Wind affects directly the benthos-pelagos interconnectivity by partly regulating sea-ice and polynya formation, sea-ice displacement, and mixed layer depth. While during winter periods, cold winds absorb heat from the water surface enhancing sea-ice formation, in summer periods strong winds push away sea-ice forming coastal polynyas (Isla 2016a). Wind-driven dispersal of the sea ice prior to its melting can prevent local release of algae trapped in the ice which would normally seed a local bloom (Riebesell et al. 1991). Furthermore, the strength of wind can also regulate the depth of the mixing layer in both a beneficial and prejudicial way. Where winds are relatively weaker a shallower mix layer is formed (especially close to the ice edge). This shallower mix layer can foster larger blooms than deeper mixed layers (Ducklow et al. 2006). Conversely, in areas where winds are relatively stronger a deeper mix layer is found. Deeper mixed layers can abruptly interrupt phytoplankton blooms, thus inhibiting primary production (Gleitz et al. 1994; Dunbar et al. 1998; Ducklow et al. 2006). While the deepening of the mix layer by wind action appears prejudicial for the coupling between pelagos and benthos by reducing primary production and thus its related particle flux, a deepening of the mix layer due to strong stormy winds has been pointed out to increase total downward particle flux. By means of sediment traps, Isla et al. (2009) found that strong stormy winds enhanced the transport of organic matter to the seabed. In their study, the flux resulting from a storm event which lasted a few days represented 53% of the total mass flux collected at mid-water during a period of 30 days.

2.3 Seasonality and Particle Flux

It is commonly accepted that the Antarctic benthic realm can be considered as a rather stable system with little variation in environmental parameters such as temperature, salinity, and water currents, whereas the pelagic realm is considered as highly seasonal with distinct summer/winter cycles, especially in primary production and sea-ice extension (Gallardo 1987; Clarke 1988; Bathmann et al. 1991; Scharek et al. 1994; Arntz et al. 1994; Arrigo et al. 1998; Palanques et al. 2002; Smith et al. 2006; Isla et al. 2009, 2011; Rossi et al. 2013; Flores et al. 2014; Isla 2016b). While the stability of the benthos and instability of the pelagos are commonly accepted, the intrinsic biotic and abiotic factors of both are highly dependent on local water mass properties and circulation, and wind-, sea ice- and topographic conditions (e.g., Barry and Dayton 1988; Barthel and Gutt 1992; Gleitz et al. 1994; Dunbar et al. 1998; Ducklow et al. 2006; Isla et al. 2009; Hauck et al. 2010; Barnes 2015).

2.3.1 Pelagic Realm

Primary production in the water column is key in regulating the flux of particles. Most of the primary production is proposed to be generated within the seasonal sea-ice zone, especially in waters close to the retreating sea-ice edge, where water column stability and nutrient concentrations are high. Driven by melting of sea-ice these locations also act as seeding grounds for primary production in the euphotic zone, enabled by released sea-ice algae and enhanced input of nutrients (Scharek et al. 1994; Sedwick and DiTullio 1997; Sedwick et al. 2000; Arrigo et al. 2008; Bertolin and Schloss 2009; Isla et al. 2009; Isla 2016b). The primary production in the seasonal sea-ice zone was estimated to be 1,300 Tg C y^{-1}, of which 420 Tg C y^{-1} are generated in the marginal sea-ice zone, and roughly 5% of production of the seasonal sea-ice zone is produced by sea-ice algae (Lizotte 2001). The importance of primary production regulating particle fluxes matches with zooplankton activities, because zooplankton quickly reacts to phytoplankton blooms (Flores et al. 2014). Grazing pressure is one of the main regulators of phytoplankton blooms. Faecal pellets resulting from this grazing largely contribute and regulate particle fluxes (Bathmann et al. 1991; Palanques et al. 2002; Isla et al. 2009; Rossi et al. 2013), change the chemical composition of these fluxes and their size structure (Isla 2016b). Summer primary production and zooplanktonic grazing amount for >95% of the yearly total mass flux. This particle flux provides carbon to the benthos, which equals between <1 up to 18% of the annual primary production of a region (Bathmann et al. 1991; Palanques et al. 2002; Isla et at. 2006a, 2009). Although the proportion of carbon reaching the seafloor appears negligible to low, it is still enough to support biomass rich benthic communities and to form "food banks" (Gutt et al. 1998; Smith et al. 2006; Isla et al. 2009, 2011), as observed, e.g., on the EWSS, where benthic biomass is high and communities are mainly constituted by sessile suspension feeders (Gerdes et al. 1992; Gutt and Starmans 1998).

Vertical migration by zooplankton, fish, or diving vertebrates is regarded as a common feature of aquatic environments, and on an individual level, these provide a trade-off between nutrition and survival (Schmidt et al. 2011). In the context of this review, vertical migration refers to any causal vertical movement (e.g., foraging expeditions, avoidance of predators). The benthic realm works as feeding ground for various vertebrates, thus promoting vertical migrations. Arntz et al. (1994) pointed out that seals and penguins often dive deep to feed on benthic invertebrates. Antarctic krill *Euphausia superba* has also been found to migrate down to 3000 m depth to either feed on the seabed, or as a result of being satiated (Ligowski 2000; Tarling and Johnson 2006; Schmidt et al. 2011). While migrating, swimming organisms release carbon and nutrients in form of faeces. Release of faeces near the benthos could mean an extra input of available food for benthic organisms. Conversely, excretion of a mix of benthic organic material and lithogenic particles in the upper water column would increase the concentration of labile iron which could enhance primary production (Schmidt et al. 2011).

2.3.2 Deposition and Resuspension

Specific particle composition and flux rates in a region are not just a question of primary production and associated zooplanktonic activity. They also are affected by local deposition and resuspension processes. Water currents, especially near the seabed, are one key environmental factor regulating deposition and resuspension. Another key environmental factor are icebergs. Iceberg scours change the seabed topography, affect the near seabed current regime and modify the deposition regime in the area by trapping particles in the scours mark (working as a sort of "sediment trap"). Iceberg scour marks can be 10s to 100s meters wide, several meters deep and 10s of meters or even kilometres long (Gutt 2001; Gerdes et al. 2003). On the other hand iceberg scours can also enhance resuspension by generating an upward particle flux (Gutt 2001; Barnes et al. 2018). A recent study on the effect of icebergs and sea ice on “blue carbon” (carbon in organisms) pointed out that in March 2017, 47 giant icebergs larger than 30 km^2 occurred in Antarctica, six of which exceeded 1000 km^2 in area (Barnes et al. 2018). Initially, any iceberg scour would resuspend already fixed blue carbon and increase the open water area by breaking and displacing sea ice. The combination of additional resuspended material and open water area would result in an increase of primary production, which in turn would promote benthic growth. As a result, deposition would be increased not only by the enhanced primary production, but also by the proportional increase of benthic suspension feeder biomass (Barnes et al. 2018).

The studies of Mercuri et al. (2008), Tatián et al. (2008) and Barnes et al. (2016, 2018) are examples of how benthic organisms affect deposition and resuspension. Micro-, macro-, and megafauna as well as marine flora directly affect the sediment erodibility and regulate sediment mixing, which greatly affects the benthos-pelagos interconnectivity (Orvain et al. 2012; Queirós et al. 2015). Benthic organisms may decrease sediment roughness by mucus, bacterial mats or diatom film production, thus reducing the resuspension ability of sediments (de Jonge and van den Bergs 1987; Grant and Bathmann 1987; Patterson 1989; Self et al. 1989; Delgado et al. 1991; Dade et al 1992; de Jonge and van Beusekom 1991). In Antarctic benthos, hexactinellid sponges exemplify how organisms can reduce resuspension and enhance deposition. These sponges cement and consolidate sediments, enhance biodiversity by promoting the immigration of other sponge species, provide refuges to other taxa, and generate spicule mats (Fig. 4), which work as silicon traps (Barthel 1992; Barthel and Gutt 1992; Gutt et al. 2013a). Sponges and other filter feeders collect particles from the water column, thus enhancing the downward flux of particles and their deposition (Barthel 1992; Mercuri et al. 2008; Tatián et al. 2008). This biodeposition effect is enhanced by the increase of biodiversity provided by sponges. Furthermore, spicule mats reduce resuspension by covering the sediment, thus reducing its erodibility. Other structures that enhance deposition are tube formations (Fig. 4). High density of polychaete tubes could generate an attracting effect equal to that of baffles in sediment traps, albeit in a reduced area (Frithsen and Doering 1986). Contrastingly, other activities of benthic organisms such as pellet production and bioturbation with formation of mounds, pits, tubes, and tracks, can change the sediment structure and enhance particle resuspension (Eckman et al. 1981; Eckman and Nowell 1984; Luckenbach 1986; Davis 1993). Resuspended material tends to be rich in nutrients and contains also micronutrients such as iron, which could, in shallower shelf areas with upwelling or those shelf areas where deep mixing occur, enhance summer primary production (Doering 1989; Sedwick et al. 2000).

2.3.3 Benthic Realm

The marked seasonal differences in the pelagic realm, especially the reduction of carbon flux in winter (see Sects. 2.1 and 2.3.1), has been thought to directly regulate benthic processes such as reproduction, growth, feeding activity, sexual development, recruitment of juveniles, and also benthic distribution patterns. However, studies on bentho-pelagic and pelago-benthic coupling in Antarctic waters have shown differences between benthic and pelagic seasonality to be less important in regulating benthic processes, and that both compartments could be less coupled than thought, partly due to the effect of currents, lateral advection and tides (see Sect. 2.2). Stanwell-Smith et al. (1999) studied meroplanktonic larvae released by benthic organisms and described these larvae to be present throughout the year. In some cases, the larval peak was clearly decoupled from the summer bloom, and the recruitment of benthic organisms was described to occur year-round or with a tendency to happen during winter months (Bowden 2005; Galley et al. 2005). Similarly, Sumida et al. (2008) found recruitment of holothurians to occur during winter, but these deposit feeders were actively feeding throughout the whole year. Measurements of metabolic activity via thorium (Th) isotopes made by McClintic et al. (2008) confirmed benthos to be metabolically active year-round. Results from the studies of Sumida et al. (2008) and McClintic et al. (2008) conducted in the WAP agreed with earlier findings made by Barnes and Clarke (1995), who recorded feeding activities of bryozoans, holothurians, polychaetes, and hydroids at Signy Island (Fig. 1D). However, Barnes and Clarke (1995) did not find any feeding activity during short periods of time during winter. Similarly, a study conducted at Rothera Point (Fig. 1E) by Brockington et al. (2001) on the feeding activity and nutritional status of the sea urchin *Sterechinus neumayeri*, found this species to completely stop feeding during winter. In a recent study, Souster et al. (2018) measured the seasonality of oxygen consumption of five benthic invertebrates and found the oxygen consumption of suspension and deposit feeders to be independent from the input provided by the local summer flux. It has been proposed that benthic organisms can feed or be metabolically active year-round by changing their feeding mechanism, as is known for some sponges, polychaetes, bivalves, and cnidarians (Cattaneo-Vietti et al. 1999; Orejas et al. 2001).

3 Regional Patterns in Coupling Processes

The interaction between biotic and abiotic factors regulating the benthos-pelagos interconnectivity will have direct implications on how “strong” or “weak” the coupling between realms is, and how changes in one of the compartments may affect its counterpart. When comparing different Antarctic regions we observe differences in flux regulators and in the structure of the respective benthic communities. These differences reflect how variable the strength of the coupling between benthos and pelagos is. To exemplify how coupled or decoupled systems appear, I compared data obtained in WAP and EWSS waters. Furthermore, I include the example of the Larsen area (Fig. 1F) to exemplify how changes in the pelagos affect and modify the benthos.

3.1 West Antarctic Peninsula

To describe the benthos-pelagos interconnectivity on the WAP shelf, I focused on studies from the Bransfield Strait (Palanques et al. 2002; Isla et al. 2006b), Rothera Point (Souster et al. 2018), and those conducted within the frame of the “Food for Benthos on the Antarctic Continental Shelf” project (FOODBANCS; e.g., Smith et al. 2006; McClintic et al. 2008; Sumida et al. 2008). All locations are marked in Fig. 1B, E. According to these studies, the coupling between the pelagic primary production and benthic biological processes in these areas appears “weak”. As already stated, the study of McClintic et al. (2008) with Th isotopes not only showed benthos to be metabolically active the whole year, it also showed that the delivery of this isotope to the sediment was not related to local downward flux, suggesting more influence from advected material than from local production. Investigation of the shelf fauna via video recordings (Sumida et al. 2008, 2014) also shows proof of a “weak” local coupling. They found holothurians to recruit during winter, i.e., independently from local food input. Sumida et al. (2008, 2014) also recorded faeces of holothurian year-round, but with hints to higher feeding rates during summer, which appears to be the result of better food quality in this season (Sumida et al. 2014). The study of Souster et al. (2018) found results partly different to those of Sumida et al. (2008, 2014). Souster et al. (2018) described primary consumers (suspension and deposit feeders) to maintain a rather stable metabolic activity year-round, regardless of food input, while secondary consumers (scavengers and predators) showed higher metabolic activity during summer than winter. These authors attributed the seasonal metabolic differences of secondary consumers to be related to better quality of food items rather than to their quantity.

Studies conducted in the WAP evidence advection of material to be more important than locally produced particle fluxes. Palanques et al. (2002) found a high amount of the sediments captured by their traps located in the deeper Bransfield Strait (BS; Fig. 1B) to originate from shallower areas of the BS. The sediment fluxes near the bottom accounted for 18% of the annual primary production and these fluxes included benthic organisms and particles resuspended and laterally transported from shallower adjacent areas. The study of Isla et al. (2006b) found that sedimentation generated by the Johnson's Glacier (Johnson's Dock, Fig. 1B) was comprised mostly of fine sediment. These particles were rich in organic matter, and near-bottom lateral transport of this resuspended matter was the main source of carbon flux into deeper basins (Isla et al. 2006b). These evidences suggest the shallow coastal areas of the WAP to be highly nutritive. Via advection from these shallower areas, the adjacent deeper basins are provided with organic matter. This material is accumulated and forms green mats or "food banks". These green mats ensure the presence of food for benthos during the low production autumn and winter seasons (Smith et al. 2006). The formation of these "food banks" via advected material and a dominance of deposit feeders might explain the restricted meaning of locally generated particle fluxes between pelagic and benthic realms in the WAP (McClintic et al. 2008; Sumida et al. 2008; Souster et al. 2018).

3.2 Eastern Weddell Sea Shelf

The "weak" interconnectivity in the WAP appears to be connected to how particle fluxes are mainly regulated by advection processes from shallower shelves to deeper basins, where "food banks" are formed (Isla et al. 2006b; Smith et al. 2006; McClintic et al. 2008; Sumida et al. 2008). On the EWSS, downward particle transport off Austasen and Kapp Norvegia (Fig. 1A) has been described to be fast (Bathmann et al. 1991; Isla et al. 2009), despite the relatively stronger currents caused by the narrow shelf. This "fast" downward flux is evidenced by a) how sediments quickly reflect the local bloom and its associated characteristics (Bathmann et al. 1991; Isla et al. 2009), and b) how bottom sediments are especially nutritive during summer/autumn (Isla et al. 2011). The efficient transport of carbon from the pelagic to the benthic realm in combination with the resuspension of particles could explain the benthic community characteristic on the EWSS. Benthic communities in this region have been described as rich in sessile suspension feeders, especially glass sponges, which not only increase diversity by creating three-dimensional structures with space for many other species, but also explain the high biomass of the EWSS benthos, which is higher than that of other subregions in the Weddell Sea including the tip of the Antarctic Peninsula

(Table 1; Barthel 1992; Barthel and Gutt 1992; Gerdes et al. 1992; Arntz et al. 1994; Gutt and Starmans 1998; Sañé et al. 2012; Gerdes 2014a, b; S.E.A. Pineda-Metz unpublished data). This high biomass of suspension feeders also influences deposition and sediment chemistry. It seems feasible that suspended particles are largely consumed by suspension feeders, thus transforming the chemical composition of these particles and reducing the amount of organic carbon remaining for incorporation into the sediment. The efficient local flux patterns in combination with particle resuspension and high biomass of suspension feeders which benefit from these conditions, might explain the "stronger" coupling between benthic and pelagic realms on the EWSS contrarily to what was found in the WAP region.

3.3 The Changing Situation of Larsen

The Larsen embayments on the eastern coast of the Antarctic Peninsula (Fig. 1F) may serve as an example of how changes in the pelagic system influence benthos. Studies in the embayments formerly covered by the Larsen A and B ice shelves reflected a shift from an oligotrophic system to one with enhanced production and flux rates (Sañé et al. 2011). Before the disintegration of the shelf ice in 1995 and 2002, respectively, the shelf benthos appeared impoverished and in an early developmental stage as compared to the EWSS. Sessile suspension feeders showed low biomasses and several deep-sea species on the shelf reflected the oligotrophic conditions resembling the deep-sea (Gutt et al. 2011; Sañé et al. 2012; Gerdes 2014a, b). The disintegration of shelf-ice created new space offshore for enhanced local primary production, shifting towards a more eutrophic and productive pelagic realm (Bertolin and Schloss 2009). Within a relatively short time, this enhanced pelagic production led to a shift also in the composition of the benthos (Fillinger et al. 2013; Gutt et al. 2013b). Benthos shifted from an ascidian dominated to a sponge and ophiuroid dominated fauna. Suspension feeding ophiuroids were replaced by a more abundant deposit feeding ophiuroid fauna, and sponges increased two- to three-fold in terms of abundance and biomass (Fillinger et al 2013; Gutt et al. 2013b).

4 Outlook

Studies on the coupling between the benthic and pelagic realms are difficult approaches with complex sampling programs, which require similar temporal and spatial scales for drawing accurate conclusions about coupling processes and their meaning for both compartments (Raffaelli et al. 2003; Renaud et al. 2008). This review on benthos-pelagos interconnectivity includes attempts to describe regulating factors that connect the benthic and pelagic both realms.

Based on "real data" I draw assumptions to distinguish between specific coupling processes in different Antarctic regions. These assumptions are made on only very few studies, which were not all intended to study the benthos-pelagos interconnectivity per se but aimed to study processes individually. This implies that my hypothetical assumptions need further testing. This shows also that many gaps remain and filling them will be of paramount importance to better understand how both realms are connected and how carbon cycling works on Antarctic shelves.

There have been a series of attempts to connect the Antarctic benthic and pelagic realms, reflected (but not restricted) to the works of Barry (1988) Barry and Dayton (1988), Dayton (1989), Ligowski (2000), Schnack-Schiel and Isla (2005), Barnes et al. (2006, 2016, 2018), Isla (2006a, b), Smith et al. (2006, 2008), McClintic et al. (2008), Mercuri et al. (2008), Tatián et al. (2008), Schimdt et al. (2011), Sañé et al. (2011, 2012), Barnes (2015), Jansen et al. (2018), and Souster et al. (2018). Promising attempts to fill regional gaps have also been made. The FOODBANCS project (Smith et al. 2006, 2008) gives a clear hint of how the coupling (or decoupling) between benthos and pelagos works in shelves of the WAP. In this modern age, modelling has gained great importance. Models on how pelagic particles are distributed and are related to benthic distribution patterns are starting to be developed (e.g., Jansen et al. 2018). While promising, attempts on modelling and correlating benthic and pelagic processes are still in early stages. Other Antarctic areas with a long history of studies such as the Weddell Sea need the available data to be reviewed, sorted, and used to start drawing lines between benthic and pelagic realms, as attempted in this review. This first step will help to set the course of future studies and point out a red line on how benthos-pelagos interactions could be investigated in different Antarctic regions, which in turn will provide an excellent tool to understand how the ongoing and predicted climate change will affect the Antarctic shelves.

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Tables and corresponding legends

Table 1 Depth ranges and wet weight biomass data (g_{ww} $m^{-2)}$ from multi-box corer samples collected in four sub-regions of the Weddell Sea: Tip of the Antarctic Peninsula (TAP), Larsen embayments (LA), Filchner Region (FR), and Eastern Weddell Sea Shelf (EWSS) (S.E.A. Pineda-Metz, unpublished data)

Sub-Region	Depth Range (m)	Biomass (g_{ww} m^{-2})		
		Range	Mean	Median
TAP	187 – 934	30 – 3485	423	223
LA	202 – 850	2 – 786	78	16
FR	254 – 1217	1 – 335	51	24
EWSS	248 – 1486	1 – 103235	4811	134

Figures and corresponding captions

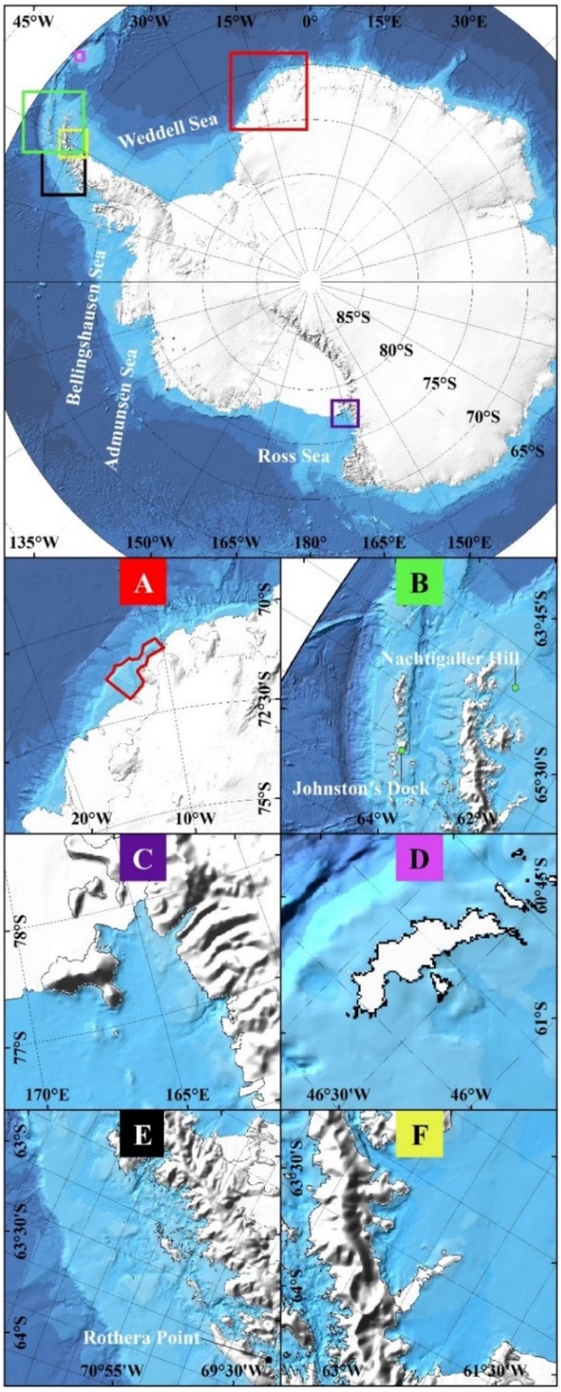

Fig. 1 Map of the Antarctic continent including locations mentioned in the review. A) Austasen and Kapp Norvegia, EWSS; B) Bransfield Strait and tip of the Antarctic Peninsula; C) McMurdo Sound, Ross Sea; D) Signey and Orcadas Islands; E) Rothera point and area studied within the frame of the Food for Benthos on the Antarctic Continental Shelf (FOODBANCS) project in the WAP, and; F) Larsen embayments, east coast of the Antarctic Peninsula. Modified after Arndt et al. (2013).

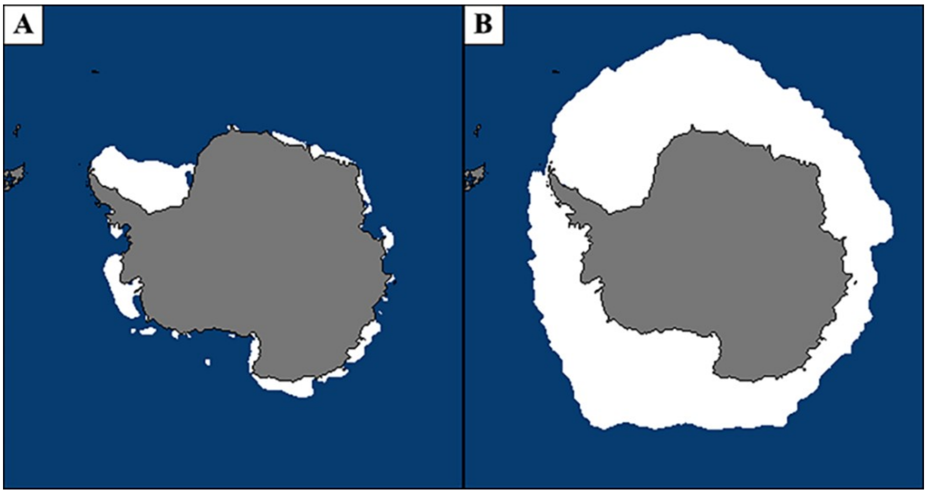

Fig. 2 Examples of sea-ice extension during A) summer (February 2018), and B) winter (August 2018). Modified after Fetterer et al. (2018).

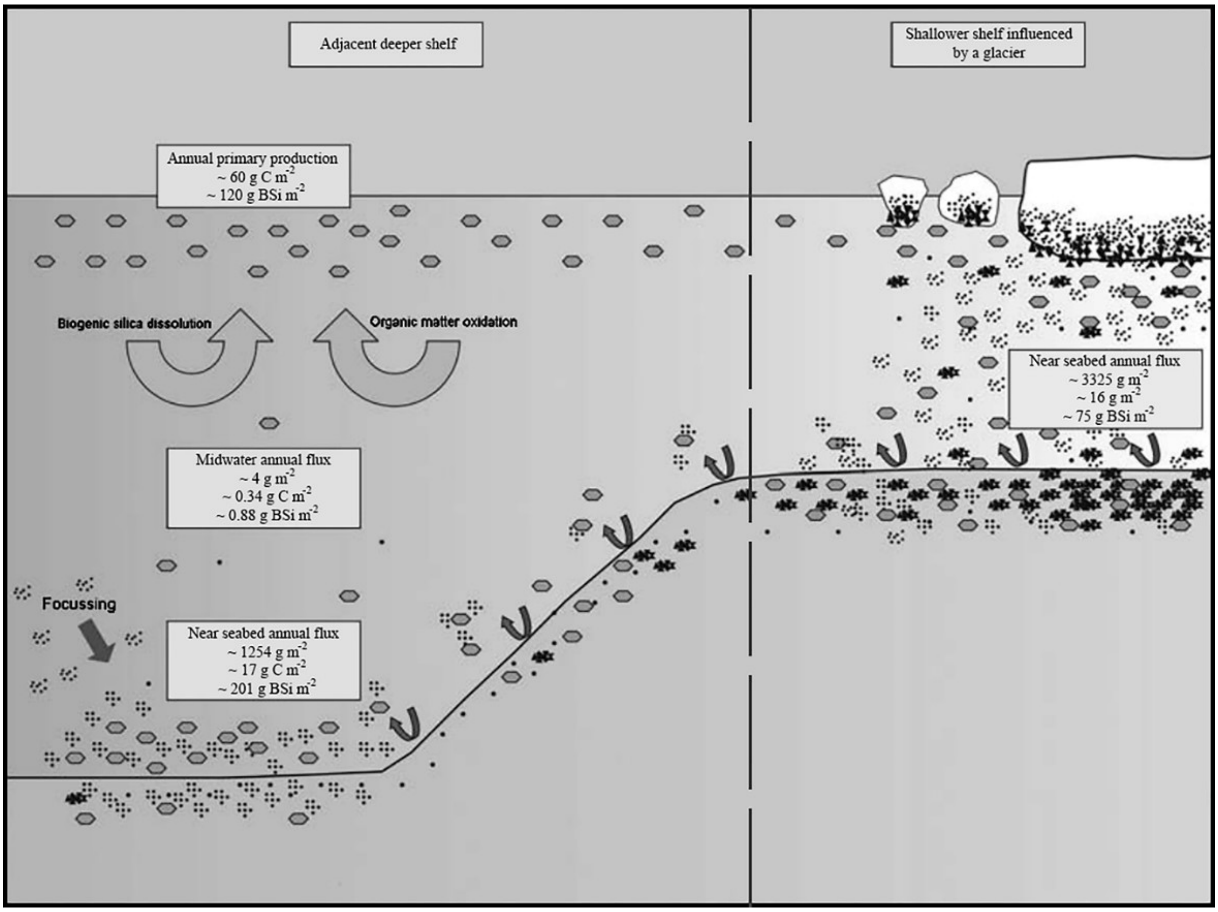

Fig. 3 Main particle fluxes at mooring sites around Johnston's Glacier (Johnston's Dock) studied by Isla et al. (2006b). Approximate annual total mass (g m^{-2}), organic carbon (g C m^{-2}) and biogenic silica (g BSi m^{-2}). The sketch shows that most particles produced off-shore over the deep shelf (polygons) do not reach mid water; the material settling in the shallower shelf feeds the deeper shelf via advection. Glacier and floating icebergs deliver coarse and fine sediments (dense clusters and circles, respectively) onto shallow areas but mostly the latter reaches the deeper shelf. Near the seabed, resuspension of sediments is represented by curved arrows. Modified after Isla et al. (2006b) with permission from Springer.

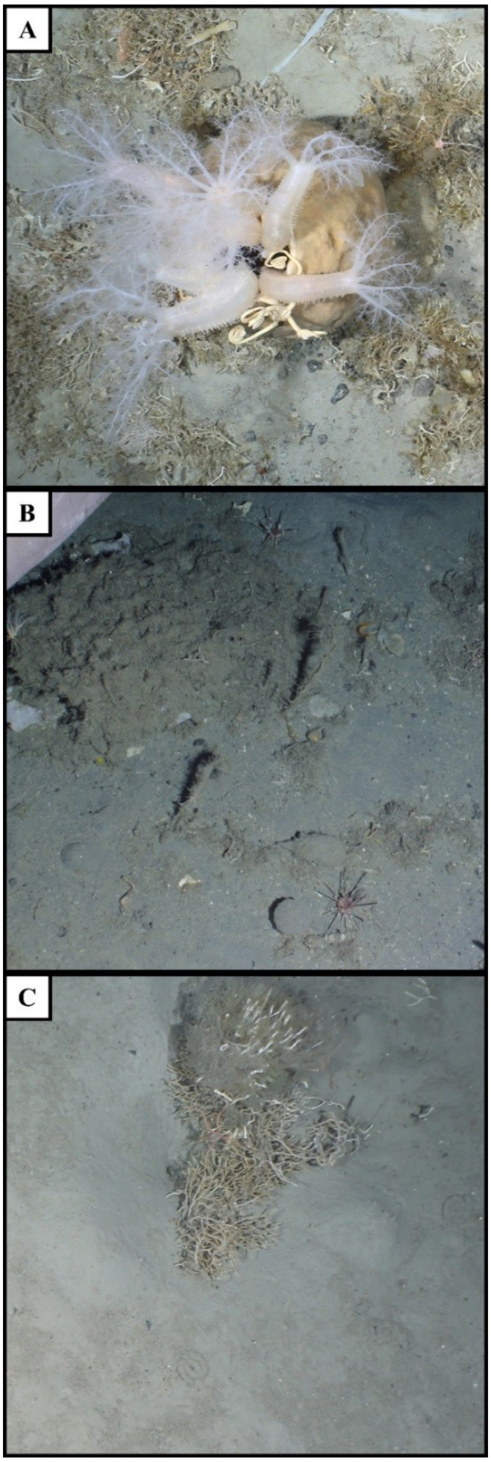

Fig. 4 Examples of benthic structures which modify particle resuspension and deposition: A) a three-dimensional structure provided by sponges and associated organisms; B) a spicule mat covering part of the seabed, and; C) a cluster of polychaete tubes. Images A) and C) were modified after Piepenburg (2016). Image B) was kindly provided by D. Gerdes and modified.

MANUSCRIPT 3: Benthic communities of the Filchner Region (Weddell Sea, Antarctica)

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Benthic communities of the Filchner Region (Weddell Sea, Antarctica)

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ABSTRACT

Due to extreme pack-ice the Filchner Region in southern Weddell Sea is one of the least studied regions on the planet. Here, we report the results on benthic communities of this high-Antarctic ecosystem and assess the relationship between environmental factors and benthic distribution patterns. We used a combination of multibox corer (MBC) and seabed images (SBI) data, from which we differenced six station groups. While one of these groups was comprised of a single station, the other five groups represented distinct benthic communities. Three of these correspond to the previously described Eastern Shelf, Southern Shelf, and Southern Trench communities. However, we found distribution shifts and MBC abundance and biomass reductions, when comparing our results to early studies. The other two groups with novel characteristics are presented here as an Ice/Ice Shelf Water (ISW) related community, and a Continental slope community (Group "E"). Water depth in combination with two or three other environmental variables (out of 7 available) explained <30 % of the benthic distribution and composition. We found a tighter relation between water mass circulation and spatial distribution of the communities, water-mass related characteristics (e.g. productivity regime, water currents) to better explain benthic spatial distribution patterns.

Keywords: Southern Ocean, infaunal benthos, epifaunal benthos, mega- and macrofauna, zoobenthic distribution patterns, sediment cores, seabed images, environment-benthic relationships

1. INTRODUCTION

Antarctic benthos has been studied for over a century (Clarke 2008). In the Weddell Sea, quantitative studies have focused more on the northwestern and eastern shelf areas (e.g. Gerdes et al. 2003, Sañé et al. 2012, Gutt et al. 2013). In contrast, the hardly accessible pack-ice covered southern Weddell Sea remains poorly studied (e.g. Voß 1988, Gerdes et al. 1992, Gutt & Starmans 1998). The present study attempts to reduce this gap by providing benthic community data from an area of ~ 476,000 km^2, covering the Filchner Trough and the adjacent continental shelf at the southern margin of the Weddell Sea (Fig.1).

The study area hereafter referred as the Filchner Region is characterized by heterogeneous topography, hydrography and sea-ice conditions. The continental shelf in front of the Filchner Ice Shelf is incised by the Filchner Trough with water depths >1000 m (Arndt et al. 2013). The Filchner Trough is considered the main conduit for Ice Shelf Water (ISW) from underneath the Filchner-Rønne Ice Shelf towards the continental slope where it mixes with open ocean waters forming the deep and bottom waters of the Weddell Sea (Schröder 2016), making the Filchner Region key for the formation of Antarctic bottom water and the regulation of the global water mass circulation (Gammelsrod et al. 1994, Foldvik et al. 2004, Ryan et al. 2017). Another conspicuous characteristic of the Filchner Region is the presence of the grounded iceberg A23-A. Iceberg A23-A is located on the Berkner Bank on the western shelf of the Filchner Region. The iceberg separated from the Filchner Ice Shelf in April 1986 and changed the circulation of High Salinity Shelf Water (HSSW) in the Filchner Region (Grosfeld et al. 2001). Previous to the calving of A23-A, HSSW flowed directly from the Berkner Bank into the Filchner Trough; after this event, the HSSW started to flow southwards to the Rønne Ice Shelf before entering the Filchner Trough as ISW (Grosfeld et al. 2001, Ryan et al. 2017).

The Filchner Region is characterized by two main sea-ice regimes (Fig.2). On the shelf east of the Filchner Trough and in of front the Rønne Ice Shelf sea-ice cover is seasonal, i.e., while during summer open water conditions prevail, during winter the sea surface is sea-ice covered. Contrastingly, over the Filchner Trough and continental shelf west of it, heavy year-round sea-ice cover dominates, as reported from previous campaigns to the Filchner Region (Knust & Schröder 2014, Schröder 2016). Sea ice not only directly regulates primary production (Arrigo et al. 2015) but also the particle flux from the euphotic zone to the benthic realm (Isla 2016), especially in the marginal sea-ice zones, where primary and secondary planktonic production are enhanced and higher than in open water areas (e.g. Bathmann et al. 1991, Isla et al. 2009, Isla 2016). Due to the opening of a polynya during summer, productivity on the eastern shelf of the Filchner region should be considerably higher than productivity at the heavy year-round sea-ice covered Filchner Trough and the continental shelf west of it. Based on these productivity differences, benthic abundance and biomass should be higher in high productive regions as compared those with lower productivity. The composition of infaunal- and epifaunal communities should also reflect such local productivity regimes. However, advection of primary produced carbon to areas adjacent to polynyas here could support benthic communities similar to those within the polynyas with even high benthic abundance and biomass (e.g. Grebmeier & Cooper 1995, Smith et al. 2006, Jansen et al. 2018).

Changes in sea-ice cover and volume directly affect water mass characteristics and planktonic productivity, thus affecting benthos. During the last decades, sea-ice cover in the eastern Weddell Sea, including a large part of our study are in the Filchner Region, has increased (Fig.2; Turner et al. 2016), in response to a decrease of surface water temperatures and a stronger positive Southern Annual Mode (Liu et al. 2004, Turner et al. 2016, Comiso et al. 2017). Thus, distinct differences in spatial and time scales of sea-ice and productivity regimes should be expected on the eastern shelf of the Filchner region, in the Filchner Trough and on the shelf west of the trough.

The first description of the benthic fauna in this region was published in the late 1980s (Voß 1988). It differentiated among three community types: a) a highly abundant and diverse Eastern Shelf community dominated by suspension feeders, especially sponges; b) a Southern Shelf community less diverse and abundant than the Eastern Shelf community, dominated by bryozoans; and c) a Southern Trench community with low diversity, high abundances, and a clear dominance of holothurians. This description was, however, exclusively based on trawl catches. Later campaigns on the eastern shelf collected quantitative data on benthic assemblages by means of a multibox corer (MBC; Gerdes et al. 1992) and seabed images (SBI; Gutt & Starmans 1998). Based on benthic abundance and biomass data, these studies reported assemblages that resembled the Eastern Shelf and Southern Trench communities *sensu* Voß (1988). These descriptions encompassed either only infaunal (based on MBC data) or only epifaunal benthos (based on SBI data), while an approach combining both benthic faunal compartments and even more, integrating the whole study area, is still missing.

Recent studies in the Filchner Trough and its adjacent shelves, based on MBC and SBI samples, concluded that both methods should be used in combination whenever possible to allow a more comprehensive representation of the benthic fauna, including both infaunal- and epifaunal benthos (Pineda-Metz & Gerdes 2018). Due to a focus on the methodological approach this recent description of the benthic fauna lacked the detail of previous studies. Here, we attempt to provide a detailed description of the benthic communities in the Filchner Region and their distribution by using a comprehensive methodological approach which considers both, infaunal- and epifaunal benthos. In a further step, we relate the observed benthic distribution with environmental factors which have already been affected by climate change and which are predicted to further vary. To these belong e.g. near seabed water temperature and salinity, and sea-ice cover (Timmerman & Hellmer 2013, Turner et al. 2016, Hellmer et al. 2017), but also other factors which are considered to be important for the benthos as e.g. sediment organic carbon content as food source and e.g. water depth and sediment grain size (Cummings et al. 2010) as regulators for benthic distribution. Based on this approach, we aim to observe how the different environmental parameters drive the structure, composition and distribution of the benthic communities of the Filchner Region.

2. MATERIAL & METHODS

Fieldwork was performed in the austral summers of 2013/14 and 2015/16 during the R/V *Polarstern* cruises PS82 (ANT-XXIX/9; Knust & Schröder 2014) and PS96 (ANT-XXXI/2; Schröder 2016). At 37 stations with water depths ranging from 243 to 1,217 m, the benthos fauna was investigated by means of a multibox corer (Gerdes 1990) and seabed images (Table S1; Fig. 1).

A 10 cm diameter multicorer (MUC) was deployed at 22 stations (Table S1) to obtain data on sediment grain size, organic carbon (OC) and biogenic silica (bSi). The upper 9 cm of the sediment cores were subsampled on board and frozen at -20 ºC in darkness until further treatment in the laboratory. Sediment grain size was measured with laser diffraction in a Horiba Partica LA950V2 laser scattering particle size distribution analyzer after removal of organic matter in a 20 % hydrogen peroxide solution. The fine sediment fraction, expressed in weight %, is equal to the combined proportion of silt- and clay-sized material, whereas the coarse fraction represents the combination of the sand and gravel fractions. OC was measured in a LECO Truspec CN analyzer and expressed as weight %. bSi was calculated following sequential alkaline extractions with Na_2CO_3 (DeMaster 1981, Mortlock & Froelich 1989, DeMaster 1991) to distinguish the biogenic and lithogenic silica fractions, both also expressed as weight %. The OC and bSi inventories for the upper 9 cm sediment column were calculated as the product of their concentrations, dry bulk density (mg cm^{-3}) and the height of the sub-sample sediment layer and expressed as mg cm^{-2}. Additional to MUC grain size data, areal cover (%) of fine sediments, gravel, and rocks/stones were estimated at each SBI station (Table S2).

To assess the effect of sea-ice on the benthic distribution and composition, we first collected monthly sea-ice cover data from the “Sea ice Index” provided by the National Snow and Ice Data Center (NSIDC) for the period 1979 – 2017 (Fetterer et al. 2018). Monthly data were used to calculate summer and year sea-ice cover averages, and the temporal trends of sea-ice cover per year and per summer. These temporal trends were calculated as the slope of the linear function of sea-ice cover over time for the period 1979 – 2017.

Additional to MUC samples and sea-ice cover, a CTD (Seabird *SBE-911 plus*) was deployed at 201 stations to obtain oceanographic data on water column parameters (Schröder & Wisotzki 2014, Schröder et al. 2016). From these data, we extracted near seabed water temperature, salinity, density, and dissolved oxygen to use in the correlation analyses.

While sea-ice data were already in raster format, CTD and sediment data were first imported to the GIS environment and interpolated for the study area with the Kriging method of the ArcMap 10 (ESRI). The “extract multi values to points” toolbox of ArcMap was used to extract environmental data from each raster derived from CTD, MUC, and sea-ice cover at all stations where both, SBI and MBC benthic data were obtained (Table S1 & S2). The extracted environmental data were used to assemble an environmental data matrix consisting of 20 environmental variables. To avoid co-correlation when conducting a BEST test (see below), the environmental variables were correlated with each other. We then selected against environmental variables with significant correlations. The final environmental matrix consisted of six of the 20 environmental variables (Table S3).

Sediment cores for benthic analyses were sieved on deck over a 500-µm mesh. Material retained on the sieves was fixed in a 5 % sea water-formaldehyde solution buffered with borax. In the laboratory, benthic organisms were sorted, identified to the lowest identifiable taxon via a stereomicroscope and classified into taxonomic units (TUs) similar to those used in previous MBC studies, in order to enable a comparison with previous data obtained in the Filchner Region (Gerdes et al. 1992) other areas of the Weddell Sea (Gerdes 2014a-h). Although the use of larger TUs such as e.g. class or order is not common, other studies have shown little loss of statistical resolution regardless of the low taxonomic resolution (e.g. Warwick 1988). Abundance (ind m^{-2}) and wet-weight biomass (g ww m^{-2}) values were calculated for each TU and sample. Abundance of colonial (e.g. bryozoans and hydrozoans) and large benthic organisms (e.g. sponges) was counted as presence only.

MBC abundance and biomass data were fourth root transformed and used to calculate between-station Bray-Curtis (Bray & Curtis 1957) similarity matrices. These MBC matrices were used in a PERMANOVA (Anderson 2001) to test for differences with older comparable MBC benthic abundance and biomass data from the Filchner Region (Gerdes et al. 1992) and other regions of the Weddell Sea (Gerdes 2014a-h). These multivariate statistics were performed by means of the software package PRIMERv6 with its PERMANOVA+ add on (Clarke & Gorley 2006, Anderson et al. 2008).

A RELATE test between MBC abundance and biomass data showed benthic distribution patterns derived from abundance and biomass to be significantly correlated (Spearman rank correlation Rho = 0.893; $p < 0.001$). Based on this result, we only used MBC biomass values in combination with SBI abundance values for the subsequent statistical analysis. All TUs from this benthic matrix were classified into four feeding guilds (deposit feeders, suspension feeders, scavengers, and predators) according to specialized literature (Table S4).

During PS82, SBI were taken every 15 seconds during a 15-min drift phase with a camera (Canon EOS D100) installed in an underwater housing attached to the MBC, resulting on an average of 55 images per station. Before treating SBI for analyses, all images out of focus or blurred by suspended particles were discarded, resulting in an average of 35 usable images per station (for more details on SBI sampling and treatment previous to the analyses see Pineda-Metz & Gerdes, 2018). At four stations (033, 040, 052 and 206), all SBI were analysed to calculate the number of images per station sufficient to identify at least 75 % of all TUs differentiated. These curves were extrapolated to 35 images whenever necessary to reach the mean number of SBI per station. All taxon accumulation curves were calculated using the EstimateS software (Colwell 2013). The taxon accumulation curves at these four stations clearly indicated that the analysis of 15 images was sufficient for this purpose (Fig.S1). For this reason, at all other stations a subset of 15 randomly selected SBI was used to describe epifaunal benthos. During PS96, SBI were obtained by means of the Ocean Floor Observation System (OFOS; for details of the gear see Piepenburg et al. 2017). From each OFOS transect, 50 SBI taken on the closest position to the corresponding MBC station were selected, and a subset of 15 randomly selected SBI was analysed and used to calculate the taxon cumulative curve, as it was described above for the SBI obtained with the underwater camera attached to the MBC. All images obtained by means of the OFOS can be found in the PANGAEA virtual data base (Piepenburg 2016).

In the laboratory all organisms visible in the images were counted, identified to the lowest identifiable taxonomic level, and classified into TUs similar to those defined for MBC samples. Whenever possible TUs lower than those defined for the MBC were used. Organism counts were standardized to abundance figures (ind m^{-2}). The abundance of colonial organisms (e.g. bryozoans, gorgonians, and hydrozoans) was calculated as the area covered by the colonies (m^2).

Previous to multivariate analysis and to eliminate the influence of different units in the benthic data matrix (i.e. ind m^{-2}, m^2, and g ww m^{-2}) all data were first pre-treated to conform a benthic data matrix of the SBI abundance ratios and MBC biomass ratios of each TU at every station. Ratios were calculated by dividing TU abundance/biomass values at each station by the corresponding total abundance/biomass value of the station (Text S1).

Multivariate statistics were applied by means of the software package PRIMERv6 with PERMANOVA+ (Clarke & Gorley 2006, Anderson et al. 2008). Prior to analysis, benthic data were log (x+1) transformed. Between-station similarities were calculated using the Bray-Curtis Index (Bray & Curtis 1957). The benthic data matrix was used in a Cluster and SIMPROF analysis (Clarke & Gorley 2006) to differentiate and define station groups, and the resemblance pattern was visualized using 2-d multidimensional scaling (MDS) plots. Additionally, one-way PERMANOVA (Anderson 2001) and SIMPER analyses (Clarke & Warwick 1994) were performed to test for significant differences among and between station groups, to establish the mean dissimilarity between groups, and to determine which TUs mainly contributed to these between group differences.

Additional to these tests, the similarity matrix derived from the benthic data matrix was used in a BEST analysis (Clarke & Gorley 2006) to test for correlations with the environmental data matrix and thus the influence of environmental variables over benthic distribution patterns. This exploratory test was followed by a BEST analysis with 999 permutations to test for significant correlations.

3. RESULTS

Fine (clay and silt) and coarse (sand and gravel) sediments were unevenly distributed among stations in the Filchner Region. Shelf and trough stations were characterized by high proportions of fine sediments, whereas coarse sediments prevailed at slope stations (Fig.3). In SBI, >50 % of the seabed was covered by fine sediments. OC inventories varied from 8.0 to 70.4 mg cm^{-2}, with higher OC concentrations along the northern slope of the Filchner Region and lower concentrations on some parts of the eastern and western shelves of the region (Fig. 4). bSi inventories ranged from 50.7 to 560.6 mg cm^{-2}; lower bSi concentrations were found at the western shelf stations, while higher values were observed in the deep trough and along the eastern shelf of the Filchner Region (Fig. 4).

Near-seabed water temperatures in the Filchner Region varied between -1.97 and -0.63 °C (Fig.5). Lower temperatures were recorded at the southernmost stations in the southern Filchner Trough on the eastern and western shelves, while higher temperatures were recorded on the northern slope of the Filchner Region (Fig.5). Stations within the Filchner Trough were characterized by highest salinity values (Fig.5).

The highest average summer and year sea-ice cover occurred over the Filchner Trough (Fig.2a, b). The sea-ice cover temporal trend over the years 1979 to 2017 showed similar patterns for summer and year averages with gain of sea-ice cover especially in the trough area and loss of cover west of the A23-A Iceberg and on the eastern shelf close to the shelf ice edge (Fig.2a, b). Average loss of sea-ice cover on the eastern shelf was greater in summer (-0.19 % y^{-1}) than over the year (slightly <0 % y^{-1}; Fig.2c,d), whereas west of the A23-A iceberg, average loss in summer (-0.19 % y^{-1}) was smaller than over the year (-0.4 % y^{-1}; Fig.2c,d).

Thirty-five TUs were distinguished in MBC samples at the Filchner Region stations (Table S5). The number of TUs at MBC stations ranged from 3 (St-066) to 26 (St-163 and 164); only at six MBC stations <10 TUs were found. In the SBI analysis, a total of 31 TUs were distinguished. The number of TUs per SBI station ranged from 6 (St-144) to 23 (St-164, 179 and 190), in all but one station >10 TUs were identified. Combining MBC and SBI data, a total of 46 benthic TUs were distinguished (Table S3). Fifteen TUs were exclusively found in MBC samples (unidentified anthozoans, sipunculids, flatworms, nemerteans, priapulids, aplacophorans, scaphopods, clitellate worms, echiurids, acari, cumaceans, harpacticoid copepods, cirripeds, tanaids, and ostracods), and 11 TUs were exclusively found in SBI (unidentified medusae, stauromedusae, gorgonians, pennatulaceans, actinarians, scleractinians, nudibranchs, cephalopods, mysids, serolids, and decapods).

The mean total benthic abundances at the 31 MBC stations ranged from 104 to 4,627 ind m^{-2}, with an overall mean of 1,526 ind m^{-2} and an overall median of 1,270 ind m^{-2}. Dominant TUs, which together contributed >75 % to overall mean abundance, were polychaetes, clitellate worms, amphipods, ophiuroids and bivalves (Table 1). Deposit feeders were the most abundant feeding guild, with an overall mean of 672 ind m^{-2} (range: 44 – 2,229 ind m^{-2}), followed by predators (mean: 460 ind m^{-2}; range: 20 – 1,532 ind m^{-2}), suspension feeders (mean: 360 ind m^{-2}; range: 20 – 1,172 ind m^{-2}), and scavengers (mean: 34 ind m^{-2}; range: 1 – 117 ind m^{-2}).

The mean benthic biomass expressed as wet-weight (ww) ranged from 1.31 to 335.47 g ww m^{-2}, with an overall mean of 51.08 g ww m^{-2} and an overall median of 23.85 g ww m^{-2}. Following the criteria given for MBC abundance data, bryozoans, sponges, polychaetes, ophiuroids, and tunicates were identified as dominant TUs (Table 1). Suspension feeders contributed most to biomass, with an overall mean of 33.04 g ww m^{-2} (range: 0.38 – 321.49 g ww m^{-2}), followed by deposit feeders (10.81 g ww m^{-2}; range: 0.47 – 56.06 g ww m^{-2}), predators (6.89 g ww m^{-2}; range: 0.23 – 37.07 g ww m^{-2}), and scavengers (0.34 g ww m^{-2}; range: 0.01 – 2.20 g ww m^{-2}).

The quantitative benthic data obtained from MBC samples in the Filchner Region study allow unbiased comparison with MBC data obtained at the Tip of the Antarctic Peninsula (TAP), the Larsen embayments (LA), and the South-Eastern Weddell Sea Shelf (SEWSS, cf. Gerdes 2014 a-h). Benthic abundance and biomass as well as faunal community composition differed significantly among regions (PERMANOVA pseudo-F = 5.549; $p < 0.001$) and between regions (Pairwise PERMANOVA p values < 0.05; Table S6). In terms of abundance, dominant taxa were polychaetes, bivalves, amphipods and ophiuroids. Polychaetes contributed most to abundance in all four regions, but their dominance declined from west to east (Table 2). Composition based on biomass data clearly showed that sponges dominated in TAP and especially the SEWSS, where they contributed 57.5 and 80.5 % to total benthic biomass, respectively; in the Filchner Region sponges contributed 22.2 % of the biomass. In LA echiurids dominated (71 % of the total biomass) and sponges represented only < 2 % of the total benthic biomass (Table 2). Further comparison of our MBC data set with previous data from the Filchner Region (Gerdes et al. 1992) also showed significant differences (PERMANOVA pseudo-F = 6.289; p < 0.001). The mean abundance (1,539 ind m-2) and biomass (52.76 g ww m-2) resulting from the 2013/14 and 2015/16 Filchner Region cruises were almost half the values (2,758 ind m-2 and 108.13 g ww m-2) recorded in the late 1980s (Gerdes et al. 1992). In terms of abundance, polychaetes, bivalves, amphipods, tanaids, and isopods were most abundant in the late 1980s, while sponges contributed most to biomass, followed by holothurians, polychaetes, priapulids and ascidians.

For the Filchner Region mean total benthic abundance at the 35 SBI stations ranged from 2 to 170 ind m^{-2}, with an overall mean of 61 ind m^{-2} and an overall median of 55 ind m^{-2}. Dominant TUs were ophiuroids, polychaetes, holothurians, tunicates and unidentified organisms, constituting > 75% of the overall abundance (Table 1). Suspension feeders were the most abundant feeding guild, with an overall mean of 28 ind m^{-2} (range: <1 – 124 ind m^{-2}) followed by deposit feeders (22 ind m^{-2}; range: 1 – 106 ind m^{-2}), predators (10 ind m^{-2}; range: <1 – 31 ind m^{-2}), and scavengers (1 ind m^{-2}; range: <1 – 5 ind m^{-2}).

Colonial organisms were not recorded at six SBI stations, and at the other SBI stations their coverage ranged from 0 to 0.585 m^2, with an overall mean of 0.051 m^2 and an overall median of 0.012 m^2. Bryozoans were the most abundant colonial TU, with an overall mean coverage of 0.045 m^2 (range: 0 – 0.569 m^{-2}), followed by hydrozoans (0.003 m^2; range: 0 – 0.045 ind m^{-2}), and gorgonians (0.003 m^2; range: 0 – 0.045 ind m^{-2}).

MBC and SBI data obtained parallel at 29 stations were combined in a single matrix. The cluster and SIMPROF analyses based on these benthic data differentiated six station groups named with the letters “A” to “F” in the Cluster and SIMPROF analyses (Fig.S2). A summarized description of these groups and their composition is given in Table 3 and one representative UW picture of each station group is shown in Fig.6. The composition in these six station groups differed significantly among them (PERMANOVA pseudo-F = 4.69; p < 0.001). A pairwise PERMANOVA showed almost all groups to be significantly different between each other. Group “C” as a “one station group” was significantly different only from group “F” (Table 4). SIMPER test “within group similarities” ranged from 50 to 71%, while between group dissimilarities ranged from 56 to 85%. SBI abundance of holothurians, ophiuroids, bryozoans, and polychaete MBC biomass contributed most to the between group dissimilarities (Table 4).

Based on the PERMANOVA among and between group comparisons we differentiated between the one-station group “C” and all other groups. We considered the later groups to represent distinct benthic communities in the Filchner Region. Group “A” consisted of two stations (St. 066 and 116) located close to each other in the deep southern Filchner Trough (Fig.1). This group represents a deposit-feeding epifauna dominated community, characterized by a relatively low number of taxa, high epifaunal abundance (not as high as group “D”), and low infaunal abundance and biomass. Holothurians contributed most to epifauna abundance, whereas the infauna was dominated by polychaetes. Group “B” consisted of four stations (Fig.1), one located on the western shelf near the iceberg A23-A (St. 037), two at the eastern slope of the Filchner Trough (St. 033 and 072), and one off the Brunt Ice Shelf (St. 144). This group represents a mixed community, with suspension- and deposit-feeding epifauna and a predator/deposit feeding dominated infauna (Table 3). Abundance, biomass, and colonial organism cover showed low values. The number of taxa was intermediate (Table 3) and ophiuroids and polychaetes were the main TUs in terms of abundance and biomass, respectively. Group "C" was comprised of only one station (St-098) located at the eastern slope of the trough (Fig.1), dominated by ophiuroids and anthozoans (Table 3), and characterized by intermediate number of TUs; MBC abundance and biomass were higher as compared to groups "A" and "B". Group "D" consisted of two stations (St. 079 and 089) located close to each other (Fig.1) on the eastern shelf. A sessile suspension-feeder community dominated in terms of biomass and total organism cover by bryozoans. The number of TUs was intermediate, and biomass, colonial organism coverage and epifaunal abundance values were high (Table 3). Group "E" was formed by three stations (St. 163, 226, 270) on the shelf break of the Filchner Region (Fig.1). This group represents a sessile suspension-feeder community with a high number of TUs, high abundance and biomass, and intermediate colonial organism cover mainly by hydrozoans. Ophiuroids showed the highest abundance and biomass values (Table 3), followed by a combination of suspension-feeding tunicates, bryozoans and sponges. Group "F" as the biggest group spread with 17 stations especially over the northern parts of the Filchner Region. This group is dominated by a mixture of suspension- and deposit-feeders, which accounted for up to 80 % of abundance and 57 % of biomass (Table 3). This community was characterized by the highest number of TUs and by intermediate abundance, biomass and colonial organism coverage. Ophiuroids dominated in terms of SBI abundance, while sponges contributed most to MBC biomass.

The exploratory BEST analysis indicated only rather weak correlations between the environmental data and the benthic data matrix conformed by MBC biomass and SBI abundances. The combination of the seven selected environmental parameters explained <30 % of the overall benthic variation (Spearman Rank correlation Rho = 0.275; p = 0.006). When testing each environmental variable individually, water depth was found to be the "best explanatory variable" (Spearman Rank correlation Rho = 0.264; p = 0.014). Combinations of two or three environmental parameters with water depth were found to be the "best explanatory" variable combinations, but even these combinations explained <30 % of the benthic variation (Spearman Rank correlation = 0.284; p = 0.023; Table 5).

4. DISCUSSION

4.1. BENTHIC COMMUNITIES IN THE FILCHNER REGION

Our approach to describe benthic communities by combining corer samples and seabed imagery into a single data matrix, also including stations in the difficult-to-access sea-ice covered western shelf of the Filchner Region, considerably extended and updated the current knowledge of the benthic fauna in this high-Antarctic region. Furthermore, our correlation analyses between benthic distribution and environmental parameters could help us to understand how benthos in the Filchner Region might be affected by the ongoing climate change. Such analysis could help us to recognize environmental variables affecting benthic spatial distribution such as near-seabed temperature and sea-ice cover, which are predicted to change by the end of the century due to climate change (Timmermann & Hellmer 2013, Hellmer et al. 2017).

We differentiated six station groups, five of which represented distinct communities (see Results). We consider group “C” as a one station group separately. In terms of epifaunal benthos, this station appears similar to group “B”, whereas its infauna was different from other groups (Table 3). Whether the infaunal composition at this station is driven more by local environmental characteristics or by the efficiency of the MBC to catch e.g. few but large anthozoans, which characterize the infauna at this station remains unclear. Assessing why group “C” is so peculiar will require further sampling in the southeast end of the Filchner Region.

From the remaining groups, we assume groups “A”, “D” and “F” to correspond to benthic communities previously described for the Filchner Region (Voβ 1988, Gerdes et al. 1992, Gutt & Starmans 1998). However, our results point to distribution shifts and expansion of previous distribution ranges. Group “A” corresponds to the Southern Trench community *sensu* Voß (1988). In contrast to the original description of the Southern Trench community (Voß 1988), we found this group only in the southern deepest part of the Filchner Trough and not along the whole trough, making it a “Deep Trough community” rather than a Southern Trench Community (Fig.S3). Group “F” corresponds to the Eastern Shelf community *sensu* Voβ (1988). This group was distributed not only on the eastern shelf of the Filchner Region, but also on the western shelf, the continental slope and the slope of the inner trough, hence extending the distribution borders of this community considerably. This agrees with previous descriptions of the Eastern Shelf community, which pointed out also an extended distribution range for this community (Gerdes et al. 1992, Gutt & Starmans 1998). The extended distribution of the Eastern Shelf community to the deeper continental slope and also to the northern part of the western shelf of the Filchner Region suggests a connection between these shelves. Group “D” corresponds to the Southern shelf community *sensu* Voß (1988). The Southern Shelf community was originally described to be mainly distributed along the ice shelf edge southwest of the Filchner Trough and in one small area on the continental shelf off Halley Bay (Fig.S3; Voß 1988). According to our results group “D” seems to have shifted southwards on the southeastern shelf. However, heavy sea-ice conditions in the entire southern Filchner Region, especially off the Rønne Ice Shelf, did not allow extensive station work in this area, thus making the confirmation of the original distribution range of this community impossible.

The two other communities we differentiated are described for the first time in the Filchner Region. One of these corresponds to group “B”, defined as a poor and mixed community with low abundance, biomass and number of taxa. This community was found in 700 m water depth at the inner slope of the continental shelf northeast of Halley Bay, at the inner slope of the central part of the Filchner Trough, and in the proximity of the large iceberg A23-A on the western shelf in 380 m water depth. We defined the heterogeneous group “B” as an “Ice/ISW related community”. Although located in different areas of the Filchner Region (St-033, 072, and 037), they share hydrographic characteristics which might explain benthic similarities among them (Fig.S4). The second newly defined benthic community was represented by group “E” and occurred along the continental slope at water depths between 600 to 800 m. This community living on sediments highly covered by gravel was dominated by ophiuroids and defined as the “Continental Slope community”.

4.2. FILCHNER REGION COMPARED TO OTHER WEDDELL SEA REGIONS

The MBC quantitative benthic data we presented for the Filchner Region allowed for comparing our results with other Weddell Sea regions. PERMANOVA analyses of benthic abundance and biomass as well as faunal community composition showed significant differences among these Weddell Sea regions (Table 2). As a general pattern, high benthic abundance and biomass prevailed in regions with low sea-ice cover, such as TAP and the SEWSS with a yearly average sea-ice cover of 12 and 58 % and summer averages of 2 and 29 %, respectively (Fetterer et al. 2018). Contrastingly, lower abundance and biomass values were observed in regions with higher sea-ice cover, e.g. in the Filchner Region and LA, where yearly average sea-ice cover reached 76 and 69 % and summer sea-ice cover 50 and 75 %, respectively (Fetterer et al. 2018). Sea-ice cover, its extension and persistence, are key factors regulating primary production (Arrigo et al. 2015). Thus, the between region sea-ice regime differences would imply differences in the primary production regime, which in turn would cause different particle fluxes and food input for benthos (Gutt 2001, Isla 2016). We therefore attribute the regional differences of benthic abundance, biomass and composition to differences in local production and particle flux regimes, regulated by sea ice (e.g. cover, ice free days).

4.3. FILCHNER REGION PAST VS PRESENT

The comparison of the present MBC data set with previously reported data from the Filchner Region (Gerdes et al. 1992) showed significant differences with reduced abundance and biomass as well as changes in the faunal composition. The MBC abundance and biomass values we found were half of those previously recorded in the Filchner Region during the late 1980s. In terms of abundance-based composition, we found groups such as tanaids and isopods to lose importance, being “replaced” by clitellate worms and ophiuroids. In terms of biomass-based composition, bryozoans gained importance, contributing more to overall average biomass than sponges, which were formerly found to dominate the fauna (Gerdes et al. 1992). These observations might already evidence climate (sea-ice cover increase; Fig.2 & S5) induced changes in community parameters, including also modifications in composition patterns of benthic communities. We hypothesize this to be related to an increase of sea-ice cover (Fig.S5; Turner et al. 2016, Fetterer et al. 2018), which reduces size and duration of the summer polynya, thus reducing also the primary productivity in the area (Arrigo et al. 2015).

Comparing our epifauna results with older data, too, reveals differences. Previous studies based on SBI data defined six clusters in the Filchner Region. These assemblages, however, were also found on the SEWSS and on the Lazarev Sea shelf (Gutt & Starmans 1998). The holothurian “deposit-feeder dominated” cluster sensu Gutt & Starmans (1998) in the deep southern Filchner Trough corresponds to our group “A. The “suspension-feeder-rich” and “suspension-feeder-poor” clusters (*sensu* Gutt & Starmans 1998) in the northern part of the eastern shelf of the Filchner Region partially overlapped with our station groups “E” and “F”. However, while both suspension feeder clusters were bryozoan-dominated (Gutt & Starmans

1998), these were less abundant in our groups “E” and “F”. This holds especially true for group “E” along the outer slope of the Filchner Region, where hydrozoans were the dominant TU. Bryozoan dominance appears to have shifted towards the south of the eastern shelf of the Filchner Region, a shift which could be driven by the increased sea-ice cover over the outer slope, and decreased sea-ice cover over the eastern shelf.

4.4. ENVIRONMENTAL DRIVERS FOR BENTHIC DISTRIBUTION

Our analyses did not indicate any strong correlation between the assessed set of environmental parameters and benthic distribution patterns (all correlation coefficient values of the BEST analyses were <0.3). This agrees with studies conducted in the Bellingshausen, Weddell and Lazarev Seas, which found rank correlation coefficients <0.550 by means of an analysis similar to the BEST test (Gutt & Starmans 1998, Saiz et al. 2008).

Water depth as a single variable showed the highest correlation value to explain benthic variability, although the correlation was weak (Table 5). Water depth is proposed to regulate benthic food input, its quantity and quality, by modifying particle residence time in the water column (Smith et al. 2006), thus also regulating benthic distribution. This could explain why some TUs such as polychaetes, isopods, amphipods and bryozoans have been described as water depth dependent groups on Antarctic shelves (Ellingsen et al. 2007, Saiz et al. 2008, Jazdzewska & Sicinski 2017). Contrastingly, e.g. sponges, ascidians, and bivalves, have been proposed to rely on water circulation and re-suspended particle supply instead (McClintock et al. 2005, Ellingsen et al. 2007, Segelken-Voigt et al. 2016), hence being more water depth “independent”. The mix of water depth “dependent” and “independent” TUs could partially explain the low correlation between water depth and benthic spatial distribution patterns. This coincides with benthic distribution patterns described for the Ross Sea (Cummings et al. 2010) and Bellingshausen Sea (Saiz et al. 2008) and would support the proposed capacity of Antarctic benthos to distribute over large depth ranges (Brey et al. 1996).

The content of organic matter in or on the seabed is commonly regarded as an important food source for benthos (Sañé et al. 2011, Zhang & Wirtz 2017). In our study, OC inventories in the sediment were just defined as quantities and quality was not regarded. The OC inventories did not show any correlation with benthic distribution patterns. This lack of correlation between OC as a single variable with benthic distribution would comply with a recent study, where OC quality was said to be more important than its quantity for explaining the structure of benthic communities (Zhang & Wirtz 2017). Thus, our observations reaffirm the idea that benthos distributes independently of the amount of OC found in the sediment column.

Sea ice affects the benthos in an indirect way by regulating primary production (Arrigo et al. 2015) and thus the food supply for benthic organisms. Despite these effects, sea-ice cover or its temporal trend were not listed as variables in our correlation analyses (Table 5). However, we found hints pointing to a combination of polynya location and water mass circulation to be related to the benthic spatial distribution, as proposed by bentho-pelagic coupling and benthic distribution studies in other Antarctic regions (Grebmeier & Cooper 1995, Isla et al. 2006, Jansen et al. 2018). The main polynya in the Filchner Region is formed on the eastern shelf (Fetterer et al. 2018), where water from the Weddell Sea Gyre enters and flows southwards towards the Filchner Ice Shelf (Ryan et al. 2017). While the polynya enhances primary production, the water mass circulation distributes this matter towards the south, supporting the presence of suspension feeders even in areas with relatively high sea-ice cover (e.g. southern end of the eastern shelf, where the Southern Shelf community was found). Conversely, water masses in the Filchner Trough originating from underneath the Filchner Ice Shelf flow northwards towards the continental break (Ryan et al. 2017). Due to its sub-ice shelf origin and to heavy ice conditions in the trough, these water masses should be less productive and transport less suspended organic matter, which might explain the high dominance of deposit feeders such as elasipodid holothurians and the concomitant absence of suspension feeders. A similar situation was described for McMurdo Sound in the Ross Sea. Benthos production was higher in the eastern Sound, where water masses flow towards the Ross Ice Shelf and lower in the western Sound, where water masses come from underneath the Ross Ice Shelf (Barry 1988, Barry & Dayton 1988).

Water mass circulation patterns in the Filchner Region appear to explain the general benthic distribution pattern (Fig.S4). The “Deep Trough community” occurs in the deep Filchner Trough where dense water originating at the Rønne Trough circulates (Fig.S4; Ryan et al. 2017). The “Ice/ISW related community” was found outside of the Filchner Trough, either close to the iceberg A-23A on the Berkner Bank, off the Brunt Ice Shelf, or in the ISW flow path (Fig.S4). The influence of water masses on benthic community distribution also becomes evident in the Southern Shelf community, represented in our study by two closely located stations in the south of the eastern shelf of the Filchner Region, likely related to the southern limit of modified Warm Deep Water (WDW; Fig.S4) coming from the north. Furthermore, the Continental Slope and Eastern Shelf communities (groups “E” and “F”) appear to live in warmer waters, most likely WDW and modified WDW from the Weddell Gyre. The circulation of WDW along the continental slope of the Filchner Region could also explain the connectivity between eastern and western shelves of the Filchner Region, which we assume from the distribution of the Eastern Shelf community also on the western shelf.

5. CONCLUSION

Our approach using a combination of SBI and MBC data allowed for a comprehensive benthic community description by including data from both infaunal- and epifaunal benthos. With this approach we found the benthos of the Filchner Region to be highly heterogeneous and composed of five distinct communities. Comparison of our data with previous benthic studies in the Filchner Region and other areas of the Weddell Sea show distinct differences among the benthic communities from the Filchner Region, the Tip of the Antarctic Peninsula, the Southeastern Weddell Sea Shelf, and the Larsen Embayments. We attribute these differences to specific sea-ice and production regimes in these regions. Our results also provide partial evidence that benthos in the Filchner Region underwent changes in terms of abundance, biomass and composition between the late 1980s and mid-2010s. Shifts in the distribution ranges of the benthic communities, too, became obvious. These changes are most likely related to water mass circulation patterns and increased sea-ice cover in the area. Our correlation analysis showed that the environmental parameters considered explained <30 % of the benthic spatial distribution. These results suggest further drivers for benthic community structure and composition such as water mass circulation patterns, planktonic productivity, particle flux and lateral transport, and planktonic community abundance and composition.

Due to lack of data we unfortunately could not include these parameters into our analyses. Nevertheless, the results of our correlation analyses can prove useful to further define environmental parameters to be considered for predicting future climate change effects on the Antarctic benthic fauna. Thus, we strongly recommend future studies to take a coordinated multidisciplinary approach. Such approach should include also comprehensive bentho-pelagic coupling studies, which will provide a better tool to understand how benthos is (and could be) shaped by its environment.

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Tables and corresponding legends

Table. 1: Abundances derived from all seabed images (SBI; n = 35), abundances and biomass derived from all multibox corer (MBC) samples (n = 31) and their respective dominance and frequency of occurrence for dominant taxonomic unit (TUs). Minimum and maximum abundances/biomass are in brackets, dominance is calculated from mean abundance/biomass values.

TUs	SBI			MBC				
	Mean abundance (ind m^{-2})	Dom.[a] (%)	Frec.[b] (%)	Mean abundance (ind m^{-2})	Mean biomass (g ww m^{-2})	Dominance (%)		Frec.[b] (%)
						Abundance	Biomass	
Porifera	3 (0 – 38)	4.5	80	1[d]	11.4 (0 – 87.7)	0.1	22.2	71
Bryozoa[d]	0.045 (0 – 0.569)	48.5	83	1[d]	13.6 (0 – 315.4)	0.1	26.7	55
Bivalvia	<1 (0 – 5)	0.2	17	101 (0 – 542)	0.5 (0 – 1.9)	6.6	0.9	97
Polychaeta	11 (<1 – 95)	17.3	100	763 (57 – 2181)	11.3 (0.4 – 101.9)	50.0	22.0	100
Clitellata	-	-	-	143 (0 – 1292)	0.2 (0 – 2.1)	9.4	0.4	74
Amphipoda	<1 (0 – 3)	0.5	74	108 (0 – 750)	0.4 (0 – 1.9)	7.1	0.7	84
Holothuroidea	8 (0 – 166)	13.	97	9 (0 – 73)	1.3 (0 – 15.3)	0.6	2.6	48
Ophiuroidea	24 (<1 – 95)	39.7	100	100 (0 – 573)	4.8 (0 – 39.3)	6.6	9.2	81
Tunicata	7 (0 – 76)	11.8	89	8 (0 – 73)	2.4 (0 – 38.0)	0.6	4.7	45
Unidentified	3 (0 – 16)	5.0	97	2 (0 – 28)	<0.1 (0 – 0.4)	0.1	<0.1	16

-: No data available

a: Dominance

b: Frequency of occurrence.

c: Abundance given in m^2; Relative abundances based on organism coverage in SBI.

d: Abundance recorded as presence/absence (see Methods section).

Table. 2: Statistics based on MBC data of each sub-region of the Weddell Sea; Tip of the Antarctic Peninsula (TAP), Larsen embayments (LA), Filchner Region (FR), and South Eastern Weddell Sea Shelf (SEWSS). MBC data of AP, LA and SEWSS modified after Gerdes (2014 a-h).

Sub-Region (Number of samples)	**Depth Range (m)**	**Number of Taxonomic units (TUs)**	**Abundance (ind m-2)**				**Biomass (g ww m-2)**			
			Range	**Mean**	**Median**	**Dominant TUs**	**Range**	**Mean**	**Median**	**Dominant TUs**
TAP (15)	187 – 934	34	608 – 16,894	3,784	2,723	Polychaeta (62.2 %) Bivalvia (10.9%) Clitellata (7.2%)	30.11 – 3,484.53	422.98	223.30	Porifera (57.9 %) Polychaeta (13.8%) Anthozoa (10.1%)
LA (21)	202 – 850	32	129 – 2,016	682	568	Polychaeta (59.2 %) Bivalvia (8.7%) Isopoda (4.3%) Sipuncula (4.1%)	1.64 – 785.70	77.73	16.00	Echiurida (70.6 %) Echinoidea (8.3%)
FR (31)	254 – 1,217	33	104 – 4,627	1,526	1,270	Polychaeta (50.0 %) Clitellata (9.4%) Amphipoda (7.1%) Bivalvia (6.6%) Ophiuroidea (6.6%)	1.31 – 335.47	51.08	23.85	Bryozoa (26.7 %) Porifera (22.2 %) Polychaeta (22.0 %) Ophiuroidea (9.3%)
SEWSS (41)	248 – 1,486	35	29 – 6,220	2,133	1,786	Polychaeta (36.1 %) Amphipoda (10.8 %) Ophiuroidea (10.5%) Bivalvia (9.9%) Sipuncula (4.7%) Isopoda (4.0%)	1.07 – 103,234.71	4810.75	134.24	Porifera (80.5 %)

Table. 3: Standardized group parameters for station groups defined after the Cluster and SIMPROF analyses. Abundances, biomasses and coverage are given as average for the station group. Main MBC TUs and feeding guilds are based on biomass data.

Station Group (Stations per Group)	Number of TUs (SBI/MBC)	SBI				MBC			
		Abundance (ind m^{-2})	**Colonial coverage (%)**	**Main TUs**[a]	**Main feeding guild(s)**[a]	**Abundance (ind m^{-2})**	**Biomass (g ww m^{-2})**	**Main TUs**	**Main feeding guild(s)**
A (2)	21 (14/10)	95 (21-170)	0	Holothuroidea	Deposit feeders (58 %)	223 (104-341)	2.4 (1.31-3.50)	Polychaeta	Deposit (44 %) and suspension feeders (31 %)
B (4)	26 (23/19)	11 (2-22)	2.7 (0.0-59.0)	Ophiuroidea	Deposit (38 %) and suspension feeders (37 %)	373 (146-839)	4.6 (2.51-7.40)	Polychaeta	Predators (42 %) and deposit feeders (39 %)
C (1)	25 (11/17)	28	3.4	Ophiuroidea	Deposit (48 %) and suspension feeders (41 %)	1352	50.0	Anthozoa	Predators (74 %)
D (2)	32 (20/29)	114 (82-147)	84.1 (68.3-99.0)	Polychaeta	Deposit (42 %) and suspension feeders (34 %)	2,330 (1,894-2,766)	204.5 (73.44-335.47)	Bryozoa	Suspension feeders (92 %)
E (3)	37 (23/27)	81 (16-123)	46.0 (23.5-64.5)	Ophiuroidea	Suspension feeders (52 %)	3,127 (1,449-4,627)	83.0 (20.43-134.06)	Ophiuroidea	Suspension feeders (46 %)
F (17)	43 (30/27)	60 (4-131)	33.3 (5.3-69.1)	Ophiuroidea	Suspension (45 %) and deposit feeders (35 %)	1,606 (306-4,474)	47.0 (3.70-160.14)	Polychaeta	Suspension feeders (57 %)

[a] Based only abundance on ind m^{-2}

Table. 4: Within group similarities, between group dissimilarities (%), and TUs contribution (%) resulting from the SIMPER analysis of benthic station groups based on seabed image abundances (S) and multibox corer biomasses (M). Marked station group combinations (*) were significantly different ($p < 0.05$) in a pairwise PERMANOVA.

		A	B	C	D	E	F
Within-group similarity		**70.62** Holothuroidea (S) 42.24% Polychaeta (M) 40.14%	**52.20** Polychaeta (M) 54.53%	Only one statoin	**67.84** Bryozoa (S) 32.48% Polychaeta (S) 28.74%	**66.67** Ophiuroidea (M) 18.88% Ophiuroidea (S) 18.06% Porifera (M) 11.93% Tunicata (S) 11.03%	**50.24** Ophiuroidea (S) 35.38% Polychaeta (M) 20.49%
Between-group dissimilarity	**A**						
	B	**61.97*** Holothuroidea (S) 27.14% Bivalvia (M) 8.33% Crustacea (S) 7.78% Anthozoa (M) 7.14%					
	C	**70.55** Anthozoa (M) 26.28% Polychaeta (M) 20.01% Ophiuroidea (M) 16.99%	**73.43** Polychaeta (M) 20.14% Anthozoa (M) 18.52% Ophiuroidea (S) 12.24%				
	D	**84.65*** Bryozoa (S) 18.17% Holothuroidea (S) 16.43% Polychaeta (S) 13.77% Polychaeta (M) 13.76%	**78.61*** Bryozoa (S) 18.29% Bryozoa (M) 16.32% Polychaeta (M) 15.60%	**83.87** Bryozoa (S) 18.18% Anthozoa (M) 18.14% Bryozoa (M) 15.57%			
	E	**82.94*** Holothuroidea (M) 18.08% Polychaeta (M) 12.24% Ophiuroidea (M) 10.82% Ophiuroidea (M) 9.37%	**74.33*** Polychaeta (M) 14.57% Ophiuroidea (M) 11.83% Hydrozoa (S) 8.89% Ophiuroidea (S) 8.12% Porifera (M) 6.61%	**70.93** Anthozoa (M) 21.29% Ophiuroidea (M) 12.32% Holothuroidea (S) 10.72% Hydrozoa (S) 9.49%	**67.39*** Bryozoa (S) 18.88% Polychaeta (S) 15.06% Bryozoa (M) 14.11% Hydrozoa (S) 8.09%		
	F	**74.41*** Holothuroidea (S) 21.14% Ophiuroidea (S) 15.04% Polychaeta (M) 9.05% Bryozoa (S) 7.15%	**63.46*** Ophiuroidea (S) 13.91% Polychaeta (M) 11.89% Bryozoa (S) 7.62% Crustacea (S) 6.69% Porifera (M) 6.67% Anthozoa (M) 6.29%	**66.61*** Anthozoa (M) 23.42% Holothuroidea (S) 11.89% Polychaeta (M) 10.15% Bryozoa (S) 7.93%	**63.90*** Bryozoa (M) 18.12% Bryozoa (S) 14.83% Polychaeta (M) 12.28% Ophiuroidea (S) 1.37%	**56.70*** Ophiuroidea (M) 10.82% Hydrozoa (S) 9.79% Porifera (M) 8.43% Polychaeta (M) 8.32% Bryozoa (S) 7.31% Ophiuroidea (S) 7.03%	

Table. 5: Single and combination of variables "best explaining" distribution patterns of benthic communities.

Single variable (Spearman Rank correlation Rho)	Combination of variables (Spearman Rank correlation Rho)
Water depth (0.264)**	Water depth, near-seabed temperature, gravel cover in SBI (0.278)**
Gravel cover in SBI (0.203)*	Water depth, gravel cover in SBI (0.278)**
Near-seabed Temperature (0.098)	Water depth, gravel cover in SBI, OC inventory (0.277)**
Coarse sediment (%) in sediment column (0.068)	Water depth, near-seabed temperature, gravel cover in SBI, OC inventory (0.277)**
OC inventory (-0.061)	Water depth, summer sea-ice cover, gravel cover in SBI, OC inventory (0.275)**

*= Correlation $p < 0.05$.
**= Correlation $p < 0.01$.

Figures and corresponding captions

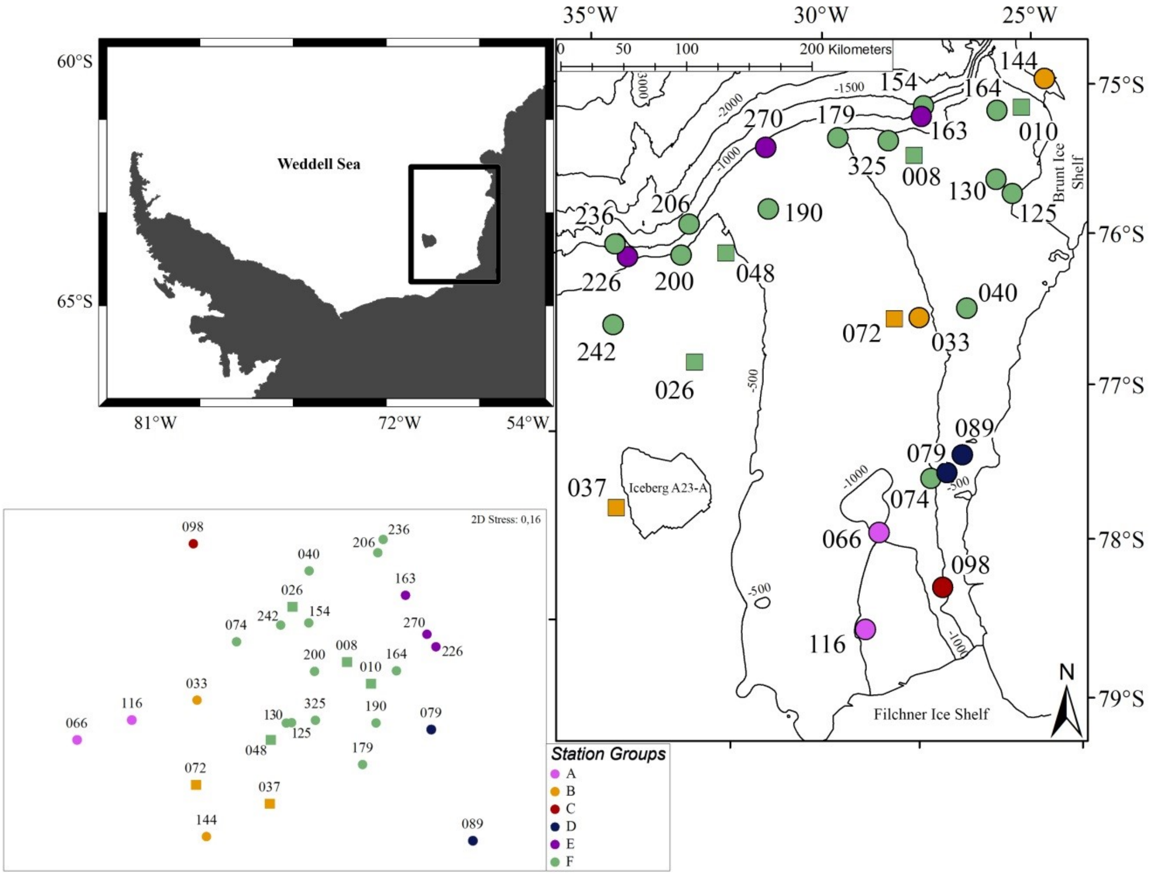

Fig. 1: Locations of stations where multibox corer (MBC) and seabed images (SBI) data were collected in the Filchner Region (Southern Weddell Sea) during R/V *Polarstern* cruises PS82 (circles) and PS96 (squares). Bathymetric data from IBCSO (Arndt et al. 2013). Two-dimensional MDS plot visualizing the among-station resemblance pattern of the benthic fauna identified in MBC and SBI samples collected during R/V *Polarstern* cruises PS82 and PS96. The pattern is based on between-station Bray-Curtis similarities calculated from MBC biomass and SBI abundance data. Grouping obtained from Cluster and SIMPROF analyses and its distribution in the Filchner Region is shown (colors).

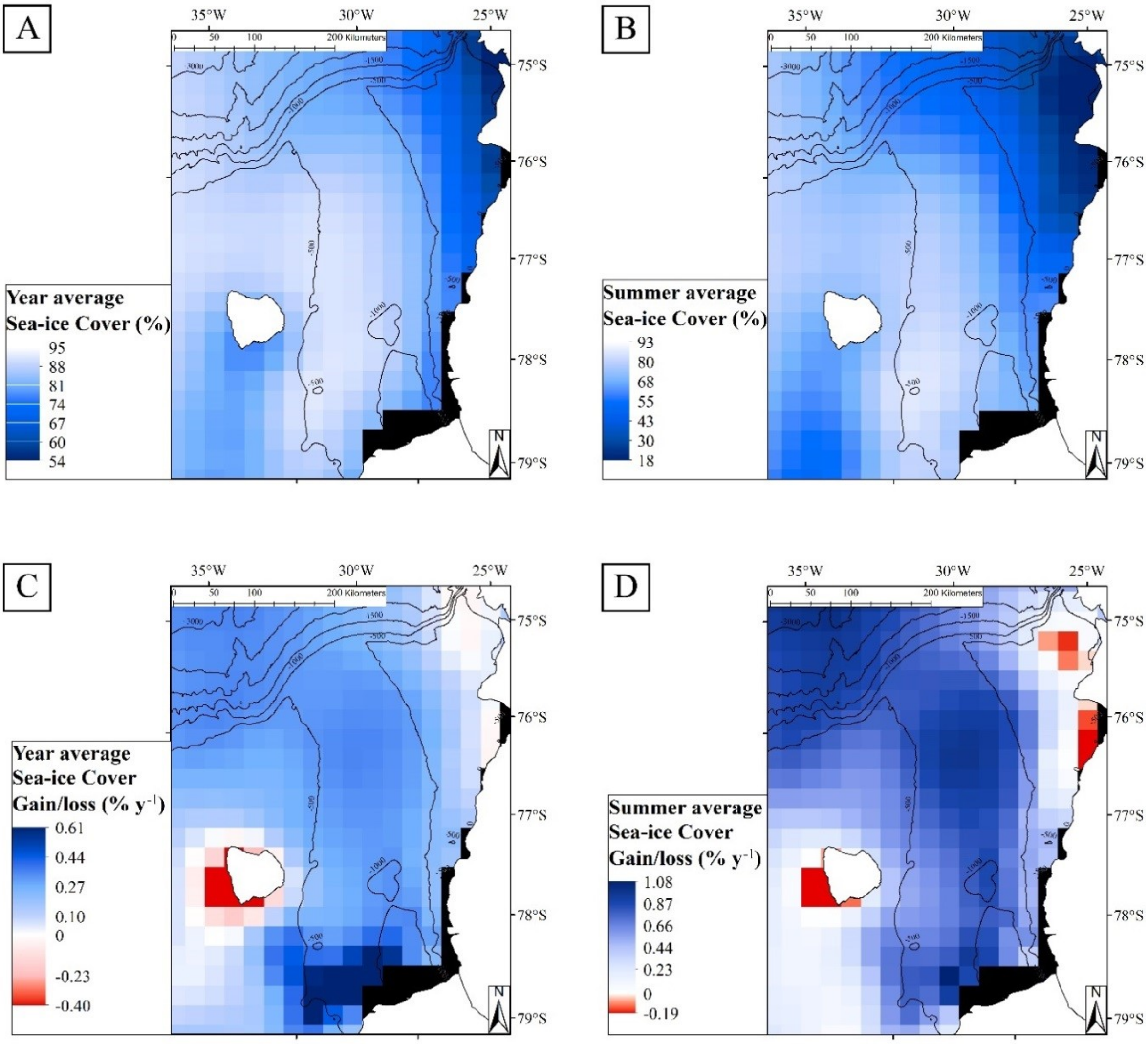

Fig. 2: Year (A) and summer (B) average sea-ice cover, and average year (C) and summer (D) sea-ice cover gain/loss (in % y^{-1}) for the period 1979 to 2017 in the study area in the Filchner Region (Weddell Sea, Antarctica). Year and summer average sea-ice cover was calculated considering values for the period 1979-2017. Note that each plot has its own scale. Modified after Fetterer et al. (2018).

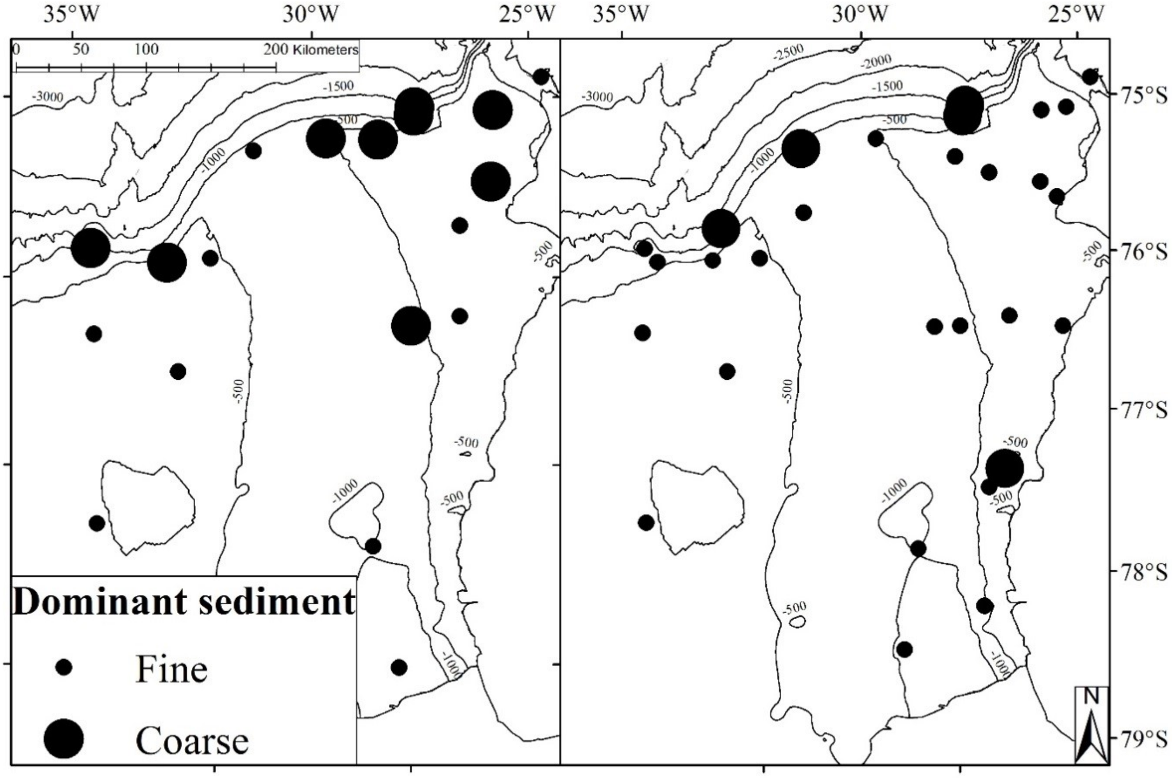

Fig. 3: Dominant sediment in the sediment column calculated from MUC stations (left) and dominant sediment at the seabed surface (derived from SBI) for all stations where mulibox corer and seabed images data were collected (right) in the Filchner Region (Southern Weddell Sea) during R/V *Polarstern* cruise PS82 and PS96.

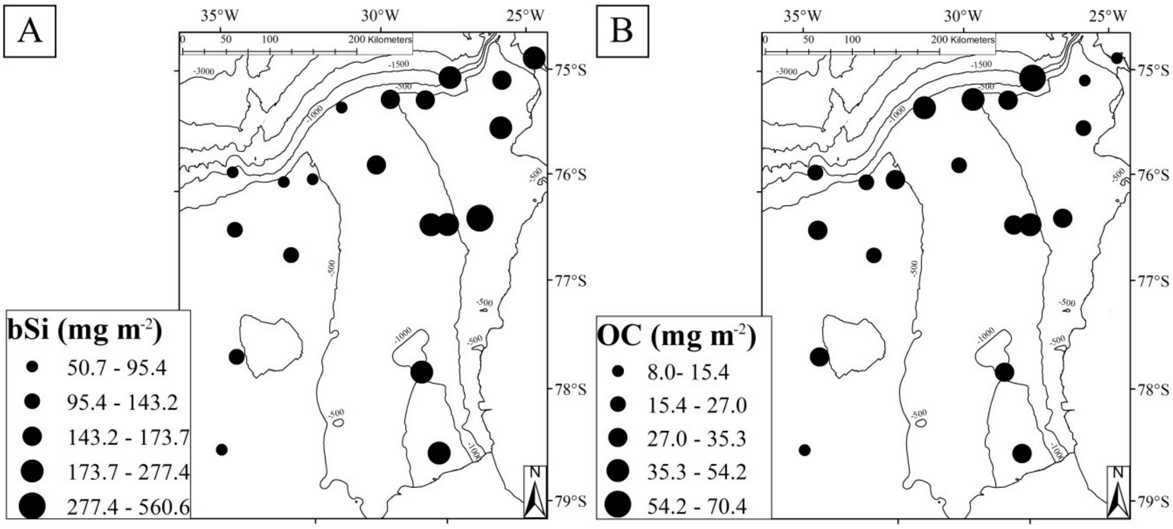

Fig. 4: Biogenic silica (bSi) inventory (A) and Organic carbon (OC) inventory (B) for all stations where mulibox corer and seabed images data were collected in the Filchner Region (Southern Weddell Sea) during R/V *Polarstern* cruise PS82 and PS96. Value breaks are based on the "Natural Breaks (Jenks)" criterion.

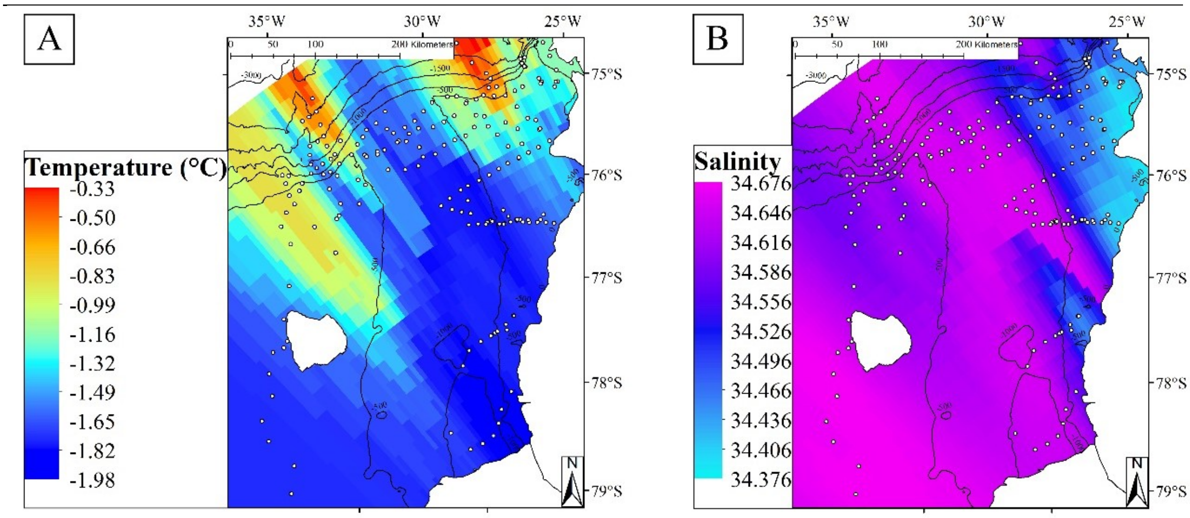

Fig. 5: Near seabed temperature (A) and salinity (B) in the Filchner Region (Southern Weddell Sea) during R/V *Polarstern* cruise PS82 and PS96. Modified from Schröder and & Wisotzki (2014) and Schröder et al (2016). White circles represent CTD cast locations.

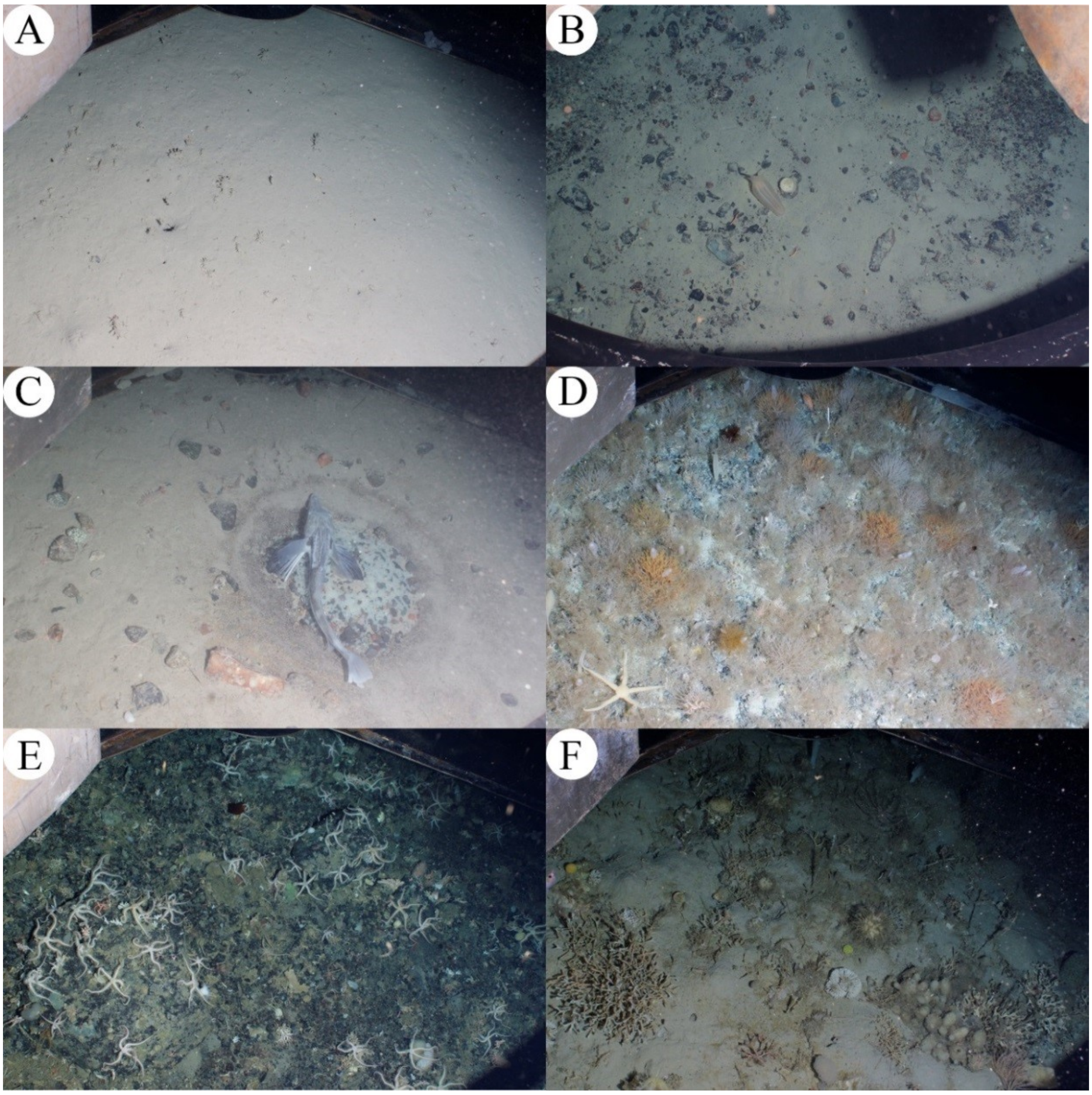

Fig. 6: Seabed images representing the typical appearance of the benthic fauna for all station groups defined by the Cluster and SIMPORF analyses.

MANUSCRIPT 4: Decadal decrease in benthic fauna on a high-Antarctic Weddell Sea shelf

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Decadal decrease in benthic fauna on a high-Antarctic Weddell Sea shelf

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ABSTRACT

The Antarctic seafloor harbours a rich and unique fauna, which has been shown to react locally to benthic disturbance, glacier retreat, and increases in primary productivity due to ice shelf disintegration and iceberg-induced changes in currents. However, the community-scale response of high Antarctic macrobenthos to long-term changes of the environment is so far unknown. Here, we report 26 years of quantitative macrobenthos data from Austasen, a high Antarctic shelf region in the eastern Weddell Sea characterized by long-term increases in sea-ice cover and iceberg frequency. Macrofauna abundances dropped to less than half of the late 1980s values, and macrofauna biomass by more than one order of magnitude, respectively, suggesting that less pelagic food reaches a seafloor community that is more heavily scoured by icebergs. Our findings underscore the importance of long-term observations to monitor the ecological changes in an area particularly vulnerable to future warming and ice-shelf collapse.

KEYWORDS: long-term observations, Antarctica, macrobenthos, climate change, iceberg scour, sea-ice cover, data bases

SHAPED by millions of years of isolation in a freezing environment, Antarctic benthic communities boast unusually high levels of biodiversity and endemism, abundance and biomass (Arntz et al. 1994, Gerdes et al. 1992, Gutt and Starmans 1998, Gutt et al. 2004, 2013). The high latitude entails a highly seasonal primary production and long periods of starvation in response to a spatio-temporally variable sea-ice cover. Although ice-algae are important in sea-ice covered areas, primary production is often eclipsed by snow cover, and most of the carbon flux reaching the seabed is in ice-free areas (Arrigo et al. 2008). Calving events along the numerous glaciers and ice shelves rimming the glaciated continent provide a notorious source of icebergs. With drafts of up to more than 500 m at calving front (Robin et al. 1983) these behemoths wreak havoc on the seafloor (Clarke 1988), as they circle the glaciated continent down to the lower reaches of the deep continental shelf. One of the gates of entry of the highway of icebergs into the Weddell Sea is the Austasen area (Fig. 1; Ranckow 2017), which also happens to be in a region of increasing sea-ice cover (Liu et al. 2004, Turner et al. 2016, Comiso et al. 2017). Located ~81 sm SE of Germany's *Neumayer* overwintering station, this area has been re-visited over a series of eight expeditions with the ice-breaking research vessel *Polarstern* over a period of 26 years. Multiple box core samples, collected, sorted and processed by the same staff provide a unique quantitative data base to explore the long-term effects of changing sea-ice cover and iceberg scouring on high Antarctic macrobenthos communities.

LOSS OF BENTHIC ABUNDANCE AND BIOMASS

Total benthic abundance and biomass, as well as abundance and biomass of major benthic groups decreased during the period 1988-2014 (Fig. 2). These abundance and biomass losses occurred after 1998, a fact we used to differentiate two periods in our time series, a pre-2000 and a post-2000 period.

Total benthic abundances registered almost 2-fold decrease during the post-2000 period, whereas total benthic biomass suffered almost a 4-fold decrease (Fig. 3), making total benthic abundance and biomass, significantly lower for the post-2000 period as compared to the pre-2000 period (p values < 0.05). Major components of the benthos showed similar trends, as well as minor components of the benthic community, represented by "others". Groups such as isopods and ophiuroids which show abundance ratios close to 1, but almost 2-fold biomass decrease (Fig. 3) would evidence some benthic groups to be able to cope with environmental variability at the cost of biomass. Interestingly, while abundance and biomass values decreased, composition remained almost un-altered for all sampling campaigns, especially in terms of abundance (Fig.S1).

INCREASED SEA-ICE COVER AND ICEBERG SCOURING, DECREASED PRODUCTIVITY

Sea-ice cover and scouring (see Methods) significantly increased during the post-2000 period ($p < 0.05$), whereas productivity (see Methods) significantly decreased after 2000 ($p < 0.05$; Fig. 2). This evidences a loss of food input for the benthic realm, related to a decrease of polynya area and duration. An increased scouring implies benthos to be more susceptible to disturbance by icebergs, especially after the year 2000 (Fig. 2).

Increases of sea-ice cover for the eastern Weddell Sea correspond with studies on sea-ice trends in the Southern Ocean. These studies relate the increased sea-ice cover to a strengthening of the Southern Annular Mode (SAM; Liu et al. 2004, Turner et al. 2016, Comiso et al. 2017). The term SAM refers to an alteration of atmospheric mass between mid-latitude surface pressure and high latitudes surface pressure (Gong & Wang 1999). SAM phase shifts regulate sea ice by modifying mean surface heat flux and ice advection (Liu et al. 2004); where positive phases of the SAM resulted in sea-ice increase in the eastern Weddell Sea (Turner et al. 2016). When considering the relation of polynya primary production and sea-ice cover, we could attribute our observed decrease of productivity to observed stronger positive phases of the SAM (Marshall et al. 2019). Pelagic productivity in Antarctica is directly influenced by mean daily photo-synthetically usable radiation, number of ice-free days, ice-free area, sea surface temperature, continental shelf width, and basal melt rate (Arrigo et al. 2015). From these factors, just ice-free days and ice-free area are directly related to sea-ice cover changes, which in turn are regulated by the phases of the SAM.

ENVIRONMENTAL INFLUENCE OVER BENTHIC ABUNDANCE AND BIOMASS LOSSES

We found losses of total benthic abundance to be driven by the increased scouring, whereas losses of total benthic biomass were related to a decrease in productivity (Fig. 4).

The increased scouring observed in the post-2000 period was related to abundance loses of all benthic groups (Fig. 4). This further evidences the negative impact of increased susceptibility of benthos to scouring, and its known devastating effect over benthic biomass (Gutt 2001, Barnes & Souster 2011, Barnes 2017). On the other side, productivity was mainly related to biomass losses, which would further support the hypothesis of Antarctic benthos being food limited (Brey & Clarke 1993). However, exceptions such as amphipods for which the decreased productivity in the post-2000 period should have contributed to abundance and biomass gains, could imply that some benthic groups are better adapted to unfavourable conditions and benefit from ecological space left by other taxa, which are limited by local primary production.

EASTERN WEDDELL SEA VERSUS ANTARCTIC PENINSULA BENTHOS

Studies conducted around the Antarctic Peninsula have linked lower sea-ice cover and collapse of ice-shelves to an increased productivity (Bertolin and Schloss 2009, Barnes 2017). This enhanced productivity has, in turn, been linked to increments in bryozoan and sponge abundance and biomass (Peck et al. 2010, Fillinger et al. 2013, Barnes 2015, Barnes et al. 2018), although this increase still is controlled by giant icebergs (Barnes 2017). The results from our long-term study in the Austasen region also showed a direct link between productivity and benthic abundance and biomass. We assume a clear productivity loss after the year 2000, which we link to benthic abundance and biomass loss. This also holds true for bryozoan biomass, which has been proposed to have increased in recent years in the Weddell Sea (Barnes 2015). Furthermore, we also relate benthic abundance loss to an increased scouring in Austasen after the year 2000, thus, to a possible increased susceptibility of benthos to iceberg scour. Our 26-year study shows benthos in the Austasen region to be negatively affected by ongoing climate change, contrasting the situation described for the Antarctic Peninsula (Peck et al. 2010, Fillinger et al. 2013, Barnes 2015, Barnes et al. 2018).

AUSTASEN BENTHOS: PRESENT AND FUTURE

We found benthos to be negatively affected by climatic variations during our 26-year study period with abundance and biomass losses at community and taxonomic unit level. These losses were mainly due to decreased productivity, increased sea-ice cover, and scouring. Based on our statistical results and findings in the Antarctic Peninsula (Peck et al. 2010, Fillinger et al. 2013, Barnes 2015, Barnes et al. 2018), we could assume benthos in the eastern Weddell Sea to benefit from the predicted decrease of sea-ice cover (Timmermann and Hellmer 2013). Such a decrease would imply an increased productivity. We therefore could expect abundance and biomass increments by the end of the century, thus supporting the idea of Antarctic shelves as carbon sinks and negative feedbacks to climate change (e.g. Peck et al. 2010, Barnes 2015, Barnes et al. 2018). However, before drawing further conclusions we need to consider physiological constrains in Antarctic benthos affected by increasing temperature. Most Antarctic benthic species appear stenothermal with narrow thermal windows of just few degrees (Peck 2002, 2005, 2014, Pörtner et al. 2007). Predictions suggest near-seabed temperature to rise up to 0°C (Hellmer et al. 2017), a temperature proposed to greatly decrease or fully stop biological functions of some taxa, e.g. bivalves and asteroids (Peck 2002, 2005, Brandt 2005, Peck et al. 2014). Finally, although our simple approach lacks the complexity of modern modelling tools, it provides baseline data and indices to be considered in future sampling strategies and modelling approaches.

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ON-LINE ONLY METHODS

QUANTIFICATION AND STATISTICAL ANALYSIS

Except for the benthic data (see below), all other data used for our analyses were obtained from the National Sea Ice Data Center data repository (sea-ice cover; Fetterer et al. 2018), the OceanColor web data repository (Chl *a* and particulate organic carbon; NASA 2018a-d), Solar Geometry Calculator of the National Oceanic and Atmospheric Administration (NOAA 2018), ALTIBERG Iceberg data base (Tournadre et al. 2016), and the Antarctic Iceberg Tracking Database (Budge and Long 2018).

The area corresponding to the Austasen region, which was used as boundary for sample selection and extrapolation of environmental data (Fig.1), was drawn as a polygon shapefile using the ArcGIS 10.4 software. We based the boundaries of the Austasen polygon on previous studies conducted there (e.g. Gerdes et al. 2003, Isla et al. 2009), and used the International Bathymetric Chart of the Southern Ocean (IBCSO; Arndt et al. 2013) as reference to only include the shelf area down to 1000m depth. The approximate area of this polygon was 9180 km^2.

All statistical tests mentioned below were done using the StatView and SigmaPlot 12 softwares. Figures were done using the OriginPro 8, RStudio, and ArcGIS 10.4.

BENTHIC ABUNDANCE AND BIOMASS DATA

Benthic total abundance and biomass, and abundance and biomass data of 35 benthic taxa corresponds to stations of the *R/V* Polarstern cruises ANT-VI/3, VII/4, XIII/3, XV/3, XVII/3, XXI/2, XXVII and PS82 (Fütterer 1988, Arntz et al. 1990, Arntz and Gutt 1997, 1999, Arntz and Brey 2001, 2005, Knust et al. 2012, Knust and Schröder 2014), which represent years 1988, 1989, 1996, 1998, 2000, 2004, 2011, and 2014, respectively. Only shelf stations were selected, i.e. all those stations located within 100-700 m depth, based on the definition of Antarctic shelf given by Gallardo (1987), Arntz et al. (1994), and Smith et al. (2006). Furthermore, we also excluded stations located in the long-term "BEnthic Disturbance Experiment" (BENDEX) study area (Gerdes et al. 2008). Under these criteria, a total of 71 stations sampled by a multibox corer (Gerdes 1990) were considered (Table S2). From these, whenever possible, we extracted data of each box recovered. In total, our database consisted of 337 cores from 63 stations. Only for the year 2000 no data for each box recovered were available, we instead used the average station values at 8 sampled stations (Table S2).

The locations of each station were imported as a single multipoint shapefile to the GIS environment using ArcGIS 10.4. This shapefile was used to extract environmental data from all environmental raster for each station. Extraction of environmental data was done with the "Extract multi value to point" tool of ArcGIS 10.4.

ENVIRONMENTAL DATA AND TREATMENT

Daily sea-ice cover (SIC) from the "Sea ice Index" provided by the National Snow and Ice Data Center (NSIDC) was extracted for the summer months of the period 1987-2014 (Fetterer et al. 2018). We considered as summer months the period November to March, which represent the months when the local polynya is open (Arrigo et al. 2015). The daily SIC data were used to calculate summer ice-free days and percentage of ice-free area in summer for the Austasen polygon. Additionally, data from the Solar Geometry Calculator of the National Oceanic and Atmospheric Administration (NOAA 2018) were used to calculate percentage of the day with sun light during summer for the period 1987-2014.

Sea-ice and solar data were used to calculate a summer productivity index, referred in the main text as “productivity”. Arrigo et al. (2015) found polynya productivity to be directly related to mean daily photo-synthetically usable radiation, number of ice-free days, ice-free area, sea surface temperature, continental shelf width, and basal melt rate. Based on this, we calculated the productivity for the 1987-2014 period as the product of ice-free days, percentage of the day with sun light, and percentage ice-free area.

To test if the calculated productivity works as a proxy for Chl *a* and particulate organic carbon concentration, we correlated productivity with summer Chl *a* and particulate organic carbon data obtained from the NASA Ocean Color web (NASA 2018a-d) and Arrigo et al. (2008). The correlations had coefficients > 0.7, thus we assumed our calculated productivity to correctly represent Chl *a* and particulate organic carbon variations. Productivity values were then extracted for each multibox corer station.

Data on the area covered by giant icebergs passing within the Austasen polygon and average area covered by small icebergs were used to calculate a scouring index, referred as “scouring” in the main text. Scouring consists in the sum of the fourth root transformed area of giant and small icebergs. Both areas were fourth root transformed to reduce the magnitude of differences between areas, which were 4 to 6 orders of magnitude, and to amplify the effect of small icebergs, which are more numerous than the giants (Tournadre et al. 2016). Scouring represents the seabed area in km^2 which can be potentially affected by icebergs, hence, a proxy for benthic susceptibility to be disturbed by an iceberg scour.

STATISTICAL ANALYSIS

Values for each box considered as well as year and station averages were plotted (Fig.2). Based on these plots we grouped all sampling years into a pre-2000 and a post-2000 period. This grouping was also applied for environmental data. To test for significant differences between periods, a Mann-Whitney U test including all benthic data was conducted for total benthic abundance and biomass. Further Mann-Whitney U tests were calculated to test for between period differences in terms of sea-ice cover, productivity and scouring.

Benthic data from all boxes was used to calculate total abundance and biomass ratios, as well as abundance and biomass ratios for all taxonomic units. For colonial (e.g. bryozoans and hydrozoans) and large macrobenthic organisms (e.g. glass sponges) abundance data were available only as presence/absence data. Before calculating all ratios, benthic taxa with low occurrence (i.e. many values = 0) were grouped in the category “Others”. This category of minor benthic groups included: hydrozoans, anthozoans, brachiopods, sipuncunculids, nemerteans, priapulids, flat worms, gastropods, polyplacophors, aplacophors, scaphopods, clitellate worms, echiurids, acari, cumaceans, harpacticoid copepods, barnacles, tanaids, ostracods, unidentified crustaceans, echinoids, holothurians, asteroids, crinoids, hemichordates, ascidians, and unidentified organisms.

Abundance and biomass ratios were calculated considering all cores and every possible post-2000 / pre-2000 combination (i.e. 2000/1988; 2000/1989; 2000/1996; 2000/1998; 2004/1988; 2004/1989; 2004/1996; 2004/1998; 2011/1988; 2011/1989; 2011/1996; 2011/1998; 2014/1988; 2014/1989; 2014/1996; 2014/1998). These ratios were log transformed and used in a one-sample t-test to look for siginifcant differences between the mean of ratios and 0. Means significantly < 0 would imply abundance or biomass losses in the post-2000 period, whereas means significantly > 0 would imply the opposite. Means were then back transformed to calculate abundance and biomass gains/losses.

To estimate the influence of each environmental variable on benthic abundance and biomass, data of all cores were first fourth root transformed to reduce the influence of outliers. Once transformed, Pearson correlation coefficients were calculated to test significant influence of depth, sea-ice cover, productivity, and scouring on benthic total abundance and biomass, and of that of the taxonomic units. Negative coefficients named "reduced" would imply a reduction of benthic abundance and biomass, e.g. higher sea-ice cover, lower abundance. Positive coefficients were named "increased" and imply an increase of benthic abundance and biomass, e.g. higher productivity, higher biomass. Results of the correlation analyses were introduced in Fig. 4.

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Figures and corresponding captions

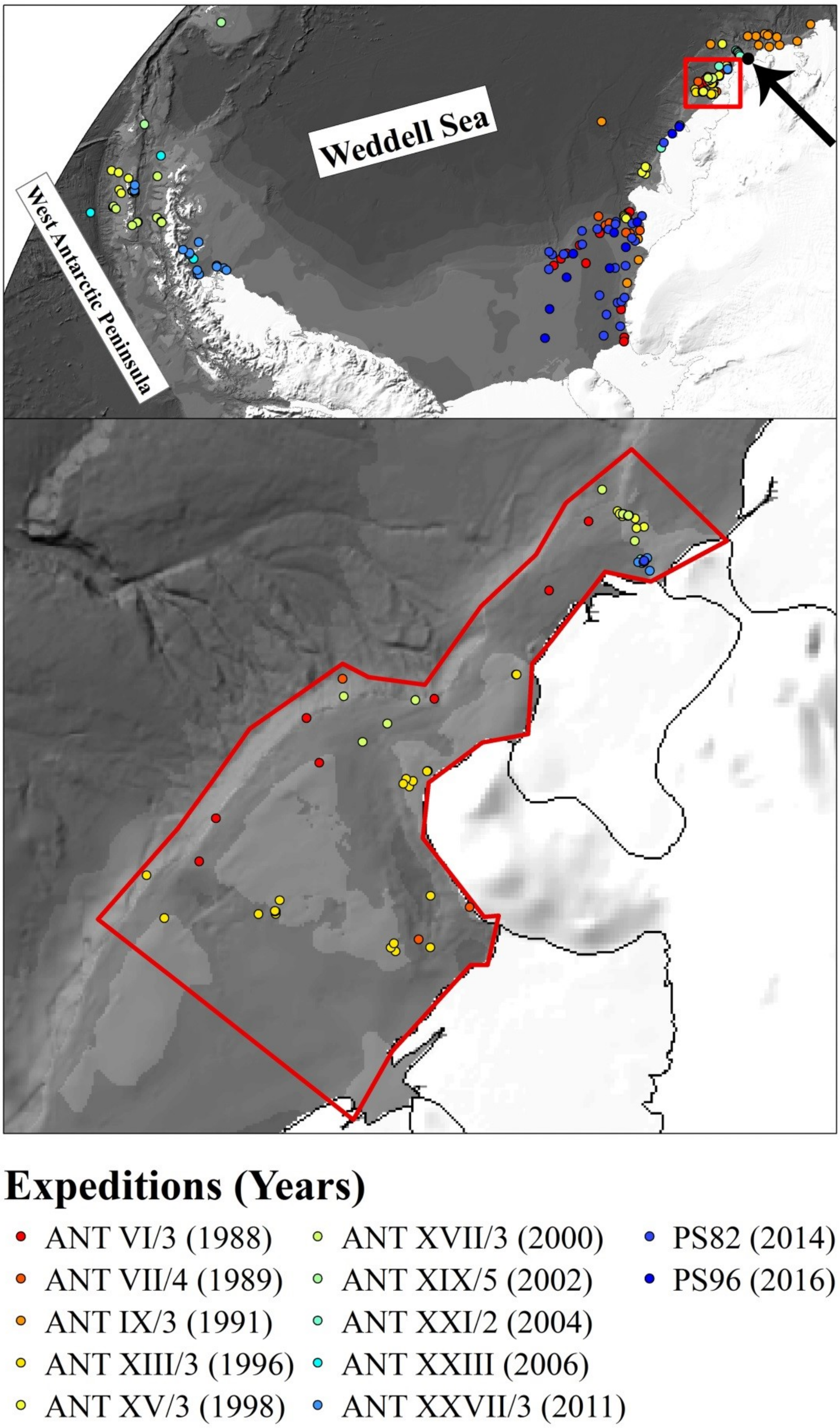


Fig. 1 Multibox-corer stations sampled in the Weddell Sea (above) and on the shelf off Austasen (below) between 1988 and 2014. Bathymetric chart modified after Arndt et al. (2013). Black arrow and point mark the location of Germany's *Neumayer III* overwintering station.

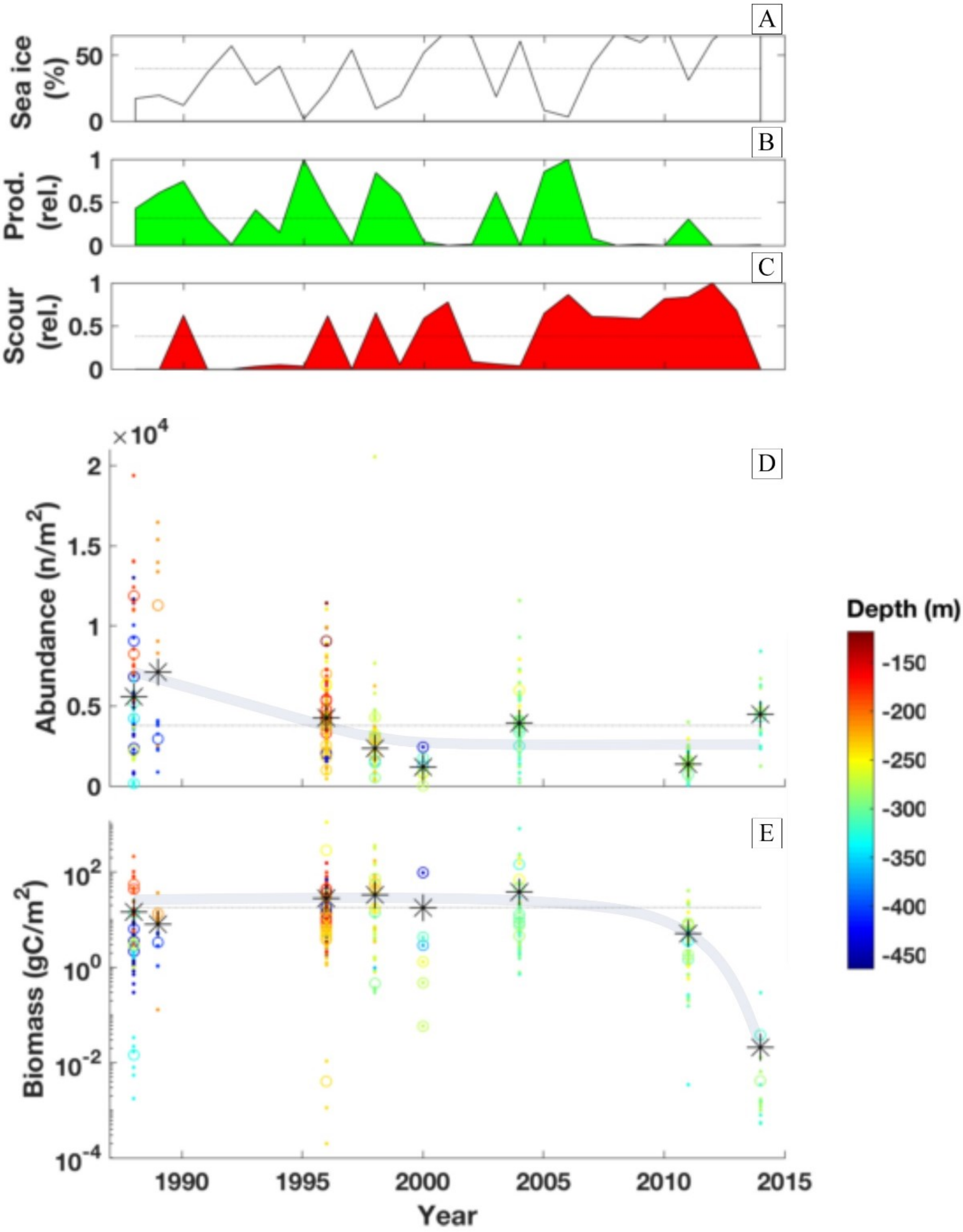


Fig. 2 Sea-ice cover (A), productivity (B), scouring (C), and benthic abundance (D) and biomass (E, in semilog scale) for the time period 1988-2014. Benthic abundance and biomass are represented as annual means (stars), stations means (circles) and for each core (dots). Dotted horizontal lines represent the mean over the 26-year study period.

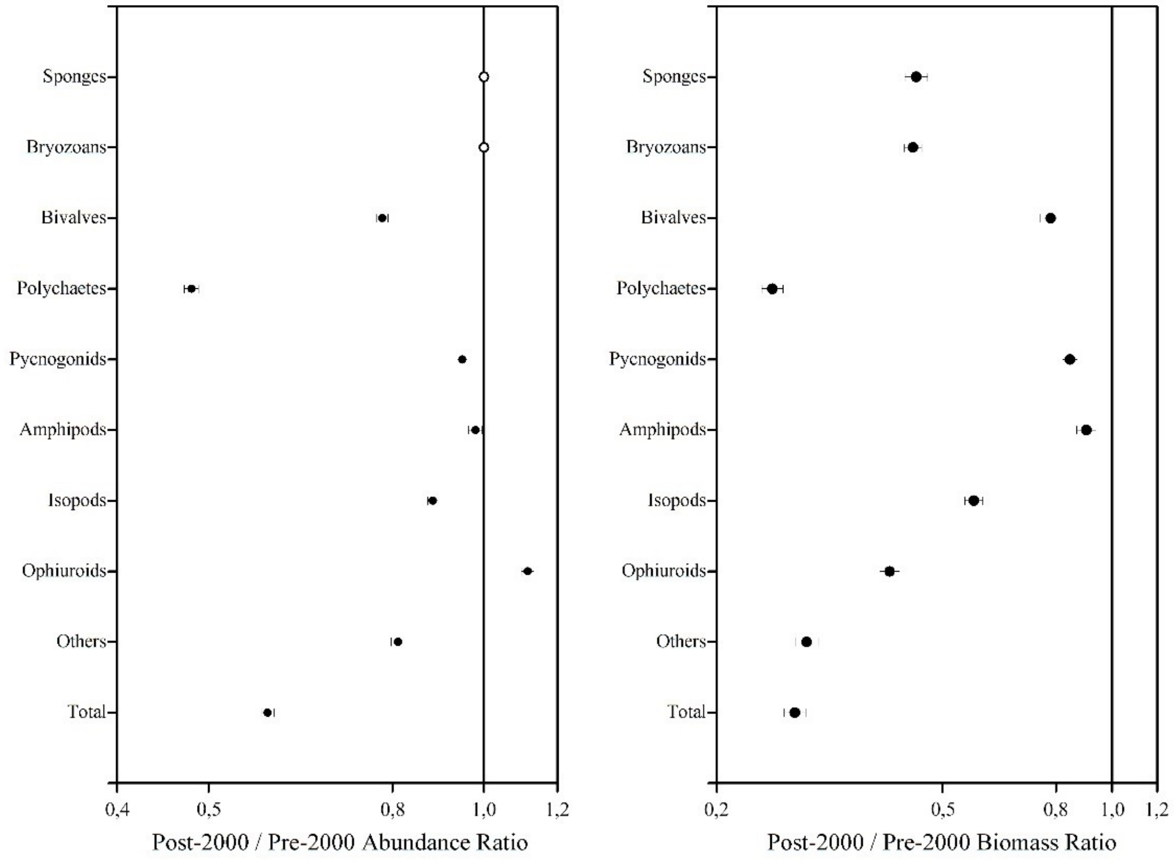
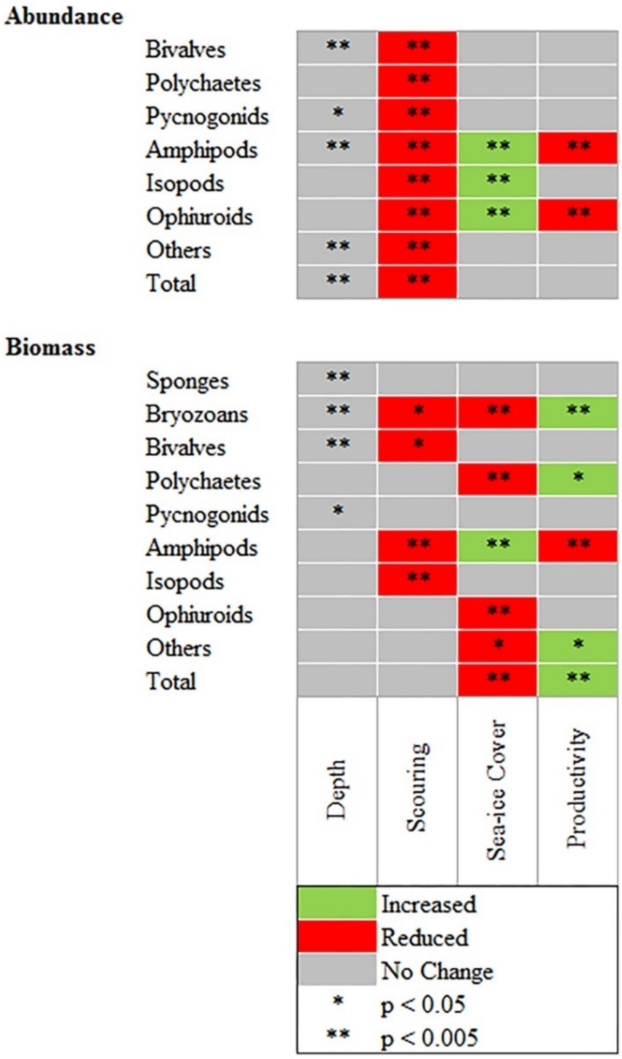


Fig. 3 Post-2000 / Pre-2000 ratios for total benthic abundance and biomass, and abundance and biomass of major components of the benthic community on the shelf off Austasen, eastern Weddell Sea. Lines represent 95% confidence intervals. Filled circles correspond to ratios significantly different from 1 ($p < 0.05$). “Others” includes minor benthic groups (see Method section).



	Depth	Scouring	Sea-ice Cover	Productivity
Abundance				
Bivalves	▨ **	🟥 **	▨	▨
Polychaetes	▨	🟥 **	▨	▨
Pycnogonids	▨ *	🟥 **	▨	▨
Amphipods	▨ **	🟥 **	🟩 **	🟥 **
Isopods	▨	🟥 **	🟩 **	▨
Ophiuroids	▨	🟥 **	🟩 **	🟥 **
Others	▨ **	🟥 **	▨	▨
Total	▨ **	🟥 **	▨	▨
Biomass				
Sponges	▨ **	▨	▨	▨
Bryozoans	▨ **	🟥 *	🟥 **	🟩 **
Bivalves	▨ **	🟥 *	▨	▨
Polychaetes	▨	▨	🟥 **	🟩 *
Pycnogonids	▨ *	▨	▨	▨
Amphipods	▨	🟥 **	🟩 **	🟥 **
Isopods	▨	🟥 **	▨	▨
Ophiuroids	▨	▨	🟥 **	▨
Others	▨	▨	🟥 *	🟩 *
Total	▨	▨	🟥 **	🟩 **

🟩	Increased
🟥	Reduced
▨	No Change
*	$p < 0.05$
**	$p < 0.005$

Fig. 4 Influence of depth, scouring, sea-ice cover, and productivity on total benthic abundance and biomass, and abundance and biomass of major benthic taxa. "Others" includes minor benthic groups (see Method section).

GENERAL DISCUSSION

This thesis is based on the most comprehensive data set of benthos living on the high-Antarctic Weddell Sea shelf. Continuous research on benthos has been carried out in the Weddell Sea since the 1980s. The regional focus of the macrobenthos surveys was the shelf of the eastern Weddell Sea in the vicinity of the German research station *Neumayer III* but also the heavily sea-ice covered south was sampled at an early stage (e.g. Voß 1988). Recently, the areas of disintegrating Larsen A and Larsen B ice shelves off the tip of the Antarctic Peninsula in the western Weddell Sea were included into the research program (e.g. Gutt et al. 2011, 2013b, Sañé et al. 2011, 2012, Fillinger et al. 2013). Benthic studies in the Weddell Sea also included long-term studies such as the BENthic Disturbance EXperiment (BENDEX; Gerdes et al. 2008), which was initiated off Austasen in order to simulate the impact of grounding icebergs on the seabed and follow the stages and time scales of recovery of disturbed benthos and demersal fish communities. Benthic data included in this thesis were collected on 12 research cruises of RV *Polarstern* between 1988 and 2016. All campaigns were accompanied by intensive oceanographic studies via CTD measurements and numerous moorings. The manuscripts within this thesis include data of > 200 biological stations (Gerdes 2014a-n, Knust and Schröder 2014, Schröder 2016): 35 seabed imagery stations in the Filchner Region, and 175 multibox corer stations from the Filchner Region (66), tip of the Antarctic Peninsula (15), the shelf formerly cover by the Larsen A and B ice-shelves (21), and the eastern Weddell Sea (73).

Based on this benthic data base and descriptions on the Antarctic environment (e.g. Constable et al. 2014, Gutt et al. 2015, Turner et al. 2016, Comiso et al. 2017) I divided the Weddell Sea into three sub-regions: a) the western Weddell Sea, also including the tip of the Antarctic Peninsula influenced by water masses of the Weddell Sea, b) the southern Weddell Sea, and c) the eastern Weddell Sea (Fig.1). The shelves of these sub-regions represent an area of approximately ~849,000 km^2. They are comparatively deep, with a mean depth of 500 m (Haid 2013) and a shelf break two to four times deeper than elsewhere in the oceans (Knox 2007), as a result of the isostatic pressure generated by the continental ice cap covering Antarctica (Smith et al 2006).

The four manuscripts this thesis is based on consider complementing approaches to investigate the seabed fauna of the eastern and southern Weddell Sea sub-regions under different aspects. Manuscript 1 focuses on comparing two benthic sampling methods, corer sampling and seabed imaging (SBI), and demonstrated the huge advantages of using them in parallel. This approach was shown to be a time-efficient way to study benthic communities by adequately targeting both the infauna and the epifauna, respectively. Manuscript 2 combines publicly available benthic and pelagic data on biotic and abiotic components of both realms, to comparatively investigate bentho-pelagic coupling looks like in the eastern Weddell Sea and off the northern Antarctic Peninsula. Based on these studies, Weddell Sea benthic communities were researched on spatial (Manuscript 3) and temporal scales (Manuscript 4).

Manuscript 3 deals with the diverse and heterogeneous infaunal- and epifaunal benthos of the Filchner Region in the southern Weddell Sea. It reports changes since this area was last investigated in the late 1980s and early 1990s, as well as investigates how similar the benthos of this region is to that of other sub-regions of the Weddell Sea. This comparison aimed to understand between-region differences in terms of benthic characteristics, for which data from the shelf formerly covered by the Larsen Ice Shelf, the east of the Antarctic Peninsula in the western Weddell Sea, and the southeastern Weddell Sea shelf were included. Finally, Manuscript 4 describes the past and present of benthos off Austasen in the eastern Weddell Sea, and includes bentho-pelagic coupling concepts to link benthic changes to environmental variation, to estimate how the future of benthos in this high-Antarctic region may look like.

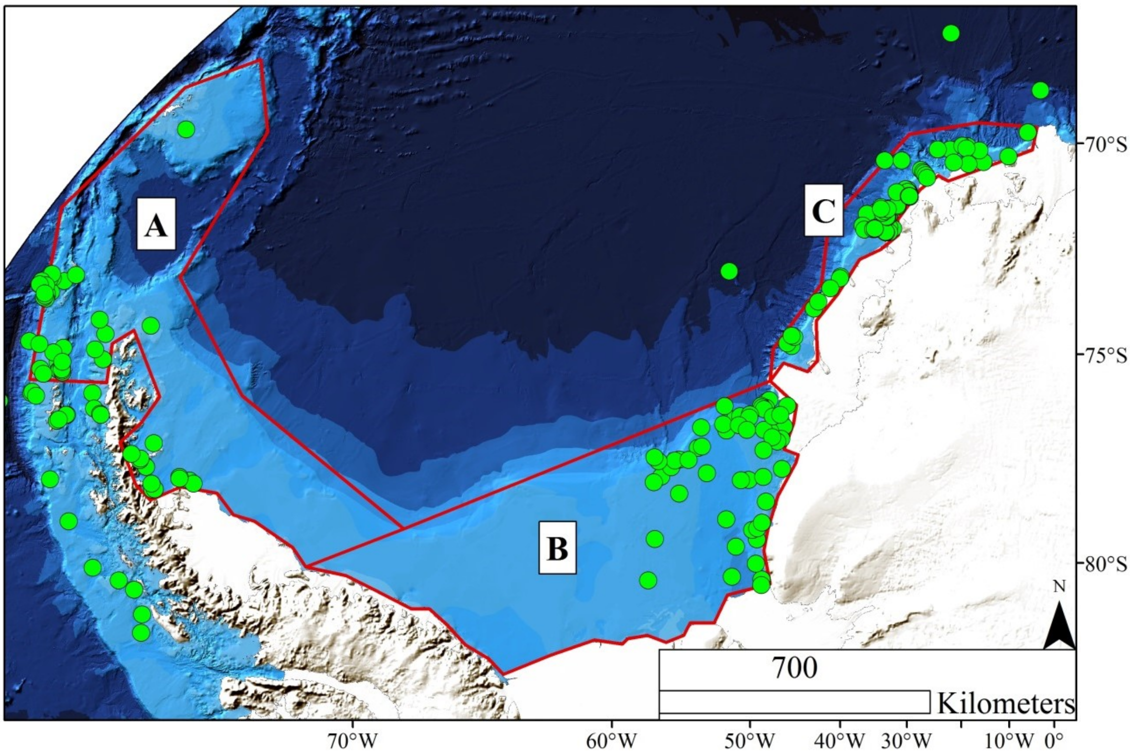


Fig.1. Schematic map of the Weddell Sea showing the locations of all multibox samples obtained on during RV *Polarstern* cruises between 1988 and 2016. Red polygons represent the western (A), southern (B) and eastern (C) Weddell Sea sub-regions.

In the Weddell Sea, extensive benthic studies started in the 1980s with the first icebreaker-based expeditions (e.g. Voß 1988, Gerdes et al. 1992, Gutt and Starmans 1998). The benthic research conducted during these expeditions (and even in the course of most recent ones) proved right the statement made by Arntz et al. (1994): *"Benthologists are comparatively conservative in their methods"*. This is clearly demonstrated in various RV *Polarstern* cruise reports (e.g. Fütterer 1988, Arntz et al. 1990, Arntz and Gutt 1997, 1999, Arntz and Brey 2001, 2005, Knust et al. 2012, Knust and Schröder 2014), since in all these cruises, Antarctic benthos was studied quantitatively by means of coring and SBI. However, data from these two methods were rarely combined in order to achieve a more comprehensive benthic analysis, the studies were focused on either infaunal- (corer data) or epifaunal benthos (SBI data).

The recurrent use of the same methodological approach allows for benthic comparisons in space and time, such as the BENDEX studies (Gerdes et al. 2008) that followed the recolonization of benthos in an area artificially disturbed, long-term studies on bryozoan populations in waters of the Antarctic Peninsula and around sub-Antarctic Islands (Barnes 2015), studies of the sponge-dominated community in McMurdo Sound, Ross Sea (Dayton et al. 1989), and the benthic study reported in Manuscript 4.

It is commonly acknowledged that infaunal- and epifaunal benthos should both be considered to comprehensively study the entire benthic community, since these two community fractions represent “two sides of the same coin”, with both sides having their own “truth” and together forming the “coin” as a whole. Corers and SBI are two “typical” methods used to study Antarctic benthos (e.g. Gerdes et al. 1992, 2008, Gutt and Starmans 1998, Gutt et al. 2011, Sañé et al. 2012, Fillinger et al. 2013, Segelken-Voigt et al. 2016). However, both are seldom studied together by parallel SBI and corer deployments, as done e.g. by Piepenburg et al. (2002). The concomitant use of corers and SBI in Manuscript 1 showed infaunal- and epifaunal benthic abundances to be orders of magnitude different, and to be dominated by different taxonomic units. This suggests the need of further studies including both approaches, in order to better understand how infauna and epifauna contribute to a benthic community. The complementary nature of corer samples and seabed images for benthic studies is a widely accepted concept but hardly applied on board research vessels, due to deployment time constrains. The combined use of corer and camera on one gear was shown to be a meaningful and practical method to study benthic fauna with all its compartments (Manuscript 1). Combining both data sets into one file for further statistical analyses of benthic distribution patterns, allowed for a more comprehensive description of benthic community distribution (Manuscript 3).

To understand benthic spatial patterns and temporal dynamics we need also to take water-column processes into account. This is especially true, when considering that the benthic habitats are inherently coupled to the pelagic realm. Pelagic productivity is directly reflected in benthic characteristics (e.g. Barnes et al. 2016, Manuscript 4). Manuscript 2 explores this relationship by including and combining available benthic and pelagic data from the Weddell Sea and other Southern Ocean regions.

The benthos of the eastern Weddell Sea has been described as being dominated by sponges (e.g. Barthel 1992, Barthel and Gutt 1992, Gerdes et al. 1992, Arntz et al. 1994, Gutt and Starmans 1998, Sañé et al. 2012). Sponge aggregations and their spicule mats provide a three-dimensional habitat which facilitates higher levels of diversity, biomass and abundance than on other Southern Ocean shelves (Barthel 1992, Barthel and Gutt 1992, Gerdes et al. 1992, Arntz et al. 1997, Gutt et al. 2013a). The sponge-dominated benthic communities are most likely supported by a relatively fast downward flux of highly nutritive particles (Bathmann et al. 1991, Isla et al. 2009, 2011). The situation in the eastern Weddell Sea is the situation for benthic organisms living on the shelf formerly covered by the Larsen A and Larsen B ice shelves in the western Weddell Sea. After the collapse of the ice shelves in 1995 (Larsen A) and 2002 (Larsen B), the region was abruptly subjected to a seasonal sea-ice regime and increased local primary productivity (Bertolin and Schloss 2009), which resulted in an increase of benthic abundance and biomass within a relatively short 3-year period (Gutt et al. 2013b, Fillinger et al. 2013).

The above-mentioned examples (included in Manuscript 2) provide ample evidence for the need to incorporate benthic abiotic parameters, as well as pelagic abiotic and biotic variables, in benthic ecological studies. By considering pelagic parameters such as Chl *a*, particulate organic carbon, sea-ice cover, persistence, and duration, presence of icebergs, temperature, and water currents, we can relate these to benthic characteristics in both space and time. On a spatial scale, these environmental factors are to be considered to understand why benthic communities are different among locations/regions (as done in Manuscript 3). On a temporal scale, coupling environmental and benthic dynamics could help shed light on how the benthic communities have been shaped, and how their future could look like (see Manuscript 4). However, understanding benthic changes in long-term studies requires understanding how “quickly” or “slowly” benthos responds to environmental variations. This fact has recently raised some discussion. Temperature, for instance, is an abiotic key factor for the development of organisms. It has a strong influence on metabolic rates, larval development and oxygen availability, among other factors, which control the organism performance and success and limit their distribution (e.g. Gillooly et al. 2001, O’Connor et al. 2007, Pörtner et al. 2007, Peck 2018). Low temperatures are proposed to induce slow reactions of Antarctic benthos (Peck 2002, 2005, 2014, Pörtner et al. 2007), but recolonization studies in the eastern Weddell Sea and benthic studies in the Larsen area have proven that some benthic taxa (e.g. sponges) developed quicker than formerly thought (Gerdes et al. 2008, Gutt et al. 2013b, Fillinger et al. 2013). Thus, understanding benthic reaction times could prove a challenge, which could allow a better understanding of the fate of Antarctic benthos.

Understanding pelagic processes and their influence on seabed systems is key to understand benthic dynamics. However, sampling and methodological constraints limit the quality and quantity of data that can be obtained during time-limited expeditions or via remote-sensing tools. Thus, the development of environmental indices, whenever data is unavailable, is essential. To cope with lack of data obtained in-situ or via satellite, I developed two indices (see Manuscript 4) which work as proxies for factors which directly influence benthic abundance and biomass (i.e. food input and disturbance), and can be easily calculated by using publicly available satellite data (see Tournadre et al. 2016, Fetterer et al. 2018, Budge and Long 2018). One is a “productivity index” calculated from ice-free days and ice-free area, as well as days with sun light, considered as a proxy for primary production, and the other, a “scouring index” calculated from the area of giant and small icebergs, considered as a proxy for the potential seabed area impacted by iceberg scouring.

These methodological considerations and bentho-pelagic concepts are included in each manuscript to tackle specific questions (see General Introduction). Most questions regard benthic spatial distribution and temporal variation, as well as to point out environmental parameters which drive benthic variability. If we were to condense the answers found by the four manuscripts, we would end up with two main aspects: the spatial and the temporal. When considering the spatial scales in the Weddell Sea, a general question would be*: how dis/similar are the benthic communities inhabiting the three sub-regions of the Weddell Sea?* This question can be tackled after having updated our knowledge on benthic spatial distribution in the Filchner Region in the southern Weddell Sea. On the other side, when considering the temporal scales, the general question would be: *how has benthos reacted to the observed environmental variation?* To answer this, we can consider benthic studies in all three sub-regions of the Weddell Sea, and include the benthic studies performed by e.g. Fillinger et al. (2013) and Barnes (2015) in the western Weddell Sea. However, to answer these questions we also need to include diverse environmental variables which affect benthos directly (e.g. icebergs, temperature) and indirectly (e.g. sea-ice cover), and modify its distribution as well as abundance, biomass, and composition. By answering these two general questions and transition from the past to the present, we can start making predictions on what could happen to benthos in the future.

SPATIAL SCALES OF WEDDELL SEA BENTHIC COMMUNITIES

Benthic studies in the eastern and southern Weddell Sea defined three community types (Voß 1988, Gerdes et al. 1992, Gutt and Starmans 1998): a) an Eastern Shelf community, b) a Southern Shelf community, c) a Southern Trench community. Recently, Gutt (2007; updated by Turner et al. 2009) modified this concept and defined three large biological associations for the entire Southern Ocean shelves based on dominating feeding guilds: a) a sessile suspension feeder community with associated fauna, b) a mobile deposit feeders, infauna and grazers dominated fauna community, and c) a “mixed assemblage”, composed of a combination of the two larger communities.

All three benthic communities *sensu* Voß (1988) were also found in the Filchner Region. However, the spatial distribution range of the Eastern Shelf and Southern Trench communities was slightly different. The distribution of the Eastern Shelf community expanded from its original position and now also includes parts of the western shelf of the Filchner Region, whereas the distribution of the Southern Trench community now appears restricted to the deeper parts of the Filchner Trough (Annex 1 Fig.S3). The Southern Shelf community seems to have shifted its distribution towards the southern end of the shelf east of the Filchner Trough (Annex 1 Fig.S3). Despite these shifts, the communities described by Voß (1988), as well as the clusters found by Gerdes et al. (1992) and Gutt and Starmans (1988), maintain their original composition characteristics. The observed abundance and biomass decrease, likely related to observed sea-ice cover increments in the last decades, will be discussed in more detail in the next section.

Additionally to the previously described “old” communities, two new were found: 1) the Ice/Ice Shelf Water (ISW) related community situated in proximities of the Brunt Ice Shelf and the giant iceberg A23-A. This community was also found in the Filchner Trough, where ISW, originated on the Berkner Bank, flows (Annex Fig.S4). 2) Another new community, defined as the Continental Slope Community, distributed along the northern slope of the Filchner Region, where Warm Deep Water (WDW) from the Weddell Gyre flows. While the Ice/ISW related community was found in areas previously “occupied” by the Southern Trench community, the Continental Slope community overlaps with the Eastern Shelf community.

The spatial distribution found in the Filchner Region was poorly explained by environmental parameters typically considered in benthic studies (e.g. Gutt and Starmans

1998, Ellingsen et al. 2007, Saiz et al. 2008, Cummings et al. 2010, Segelken-Voigt et al. 2016). However, each benthic community in the Filchner Region appeared tightly related to water mass circulation patterns:

- The “Eastern Shelf community” distributed along the eastern shelf under the influence of modified WDW, and also on the shelf west of the trough;
- The “Southern Shelf community” was found at the southern end of the shelf east of the Filchner Trough, close to where modified WDW enters a heavy sea-ice covered area before flowing into the trough;
- The “Southern Trench community” distributed in the deepest parts of the Filchner Trough, where the densest ISW leaves the Filchner-Rønne shelf cavity;
- The “Ice/ISW related community” was found, where less dense ISW flows, and in proximities of ice bodies large enough to influence water mass characteristics (e.g. Giant iceberg A23-A and the Brunt Ice shelf);
- The “Continental Slope community” was distributed along the continental slope under the influence of Warm Deep Water (WDW) from the Weddell Gyre.

Based on the conceptual background given in Manuscript 2, we can hypothesize water-mass-related characteristics to better explain benthic spatial distribution in the Filchner Region. Such characteristics include e.g., productivity regimes, local particle flux and input from adjacent regions, and planktonic community composition (e.g. Barry 1988, Barry and Dayton 1988, Bathmann et al. 1991, Scharek et al. 1994, Kang et al. 2001, Palanques et al. 2002, Isla et al. 2009, Hauck et al. 2010; 2012, Isla et al. 2011, Flores et al. 2014). These characteristics seem to play a major role in defining benthic spatial distribution patterns, thus, it will be key to better understand these processes in order to assess their importance for specific patterns in the benthic realm. Including them in future studies will require better campaign planning with a multidisciplinary approach, and less constrained statistical approaches.

When considering benthic data from the Filchner Region in a sub-region comparison, we find the southern Weddell Sea benthos to be dominated by suspension feeders (mainly bryozoans). This already demonstrates differences between this region and the eastern and western Weddell Sea sub-regions, described as sponge dominated (e.g. Barthel 1992, Barthel and Gutt 1992, Gerdes et al. 1992, Arntz et al. 1994, Gutt and Starmans 1998, Sañé et al. 2012, Fillinger et al. 2013, Gutt et al. 2016). In terms of abundance and biomass, higher values correspond to regions where sea-ice cover is less persistent (e.g., with marked seasonality), as is the case at the tip of the Peninsula in the western and in the eastern Weddell Sea (Fetterer et al 2018). Contrastingly lower abundance and biomass values were observed in regions where sea ice persists for more than one season, as is the case in the southern Weddell Sea (Fetterer et al. 2018).

The Weddell Sea is covered by thick ice in winter but returns to ice-free conditions in large areas during summer. Areas with this seasonal sea-ice regime are defined as sea-ice marginal zones and regarded as areas where planktonic production is enhanced and higher than in open ocean waters (e.g. Clarke 1988, Donnelly et al. 2006, Isla et al. 2009, Flores et al. 2014). The eastern Weddell Sea benthos is under such regime with enhanced production, which provides higher particle fluxes to the benthos, thus sustaining a sponge-dominated suspension-feeder rich fauna. In the southern Weddell Sea, only the shelf east of the Filchner Trough can be regarded as a sea-ice marginal zone being comparatively smaller than in the eastern Weddell Sea shelf. Additionally, sea-ice cover, its extension and persistence play a major roles in regulating primary production in the Southern Ocean (Arrigo et al. 2015), and, in turn, the particle flux to the benthos (Gutt 2000, Isla 2016). Thus, we can attribute regional differences in benthic abundance and biomass to differences in local production and particle flux regimes, driven mainly by different sea-ice regimes.

Other factors which could “conspire” with regional sea-ice and productivity differences are shelf topography and water masses and their respective circulation pattern. Shelf topography modifies water current pathways and their strength (e.g. Gutt et al. 1998, Dorschel et al. 2014), thus regulating transport and deposition of suspended particles (Isla 2016). In this context, shelf width has been found to influence current speed. Narrower shelves are associated with relatively faster current regimes, where settled particles are easily resuspended, thus favouring suspension-feeder-dominated communities with high abundance, biomass, and diversity (Gutt et al. 1998), such as the Eastern Shelf community. On the other hand, wider shelves are associated with slower water current regimes that favor particle deposition (Gutt et al. 1998). The western and southern Weddell Sea shelves are wider as compared to the eastern Weddell Sea, reflected in total shelf area differences (approximately 340,000, 477,000 and 32,000 km^2 respectively). This would imply faster current regimes in the eastern Weddell, which in turn would support the higher abundance and biomass found in this sub-region, especially that of sponges.

While topography affects current velocities and thus deposition/resuspension of particles, water masses and their respective circulation patterns are related to different local productivity regimes and quantity/quality of particulate organic carbon. An example for this is the McMurdo Sound in the Ross Sea, where two contrasting regimes and benthic communities are found related to water mass circulation (Barry 1988, Barry and Dayton 1988). On the eastern shelf of the sound the water mass flows from the sea-ice marginal zone towards the Ross Ice Shelf, whereas the water mass on the western shelf comes from underneath the Ross Ice Shelf. As a result, the water mass on the eastern shelf is more productive and the benthic community more abundant than on the western shelf of the sound (Barry 1988, Barry and Dayton 1988). The predominant water mass found at the sampling stations in the eastern and western Weddell Sea sub-regions mainly flows through sea-ice marginal zones (Muench and Gordon 1995, Beckmann et al. 1999, Schröder and Fahrbach 1999), thus being more productive and supporting the higher benthic abundance and biomass in the eastern and western Weddell Sea sub-regions. In the southern Weddell Sea, water masses on the shelf in front of the Rønne Ice Self and in the Filchner Trough originate from underneath the Filchner Ice Shelf or from areas heavily covered by sea-ice (Gammelsrod et al. 1994, Grosfeld et al. 2001, Foldvik et al. 2001, 2004, Ryan et al. 2017). This would suggest these water masses to be less productive, thus explaining why benthic abundance and biomass are lower in the southern Weddell Sea. The different water masses with their complex current patterns and the environmental heterogeneity in the southern Weddell Sea might help to explain the existence of a larger number of community types in this sub-region of the Weddell Sea.

WEDDELL SEA BENTHIC COMMUNITIES AND TIME SCALES

Comparison of the results of Manuscript 3 with previous studies in the southern Weddell Sea demonstrated changes of benthic distribution ranges, abundance and biomass. In a period of almost 25 years, benthic infauna abundance and biomass values were half of those previously recorded by Gerdes et al. (1992). Furthermore, sponges, a major component of the biomass were replaced by bryozoans, evidencing a composition shift. A similar shift also became obvious in the epifauna. Previous descriptions of southern Weddell Sea benthos described bryozoan dominated communities in the north of the Filchner Region (Voß 1988, Gutt and Starmans 1998). These bryozoan dominated communities appear to have shifted towards the southeast of the Filchner Region. These differences between stations sampled in the 1980s and the mid-2010s appear related to sea-ice variations.

Similar to the situation in the southern Weddell Sea is that of the benthos in the eastern Weddell Sea. On the eastern Weddell Sea shelf, total benthic abundance and biomass and that of most benthic community major and minor components showed a clear decrease during the 1988 to 2014 period. This demonstrates the present situation on the eastern Weddell Sea shelf to be unfavorable for the benthic community as a whole. However, it is still unclear how productivity and sea-ice cover variations interact with different taxonomic units.

These results suggest a clear effect of ongoing climatic variation on the benthic communities in this part of the Weddell Sea. Sea-ice cover affects benthic community indirectly by modifying the primary production regime. In polynyas, primary production is directly related to polynya extension and duration (Arrigo et al. 2015), both regulated by sea-ice cover and sea-ice persistence. The latter have increased in the eastern and southern Weddell Sea during the last decades (Turner et al. 2016), especially after the year 2000 (Fetterer et al. 2016). We could relate the observed abundance and biomass losses in these sub-regions of the Weddell Sea, as well as the observed community distribution shifts in the southern Weddell Sea, to the observed climatic variation. Sea-ice cover in the southern and eastern Weddell Sea increased between 1979 and 2017, which could explain the observed benthic abundance and biomass losses. On a finer spatial scale, however, some sectors in the eastern Filchner Region showed losses of sea-ice cover during the same time period (Annex 1 Fig.S5). This could explain the shift of the bryozoan-dominated community from the shelf edge off Halley Bay from its original position towards southern areas with increased primary production and less sea-ice cover.

Another important factor shaping benthos is iceberg scouring (Arntz et al. 1994, Gutt 2000, 2001, Gerdes et al. 2003, Barnes and Souster 2011). Scours are a catastrophe-like disturbance, which completely eliminates benthos in affected locations (Dayton et al. 1989, Gutt 2001, Gerdes et al. 2003). The susceptibility of benthos to iceberg scours is directly related to the number and size of icebergs. The higher “scouring index” found after 2000 points to a larger seabed area potentially affected by iceberg scours. Thus, we could relate observed abundance and biomass losses to the increasing number of giant (Budge and Long 2018) and smaller icebergs (Tournade et al. 2016), both the product of higher basal melting rates.

Contrasting to the situation in the eastern and southern Weddell Sea is that in the western Weddell Sea and in waters west of the Antarctic Peninsula. Sea-ice cover has decreased, and sea-surface temperature has increased (Liu et al. 2004, Turner et al. 2016, Comiso et al. 2017). Consequently, the situation of benthos is also contrasting with pronounced gains in abundance and biomass gains (e.g. Fillinger et al. 2013, Barnes 2015). In waters west of the West Antarctic Peninsula, South Georgia and South Orkney Islands, biomass and productivity of major benthic components have been estimated to increase related to an increase in the number of ice-free days per year (Barnes 2015). Similarly, on the shelf previously covered by the Larsen ice shelves, benthos appears to have steadily developed following a shift from an oligotrophic system with low pelagic primary productivity (Sañé et al. 2011) to a system with higher pelagic primary productivity (Bertolin and Schloss 2009). Striking is the speed at which the abundance and biomass of the sponge assemblage increased (Fillinger et al. 2013). In general, Antarctic benthos is hypothesized to live in the "slow lane", developing at slower rates than in warmer regions (Arntz et al. 1994, Peck 2002, 2005, 2016, Pörtner et al. 2007), and to recover from disturbances at a rather slow pace (Gerdes et al. 2008). The development recorded by Fillinger et al. (2013) represented a 2- and 3-fold increase of sponge abundance and biomass, respectively, in a four year period. This comparatively "fast" development shows how different benthic reaction times can be and prove the need of better understanding the speed at which benthos reacts to environmental variation. Improving our knowledge on this topic will allow better predictions on how benthos will react to predicted climatic scenarios.

SYNTHESIS

While different in benthic characteristics, the eastern and southern Weddell Sea show similar changes in sea-ice cover and sea-surface temperature: Based on satellite data collected since 1979, sea-ice cover in these Weddell Sea sub-regions has increased (Turner et al. 2016), whereas sea-surface temperature has decreased (Comiso et al. 2017). For the eastern Weddell Sea, the study of Barnes (2015) indicate increased bryozoan biomass and production despite the sea-ice increase, while the analysis of the large benthic data set collected on board RV *Polarstern* between 1988 and 2014 (Gerdes 2014a-n) suggests that bryozoan biomass has decreased. The same trend has been reported for total benthic community abundance and biomass in both the eastern and southern Weddell Sea, where abundance and biomass in the mid-2010s were half of those recorded in the late 1980s (Gerdes et al. 1992, Manuscript 3). In the western Weddell Sea, sea-ice cover and sea-surface temperature trends appear to go in opposite directions, i.e. sea-ice cover decreased, and sea-surface temperatures increased. Studies including data sets of several sampling campaigns have shown the environmental trends in the western Weddell Sea to favour benthos, resulting in increased biomass and carbon production (e.g. Fillinger et al. 2013, Barnes 2015, Barnes et al. 2018).

Temporal changes in benthic communities signal sea-ice cover as a main “culprit” for this variation. Sea-ice cover satellite data can be used to calculate ice-free area and ice-free days, two parameters regarded as direct regulators of primary productivity in the Southern Ocean (Arrigo et al. 2015). Thus, sea-ice cover gains/losses during recent decades work as indicators for primary productivity gains/losses. For the 1979-2013 period, sea-ice cover in the Bellingshausen Sea and Amundsen Sea has significantly decreased at rates of 2 to 10 %-cover dec^{-1}, whereas opposite trends with increases of 2-10 %-cover dec^{-1} have been found for other Antarctic sectors as e.g. the eastern Weddell Sea (Schwegmann 2012, Turner et al. 2016). Based on our current knowledge concerning the role of sea-ice for primary productivity and its effect on benthos, we could assume benthic abundance and biomass gains for the Bellingshausen Sea and Amundsen Sea for the 1979-2013 period, and the opposite for the Ross Sea, west Pacific Ocean and Indian Ocean sectors of the Southern Ocean.

One has to consider, however, the restricted area in which the study in the eastern Weddell Sea was conducted. Furthermore, there is a clear lack of long-term studies dealing with community-level responses to observed climatic trends. Drawing further conclusions will also require the inclusion of further environmental parameters. The so-far published results are entirely based on relations between benthos and sea-ice/productivity/iceberg variations (e.g. Barnes 2015, 2017, Barnes et al. 2018), and disregard other possible stressors, e.g. acidification, warm water intrusions, change of water mass circulation patterns, or increased terrigenous inputs due to glacier retreat. Currently ~14% of the Southern Ocean is estimated to be affected by multiple stressors, but under future climate scenarios, this percentage is estimated to be almost 86% (Gutt et al. 2015). This demonstrates the need of including further environmental parameters into sampling campaigns and future studies, as suggested by Gutt et al. (2015) and literature cited therein.

Despite clear gaps, our knowledge can be used to tentatively predict the future of the benthic communities of the three sub-regions of the Weddell Sea, as well as that of other high-Antarctic regions. Based on different IPCC scenarios, sea-ice cover in the Southern Ocean is predicted to decrease at rates of 1.1 to 3.1 % per decade until 2099 (Timmermann and Hellmer 2013). Under this context, we could assume a “brighter” future to most benthic communities, with increased food input. There are, however, some considerations to take before drawing further conclusions. Near-seabed temperature is another variable predicted to increase, reaching up to 2°C on some Antarctic shelves (Timmermann and Hellmer 2013). Physiological studies have shown warming of 1°C as a threshold at which benthic organisms respond significantly (Barnes and Peck 2008, Peck 2011, Peck et al. 2014), with loss of biological activity at temperatures close to 0°C, e.g. reducing burrowing or swimming activity as is the case in mollusks (Peck et al. 2009). The studies of Peck et al. (2009, 2010) and Richard et al. (2012) on adaptation capabilities of Antarctic benthos propose temperature ranges ~3°C above present day temperatures to be already harmful. The predicted temperature rises imply a ~2°C increase above present day temperatures, which could prove lethal to some components of the Antarctic benthic communities.

This temperature rise would also imply an increase of basal melt rates of ice shelves, which would in turn imply an increased number of icebergs. A larger number of icebergs could potentially inflict devastating short-term consequences, but positive long-term consequences (Barnes et al. 2018). On short term, more icebergs imply a higher susceptibility of benthos to scours, which are known disturbances regarded as destructive as fire in forests (Gutt 2001). The higher susceptibility of benthos to scours would result in abundance and biomass to be drastically reduced. However, once icebergs disintegrate or move onto the open ocean, the seabed areas they once covered are recolonized by benthic organisms, leading to a local diversity increase (Gutt and Piepenburg 2003). In addition, in the water column new productive areas would become available, leading to higher primary productivity (Schwarz and Schodlok 2009, Vernet et al. 2011, Barnes et al. 2018). There is, however, an important question on the post-scour recovery of benthos in areas were observed climate change resulted in decreased abundance and biomass: If benthos is already close to a tipping point due to climate-change-related decrease in, e.g., abundance and biomass, would it be able to recover from a catastrophic disturbance event, such as iceberg scouring?

Observed and predicted temperature raises could affect distribution ranges of species. On the one hand, it could reduce the range of those organisms which are less adapted. On the other it could allow invasive species to migrate into the shelves of the Southern Ocean. The expected temperature increase for the upcoming three decades would raise temperatures enough to be suitable for, e.g., king crabs to invade the Southern Ocean (Smith et al. 2012, Griffiths et al. 2013). Re-introduction of these benthic high predators would imply an increased predation pressure to organisms which, since millennia, have lived without them (Thatje et al. 2005). This could prove a worse-case scenario under projections which predict 98% of the Southern Ocean to be undersaturated with respect to aragonite by 2100 (Orr et al. 2005). This would result in organisms such as bryozoans, echinoids and mollusks dealing not only with increased temperatures, but with difficulties generate their skeletons (Watson et al. 2012). Difficulties regarding calcification of skeletons, resulting in their thinning, would lower their resistance to predation (Gazeau et al. 2013). The pelagic system would be also negatively impacted, because under an aragonite undersaturated environment the efficiency of photosynthesis and that of the biological carbon pump could be reduced (Riebesell et al. 2007, Hofmann and Schellnhuber 2009, Tortell et al. 2010). This could, in turn, imply a lower quality and quantity of food input for benthos.

The effects of single/multiple stressors on the benthos will depend on the survival capacity of benthic organisms. Animals have three main mechanisms for surviving environmental changes: a) to cope with the altered conditions using their phenotypic plasticity, b) to adapt via genetic changes on population level, and c) to migrate to environments with conditions that allow survival (Peck 2005, 2018). When considering temperature alone, it appears that the phenotypic plasticity of some benthic organisms would allow them to acclimate to the predicted temperatures of 2°C higher than present-day values (Timmermann and Hellmer 2013). As mentioned before, Peck et al. (2009, 2010) and Richard et al. (2012) propose benthos can even survive under temperatures 3°C higher than present-day values. However, how this survival window can shift for calcifying benthos under an aragonite-undersaturated environment in response to ocean acidification is still unknown. Assuming the benthic phenotypic plasticity is unable to cope with environmental changes, adaptation via genetic changes could compensate. Genetic changes involving gene frequency, genetic drift, and gene selection can take months to decades to be evident (Peck 2011, 2018). These changes can take even longer for Antarctic benthos, considering their slower metabolic rates, and long development rates (Peck 2005, 2018). This would suggest Antarctic benthos might be "too slow" to be able to develop the adaptations needed to cope with its changing environment. However, when considering that predicted changes are expected to be met in 50 to 100 years, will benthos be truly "too slow"? or will benthos be able to "go with the flow" of change? The third mechanism, migration, depends on the dispersal capability of the organisms (Peck 2005), but under a prognosis were most of the Southern Ocean will be affected by at least one stressor (e.g. temperature increments, and aragonite undersaturation), "running" away appears out of the question.

In conclusion, predictions based on future sea-ice losses would suggest benthos to benefit. However, knowledge on different stressors that might affect benthos (and pelagos) points to a highly risky and grim future. Better understanding how benthos interacts with different stressors, and how bentho-pelagic processes might be affected, will be paramount to improve the validity of our predictions and to get a more comprehensive system-level understanding on how the future of benthos might be. Another important aspect to consider is how fast benthos reacts and adapts to changes. If our assumptions on the timings and speeds of Antarctic benthos process and adaptations are off, it would imply a "brighter" future than though, even under an environment with multiple stressors. However, proving these assumptions will require filling numerous gaps and setting new redlines for future studies on benthic communities.

OUTLOOK

This thesis presents new information on benthic communities in the Filchner Region. It also provides evidence that water mass-characteristics (i.e., ocean circulation dynamics), their associated productivity, particle flux and sea-ice regimes are key drivers of spatial benthic distribution patterns. However, the relative importance of these and other environmental factors are still unclear. Therefore, future research campaigns should have a multidisciplinary approach, featuring the current use of various sampling methods and strategies, including the quantitative measurement of further water-mass-related environmental factors, such as e.g. water currents, primary production, and particle flux. Moreover, there is a need to review, sort, validate and use already available data that can be analyzed to explore the relationships between benthic and pelagic processes, as stated in Manuscript 2. This could be achieved by using large and comprehensive biological and environmental data sets, such as those found in, e.g., the PANGAEA repository, National Snow and Ice Data Center portal, NASA Ocean Color data center, the Antarctic Iceberg Tracking Database, and ALTIBERG iceberg data base. Manuscript 4 applies such an approach by combining field benthic data, satellite data, and knowledge on primary production regulators and disturbance by iceberg scours. However, due to the limitations of the statistical approach used (correlation analysis) open questions remained unanswered, such as, e.g., “how the future of a typical Weddell Sea shelf benthic community could look like in predicted climate scenarios”. Another aspect that constrains the conclusions on the future of the benthic communities of the Weddell Sea is the current lack of knowledge on the fundamental physiological limits within which different components of Antarctic benthos can live, pointing to the need of more multidisciplinary work between ecologists and physiologists.

Manuscripts 3 and 4 provide useful hints to understand spatial and temporal patterns of the Weddell Sea benthos, and how these communities have altered (and could alter) under ongoing (and predicted) climate change. However, the use of statistical approaches that are based on the assumption of linear relationships (such as, e.g., multiple correlations and regressions) impedes to match environmental with benthic parameters. Future multidisciplinary studies should apply modern approaches to assess the relation between environmental parameters and benthic spatial (and temporal) patterns, such as, machine-learning techniques like Random Forests or MaxEnt. These techniques are less constrained than linear statistics and allow, e.g., the inclusion of categorical variables (e.g. water mass type, physiological constraints). This flexibility will also allow exploring the significance of benthic response times and effects of multiple stressors, thus improving our ability to predict benthic dynamics. Moreover, both Random Forests and MaxEnt that allow the construction of spatial distribution models (e.g. Vinvenzi et al. 2011, Wang et al. 2016, Ostmann and Arbizu 2018), which could allow for a statistically rigorous test of the hypothesis made in Manuscript 3. Finally, when such distribution models are fed with environmental data from, they would allow for projecting future benthic dynamics, thus improving the results and predictions made in Manuscript 4.

This thesis exemplifies the great surplus values of “multidisciplinary work” for future benthic studies. Manuscript 2 shows that the benthos strongly depends on water-column processes, in both spatial and temporal scales. Manuscripts 3 and 4 further corroborate the prime ecological significance of the bentho-pelagic coupling and also demonstrate that the lack of a multidisciplinary sampling strategy necessarily leads to just partial answers (and lots of extra questions). Quantitatively describing and modelling the relationships between benthic and pelagic processes by means of such multidisciplinary approaches will be key that are required to develop the tools to understand how the ongoing and predicted climate change affects Antarctic benthos in the Weddell Sea, but also in other high-Antarctic regions of the Southern Ocean.

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ANNEX

ANNEX 1: Supplementary material for Manuscript 3

Supplementary Tables and legends

Table S1: Multibox corer (MBC), Seabed images (SBI), and multicorer (MUC) stations for benthos and sediment studies conducted during RV *Polarstern* cruises PS82 and PS96. Sediment characteristics correspond to the first 9 cm of the sediment column (Continued in next page).

St. Nr.	Latitude (°S)	Longitude (°W)	Sampling gear	Depth (m)	Coarse Sediment (%)	Fine Sediment (%)
PS82-033	75° 56.83'	31° 40.57'	MBC+SBI	684	34.7	65.3
034	75° 57.08'	31° 40.60'	MUC	691	48.3	51.7
040	76° 03.96'	30° 16.83'	MBC+SBI	472	34.8	65.2
041	76° 04.03'	30° 18.40'	MUC	470	8.1	91.9
052	76° 19.06'	29° 02.21'	SBI	243	-	-
064	77° 06.11'	36° 25.51'	MUC	1115	5.9	94.1
066	77° 06.09'	36° 34.39'	MBC+SBI	1111	22.3	77.7
074	76° 59.89'	34° 07.71'	MBC+SBI	571	27.7	72.3
079	77° 01.92'	33° 35.19'	MBC+SBI	390	28.4	71.6
089	76° 59.02'	32° 51.05'	MBC+SBI	254	30.1	69.9
098	77° 42.76'	35° 55.73'	MBC+SBI	585	22.3	77.7
108	77° 54.17'	38° 09.99'	MUC	1215	15.1	84.9
109	77° 53.92'	38° 08.49'	SBI	1216	21.9	78.1
116	77° 36.77'	38° 56.70'	MBC+SBI	1060	22.4	77.6
125	75° 29.48'	27° 24.60'	MBC+SBI	286	40.5	59.5
130	75° 20.28'	27° 38.48'	MBC+SBI	361	41.3	58.7
132	75° 20.27'	27° 38.44'	MUC	361	70.0	30.0
144	74° 49.80'	25° 07.44'	MBC+SBI	702	33.7	66.3
145	74° 49.80'	25° 07.44'	MUC	702	9.7	90.3
152	74° 37.01'	28° 31.83'	MUC	1152	47.6	52.4
153	74° 37.01'	28° 30.57'	MUC	1176	-	-
154	74° 36.53'	28° 28.72'	MBC+SBI	1217	41.4	58.6
163	74° 39.94'	28° 40.16'	MBC+SBI	696	41.1	58.9
164	74° 53.67'	26° 42.48'	MBC+SBI	290	39.6	60.4
165	74° 53.69'	26° 41.75'	MUC	296	54.3	45.7
178	74° 29.96'	30° 59.75'	MUC	530	54.6	45.4
179	74° 29.86'	30° 59.01'	MBC+SBI	530	39.3	60.7
190	74° 40.21'	33° 40.27'	MBC+SBI	591	29.9	70.1
198	74° 36.21'	36° 21.31'	MUC	422	49.4	50.6
200	74° 34.73'	36° 23.70'	MBC+SBI	426	28.7	71.3
206	74° 26.09'	35° 43.48'	MBC+SBI	1140	30.0	70.0
226	74° 21.12'	37° 36.14'	MBC+SBI	554	29.2	70.8
235	74° 11.62'	37° 44.00'	MUC	806	61.2	38.8
236	74° 13.23'	37° 39.67'	MBC+SBI	798	29.5	70.5
242	74° 40.84'	39° 04.43'	MBC+SBI	436	24.8	75.2
243	74° 41.31'	39° 04.53'	MUC	435	9.5	90.5
269	74° 18.05'	32° 47.56'	MUC	748	1.2	98.8
270	74° 17.05'	32° 47.81'	MBC+SBI	830	31.2	68.8
277	74° 54.42'	29° 39.80'	SBI	406	39.4	60.6
269	74° 18.05'	32° 47.56'	MUC	748	1.2	98.8
292	75° 30.60'	29° 00.44'	MUC	454	14.6	85.4
297	75° 32.61'	28° 49.88'	SBI	412	38.8	61.2
305	75° 06.53'	28° 45.83'	SBI	413	40.2	59.8
313	74° 40.06'	28° 39.77'	MUC	672	53.2	46.8
324	74° 41.61'	38° 48.29'	MUC	426	59.6	40.4
325	74° 42.28'	29° 48.41'	MBC+SBI	427	39.5	60.5
PS96-008	74° 53.70'	29° 22.77'	MBC+SBI	405	39.7	60.3
010	74° 56.75'	26° 02.87'	MBC+SBI	283	37.1	62.9

017-3	75° 00.87’	32° 52.51'	MUC	608	-	-
026	75° 16.17'	37° 55.09'	MBC+SBI	402	25.9	74.1
026-7	75° 16.19'	37° 52.96'	MUC	416	19.5	80.5
027	76° 43.12'	52° 09.30'	SBI	302	24.6	75.4
032	76° 19.36'	45° 47.17'	MBC	330	11.1	88.9
037	75° 43.27'	42° 27.49'	MBC+SBI	380	22.1	77.9
037-8	75° 43.30'	42° 27.71'	MUC	391	11.1	88.9
048	74° 45.53'	35° 20.61'	MBC+SBI	470	28.6	71.4
048-7	74° 45.52'	35° 20.91'	MUC	482	22.2	77.8
056	75° 31.02'	28° 57.18'	MBC	454	38.1	61.9
072	75° 51.47'	32° 20.01'	MBC+SBI	725	33.5	66.5
072-7	75° 51.61'	32° 17.58'	MUC	755	-	-

-: No data available

Table S2: Near seabed hydrographic variables (modified after Schröder and Wisotzki 2014; Schröder et al. 2016), and surface sediment (derived from seabed images) for each benthic station sampled during R/V *Polarstern* cruises PS82 and PS96.

St. Nr.	**Sediment cover (%)**			**Hydrography**			
	Fine	**Gravel**	**Stone/Rock**	**Dissolved O_2 (µmol L^{-1})**	**Density (sigma-theta kg m^{-3})**	**Temperature (°C)**	**Salinity**
PS82-033	92	7	0	317.6	27.91	-1.95	34.66
040	100	0	0	317.8	27.79	-1.84	34.52
052	0	0	100	321.5	27.68	-1.78	34.40
066	99	0	1	321.2	27.91	-1.94	34.65
074	92	5	3	324.6	27.85	-1.91	34.58
079	49	37	14	323.6	27.75	-1.92	34.48
089	5	94	1	323.1	27.72	-1.92	34.46
098	81	19	1	322.9	27.88	-1.97	34.63
109	82	16	2	320.8	27.90	-1.94	34.65
116	68	29	3	316.9	27.90	-1.86	34.64
125	97	1	1	313.7	27.69	-1.65	34.40
130	96	1	3	306.2	27.71	-1.50	34.43
144	99	1	0	292.7	27.70	-1.33	34.43
154	63	31	6	266.9	27.79	-0.69	34.57
163	7	78	15	264.2	27.78	-0.63	34.56
164	80	19	1	304.2	27.70	-1.45	34.42
179	51	48	1	298.1	27.81	-1.42	34.57
190	79	18	3	314.0	27.90	-1.88	34.65
200	54	44	2	308.7	27.85	-1.73	34.60
206	6	92	2	283.7	27.87	-1.18	34.63
226	88	12	0	285.3	27.83	-1.13	34.61
236	82	16	2	283.1	27.82	-1.08	34.60
242	100	0	0	286.9	27.83	-1.16	34.58
270	17	69	14	310.0	27.86	-1.77	34.63
277	93	6	1	296.9	27.74	-1.35	34.48
297	96	3	1	304.1	27.74	-1.53	34.47
305	100	0	0	295.9	27.74	-1.35	34.48
325	58	41	2	294.0	27.75	-1.26	34.49
PS96-008	92	5	3	296.9	27.73	-1.35	34.47
010	87	12	1	305.3	27.69	-1.47	34.40
026	95	5	0	283.1	27.87	-1.07	34.61
027	95	5	0	320.3	27.88	-1.90	34.63
032	-	-	-	320.2	27.92	-1.91	34.67
037	95	5	0	315.7	27.91	-1.82	34.66
048	94	5	0	296.5	27.90	-1.47	34.65
056	-	-	-	307.4	27.75	-1.61	34.47
072	95	5	0	317.3	27.90	-1.93	34.66

-: No data available

Table S3: List of 20 environmental variables (and corresponding units) included in the environmental data matrix used for the BEST analyses. Marked in bold are the environmental variables considered for the BEST test.

Environmental variable	Unit	Obtained or calculated from
Water Depth	**Meters**	**CTD[a,b]**
Dissolved O_2 concentration	µmol L^{-1}	CTD[a,b]
Near seabed density (Sigma-theta)	kg m^{-3}	CTD[a,b]
Near seabed temperature	**°C**	**CTD[a,b]**
Near seabed salinity	None	CTD[a,b]
Gravel content in sediment column	**Percentage in sediment column**	**Multicorer (MUC) cores**
Sand content in sediment column	Percentage in sediment column	MUC cores
Silt content in sediment column	Percentage in sediment column	MUC cores
Clay content in sediment column	Percentage in sediment column	MUC cores
Fine sediment content in sediment column	Percentage in sediment column	MUC cores
Coarse content in sediment column	Percentage in sediment column	MUC cores
Fine sediment cover	Percentage seabed covered	Seabed images (SBI)
Gravel cover	**Percentage seabed covered**	**SBI**
Stone/rock cover	Percentage seabed covered	SBI
Biogenic Silica (Opal) inventory	mg cm^{-2}	MUC cores
Organic Carbon (OC) inventory	**mg cm^{-2}**	**MUC cores**
Year average sea-ice cover	Percentage surface covered	Sea ice index[c]
Year sea-ice cover gain/loss	Percentage sea-ice cover gain/loss per year	Sea ice index[c]
Summer average sea-ice cover	**Percentage surface covered**	**Sea ice index[c]**
Summer sea-ice cover gain/loss	**Percentage sea-ice cover gain/loss per year**	**Sea ice index[c]**

a: Schröder & Wisotzki 2014
b: Schröder et al. 2016
c: Fetterer et al. 2018

Table S4: Feeding guild assignment for all considered taxonomic units. Assignment considering on specialized literature (Yonge 1928, Hansen 1978, Fauchald & Jumars 1979, Montiel et al. 2005, Macdonald et al. 2010).

	DF	SF	SV	PD
Porifera	0	1	0	0
Medusae	0	0	0	1
Hydrozoa	0	1	0	0
Alyonacea	0.1	0.9	0	0
Pennatulacea	0	0.1	0.9	0
Anthozoa	0	0.13	0.0	0.87
Bryozoa	0	1	0	0
Brachiopoda	0	1	0	0
Sipuncula	1	0	0	0
Platyhelminthes	0	0	0.1	0.9
Nemertina	0	0	0	1
Priapulida	0	0	0.5	0.5
Polyplacophora	0	0	0.8	0.2
Solenogastres	1	0	0	0
Bivalvia	0.28	0.70	0	0.02
Nudibranchia	0	0	0	1
Gastropoda	0,5	0.1	0.1	0.4
Scaphopoda	0	0	0	1
Cephalopoda	0	0	0	1
Polychaeta	0.52	0.16	0.02	0.3
Clitellata	0.6	0	0	0.4
Echiurida	1	0	0	0
Acari	0	0	0	1
Pantopoda	0	0	0	1
Mysida	0.7	0	0	0.3
Amphipoda	0.2	0.3	0.1	0.4
Cumacea	0.78	0.04	0	0.18
Harpacticoidea	0	0.7	0	0.3
Cirripedia	0	1	0	0
Isopoda	0.7	0	0	0.3
Tanaidacea	0	1	0	0
Ostracoda	0.3	0.2	0.4	0.2
Decapoda	0.25	0.25	0.25	0.25
Crustacea	0.3	0.4	0.1	0.2
Echinoidea	0.9	0.1	0	0
Holothuroidea	0.6	0.4	0	0
Asteroidea	0.2	0	0	0.8
Ophiuroidea	0.4	0.5	0	0.2
Crinoidea	0	1	0	0
Hemichordata	0.6	0.4	0	0
Tunicata	0	1	0	0
Unidentified	0.25	0.25	0.25	0.25

Table S5: Abundances derived from seabed images (SBI), abundances and biomass derived from multibox corer (MBC) samples and their respective dominance and frequency of occurrence for each taxonomic unit (TUs). Ranges are given in brackets.

TUs	SBI[a]			MBC[b]				
	Mean abundance (ind m^{-2})	Dom.[c] (%)	Frec.[d] (%)	Mean abundance (ind m^{-2})	Mean biomass (g ww m^{-2})	Dominance (%)		Frec.[d] (%)
						Abundance	Biomass	
Porifera	3	4.5	80	1	11.4	0.1	22.2	71
Stauromedusae	<1	<0.1	3	-	-	-	-	-
Medusae[e]	<1	<0.1	3	-	-	-	-	-
Hydrozoa[f]	0.003	3.6	66	15	0.1	1.0	0.2	55
Alcyonacea[f]	0.003	3.4	80	-	-	-	-	-
Pennatulacea	<1	<0.1	20	-	-	-	-	-
Actinaria	<1	1.2	74	-	-	-	-	-
Scleractinia	<1	0.1	37	-	-	-	-	-
Anthozoa[e]	-	-	-	16	2.1	1.1	4.2	77
Bryozoa[f]	0.045	48.5	83	1	13.6	0.1	26.7	55
Brachiopoda	<1	<0.1	17	5	0.2	0.6	0.3	32
Sipuncula	-	-	-	16	0.5	1.1	0.9	65
Platyhelminthes	-	-	-	<1	<0.1	<0.1	<0.1	6
Nemertina	-	-	-	32	0.2	2.1	0.5	81
Priapulida	-	-	-	1	0.1	0.1	0.2	10
Polyplacophora	<1	<0.1	6	1	<0.1	0.1	<0.1	13
Solenogastres	-	-	-	5	<0.1	0.3	<0.1	45
Bivalvia	<1	0.2	17	101	0.5	6.6	0.9	97
Nudibranchia	<1	<0.1	3	-	-	-	-	-
Gastropoda	<1	1.2	34	20	0.2	1.3	0.4	74
Scaphopoda	-	-	-	2	0.1	0.2	0.1	26
Cephalopoda	<1	<0.1	9	-	-	-	-	-
Polychaeta	11	17.3	100	763	11.3	50.0	22.0	100
Clitellata	-	-	-	143	0.2	9.4	0.4	74
Echiurida	-	-	-	1	1.0	<0.1	1.9	10
Acari	-	-	-	3	<0.1	0.2	<0.1	16
Pantopoda	<1	0.7	77	18	<0.1	1.2	0.1	55
Mysida	<1	0.6	71	-	-	-	-	-
Amphipoda	<1	0.5	74	108	0.4	7.1	0.7	84
Cumacea	-	-	-	21	0.1	1.4	0.1	68
Harpacticoida	-	-	-	7	<0.1	0.4	<0.1	32
Cirripedia	-	-	-	<1	<0.1	<0.1	<0.1	6
Serolidae	<1	0.2	51	-	-	-	-	-
Isopoda	<1	<0.1	14	60	0.3	4.0	0.5	84
Tanaidacea	-	-	-	35	<0.1	2.3	<0.1	77
Ostracoda	-	-	-	14	<0.1	0.9	<0.1	58
Decapoda	<1	0.3	63	-	-	-	-	-
Crustacea[e]	<1	0.7	71	1	<0.1	<0.1	0.1	6
Echinoidea	<1	0.5	97	2	0.1	0.1	0.2	26
Holothuroidea	8	13.	97	9	1.3	0.6	2.6	48
Asteroidea	<1	0.4	77	4	0.1	0.2	0.1	23
Ophiuroidea	24	39.7	100	100	4.8	6.6	9.2	81
Crinoidea	<1	1.3	80	8	0.2	0.5	0.3	26
Hemichordata	<1	0.6	40	1	<0.1	0.1	0.1	10
Tunicata	7	11.8	89	8	2.4	0.6	4.7	45
Unidentified	3	5.0	97	2	<0.1	0.1	<0.1	16

-: No data available
a: n = 35
b: n = 31
c: Dominance
d: Frequency of occurrence.
e: Unidentified.
f: Abundance given in m^2; Relative abundances based on organism coverage in SBI.

Table S6: Results of the pairwise PERMANOVA between Multibox corer (MBC) abundance and MBC-biomass data from different sub-regions of the Weddell Sea; Tip of the Antarctic Peninsula (TAP), Larsen embayments (LA), Filchner Region (FR), and South Eastern Weddell Sea Shelf (SEWSS). MBC data of TAP, LA and SEWSS modified after Gerdes (2014 a-h).

Sub-Region	**Abundance-based Pseudo-F**				**Biomass-based Pseudo-F**			
	TAP	LA	FR	SEWSS	TAP	LA	FR	SEWSS
TAP	-				-			
LA	2.3218**	-			2.0817**	-		
FR	1.5607*	1.9012**	-		2.4879**	1.6964**	-	
SEWSS	2.0808**	3.3323**	2.2476**	-	2.2217**	3.5487**	3.0764**	-

* Significantly different at $p < 0.05$

** Significantly different at $p < 0.005$

Supplementary Text and legends

Text S3: Formula used to calculate abundance and biomass ratios of each Taxonomic Unit (TU) per station, where “ij” is the i-th TU of the j-th Station. For colonial organisms, this is calculated using abundance (m^2) and the total area (in m^2) covered by organisms.

$$Ratio\ TU_{ij} = \frac{Abundance\ or\ biomass\ TU_{ij}}{Total\ abundance\ or\ biomass\ of\ Station_j}$$

Supplementary Figures and captions

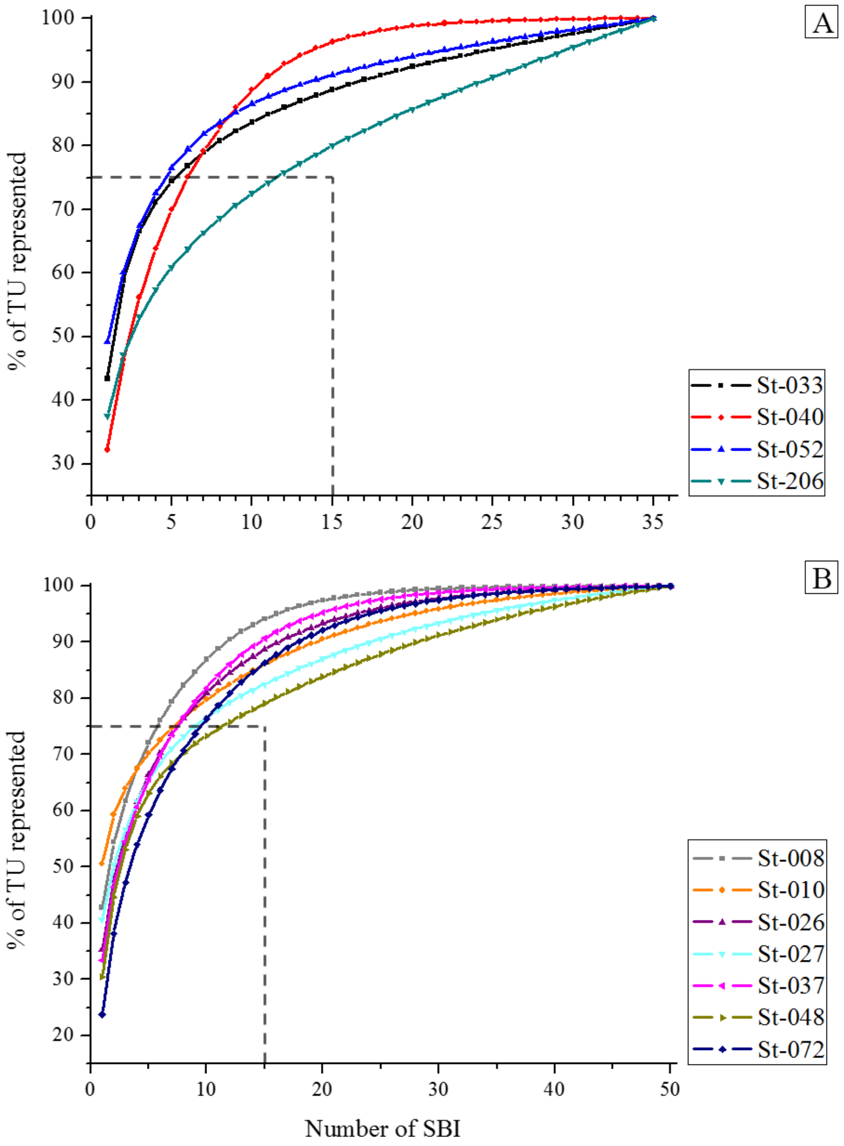

Fig.S1. Taxonomic unit (TU) cumulative curves calculated for SBI stations St-033, 040, 052, and 206 from PS82 (A) and St-008, 010, 026, 027, 037, 048, and 072 from PS96 (B). At least 75% of the TUs are represented after analysing 15 seabed images (dashed lines).

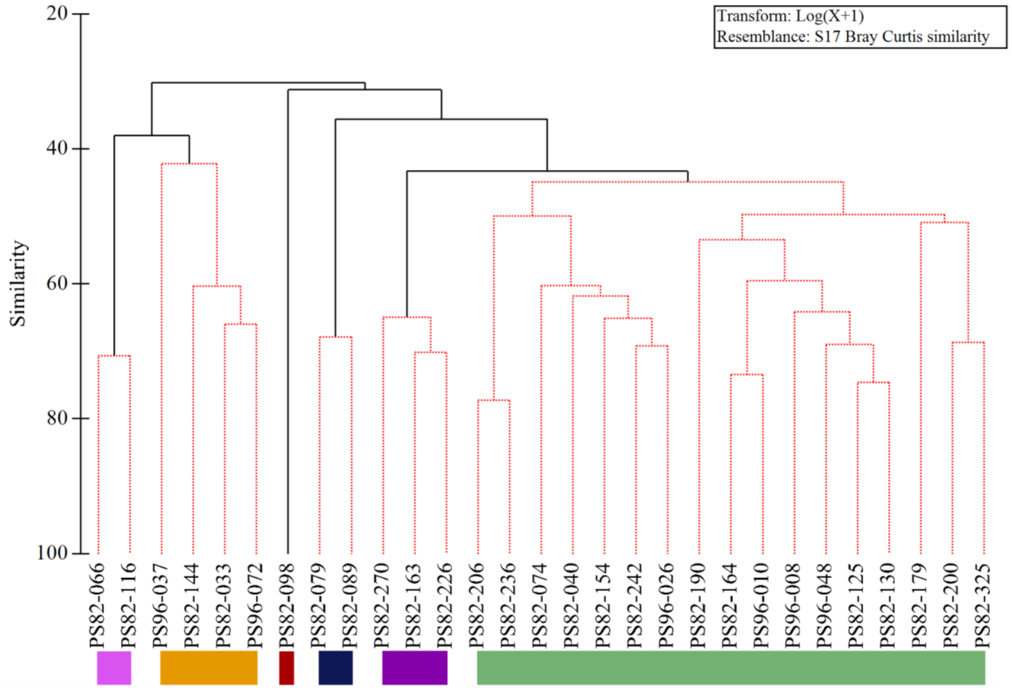

Fig.S2. Dendrogram from the Cluster and SIMPROF analyses used to differentiate station groups. Colour bars (and dashed red lines) show station groups A (pink), B (orange), C (dark red), D (dark blue), E (purple), and F (green). Stations are clustered based on group average. SIMPROF differentiated groups with *a* = 0.05, considering a mean number of permutations = 1000, and 999 simulations.

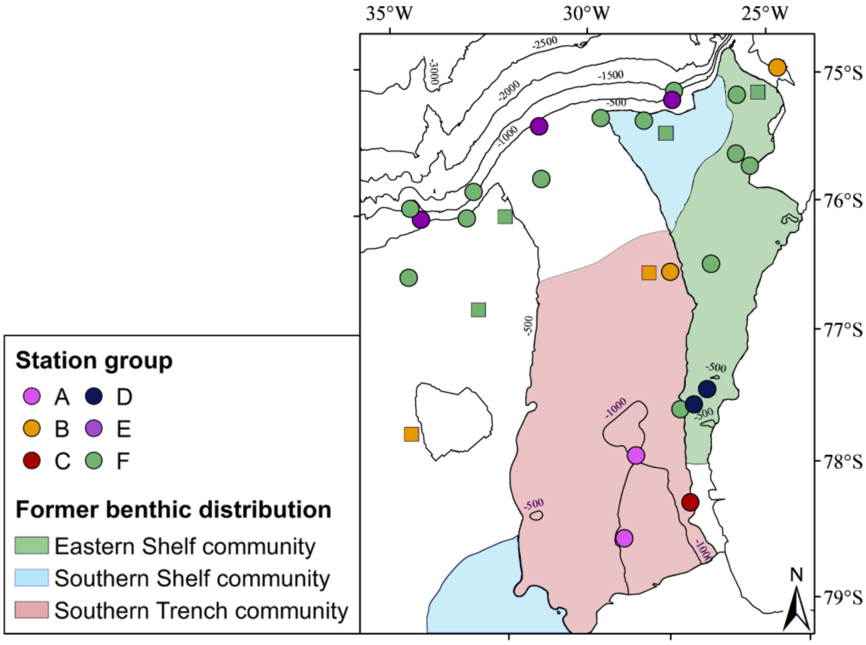

Fig.S3. Comparison of benthic communities showing only partial agreement between previously described benthic communities (Voß 1988; coloured areas) and station groups defined in this work via Cluster and SIMPROF analyses.

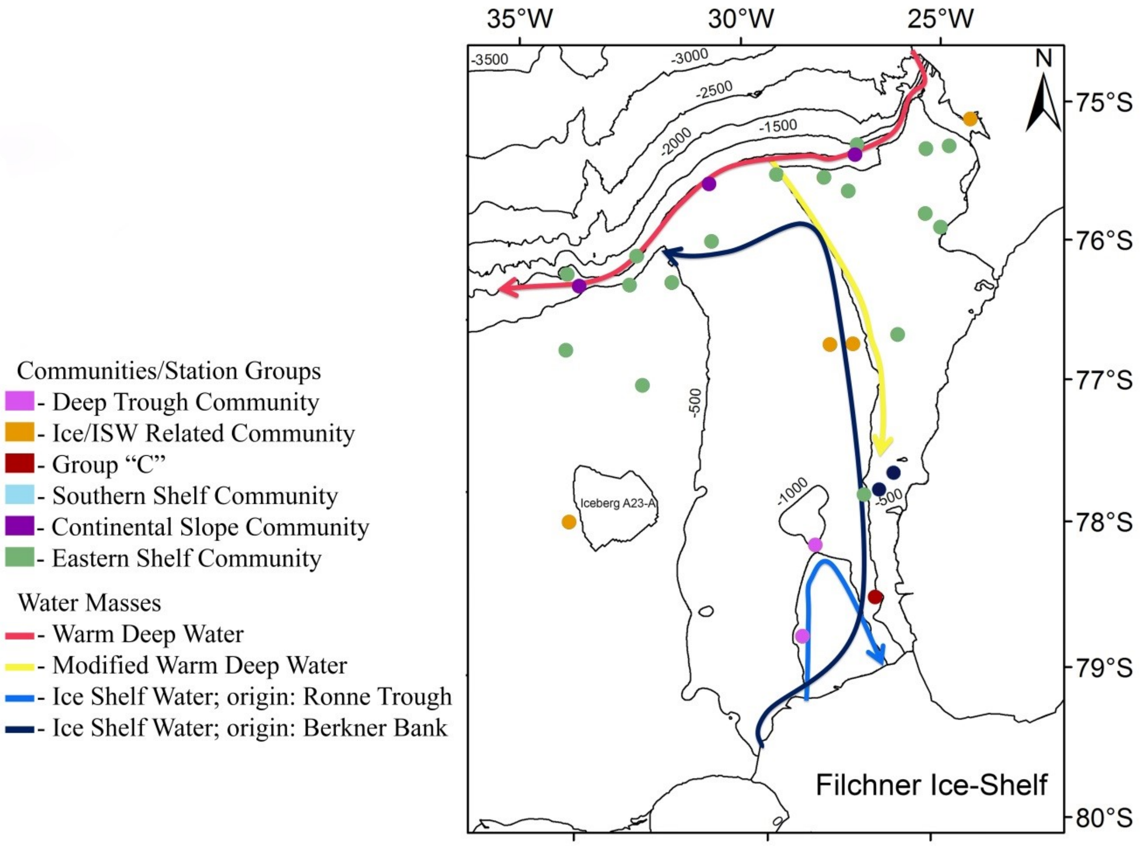

Fig.S4. Benthic faunal communities/station groups differentiated with the Cluster and SIMPER analysis. Arrows represent water mass circulation in the Filchner Trough, shelves and outer slope of the Filchner Region; modified after Ryan et al (2017).

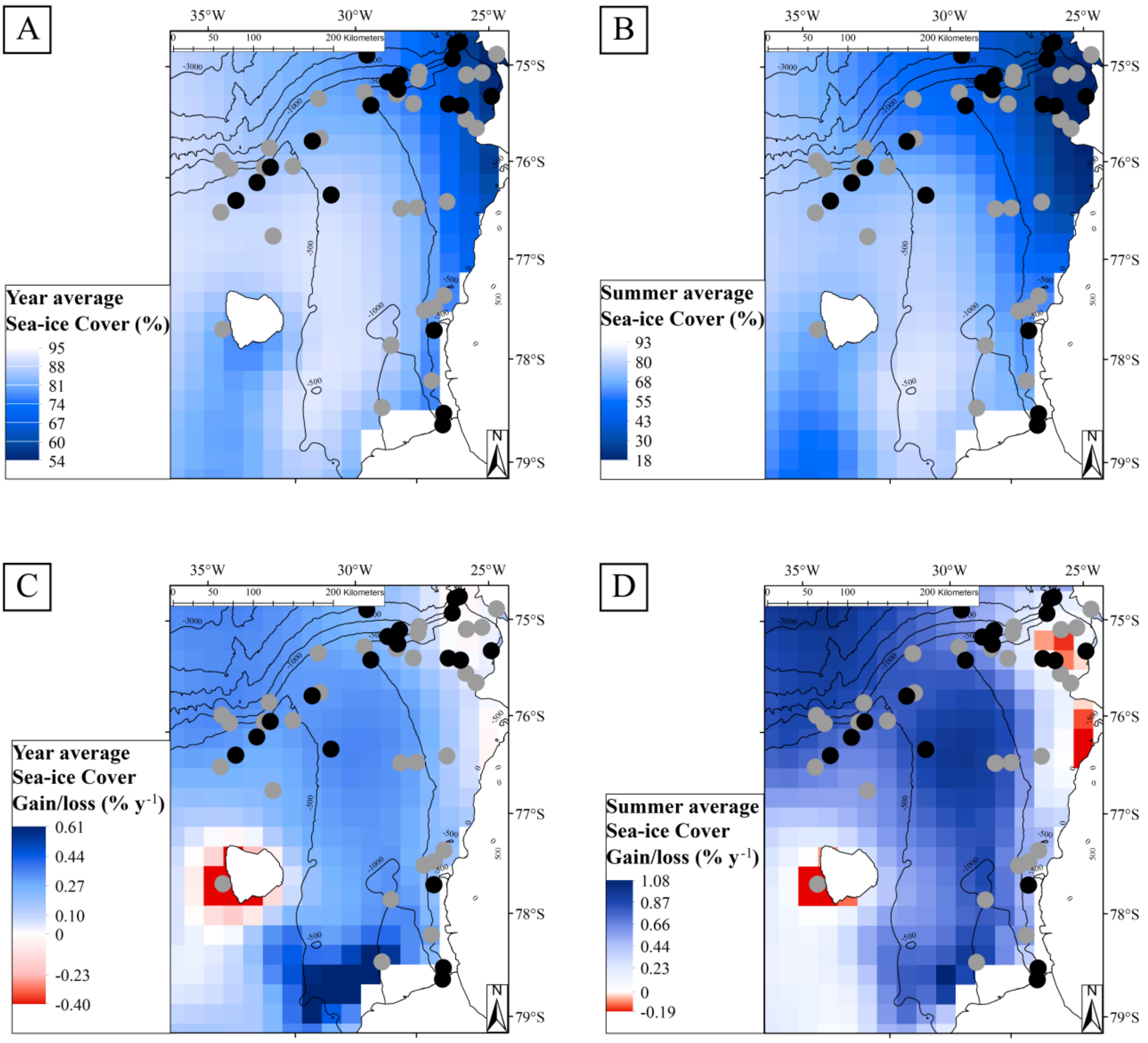

Fig.S5. Year (A) and summer (B) average sea-ice cover, and average year (C) and summer (D) sea-ice cover gain/loss (in % y^{-1}) for the period 1979 to 2017 in the study area in the Filchner Region (Weddell Sea, Antarctica). Year and summer average sea-ice cover was calculated considering values for the period 1979-2017. Note that each plot has its own scale. Modified after Fetterer et al. (2018). Black circles represent MBC stations sampled in the late 1980s (Gerdes et al. 1992), grey circles represent MBC stations sampled during the mid-2010s (this study).

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ANNEX 2: Supplementary material for Manuscript 4

Supplementary Tables and legends

Table S1. List of stations per expedition and year considered in our study. Water depth and number of cores per station is also provided (Continued in next page).

Station Number	Campaign	Year	°Latitude (+N; -S)	°Longitude (+E; -W)	Water depth (m)	Number of cores
266	ANT-VI/3	1988	-71.15	-12.1167	332	5
298	ANT-VI/3	1988	-70.8333	-10.85	464	8
305	ANT-VI/3	1988	-71.13	-13	525	8
308	ANT-VI/3	1988	-71.2333	-12.9833	190	6
387	ANT-VI/3	1988	-71.3833	-13.95	308	7
396	ANT-VI/3	1988	-71.3	-13.7667	412	3
418	ANT-VI/3	1988	-71.3167	-12.4167	181	8
437	ANT-VI/3	1988	-70.9667	-11.2	350	8
503	ANT-VI/3	1988	-70.1333	-12.2	438	7
512	ANT-VI/3	1988	-70.7833	-10.55	266	4
274	ANT-VII/4	1989	-71.6183	-12.1817	211	7
277	ANT-VII/4	1989	-71.6633	-12.5817	405	7
292	ANT-VII/4	1989	-71.0633	-12.7017	561	5
1	ANT-XIII/3	1996	-71.3033	-12.2667	246	8
4	ANT-XIII/3	1996	-71.3033	-12.27	174	1
5	ANT-XIII/3	1996	-71.3033	-12.2717	172	2
6	ANT-XIII/3	1996	-71.575	-12.4333	169	1
8	ANT-XIII/3	1996	-71.5317	-13.515	574	6
9	ANT-XIII/3	1996	-71.5333	-13.5183	234	6
10	ANT-XIII/3	1996	-71.5367	-13.52	235	6
11	ANT-XIII/3	1996	-71.51	-13.47	239	3
12	ANT-XIII/3	1996	-71.6867	-12.5133	225	6
20	ANT-XIII/3	1996	-71.6783	-12.76	438	5
22	ANT-XIII/3	1996	-71.6683	-12.7867	224	1
23	ANT-XIII/3	1996	-71.66	-12.7583	216	6
24	ANT-XIII/3	1996	-71.135	-11.535	223	4
25	ANT-XIII/3	1996	-71.135	-11.5317	119	1
26	ANT-XIII/3	1996	-71.3283	-12.4133	118	5
27	ANT-XIII/3	1996	-71.3183	-12.38	182	6
28	ANT-XIII/3	1996	-71.31	-12.4233	159	5
29	ANT-XIII/3	1996	-71.32	-12.45	181	5
30	ANT-XIII/3	1996	-71.385	-14.3283	253	4
31	ANT-XIII/3	1996	-71.4867	-14.2817	628	3
33	ANT-XIII/3	1996	-71.5283	-13.6367	218	3
35	ANT-XIII/3	1996	-71.5317	-13.52	279	6
36	ANT-XIII/3	1996	-71.5317	-13.52	241	6
37	ANT-XIII/3	1996	-71.5317	-13.5167	238	4
38	ANT-XIII/3	1996	-71.53	-13.52	234	3
47	ANT-XV/3	1998	-70.8683	-10.49	234	7

48	ANT-XV/3	1998	-70.8683	-10.4883	245	5
63	ANT-XV/3	1998	-70.8683	-10.54	234	5
67	ANT-XV/3	1998	-70.8317	-10.6083	305	2
68	ANT-XV/3	1998	-70.8367	-10.62	269	7
225	ANT-XV/3	1998	-70.085	-10.5867	276	5
227	ANT-XV/3	1998	-70.8233	-10.645	360	2
228	ANT-XV/3	1998	-70.83	-10.6333	293	4
230	ANT-XV/3	1998	-70.8467	-10.5367	229	7
90	ANT-XVII/3	2000	-71.2093	-12.6627	365	-*
98	ANT-XVII/3	2000	-71.1817	-12.4683	314	-*
108	ANT-XVII/3	2000	-71.144	-12.2458	441	-*
112	ANT-XVII/3	2000	-71.1017	-12.7183	567	-*
114	ANT-XVII/3	2000	-70.7698	-10.7203	753	-*
120	ANT-XVII/3	2000	-70.8383	-10.5833	271	-*
136-6	ANT-XVII/3	2000	-70.8367	-10.575	256	-*
137	ANT-XVII/3	2000	-70.8367	-10.5783	272	-*
105	ANT-XXI/2	2004	-70.9417	-10.5335	295	6
106	ANT-XXI/2	2004	-70.944	-10.5338	304	8
116	ANT-XXI/2	2004	-70.9468	-10.5478	321	6
124	ANT-XXI/2	2004	-70.94	-10.529	290	6
125	ANT-XXI/2	2004	-70.94	-10.526	282	6
185	ANT-XXI/2	2004	-70.9435	-10.5275	294	6
197	ANT-XXI/2	2004	-70.9382	-10.5053	253	6
201	ANT-XXI/2	2004	-70.9375	-10.5502	322	4
274	ANT-XXVII/3	2011	-70.9428	-10.5712	333	7
275	ANT-XXVII/3	2011	-70.9403	-10.527	283	8
279	ANT-XXVII/3	2011	-70.937	-10.5055	250	7
283	ANT-XXVII/3	2011	-70.966	-10.5055	284	7
295	ANT-XXVII/3	2011	-70.9438	-10.5335	303	5
297	ANT-XXVII/3	2011	-70.9433	-10.527	276	7
359	PS82	2014	-70.9445	-10.5372	322	8
360	PS82	2014	-70.9418	-10.5295	283	7

*No core data available.

Supplementary Figures and captions

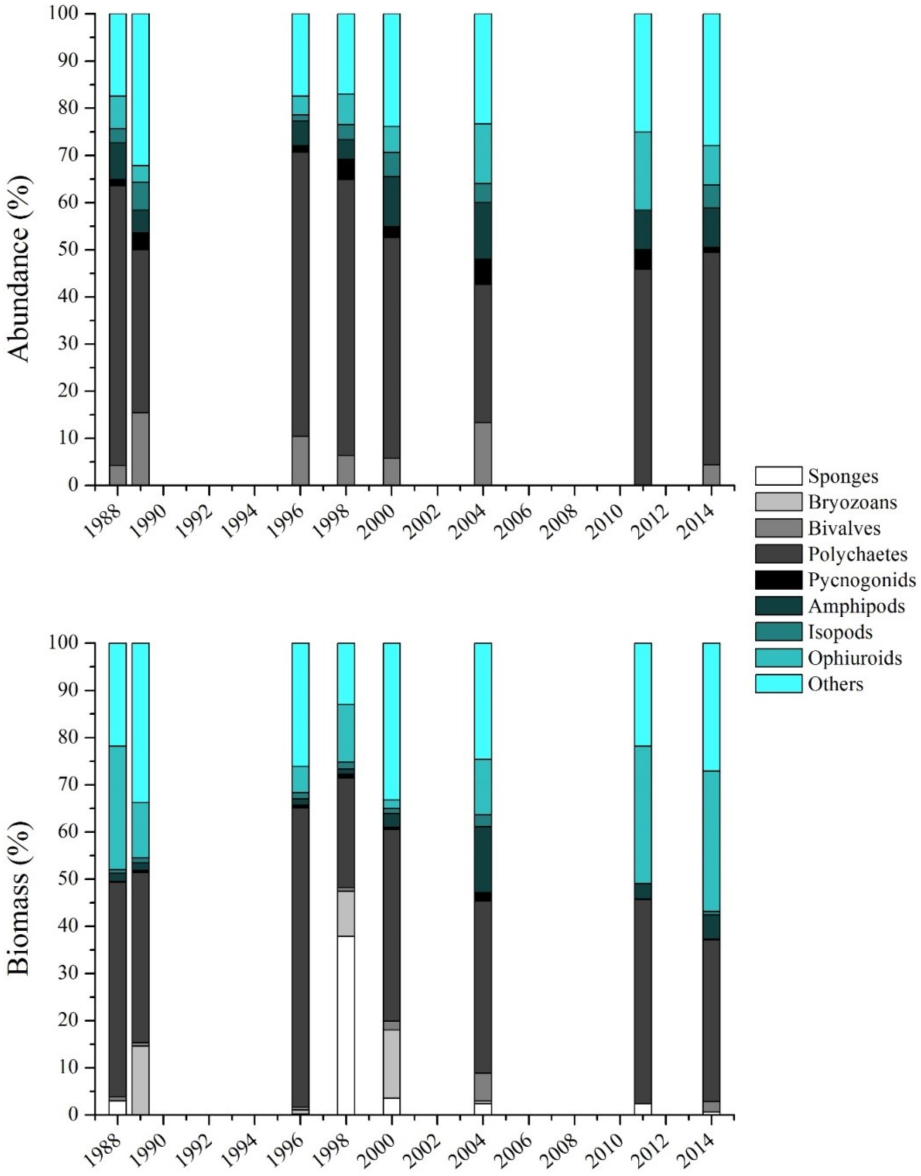

Fig.S1. Composition of the benthos in the shelf off Austasen for each sampling year. Relative abundance and biomass (%) calculated from median values per year.

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Two days before submitting this “lovely” thesis, I realize “wow, and so, three years flew by”. At that moment, well, it was actually after some hours of working on editing the text of the thesis for the n-th time, I started remembering faces, names and nicknames of those who should be included here, since I’m extremely thankful to all of them (and I owe one or two).

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And to you my dear reader, thank you too for enduring this far, and if you manage to get to this paragraph, you deserve a cookie. In case you didn’t read the whole thesis, but only this, you deserve two cookies.