Antarctic Continental Shelf Benthos under Changing Marine Icescapes – Structure, Function and Behaviour

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Preface

The following DPhil thesis investigates Antarctic continental shelf benthic assemblages, particularly their structure, function and behaviour, of marine environments within the Atlantic sector of the Southern Ocean, seldom accessed, and likely to be impacted by climate-induced environmental change, including alterations to the marine icescape.

The thesis is presented in paper format and comprises six chapters. Chapter 1 provides context to the research and closes with the research aims and objectives. Chapter 2 introduces the study areas and research methods utilised, presented in further detail in three subsequent research chapters, including: Chapter 3, which focuses on the structuring of megabenthic assemblages adjacent to an ice shelf; Chapter 4, focusing on the blue carbon storage function of zoobenthos across a southern polar gradient; and Chapter 5, which focuses on sub-ice-shelf macrobenthic assemblage behaviour, specifically spatial competition. Chapters 3 to 5 each represent a research paper and commence with a linking statement and indication of publication status. Chapter 6 closes the thesis, providing key findings, future perspectives, and concluding remarks. Supplementary materials and copies of published papers are provided in the Appendices.

Regarding the three research chapters, Chapter 3 is published in *Biology*, Chapter 4 is published in *Marine Environmental Research*, and Chapter 5 is published in *Science of the Total Environment*.

Advisors/supervisors during the DPhil include Dr David K.A. Barnes of the British Antarctic Survey, UK Natural Environment Research Council, Cambridge, and Drs Chloë M.J. Montes Strevens and Lisa M. Wedding of the School of Geography and the Environment, University of Oxford, Oxford.

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Finally, profound thanks go to my friends and family.

Abstract

As climate change and global warming advance, the coastal seas of Antarctica, although isolated oceanographically by the Antarctic Circumpolar Current, are undergoing physico-chemical transformations, including alterations to the marine cryosphere (icescape). These environmental modifications will have implications for Antarctica's varied and connected marine ecosystems, component biological communities, and associated ecosystem services, over diverse spatial and temporal scales.

Transitions of Antarctic marine icescapes from "white to blue" are being evidenced by, for example, sea-ice decline and glacier retreat over Antarctica's vast continental shelf, one-third (1.6 million km^2) of which is covered by floating extensions of the Antarctic Ice Sheet: "ice shelves". In high-/polar-latitude marine environments, loss of ice cover can create new or greater exposure to open-water conditions with opportunities for primary production and associated organic matter export (food-fall) to the benthos (communities of seafloor-dwelling organisms), which includes the majority of Antarctica's known species (biodiversity).

Constituting a critical component of the Southern Ocean ecosystem (and food web), Antarctic seabed biodiversity has evolved in partial isolation and relative constancy of physical conditions, punctuated by glaciations, and exhibits considerable endemicity in particular taxonomic groups and specific adaptations and traits. Furthermore, the benthos of Antarctica's continental shelf is becoming increasingly recognised for its role in storing carbon (as part of blue carbon), a function (and an ecosystem service) potentially supporting climate change mitigation. How such specialised biota, the communities they make up, and the services they provide will be impacted by climate- and global-warming-induced environmental changes, including marine icescape transitions, is yet to be fully realised, hindered, in part, by knowledge gaps of benthic assemblages at the margins of and beneath

ice shelves, where comparatively little ecological sampling has been conducted to date and where physical environmental change may be most profoundly/conspicuously exhibited.

This DPhil thesis aims to investigate, and enhance understanding of, the structuring, function and behaviour (three interconnected components) of contemporary Antarctic continental shelf benthic assemblages under different regimes of ice cover (e.g., sea-ice and ice-shelf environments) and in seldomly-accessed areas increasingly vulnerable to climate change, including ocean and atmospheric warming. The research encompasses varied datasets and methodologies (including the leveraging of a functional group approach), and sampling across contrasting continental shelf areas spanning the breadth of a high Antarctic to southern high-temperate region, and (i) determines megabenthic assemblage configurations adjacent to an evolving ice-shelf margin (within an intermittent rarely-accessible coastal polynya), and potential environmental drivers; (ii) discerns the variability in zoobenthic carbon storage, a function of the zoobenthos, across a southern polar gradient, and potential influences; and (iii) newly discovers macrobenthic assemblages competing for space deep beneath an ice shelf, establishes the nature of such competition, and compares findings to those of open-water environments (across latitudes).

Overall, the research contributes to increasing knowledge- and evidence-bases around Antarctic seabed life and its complexities, including of areas potentially facing significant environmental modifications, and provides new bio/ecological baselines (pertaining to structure, function and behaviour of benthic assemblages) from which change can be evaluated. The thesis outputs can support present and (near-)future marine ecosystem-based management, conservation measures, and spatial planning within national and international frameworks, including in view of evolving and emerging polar marine environments in a warming world.

Keywords

Antarctic continental shelf; megabenthic assemblage structure (and influences); zoobenthic blue carbon storage; macrobenthic spatial competition; functional groups; ice cover; ice shelves; marine icescapes; climate change

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Abbreviations

ABNJ	Area(s) Beyond National Jurisdiction
ACC	Antarctic Circumpolar Current
AFDM	Ash-Free Dry Mass
AGT	Agassiz trawl
AIS	Antarctic Ice Sheet
ANOVA	Analysis of Variance
ATS	Antarctic Treaty System
AUV	Autonomous Underwater Vehicle
AWI	Alfred Wegener Institute
BAS	British Antarctic Survey
BEST	Bio-Env (Routine)
BIIGLE	BioImage Indexing, Graphical Labeling and Exploration
CCAMLR	Commission for the Conservation of Antarctic Marine Living Resources
Chl-*a*	Chlorophyll-*a*
C_{inorg}	Inorganic carbon
CO_2	Carbon dioxide
C_{org}	Organic carbon
CTD	Conductivity-Temperature-Depth
C_{tot}	Total carbon (C_{inorg} + C_{org})
C_{zoo}	Zoobenthic carbon
EEZ	Exclusive Economic Zone
EIS	Ekström Ice Shelf (Research Area)

FOV	Field of View
FPS	Frames Per Second
GHG	Greenhouse Gas
GIS	Geographic Information System
HAC	Hierarchical Agglomerative Clustering
HD	High Definition
Ind.	Individual(s)
IMO	International Maritime Organization
IPCC	Intergovernmental Panel on Climate Change
LCP	Larsen C (Ice Shelf) Polynya (Research Area)
MC	Marian Cove (of King George Island Shelf Research Area)
MPA	Marine Protected Area
NERC	Natural Environment Research Council
NDC	Nationally Determined Contribution
nMDS	non-Metric Multidimensional Scaling
NPP	Net Primary Production
PAR	Photosynthetically Active Radiation
PCA	Principal Component Analysis
PERMANOVA	Permutational Multivariate Analysis of Variance
PRIMER	Plymouth Routines in Multivariate Ecological Research
PSU	Practical Salinity Unit
ROV	Remotely Operated Vehicle
RRS	Royal Research Ship
SAERI	South Atlantic Environmental Research Institute

SCUBA	Self-Contained Underwater Breathing Apparatus
SD	Standard Deviation
SE	Standard Error
SG	South Georgia (Shelf Research Area)
SIC	Sea-Ice Cover
SIMPER	Similarity Percentages
SIMPROF	Similarity Profile
SP	Southeast Patagonia (Shelf Research Area)
SUCS	Shelf Underwater Camera System (designed by BAS)
UKRI	UK Research and Innovation
UN	United Nations
UNFCCC	United Nations Framework Convention on Climate Change
VME	Vulnerable Marine Ecosystem
WAP	Western Antarctic Peninsula (Shelf Research Area)
WoRMS	World Register of Marine Species
WS-MPA	Weddell Sea Marine Protected Area

Chapter 1 | Introduction

Ice is a dominant environmental feature of polar marine environments. Loss of ice cover, naturally or due to anthropogenic climate change, can influence environmental conditions, with potential implications for marine life, including the benthos. To help understand how polar benthic communities may respond to ice-cover losses in a warming world, this research explores the structure, function (ecosystem service provisioning), and behaviour (species interactions) of Antarctic continental shelf assemblages under different ice-cover regimes in seldom-accessed, yet extensive, seabed environments.

The following chapter provides preliminary context to the Antarctic-based research conducted in this thesis, with more detailed contexts provided in individual research chapters, and includes particular focus on the following areas pertinent to the thesis:

i. The governing body responsible for protecting marine life of the Southern Ocean global commons: the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR)
ii. Marine ecosystem services, including an introduction to high-latitude zoobenthic blue carbon,

and, in closing, provides the overall aims and objectives of the thesis in respect of associated and dedicated research chapters.

A map of the Antarctic continent and surrounding seas, including locations of the six primary study areas encompassed in this thesis, is provided in **Figure 1.1**. More detailed maps of the study areas are provided in corresponding research chapters.

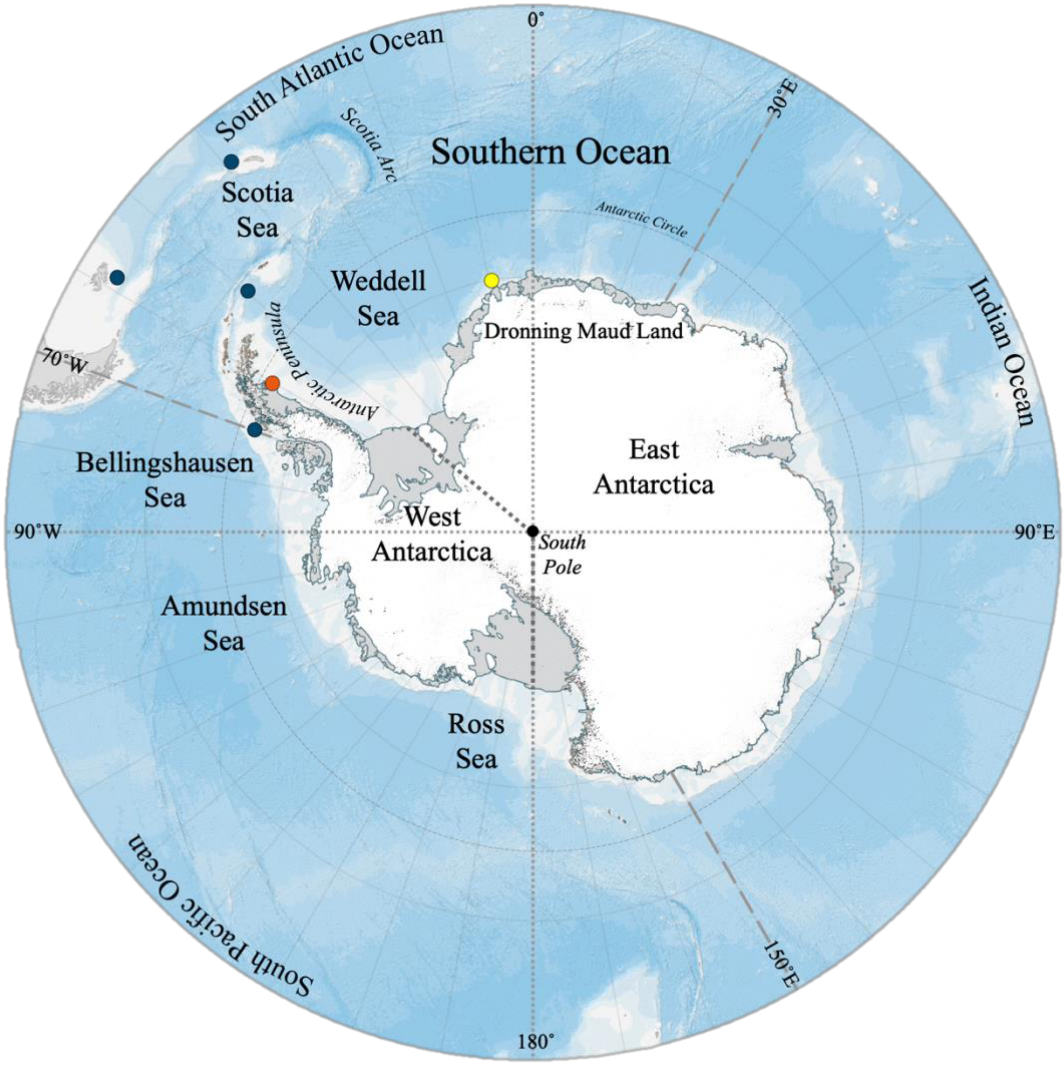


Figure 1.1: The Antarctic continent and surrounding seas, including locations of the six primary continental/island shelf study areas of the thesis (all within the Atlantic sector of the Southern Ocean, between 70°W and 30°E). Orange circle indicates study area of Chapter 3, focus megabenthic assemblage structure in the Larsen C Ice Shelf Polynya; blue circles indicate study areas of Chapter 4, focus (epi)zoobenthic carbon storage across the Scotia Arc; and yellow circle indicates study area of Chapter 5, focus macrobenthic behaviour beneath Ekström Ice Shelf. Grey areas fringing Antarctica indicate ice shelf areas.

1.1 Preliminary Context to the Antarctic-based Research

Despite being remote and partially isolated oceanographically by the Antarctic Circumpolar Current (ACC), the polar seas surrounding Antarctica are not impervious to anthropogenic impacts and are expected to undergo significant transformations as global climate change advances. Indeed, parts of the Antarctic, especially the Antarctic Peninsula (the northernmost part of the Antarctic continent), are among the regions of the world where climate change is hitting hard and fast (IPCC, 2014, 2019). Climate-induced alterations to the Antarctic cryosphere (icescape) will also likely have wide-ranging implications for Antarctica's varied and connected marine ecosystems, component living communities, and associated ecosystem goods and services over diverse spatial and temporal scales (Gutt et al., 2019; Vause et al., 2019; Rogers et al., 2020; Cavanagh et al., 2021; Gutt et al., 2021).

Transitions in Antarctica's marine icescapes, from "white to blue", are being most conspicuously evidenced by the retreat and collapse of ice shelves (see **Figure 1.2**) and glaciers (floating extensions of the Antarctic Ice Sheet) and areas of seasonal sea-ice decline (Scambos et al., 2003, 2008; Cook and Vaughan, 2010; Rignot et al., 2013; Cook et al., 2016; Turner et al., 2014; Eayrs et al., 2021; Gutt et al., 2021). Losses of formerly "permanent" ice cover, such as through ice-shelf disintegration, create large marine areas newly exposed to open-water regimes, with new or increased opportunities for photo-induced primary production and associated food fall to the seafloor (Bertolin and Schloss, 2009; Sañé et al., 2011; Gutt et al., 2013), where the majority (>95%) of Antarctica's known biodiversity resides (De Broyer et al., 2014).

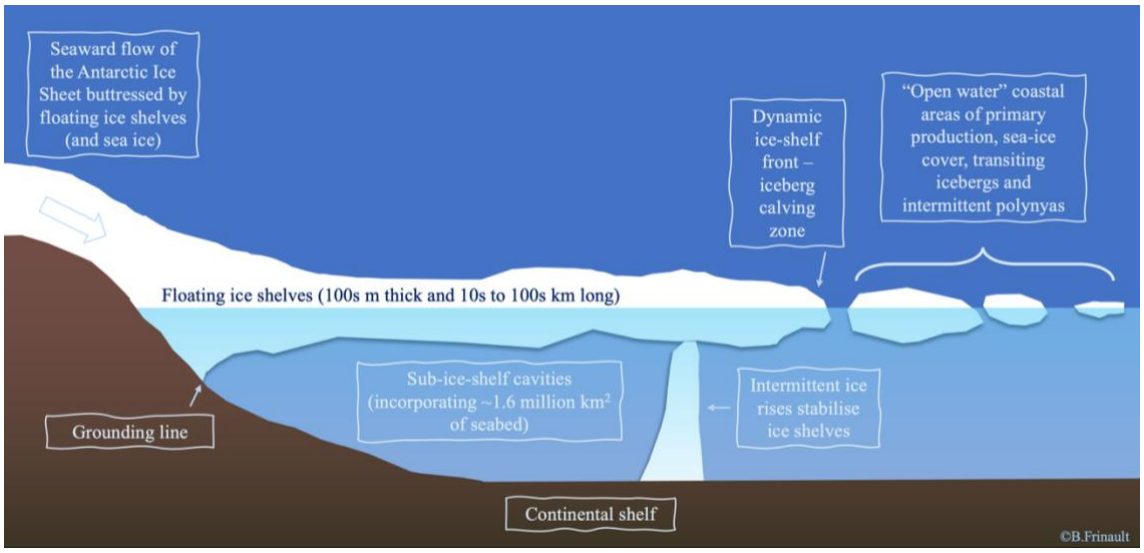


Figure 1.2: Antarctic ice shelf schematic encompassing the seaward flow of the Antarctic Ice Sheet creating floating ice shelves (100s m in thickness and 10s to 100s km in length) stabilised (in part) by ice rises. Between the grounding line and ice-shelf front exist vast sub-ice-shelf cavities and a relatively ecologically unexplored seabed area of ~1.6 million km^2. Beyond the ice-shelf front lies "open water" coastal areas of primary production, sea-ice cover, transiting icebergs and intermittent polynyas.

A critical component of the wider Southern Ocean ecosystem and food web, Antarctic seabed biodiversity (benthos) (Henley et al., 2020) is becoming increasingly recognised for its role in ocean health and carbon capture, storage and sequestration (Peck et al., 2010; Barnes, 2017, 2018; Barnes et al., 2018; Sands et al., 2023). Such life has evolved in partial isolation, afforded, in part, by the size and strength of the ACC, relative constancy of physical conditions, punctuated by glaciations, and, consequently, exhibits very high endemism in some taxonomic groups (Arntz et al., 1994). Furthermore, in response to their unique environment, many benthic taxa have developed specific adaptations and traits, exemplified by slow growth and development and great longevity (Arntz et al., 1994; Clarke and Johnston, 2003). Although climate change is advancing (Rogers et al., 2020), how such specialised biota and the communities they comprise will respond to anticipated alterations in overlying Antarctic marine icescapes, including ice-shelf loss, is yet to be fully realised. Our understanding is hindered by extensive

knowledge gaps, especially of seabed assemblages (that make up communities) residing beside and beneath ice shelves, chiefly due to challenges of access; indeed, large areas of the Southern Ocean seafloor have had little or no ecological sampling to date (Convey et al., 2009; Griffiths, 2010). Nonetheless, it is likely that benthic taxa and assemblages may respond to such environmental change in various ways, including structurally, functionally and behaviourally (e.g., Smale and Barnes, 2008; Ingels et al., 2012; Hale et al., 2014; Ashton et al., 2017; Rogers et al., 2020 and see references within; Barnes et al, 2021; Gómez-Gras et al., 2021; Weinert et al., 2022).

This DPhil thesis aims to help reduce such knowledge gaps by exploring the structure, function and behaviour within contemporary Antarctic continental shelf assemblages under different ice-cover regimes (from open-water with seasonal sea-ice cover to permanent cover by an ice shelf) and of rarely-accessed yet vast marine environments vulnerable to climate change or which have already incurred considerable ice loss. The current research incorporates sampling across contrasting seas, varied apparatus types and the full breadth of the high continental Antarctic to sub-Antarctic archipelagos. The work explores megabenthic assemblage configurations and environmental drivers in an intermittent coastal polynya (a polynya being an open-water area where sea-ice cover is expected, see Arrigo and van Dijken, 2003; Grebmeier and Barry, 2007; Arrigo et al., 2008, 2015) adjacent to an evolving ice margin, the Larsen C Ice Shelf front; assesses the carbon-storage function of zoobenthic assemblages across a latitudinal gradient (from Antarctic to sub-Antarctic waters) and with differing seasonal sea-ice cover; and determines the nature of a fundamental biotic/species interaction type, spatial competition, in macrobenthic assemblages deep beneath an ice shelf (Ekström Ice Shelf) compared to that of open-sea environments – this being the very first study to illuminate the characteristics of any sub-ice-shelf competition.

This research also aims to contribute to an increased understanding of the nature of seabed life in areas potentially facing climate-induced environmental alterations and the potential impacts of a changing icescape on the benthos of the Antarctic continental shelf. In addition, the associated explorations provide new biological/ecological baselines from which change (structural, functional and behavioural) can be assessed or monitored as environmental modifications, such as those related to marine icescape transitions, transpire. The research is also pertinent as cold-water benthic communities are becoming acknowledged as deliverers, maintainers and enhancers of carbon storage and sequestration-related ecosystem services – with a potentially increasing role in climate mitigation as climate change advances (Barnes et al., 2020; Bax et al., 2021; Sands et al., 2023). The outputs of the DPhil thesis can inform present and near-future marine ecosystem management, conservation and spatial planning in both national and international frameworks, in view of emergent polar environments.

1.2 Governance of the Antarctic Marine Commons

Researching Antarctica's marine ecosystems and resident biological communities can have many challenges, including access and resources; indeed, much of the Antarctic marine environment is, as of yet, not ecologically explored. Discoveries and the generation of new knowledge, however, can help deliver and enhance evidence bases essential for decision-making regarding, for example, marine conservation in the region.

Safeguarding the global marine commons of Antarctica principally falls under two connected multilateral regimes: the Antarctic Treaty System, which entered into force in 1961, and CCAMLR, founded in 1982 and associated with the Convention for the Conservation of Antarctic Marine Living Resources.

Essentially, CCAMLR (also known as the Commission) has influence over 35.7 million km^2 of the Southern Ocean, referred to as the "Convention Area" (see **Figure 1.3**). The area is divided into three major sectors according to contiguous ocean: the Atlantic, Pacific and Indian, designated as CCAMLR sub-areas 48, 88 and 58, respectively. For the Convention Area, CCAMLR decides on and implements conservation measures and management and protection frameworks, including the designation of Marine Protected Areas (MPAs), regulates fisheries (harvesting), e.g., through quotas, and is responsible for conserving and managing all marine life, including that making up seafloor (benthic) communities, i.e., the benthos (Rogers et al., 2020; Hughes et al., 2023) (and the exceptions being seals and whales, which are considered within other conventions).

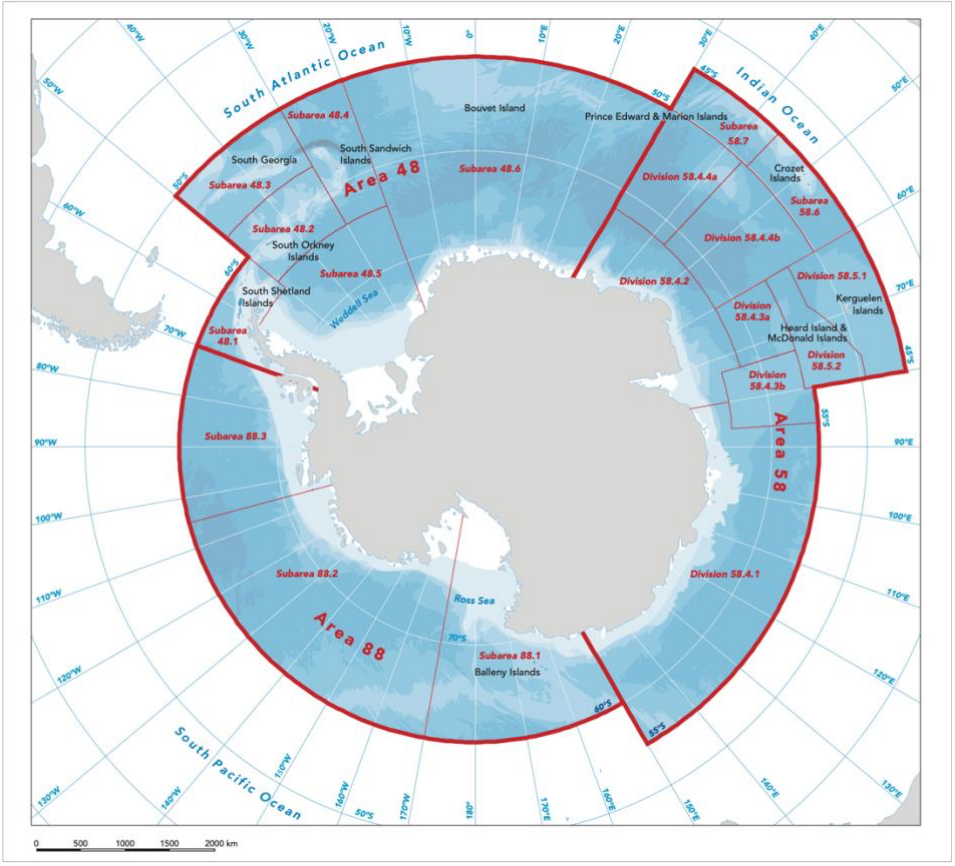


Figure 1.3: Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Convention Area and Statistical Areas and Subareas (modified from CCAMLR, 2017).

Originally, CCAMLR was created in response to concerns regarding emerging interests in bulk harvesting of a key species in the Southern Ocean food web, the malacostracan crustacean *Euphausia superba*, Antarctic krill, to help prevent a repeat of adverse outcomes associated with past harvesting activities, which had inadvertently led to the decimation and near-extinction of certain whale, seal and groundfish populations (Ainley and Brooks, 2013; Brooks, 2013; Ainley and Pauly, 2014; Rogers et al., 2020). The first CCAMLR meeting took place in Hobart, Tasmania, in 1982, and since then, the Commission has typically met on an annual basis. Today, CCAMLR aims to inclusively conserve Antarctic marine life using an ecosystem-based approach.

Parties of CCAMLR comprise 27 member states, including the European Union, each party having representation in the Commission. In the Convention Area, (propositioned) conservation measures and management and protection frameworks can only be adopted if all associated concerns raised (by parties) are remedied and all parties are in unanimous agreement. Naturally, such consensus-based decision-making can be time-consuming, challenging to achieve and may require compromise (see Nilsson et al., 2016; Brooks et al., 2019; Goldworthy, 2022). Over 20 years ago, CCAMLR committed to creating, by 2012, a representative and comprehensive network of MPAs in the Southern Ocean across nine MPA planning domains (see Brooks et al., 2020); however, various delays have impeded its realisation. Nonetheless, to date, the Commission has adopted two MPAs: the South Orkney Islands Southern Shelf MPA (established 2009) and the Ross Sea MPA (established 2016 and constituting the world's largest MPA) in sub-areas 48 and 88, and Domains 1 and 8, respectively (Brooks et al., 2020, 2021).

Other propositioned MPAs, such as the Weddell Sea MPA (WS-MPA), situated within sub-area 48 and Domain 3, have not yet been approved due to opposition from a few member states (Brooks et al., 2016, 2019; Liu and Brooks, 2018; Sylvester and

Brooks, 2020). Registered concerns have included spatial and temporal restrictions to harvesting and knowledge gaps in scientific support (e.g., see Brooks, 2013; Brooks et al., 2016; Jacquet et al., 2016; Sylvester and Brooks, 2020). It is understood that apparent knowledge gaps could, in part, be narrowed through delivery of further information, including that which is area-specific, on benthic communities inhabiting the Antarctic continental shelf, such as that pertaining to their structure (composition), function (including functions constituting ecosystem services) and behaviour (e.g., competition). Additionally, specific benthic taxa, considered by the Commission as indicative of Vulnerable Marine Ecosystems (CCAMLR, 2009; FAO, 2009; and referred to as VME taxa), if identified as present, can be utilised to support/complement management and protection frameworks within the CCAMLR Convention Area (Parker and Bowden, 2010; Brasier et al., 2018).

With climate-forced changes (current and predicted) to Antarctica's seas, such as marine icescape modifications, CCAMLR's implementation of conservation measures and MPAs to protect Antarctic marine life and ecosystems may become increasingly time-sensitive. Furthermore, as ice cover is reduced, including over the continental shelf, accessibility will increase, potentially rousing historic and novel extractive (and non-extractive, e.g., touristic; Deininger et al., 2016; Rogers et al., 2020) interest in the region, related activities of which could put adverse pressures on marine communities in addition to climate change.

1.3 Antarctic Marine Ecosystem Services

Understanding and consideration of ecosystem services can support evidence bases and decision-making, especially around ecosystem-based conservation and management (O'Higgins et al., 2020). Within the thesis the ecosystem service "blue carbon" is

presented as a function of benthic communities, and the following section provides a brief introduction to the concept of ecosystem services, with services of the Antarctic marine environment/Southern Ocean used as examples.

Ecosystem services (including goods) can be generally defined as "the benefits people obtain from ecosystems" (Millennium Ecosystem Assessment, 2005). The Southern Ocean is vital to the provisioning of an abundance of marine ecosystem services locally and globally – the futures of which are potentially vulnerable to climate change (Grant et al., 2013; Deininger et al., 2016; Rogers et al., 2020; Cavanagh et al., 2021).

Ecosystem services fall into four, at times overlapping, categories: (i) provisioning; (ii) cultural; (iii) regulating; and (iv) supporting. Examples of marine ecosystem services include: fisheries, oil and gas, tourism, climate and air regulation, cryospheric balance, carbon capture, storage and sequestration, primary production, nutrient cycling, habitat supply, maintenance of biodiversity, and biodiversity itself (Rogers et al., 2020). As can be envisaged, the delivery and extent of such services can alter with ecosystem (and biological community) shifts induced by changes in encompassing environments (Rocha et al., 2015; Rogers et al., 2020), and in Antarctica, for example, marine icescape transitions (and other environmental dynamics associated) (Barnes et al., 2018; Cavanagh et al., 2021), which can represent severe ecosystem modifications.

At a global level, Antarctic seas (and, by extension, the Southern Ocean) are fundamental to the ventilation of and provision of macronutrients to the world's great oceans, including the Pacific, Atlantic and Indian Oceans – supporting biological productivity and biodiversity; hence, humankind (Hauck et al., 2015; Keller et al., 2016; Rogers et al., 2020). Furthermore, the Southern Ocean, which represents ~10% of the global ocean network (by surface area), accounts for ~25% of global oceanic uptake of

anthropogenic carbon dioxide (CO_2) (Arrigo et al., 2008) – the most ubiquitous of the greenhouse gases. Hence, the Southern Ocean has a major, although complex, role in helping to regulate Earth's climate – this via carbon capture, storage (e.g., within its deep waters and seabed) and potential sequestration (Arrigo et al., 2008; Long et al., 2021; Friedlingstein et al., 2023).

At a local level, and particularly in the more northern marine areas of the Atlantic sector of the Southern Ocean, an important ecosystem service is the provisioning of fish stocks for international fisheries, associated activities of which have, so far, taken place outside of the Weddell Sea (Antarctica's largest sea at ~3 million km^2; see **Figure 1.1**) owing to perennially-heavy sea-ice cover challenging and precluding vessel access (see Brooks, 2013; Grant et al., 2013). Overall, in the Convention Area, the most important species by tonnage caught are the mackerel icefish (*Champsocephalus gunnari*), Patagonian toothfish (*Dissostichus eleginoides*), Antarctic toothfish (*Dissostichus mawsoni*), the latter two fishes collectively referred to as Chilean seabass and "white gold" (Brooks, 2013), and a critical Antarctic food web species, Antarctic krill, krill constituting some 95% of overall catch (and used in aquaculture feeds and dietary supplements; Nash et al., 2014) – the Atlantic sector being the dominant source of all catch (>90%; CCAMLR, 2019). Coupled with increasing global demand for animal protein and depletion of fish stocks elsewhere, the pressure to expand fisheries within Antarctica's global marine commons is building (Brooks, 2013; Brooks et al., 2016). Moreover, climate-forced ice loss, as observed in parts of West Antarctica, and including novel areas of sea-ice decline and ice-shelf retreat in the Weddell Sea, will likely improve accessibility and navigability for vessels, and may well incite interest regarding prospective fishing or the expansion of current fisheries' operations, as already demonstrated in the Arctic (Molenaar, 2015).

An ecosystem service also associated with marine living resources currently attracting much attention, and thought to have the capacity to increase with climate change, particularly in Antarctica (Peck et al., 2010; Barnes, 2015; Bax et al., 2021; Sands et al., 2023), is that of (zoo)benthic blue carbon; blue carbon being defined as the carbon captured and held by marine life (Barnes, 2018). Indeed, Antarctic benthic communities and habitats are becoming increasingly recognised for their carbon storage function, essentially acting as carbon sinks helping to moderate atmospheric CO_2 levels (Peck et al., 2010; Alurralde et al., 2019; Barnes et al., 2020, 2021). Furthermore, as ice cover is lost, the potential development or expansion of benthic assemblages, hence seabed carbon storage channels, is anticipated (e.g., Zwerschke et al., 2022). Although assessments of contemporary Antarctic blue carbon remain limited, several studies have indicated that benthic habitats of southern high-latitudes, including those projected to emerge, could represent considerable negative feedbacks on climate change through their carbon storage function (e.g., Peck et al., 2010; Barnes et al., 2020, 2021; Zwerschke et al., 2022); therefore, potentially warranting protective prioritisation of such habitats in marine spatial planning.

1.4 Thesis Aims and Objectives

This doctoral thesis aims to investigate and enhance understanding of how Antarctic benthic assemblages may respond to changes in marine icescapes, an effect of climate change. To achieve this overarching aim, contrasting yet interconnected aspects of mega- and macro-benthic life were principally investigated, with varied methodologies employed, in areas of the Atlantic sector of the Southern Ocean. The aspects of benthic life explored comprised: structure, function and behaviour, with the following corresponding objectives explored in Chapters 3, 4 and 5, respectively:

(i) To characterise the structure of megabenthic assemblages of a rarely accessed and sampled polynya bordering a dynamic and evolving ice-shelf front and determine potential environmental drivers of variability (including whether historical ice cover and distance from the ice shelf are key influences).

(ii) To ascertain how zoobenthic carbon storage (a function of and ecosystem service afforded by zoobenthos) may vary from southern high-temperate to polar latitudes (with different sea-ice cover regimes) and determine potential influences.

(iii) To establish whether macrobenthic spatial competition occurs beneath the "permanent" cover of an ice shelf and, if so, to resolve its nature and compare it with that of open-water environments of both polar and lower latitudes.

Research Chapters 3, 4 and 5 are published (Frinault et al., 2022, Frinault and Barnes, 2024 and Frinault et al., 2023, respectively).

The subsequent chapter, Chapter 2, introduces the southern high-latitude study areas (and sites) of the thesis and research methods utilised, more details of which are provided in research Chapters 3, 4 and 5.

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Chapter 2 | Study Areas and Methods

The following chapter provides an overview of the Atlantic Antarctic study areas of the DPhil thesis (see **Figure 1.1**) and the research methods used, further details of which are presented, and referenced accordingly, in research Chapters 3, 4 and 5 (see Frinault et al., 2022; Frinault and Barnes, 2024; Frinault et al., 2023, respectively).

The research methods encompass a range of data collection, generation and analysis techniques brought together to deliver the aims and objectives of the doctoral thesis. Each research chapter encompasses imagery data – such datasets considered fundamental for discovery, monitoring, and management of ocean ecosystems, including those spatially-extensive and remote (Schoening et al., 2022), and, correspondingly, visual analysis: in Chapter 3, of seafloor video-transects; in Chapter 4, of still photographs of the seabed; and in Chapter 5, of colonised sub-ice-shelf substrata via stereo microscopy.

2.1 Study Areas

The six primary study areas of the thesis are continental or island shelves (latitudinal range ~54 to 71°S; longitudinal range ~8 to 70°W; and depth range ~60 to 680 m) principally within the Atlantic sector of the Southern Ocean and encompassing both (what are termed) West and East Antarctica, the exception being the area located on the southeast Patagonian shelf in the contiguous South Atlantic Ocean and connected to the West Antarctic study areas by the Scotia Arc (see **Figure 1.1**).

Chapter 3: The study of megabenthic assemblage structuring at an ice-shelf front (see **Figure 1.2**) encompassed four continental shelf sites (of latitudes between 66 and 67°S; longitude ~60°W; and depth range ~300 to 400 m) situated within the intermittent and wind-driven coastal Larsen C Ice Shelf Polynya. The sites were adjacent to the

northernmost sector of Larsen C Ice Shelf between the Jason Peninsula and Bawden Ice Rise. The Larsen C Ice Shelf is located on the eastern side of the Antarctic Peninsula, western Weddell Sea (West Antarctica). Sites varied in distance (seaward) from the ice-shelf calving front. The study area, renowned for heavy perennial sea-ice cover, was accessed, when the polynya was open, by the South African polar supply and research vessel *SA Agulhas II* as part of a 2018/19 expedition in search of *Endurance* (funded by the Flotilla Foundation and Marine Archaeology Consultants Switzerland) (see Dowdeswell et al., 2019; Bound, 2022). Vessel access was exceptionally enabled, at the time (January 2019), not only by the opening of the polynya, but also by suitable leads (linear fractures) in the surrounding sea ice and the presence of a giant (surface area ~6,000 km^2) tabular iceberg, A-68, which shielded the study area from further influx of transiting sea ice and smaller icebergs (from the south) (Dowdeswell et al., 2020).

Chapter 4: The study of carbon storage by high-latitude zoobenthic assemblages extended southern high-temperate and high-Antarctic waters (latitudinal range ~54-67°S; longitudinal range ~38-70°W; and depths from ~60-620 m) and included four distinct study areas (with three shelf sites per area, i.e., 12 sites total) distributed across a latitudinal (and sea-ice cover) gradient and connected by the Scotia Arc. The areas comprised continental/island shelves of the Falkland Islands/Islas Malvinas (southern South Atlantic); South Georgia (which bisects the Antarctic Circumpolar Current); Marian Cove of King George Island (part of the South Shetland archipelago), just above the northern tip of the Antarctic Peninsula; and Marguerite Bay, in the Bellingshausen Sea, on the western Antarctic Peninsula (within the Antarctic Circle); the latter two areas lying within West Antarctica. All areas (and sites) were accessed by the Royal Research Ship *RRS James Clark Ross* as part of various, principally BAS-led, expeditions (within the 2011-2020 timeframe).

Chapter 5: The study of sub-ice-shelf macrobenthic spatial competition encompassed two continental shelf sites beneath Ekström Ice Shelf, eastern Weddell Sea (East Antarctica) (latitude ~71°S; longitude ~8°W; and depths ~250 and 300 m). The sites were ~20 km apart and situated >3 and ~10 km landward from the ice-shelf front. The sites were accessed via boreholes drilled through the ice shelf, which was ~200 m thick at each location. The heights of the underlying marine cavities (see **Figure 1.2**), extending from the base of the floating ice shelf to the seafloor below, were ~60 and 110 m. Borehole-related activities were carried out as part of the 2017-19 Sub-EIS-Obs Project, principally funded by the Alfred Wegener Institute (AWI) and the Federal Institute for Geosciences and Natural Resources, Germany (Kuhn and Gaedicke, 2015; Kuhn et al., 2019). The AWI research station, Neumayer III, located relatively near the boreholes, provided logistical support for drill teams. The research within this chapter constitutes the first-ever study of competition for resources under an ice shelf, and the highest latitude study of ecological competition in the Southern Hemisphere. The design of the study and results permitted comparison with findings from other marine environments of differing latitude (across both hemispheres), with the Antarctic sub-ice-shelf environment considered a global disturbance minimum.

2.2 Methods

2.2.1 Environmental Data

Environmental data, principally used in Chapters 3 and 4, were collected in situ or generated using remotely-sensed Earth Observation data. In situ oceanographical data were acquired using a CTD (conductivity-temperature-depth) system yielding, for example, measurements of temperature, salinity, dissolved oxygen and nutrient concentrations (e.g., Hutchinson et al., 2020; Flynn et al., 2021). In all cases, equipment

for collecting in situ oceanographical data was fitted with underwater acoustic positioning systems to provide corresponding latitude, longitude and depth. Primary production and ice cover (ice-shelf extent and sea-ice concentration) were computed from remotely sensed satellite data (e.g., Arrigo et al., 2008, 2015; Christie et al., 2022). Environmental data were additionally derived from appraisal of seafloor imagery, including prevailing substratum type, level of phytodetritus and rugosity (small-scale roughness) – the latter determined by shadow length of substrata (as per Barnes et al., 2019 and Souster et al., 2020).

2.2.2 Physical Biological Samples

Physical biological samples used in Chapters 4 and 5 were obtained from faunal collections/inventories arising from Agassiz or mini-Agassiz trawls (AGTs) conducted on continental/island shelves, and from sub-ice-shelf seabed sediment cores/grabs, respectively, with associated sampling activities carried out by BAS/AWI and partners, and under specialist permits as per Antarctic Treaty. In all cases, equipment for collecting physical samples was fitted with underwater acoustic positioning systems to provide corresponding latitude, longitude and depth.

The benthic fauna collected by AGTs were identified (taxonomically) and their respective carbon content determined for use in zoobenthic carbon storage evaluations. Encrusting fauna of sub-ice-shelf substrata isolated from seafloor sediment cores/grabs were identified predominantly to species-level, with competitive interactions between colonies discerned and outcomes determined using established methodologies and stereo microscopy.

2.2.3 Seafloor Imagery Collections

The seafloor imagery data used in Chapter 3 and Chapter 4 to determine benthic assemblage structure and characterise the corresponding seabed environment, encompassed videos and stills (photographs), respectively.

Video imagery: Raw video imagery (of Chapter 3) was obtained using a tethered Remotely Operated Vehicle (ROV) equipped with a high-definition colour video camera acutely angled toward the seafloor (permitting a more landscape perspective). The ROV was also fitted with scaling lasers, lights and a high-precision acoustic positioning system (to record latitude, longitude and depth). Video footage was timestamped, enabling pairing of observations with ROV positional data, as appropriate. The video imagery required extensive processing/post-processing, including continuity checks, quality enhancement (deinterlacing), as well as the extraction of still frames – the extraction rate being informed by: (i) mean ROV velocity (calculated from positional date); (ii) field of view (FOV) of the video camera (computed using trigonometry); and (iii) maps of the ROV tracks (generated in QGIS); and (iv) general inspection of corresponding video footage.

Still imagery: Still images (of Chapter 4) were acquired through deployment of the Shelf Underwater Camera System (SUCS) developed by the BAS Antarctic Marine Engineering Group. SUCS comprises a tethered (fibre-optic multimode cable) high-resolution still camera, dimmable lights and real-time ultra-short baseline positioning beacon (to record latitude, longitude and depth), all mounted on a tripod. During operations, the camera was positioned perpendicular to the seabed (the tripod is able to adjust for a sloped seafloor) and pre-set to capture images (replicates) of the same size/FOV, enabling quantitative analyses. The associated sampling method was designed

to circumvent spatial overlap between images, which could otherwise result in duplicate observations, and additionally reduces post-processing requirements.

2.2.4 Imagery Analysis

Video imagery: Extracted still frames (>3,000) were analysed using a web-based imagery annotation tool, specifically BioImage Indexing, Graphical Labeling and Exploration (BIIGLE) 2.0 (Langenkämper et al., 2017), with bespoke label trees created for the study, and the faunal label tree based on WoRMS taxonomy and informed by Antarctic benthos field guides (e.g., Gon and Heemstra, 1990; Hibberd and Moore, 2009; Rauschert and Arntz, 2015). Frame analysis included annotation (hence enumeration) of all discernible (epi)benthic megafauna (i.e., organisms large enough to be discerned within seafloor imagery; Rex, 1981) and identification of such fauna to the highest taxonomic resolution possible (with identities further verified by taxonomic experts as appropriate). The species/morphotaxa (i.e., taxa differentiated by morphological traits) observed (counted) were each ascribed a functional group. Substratum type and level of phytodetritus, seabed features (e.g., circular/elliptic depressions and cold seeps) and biotic interactions (e.g., instances of commensalism) were also identified and recorded. Faunal and functional group densities were computed for community (including assemblage structure) analyses.

Still imagery: Still images (~240) were analysed using BIIGLE 2.0, with bespoke label trees (suitable for the study areas) developed before imagery evaluation and able to be updated when new species/morphotaxa are observed. Images were appraised for: (i) all perceptible megabenthic fauna (assigned to 13 functional groups, based on skeletisation, mobility and feeding mode – traits considered important to blue carbon pathways (Barnes and Sands, 2017)); (ii) richness, i.e., the number of different morphotaxa and functional groups; and (iii) environmental setting including substratum

type (derived from the Udden-Wentworth scale) and rugosity (assessed by shadow-length of substrata). As the seafloor area represented by each image was known (being pre-set), corresponding faunal and functional group densities were able to be calculated for subsequent use in zoobenthic carbon storage estimations.

2.2.5 Assemblage Structuring and Influences – Statistical Approaches

Community (including assemblage structure) analysis of the megabenthic assemblages adjacent to an ice shelf (part of Chapter 3) comprised calculations of univariate indices, including the total number of morphotaxa (richness), and the application of multivariate statistical techniques in PRIMER v7 (Clarke and Gorley, 2015).

Prior to multivariate analysis, and adopting standardised procedures (for an overview see Clarke et al., 2014), environmental variables that displayed right-skewed distributions were log-transformed, and collinearity between variables was assessed using Draftsman plots. Of those variables that were highly correlated ($r \geq 95\%$), one variable was retained, acting as a proxy for the other(s). The remaining environmental variables were normalised to provide a common (dimensionless) scale for analysis. The megafaunal density data were fourth-root transformed to give more weight to rarer taxa and less weight to more dominant taxa.

The Bray-Curtis similarity coefficient was used to evaluate compositional similarities of faunal assemblages within and between study sites (based on the transformed faunal data), generating a resemblance matrix. Hierarchical (group-average) agglomerative clustering (HAC) analysis, based on Bray-Curtis similarities, was performed with a similarity profile (SIMPROF) test to visualise and assess the underlying structure of the biological data, clustering the data into groups previously undefined and

allowing for statistically significant clusters to be identified. The similarity percentages (SIMPER) routine was employed to: (i) quantify the contribution of each morphotaxon to the mean compositional similarity of samples within the SIMPROF-defined groups (in this case, groups = sites), i.e., identifying morphotaxa "typifying" groups; and (ii) quantify the contribution of each morphotaxon to the mean compositional dissimilarity between groups, i.e., identifying morphotaxa "discriminating" among groups. Additionally, and also using Bray-Curtis similarities, a non-metric multidimensional scaling (nMDS) ordination was used to visualise the compositional similarity of samples.

For the normalised environmental data, a resemblance matrix, based on Euclidean distance, was generated and used in a principal component analysis (PCA). The PCA was undertaken to visualise patterns in the environmental data across sites (and samples) and provide a preliminary indication of which variables may be influencing assemblage structure. In addition, the BEST (Bio-Env) routine, employing the Spearman's rank correlation coefficient and including a global BEST test (999 random permutations), was used to identify which subset of environmental variables best matched (or "explained") the observed biotic patterns (i.e., assemblage structures), and to test the statistical significance of the match. Note, the BEST procedure uses biological resemblance and normalised-environmental data matrices (and applies Euclidean distance to the latter during the process).

The statistical processes were also conducted for the functional group-based classification.

Note, several abovementioned procedures are applied within Chapter 4.

2.2.6 Zoobenthic Carbon Content and Carbon Storage Estimations

The carbon content of physical biological samples (i.e., selected individual benthic fauna obtained utilising AGTs) was determined (as part of Chapter 4 procedures) using established laboratory-based methods (Barnes, 2017; Barnes and Sands, 2017; Barnes et al., 2019; Souster et al., 2020; Zwerschke et al., 2022). Faunal samples were specifically chosen (from the existing collections/inventories) to ensure carbon storage information would be generated for all functional groups (as appropriate). Such samples were dried to constant mass and then "ashed" to procure skeletal (inorganic) mass, and hence, by extension, tissue (organic) mass. Inorganic carbon content was calculated as 12% of ash mass (in reference to calcium carbonate skeletons) and organic carbon content as 50% of ash-free dry mass; the two values added together giving total carbon content (carbon stored) per sample (individual) and from which mean carbon stored (g of C held) by each functional group could be calculated. For each SUCS image, the image area and functional group densities, were scaled to 1 m^2, and the density of each functional group multiplied by the corresponding mean carbon content to give g C m^{-2} per functional group, and, when the values per functional group totalled, total zoobenthic carbon storage (g C m^{-2}). The mean carbon storage values for site and area levels were also calculated (employing the image-derived values).

2.2.7 Characterising Sub-Ice-Shelf Macrobenthic Spatial Competition

Spatial competition research, pertaining to Chapter 5, was undertaken by examining biogenic substrata, principally dead bryozoan fragments, isolated from exceptionally rare sub-ice-shelf seafloor sediment samples. Over 320 fragments were visually studied, via stereo microscopy, for the occurrence of inhabiting fauna (referred to as macrobenthic/macrobenthos rather than megabenthic/megabenthos as generally too small

to be discerned within seafloor imagery; Rex, 1981) and evidence of spatial (contest) competition between them. Fragment-residing fauna were predominantly encrusting colonies of Bryozoa which were counted and identified, in almost all cases, to species level (with the aid of taxonomic literature; Hayward, 1995). To enable comparison with findings from elsewhere, competition for space between the colonies was examined following established methods (e.g., Stebbing, 1973; Buss and Jackson, 1979; Barnes and Kuklinski, 2004; Liow et al., 2016, 2019), including identification of a competitive encounter and classification of the respective outcome. Sub-ice-shelf competition was characterised using an array of measures based on literature-derived definitions (e.g., see Barnes et al., 2021), including competition intensity, severity, identity, dominance (by the most frequent competitor), complexity, taxonomic divergence between competitors, and interclade competitive performance. The use of standardised competition measures permitted the comparison of novel under-ice-shelf competition findings with those of equivalent assemblages from global open-sea continental/island shelf environments (i.e., where "permanent" ice cover is not present) of differing latitudes, leveraging past sampling in polar (Arctic and Antarctic), temperate and tropical regions, and additionally gaining of insight as to how sub-ice-shelf competition may alter with ice-shelf loss.

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Chapter 3 | Antarctic Seabed Assemblages in an Ice-Shelf-Adjacent Polynya, Western Weddell Sea

Linking statement

This chapter helps achieve the first objective of the thesis:

"*To characterise the structure of megabenthic assemblages of a rarely accessed and sampled polynya bordering a dynamic and evolving ice-shelf front and determine potential environmental drivers of variability (including whether historical ice cover and distance from the ice shelf are key influences).*"

In recent decades, the retreat and disintegration of ice shelves has taken place along the eastern Antarctic Peninsula, with Antarctica's ice shelves becoming increasingly vulnerable to climate-forced warming. As ice-shelf cover is lost, formerly aphotic marine environments transform into new spaces of photo-induced primary production and increased organic matter flux to the benthos. Predicting how seafloor assemblages may compositionally develop following ice-shelf loss requires knowledge of assemblages bordering the ice-shelf margins; however, such knowledge is presently very limited.

In response, this chapter investigates the structure of seabed assemblages (taxonomically and by functional groups) adjacent to the Larsen C Ice Shelf, eastern Antarctic Peninsula, western Weddell Sea. This area is seldom accessible, at the forefront of climate-induced change, and under consideration by the Commission for the Conservation of Antarctic Marine Living Resources to be designated as an international marine protected area. The research within this chapter encompasses continental shelf

study sites within a coastal polynya at various distances from the ice-shelf calving front, newly uncovering megabenthic assemblage configurations and potential environmental drivers, with environmental data determined from in situ collections and by remote sensing.

Status

This research chapter is published (in an adapted form) in *Biology* as part of a special issue "Polar Ecosystem: Response of Organisms to Changing Climate" (see Appendix B for published research paper).

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3.1 Abstract

Ice shelves cover ~1.6 million km^2 of the Antarctic continental shelf and are sensitive indicators of climate change. With ice-shelf retreat, aphotic marine environments transform into new open-water spaces of photo-induced primary production and associated organic matter export to the benthos. Predicting how Antarctic seafloor assemblages may develop following ice-shelf loss requires knowledge of assemblages bordering the ice-shelf margins, which are relatively undocumented. This study investigated seafloor assemblages, by taxa and functional groups, in a coastal polynya adjacent to the Larsen C Ice Shelf front, western Weddell Sea. The study area is rarely accessed, at the frontline of climate change, and located within a CCAMLR-proposed international marine protected area. Four sites, ~1 to 16 km from the ice-shelf front, were explored for megabenthic assemblages, and potential environmental drivers of assemblage structures were assessed. Faunal density increased with distance from the ice shelf, with epifaunal deposit-feeders a surrogate for overall density trends. Faunal richness did not exhibit a significant pattern with distance from the ice shelf and was most variable at sites closest to the ice-shelf front. Faunal assemblages significantly differed in composition among sites, and those nearest to the ice shelf were the most dissimilar; however, ice-shelf proximity did not emerge as a significant driver of assemblage structure. Overall, the study found a biologically-diverse and complex seafloor environment close to an ice-shelf front and provides ecological baselines for monitoring benthic ecosystem responses to environmental change, supporting marine management.

3.2 Keywords

Climate change; ice shelf; continental shelf; coastal polynya; benthic assemblages; benthic biodiversity; functional groups; Larsen C Ice Shelf; Antarctica; Weddell Sea

3.3 Introduction

Previously long-constant Southern Ocean ecosystems are in transition, with climate change considered the greatest influencer (Arntz et al., 1994; Gutt et al., 2021). Despite being geographically remote, and partially protected oceanographically by the Antarctic Circumpolar Current (ACC) for ~34 million years (Barker et al., 2007; Dayton et al., 2016), the cold-water coastal seas of Antarctica are undergoing profound transformations, some of which are climate-linked (Turner and Comiso, 2017; Rogers et al., 2020). These environmental transitions are perhaps most conspicuously evidenced by changes in the marine cryosphere (icescape), including areas of sea-ice decline, glacier recession, large iceberg calving and ice-shelf retreat and collapse, particularly in the Antarctic Peninsula and West Antarctic Ice Sheet regions (Scambos et al., 2003; Scambos et al., 2008; Cook and Vaughan, 2010; Turner et al., 2014; Cook et al., 2016; Eayrs et al., 2021; Christie et al.; 2022a). Such ice losses are "blue-ing" the Southern Ocean, potentially opening up areas to new or enhanced primary production, and will likely have wide-ranging implications for Antarctica's varied marine ecosystems, living resources, and ecosystem services over different spatial and temporal scales (Gutt et al., 2019; Vause et al., 2019; Rogers et al., 2020; Cavanagh et al., 2021; Grant et al., 2021).

The majority (~95%) of Antarctica's known marine biodiversity is seafloor-dwelling, i.e., benthic (De Broyer et al., 2014). Benthos is a key component of the Southern Ocean ecosystem and food web (Henley et al., 2020), and is becoming increasingly recognised for its role in ocean health and carbon capture, storage and sequestration (Peck et al., 2010; Barnes, 2017a; Barnes, 2018; Barnes et al., 2018). Antarctic seabed life (e.g., sponges, corals, brittle stars and feather stars) has evolved in partial isolation, afforded by the ACC (and its role as a barrier to meridional exchange),

and relative constancy of physical conditions (Arntz et al., 1994), punctuated by the seaward advance of the Antarctic Ice Sheet (AIS) during glaciations. Where such ice sheet extensions occur as grounded ice, much seafloor life is erased off the continental shelf. In contrast, the warmer interglacial periods are characterised by a comparatively much retreated AIS, and bring intense seasonality of light, sea-ice cover and food availability, and disturbance. Consequently, Southern Ocean seafloor biota is unlike any other, with very high levels of endemism – some taxonomic groups having undergone extensive evolutionary radiations (e.g., sea spiders and notothenioid fish) (Arntz et al., 1994; Matschiner et al., 2015). In comparison, other taxa are notably rare or absent (perhaps yet to be detected), such as durophagous (shell-crushing) predators (e.g., crabs and sharks; Aronson et al., 2007). Furthermore, many benthic taxa possess specific adaptations and traits, exemplified by antifreeze glycoproteins (Matschiner et al., 2015), slow growth and development, and great longevity (Arntz et al., 1994; Clarke and Johnston, 2003). How such specialised biota and the communities they make up will respond to ongoing and anticipated changes in the Antarctic environment, including to a rapidly changing marine icescape, is, however, not yet clear (Ashton et al., 2017; Griffiths et al., 2017; Morley et al., 2019; Rogers et al., 2020).

Approximately one-third of Antarctica's extensive (~4.6 million km^2) and deep (mean depth >450 m) continental shelf is overlain by a unique environment: ice shelves (Clarke and Johnston, 2003). Ice shelves are the floating extensions of the AIS, often hundreds of meters thick and hundreds of km wide, and inhibit the flow of inland grounded ice into the ocean (Rignot et al., 2013; Fürst et al., 2016; Hogg and Gudmundsson, 2017; Christie et al., 2022a). The marine cavities beneath ice shelves (i.e., sub-ice-shelf; between the grounding line and the ice-shelf front) experience aphotic conditions, some for thousands of years, and are arguably the least biologically-explored

large-environment on Earth, in part due to challenges of access (Barnes et al., 2021). Benthic life beneath ice shelves has generally been posited as increasingly depauperate with increasing distance into the cavity (Clarke and Johnston, 2003; Griffiths et al., 2021). This is hypothesised, in part, because sub-ice-shelf benthic communities, in particular the primary consumers, are considered as having some dependency on food supplies laterally advected under the ice shelf from open-water areas, although chemotrophic communities may also be present (Domack et al., 2005a). However, examples of sessile suspension feeders (e.g., sponges and bryozoans) have been observed as far as 260 km landward of an ice-shelf front, this being in addition to mobile scavengers and predators (e.g., Riddle et al., 2007; Post et al., 2014; Kim, 2019; Barnes et al., 2021; Griffiths et al., 2021). These faunal observations suggest that such marine spaces are potentially more habitable than previously long-thought.

The remaining two-thirds of Antarctica's continental shelf (~3 million km^2) can be viewed as an "open-water" system, typically with regimes of seasonal sea-ice cover (extended winter sea-surface freezes and summer melts) and primary productivity (phytoplankton blooms) (Arntz et al., 1994); however, some open-water shelf areas, for example, in the Weddell Sea embayment, can be dominated by multi-year sea ice (Dowdeswell et al., 2020). Although extensive sampling and knowledge gaps remain (Convey et al., 2009; Griffiths, 2010), far more is known about Antarctic open-water continental shelf communities. In this respect, rich and abundant benthic communities have been documented in some areas (Gutt and Starmans, 1998), as well as, more recently, expansive breeding colonies of icefish (Purser et al., 2022), while in other areas, communities shaped by intense disturbance from iceberg scouring or ploughing (Barnes, 2017b), and nearby glacier retreat (Sahade et al., 2015) and rapid ice-shelf collapse (Domack et al., 2005a).

Ice-related seafloor disturbance is a major driver of Antarctic shelf community patterns, and the severity and impact of such disturbances can differ over spatial scales, and temporally. For example, while iceberg scouring or ploughing of the seabed can be catastrophic to benthos at local scales, it can also, over time, promote higher regional diversity as mosaics of different faunal successional stages emerge across the seafloor (Peck et al., 1999; Gutt, 2001; Gutt and Starmans, 2001; Gutt and Piepenburg, 2003; Smale et al., 2008). A transfer from an ice-shelf-covered to open-water state, and vice-versa, can also represent a disturbance (Robinson et al., 2022), with energy dynamics considerably changing through the introduction of, for example, seasonal fluxes of light, and new occurrences of localised photosynthetic primary productivity (Bertolin and Schloss, 2009; Sañé et al., 2011). Such changes can have implications for depositional and trophic regimes of benthic habitats, hence the structure of resident biotic communities (Gutt et al., 2013; Post et al., 2014). Abrupt ice-shelf retreats, such as those associated with the 2002 disintegration of Larsen B Ice Shelf, eastern Antarctic Peninsula (Domack et al., 2005b), can result in a forfeiture of some species living under the ice shelf, potentially accustomed to sub-ice-shelf environmental conditions. However, such environmental transitions can also create new opportunities for colonisation of the seafloor and initiation of recruitment and community successional processes (Fillinger et al., 2013).

Following ice-related disturbance, (re)colonisation of the Antarctic continental shelf can involve some predictable taxa and assemblage dynamics and, depth-depending, take from just several to hundreds of years for mature communities to (re)establish (Peck et al., 1999; Gutt and Starmans, 2001; Zwerschke et al., 2021). Faunal colonisation, recruitment, and succession processes have been predominantly studied in the shallows near established research stations using settlement panels and SCUBA-based

photographic surveys (e.g., Bowden et al., 2006; Dayton et al., 2013; Sahade et al., 2015; Dayton et al., 2016), and in deeper shelf waters using underwater cameras, towed collection apparatus and sediment cores (e.g., Teixidó et al., 2004; Teixidó et al., 2007; Gerdes et al., 2008). In such studies, the density and composition of proximate, or oceanographically-connected, communities are recognised as important to colonisation and recovery patterns. However, temporal investigations of benthic-community dynamics following the retreat of an ice shelf above remain relatively rare, yet nevertheless include, for example, pivotal studies by Fillinger et al. (2013) and Gutt et al. (2013) at the Larsen Ice Shelf System, eastern Antarctic Peninsula – a region where pronounced ice-shelf loss has been observed over the satellite observation era (Cook and Vaughan, 2010; Wellner et al., 2019; Christie et al., 2022a).

Over the last 50 years, considerable ice-shelf loss has occurred in Antarctica, which is predicted to continue in a warming world. Indeed, a recent study by Gilbert and Kittel (2021) has suggested that within this century, one-seventh to over one-third of Antarctica's ice shelves are at risk of destabilisation and potential collapse if the global mean atmospheric temperature reaches 1.5 to 4 °C above pre-industrial temperature, respectively. Furthermore, Gilbert and Kittel (2021) also identified Larsen C Ice Shelf, once neighboured to the north by the now-collapsed Larsen A and B Ice Shelves, as one of the most at-risk and vulnerable ice shelves in Antarctica. With such future ice-shelf losses projected, it can be anticipated that there will be intensification in disruption to continental shelf environments, ecosystems, and associated biotic communities, particularly near to and underneath ice shelves, with potential implications for their structure, functioning and carbon sink capacity (Peck et al., 2010; Barnes, 2017a; Barnes, 2017b Barnes et al., 2018; Bax et al., 2021).

As a centre of ice-shelf loss, and with the regional benthos well-studied by Antarctic standards (e.g., Domack et al., 2005a; Gutt et al., 2011; Hauquier et al., 2011; Fillinger et al., 2013; Gutt et al., 2013; Almond et al., 2021; Drennan et al., 2021), the eastern Antarctic Peninsula is a key region for studying how seafloor communities develop, over time, in response to a transition from once ice-shelf-covered to open-water coastal conditions. The current study explored four continental shelf sites adjacent to the Larsen C Ice Shelf front (a border between sub-ice-shelf and open-water shelf habitats), in an area falling within a proposed marine protected area (MPA): the Weddell Sea MPA (WS-MPA), under consideration by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (Brooks et al., 2020; Teschke et al., 2021). All study sites were within an occasionally-present coastal polynya and situated at various distances seaward from the ice-shelf edge, with two sites covered by ice shelf in recent-time. The study aimed to: (1) Compare ice-shelf-adjacent benthic habitats and assemblages; (2) Determine whether density and richness of benthos alter with distance from an ice-shelf front (and with substratum type), and subsequently discern potential functional group surrogates of the patterns observed (note, a surrogate is herein defined as a taxon that serves as a proxy for wider faunal patterns while not driving them); and (3) Identify potential environmental drivers of assemblage structures discerned. A broader goal of the research was to increase understanding of the nature and variability of seabed habitats and life at the ice-shelf margins in areas at the cusp of environmental change. As such, the study provides an ecological baseline of benthic megafaunal structure from which change can be assessed and contributes to the wider understanding of the impact of a changing icescape on the benthos of the Antarctic continental shelf.

3.4 Materials and Methods

3.4.1 Study Area and Sites

The Weddell Sea lies within the Atlantic sector of the Southern Ocean. It is a coastal sea bordered by the Antarctic continent, including the Antarctic Peninsula, and the Scotia Arc, and is characterised by a broad and deep continental shelf (maximal depths exceeding 1 km), vast ice shelves, perennially-heavy sea-ice cover (Clarke and Johnston, 2003; Knox, 2006; Dowdeswell et al., 2020), and the presence of the strong cyclonic Weddell Gyre; the latter implicated in the northward transit of icebergs and sea ice along the eastern Antarctic Peninsula (Vernet et al., 2019).

The study area is situated on the inner continental shelf of the western Weddell Sea adjacent to the northeast sector of the Larsen C Ice Shelf (maximum width ~200 km and thickness of ice front ~200 m) (Arrigo et al., 2015; Wellner et al., 2019), between Jason Peninsula and Bawden Ice Rise (**Figure 3.1**). It is within CCAMLR Statistical Subarea 48.5 and MPA Planning Domain 3, and proposed WS-MPA (Brooks et al., 2020; Teschke et al., 2021). Associated fieldwork was carried out in January and February 2019 (austral summer 2018/19) aboard the South African polar supply and research vessel *SA Agulhas II* (IMO: 9577135), as part of the Weddell Sea Expedition 2019 data collection program (Dowdeswell et al., 2019). At the time of sampling, study sites were located within the intermittent and wind-driven Larsen C Ice Shelf Polynya (LCP), averaging, when present, an open-water area of ~4,700 km^2 for 128 days per annum (pa), with phytoplankton blooms for 69 days pa (Arrigo et al., 2015); the area is otherwise covered in first- to multi-year sea ice up to 5 m thick (Dowdeswell et al., 2020). Benthic megafaunal assemblages were investigated at four sites, LCP1-4 (**Table 3.1**), situated at various distances from the nearest ice-shelf front, i.e., coastline (ranging from <1 to ~16

km, and labelled accordingly, with LCP1 being closest to the ice shelf and LCP4 farthest away). The sites were located on either side of the glacially-deepened Jason Trough (Ó Cofaigh et al., 2014; Batchelor et al., 2022). LCP1 was the most southerly site, close to Bawden Ice Rise, and LCP2-4 were located north of Jason Trough, near Cape Framnes at the tip of Jason Peninsula. Sites were 15 to 75 km apart (**Table S3.1**), with LCP1 (the Bawden Ice Rise site) situated between ~57 to 75 km south of the Jason Peninsula sites, the latter all within ~19 km of each other. Sites were of depths ranging from ~300 to 400 m. At the time of sampling, a large tabular ice-berg (A-68) was pivoting towards the study zone (see Figure 6A in Dowdeswell et al., 2020), in part shielding the area from the influx of sea ice and enabling vessel access.

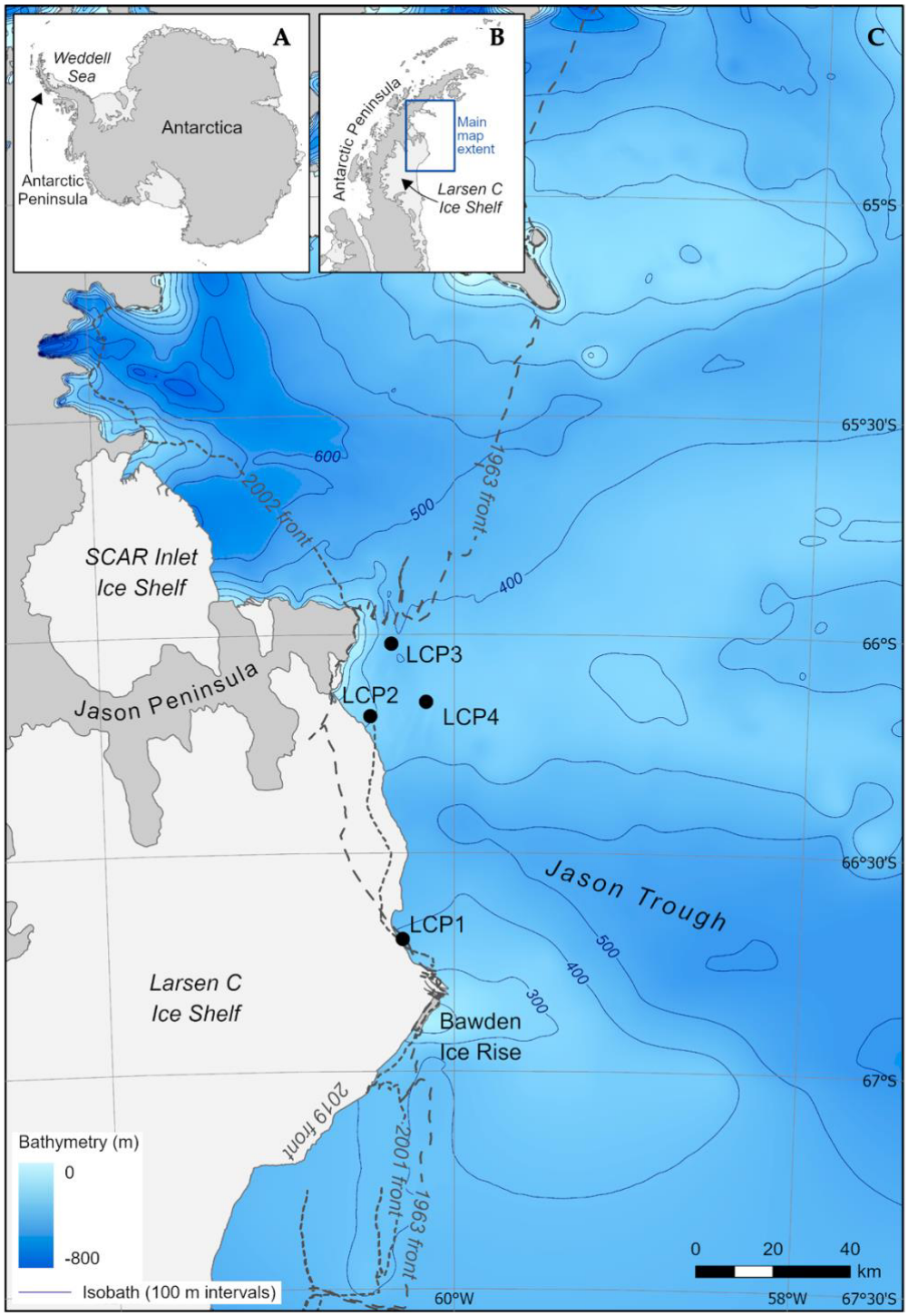


Figure 3.1: Study zone and sites. Inset (**A**) Antarctica indicating the Antarctic Peninsula and Weddell Sea; inset (**B**) Antarctic Peninsula indicating Larsen C Ice Shelf and the extent of the main map; and (**C**) main map of western Weddell Sea study area, showing the modern-day (2019) ice front and the locations of continental shelf study sites, LCP1-4 (black circles), investigated for benthic mega-faunal assemblages. Light grey indicates ice shelves and darker grey indicates ice-covered land/grounded ice. Bathymetry is from the International Bathymetry Chart of the

Southern Ocean v2 (Dorschel et al., 2022), with 100 m contours. The ice-shelf fronts are from Cook and Vaughan (2010), Cook et al. (2021) and Christie et al. (2022b).

Table 3.1: Western Weddell Sea continental shelf study sites, LCP1-4, investigated for benthic megafaunal assemblages, including date(s) sampled (seafloor imagery collection), position in decimal degrees latitude (°S) and longitude (°W), and water depth (m) (mean across associated seafloor imagery), and distance from the ice-shelf front at the time of sampling (m).

Site	Date(s) sampled	Latitude (°S)	Longitude (°W)	Water depth (m)[1]	Distance from ice-shelf front (m)[2]
LCP1 – Bawden Ice Rise	21-22 Jan 2019	-66.6975	-60.2981	397	777
LCP2 – Jason Peninsula	20 Jan 2019	-66.1868	-60.4742	299	2,752
LCP3 – Jason Peninsula	14 Jan 2019	-66.0219	-60.3526	400	9,024
LCP4 – Jason Peninsula	23 Jan 2019	-66.1544	-60.1594	349	16,459

[1]Measured during sampling by high-precision acoustic positioning system (section 3.4.3)

[2]Calculated following sampling using Vector Analysis Tools in QGIS v3.16.6.

3.4.2 Collation of Environmental Data Used in the Study

To discern how sites differed environmentally, and to help identify environmental variables potentially responsible for structuring megabenthic assemblages, various

environmental datasets (remotely-sensed, collected in situ and seafloor-imagery derived) were used.

Ice-shelf cover and ice-shelf front proximity. The distance of each site from the nearest ice-shelf front, at the time of sampling, was calculated using Vector Analysis Tools in QGIS (see **Table 3.1**), and employed in the same way as distance from a coastline (or glacier front) is utilised (e.g., Galeron et al., 1992; Gutt and Starmans, 1998; Kim et al., 2021). Historical areal extent and ice-shelf front positions of Larsen C (and its environs), available from 1963 onwards (with annual observations from 2009), were obtained from several published satellite-based datasets (Cook et al., 2005; Ferrigno et al., 2005; Cook and Vaughan, 2010; Haran et al., 2012; Wuite et al., 2015; Christie et al., 2022b). These datasets were used to estimate for each site for the 1963-2018 observation period, the number of years ice-shelf covered (or open-water), the number of years since last covered by ice shelf, and when ice-shelf retreats occurred.

Sea-ice concentration. Mean monthly sea-ice concentration (SIC; %) data, spanning 1979 to 2019 and derived from Nimbus-7 SMMR and DMSP SSM/I-SSMIS passive microwave observations (Cavalieri et al., 2022), were obtained from the US National Snow and Ice Data Center. These records have a grid cell resolution of 25 x 25 km and were processed in the same manner as described by Christie et al. (2022a). Using this data, mean SIC was calculated for each site for the 1997-2018 period, complementing available primary production data.

Primary productivity. Mean daily net primary production (NPP; mg C m^{-2} day^{-1}) data, spanning 1997 to 2018, were generated following the methods of Arrigo et al. (2008, 2015). From such data, both mean daily NPP and mean peak NPP were calculated for each site for the 1997-2018 period.

Oceanography. Oceanographical data were acquired by deployment of a CTD (conductivity-temperature-depth) system (Sea-Bird Scientific SBE 911plus), which included auxiliary sensors (e.g., oxygen and photosynthetically active radiation; PAR) and a rosette of 24 12-L Niskin bottles enabling collection of water samples (see Hutchinson et al., 2020 and Flynn et al., 2021). The CTD was deployed from the sea surface to within 10 m of the seafloor at 19 stations in the study area. Measurements of temperature, salinity (from conductivity), and dissolved oxygen (to which a correction was applied (see Hutchinson et al., 2020) were obtained, and from associated water samples, an array of nutrient concentrations determined (see Flynn et al., 2021). For each site, data from the nearest CTD station were used, and associated measurements depth-matched wherever possible to the imagery; otherwise, the bottom-most measurements were utilised. CTD variables that varied negligibly between sites, including, for example, turbidity and PAR, were not included in further analyses, with those remaining given in **Table S3.3**.

Substratum and phytodetritus. Both substratum type (hardness) and level of phytodetritus cover were determined during seafloor imagery analysis.

3.4.3 Seafloor Imagery Collection

At each site, three seafloor video-transects were conducted using a remotely operated vehicle (ROV) (EGI GP-50 Work Class; Eclipse Group Inc, Annapolis, MD, USA) (piloted by Eclipse Group Inc and supported by Deep Ocean Search Ltd and Ocean Infinity Inc) equipped with a high-definition (HD) 1080i/29.97 fps colour video camera (DSP&L HD Zoom SeaCam; DeepSea Inc, San Diego, CA, USA); the camera was forward-facing and angled obliquely towards the seabed. The ROV was fitted with two red parallel scaling lasers (DSP&L Micro SeaLaser; DeepSea Inc), 10 cm apart, and six

lights (DSP&L LED SeaLite; DeepSea Inc). During dives, the three-dimensional position (i.e., latitude, longitude and depth) of the ROV was provided by a high-precision acoustic positioning system (Kongsberg HiPAP 502; Kongsberg, Norway). Videos were time-stamped, enabling the pairing of observations with positional data. Mean transect length was 847 m and depth within transects varied by <15 m.

3.4.4 Post-Processing of Collected Imagery

Raw transect videos (three per study site, 12 in total) were de-interlaced in Hand-Brake 1.3.3 (www.handbrake.fr), an open-source video transcoder. Frames were extracted from re-encoded videos every 20 seconds to avoid spatial overlap between successive frames. Frames not viable for analysis (e.g., too high above the seafloor, significantly obscured by sediment kick-up and/or laser points non-discernible) were discarded, the mean discard rate being ~25 %. A 250 m sample was taken from each transect for analysis (and standardised to 100 m^2 for richness calculations). Examples of seafloor imagery from the study are provided in **Figures S3.1** and **S3.2.**

3.4.5 Frame Analysis and Assignments

As per Jones et al. (2009), video frame appraisal methodologies were identical to those of still photographs. Frames were analysed using the web-based imagery annotation tool BIIGLE 2.0 (www.biigle.de) (Langenkämper et al., 2017). Analysis was restricted to the lower-half of each frame (below the laser points), and frames were examined in random order. For each frame, all discernible epibenthic megafauna were annotated (hence counted) and identified to the highest taxonomic resolution possible or assigned a practicable morphotaxon/operational taxonomic unit (with taxonomic specialists and literature consulted, as appropriate, during the appraisal process). Substratum type was categorised as soft (i.e., mud or sand), assorted hard (varied coarse grain sizes from pebble

to boulder [with soft sediment interstices]), boulder, or mixed sediment; the latter a ~50:50 mixture of soft and hard sediment. At sample-level, where frames became aggregated, substratum type assignment was based on the two most dominant substratum categories and then converted to a scale of "hardness" from 1-6 (1 being the softest substratum and 6 the hardest) (**Table S3.2**). The level of phytodetritus cover (indicated by a greenish layer on the seafloor) was recorded on a scale of 1-5 (1 being the lowest cover and 5 the highest; see supplementary information). Laser points were marked and used to calculate the width of the field of view at the laser line, enabling computation of the seafloor area analysed (mean of 2.2 m^2 per frame). To provide further ecological context to the megabenthic diversity observed, and also to potentially identify ecological proxies to facilitate future monitoring, a functional group (one of 14; see **Table 3.2**), based on functional traits of feeding-strategy, mobility, and "skeletisation", was ascribed to each morphotaxon; groups being adapted from Barnes and Sands (2017) and Barnes et al. (2020). For each frame and sample, epibenthic megafauna and functional group counts were converted into densities, i.e., individuals per m^2 (ind. m^{-2}).

Table 3.2: Functional group categories based on Barnes and Sands (2017) and Barnes et al. (2020), and example taxa discerned in Larsen C Ice Shelf Polynya.

Functional group	Example taxa
Deposit-feeding crawlers (epifaunal)	Holothurians
Soft infaunal deposit-feeders	None discerned
Hard burrowing deposit-feeders	Irregular echinoids
Flexible strategists	Ophiuroids
Grazers	Regular echinoids
Soft sessile predator/scavengers[1]	Pennatulaceans, soft corals, anemones (actiniarians), hydroids
Hard sessile predator/scavengers[1]	Scleractinian corals, calcaxonian whips, hydrocorals
Soft mobile predator/scavengers	Nemerteans, nudibranchs, octopi
Hard mobile predator/scavengers	Fish, gastropods, asteroids
Arthropod predator/scavengers	Pycnogonids, decapod shrimps
Pioneer sessile suspension feeders	Encrusting bryozoans, ascidians, some polychaetes
Climax sessile suspension feeders	Demosponges, hexactinellids, brachiopods, some bryozoans
Sedentary suspension feeders	None discerned
Mobile suspension feeders	Crinoids

[1]Can also be considered as "active and passive filter feeders" (see Hogg et al., 2018, Hogg et al., 2021).

3.4.6 Statistical Analyses to Explore Biotic Differences and Potential Environmental Drivers

Statistical analysis comprised calculations of univariate indices, including the total number of morphotaxa (richness), as well as the application of multivariate statistical techniques in PRIMER v7 (Clarke and Gorley, 2015) with PERMANOVA+ add-on (Anderson et al., 2008).

Prior to multivariate analysis, and adopting established procedures (see Clarke et al., 2014; Clarke and Gorley, 2015; and references therein), environmental variables that displayed right-skewed distributions were log-transformed, and collinearity between variables was assessed using Draftsman plots. Of those variables that were highly correlated (or anticorrelated) ($r \geq 95\%$ [or $\leq -95\%$]), one variable was retained, acting as a proxy for the other(s) (**Table S3.3**). The remaining environmental variables were normalised to provide a common (dimensionless) scale for analysis. The megafaunal density data were fourth-root transformed to give more weight to rarer taxa and less weight to more dominant taxa (Clarke and Green, 1988).

The Bray-Curtis similarity coefficient (Bray and Curtis, 1957) was used to evaluate compositional similarities of faunal assemblages within and between sites (based on the transformed faunal data), generating a resemblance matrix. Hierarchical (group-average) agglomerative clustering (HAC) analysis (Everitt, 1980), based on Bray-Curtis similarities, was performed with a similarity profile (SIMPROF) test to visualise and assess the structure of the biological data, clustering the data into groups previously undefined and allowing for significant clusters to be identified (Clarke et al., 2008). The similarity percentages (SIMPER) routine (Clarke, 1993) was employed to: (i) quantify the contribution of each morphotaxon to the average compositional similarity of samples

within the SIMPROF-defined groups (in this case, groups = sites), i.e., identifying morphotaxa "typifying" groups; and (ii) quantify the contribution of each morphotaxon to the average compositional dissimilarity between groups, i.e., identifying morphotaxa "discriminating" among groups. Additionally, and also using Bray-Curtis similarities, a non-metric multidimensional scaling (nMDS) ordination (Kruskal, 1964) was used to visualise the compositional similarity of samples.

For the normalised environmental data, a resemblance matrix, based on Euclidean distance, was generated and used in a principal component analysis (PCA) (Chatfield and Collins, 1980). The PCA was undertaken to visualise patterns in the environmental data across sites (and samples) and provide a preliminary indication of which variables may be influencing assemblage structures. In addition, the BEST (Bio-Env) routine, employing the Spearman's rank correlation coefficient and including a global BEST test (999 random permutations) (Clarke and Ainsworth, 1993; Clarke et al., 2008), was used to identify which subset of environmental variables best matched (or "explained") the observed biotic patterns (i.e., assemblage structures), and to test the statistical significance of the match. Note, the procedure uses biological resemblance and normalised-environmental data matrices (and applies Euclidean distance to the latter during the process).

The abovementioned statistical processes were also conducted for the functional group-based classification.

3.5 Results

3.5.1 Seafloor Habitat of the Study Area – Observations and Features

Across and within the study sites, the seafloor varied considerably in terms of rugosity (roughness) and dominant substratum type. Expanses of poorly-sorted coarse-grained (pebbles to boulders) substratum were particularly prominent at site LCP2, closest to Jason Peninsula. Such material appeared similar to that observed northward along the Larsen A Ice Shelf front (Evans and Cofaigh, 2003); indeed, the angularity and separateness of the boulders, in particular, suggested presence of supraglacially-derived ice-rafted debris (Batchelor et al., 2020).

Recent iceberg-scouring, such as that observed by Gutt and Piepenburg (2003) and Gutt et al. (2013) via ROV, was not evident in the imagery, although wide and deep furrows were observed in the seabed at the two shallower sites, LCP2 and LCP4 (both <350 m deep).

Phytodetritus cover of the seafloor, indicative of potential "food banks" (Mincks et al., 2005; Smith et al., 2006), was heaviest at the sites farthest offshore (i.e., LCP3 and LCP4), with lighter cover observed at the sites closest to the ice shelf, LCP1 and LCP2 (both within 3 km of Larsen C).

Small circular/elliptic seabed depressions (~10 to 25 cm in diameter), very similar to those captured (also by a video-camera-equipped ROV) by Gutt et al. (2010) just northward of Jason Peninsula, were observed at each study site. These depressions appeared individually and in clusters (see **Figure S3.2**), with more and larger clusters observed at the shallower sites, LCP2 and LCP4. Most depressions were free of phytodetritus as if maintained or freshly formed and were, at times, accompanied by

holothurians, potentially resting or feeding, and notothenioid fish. Although speculative, it is possible that these depressions constitute nursery areas for juvenile fish or holes for egg fertilisation (Hollyman, 2020); however, compared to the icefish nests observed at scale by Purser et al. (2022) in the Filchner Trough, southern Weddell Sea, the depressions near Larsen C were smaller and much less uniform in size and distribution across the seafloor (and far less spatially expansive). Alternatively, the depressions could have been feeding marks or pits of large vertebrates (Hollyman, 2020; Marsh et al., 2018) or even of geological origin, representing sources of seeps (Gutt, 2020) – although no bacterial mats were seen, and sampling would be required to confirm this.

Similar to the documented video-derived observations of Domack et al. (2005a) and Niemann et al. (2009) of the continental shelf of the Larsen B embayment, potential chemotrophic habitats were observed. Such habitats presented as shallow indentations in the seabed (~0.75 to 2.5 m across) with soft sediment within (i.e., mud/sand), and were occasionally edged by bedrock. These habitats are likely inactive or low-activity cold seeps, evidenced by a faunistic legacy of *Calyptogena*-like shells and weedy worm-tubes (possibly Siboglinidae; see Georgieva et al., 2015), and the occurrence of potential bacterial mats within or around the features. Such chemotrophic habitats were observed at sites with the most contrasting ice-shelf-cover history, LCP1 and LCP4 (see Section 2.5.2), although further examples may have been camouflaged across the study area by sedimentation.

Across the study sites, biota, and associated functional groups, were, at times, highly variable in terms of abundance, diversity and composition – indicating a degree of faunal patchiness. Some areas could be depauperate, with little or no perceptible biota, or comparatively dominated by a particular taxon or functional group (e.g., corals and ophiuroids). In contrast, other areas could host multiple encrusting fauna (e.g., ascidians,

sponges and pioneering bryozoans) on hard substratum (mainly larger rocks and boulders). Giant predatory and suspension-feeding asteroids, e.g., *Perknaster* sp. and brisingids, respectively, were observed in higher numbers at LCP2, the latter consistently on large boulders (potentially glacial dropstones). Instances of commensalism were evident throughout much of the study area, including, for example, crinoids and ophiuroids on top of corals or large sponges (Gutt and Schickan, 1998).

3.5.2 Environmental Differences Determined from Remotely-Sensed Data

Ice-shelf cover and ice-shelf front proximity. Observations of changing areal extent of Larsen C throughout the satellite era revealed varying degrees of ice-shelf cover over the study sites. Specifically, it was found that LCP1 and LCP2 had intermittently been covered by ice shelf in the observation period (1963-2018), consistent with the natural advance and calving of small icebergs along this particular stretch of the Larsen C front through time (Cook and Vaughan, 2010; Christie et al., 2022a). LCP1 and LCP2 were last ice-shelf covered around 2009 and 2003, i.e., 10 and 16 years prior to sampling, respectively. It was observed that LCP1 had experienced (at least) two retreats, remained in close proximity (<1 to ~3 km) to the Larsen C ice-shelf front, and was ice-shelf-covered for (at least) two separate periods totalling 23 years (of the 56 years of observations). LCP2 also experienced two retreats and was covered for two distinct periods (totalling 7 years), and was proximate to Larsen C from the 1990s onwards. In contrast, LCP3 and LCP4 were free of ice-shelf cover throughout the observation period (Christie et al., 2022a), and possibly for longer (Smith et al., 2021). LCP3 was, in certain years, notably close to the Larsen B Ice Shelf margin (e.g., in 1968, 1986, and 1993), whereas LCP4 was comparatively (and consistently) distant from any ice-shelf fronts.

Sea-ice concentration. Mean monthly SIC (± 1 SD), for the 1997-2018 period, was lowest at LCP1 (65.1% [± 22.7]) and highest at LCP2-4 (69.6% [± 25.7]). The low SIC values observed are indicative of the presence of the polynya.

Primary productivity. Mean daily NPP and mean peak NPP, for the 1997-2018 period, were highest at LCP4 and showed a significant increase with increasing distance from the ice-shelf front (regression-associated ANOVAs, $R^2 = 0.93$ and 0.94, $F = 129.37$ and 152.16, respectively, with both p-values < 0.001). For LCP1-4, the mean daily NPP values (± 1 SD) were 123.5 (± 202.8), 165.9 (± 226.4), 199.4 (± 245.2), and 243.8 (± 309.3) mg C m^{-2} d^{-1}, respectively, and mean peak NPP values (± 1 SD) 264.5 (± 329.7), 372.6 (± 207.7), 435.4 (± 309.5), and 791.7 (± 552.9) mg C m^{-2} d^{-1}, respectively.

3.5.3 Megafaunal Richness: Accumulation with Area, and Pattern with Ice-Shelf Proximity and Substratum Hardness

Overall, a total of 98 morphotaxa from 23 classes of 10 phyla were observed across the study zone.

The relationship between richness and area surveyed was examined at each site and compared to determine if megafaunal richness accumulated differently across sites. As expected, faunal richness increased from the area of a single frame to a sample (mean 165.7 m^2), the latter peaking at 32 morphotaxa (**Figure 3.2**). The lowest intercept and most gradual slope (indicative of richness accumulation) were at LCP2, equating to half the level of richness observed at LCP1 and LCP4 (the sites closest to and farthest from the ice-shelf edge, respectively). LCP1 and LCP4 were not significantly different in terms of richness accumulation ($p > 0.2$), while all other pairwise comparisons indicated slopes to be significantly different.

Larger areas increasingly accumulated the less abundant and rarer morphotaxa (e.g., particular sponges, asteroids, anthozoans, ascidians, and brachiopods), including "singletons" (morphotaxa that only appeared once), and this mainly drove the increased richness observed at LCP1 and LCP4, with different taxa contributing to the morphotaxa count of each site.

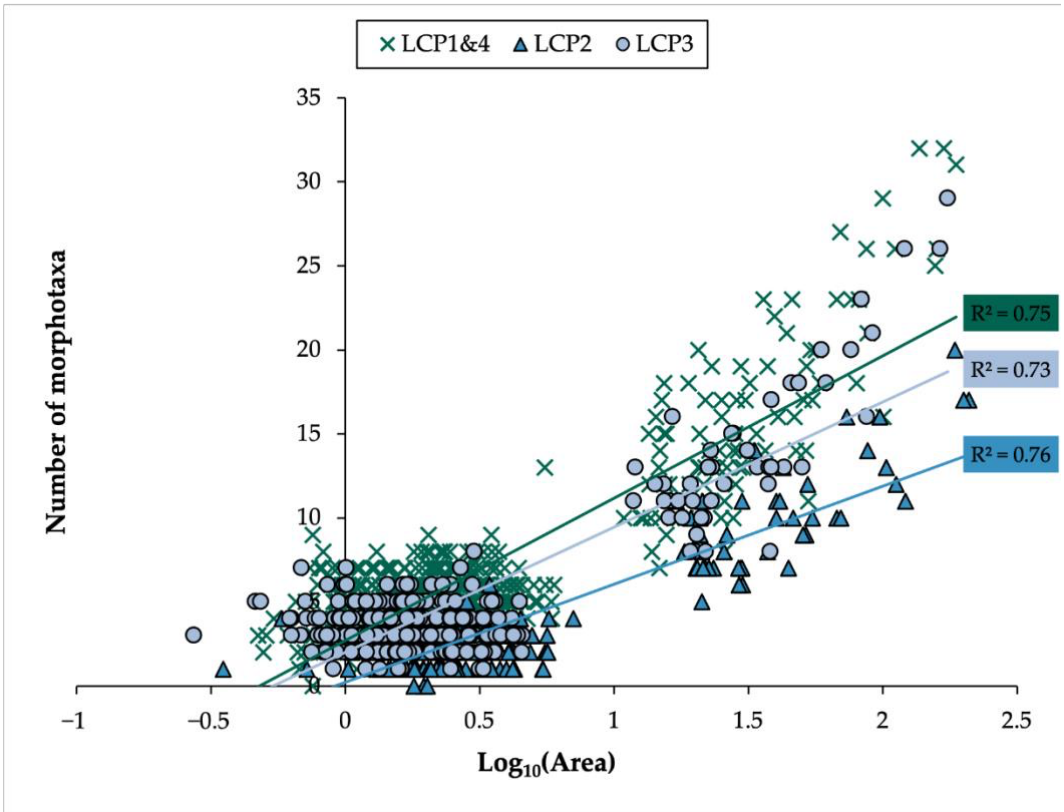


Figure 3.2: Ice-shelf-adjacent sites accumulate faunal richness differently. Morphotaxa richness with area surveyed for sites LCP1-4 (note, slopes for LCP1 and LCP4 were not significantly different from each other, $p > 0.2$, therefore, datasets pooled). Significantly different slopes are shown (p-values for differences between slopes all < 0.01). For regression lines, F-values = 1546.39, 767.44, and 930.35, for LCP1 and LCP4 combined, LCP2, and LCP3, respectively, with p-values all < 0.001.

When comparing standardised 100 m^2 samples (three per site), the lowest richness was observed in an LCP2 sample and the highest in an LCP4 sample, with 11 and 31

morphotaxa recorded, respectively. An LCP1 sample exhibited the second-highest richness at 27 different morphotaxa. The richness of LCP4 samples was varied, with the value of one sample being almost double of another (16 and 31), whereas the richness of LCP3 samples was noticeably more uniform (23, 24 and 25). Marked variability in richness was found at the sites closest to the ice-shelf front, with more than a doubling from the poorest to richest sample (11 and 27).

In terms of a relationship with proximity to the ice shelf, richness did not significantly alter with increasing distance from the ice-shelf front (regression-associated ANOVA, $F = 1.0$, $p = 0.33$). However, when LCP1 samples were excluded from the exploration, as they were located within a different water mass (see Hutchinson et al., 2020), the relationship became more robust although remained non-significant (R^2 value = 0.4, and regression-associated ANOVA, $F = 4.6$, $p = > 0.06$).

Overall, a weak (inverse) relationship was observed between richness and "hardness" of substratum (**Figure S3.3**, $F = 6.59$, $p = 0.03$), although richness did halve from predominantly soft-sedimented (with incidences of mixed) substratum through to assorted hard sediment-boulder fields.

3.5.4 Megafaunal Density and Pattern with Ice-shelf Proximity and Substratum Hardness

Across samples, mean benthic megafaunal density varied by nearly an order of magnitude, from 2.5 to 9.7 ind. m^{-2} (see y-axis of **Figure 3.3**). The lowest densities were typically found at LCP2 (all three samples observed to be faunally depauperate) and the highest densities generally at LCP4; although, at LCP1, closest to the ice-shelf edge, faunal densities could also be high, although more variable. When considered together,

the two sites nearest to the ice shelf were more variable in terms of faunal density than the two sites farthest away.

With increasing distance from the ice-shelf front, it was observed that density generally increased (regression-associated ANOVA, $R^2 = 0.35$, $F = 5.39$, $p = 0.04$). To control for water mass differences, this trend was also explored without LCP1, where it became more significant (**Figure 3.3**, regression-associated ANOVA, $F = 43.3$, $p < 0.01$).

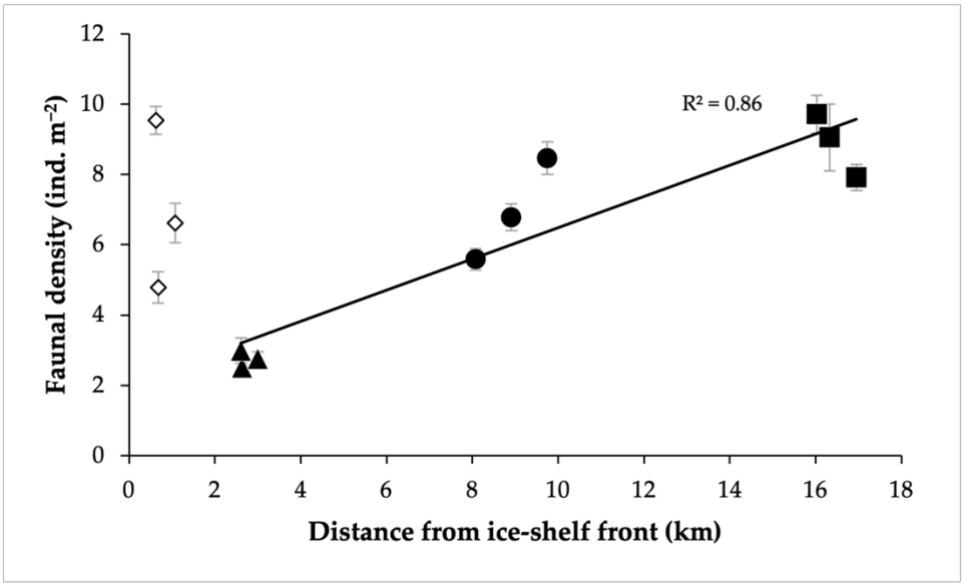


Figure 3.3: Megafaunal density generally increases with distance from the ice shelf. Mean benthic megafaunal density (ind. m^{-2}) (± SE) of each sample (three per site) with distance from the ice-shelf front (km). Mean density (± SE) calculated for each sample using associated frames (minimum of 44 frames per data point). Site LCP1 = diamonds, LCP2 = triangles, LCP3 = circles, and LCP4 = squares. Symbols filled in white excluded from regression statistics (hence trend-line generation) (owing to water mass differences, see Hutchinson et al., 2020).

The general relationship of increased faunal density from the ice-shelf front to farther offshore was principally caused by increases in densities of bottlebrush corals (e.g., Primnoidae, including *Thouarella* spp.), ophiuroids (e.g., *Ophionotus*) and

encrusting lithophilic fauna (e.g., pioneering bryozoans, ascidians and sponges). Bottlebrush corals and encrusting fauna mainly drove the high variability in density and occasionally high values at LCP1.

The nature of the substratum also appeared to influence faunal densities, with faunal density significantly decreasing with increasing substrate hardness (**Figure 3.4**, regression-associated ANOVA, $F = 13.7$, $p < 0.01$). The lowest density values were observed in the samples categorised as having the "hardest" substratum type. This trend was principally driven by decreased densities across the majority of faunal groups at LCP2 (closest to Jason Peninsula), but particularly in encrusting suspension feeders, and the apparent absence of certain taxa, including bottlebrush corals (see section 3.5.6).

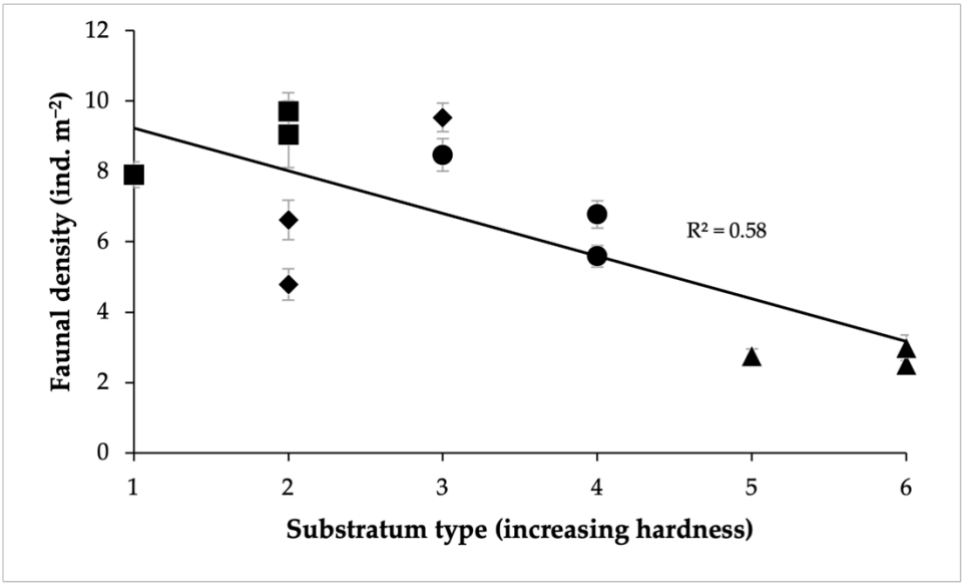


Figure 3.4: Megafaunal density generally decreases with increasing hardness of the substratum. Mean faunal densities (ind. m^{-2}) (± SE) of samples (three per site) with substratum type (scale of increasing hardness from left to right), where 1 = soft-sediment: mixed; 2 = mixed: soft-sediment; 3 = mixed: boulder; 4 = assorted hard: mixed; 5 = assorted hard: boulder/mixed; and 6 = assorted hard: boulder. Site LCP1 = diamonds, LCP2 = triangles, LCP3 = circles, and LCP4 = squares.

3.5.5 Functional Group Richness and Density Patterns with Ice-Shelf Proximity and Substratum Hardness, and Potential Surrogacy of Wider Faunal Patterns

Of the 14 functional groups (**Table 3.2**), 12 were represented by the fauna discerned in the imagery. Whether such functional groups reflected taxonomic patterns in richness and overall density was assessed.

With respect to richness, functional group richness, like morphotaxa richness, did not significantly change with increasing distance from the ice-shelf front, including when removing groups represented by singletons (both p-values > 0.3). However, in contrast, functional group richness did not exhibit a relationship with substratum hardness, including when removing singleton groups (both p-values > 0.7).

As with taxonomic groups, the density of some functional groups altered with distance from the ice shelf. Deposit-feeding crawlers (all holothurians), pioneer-sessile suspension feeders (primarily encrusting lithophiles) and hard-sessile predator/scavengers (principally bottlebrush corals) all showed similar patterns to the overall faunal trend (**Figure 3.5A-C**); this including high densities at LCP1 (cf. **Figure 3.3**). In contrast, grazers and hard deposit-feeders (both groups predominantly echinoids) showed high densities at LCP1 and no trend with increased distance away from the ice shelf (**Figure 3.5D,E**). Some fauna, such as soft-sessile predator/scavengers (primarily anemones), increased in density with distance from the ice shelf (**Figure 3.5F**) and did not display high densities at LCP1 (hence, differed from the overall faunal pattern).

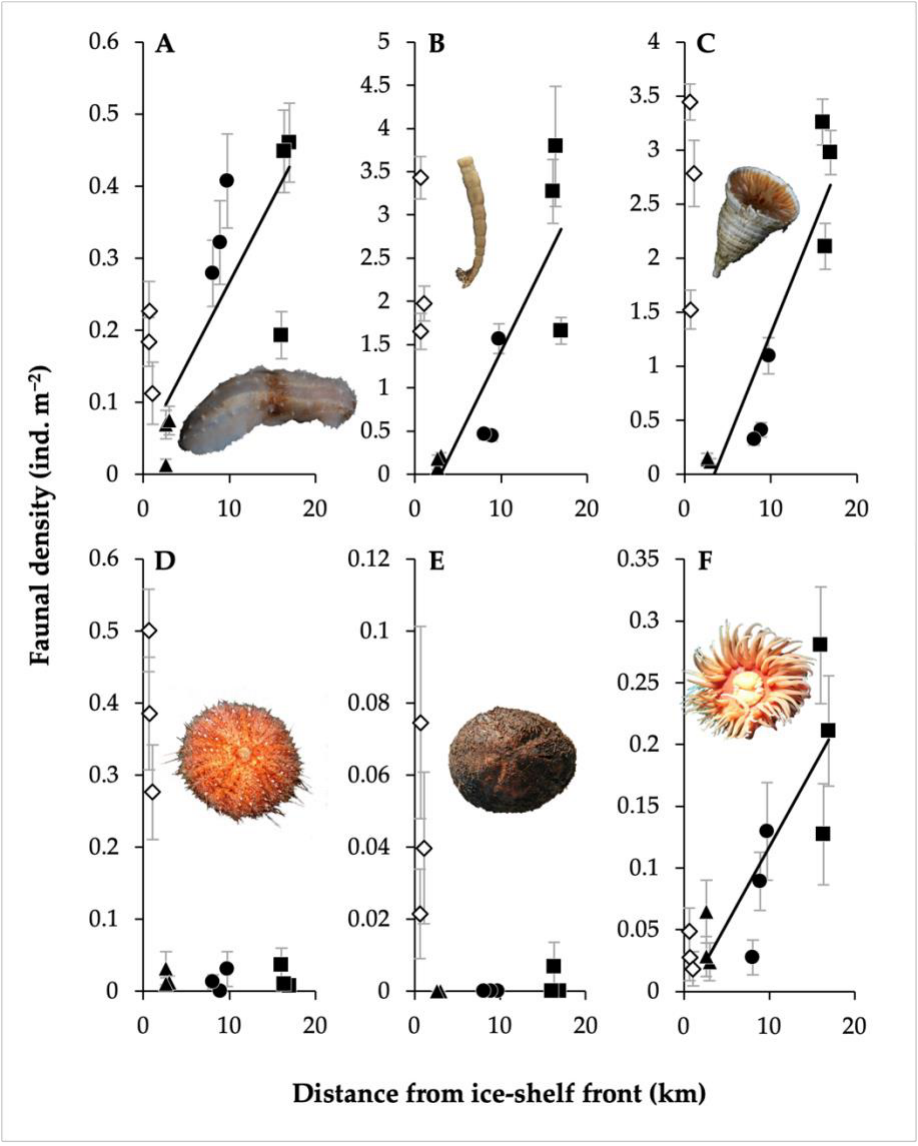


Figure 3.5: Functional group densities can alter differently relative to ice-shelf proximity. Mean functional group densities (ind. m^{-2}) (± SE) of samples with distance from the ice-shelf front (km), with an example taxon for each group (images provided by D.K.A.B.): (**A**) deposit-feeding crawlers; (**B**) pioneer sessile suspension feeders; (**C**) hard sessile predator/scavengers; (**D**) grazers; (**E**) hard deposit-feeders; and (**F**) soft sessile predator/scavengers. Site LCP1 = diamonds, LCP2 = triangles, LCP3 = circles, and LCP4 = squares; white-filled symbols indicate (due to water mass disparities, see Hutchinson et al., 2020) data not included in trend-line generation. R^2 values for 5A-C and F = 0.63, 0.85, 0.74 and 0.7, respectively, and regression statistics indicated all associated p-values ≤ 0.01.

With regard to substratum type, deposit-feeding crawlers, hard sessile predator/scavengers, and pioneer sessile suspension feeders, like the overall fauna pattern, decreased in density with increased substratum hardness (regression-associated ANOVAs, $F = 7.4$, 19.88 and 11.64, $p = 0.02$, 0.001 and 0.007, respectively). Whereas other functional groups (and component taxa), e.g., climax suspension feeders, flexible strategists (all ophiuroids), sedentary suspension feeders (all crinoids), and mobile hard predator/scavengers (principally asteroids and notothenioid fish) did not show clear trends with substratum hardness (p-values > 0.1).

On exploring whether any functional groups could be considered a proxy (surrogate) for the wider faunal patterns observed, e.g., in density, deposit-feeding crawlers appeared to be the strongest surrogacy candidate (**Figure 3.6**; and see **Figure S3.4** for pioneer sessile suspension feeders and hard sessile predator/scavengers). The functional group individually reflected the density pattern, and when removed from the broader dataset, the pattern remained, supporting that deposit-feeding crawlers did not drive the trend. Furthermore, and as abovementioned, the density-trend of deposit-feeding crawlers with substratum type also reflected that of the overall fauna.

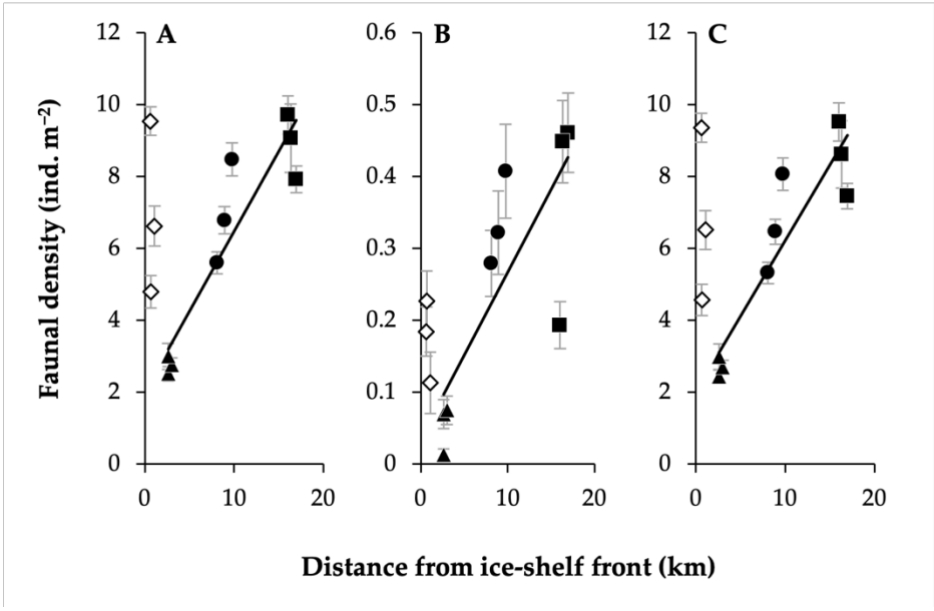


Figure 3.6: Deposit-feeding crawlers as an effective surrogate of the overall faunal density trend observed with distance from the ice shelf. Mean densities (ind. m^{-2}) (± SE) with distance from the ice-shelf front (km) of: (**A**) overall fauna; (**B**) deposit-feeding crawlers; and (**C**) overall fauna excluding deposit-feeding crawlers. Site LCP1 = diamonds, LCP2 = triangles, LCP3 = circles, and LCP4 = squares; white-filled symbols indicate data not included in trend-line generation (because of water mass differences, see Hutchinson et al., 2020). R^2 values for A-C = 0.86, 0.63 and 0.85, respectively. Regression statistics for C presented a p-value of ≤ 0.001.

3.5.6 Megafaunal Assemblage Composition

The nMDS ordination of megafaunal assemblages of samples showed a robust two-dimensional representation of non-metric multidimensional space (stress 0.05, **Figure S3.5**). This analysis revealed that the sites closest to the ice shelf were not compositionally homogeneous, in fact LCP1 and LCP2 had the most dissimilar assemblages (61.2% dissimilarity) of any two sites. The highest Bray-Curtis similarities were observed from intra-site comparisons (highest = 77.6% at LCP4) and the lowest from inter-site comparisons (lowest = 35.6% between LCP1 and LCP2). The key morphotaxa found to be driving similarity between samples within sites were ophiuroids (particularly for LCP2

and LCP3), encrusting lithophiles and bottlebrush corals (**Table S3.4**). Key morphotaxa driving dissimilarity between sites included bottlebrush corals, particularly when comparing LCP2 samples with others (although not key for LCP1 and LCP4 dissimilarity), *Sterechinus antarcticus* (as well as other echinoid species), principally when comparing LCP1 with offshore sites, and, in some site comparisons, encrusting lithophilic organisms and *Pyura* sp. (potentially *Pyura bouvetensis*) (see **Table S3.5**).

The differences between LCP2 samples and those of other sites appeared to be driven by absences and much lower densities of various taxa, although LCP2 was the only site in which the holothurian *Peniagone vignoni* was observed. Notably, LCP1 had higher densities of echinoids (of at least three different morphospecies). At LCP4, an athecate hydroid species occurred in higher densities than at other sites. Compared to LCP3, LCP4 had more bottlebrush corals, the aforementioned hydroid species, and the *Pyura* sp. In general, LCP3 and LCP4 had higher densities of holothurians (of differing species), particularly those (visually) identified as *Pseudostichopus mollis*.

HAC analysis with a SIMPROF test identified four distinct groupings among samples, corresponding to the four individual sites (**Figure 3.7**). Further examination of the HAC dendrogram showed that LCP2 samples were compositionally more distinct from those of the other sites; this was followed by LCP1, and then LCP3 and LCP4. The results of this analysis were reflected in the nMDS findings showing that the sites closest to the ice-shelf front were the most compositionally dissimilar.

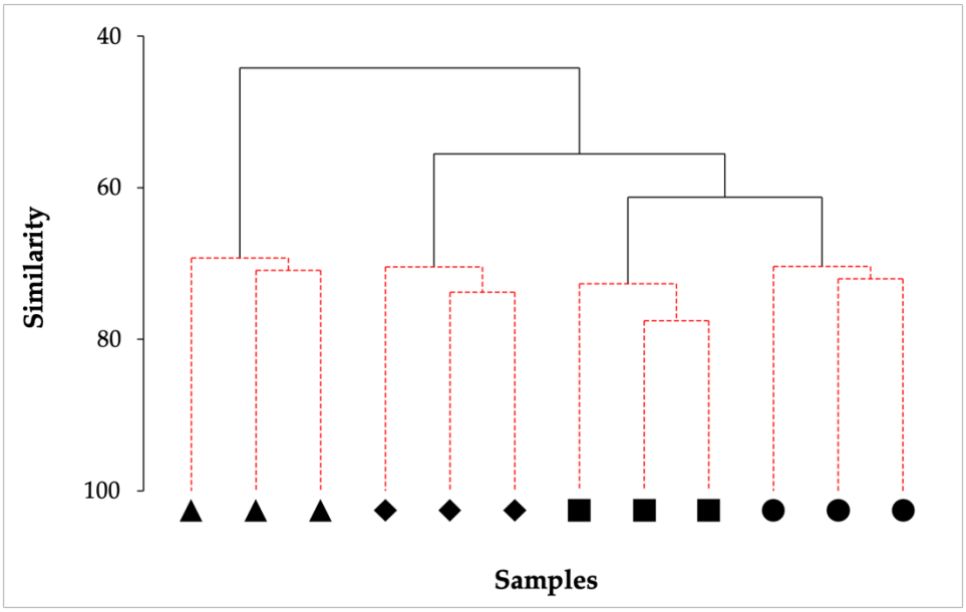


Figure 3.7: Clustering of samples corresponds with respective study site. Dendrogram resulting from hierarchical agglomerative cluster analysis of samples from Larsen C study sites (based on Bray-Curtis similarities and using group-average linking). Black continuous lines indicate significant clusters, identified by a SIMPROF test, and red dashed lines non-significant clusters. Site LCP1 = diamonds, LCP2 = triangles, LCP3 = circles, and LCP4 = squares.

When HAC (plus SIMPROF) analysis was performed for functional groups, results were similar to that of the morphotaxa in that the samples were again clustered by their respective study site (**Figure S3.6**).

3.5.7 Environmental Differences between Study Sites

A range of environmental variables (15 in total and 9 following correlation analysis, see **Table S3.3**) was examined to discern how sites differed in terms of environmental context. The PCA and associated ordination (**Figure 3.8**) showed that the first two principal components accounted for >85% of the environmental variability (52.9% and 32.4%, respectively). The first principal component explained environmental differences among samples due to sea-ice cover, nitrate, salinity, and water physico-chemistry

(represented by temperature and correlation with oxygen concentration) (Eigenvectors = 0.45, 0.43, 0.39, and -0.38, respectively). The second principal component further showed the factors of substratum type, distance from the ice-shelf front, depth, and phosphate (Eigenvectors = -0.55, 0.38, 0.38 and -0.38, respectively).

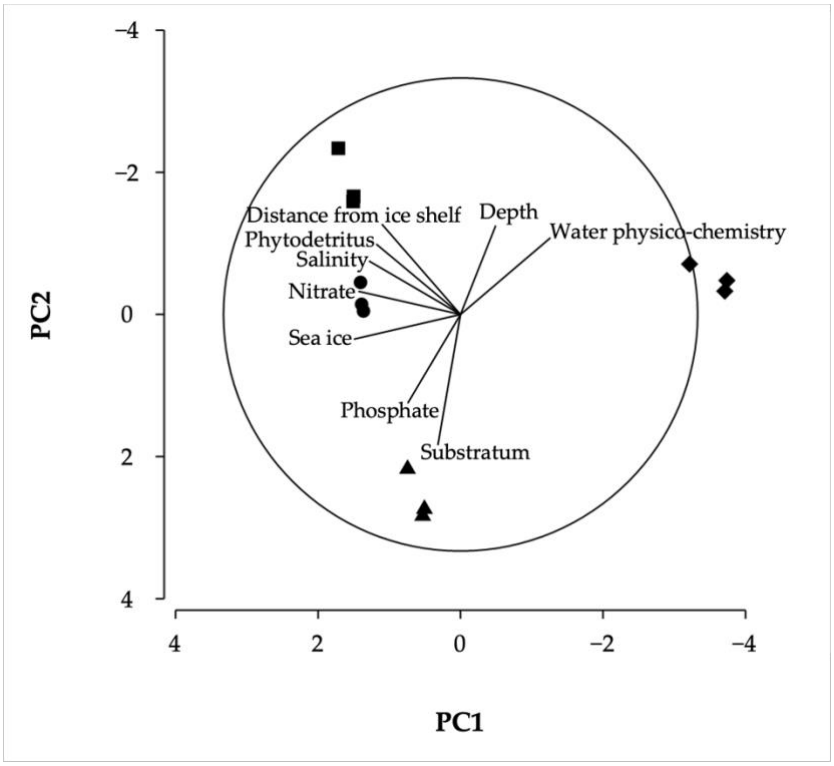


Figure 3.8: Differences in the environmental setting of sites (and samples). PCA ordination showing spatial variation in environmental variables among the 12 samples. Site LCP1 = diamonds, LCP2 = triangles, LCP3 = circles, and LCP4 = squares. PC = Principal Component.

Overall, the PCA indicated the importance of measuring a range of environmental variables when studying multiple sites, as water physio-chemistry appeared the most influential in differentiating LCP1 from the other sites (hence separation in **Figure 3.3**), substratum at LCP2, and distance from the ice shelf and phytodetritus cover at LCP3 and LCP4.

3.5.8 Environmental Influences on Megafaunal Assemblage Composition Differences

Having established environmental differences among sites, BEST analysis was performed to determine which variables correlated with, and hence could be potentially influencing, megabenthic assemblage compositional differences in space. The results showed that specific combinations of environmental variables were more likely to be underpinning faunal differences.

The BEST analysis indicated that a subset of three environmental variables most highly correlated with (or "best explained") the variation in faunal assemblage structure (Rho correlation = 0.93, $p < 0.01$). This subset included mean depth, water physico-chemistry and substratum hardness. The single variable showing the highest Rho correlation (0.77) was substratum type, considered a local-scale variable.

When comparing BEST analysis results of all faunal grouping methods, i.e., morphotaxa, class and functional groups, the most highly correlated subsets of potential explanatory variables each included water physico-chemistry and substratum hardness (Rho correlations for the latter two faunal groupings = 0.87 and 0.93, respectively, with associated p-values < 0.01). As such, there appears to be some consistency in which environmental variables emerged as potential key drivers of the biotic variation observed, irrespective of whether the benthic biodiversity was classified by taxonomic levels or functional groups.

3.6 Discussion

The Southern Ocean can be characterised by relative constancy (Arntz et al., 1994) and also sharp marine environmental gradients, the latter exemplified by conditions either

side of the Polar Front (the strongest jet of the ACC) (Moore et al., 1999), the continental shelf break (the terminus of grounded ice in glaciations) (Knox, 2006; Gili et al., 2015; Cummings et al., 2021), the marginal sea-ice zone and the ice-shelf front (Clarke, 1988). With ocean and atmospheric warming, Antarctic icescapes and associated marine ecosystems are expected to change, with implications for biota (Rogers et al., 2020; Gutt et al., 2021). While there have been various studies of biological response to Antarctic glacier retreat (e.g., Torre et al., 2012; Pasotti et al., 2015; Sahade et al., 2015; Zwerschke et al., 2022), few have covered life underneath ice shelves (see Kim, 2019; Barnes et al., 2021; Griffiths et al., 2021) and even fewer on what shapes biodiversity, and how it develops, in areas that have recently experienced ice-shelf loss (Fillinger et al., 2013; Gutt et al., 2013; Almond et al., 2021). The current study investigated megabenthic biodiversity (richness, density and composition) and potential environmental drivers at a key Antarctic marine frontier that is arguably one of the most sensitive to climate change, the ice-shelf edge. Furthermore, the respective study area sits entirely within the constraints of an important and characteristic Antarctic marine feature, a coastal polynya (Arrigo and van Dijken, 2003; Arrigo et al., 2015). The seafloor biology where these two systems cooccur is little known (Post et al., 2017), and yet, potentially representative of how seabed communities may develop in new areas of open-water as Antarctic ice shelves retreat in a warming world.

The present study found a trend in the overall density of megafauna with increasing distance from the ice-shelf front; however, perhaps surprisingly, not in richness (biodiversity). When individual taxa and functional groups were explored, some groups were found to reflect the overall density trend (i.e., could potentially be used as proxies), some contrasted, and some showed no clear pattern. Substratum type appeared to strongly influence megafaunal density, although it did not appear to exert the same

impact on richness. Distance from the ice-shelf edge, which, in the confines of the study, correlated with the remotely-sensed primary-production-related variables, did not emerge as a significant environmental driver of assemblage composition. Instead, different environmental variables appeared to be important locally at each study site. Compared to offshore sites, assemblages closest to the ice-shelf front could be expected to be more similar to each other (having had less time in terms of environmental exposure to diverge), yet they were actually the most dissimilar. Overall, results suggested that a study zone, where a polynya abuts the ice shelf, can be a complex coastal environment, both physically and biologically.

Large-scale alterations in faunal richness have been widely observed across geological time (Jablonski, 1999) and space, e.g., latitude (Hillebrand, 2004; Tittensor et al., 2010), with pronounced hemispherical asymmetry (Arntz et al., 1994; Chown et al., 2004) due to the Antarctic Ocean being anomalously highly biodiverse (Clarke and Johnston, 2003; De Broyer et al., 2014). Various reasons for changes to faunal richness across scales have been presented, including energy availability (Woolley et al., 2016) and species turnover (Rabosky et al., 2018). Given that the number of species encountered generally increases with the size of area surveyed (e.g., **Figure 3.2**), it is important to evaluate richness levels within comparable area sizes (i.e., standardised samples), for example, when comparing findings, such as the current study's, with those of other regions. In the case of the present study, investigating continental shelf assemblages proximate to Larsen C, morphotaxa richness increased (at each site) with the size of area examined, however, less rapidly than, for example, at Ryder Bay (western Antarctic Peninsula) (Barnes, 2017a), around the island of South Georgia (Barnes and Sands, 2017), and in the Barents Sea (Arctic) (Souster et al., 2020) (**Figure 3.9**, using associated datasets).

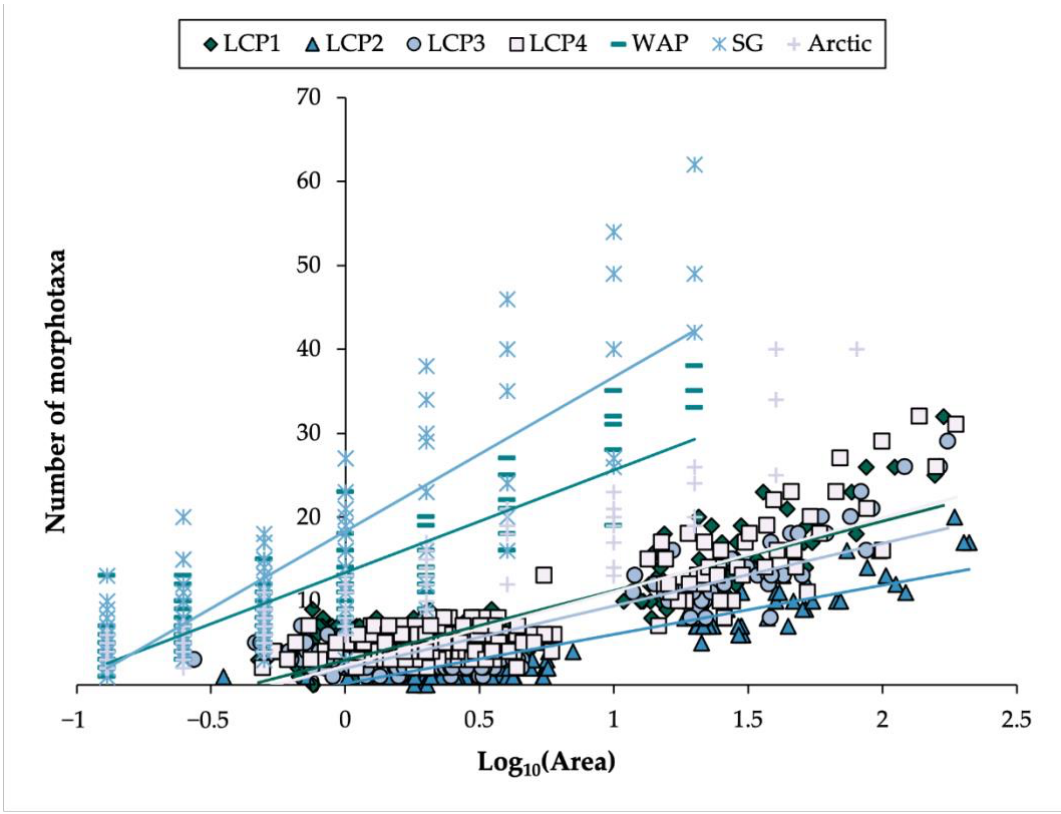


Figure 3.9: Geographical regions accumulate faunal richness differently. Morphotaxa richness with area examined for Larsen C Polynya study sites, LCP1-4, compared to photographic studies from Ryder Bay (western Antarctic Peninsula, WAP), around the island of South Georgia Island (SG), and the Barents Sea (labelled here as "Arctic") (sources of external datasets used are provided in the text).

Potentially having experienced greater historic disturbance (e.g., from iceberg scouring), Antarctica's coastal open-water shelf areas can harbour a great array of habitat types and niches, and hence resident biota, including those associated with different successional stages. As such, it was envisaged that a positive richness gradient would be observed with increasing distance from the ice-shelf front (i.e., farther offshore). However, within the study confines, no significant increase (or change) in faunal richness was discerned (including when examining Jason Peninsula sites exclusively). Furthermore, richness values were particularly variable at the sites closest to the ice-shelf

front. Similarly, Grange and Smith (2013) found no increase in richness with distance from western Antarctic Peninsula glacier termini, whereas Kim et al. (2021) found the greatest richness at a location farthest from a glacier front in Marian Cove, King George Island. The results of the current study could be due to several reasons, including: (1) the nature of the seabed environment close to the ice-shelf front being similarly (or more) variable to that of open shelf farther away (e.g., reflected in the different prevailing substratum types); and, alternatively or additionally, (2) the principal environmental influences driving biodiversity patterns are site-specific, i.e., differ according to the site (**Figure 3.8**; and as found by Post et al. 2020a with regard to rugosity), and are more influential than ice-shelf-edge proximity (and respective correlates, i.e., mean daily and mean peak NPP). However, examining biodiversity differences using richness alone can obscure underlying variances and changes (Hillebrand et al., 2018) and is better evaluated in coordination with other measures such as density and faunal composition.

Biota responses to major environmental gradients can be reflected in faunal density in both space and time. In the polar regions, this can be exemplified by (re)colonisation of seafloor on ecological timescales in response to ice scour, glacier retreat and ice-shelf collapse (Gutt et al., 1996; Fillinger et al., 2013; Grange and Smith, 2013; Gutt et al., 2013; Barnes, 2017b), and by (re)colonisation of the continental shelf on evolutionary timescales following the recession of the AIS and associated grounded ice (e.g., following the Last Glacial Maximum ~20,000 years ago) (Thatje et al., 2005; Barnes et al., 2016). Significant changes in the density of benthos can occur from the abyssal plain through continental slope to continental shelf (Cummings et al., 2021), i.e., spatially, and over time, for example, in association with food-fall (Smith et al., 2006; Jansen et al., 2018). However, some studies have shown that faunal abundance does not always directly reflect observed phytodetritus fall and cover of the seafloor (Gutt et al.,

1998; Sumida et al., 2008). The present study found that faunal density generally increased with increasing distance offshore. This result is in some contrast to the findings of Grange and Smith (2013), which showed lower densities on the open-water continental shelf compared to study locations at glacial termini, albeit on a larger spatial scale. However, in the current study, the Bawden Ice Rise site (LCP1), closest to the ice shelf and with the greatest ice-shelf cover over the observation period, had some of the highest faunal densities observed in the study area. These high densities may have been driven by the site experiencing different water mass conditions (see **Figures 3.3 and 3.8**, and Hutchinson et al., 2020); in particular, water temperatures were higher, possibly influencing the occurrence and growth of taxa (e.g., see Ashton et al., 2017) and/or parts of the site being serviced by bottom currents rich in organic matter.

Additionally, the seafloor (hence benthos) at LCP1 may have been more protected from ice-mediated disturbance than the Jason Peninsula sites due to being more consistently ice-shelf-covered, and for a more extended period, at least within the satellite era. Furthermore, when open-water, LCP1 may have been afforded further protection from disturbance by Bawden Ice Rise and associated shallow seafloor, known to constrain iceberg-flow into and within the area (Han et al., 2019). Nonetheless, it is notable that farther north on the western Weddell Sea continental shelf, it has been observed that in just a few years of areas becoming ice-shelf-free, density and biomass of benthos can increase considerably, i.e., in response to new exposure to open-water conditions and associated food regime changes (Fillinger et al., 2013; Gutt et al., 2013).

The site with the lowest faunal densities was LCP2, closest to Jason Peninsula. Such density values may be explained in reference to the aerial/satellite imagery that showed the site had often been proximate to the ice-shelf edge and had undergone ice-shelf advance and retreat (at least twice) in recent-time. Additionally, the site is at a water

depth within reach of modern iceberg keels in an area of iceberg transit (conditions also particularly pertinent to LCP4 and potentially explaining the faunal patchiness observed there). Hence, the respective site may have been especially subject to disturbance such as scouring and the deposition of ice-rafted debris (associated with calving-front dynamics, ice-shelf basal melt, and transiting icebergs) (Clarke, 1996; Nicholls et al., 2012).

Although all sites in the study occurred within a polynya, and therefore an area of potentially elevated primary production and related organic matter export to the seabed (Grebmeier and Barry, 2007; Arrigo et al., 2015), megafaunal density values were not necessarily as high as those recorded for other open-water continental shelf areas (e.g., Gutt and Starmans, 1998; and see Table VI of Post et al., 2017). The lower faunal densities observed could be related to the fact that the polynya only occurs intermittently, and the study area is otherwise covered in heavy year-round sea ice. Furthermore, there is a contrasting seasonality of sea-ice cover in the polynya compared to other Southern Ocean areas – sea-ice cover in the polynya being at a maximum during the austral summer (when phytoplankton blooms are typically most productive) as opposed to winter. Such aspects may compromise primary production potential, and thus associated organic matter flux to the Antarctic seabed.

Biological patterns were not only explored by looking at the megafaunal assemblage as a whole, but also through the 12 functional groups represented by fauna detected (**Table 3.2**; **Figure 3.5**). Such an approach has advantages in examining the functionality of biodiversity and also potentially helping reduce imagery appraisal times. In the study, specific taxa and functional groups, e.g., anemones and hydroids – both components of the soft sessile predator/scavengers group, showed significant density increases as distance from the ice shelf increased. Some taxa, e.g., echinoids of grazing and deposit-feeding types, showed exceptionally high densities at the Bawden Ice Rise

site (LCP1), and low densities (or absences) elsewhere, while others, e.g., climax suspension feeders, showed no discernible trends. It could be predicted that pioneer species would be of higher density in more-recently ice-shelf-uncovered areas and climax species in more established (Gutt and Starmans, 2001; Gutt and Piepenburg, 2003). However, the study found high pioneer densities at LCP4, free of ice-shelf cover during and potentially before the satellite era, and LCP1, the site most consistently ice-shelf-covered and still situated very close to the ice-shelf edge. In addition, pioneer suspension feeders displayed a significant positive density relationship with distance from the ice-shelf edge, particularly when the Jason Peninsula sites were considered exclusively. Climax suspension feeders, e.g., sponges and bryozoans, did not show a trend with distance from the ice shelf, and interestingly, the highest densities were found within an LCP1 sample, challenging the assumption that climax suspension feeders would be more prevalent in areas farther from the ice shelf where primary production may be higher. Additionally, it could also be predicted that grazers would be better represented in seabed spaces featuring more hard substratum (hence potential attached food sources), and deposit-feeders in soft-sedimented areas (Arntz et al., 1994). While this was not the case for grazers in this study, densities of epifaunal deposit-feeders did increase with increasing substratum softness.

Partitioning faunal density and richness into various taxonomic levels, or by function, permits further insight into how different elements of biodiversity respond to environmental conditions. Finding appropriate surrogacy, or indicators, can also help simplify ecosystem monitoring, accelerate data processing and results-delivery, and thus enhance the timeliness of informing marine management, which is particularly important for rapidly changing environments. Suitable surrogates should reflect the overall biotic pattern of interest while not driving it. In the present study, deposit-feeding crawlers, all

of which were holothurians, were found to be the strongest surrogacy candidate for overall megafaunal density (**Figure 3.6**). Although preliminary, this finding could be especially advantageous for imagery-based seafloor assessments given that holothurians are relatively easy to detect and identify due to their visual characteristics and mobility, making them also potentially ideal candidates for the development of automated appraisal and monitoring tools (e.g., Li et al., 2021). Nevertheless, it remains important to continue testing proposed surrogates. For example, gastropods have been used as indicators of latitudinal trends in the reproductive strategy of benthic invertebrates, i.e., Thorson's rule (Mileikovsky, 1971), yet when exploring this rule in echinoderms (Pearse et al., 1991), quite different patterns were uncovered; rather than brooding becoming a more dominant reproductive strategy with increasing latitude, lecithotrophy (non-feeding larvae) became more common. Additionally, in Southern Ocean seabed conservation and management, taxa considered representative of Vulnerable Marine Ecosystems (VMEs) (CCAMLR, 2009; FAO, 2009) can be employed to pinpoint and designate VMEs. While such taxa are invaluable tools, it is not yet fully known whether all are true indicators of VMEs and/or are vulnerable themselves (see Dayton et al., 2013; Fillinger et al., 2013; Dayton et al., 2016).

Ordination techniques, such as nMDS, can help reveal underlying structural differences in biodiversity at various scales, for example, between islands and seamounts (Bridges et al., 2021), along fjords (Grange and Smith, 2013), and across depths (Cummings et al., 2021). Given that offshore sites were considered more likely to have experienced historic disturbance, hence display differing successional/colonisation stages, such sites were expected to be the most compositionally dissimilar (within and between respective sites). The nMDS visualisation, however, revealed two particular aspects of note. Firstly, variability, in terms of assemblage composition, was similar

within sites irrespective of distance from the ice-shelf edge, and secondly, sites closest to the ice shelf were the most compositionally dissimilar. A potential explanation is that the ice-shelf margin is a similarly (or more) variable continental seabed environment to that of offshore. This variability at the ice front may be due to the differing retreat-advance dynamics of the ice shelf, and the varying degrees (and nature) of sediment loading and stochasticity of release, which will impact the seafloor in terms of disturbance and substratum make-up, hence benthic assemblage structures.

One of the striking biological differences between Jason Peninsula site LCP2 and other sites was that it did not appear to host calcaxonian corals, despite the availability of plentiful hard surfaces, i.e., attachment points. However, the distribution of such biota is also thought to be strongly influenced by water depth, coincident iceberg scouring, and the flow of organic matter (Post et al., 2010), so these factors may play an important role around this part of the Larsen C Ice Shelf margin. Furthermore, LCP2 was also the only site observed to host elasipod holothurians, which could indicate a food-poor habitat as the taxon is considered well-adapted to food scarcity (Sumida et al., 2008). Larsen-marginal habitat differences appear complex, perhaps even enigmatic. Nevertheless, the underlying drivers of assemblage differences are ultimately environmental, with various biota elements responding differently.

A priori considerations that ice-shelf proximity may be a major influencer of megafaunal assemblage composition were not directly supported by the BEST analysis findings of this study. However, such a factor (as aforementioned) could be linked to other environmental variables such as prevailing substratum type. As found in other polar locations and farther afield (e.g., Jones et al., 2007; Grange and Smith, 2013; Post et al., 2017; Ziegler et al., 2017; Post et al., 2020b), substratum type and depth were also found to be important drivers of faunal composition, although the impact of depth is not always

clear in the Antarctic owing to wide bathymetric ranges of many benthic species (Thatje et al., 2005). Given that areas exhibiting hard substratum are expected to be more heavily colonised and display characteristic taxa (Ziegler et al., 2017; Post et al., 2020b), the substratum results of the present study were somewhat counterintuitive. For instance, the "hardest" site, LCP2, had notably low faunal densities, including very few encrusting lithophiles, and corals appeared unrepresented. It is thus likely that further factors were influential at LCP2, including, for example, potentially organic-poor (oligotrophic) bottom currents coming from beneath the ice shelf, as described by Dayton and Oliver (1977) for an area on the west flank of the McMurdo Sound, next to Ross Ice Shelf. Alternatively, the substratum at LCP2 (as per above) was indicative of a more frequently disturbed environment in relation to ice-shelf processes and dynamics; hence faunal assemblage components and densities are reflective.

In the polar seas, sea-ice cover (concentration, timing and duration) is a key influencer of seabed biodiversity dynamics, in part through associated impacts on light penetration, primary production, and flux of particulate organic matter to the seafloor (Clark et al., 2017; Pineda-Metz et al., 2020). However, in this study, sea-ice cover was not significantly coincident with differences in assemblage structure. This result may be because the sea-ice data (alone) did not sufficiently differentiate between the sites and/or the associated variable did not account for periods of ice-shelf cover. Water physico-chemistry was also found to be important in influencing faunal composition. This variable notably included ocean temperature, considered highly likely to be impacted by climate change, with implications for biotic communities, in particular those of coastal habitats and habitats at continental shelf depths (Rogers et al., 2020). As an assortment of variables, i.e., depth, substratum type and water physico-chemistry, were the best explanatory set of environmental factors, this supports the view that the Antarctic

continental shelf is a complex environment. Exploration of further variables/parameters, in particular those related to biological interactions such as predation and competition, may provide additional, potentially important, ecological insights, particularly in the case of likely alterations to benthic assemblages in response to environmental change. Furthermore, extending studies to other ice-shelf-adjacent polynyas (e.g., those pinpointed in Arrigo, et al., 2015) would help determine if there is a degree of commonality (or not) among polynyas in terms of benthic assemblage structuring and drivers, and, together with the present study, additionally offer a collective ecological baseline for conservation and management purposes.

3.7 Conclusions

This study explored benthic assemblages of four western Weddell Sea continental shelf sites, all within an ice-shelf-adjacent coastal polynya, and two of which have recently experienced ice-shelf retreat. The research revealed distinct faunal patterns in density (but not in richness), and identified a taxonomic and functional group (deposit-feeding crawlers [all holothurians]) that could potentially be a surrogate for the wider megafauna, hence contributing to simplifying, and potentially expediting, future marine environmental monitoring efforts. Distance from the ice shelf was not identified as a key driver of assemblage composition; however, results evidenced that at the ice-shelf front, habitats and assemblages can be very different across space. The study further showed that different environmental variables were potentially important in structuring benthic assemblages at each study site (e.g., water physico-chemistry at LCP1), emphasising the complexity of Antarctic continental shelf environments, particularly those at the edge of ice shelves.

The current findings provide an indication of how seabed communities may develop along the eastern Antarctic Peninsula as further ice-shelf cover is lost, and narrow biological knowledge gaps of a very rarely accessed and distinctive area within a CCAMLR-proposed MPA.

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Chapter 4 | Variability in Zoobenthic Blue Carbon Storage across a Southern Polar Gradient

Linking statement

This chapter helps achieve the second objective of the thesis:

"*To ascertain how zoobenthic carbon storage (a function of and ecosystem service afforded by zoobenthos) may vary from southern high-temperate to polar latitudes (with different sea-ice cover regimes) and determine potential influences.*"

High-latitude zoobenthic continental shelf communities of cold sub-Antarctic and Antarctic waters are increasingly being recognised for their (blue) carbon storage function and its potential role in helping mitigate climate change. Seasonal phytoplankton blooms (which constitute a carbon drawdown mechanism) provide food to consumers, including via "food fall", relaying carbon from the ocean surface through the pelagic zone to the benthic communities of the seafloor, where it can be stored, over time, in expansive and often long-lived benthic assemblages; this carbon storage function can be considered as an ecosystem service, i.e., of benefit to humankind.

Benthic assemblages and their functions, including carbon storage, are expected to be affected by environmental shifts brought about by climate change, including alterations to ice cover, and it is yet to be fully realised what this may mean for the continuation of benthic ecosystem services. This research chapter, therefore, explores and compares the carbon stored in high-latitude (epi)zoobenthic assemblages of the Scotia Arc study region in marine areas both sides of the Antarctic Circumpolar Current, and of differing ice-

cover regimes – examining, in addition, the influence of assemblage structuring and potential environmental drivers.

Status

This research chapter is published (in an adapted form) in *Marine Environmental Research* (see Appendix B for published research paper).

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4.1 Abstract

The seabed of the Antarctic continental shelf hosts most of Antarctica's known species, including taxa considered indicative of vulnerable marine ecosystems (VMEs). Nonetheless, the potential impact of climatic and environmental change, including marine icescape transition, on Antarctic shelf zoobenthos, and their blue carbon associated function, is still poorly characterised. To help narrow knowledge gaps, four continental shelf study areas, spanning a southern polar gradient, were investigated for zoobenthic (principally epi-faunal) carbon storage (a component of blue carbon) and potential environmental influences, employing a functional group approach. Zoobenthic carbon storage was highest at the two southernmost study areas (with a mean estimate of 41.6 versus 7.2 g C m^{-2}) and, at each study area, increased with morphotaxa richness, overall faunal density, and VME indicator density. Functional group mean carbon content varied with study area, as did each group's percentage contribution to carbon storage and faunal density. Of the environmental variables explored, sea-ice cover and primary production, both likely to be strongly impacted by climate change, featured in variable subsets most highly correlating with assemblage and carbon storage (by functional groups) structures. The study findings can underpin biodiversity- and climate-considerate marine spatial planning and conservation measures in the Southern Ocean.

4.2 Keywords

Zoobenthic carbon storage; blue carbon; Antarctic; benthos; climate change; ecosystem function; functional groups; vulnerable marine ecosystems; dropstones; ecosystem service; ice-cover loss

4.3 Introduction

This century sees the tercentenary of the Industrial Revolution, and over the corresponding period, atmospheric levels of greenhouse gases (GHGs) have been rising. The atmospheric concentration of the most ubiquitous GHG, carbon dioxide (CO_2), has increased from around 280 parts per million (ppm) in 1750, i.e., pre-industrial-era, to a 2022 average of ~417 ppm; this rise being particularly significant in the last 75 years and mainly from intensities of fossil-fuel combustion, cement production, and deforestation, i.e., anthropogenic (Friedlingstein et al., 2023; IPCC, 2023). The cumulative effect of GHG emissions is global climate change, including warming, the impacts of which are increasingly experienced across the world and considered intertwined with the biodiversity crisis (IPCC, 2022, 2023; Pörtner et al., 2023; Siegert et al., 2023). To reduce levels of atmospheric CO_2, societal efforts centre on minimising emissions at source (i.e., decarbonisation methodologies) and large-scale CO_2 capture; the captured CO_2 later used in further processes or potentially placed in long-term geological storage, e.g., within depleted oil and gas reservoirs of continental shelves – legacies of hydrocarbon extraction (Holloway and Burnard, 2009; Luo et al., 2023). In parallel, protection and capacity enhancement of natural carbon sinks, including, for example, the living resources/biomass of various marine ecosystems such as those present along tropical and temperate shorelines (e.g., McLeod et al., 2011; Greiner et al., 2013; Howard et al., 2014; Song et al., 2023) and on high-latitude/polar continental shelves (e.g., Gogarty et al., 2020; Cavanagh et al., 2021; Bax et al., 2022), are also being pursued.

The vast ocean network, constituting >70% of the world's surface, plays a major role in mitigating climate change by helping regulate atmospheric levels of CO_2, the oceans collectively absorbing ~26% of anthropogenic CO_2 emissions (Friedlingstein et

al., 2023) and the Southern Ocean, representing ~10% of the ocean network, disproportionately accounting for around one-quarter of total oceanic uptake of atmospheric CO_2 (Arrigo et al., 2008). Marine biodiversity can help support this process through "blue carbon", a component of which can be defined as the carbon captured and stored by marine life, i.e., the carbon within living marine biomass (Barnes, 2018). Blue carbon is also considered a marine ecosystem service benefitting humankind (Grant et al., 2013; Rogers et al., 2020; Cavanagh et al., 2021). Marine primary producers, such as phytoplankton and macroalgae, initially capture CO_2 via photosynthesis, and thereafter, carbon is exported/transferred within associated and conjugated ecosystems (Cavan and Hill, 2022), being stored across the marine food web over diverse timespans and spatial scales, eventually leading to, for example, its sequestration within seabed sediments (Barnes, 2018).

In the polar regions, biological carbon pathways (and fates) are yet to be fully understood (Cartapanis et al., 2016; Henley et al., 2020; Sands et al., 2023); however, at high-temperate, sub-polar and polar latitudes, marine food webs can be based on macroalgae (e.g., kelp; see Vilas et al., 2020) and phytoplankton (microalgae), and at the very highest latitudes of the Southern Ocean, and its constituent seas, phytoplankton dominate primary production (Deppeler and Davidson, 2017). In the cold surface waters of the Antarctic, where atmospheric CO_2 more readily dissolves (Arrigo et al., 2008), huge seasonal (austral spring and summer) accumulations (blooms) of phytoplankton capture CO_2, incorporating it into the biological carbon cycle and initiating pathways for carbon storage in the Antarctic marine food web, including in the benthos (seafloor-dwelling organisms), by which an estimated 12-18% of Southern Ocean primary production is consumed (Barnes, 2017; Figure 8 in Henley et al., 2020). The seafloor is also where the majority of Antarctica's known biodiversity resides (De Broyer et al.,

2014) and where taxa considered indicative of vulnerable marine ecosystems (VMEs), as defined by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR; CCAMLR, 2009), have been observed (CCAMLR, 2019; Lockhart and Hocevar, 2021). The presence of VME indicator taxa can strengthen justification for the adoption of proposed regional protection frameworks, such as Marine Protected Areas (MPAs) (Lockhart and Hocevar, 2021), and some VME indicators, e.g., corals, owing to their carbonate skeletons, are particularly proficient at storing carbon (and enhancing sequestration, i.e., long-term storage potential) (Barnes, 2018) whilst some are also important habitat providers/ecosystem engineers (Miller et al., 2012); hence, can help amplify carbon storage through associated inhabitants.

Similar to terrestrial forests and coastal wetlands (Howard et al., 2014; Mildrexler et al., 2020), marine biodiversity can be important in capturing, storing and facilitating sequestration of carbon. Carbon that might otherwise be broken down and recycled by the microbial loop is taken up and bound into tissues (and skeletons) of marine biota (Barnes, 2018). Benthic habitats, including, for example, their biological/zoobenthic communities (and component assemblages), i.e., the fauna living on (epi-faunal) and within (in-faunal) the seabed, can function as carbon sinks, accumulating and immobilising carbon (see Peck et al., 2010; Alurralde et al., 2019; Barnes et al., 2020). Zoobenthic assemblages, in terms of their composition, are known to be shaped by various combinations of environmental variables, such as ice cover, substratum type and physical/chemical features of the seabed (e.g., Domack et al., 2005; Isla et al., 2006; Niemann et al., 2009; Clark et al., 2017; Post et al., 2017; Ziegler et al., 2017; Almond et al., 2021). Alterations in such variables may impact the structure and function (including performance) of assemblages. Disentangling bio-physical relationships can be helpful for predictions regarding biological responses to environmental change (Cummings et al.,

2018). To discern benthic community/assemblage structure, epi-zoobenthos (the epifaunal component of zoobenthos) can be sampled/surveyed by relatively non-destructive means, e.g., via seafloor imaging techniques, whereas in-fauna are generally sampled by (more intrusive) sediment cores and grabs (Pineda-Metz and Gerdes, 2018). Although in-faunal organisms do not fall within the remit of the current study, they can account for ~50% of the carbon stored in the benthos (when epifauna and infauna are both considered), for example, of Antarctic fjords (Zwerschke et al., 2022).

Studies assessing high-latitude benthic blue carbon, including within the context of ecosystem services and nature-based solutions to moderating climate change, are growing yet still relatively rare. Furthermore, such studies are primarily in exclusive economic zones or performed in consideration of unilateral marine protection zones (e.g., Barnes et al., 2019, 2021a; Bax et al., 2022); opposed to, for example, internationally-shared waters or areas beyond national jurisdiction. If left undisturbed, these seabed ecosystems may continue functioning as carbon sinks and store carbon delivered to them through the food web. However, given ongoing and anticipated environmental shifts in high-latitude marine environments brought about by climate change and direct human impacts associated with the Anthropocene (Steffen et al., 2011), Antarctic seafloor habitats, component communities/assemblages, and their associated functions and ecosystem services may alter in response or indeed be at risk (Rogers et al., 2020; Cavanagh et al., 2021; Gutt et al., 2021).

Over the past few decades, carbon storage in polar zoobenthic communities has garnered attention in both hemispheres. Several investigations have now employed blue-carbon-oriented "functional groups" – a faunal grouping method in which fauna are grouped based on functional traits considered important in benthic blue carbon pathways (see Barnes and Sands, 2017). For example, studies in the Barents Sea, where carbon

storage capacities, also referred to as "carbon standing stocks", of sedimented continental shelf assemblages were assessed (Souster et al., 2020, 2024), and in deglaciating fjords of the western Antarctic Peninsula, where blue carbon of emerging coastal benthic ecosystems was evaluated (Barnes et al., 2020; Zwerschke et al., 2022). Emergent polar marine habitats experiencing losses of overlying ice (e.g., sea ice, glaciers and ice shelves) are, in particular, regarded as potentially large-scale negative feedbacks on climate change (Peck et al., 2010; Morley et al., 2022; Zwerschke et al., 2022; Sands et al., 2023).

Antarctic seabed biodiversity, having developed in relative constancy of physical conditions and partial isolation due to the presence of the Antarctic Circumpolar Current (ACC) (Arntz et al., 1994), is likely vulnerable to climate change and associated environmental alterations (Rogers et al., 2020; Gutt et al., 2021; Casado et al., 2023). Nevertheless, considerable knowledge gaps exist around how high-latitude zoobenthic communities, and their carbon storage function, may alter in a warming world and as marine icescapes modify (however, see Barnes, 2017; Pineda-Metz et al., 2020). In respect, this study aims to discern how zoobenthic carbon storage varies across a southern polar gradient and examines zoobenthic (principally epi-zoobenthic) assemblages of four continental/island shelf study areas, all connected by the Scotia Arc, and representative of a transition from cool to seasonally-surface-freezing marine waters. The study includes the following objectives: (i) to ascertain whether zoobenthic carbon storage variance aligns with biodiversity measures (richness) and faunal density; (ii) to determine if VME indicator taxa substantially contribute to zoobenthic carbon storage; (iii) to explore functional groups' contributions to zoobenthic carbon storage; and, finally, (iv) to identify potential environmental drivers of zoobenthic carbon storage, including whether dropstones, physical features of the seabed, exhibit a discernible influence. The wider aims of this study include furthering the knowledge base of very high-latitude blue carbon

estates in a warming world with anticipated marine icescape transformations, and providing an indication of the zoobenthic carbon storage capacity of the southern high-latitude/polar region. The study is also conducted in view of underpinning marine spatial planning and supporting conservation measures, present and future.

4.4 Materials and Methods

4.4.1 Scotia Arc Study Areas and Sites

Situated in the southern South Atlantic Ocean and Atlantic sector of the Southern Ocean, the four study areas, collectively making up the "study region", lie within the latitudinal and longitudinal ranges of ~53-67°S and ~37-70°W, respectively (**Figure 4.1A**; **Table 4.1**). The study areas are ~760 to 2,200 km apart and are connected by the underwater ridge and island system of the Scotia Arc, which links the Terra del Fuego region of South America to the Antarctic Peninsula and semi-encloses the Scotia Sea. The northernmost study area falls within the southern South Atlantic Ocean and is situated on the southeast Patagonian shelf and the western side of the North Scotia Ridge. The most easterly study area is the shelf around the island of South Georgia, positioned south of the Polar Front, the strongest jet of the ACC, at a cusp between sub-Antarctic and Antarctic waters. Following the Scotia Arc clockwise from South Georgia toward higher latitudes leads to the third study area, Marian Cove (a relatively enclosed fjord basin) of King George Island – the largest island of the South Shetland Islands. This archipelago is at the southern boundary of the Drake Passage, and the study area is separated from the South Scotia Ridge and the Antarctic Peninsula by the Bransfield Strait. The fourth and most southerly study area is some 760 km from King George Island, situated west of Marguerite Bay and Adelaide Island on the outer continental shelf of the western Antarctic Peninsula in the Bellingshausen Sea, and falls within the Antarctic Circle. The

study areas of the Scotia Arc study region are herein referred to as SP for southeast Patagonia, SG for South Georgia, MC for Marian Cove and WAP for the western Antarctic Peninsula.

Each Scotia Arc study area was represented by three continental/island shelf sites (**Figure 4.1B-E**; **Table 4.1**) with associated field datasets acquired during various ship-based, chiefly Royal Research Ship *RRS James Clark Ross*, scientific expeditions occurring during austral summers spanning 2009-2020. The southeast Patagonian shelf sites include two at the shallow seamount Burdwood Bank (~18,000 km^2 in area) lying ~200 km south of the Falkland Islands (Islas Malvinas); the sites correspond to SP1 and SP2 and are of ~610 and 110 m water depth, respectively. The third site, SP3 (~570 m depth), lies south of Beauchêne Island – the southernmost and most remote island of the Falkland archipelago at >60 km from East Falkland. At South Georgia, two sites are situated on the island's southern shelf, SG1 (at ~170 m depth) mid-shelf and SG2 (~240 m depth) at the shelf break, while SG3 (~680 m depth) is located on the western shelf of the island. At King George Island, the specific area of focus is Marian Cove fjord, bordered by the Weaver and Barton Peninsulas and situated within Maxwell Bay. With regard to Marian Cove sites, MC1 (at ~200 m depth) sits just outside the fjord (at the entrance), while MC2 (~80 m depth) lies deep within and is closest to the glacier terminus, and MC3 (~60 m depth) is located on the sill of the cove. On the outer continental shelf of the WAP, all three sites, WAP1-3, are situated westward of Marguerite Bay and Adelaide Island, with a depth range of ~360-620 m.

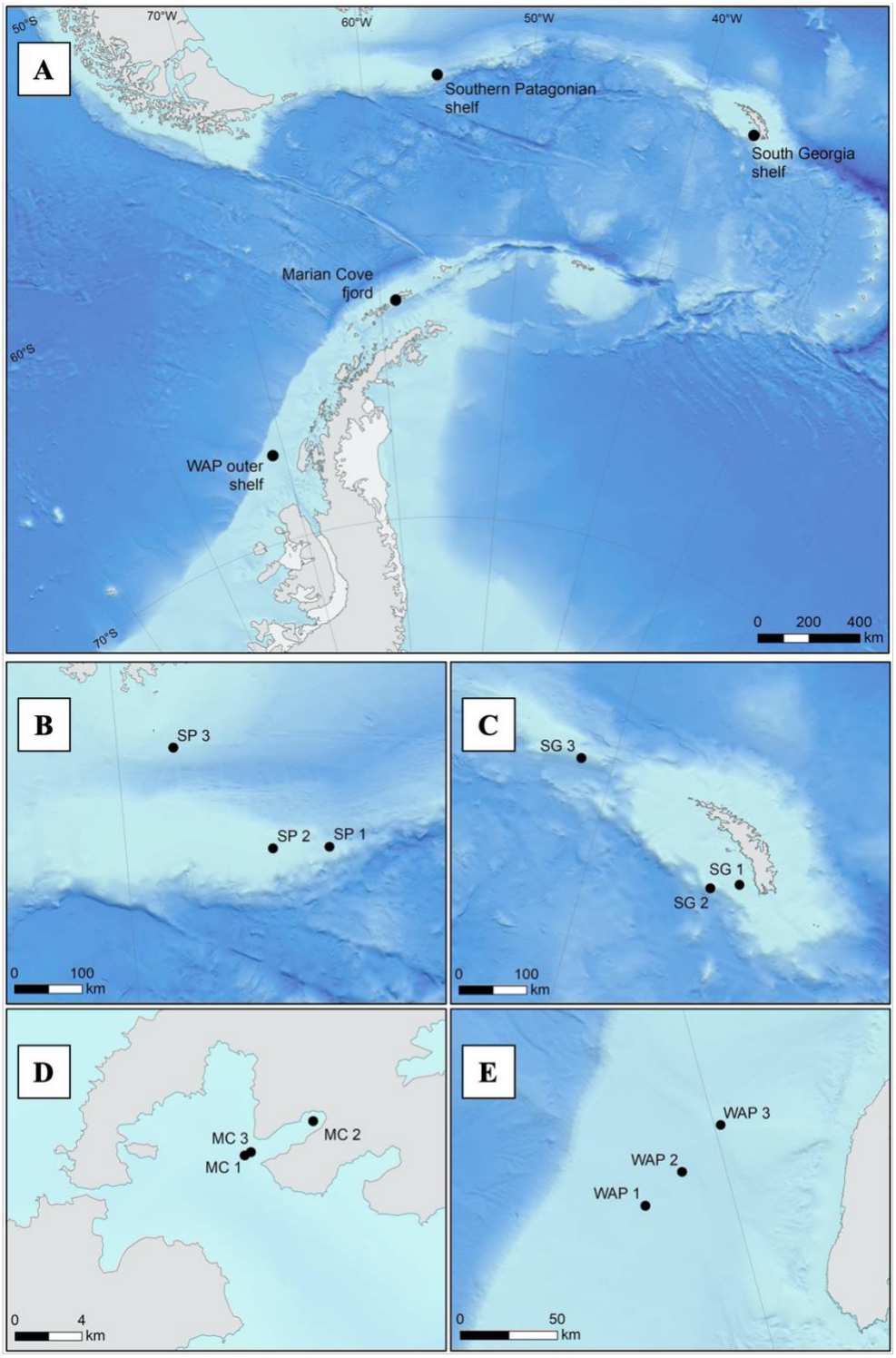


Figure 4.1: Southern South Atlantic and Antarctic study areas and respective sites where benthic imagery was captured by the bespoke Shelf Underwater Camera System (SUCS). (**A**) Location of study areas in the wider context of the southern South Atlantic Ocean and Atlantic sector of the Southern Ocean, including the southern Patagonian shelf, South Georgia shelf, Marian Cove fjord (of King George Island), and the western Antarctic Peninsula (WAP) outer continental shelf; (**B**) Southern Patagonian shelf sites SP1-3; (**C**) South Georgia island shelf sites SG1-3; (**D**)

Marian Cove fjord sites MC1-3; and (**E**) WAP outer continental shelf sites WAP1-3. White areas of the main map denote ice shelves, and grey areas of all maps represent land or ice-covered land/grounded ice (as appropriate). The bathymetric data is from the International Bathymetry Chart of the Southern Ocean v2 (Dorschel et al., 2022), with 100 m contours.

Table 4.1: Southern South Atlantic and Antarctic study areas and sites, including latitude (◦S), longitude (◦W) (in decimal degrees) and water depth (m) (all means across associated benthic imagery), and habitat type.

Study area	Site	Latitude[1]	Longitude[1]	Depth[1]	Habitat type
Southern Patagonian shelf	SP1	-54.4949	-55.5205	610	Shelf bank
	SP2	-54.4997	-56.7649	109	
	SP3	-53.1558	-58.8065	572	
South Georgia shelf	SG1	-54.8735	-36.5875	166	Shelf bank
	SG2	-55.0314	-37.1792	236	
	SG3	-53.7746	-40.6700	678	
Marian Cove (of King George Island)	MC1	-62.2200	-58.8159	205	Fjord
	MC2	-62.2031	-58.7313	83	
	MC3	-62.2174	-58.8065	62	
WAP outer continental shelf	WAP1	-66.9342	-71.0422	479	Trough
	WAP2	-66.7882	-70.4847	620	
	WAP3	-66.6648	-69.9220	358	

[1] Recorded during collection of benthic imagery by an underwater acoustic positioning system – all depths fall within the depth range of the Antarctic continental shelf (Clarke et al., 2004).

4.4.2 Environmental Data Collection

To determine how study sites and/or areas differed environmentally and to help identify environmental variables potentially responsible for biological structuring, various environmental datasets, collected in situ (during seabed imagery collection campaigns), remotely sensed and imagery-analysis-derived, were utilised.

In situ oceanographical data were acquired for each site (during corresponding imagery acquisition efforts) by deploying a Conductivity-Temperature-Depth system (CTD) fitted with auxiliary sensors. The CTD was cast from the sea surface to within ~10 m of the seabed, obtaining near-seafloor temperature (°C), salinity (Practical Salinity Unit; PSU), dissolved oxygen (O_2; μmol L^{-1}), chlorophyll-*a* (μg L^{-1}) and turbidity (beam transmittance; %) measurements.

Daily sea-ice concentration (SIC; %) data, spanning October 1978 to December 2021, and derived from passive microwave observations, were obtained from the US National Snow and Ice Data Center (NSIDC) (in conjunction with the US National Oceanic and Atmospheric Administration; NOAA). The dataset used was the NOAA/NSIDC Climate Data Record of Passive Microwave Sea Ice Concentration, Version 4 (G02202) (Meier et al., 2021), with a 25 by 25 km grid cell resolution. These records were used to calculate mean SIC for each site and area for the 14-year period prior to respective imagery collection, the period complementing available primary production data. As per Cummings et al. (2021), a year was considered as being from July through to June. In addition, the mean number of days sea-ice-covered per year was also computed for each site and area for the same period, with ≥ 85% sea-ice concentration/cover considered sea-ice-covered (as per Souster et al., 2020). For the

purpose of the study, study sites were defined as "sea-ice sites" when the mean number of days of sea-ice-covered per year was at least 40.

Daily net primary production (NPP; mg C m^{-2} day^{-1}) data, spanning September 1997 to July 2019, were generated following the methods of Arrigo et al. (2008) and (2015). From such data, mean daily NPP and mean peak NPP were calculated for each site and area for the 14-year period prior to respective imagery collection.

Daily sea surface temperature (SST; °C) data, spanning September 1981 to March 2022, were obtained from NOAA. The dataset used was the NOAA 1/4° Daily Optimum Interpolation Sea Surface Temperature dataset (Huang et al., 2020). From such data, mean daily SST was calculated for each site and area for the 14-year period prior to respective imagery collection, again the period complementing available primary production data.

Substratum type and rugosity of each image were determined during seafloor imagery analysis (section 4.4.4), and corresponding (mode-based) assignments assigned to each site.

4.4.3 Continental Shelf Imagery Collection

Seabed imagery (for example images see **Figure S4.1**) was acquired for each study site using the Shelf Underwater Camera System (SUCS; developed by the British Antarctic Survey Antarctic Marine Engineering Team). SUCS comprises a high-resolution still camera, lights, and a real-time ultra-short baseline positioning beacon, all mounted on a tethered (fibre-optic multimode cable) tripod, which can adjust for slope (see Barnes et al., 2020; Zwerschke et al., 2022). The camera was positioned perpendicular to the seabed at the same pre-set distance to capture images with a known field of view (area), enabling faunal density calculations. Images were captured when the tripod was at rest and spaced

~5 m apart to avoid spatial overlap. Typically, 20 images (replicates) were taken per site; hence, 60 per study area and ~240 across the Scotia Arc region.

4.4.4 Imagery Analysis and Functional Group and VME Indicator Assignments

Each seafloor image collected was analysed for discernible zoobenthic megafauna using the web-based imagery annotation software BIIGLE 2.0 (www.biigle.de; Langenkämper et al., 2017). For each image, the number of different morphotaxa (morphotaxa richness) was recorded, and counts of individual functional groups (see **Table 4.2**; adapted from Barnes and Sands, 2017 and Frinault et al., 2022) were conducted; hence, functional group richness was also recorded. Functional groups were based on mobility, feeding strategy and skeletal support – as aforementioned, attributes considered important in blue carbon pathways (see Barnes and Sands, 2017) – and included three suspension-feeding groups, three deposit-feeding groups, a flexible feeding strategy group (typified in the study by ophiuroids), a grazing group and five predating/scavenging groups. The utilisation of such functional group categorisations enables direct comparison with findings of other studies employing the same functional group categorisation scheme (e.g., Souster et al., 2020). The number of taxa considered indicative of VMEs, as per CCAMLR (2009), was also determined (referred to herein as VME indicator taxa or simply VME taxa). As the area of each image was known, taxonomic group, functional group, and VME taxa counts could be converted into corresponding densities, i.e., individuals per m^2 (ind. m^{-2}) – standardisation permitting direct comparisons.

Table 4.2: Functional groups based on Barnes and Sands (2017) and Frinault et al. (2022), with example taxa discerned in this study.

Functional group	Example taxa
Pioneer sessile suspension feeders	Ascidians, encrusting bryozoans, some tubicolous polychaetes
Climax sessile suspension feeders	Brachiopods, some erect bryozoans, poriferans (of classes Demospongiae and Hexactinellida)
Sedentary/mobile suspension feeders	Crinoids, some holothurians
Crawling (epi-faunal) deposit feeders	Holothurians
Soft (in-faunal) deposit feeders	Echiurans, some polychaetes, sipunculans
Hard (burrowing) deposit feeders	Bivalves, irregular echinoids, scaphopods
Flexible strategists	Ophiuroids
Grazers	Regular echinoids, gastropods
Soft sessile predator/scavengers	Actiniarians, hydroids, pennatulaceans, soft corals, staurozoans
Hard sessile predator/scavengers	Calcaxonian whips, hydrocorals, scleractinians
Soft mobile predator/scavengers	Octopi, nemerteans, nudibranchs
Hard mobile predator/scavengers	Asteroids, fish, some gastropods
Arthropod predator/scavengers	Amphipods, decapod shrimps, pycnogonids

Additionally, for each image, substratum type was categorised as mud/fine sand, coarse sand, fine pebbles, coarse pebbles, cobbles, boulders/bedrock, or biogenic. The seven categories (principally of increasing sediment grain size) were based on the modified Udden-Wentworth sediment classification scheme (Blair and McPherson, 1999) and categorisations by Barnes et al. (2019) and Souster et al. (2020). Further to substratum categorisation, an image was also defined as a "dropstone image" if a dropstone or boulder was present at least three sediment-size classes larger than proximate substrata (for more information regarding glacial dropstones, see Ziegler et al., 2017 and Post et al., 2020) in order to assess if such features had any influence on zoobenthic carbon storage and other biological variables in the study region. Finally, rugosity, the small-scale roughness of the seabed, was graded by measuring the "shadow length" of substrata (again following Barnes et al., 2019 and Souster et al., 2020). The seven categories (of increasing rugosity) included <1 mm (i.e., smooth), 1–10 mm, >10–20 mm, >20–30 mm, >30–40 mm, >40–50 mm and ≥50 mm (i.e., rough).

4.4.5 Zoobenthos – Acquisition and Carbon Content Analysis, and Zoobenthic Carbon Storage Estimations

Zoobenthic specimens were collected in the vicinity of SUCS deployments (and oceanographical data collections) using Agassiz or mini-Agassiz trawls. Specimens were washed and morphologically-identified prior to storage, with the carbon contents of identified taxa later determined and used to calculate the mean carbon content of each functional group for each study area. The total number of specimens used in such calculations varied from 84 to 102 per study area. For three study areas, zoobenthic carbon content data of associated specimens were acquired from previous studies which employed identical methodologies (Barnes, 2017; Barnes and Sands, 2017; Bax, *pers.*

comms.), and for Marian Cove, the carbon content of respective zoobenthos was determined as part of this study, with associated methods reported below.

The carbon content of Marian Cove zoobenthic specimens was determined following standardised methods (see Barnes, 2017; Barnes and Sands, 2017; Barnes et al., 2019; Souster et al., 2020), facilitating direct comparability with the results of those studies. Specimens were first washed with deionised water (Millipore Elix® Type 2) and placed into pre-etched and pre-weighed aluminium weighing boats for the duration of the analysis; a specimen was divided between more boats as necessary. Specimens were then dried for 12-24 hours in a drying oven (Genlab OV/125/F/DIG) at 70 °C until constant mass achieved and subsequently incinerated for 12 hours in a muffle furnace (Carbolite ESF 12/10) at 480 °C and reweighed – the tissue mass, equivalent to ash-free dry mass (AFDM), having been burnt off and skeletal mass isolated. The organic carbon content of a specimen, C_{org}, was calculated as 50% of AFDM (this percentage based on prior studies which found that, in most taxa, ~50% of their organic matter is carbon, e.g., Salonen et al., 1976; Schlesinger, 1991), while the inorganic carbon content, C_{inorg}, was computed as 12% of the residual skeletal mass; however, if a specimen was siliceous (e.g., a Hexactinellid sponge), C_{inorg} was calculated as 1% of the residual skeletal mass (as per Barnes and Sands, 2017). A specimen's total carbon content, C_{tot}, i.e., g of C held, was obtained by summing the corresponding values of C_{org} and C_{inorg}.

Using C_{tot} of all corresponding specimens, the mean C_{tot} of each functional group was computed for each study area. – note, the mean C_{tot} a functional group will be influenced by which specimens are (able to be) collected. To estimate zoobenthic carbon storage per m^2 (C_{zoo}; g C m^{-2}), functional group densities, determined during section 4.4.4 procedures, were multiplied by respective values for mean C_{tot}. Around 20 separate C_{zoo} values were generated per study site, thus 60 for each study area.

4.4.6 Statistical Analyses

Differences in C_{zoo} and faunal density among study areas were tested using non-parametric (Kruskal Wallis) tests (with Dunn's post-hoc tests) as associated data did not meet the assumptions of Analysis of Variance (ANOVA), even after transformation. The relationship between C_{zoo} and various biological variables (i.e., richness and density) was explored via linear regression.

In advance of multivariate analyses, performed in PRIMER v7 (Clarke and Gorley, 2015) with PERMANOVA+ add-on (Anderson et al., 2008), and following established procedures (Clarke et al., 2014; Clarke and Gorley, 2015), all environmental/abiotic variables were assessed for collinearity (via Draftsman plots and an accompanying correlation matrix). For variables exhibiting a high correlation coefficient, r ≥95%, a single variable was retained as a proxy for the other (**Table S4.1**); the remaining variables were then normalised onto a common dimensionless scale for analysis. Biological data, i.e., functional group densities (assemblage structure) and C_{zoo} values split by functional group (carbon storage structure), were fourth-root transformed, permitting rarer/less numerically dominant groups to have some influence in subsequent similarity calculations (Clarke and Green, 1988).

The similarity between study sites' biological structuring was investigated using the Bray-Curtis similarity coefficient (which generates a resemblance matrix; Bray and Curtis, 1957), followed by hierarchical agglomerative cluster (HAC) analysis (based on the resemblance matrix; Everitt, 1980), with a similarity profile (SIMPROF) test (Clarke et al., 2008), and the similarity percentages (SIMPER) procedure (see Clarke, 1993).

The BEST (Bio-Env) routine, employing the Spearman's rank correlation coefficient, was used to identify which subset of environmental variables (**Table S4.1**)

best matched, or "explained", the biological structuring observed, accompanied by a global BEST test (999 random permutations) to determine the statistical significance of the match (Clarke et al., 2008; Clarke and Ainsworth, 1993). The BEST routine uses biological resemblance and normalised-environmental data matrices (and applies Euclidean distance to the latter during the process). Total C_{zoo} was also explored as a single response variable, with the corresponding resemblance matrix being based on Euclidean distance (Clarke and Gorley, 2015).

In addition, Wilcoxon matched-pair signed-rank tests were used to compare the means of several biological variables of dropstone images and randomly-selected non-dropstone images (paired from the same study site).

4.5 Results

4.5.1 Environmental Differences of Study Areas

In terms of CTD-derived environmental (i.e., in situ oceanographical) differences, and for SP, SG, MC and WAP collectively, mean (±1 SD) near-seafloor temperature (°C) ranged from 0.1 (±0.2) to 7.4 (±0.1); salinity (PSU) from 33.4 (±1.2) to 34.7 (±0.0); dissolved oxygen (μmol L^{-1}) from 177.8 (±6.3) to 346.6 (±19.8); chlorophyll-a (μg L^{-1}) from 0.02 (±<0.1) to 0.21 (±0.1); and turbidity (beam transmittance; %) from 93.8 (±2.3) to 97.9 (±0.3).

From remotely-sensed data, it was found that mean SIC (%, ±1 SD where applicable) for the 14-year period prior to respective imagery collection was 0 for SP and SG, 10.1 for MC (within one grid cell), and 39.8 (± 1.4) for WAP. The mean number of days per annum sea-ice-covered (days) varied from 0 for SP and SG to 117.4 (± 7.4) for WAP.

Mean daily and peak NPP for the 14-year period prior to respective imagery collection were highest at WAP and SP, respectively. For SP, SG, MC and WAP collectively, mean (±1 SD) daily NPP values (mg C m^{-2} d^{-1}) ranged from 300.3 (±0.2) to 389.3 (±36.5), and mean (±1 SD) peak NPP values (mg C m^{-2} d^{-1}) from 520.4 (±0.9) to 1126.8 (±548.4).

Mean (±1 SD) sea surface temperature (°C) for the 14-year period prior to respective imagery collection ranged from 5.8 (±0.4) (for SP) to −0.8 (±0.0) (for WAP).

Study area-specific means of environmental data can be found in **Table S4.2**.

Regarding imagery-informed environmental differences, the finest sedimented (i.e., mud/fine sand) and smoothest seabed (i.e., lowest rugosity) was observed at sites MC2, WAP2 and WAP3. The site with the coarsest sediment (largest grain size) and highest rugosity was SP3, which featured boulders. Coarse pebbles were observed at SG3 and WAP3.

4.5.2 Zoobenthos of the Scotia Arc Imagery

Over 9,400 individual fauna were detected across the Scotia Arc imagery, with all functional groups (**Table 4.2**) being represented. Overall, images were dominated by pioneer sessile suspension feeders (e.g., ascidians and encrusting bryozoans) and mobile flexible-feeding ophiuroids. Specifically, 39.4% of individuals belonged to the pioneer sessile suspension feeder group, 25.7% to the flexible feeding strategy group, 11.9% to the climax sessile suspension feeder group, which included, for example, demosponges, and 7.3% to the soft sessile predator/scavenger group (exemplified by sea anemones and hydroids) – the remaining individuals were distributed across the nine other functional groups. In addition, 46.8% of all zoobenthic taxa observed were classified as VME taxa, i.e., >4,400 individuals.

4.5.3 Zoobenthic Carbon Storage across Study Areas

A zoobenthic specimen of the Scotia Arc study region held, on average, 0.3 g of carbon (with a standard deviation of ±0.6). When looking at the mean (±1 SD) C_{tot} of individual functional groups across all study areas, 0.001 (±0.0007) g was the lowest value calculated (the responsible functional group type being crawling deposit feeders – i.e., holothurians) and 2.1 (±2.3) g the highest (the responsible functional group type being soft mobile predator/scavengers) (see **Figure S4.2**). The mean C_{tot} of a particular functional group varied between the four study areas. Considering all respective specimens, mean C_{tot} was lowest for SG (which bisects the ACC), followed by SP and MC, and highest for WAP.

At site level, means (plus standard deviations) for zoobenthic carbon storage ranged from 2.4 (±2.5) C m^{-2} at SP1 to 76.0 (±39.4) C m^{-2} at WAP3. At study area level, means for zoobenthic carbon storage were 8.2 (±8.9), 6.2 (±5.1), 38.6 (±28.8), and 44.6 (±57.9) g C m^{-2} for SP, SG, MC, and WAP, respectively, i.e., the two polar study areas south of the ACC exhibited higher mean carbon storage values compared to the other two areas, collectively averaging 41.6 (±45.6) and 7.2 (±7.3) g C m^{-2}, respectively. Kruskal Wallis tests indicated that all study areas significantly differed in terms of carbon storage except the two lower-latitude areas, SP and SG (**Table 4.3**).

Table 4.3: P-values (with Bonferroni correction) resulting from Kruskal-Wallis tests between Scotia Arc study areas for zoobenthic carbon storage (C_{zoo}; g C m^{-2}) and faunal density (ind. m^{-2}). Regarding continental/island shelf study areas: SP = South Patagonia (specifically the shelf of the Falkland Islands/Islas Malvinas); SG = South Georgia; MC = Marian Cove (of King George Island); and WAP = western Antarctic Peninsula (westward of Marguerite Bay and Adelaide Island). Significant p-values are shown **in bold** and asterisked.

	SP vs SG	**SP vs MC**	**SP vs WAP**	**SG vs MC**	**SG vs WAP**	**MC vs WAP**
C_{zoo}	$p > 0.05$	**$p < 0.001$****	**$p < 0.001$****	**$p < 0.001$****	**$p < 0.001$****	**$p = 0.049$***
Faunal density	***$p < 0.001$*****	***$p < 0.001$*****	***$p < 0.001$*****	*$p > 0.05$*	*$p > 0.05$*	*$p > 0.05$*

4.5.4 Zoobenthic Carbon Storage and Morphotaxa and Functional Group Richness

An objective of the current study was to investigate relationships between marine biological carbon storage and biodiversity measures (morphotaxa and functional group richness). For all study areas, statistically significant positive relationships were found between zoobenthic carbon storage and morphotaxa richness; however, some relationships appeared stronger than others, in particular, those of SP and WAP (see **Figure 4.2A**) – the most northerly and southerly areas, respectively. Thus, it appeared that greater carbon storage function, within the study region, generally aligned with higher biodiversity (richness). In addition, the carbon-morphotaxa richness relationships of the study areas were all statistically significantly different.

Significant positive relationships were also found between C_{zoo} and functional group richness (**Figure 4.2B**); however, these relationships were not as strong as those

observed for C_{zoo} and morphotaxa richness. WAP exhibited the strongest relationship of all areas. Nonetheless, almost all carbon-functional group richness relationships were statistically significantly different, with the relationship of SP and SG the exception (i.e., not significantly different).

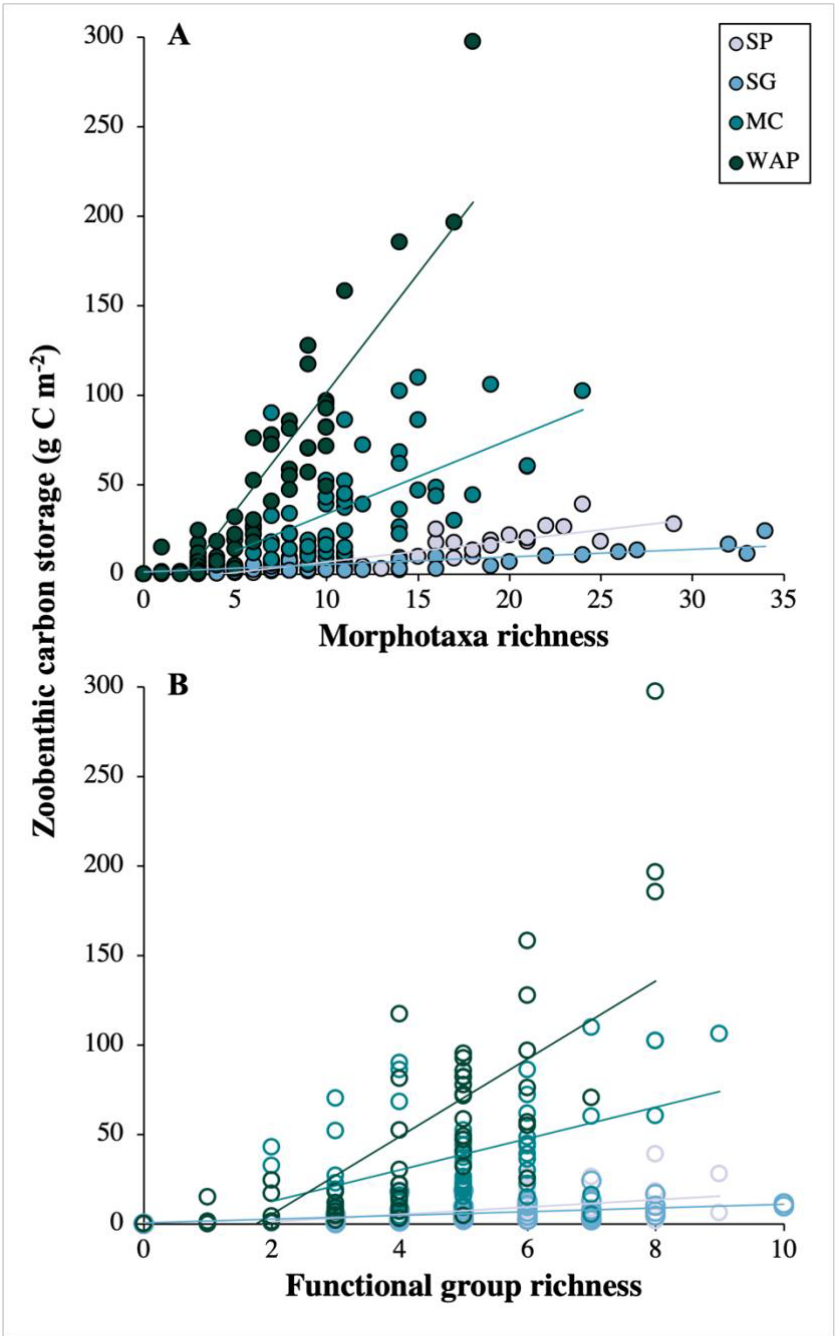


Figure 4.2: Carbon storage by zoobenthos (C_{zoo}; g C m^{-2}) versus faunal richness for (**A**) morphotaxa richness and (**B**) functional group richness. R^2 for (**A**): SP = 0.82; SG = 0.42; MC = 0.35; and WAP = 0.82. R^2 for (**B**): SP = 0.19; SG = 0.21; MC = 0.19; and WAP = 0.53. Regarding continental/island shelf study areas: SP = South Patagonia (specifically the shelf of the Falkland Islands/Islas Malvinas); SG = South Georgia; MC = Marian Cove (of King George Island); and WAP = western Antarctic Peninsula (westward of Marguerite Bay and Adelaide Island). For C_{zoo} versus morphotaxa richness, all slopes were statistically significantly different (p-values all < 0.001). For C_{zoo} versus functional group richness, all slopes were significantly different (p-values all < 0.001, bar SP versus MC, where the p-value was 0.004) except for SP versus SG, where the

p-value was non-significant. Regression-associated ANOVA results for C_{zoo} versus morphotaxa richness: F = 258.33, 39.85, 31.69, and 267.30 for SP, SG, MC, and WAP, respectively, and p-values all <0.001, and for C_{zoo} versus functional group richness: F = 12.84, 13.33, 15.76, and 78.87 for SP, SG, MC, and WAP, respectively, and p-values all < 0.001.

4.5.5 Faunal Density and Zoobenthic Carbon Storage

In terms of seabed megafaunal densities, WAP exhibited the highest image level faunal density value, 484.9 ind. m^{-2}, and also the highest estimated zoobenthic carbon storage value, 297.5 g C m^{-2} (**Figure 4.3**). When examining lowest faunal densities, some images had no discernible fauna, i.e., faunal densities of zero (including imagery of sites SG2, WAP1 and WAP2). The lowest density greater than zero was observed in an SP1 image at 2.5 ind. m^{-2}. At site level, the highest mean faunal density was 255.1 (±88.4) ind. m^{-2} at WAP3, and the lowest was 12.8 (±2.4) ind. m^{-2} at SP1 – the former aligning with the highest average for carbon storage and the latter aligning with the lowest average for carbon storage (see section 4.5.3). Kruskal Wallis tests indicated that SP statistically significantly differed from all other study areas in terms of faunal density, while SG and MC, SG and WAP, and MC and WAP did not significantly differ (see bottom row of **Table 4.3**).

For all study areas, significant positive relationships were found between zoobenthic carbon storage and faunal density, and carbon-faunal density relationships were all statistically significantly different (**Figure 4.3**). Generally, C_{zoo} exhibited a stronger relationship with faunal density than with morphotaxa and functional group richness; the exception being WAP, where the carbon-morphotaxa richness relationship appeared the strongest of the relationships examined.

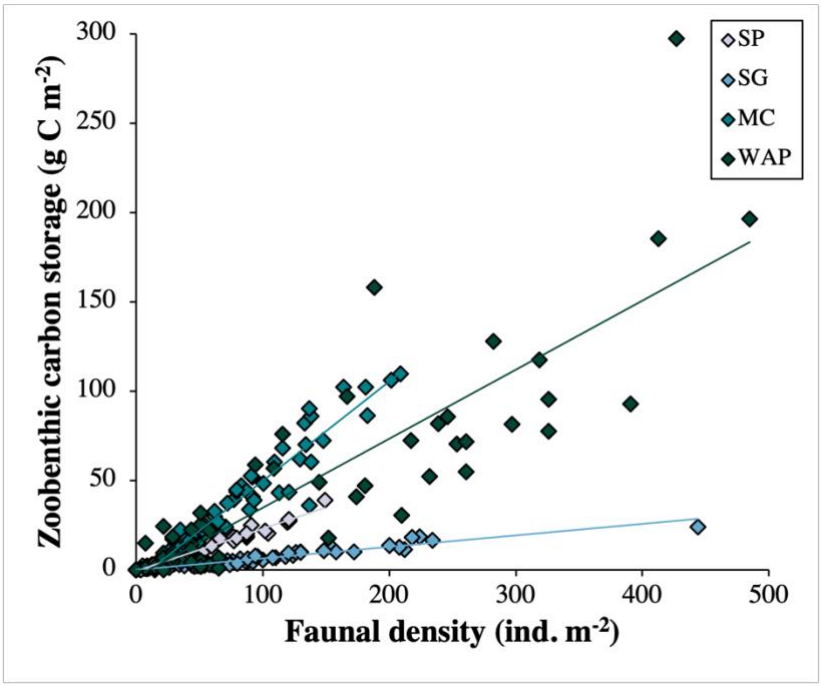


Figure 4.3: Carbon storage by zoobenthos (C_{zoo}; g C m^{-2}) versus faunal density (ind. m^{-2}). R^2: SP = 0.97; SG = 0.92; MC = 0.92; and WAP = 0.75. Regarding continental/island shelf study areas: SP = South Patagonia (specifically the shelf of the Falkland Islands/Islas Malvinas); SG = South Georgia; MC = Marian Cove (of King George Island); and WAP = western Antarctic Peninsula (westward of Marguerite Bay and Adelaide Island). All slopes were statistically significantly different (p-values all < 0.001). Regression-associated ANOVA results for C_{zoo} versus fauna density: F = 1874.79, 672.35, 639.96, and 172.68 for SP, SG, MC, and WAP, respectively, and p-values all < 0.001.

4.5.6 VME Taxa and Zoobenthic Carbon Storage

VME taxa contributed at least 53% to zoobenthic carbon storage at eight (out of 12) study sites. In the SP study area, VME taxa contributed 81, 87 and 31% at sites SP1-3, respectively; hence, VME taxa contribution to zoobenthic carbon storage was highest at the two Burdwood Bank sites, corresponding with previous observations (Bax, *pers. comms.*). For the SG study area, SG3 (situated on the western shelf) exhibited the highest VME taxa contribution at 56%, while contributions at SG1 and SG2 (both on the southern shelf) were lower at 23 and 7%, respectively. In MC, VME taxa contributions to

zoobenthic carbon storage were high across study sites at 53, 82 and 66% for MC1-3, respectively. Finally, VME taxa contributed 86, 31 and 64% at WAP1-3, respectively. Overall, WAP1 (the southernmost site of the study) displayed the highest site-level VME taxa contribution to zoobenthic carbon storage of all sites, and SG2 the lowest.

In addition, the relationship between zoobenthic carbon storage and VME taxa density was also examined for each study area (**Figure 4.4**). All carbon-VME density relationships were positive and significant and significantly differed from one another. Compared to carbon and complete faunal density relationships (**Figure 4.3**), the carbon-VME density relationships displayed slightly lower R^2 and less significant p-values for SP and MC, and a much lower R^2 and less significant p-value for SG; however, a higher R^2 and more significant p-value for WAP.

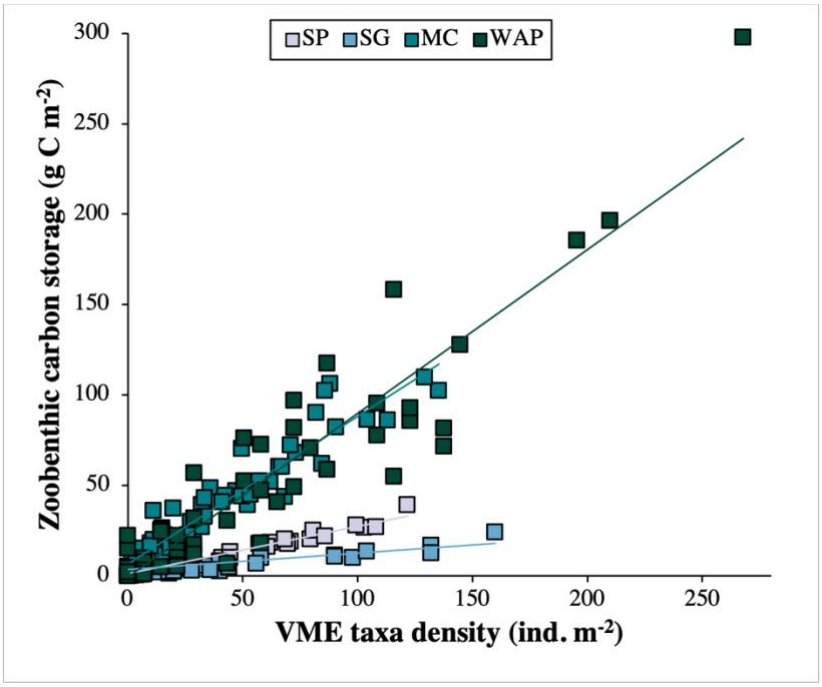


Figure 4.4: Zoobenthic carbon storage (C_{zoo}; g C m^{-2}) versus density of Vulnerable Marine Ecosystem (VME) indicator taxa (ind. m^{-2}). R^2: SP = 0.96; SG = 0.40; MC = 0.90; and WAP = 0.87. Regarding continental/island shelf areas: SP = South Patagonia (specifically the shelf of the Falkland Islands/Islas Malvinas); SG = South Georgia; MC = Marian Cove (of King George Island); and WAP = western Antarctic Peninsula (westward of Marguerite Bay and Adelaide Island). All slopes were statistically significantly different (p-values all < 0.001). Regression-associated ANOVA results for C_{zoo} versus VME taxa density: F = 1289.91, 37.17, 498.79, and 404.72 for SP, SG, MC, and WAP, respectively, and p-values all < 0.001.

4.5.7 Functional Group Contributions to Zoobenthic Carbon Storage and Faunal Density

Overall, nine functional groups were found to be substantial contributors (i.e., ≥ 10%) to zoobenthic carbon storage at site level (**Figure 4.5**), the exceptions being sedentary/mobile suspension feeders and all deposit-feeding groups. At area level, six functional groups were substantial contributors (see **Figure S4.3**), including pioneer sessile suspension feeders, climax sessile suspension feeders, grazers, soft and hard

sessile predator/scavengers, and flexible strategists. No individual functional group was found to be a substantial contributor to zoobenthic carbon storage at all 12 sites, and similarly, no individual group was found to be a major contributor in all four study areas.

Functional groups which contributed most substantially to the zoobenthic carbon stored at each study area (**Figure S4.3**) included climax sessile suspension feeders at both SP and WAP (49.0 and 50.5%, respectively), flexible strategists (i.e., ophiuroids) at SG (54.9%), and pioneer sessile suspensions feeders at MC (80.7%). Other substantial contributors to zoobenthic carbon storage included hard sessile predator/scavengers and grazers at SP, climax sessile suspension feeders and pioneer sessile suspension feeders at SG, flexible strategists at MC, and pioneer sessile suspension feeders and soft sessile predator/scavengers at WAP. The "mixed" group, which included functional groups that individually contributed <10% to zoobenthic carbon storage, also substantially contributed in three out of four study areas (ranging from 13.1 to 20.8%), the exception being MC (at 6.4%).

At a more granular level (i.e., site level; **Figure 4.5**), different combinations of functional groups substantially contributed to zoobenthic carbon storage. For example, functional groups substantially contributing at SP sites included hard sessile predator/scavengers at SP1-3 (53.6, 21.7, and 29.8%, respectively), climax sessile suspension feeders at SP1 and SP2 (25.9 and 63.7%, respectively), and grazers (made up of grazing gastropod molluscs), rather than climax sessile suspension feeders, at SP3 (56.7%). At SG1, flexible strategists (64.3%) and climax sessile suspension feeders (11.1%) were substantial contributors, as well as the mixed group (24.6%). At SG2, flexible strategists were the dominant carbon storage contributors (84.8%), the remaining contributors all within the mixed group (15.2%). At SG3, four individual functional groups substantially contributed to zoobenthic carbon storage: flexible strategists (22.5%;

as observed at SG1 and SG2), climax sessile suspension feeders (33.2%; and consistent with SG1), and, in addition, hard sessile predator/scavengers (19.8%) and pioneer sessile suspension feeders (15.7%). The most considerable contribution to zoobenthic carbon storage at MC1-3 was from the pioneer sessile suspension feeders functional group (with a percentage contribution range of 69.7-94.2%), and, at MC1 and MC3, a substantial contribution was also observed from flexible strategists (21.8 and 16.0%, respectively). The mixed group did not contribute substantially at any MC site (all ≤8.5%). At both WAP1 and WAP3, climax sessile suspension feeders were the major contributor to carbon storage (at 58.0 and 48.9%, respectively), although not at WAP2. Site WAP2 appeared to be the most complex with respect to major contributor make-up, with five functional groups substantially contributing to zoobenthic carbon; groups included soft sessile predator/scavengers (in common with WAP1), pioneer sessile suspension feeders (in common with WAP3) and, additionally (and contrary to WAP1 and WAP3), soft mobile predator/scavengers (27.9%), arthropod predator/scavengers (17.5%), and hard mobile predator/scavengers (12.4%).

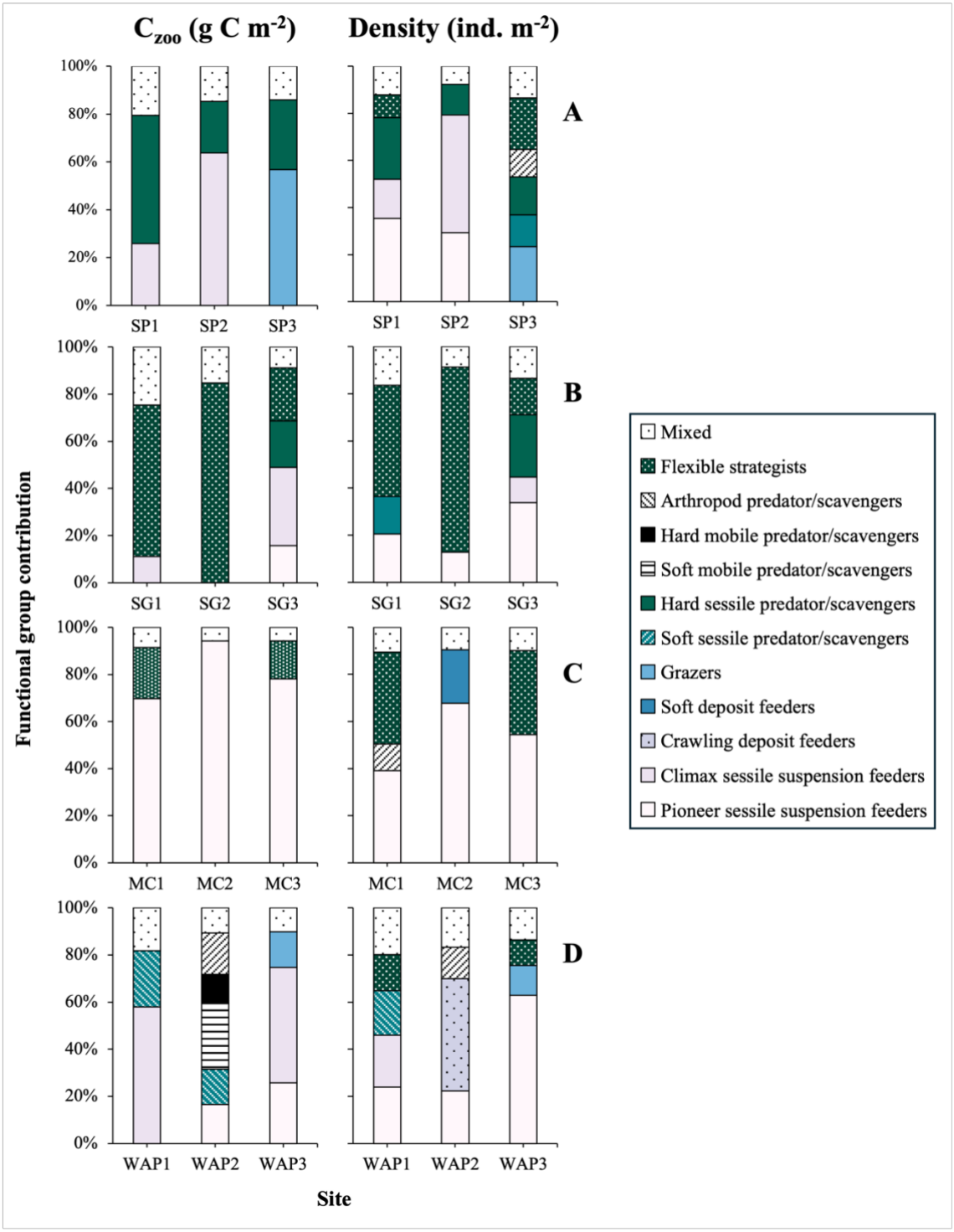


Figure 4.5: Average functional group contribution (%) to zoobenthic carbon storage (C_{zoo}; g C m^{-2}) and faunal density (ind. m^{-2}) for continental/island shelf study sites of (**A**) South Patagonia (specifically the shelf of the Falkland Islands/Islas Malvinas), (**B**) South Georgia, (**C**) Marian Cove (of King George Island), and (**D**) the western Antarctic Peninsula (westward of Marguerite Bay and Adelaide Island). Individual functional groups are shown where their contribution was ≥

10%. Otherwise, groups were pooled with others whose contributions were also < 10% and designated as the "mixed" group.

Across the study region, at both study area and site level, functional group (percentage) contributions to zoobenthic carbon storage differed from respective contributions to faunal density (see **Figures 4.5** and **S4.3**, respectively). For example, at area level, some functional groups had greater contributions to C_{zoo} than density, e.g., climax sessile suspension feeders at SP, SG and WAP, grazers and hard sessile predator/scavengers at SP, flexible strategists at SG, pioneer sessile suspension feeders at MC, and soft sessile predator/scavengers at WAP. Conversely, some functional groups had smaller contributions to C_{zoo} than density, including pioneer sessile suspension feeders at SP, SG, and WAP, soft sessile predator/scavengers at SG, and hard sessile predator/scavengers at MC and WAP (the two polar study areas south of 60°S). This observation was similarly the case for site-level functional group percentage contributions (**Figure 4.5**), where some functional groups contributed greatly to C_{zoo} and not faunal density, and vice versa.

4.5.8 Assemblage and Zoobenthic Carbon Storage Structures and Potential Environmental Drivers

With regard to assemblage structure (by functional groups), HAC analysis (with SIMPROF) identified four distinct groupings among the 12 sites (**Figure S4.4A**). WAP2, MC2 and SP3 were each compositionally distinct (hence, each their own group), while the remaining nine sites formed one group (with an average similarity of 75.6% and with pioneer sessile suspension feeders, flexible strategists and climax sessile suspension feeders being the top functional groups contributing to similarity [according to

SIMPER]). WAP2 and the group comprising the nine sites were the most compositionally dissimilar (with an average dissimilarity of >44% – principally due to an abundance of crawling deposit feeders and a lack of climax sessile suspension feeders and hard sessile predator/scavengers at WAP2). For more details, see **Table S4.2**.

Regarding carbon storage (by functional group) structure, HAC analysis (with SIMPROF) identified six distinct groupings among sites (**Figure S4.4B**). MC2 and WAP2 constituted one group, which had the lowest average similarity at 59.7%, SP3 was compositionally distinct in its own right (hence, its own group), WAP1 and WAP3 formed another group, SP1 and SP2 another, and SG1-3, MC1 and MC3 the final group (with an average similarity of 74.2%). The MC2 and WAP2 group (both polar sites) and the SP1-2 group (the northernmost sites) were the most compositionally dissimilar (with an average dissimilarity of 54.7%). For the SP1-2 group and the MC2 and WAP2 group, dissimilarities were principally driven by hard sessile predator/scavengers, climax sessile suspensions feeders, pioneer sessile suspension feeders, and in-faunal deposit feeders. For more details, see **Table S4.3**.

BEST analyses indicated that a subset of four environmental variables most highly correlated with the variation in faunal assemblage structure (by functional groups) (Rho correlation = 0.34, p-value < 0.01). The subset comprised sea-ice cover, peak NPP, turbidity, and substratum.

For the carbon storage by functional group data, a subset of three environmental variables was identified as the most highly correlating (Rho correlation = 0.41, p-value < 0.01). The subset included sea-ice cover, peak NPP, and temperature.

Sea-ice cover was the single variable with the highest correlation with assemblage and carbon storage by functional groups structures (Rho correlations all > 0.32), and sea-

ice cover and peak NPP were encompassed in all optimal subsets of environmental variables. The subsets, therefore, included a mixture of remotely sensed and local-scale environmental variables.

Additionally, when examining zoobenthic carbon storage as a single response variable, sea-ice cover was both the single variable with the highest correlation and the optimal subset (Rho correlation = 0.26, p-value < 0.01).

4.5.9 Influence of Dropstones

The influence of dropstones and boulders (relatively raised physical seabed features) on zoobenthic carbon storage and other biological variables was also examined. All dropstones observed were of boulder grain sizes (i.e., >256 mm; Blair and McPherson, 1999). Dropstone images, although relatively rare, representing just 3% of the Scotia Arc imagery analysed, displayed higher values (means) than non-dropstone images for all biological variables explored, i.e., morphotaxa and functional group richness, zoobenthic carbon storage and faunal density; however, Wilcoxon matched-pair signed-rank tests revealed these differences to be statistically non-significant (Table 4) – perhaps due to the limited sample size. SP1, SP2, SG3, MC1-3, and WAP3 each presented paired samples.

Table 4.4: Results of Wilcoxon matched-pair signed-rank tests for various biological variables of dropstone images and non-dropstone images of Scotia Arc continental/island shelf study areas. "N" indicates sample size (i.e., number of images) and the biological variables examined included morphotaxa and functional group richness, zoobenthic carbon storage (C_{zoo}; g C m^{-2}), and faunal density (ind. m^{-2}).

	Dropstone images $\bar{x}$ **(±1 SD)** **N = 7**	**Non-dropstone images** $\bar{x}$ **(±1 SD)** **N = 7**	**Wilcoxon matched-pair test result**
Morphotaxa richness	18.9 (±7.5)	11.3 (±5.3)	**p = 0.06**
Functional group richness	6.0 (±1.3)	5.0 (±1.3)	**p = 0.07**
Zoobenthic carbon storage	61.1 (±66.1)	30.1 (±44.1)	**p = 0.06**
Faunal density	191.8 (±190.3)	84.1 (±94.0)	**p = 0.09**

4.6 Discussion

The Scotia Arc study region, which encompasses the southern South Atlantic Ocean and Atlantic sector of the Southern Ocean, is a collective hotspot of climate change, high-latitude biodiversity, and ecosystem services; however, not, as of yet, protection (Rogers et al., 2020; Cavanagh et al., 2021). Much of the study region falls within a proposed network of marine protected areas (MPAs) under consideration by CCAMLR (Brooks et al., 2020). Building evidence bases, such as those concerning biodiversity and blue carbon (as an ecosystem service), and VME taxa presence and their contributions to the former, is vital in supporting MPA designations; the current study contributes to such evidence

bases. Additionally, a recent review, supported by the Intergovernmental Panel on Climate Change, has recommended a synergistic approach to alleviating the biodiversity and climate crises (i.e., Pörtner et al., 2023). Although such an approach is seemingly yet to be implemented in polar waters, evidence is building, including from this study, with regard to high-latitude benthic biodiversity supporting carbon storage, and potentially climate change mitigation (Morley et al., 2022; Zwerschke et al., 2022; Sands et al., 2023).

4.6.1 Variation in Zoobenthic Carbon Storage

Reflecting the complex and patchy nature of southern high-latitude continental/island shelf habitats, zoobenthic carbon storage was here found to vary within and between study sites and study areas – i.e., over different spatial scales. Nonetheless, when comparing the combined average for carbon storage by zoobenthic assemblages of the two southernmost study areas with that of the two northernmost areas, the former was six times greater than that of the latter. This considerable difference in ecosystem function could be for several reasons, including, for example, the two areas south of the ACC being comparatively less disturbed, naturally and/or anthropogenically; both areas experience periods of sea-ice cover, which can afford protection from various physical disturbances such as iceberg scouring (Smale et al., 2008; Clark et al., 2017). In addition, some sites, such as WAP1-2 of the Bellingshausen Sea, are also situated at depths beyond the reach of many modern iceberg keels (Dowdeswell and Bamber, 2007); thus, should evade most ice scouring. This attribute, however, is not shared by WAP3 (the respective site exhibiting the highest zoobenthic carbon storage and faunal density values), which is at a depth of 358 m, and hence, at greater risk of experiencing iceberg-mediated disturbance. Nevertheless, areas with more constant environmental conditions (e.g., deprived of or

with minimal disturbance) could promote the development/advancement of benthic communities to later (more complex) successional stages (Teixidó et al., 2007) with potentially positive implications for carbon storage capacity (Barnes et al., 2020). Furthermore, in sea-ice covered areas, sympagic (ice-affiliated) primary production can also be taking place, with the organic matter produced principally reaching and consumed by the benthos (Cautin et al., 2022).

4.6.2 Extrapolating Zoobenthic Carbon Storage to the Antarctic Continental Shelf

In blue carbon studies, findings are occasionally extrapolated to a wider region/environment (e.g., Barnes et al., 2019, 2020; Sands et al., 2023). For the current study, an extrapolation is made for the Antarctic continental shelf, which is deep (up to 1,000 m) and extensive, constituting an area of 4.6 million km^2 (Clarke and Johnston, 2003). However, as around one-third of the Antarctic continental shelf is overlain by ice shelves, floating seaward extensions of the Antarctic Ice Sheet, and very little is known about or documented for the benthic assemblages residing beneath ice shelves, for example, compositional, functional or behavioural traits (see Barnes et al., 2021b; Griffiths et al., 2021; Frinault et al., 2023), this study's extrapolation extends the ice-shelf-free continental shelf only. Based on mean zoobenthic carbon storage from MC and WAP data (south of the ACC), it is therefore estimated that ~125 million tonnes of carbon could be stored on the open-water continental shelf by epi-zoobenthic assemblages alone. This estimate, although conjectural, is equivalent to a CO_2 drawdown of 458 million tonnes, which, for contextualisation purposes only, is a greater amount than the CO_2 (including equivalents) estimated to have been emitted by the United Kingdom in 2022 (DESNZ, 2023). If in-faunal benthic carbon storage were to be included in the appraisal,

the amount of carbon stored in Antarctic open-shelf benthos, and equivalent GHG drawdown, is potentially considerably higher (Zwerschke et al., 2022). Such extrapolations should, nonetheless, be treated with caution, especially in Antarctica, given the innate heterogeneous and patchy nature of its seabed habitats and communities – some areas of the continental shelf appear depauperate while others are highly abundant and biodiverse (Post et al., 2017; Almond et al., 2021; Brasier et al., 2021). Although, in this study, the highest latitude areas of interest already displayed the highest estimated zoobenthic carbon storage values per unit area, it is thought that the capacity of Antarctica's continental shelf to store carbon will, in the absence of disturbance, e.g., from fishery activities, increase with loss of ice cover – potentially acting as a negative feedback on climate change (Peck et al., 2010; Barnes et al., 2020; Morley et al., 2022; Zwerschke et al., 2022; Sands et al., 2023).

4.6.3 Zoobenthic Carbon Storage Aligns with Richness and Faunal Density

The climate change crisis is considered intertwined with the dilapidation of ecosystems, hence, the degradation or forfeiture of associated functions (IPCC, 2022, 2023; Pörtner et al., 2023; Siegert et al., 2023). Marine ecosystems that can be identified as assisting with moderating climate change (e.g., through their carbon storage capacity), by virtue of hosting diverse biological communities, could be prioritised for protection in marine spatial planning to help address these entangled issues. A key objective of the current study, therefore, was to ascertain whether zoobenthic carbon storage variance aligns with biodiversity measures (richness), and also faunal density. For all study areas, zoobenthic carbon storage increased with richness (biodiversity), particularly morphotaxa richness. Thus, species-rich or carbon-rich areas could be priority areas for protection (permitting both bio/ecological elements to be protected simultaneously). For each area,

zoobenthic carbon storage also exhibited a particularly strong relationship with density. Such an alignment has been observed elsewhere, including in the Barents Sea, in the northern hemisphere (Souster et al., 2020), and on the South Georgia shelf (see Figure 2 of Barnes and Sands, 2017), and potentially indicates that ecosystem monitoring and MPA efficacy evaluations could be supported by higher-level data.

4.6.4 VME Taxa Prevalent and Major Contributors to Zoobenthic Carbon Storage

In the Southern Ocean, seabed conservation and management tools include an array of benthic taxa classified by CCAMLR as VME indicators (CCAMLR, 2009; FAO, 2009). While the approach can be important for decision-making, e.g., regarding CCAMLR MPA design and designation, it is not yet fully known whether all such taxa indicate VMEs or, indeed, are vulnerable themselves (see Dayton et al., 2013, 2016; Fillinger et al., 2013). However, advances are being made to better characterise the vulnerability of these taxa based on morphology (e.g., see Gros et al., 2023). The current study importantly has shown that VME indicator taxa are both prevalent components of benthic assemblages observed, particularly those assemblages of Burdwood Bank (and polar site WAP1), and major contributors to zoobenthic carbon storage in all study areas explored (although not uniformly so). This finding is of further interest as VME taxa are also often habitat formers/providers (correspondingly termed ecosystem engineers); hence, a co-benefit resulting from their presence (and protection) is the elevation of biodiversity levels and attendant functions (Buhl-Mortensen et al., 2010). In addition, as VME density-carbon relationships were similar to faunal density-carbon relationships, this may be potentially useful information for CCAMLR (or other regional management organisations) which exclusively (or particularly) monitor VME taxa. Such findings

concerning VME taxa could be leveraged in marine spatial planning and protection prioritisation decisions in (and beyond) the study region.

4.6.5 A Functional Group Approach for Benthic Assemblage Analysis Under Environmental Change

Several investigations, across both hemispheres, have employed a functional group approach to characterising benthic community structures and functions, for example, via grouping taxa by feeding mode (e.g., Jansen et al., 2020; Thyrring and Peck, 2021). A functional group approach has varied advantages, such as enabling the functionality of biodiversity to be examined and vastly reducing imagery appraisal times – the latter a renowned bottleneck between the acquisition of seabed images/video and desired outputs (Bowden et al., 2020) and ever more critical given the rate of environmental change, particularly, for example, in West Antarctica. Notably, in this study, different and multiple functional groups were major contributors to zoobenthic carbon storage across study areas (and sites). This finding indicates that, as at South Georgia (Barnes and Sands, 2017), all functional groups should be considered in view of protecting the carbon storage function of the benthos and benthic habitats. When comparing which groups majorly contributed at sites, MC1 and MC3 were the most similar – of all the sites, these sites were the closest in distance (<1 km) and situated within a relatively enclosed fjord basin.

4.6.6 Biological Patterns and their Environmental Context, including Sea-ice Incidence

Consideration of the environment in which organisms live and habitats persist provides the opportunity to detect bio-environmental relationships (e.g., Cummings et al.,

2018; Gutt et al., 2019) – helpful for understanding and predicting the effects of environmental change. In the current study, environmental data, of various spatial and temporal scales, were derived from in situ measurements, remote sensing and imagery, providing a contemporary environmental context to biological observations in the Scotia Arc study region. However, some of the environmental variables considered, and found to be coincident with zoobenthic carbon storage, are expected to be modified by climate change (Rogers et al., 2020), for example, long-projected sea-ice decline (Fox-Kemper et al., 2020). In the polar seas, sea-ice cover, including concentration, extent, timing and duration (the latter two features also referred to as "seasonality"), is regarded as a key environmental influencer of seabed habitat biodiversity and functionality (Lohrer et al., 2013; Clark et al., 2017; Pineda-Metz et al., 2020). Nonetheless, sea-ice cover (as well as other types of ice cover, e.g., ice shelf; Gilbert and Kittel, 2021) will likely be reduced due to the impacts of climate change (depending on timescale, and societal action to mitigate [Pörtner et al., 2023]), with implications for marine community structuring and associated ecosystem services (Rogers et al., 2020; Cavanagh et al., 2021). Given the current climatic situation, it is particularly notable when environmental variables likely to modify with climate change are identified as potential drivers of contemporary biological patterns.

Greater zoobenthic carbon storage might be expected in areas void of extensive sea-ice cover, given potentially greater access by benthic fauna to primary-production-derived food, hence, for example, higher faunal densities (Smith et al., 2006; Lohrer et al., 2013). In this study, however, the opposite was observed (for both carbon storage and faunal density). Furthermore, when comparing southern (this study) and northern (Arctic; Souster et al., 2020) high-latitude study regions, C_{zoo} significantly differed between sea-ice-covered and non-sea-ice-covered sites (**Figure 4.6**). For both of the polar regions,

sites that experience sea-ice cover exhibited higher C_{zoo} values on average than sites that do not; however, for both sea-ice-cover conditions, the Antarctic study region had greater zoobenthic carbon storage means than the Arctic (though with large standard deviations). Again, this finding could be related to disparities in disturbance regime, where sites covered by sea ice are more shielded from disturbance than those that are not. This observation is similar to that of Frinault et al. (2022) at the Larsen C Ice Shelf front, in that biological variations (faunal densities) did not meet expectations based on ice-cover regime. The Antarctic observations are further interesting as the Bellingshausen Sea (where the sea-ice sites of the current study are situated) is considered a warm polar sea region, and the Weddell Sea (which hosts the Larsen C) is a cold polar sea region (of significance for bottom water formation; Meredith, 2013; Zhou et al., 2023). Thus, irrespective of being a warm or cold southern high-latitude marine region, similar unexpected density relationships appeared with sea-ice incidence. Whether the findings are related to sea-ice cover in terms of sympagic primary production and affiliated food-fall to the benthos may also be potentially important to determine (see Cautain et al., 2022).

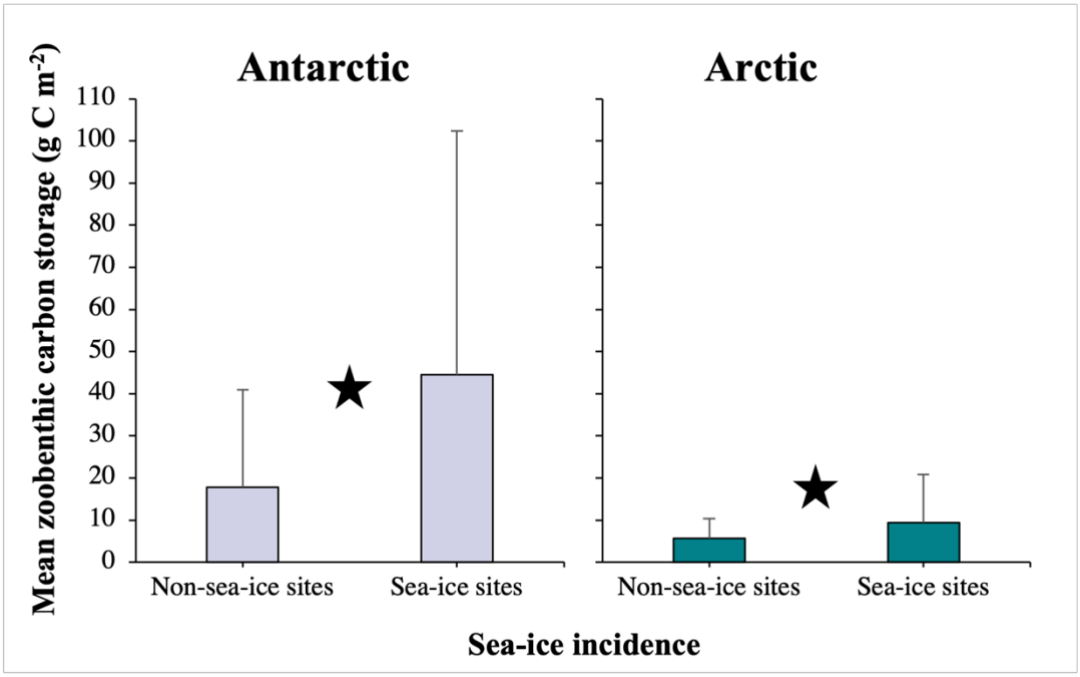


Figure 4.6: Mean zoobenthic carbon storage (C_{zoo}; g C m^{-2}) of non-sea-ice and sea-ice sites for Antarctic and Arctic regions. Sea-ice sites correspond to those with a mean annual sea-ice cover of >10%. Data for the Antarctic are from this study, and for the Barents Sea (Arctic), from Souster et al. (2020). A black star indicates a statistically significant difference between non-sea-ice and sea-ice sites (t = -3.480 and -4.225 for the Antarctic and Arctic, respectively, with both p-values < 0.001).

4.6.7 Dropstones as Potential Islands of Zoobenthic Carbon Storage

Dropstones are considered important physical seabed features, sometimes referred to as "islands", offering hard substrata/surfaces for benthic colonisation across swathes of soft/fine sediment (Zeigler et al., 2017), as well as providing platforms for elevation of suspension-feeding fauna into passing bottom currents in search of sustenance, as exemplified below the Filchner-Ronne Ice Shelf, southern Weddell Sea (Griffiths et al., 2021). In the present study, dropstones were relatively rare, constituting just a few percent of the seabed surface analysed, echoing findings of Post et al. (2020) for the Sabrina continental shelf, East Antarctica, where dropstones (in particular) accounted for <1% of

the seafloor surface examined. Similar to results of Zeigler et al. (2017), for fjords of the western Antarctic Peninsula, the current study also found that dropstones supported higher morphotaxa richness and faunal densities and, in addition, zoobenthic carbon storage. Although in this study (as observed in others), dropstones were of low occurrence, given their association with ice-rafted debris, including of supraglacial provenance, it may be anticipated that dropstones will become more prevalent as icescapes transform in a warming world, especially in areas undergoing ice-shelf retreat and experiencing increased iceberg generation and transit. In consequence, respective areas may also eventually experience enhanced biodiversity (richness) and faunal densities, and, potentially, increased zoobenthic carbon storage, although other environmental factors (and changes to them) will also shape benthic community structure and function (Rogers et al., 2020).

4.6.8 Protection of Benthic Biodiversity Aligns with Safeguarding of Zoobenthic Carbon Storage

Antarctica, its surrounding seas, and hence marine ecosystems and associated components, are currently under the protection of the Antarctic Treaty (due for renegotiation by 2048; Rogers et al., 2020) and attendant conventions, including those prohibiting mineral exploration (and exploitation), whaling and sealing, and restricting fishing activities, including pertaining to Antarctic krill, *Euphausia superba* – a key species of the Southern Ocean food web (Trathan and Hill, 2016; Rogers et al., 2020). Nonetheless, no convention presently exists directly addressing the safeguarding of Antarctic benthos (which includes most of Antarctica's known species), thus related functions. Nevertheless, as climate change intensifies and further ice-cover loss is experienced, the Southern Ocean and the Antarctic continental shelf will become more

accessible; thus, novel challenges may be presented regarding the protection and endurance of benthic blue carbon estates of this southern high-latitude region. Further protections could be placed on blue carbon and possibly in a way that benefits international stakeholders – for example, via sharing the value of carbon stored by benthic or other marine habitats of the region between Antarctic Treaty nations, e.g., for incorporation into corresponding nationally determined contributions (as appropriate, and as per the 2015 Paris Agreement; UNFCCC, 2023). Given that benthic carbon storage and biodiversity have been shown to align, protecting blue carbon habitats and ecosystems could support both climate change mitigation and the safeguarding of biodiversity, and hence contribute to alleviating the associated crises.

4.7 Conclusions

Exploring four distinct continental shelf areas, all connected by the Scotia Arc, has provided an indication of how zoobenthic carbon storage capacity can vary along a southern polar gradient, with seabed habitats of the southernmost areas, i.e., those south of the ACC, currently supporting greater carbon storage (with a sixfold higher storage average presented). This exploration has also revealed that high-latitude zoobenthic carbon storage consistently aligned with faunal richness and density, as well as density of VME indicator taxa – the former finding supporting that the protection of benthic biodiversity could be complementary to the protection of benthic blue carbon (and vice versa), and the lattermost finding confirming that VME indicators can be important contributors to benthic blue carbon. Functional group contributions to carbon storage were also found to vary within and between study areas, advocating the notion of "collective protection" of high-latitude and polar benthic assemblages to best support their carbon storage function. In addition, and although other variables are likely

influential, zoobenthic blue carbon, in the confines of this study, appeared coincident with sea-ice cover – an environmental variable sensitive to ocean and atmospheric warming.

The current study has provided contemporary estimates of benthic blue carbon in terms of principally (epi-)zoobenthic carbon storage, as well as ecological and environmental baselines, and supports the protection of the benthos as a whole when considering, by example, the protection and endurance of their carbon storage function. Furthermore, findings may also contribute to evidence bases supporting high-latitude marine conservation measures and climate-considerate marine spatial planning.

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Chapter 5 | Spatial Competition in a Global Disturbance Minimum; the Seabed Under an Antarctic Ice Shelf

Linking statement

This chapter helps achieve the third objective of the thesis:

"*To establish whether macrobenthic spatial competition occurs beneath the "permanent" cover of an ice shelf and, if so, to resolve its nature and compare it with that of open-water environments of both polar and lower latitudes.*"

Although floating ice shelves cover around one-third (~1.6 million km^2) of Antarctica's continental shelf, life in the marine cavities beneath them is rarely documented, principally due to challenges of access. The corresponding sub-glacial shelf is arguably one of the least biologically-explored large ecosystems on Earth, hosting unreported habitats predicted to be lost, at scale, with ice-shelf losses being potentially significant consequences of climate change. Furthermore, and contrary to much of Antarctica's open-water continental shelf, the sub-ice-shelf seabed environment is a potential global disturbance minimum, having been protected (e.g., from ice scour) by overlying ice shelves for millennia.

To help address the paucity of knowledge and better understand life, its interactions, and habitats underneath ice shelves, this research chapter encompasses shelf study sites below Ekström Ice Shelf, eastern Weddell Sea – the southernmost study area visited in the thesis. Thus far, this area is regarded as relatively unaffected by climate change and recognised as an important area for ecological monitoring (systematic and long-term) and

associated research activities. The study uses exceptionally rare sub-ice-shelf seabed sediment samples, the collection of which was enabled by boreholes drilled through the ice shelf. The research aimed to determine, using stereo microscopy, whether competition for space, a major structuring force of benthic communities, occurs under ice shelves and, if so, to characterise its nature and compare it with that of open-water continental shelf systems.

Status

This research chapter is published (in an adapted form) in *Science of the Total Environment* (see Appendix B for published research paper).

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5.1 Abstract

The marine habitat beneath Antarctica's ice shelves spans ~1.6 million km^2, and life in this vast and extreme environment is among Earth's least accessible, least disturbed and least known, yet likely to be impacted by climate-forced warming and environmental change. Although competition among biota is a fundamental structuring force of ecological communities, hence ecosystem functions and services, nothing was known of competition for resources under ice shelves, until this study. Boreholes drilled through a ~200 m thick ice shelf enabled collections of novel sub-ice-shelf seabed sediment which contained fragments of biogenic substrata rich in encrusting (lithophilic) macrobenthos, principally bryozoans – a globally-ubiquitous phylum sensitive to environmental change. Analysis of sub-glacial biogenic substrata, by stereo microscopy, provided first evidence of spatial contest competition, enabling generation of a new range of competition measures for the sub-ice-shelf benthic space. Measures were compared with those of global open-water datasets traversing polar, temperate and tropical latitudes (and encompassing both hemispheres). Spatial competition in sub-ice-shelf samples was found to be higher in intensity and severity than all other global means. The likelihood of sub-ice-shelf competition being intraspecific was three times lower than for open-sea polar continental shelf areas, and competition complexity, in terms of the number of different types of competitor pairings, was two-fold higher. As posited for an enduring disturbance minimum, a specific bryozoan clade was especially competitively dominant in sub-ice-shelf samples compared with both contemporary and fossil assemblage records. Overall, spatial competition under an Antarctic ice shelf, as characterised by bryozoan interactions, was strikingly different from that of open-sea polar continental shelf sites, and more closely resembled tropical and temperate latitudes. This study represents the first analysis of sub-ice-shelf macrobenthic spatial competition and provides a new

ecological baseline for exploring, monitoring and comparing ecosystem response to environmental change in a warming world.

*Please see **Figure S5.1** for graphical abstract of corresponding published research paper, a requisite of the respective journal and designed to succinctly represent the research.*

5.2 Keywords

Global climate change; Weddell Sea; boreholes through ice shelves; stereo microscopy; macrobenthos interactions; Bryozoa

5.3 Introduction

With anthropogenic greenhouse gas (GHG) emissions at unprecedented levels and atmospheric carbon dioxide concentrations still rising (Friedlingstein et al., 2022), one of the most significant, and perhaps most conspicuous, changes to a warming world is the shrinking of the cryosphere (icescape) (Turner and Comiso, 2017; IPCC, 2019; Parkinson, 2019; Rogers et al., 2020). In particular, losses of ice, including sea ice, floating glaciers and ice shelves, are transforming parts of the ocean surface of polar regions from white to blue, with implications for Earth's albedo (Barnes and Souster, 2011; Barnes, 2013).

In the southern polar region, ice shelves are the floating extensions of the Antarctic Ice Sheet, dominate most of the Antarctic coastline, fringing ~75% (Rignot et al., 2013), and overlie one-third of Antarctica's continental shelf (Clarke and Johnstone, 2003). The under-ice-shelf marine environment is aphotic and vast, ~1.6 million km^2 (Clarke and Johnstone, 2003), and, mainly on account of challenges of access, one of the least known habitats on Earth (Barnes et al., 2021a; Griffiths et al., 2021), as well as one

vulnerable to GHG-induced global warming (Miles et al., 2017; Lai et al., 2020; Gilbert and Kittel, 2021). Furthermore, the seabed underneath ice shelves is ostensibly among the least disturbed marine surface habitats on the planet (Barnes, 2017), this being both naturally and anthropogenically, a distinctive characteristic that may be forfeited with climate-forced ice-shelf loss.

In Antarctica, episodic retreats and collapses of ice shelves at their outer marine termini, calving fronts, constitute a major source of icebergs (Bigg, 2015). Such icebergs can cause disturbance by colliding with the seafloor of the open-water polar continental shelf (Gutt, 2001). These collisions, referred to as "ice scours" or "iceberg ploughmarks", can be ubiquitous across the shallower shelf of the seasonal sea ice zone and occur to maximum depths of 650 m (Dowdeswell and Bamber, 2007), and are considered one of the most catastrophic natural disturbance events to benthic marine systems (Gutt and Starmans, 2001), with impacts akin to those of anthropogenic physical disturbances, e.g., generated by intense trawling and dredging (Conlan et al., 1998; Barnes and Conlan, 2007). Ice scouring has the potential to cause almost complete local mortality, at levels ≥95% (Peck et al., 1999; Smale et al., 2008), from which recovery of the benthos may take decades in the shallows to centuries in deeper shelf waters (Gutt and Starmans, 2001; Conlan and Kvitek, 2005; Zwerschke et al., 2021). In contrast, the expansive seafloor underneath ice shelves is relatively undisturbed, the presence of (permanent) ice shelf above affording it protection from ice-mediated disturbance, in some instances over millennia timescales. Thus, in terms of natural disturbance, Antarctica's continental shelf comprises some of the most and least disturbed seabed habitats on Earth (Gutt and Starmans, 2001; Barnes, 2017), with the under-ice-shelf environment representing a rare example of a disturbance minimum for life.

Sampling the environment under ice shelves is challenging and costly, and thus collections of sub-ice-shelf biological samples, particularly biological, are a rarity, constraining our understanding of this vast space. Boreholes hot-water-drilled through ice shelves, however, are an essential method for accessing and enabling the sampling/surveying of sub-ice-shelf marine ecosystems, and various sampling devices can be passed through them into the water column and to the seafloor below. Such access holes, created through less than ten Antarctic ice shelves to date (see Gong et al., 2019), have facilitated some remarkable ecological discoveries, including those related to the underlying seabed habitat and its biotic components. For example, cameras passed down boreholes in the Ross, Amery and McMurdo Ice Shelves uncovered a surprising abundance and variety of seabed-dwelling life – generally unexpected considering the lack of in situ photo-induced primary production, i.e., potential food sources, and thus possible reliance on food particles/phytoplankton blooms being physically advected underneath by ocean currents (Pawlowski et al., 2005; Riddle et al., 2007; Kim, 2019). More recently, borehole cameras through Filchner-Ronne Ice Shelf revealed colonisation of hard substrata (a boulder in the particular example) by primary consumers, including suspension-feeding sponges, is possible hundreds of km from the ice-shelf front, and considerable distances from light and open-water (Griffiths et al., 2021). Furthermore, physical seafloor samples obtained via sediment grabber and corers dropped through boreholes in the Ekström Ice Shelf, eastern Weddell Sea (Kuhn et al., 2019), provided evidence of benthic life in the underlying marine cavity spanning circa 5,800 years as well as an unprecedented richness in bryozoan species exceeding even that of the open-sea continental shelf (Barnes et al., 2021a), such assemblages and novel observations of interactions between individual biota/colonies being the basis of the current study.

Bryozoa, invertebrate principally-sessile (substrata-attached) clonal and colonial filter-feeders (primary consumers), are ubiquitously distributed across the globe and found in both freshwater and marine environments, including the Southern Ocean and its seas, where they constitute a significant component of open-water continental shelf communities (Hayward, 1995). Marine bryozoan species fall into two major clades: Cheilostomatida (cheilostomes), to which most (~85%) extant species belong (based on information provided in WoRMS, 2022; accessed 13th December 2022), and Cyclostomatida (cyclostomes). In the marine environment, bryozoans can be important ecosystem architects, with a role in biodiversity enhancement (Cocito, 2004; Wood et al., 2012; Santagata et al., 2018), and also constituents of the seabed sediment (Bone and James, 1993; Taylor, 2020), including as dead fragments, and hence, agents of seafloor carbon storage and sequestration (Barnes et al., 2016). In terms of growth morphology, and beyond erect and "massive" forms, most contemporary bryozoan species grow as two-dimensional encrusting sheets (McKinney and Jackson, 1991); hence a critical limiting resource for the latter is space on suitable "hard" substrata (such as boulders, rocks, shells, reef rubble, settlement panels, macroalgae and even other bryozoans) (e.g., Maughan and Barnes, 2000; Centurión and López Gappa, 2011; Cocito et al., 2012; López Gappa and Zelaya, 2021; Sanjay et al., 2021), and space is often intensely competed for (Taylor and Wilson, 2003). The majority of bryozoans have calcium carbonate skeletons, meaning that, in certain environmental conditions, bryozoans fossilise well (Brood, 1998; Taylor, 2016, 2020), and, somewhat uniquely, interactions between colonies, including those competitive in nature, can be preserved and thus interpreted (Taylor, 2016; Taylor and Wilson, 2003). Indeed, the bryozoan fossil record extends hundreds of millions of years, enabling temporal studies of vast time spans (e.g., McKinney, 1995; McKinney et al., 1998). The taxon has also been proposed as an environmental indicator (e.g., Okamura

and Bishop, 1988; Hageman et al., 1997; Amini et al., 2004) and utilised in exploring ecological theories, including the use of encrusting colony dynamics to investigate competition (e.g., Barnes, 2003). There is also evidence that monitoring bryozoan competition dynamics could provide an earlier warning of biodiversity response to global warming, at least in polar seas, than more traditional techniques of surveying whole assemblage composition, richness or diversity change (Barnes et al., 2021b).

Competition is a fundamental component and structuring force of communities (Dayton, 1971; Turner and Todd, 1994; Lomolino et al., 2004), hence influences associated ecosystem services. However, the nature of any competition under ice shelves was, until the current study, unknown or unreported. Borehole-derived samples of the lithophilic benthos residing under the Ekström Ice Shelf recently revealed that both cheilostome and cyclostome encrusting bryozoans are represented (Barnes et al., 2021a). Hence, the corresponding samples and their colonisers can be harnessed to discern whether competition, particularly spatial competition, actually occurs under Antarctic ice shelves and, if so, evaluate whether it resembles open-sea polar competition, as well as where it may fit in a more global context. This research, therefore, not only helps narrow a significant knowledge gap but also provides new baseline information for future ecological monitoring and projected long-term Antarctic studies (see Gutt et al., 2022; Lowther et al., 2022). Furthermore, a rare and novel opportunity is provided in that polar latitude data can, in this instance, be decoupled from high disturbance. As the study area has been relatively unaffected by climate change thus far (e.g., especially compared to much of the Antarctic Peninsula) (Gutt et al., 2022), gaining knowledge of the interactions between the contemporary assemblage constituents is particularly valuable as future temporal change can be more confidently attributed to climate/environmental change.

Previously, Barnes and Neutel (2016) demonstrated high-latitude (polar) spatial competition to be extremely hierarchical and suggested that without disturbance, superior competitors would monopolise space. Such monopolisation should, therefore, eventually lead to most spatial competition being intraspecific (i.e., between members of the same species), hence more tie/stand-off outcomes between competitors (as competitively matched) rather than more "severe" definitive win-losses. In addition, polar substrata from continental-shelf depths have indicated low colonisation levels (Barnes and Kuklinski, 2010). Thus, it was first hypothesised that the intensity and severity of sub-ice-shelf spatial competition, being of a very high-latitude environment of minimal disturbance, would be globally low and mainly comprise intraspecific encounters between the strongest competitor(s). Hence, the second hypothesis was that the complexity of spatial competition under ice shelves would also be low, with little diversity in pairwise competitive encounters due to the majority of spatial competition involving the most dominant competitor(s). Finally, McKinney et al. (1998) previously showed that during and following a massive disturbance event (i.e., mass extinction), cyclostomes dominated over cheilostomes, but then cheilostomes recovered to dominate over cyclostomes across calmer geological time. Thus, it was also predicted that cheilostomes would be especially competitively dominant under ice shelves, given that the sub-ice-shelf seafloor environment is anticipated to be a long-standing disturbance minimum.

5.4 Materials and Methods

5.4.1 Study Area and Sites

In January 2018 (austral summer 2017/18), as part of the Sub-Ekström Ice Shelf-Observations (Sub-EIS-Obs) Project (Kuhn and Gaedicke, 2015; Kuhn et al., 2019),

seafloor material was collected from two continental shelf sites, EIS-2 and EIS-3, underneath the Ekström Ice Shelf, eastern Weddell Sea, Dronning Maud Land, East Antarctica (**Figure 5.1**, **Table 5.1**); the wider environs of particular interest for long-term systematic ecological studies related to the impacts of climate and environmental change (see Gutt et al., 2022; Lowther et al., 2022). Sites EIS-2 and EIS-3 were ~19.6 km apart, the distance determined using Vector Analysis Tools in QGIS v3.22.9. The site closest to the ice-shelf edge/front, EIS-2, was at 250 m water depth in a 58 m high sub-ice-shelf cavity and ~3.4 km from seasonally-open water. The second site, EIS-3, was at 300 m water depth in a 110 m high sub-ice-shelf cavity and ~9.6 km from seasonally-open water. Both sites, being sub-ice-shelf (and set back from the ice-shelf calving front), are protected from iceberg-mediated disturbance; indeed, seaward of Ekström's ice-shelf front transiting/drifting icebergs scour and rework the sediment of the adjacent open continental shelf (Oetting et al., 2022 and see Figure 7 within).

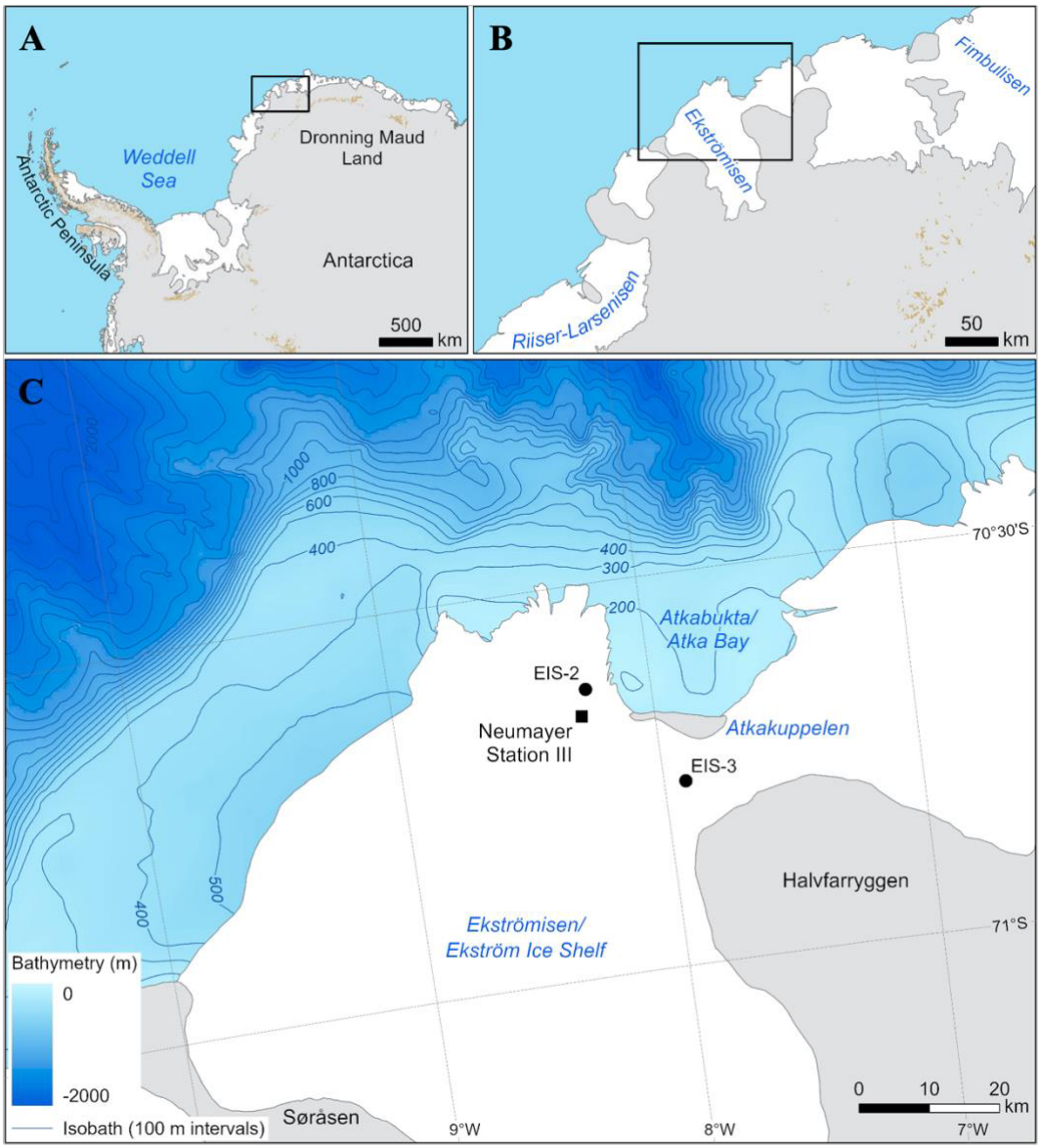


Figure 5.1: East Antarctic Southern Ocean study zone and sites. White indicates ice shelves, and grey indicates ice-covered land/grounded ice. (**A**) Weddell Sea region indicating the Antarctic Peninsula, Dronning Maud Land and general location of Ekström Ice Shelf and environs; (**B**) Ekström Ice Shelf (Ekströmisen) and neighbouring ice shelves off Dronning Maud Land with extent of main map indicated; and (**C**) main map showing locations of borehole study sites, EIS-2 and EIS-3 (black circles), where underlying seafloor substrata, investigated for macrobenthic spatial competition, was collected, and with position of nearby Neumayer III research station shown (black square). Bathymetry is from the International Bathymetry Chart of the Southern Ocean v2 (Dorschel et al., 2022), with 100 m contours.

Table 5.1: Eastern Weddell Sea, East Antarctica, continental shelf study sites under Ekström Ice Shelf, EIS-2 and EIS-3, investigated for macrobenthic spatial competition in a disturbance minimum, including position in decimal degrees latitude (°S) and longitude (°W), water depth (m), distance from the ice-shelf front (at the time of sampling; km), ice-shelf thickness (m) at the location, and sub-ice-shelf cavity height (m). All seabed surface sediment sampling was conducted in January 2018 (see Kuhn and Gaedicke, 2015; Kuhn et al., 2019).

Site	Latitude (°S)	Longitude (°W)	Water depth (m)	Distance from ice-shelf front (km)	Ice-shelf thickness (m)	Sub-ice-shelf cavity height (m)
EIS-2	-70.6353	-8.2504	250	3.4	192	58
EIS-3	-70.7679	-7.9009	300	9.6	190	110

5.4.2 Collection of Physical Samples (Seabed Substrata)

The sub-glacial seafloor samples of this study (corresponding to one sample per site) were brought up from a depth of 250-300 m to the ice-shelf surface through hot water drill (bore)holes (the ice shelf being ~190 m thick at each location) and were obtained from the seabed surface sediment layer (up to 5 cm depth) using a Wippermann grabber (Wippermann GmbH, Germany) at EIS-2 and JLU vibrocorer (Justus Liebig University, Germany) at EIS-3 (Kuhn et al., 2019; Gong et al., 2019; Kuhn et al., 2021). Dead bryozoan fragments (skeletons), i.e., the seabed substrata examined in this study, constituted 9.7 and 9.0% of the seafloor sediment samples of EIS-2 and EIS-3, respectively (see Barnes et al., 2021a).

5.4.3 Stereo Microscopy for Analysis of Spatial Competition

Spatial contest competition between encrusting colonists (predominantly bryozoans) on the isolated bryozoan fragments (158 and 166 for EIS-2 and EIS-3, respectively; 324 total) was examined using stereo microscopes (Leica M165 FC and S8 APO; Leica Microsystem (UK) Ltd, UK), with example images provided in **Figure 5.2**. Each fragment was analysed following the same procedure. For each fragment, the surface area was calculated (cm^2), and all colonies, i.e., potential competitors, residing on the fragment were counted (enabling calculations of colony density, i.e., number of colonies cm^{-2}). Each colony was identified to the highest taxonomic resolution possible, predominantly to species level, using Hayward (1995) and proceeding primary literature. Colonised fragments were further inspected for competitive interactions between colonies, determined whereby the growth boundaries of colonies physically met, with at least 5% of their perimeter being affected (as per Barnes and Kuklinski, 2004) and signs/indications that both colonies were alive at the time of the interaction, i.e., detection of defensive responses in colony morphology such as the formation of protective spines on newer zooids at the growth edge (e.g., Seroy and Grünbaum, 2018; Liow et al., 2019). Following established criteria, for every competitive encounter, the outcome was classified as either a tie/stand-off or a win-loss; a tie being, for example, where the growth of colonies ceased along the contact margin or reciprocal overgrowth occurred, and a win-loss where a colony overgrew another to cover the apertures of its zooids (Stebbing, 1973; Buss and Jackson, 1979; Barnes and Kuklinski, 2004; Liow et al., 2016). The outcome for each competing colony was also logged (as a tie, win or loss). In addition, for all competitive interactions, the lowest taxonomic divergence point of the competing colonists, i.e., kingdom, phyla, class, family, genus or species, or different colonies of the

same species, was also recorded. All data pertaining to microscopy studies were recorded in Microsoft Excel (Microsoft Corp, USA).

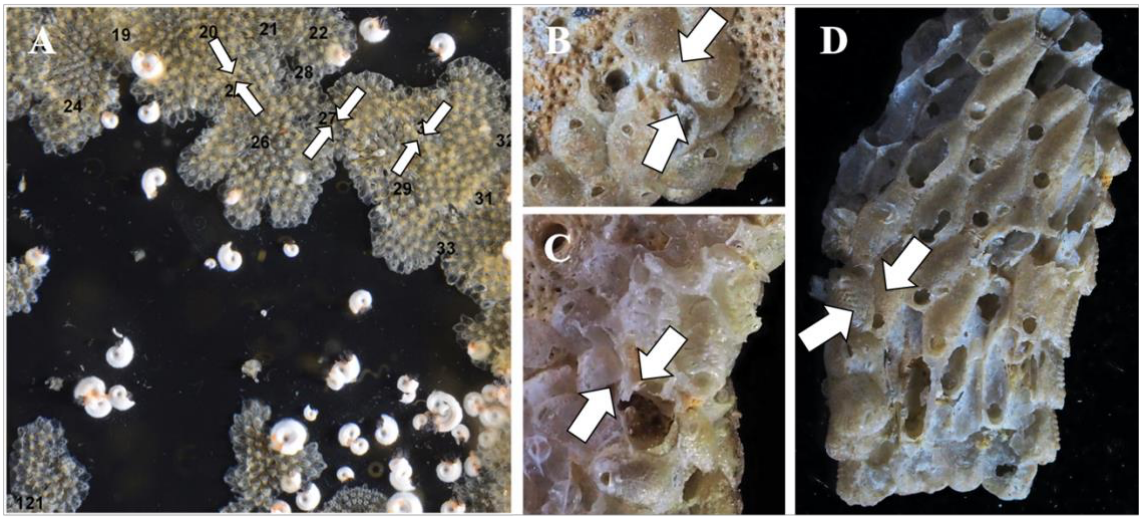


Figure 5.2: Example images showing spatial competition between bryozoan colonies (indicated by white arrows): (**A**) on a settlement panel from Antarctic shallow waters (15 m depth) (Barnes et al., 2021a) and (**B-D**) on bryozoan fragments of sub-ice-shelf sediment samples (this study), whereby (**B**) shows colonies of the same species competing for space (intraspecific competition), and (**C-D**) depict colonies of different species competing for space (interspecific competition).

5.4.4 Spatial Competition Measures Explored

Data generated from stereo microscopy analyses were subsequently used to calculate a series of differing spatial competition measures for both EIS-2 and EIS-3 samples. The measures and their associated calculations (based on literature-derived definitions; see Barnes and Neutel, 2016; Barnes et al., 2021b, and summarised in **Table 5.2**) were: **Density** – the number of competitive encounters divided by the total substratum surface area examined; **Intensity** – the number of competitive encounters divided by the total number of colonies observed, i.e., the probability of a given colony experiencing competition; **Severity** – the number of competitive encounters resulting in a definitive (win-loss) outcome divided by the total number of colonies, i.e., the probability of a

colony being involved in severe competition; **Identity** – the number of intraspecific encounters (encounters between colonies/individuals of the same species) divided by the total number of competitive encounters, i.e., the probability of a competitive encounter being intraspecific; **Dominance** – the number of competitive encounters involving the most frequent competitor divided by the total number of competitive encounters; **Complexity** – the number of different pairwise competitive encounter types (e.g., Competitor A versus B is one type); and **Taxonomic spread** – the proportion of competitive encounters falling within each of seven categories based on the lowest taxonomic divergence of the respective combatting competitors. The categories included competitors being of the same species (i.e., the most taxonomically similar category and constituting intraspecific competition) to being from different species, genera, families, classes, phyla and kingdoms (the latter being the most taxonomically divergent category). The taxonomic divergence of competitors provides a further way to examine complexity of competition.

Table 5.2: Descriptions of the seven different measures of spatial competition explored on substrata obtained from under Ekström Ice Shelf, eastern Weddell Sea, East Antarctica. Competition measures are based on a collection of literature-derived definitions (see Barnes and Neutel, 2016; Barnes et al., 2021b).

Competition measure	Description
Density	Number of competitive encounters divided by the total area of substrate examined
Intensity (probability of competition taking place)	Number of competitive encounters divided by the total number of colonies
Severity	Number of spatial contests resulting in a definitive outcome (win-loss) divided by the total number of colonies
Identity	Probability of a competitive encounter being intraspecific (between competitors of the same species) – number of intraspecific encounters divided by the total number of competitive encounters
Dominance – numerical dominance by the most frequent single competitor	Proportion/share of all competitive encounters involving the most frequent competitor (the higher the proportion, the

	less complex competition is considered to be)
Complexity – diversity/variety of competitive encounters	Number of different pairwise competitive encounter types, e.g., Competitor A versus B is one type (the higher the number, the more complex competition is considered to be)
Taxonomic spread – the taxonomic difference between competitors	Frequency of lowest taxonomic divergence of competitors engaged in competition across seven categories from same species (intraspecific) to different kingdoms (interkingdom)

5.4.5 Global Open-sea Bryozoan Assemblage Datasets

To determine where sub-ice-shelf competition fits in a more global context, competition measures for EIS-2 and EIS-3 were compared with those obtained/calculated from available and comparable global open-sea bryozoan assemblage datasets (Barnes and Kuklinski, 2010; Barnes and Neutel, 2016); it is, however, acknowledged that comparisons are constrained in power due to the scarcity of sub-ice-shelf samples necessitating comparisons of single measures with means from elsewhere. The comparison datasets encompassed a latitudinal range of 5 to 78° across the two hemispheres and were classified as either tropical, temperate or polar, defined here as ≤30, >30 to <60 and ≥60°N/S, respectively. All datasets focused on encrusting bryozoan

assemblages of island or continental shelf systems and employed comparable methods for analysing colonisation and competition. Substrata were abiotic, ranged from pebble to boulder grain sizes (with surface areas of ~2 to 500 cm^2) and collected via SCUBA, Agassiz trawls or dredging techniques. Datasets were based on multiple samples from multiple locations within a sampling area, the exception being the eastern Weddell Sea dataset (Barnes and Kuklinski, 2010), which comprised four individual samples from four locations (and only used for the competition intensity comparison). For more information regarding comparison datasets, see Barnes and Kuklinski (2010) and Barnes and Neutel (2016).

5.4.6 Interclade Spatial Competition

The relative competitive success of the two major bryozoan clades, cheilostomes (Gymnolaemata) and cyclostomes (Stenolaemata), was investigated by determining the percentage win rate of cheilostomes against cyclostomes for EIS-2 and EIS-3 using all competitive encounters in which the two clades met. Sub-ice-shelf win rates were then compared to those of literature data, encompassing fossil and recent assemblages. These assembled data span more than 100 million years before present and global space, i.e., across varying latitudes. The fossil assemblage data was compiled by McKinney (1995) and those of global living bryozoans by Barnes and Dick (2000). The probability of the sub-ice-shelf cheilostome win-rate observation was also calculated.

5.5 Results

The surface area of sub-glacial substrata (fragments) ranged from 0.2 to 7.2 cm^2, with a mean area of 0.8 cm^2. Of the 158 and 166 fragments microscopically examined from EIS-2 and EIS-3 seafloor sediment samples (constituting a total surface area of 247.2 cm^2), 39 and 48% were found to be colonised by encrusting macrobenthos, respectively. The

colonists were identified as predominantly cheilostome, followed by cyclostome bryozoans, with occasional tube-building serpulid polychaetes. Colony density for EIS-2 and EIS-3 substrata was ~1.3 and 1.6 colonies cm^{-2}, respectively. Spatial contest competition was detected on 47 and 30% of colonised substrata for EIS-2 and EIS-3, respectively, with up to 21 competitive interactions being observed on a single fragment. Competition density for the EIS-2 and EIS-3 samples was ~0.54 and ~0.79 competitive encounters cm^{-2}, corresponding to 5,443 and 7,875 competitive encounters m^{-2}, respectively. Regarding colonists, cheilostomes were the most speciose taxon, the major occupiers of space on fragments, and were involved in most competitive interactions; for EIS-2, cheilostomes were involved in ~92% of all pairwise encounters (>94% when bryozoan-bryozoan encounters considered exclusively), and for EIS-3, cheilostomes were involved in 100% of the encounters.

5.5.1 Intensity, Severity and Identity of Spatial Competition

The intensity of competition on sub-ice-shelf samples was ~41 and 49% for EIS-2 and EIS-3, respectively. Sub-ice-shelf intensity values were high relative to global levels (**Figure 5.3A**), and, in particular, very high compared to other polar data from similar depths and region, i.e., the eastern Weddell Sea open-shelf dataset; the mean intensities were 5% and 15% for the eastern Weddell Sea shelf and the collective polar region, respectively, therefore sub-ice-shelf competition intensity was nine and three times higher, respectively.

The severity of sub-ice-shelf competition was ~31 and 39% for EIS-2 and EIS-3, respectively. Sub-ice-shelf severity values were also high relative to global levels and outside corresponding 95% confidence intervals (**Figure 5.3B**). Competition severity under the ice shelf was much higher than that observed for other polar data; the mean

severity of polar data being 12.5%, hence sub-ice-shelf values almost three times higher (similar in difference to competition intensity).

Regarding competition identity, i.e., the proportion of intraspecific encounters, sites EIS-2 and EIS-3 presented very similar values at 19.4 and 18.7%, respectively. Sub-ice-shelf identity values also markedly differed from that of open-water polar data (**Figure 5.3C**), the mean intraspecificity of competition for other polar data being >45.5%, equivalent to greater than a twofold difference. Sub-ice-shelf identity values were more similar to those observed for non-polar environments.

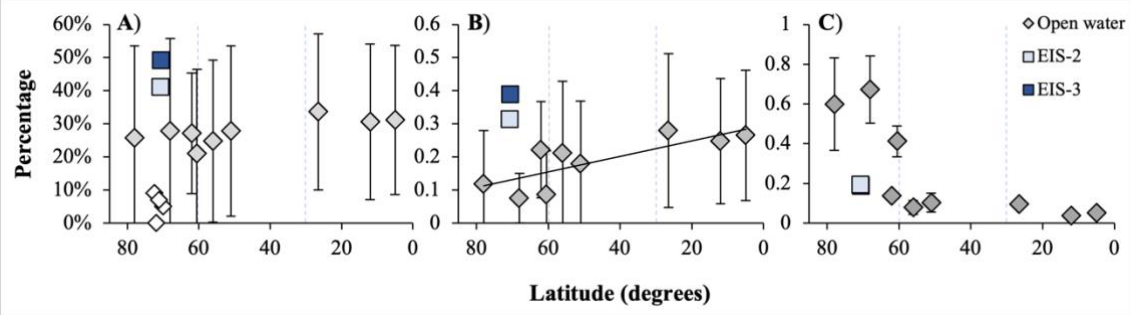


Figure 5.3: Spatial competition on marine substrata from under an Antarctic ice shelf and comparison with competition across different latitudes. Including: (**A**) Intensity; (**B**) Severity (with regression line); and (**C**) Identity. Sub-Ekström Ice Shelf (EIS) data are shown as individual samples (with light and dark blue squares for sites EIS-2 and EIS-3, respectively). Open-water data are shown as means with standard deviations for the shallows (grey diamonds, calculated using data from Barnes and Neutel, 2016) and as individual samples for ~120-650 m shelf depths (white diamonds, computed utilising data from Barnes and Kuklinski, 2010). Regression-associated ANOVA indicated a significant inverse relationship between latitude and competition severity ($R^2 = 0.61$, $F = 10.99$ and $p = 0.01$).

5.5.2 Complexity of Spatial Competition

Two initial aspects of competition complexity were investigated: the numerical dominance in encounters by the most frequent single competitor, i.e., the proportion of

competitive encounters involving the most common competitor, and the number of different pairwise competitor combinations discerned (**Figure 5.4**).

The numerical dominance by a single competitor at EIS-2 and EIS-3 was 26.4 and 42.9%, respectively (**Figure 5.4A**). Such under-ice-shelf dominance levels were found to be more comparable with that of equivalent competition in tropical and temperate samples (with means of 39.5 and ~49%, respectively), and around or less than half that previously recorded for polar regions, the collective polar mean being ~85%, and the Antarctic specific mean 94%. The species most frequently involved in competitive interactions were cheilostomes *Microporella stenoporta* for EIS-2 and *Lacerna watersi* for EIS-3.

Regarding how many types of competitive encounters were present, sub-ice-shelf samples presented 43 and 31 different types for EIS-2 and EIS-3, respectively (**Figure 5.4B**). The EIS-3 value was more similar to those of lower-latitude and Arctic samples, with the mean number of encounter types for temperate and tropical regions being ~30 and for the Arctic 28, whereas EIS-2 exhibited a particularly high diversity in pairwise competitive encounter types compared to anywhere else. Both under-ice-shelf samples exhibited a greater variety of encounter types (at least >50% more) than the open-water Antarctic region, which had a mean of 20 types.

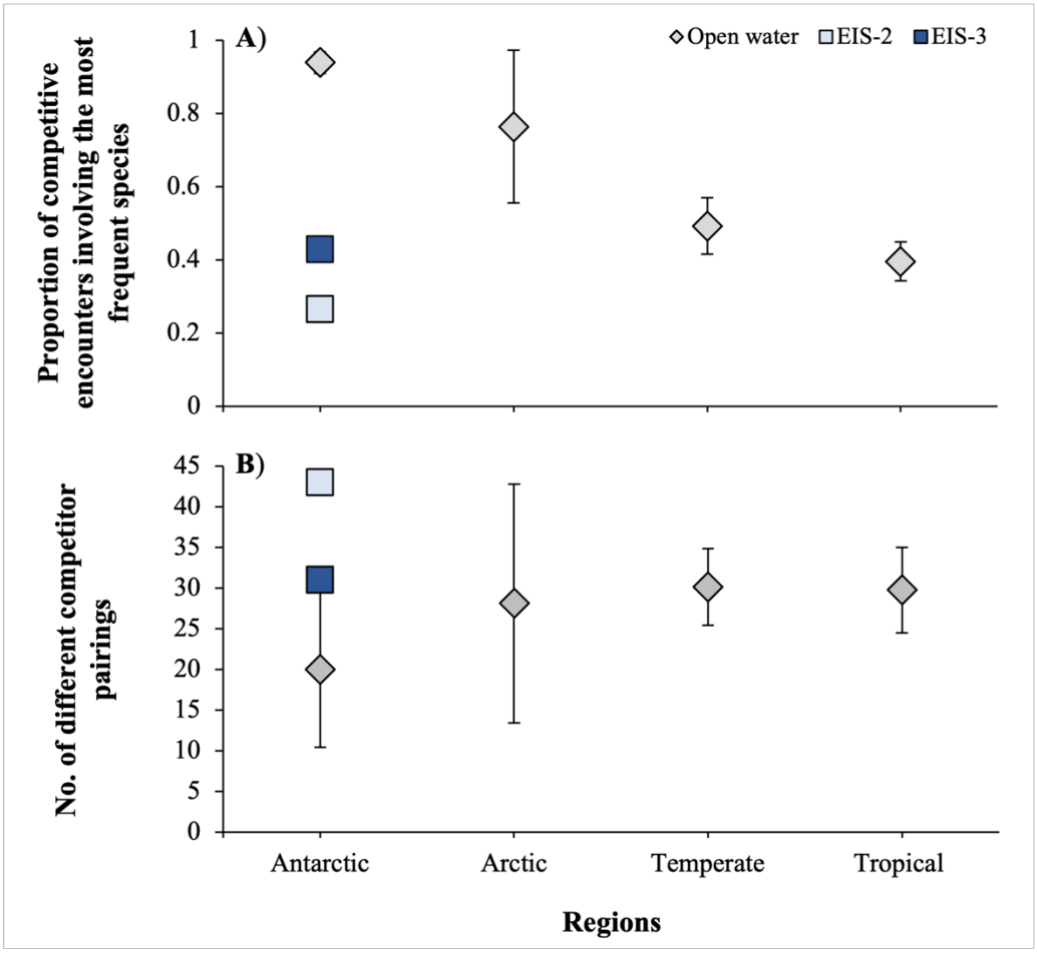


Figure 5.4: Complexity of spatial competition on marine substrata from under an Antarctic ice shelf and comparison with competition complexity of Antarctic, Arctic, temperate and tropical regions. Including: (**A**) Numerical dominance of the most frequent competitor in interactions; and (**B**) Variety of pairwise competitive encounter types. Sub-Ekström-Ice-Shelf (EIS) data are shown as individual samples (squares – light and dark blue for sites EIS-2 and EIS-3, respectively). Open-water data are shown as means with standard deviations for the shallows (grey diamonds, calculated using datasets from Barnes and Neutel, 2016).

5.5.3 Taxonomic Difference between Competitors for Space

As a broader way of realising complexity of competition, the frequencies of the taxonomic divergences (taxonomic spread) of competitors were explored for the sub-ice-shelf samples and subsequently compared with those calculated from available global datasets (**Figure 5.5**).

For EIS-2 and EIS-3, the taxonomic difference between competitors varied from within species (intraspecific), e.g., *Lacerna watersi*, to between representatives of different phyla, i.e., Bryozoa and Annelida (**Figure 5.5A**). However, the most common spatial competitive encounters found on sub-Ekström-Ice-Shelf samples (i.e., dead bryozoan fragments) were between competitors belonging to different families (of the same class, phyla and kingdom) at >45 and 55% of all encounters for EIS-2 and EIS3, respectively. The mean proportions of competition being interfamilial for tropical, temperate and polar regions were 72, 68 and 32.7%, correspondingly, i.e., the sub-ice-shelf findings sitting between that of lower-latitude and polar regions (**Figure 5.5A,B**). Under-ice-shelf patterns of spatial competition also showed comparatively moderate levels of intraspecific competition with a mean >18.4% (**Figure 5.5A**), whereas means for tropical, temperate and polar regions were ~4, ~10 and >55%, respectively, i.e., again, the sub-ice-shelf findings lying between lower latitude and polar, however, in this case, more towards tropical and temperate regions.

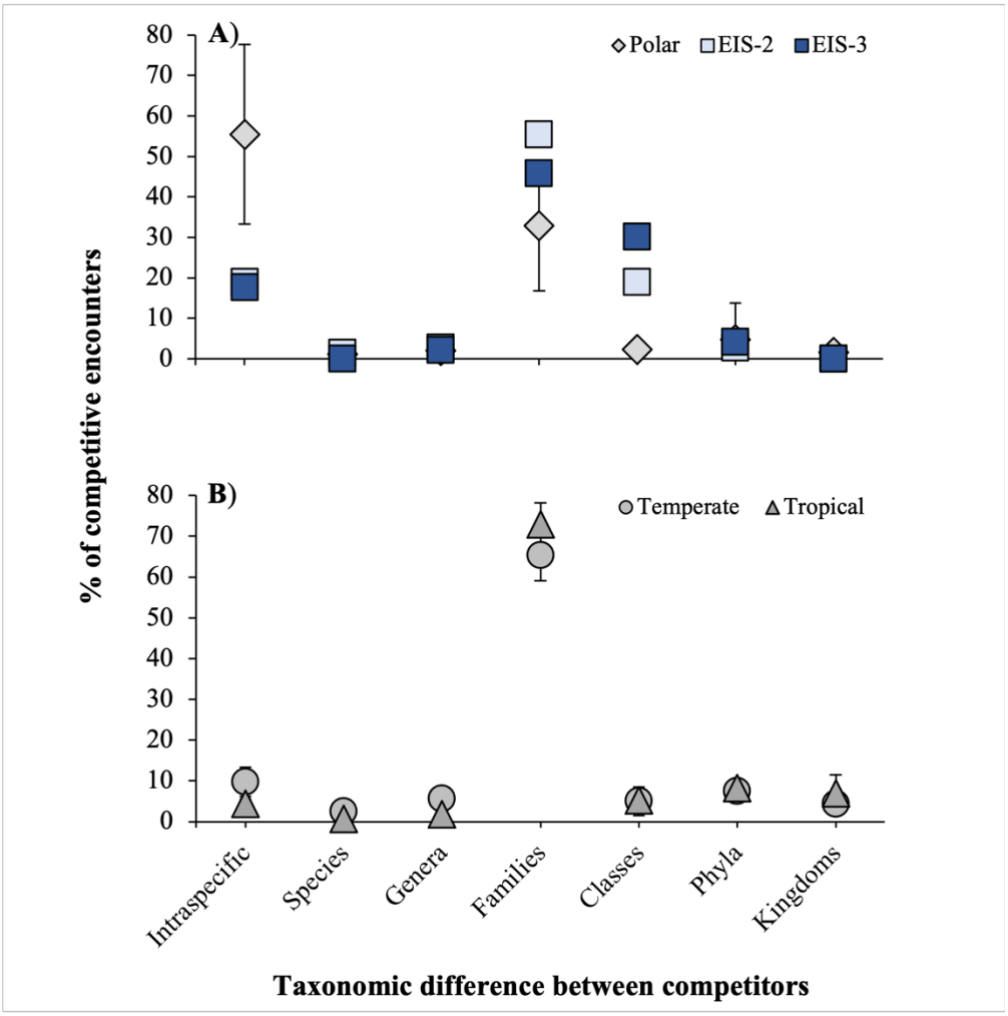


Figure 5.5: Taxonomic difference between competitors for space on marine substrata from under an ice shelf and comparison with different regions. Including: (**A**) polar – sub-ice-shelf and open water; and (**B**) temperate and tropical. Sub-Ekström Ice Shelf (EIS) data are shown as individual samples (with light and dark blue squares for sites EIS-2 and EIS-3, respectively). Open-water data are shown as means with standard deviations for the shallows (calculated utilising data from Barnes and Neutel, 2016) with symbols for polar, temperate and tropical regions being diamonds, triangles and circles, respectively.

5.5.4 Interclade Spatial Competition

The win rate between the two most abundant marine bryozoan clades: cheilostomes (all of class Gymnolaemata) and cyclostomes (all of class Stenolaemata), was established for each sub-ice-shelf sample. At both under-Ekström-Ice-Shelf sites, cheilostomes were

competitively superior and exhibited very high win rates against cyclostomes, at 92.9% for EIS-2 and 86.2% for EIS-3 (**Figure 5.6**).

When comparing sub-ice-shelf cheilostome win rates with those of present-day living assemblages and fossil assemblages, the sub-ice-shelf samples interestingly displayed not only two of the three highest win rates against cyclostomes in present-time but also when the fossil record was considered (**Figure 5.6**); the mean win rate for fossil assemblages being 66.5% across time. The probability of two of the three highest win rates occurring in the sub-ice-shelf samples (out of all 33 samples) is <0.006 (i.e., <1%).

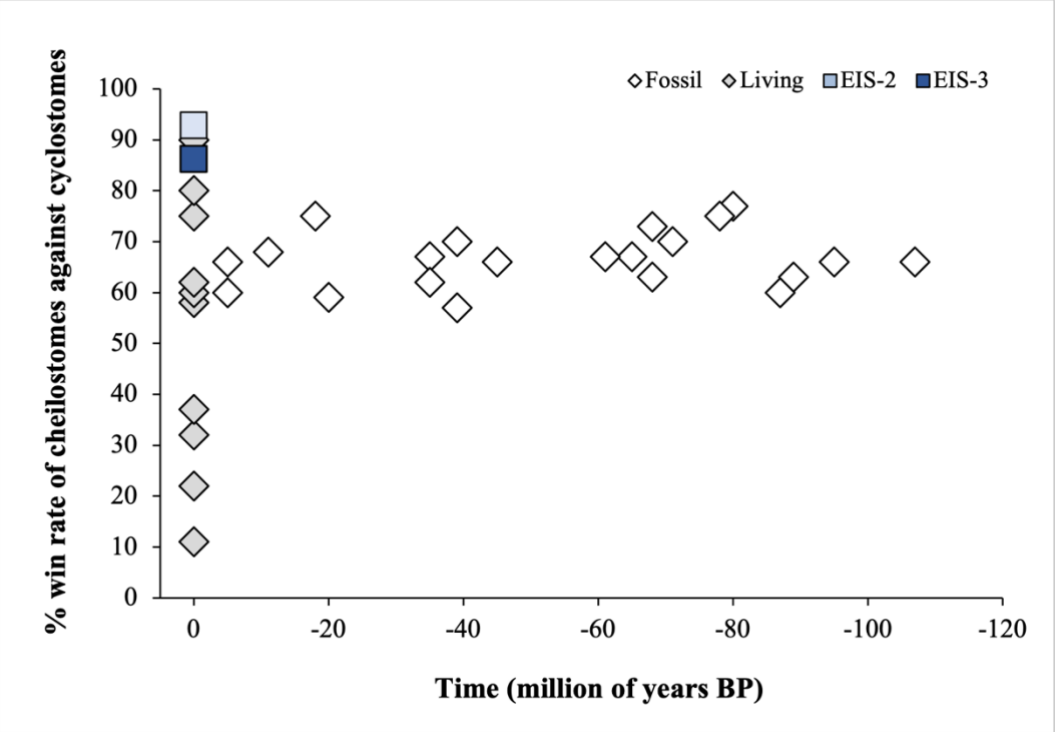


Figure 5.6: Outcomes of spatial competition between two major marine bryozoan clades: Cheilostomatida and Cyclostomatida, in terms of cheilostome win rates (%) over cyclostomes, on marine substrata from under an Antarctic ice shelf, Ekström Ice Shelf (EIS), and comparison with win rates of open-water global living and fossil assemblages (i.e., present and before present, BP) (Barnes and Dick, 2000 and references therein).

5.6 Discussion

Competition for resources, including space, food and mates, is a common and fundamental component of populations and communities across global ecosystems (Lomolino et al., 2004; Schemske et al., 2009). However, to the authors' knowledge, before this study, competition for any resource had not been described for the vast environment under the Antarctic ice shelves. Indeed, prior to recent discoveries that complex, rich and abundant life can occur on the seabed underlying ice shelves (Kim, 2019; Barnes et al., 2021a), the sheer presence of competition in this permanently dark, historically-assumed food-scarce (Clarke and Johnstone, 2003) habitat may have been a surprise. The results of the current study, however, not only show for the first time that competition is present, indeed prevalent below an ice shelf (Ekström Ice Shelf, Dronning Maud Land), but also that the nature of such sub-ice-shelf competition is quite different from any previously reported from open-water polar latitudes.

Sub-ice-shelf spatial competition was not of globally-low intensity or severity as initially hypothesised. Instead, both measures were high under Ekström Ice Shelf relative to those of the global marine data, and particularly compared to other polar data from open-water areas of the seasonal sea ice zone (**Figure 5.3A,B**). If present, under-ice-shelf competition was expected to be principally intraspecific, as observed elsewhere in polar seas; however, this was not supported – just 18-19% of competitive encounters were intraspecific compared to a non-sub-ice-shelf polar mean of ~46% (**Figure 5.3C**). The second hypothesis that competition complexity under an ice shelf would be low (as in other polar areas) was also not supported; sub-ice-shelf samples displayed higher complexity levels than all other global datasets (**Figure 5.4A,B**), and the taxonomic divergence of competitors was predominantly at the family (followed by class) level

rather than at the intraspecific level (**Figure 5.5**). The expectation, based on McKinney et al. (1998), that cheilostome bryozoans would be extremely competitively dominant over cyclostomes in such a disturbance minimum as under an ice shelf was, however, supported by the results of the study (**Figure 5.6**). Nonetheless, in all the measures of spatial competition explored, sub-ice-shelf competition bore most resemblance to lower-latitude (non-polar) rather than open-sea high-latitude (polar) competition. In respect, the nature of competition for resources in one of Earth's least known, and perhaps least disturbed habitats appears (according to the current study) to be atypical and has a distinctive mix of attributes compared to similar assemblages elsewhere (e.g., Karlson and Jackson, 1981; Quinn, 1982; Russ, 1982; Chornesky, 1989).

Competition for resources can frequently occur between competitors of differing taxonomic relatedness, as extreme as belonging to different kingdoms (Hochberg and Lawton, 1990) or phyla (Brown and Davidson, 1979). These extremes in competitor relatedness are common in the marine environment and often involve humans as competitors (Diamond, 1987), e.g., for fish stocks (Östman et al., 2013; Hansson et al., 2018) or space via coastal development/re-assignment (Richards and Friess, 2015) – such competition for such resources having considerable ramifications for society and nature's near future. Taxonomic relatedness of spatial competitors is not randomly spread in terms of frequency, and on the seabed, competition appears to be most commonly interfamilial (between members of different families) for reasons yet to be clarified. However, polar coastal shelf competition is predominantly intraspecific (Barnes et al., 2014; Barnes and Neutel, 2016), except seemingly under ice shelves (this study). The current study explored how competitive encounters were distributed across a competitor-relatedness spectrum in an environment unlike any other investigated to date – the seabed underneath an ice shelf. The spread of competitive encounters for space across the competitor-

relatedness spectrum was similar for both sub-ice-shelf sites; however, the overall pattern differed from that of other global data (**Figure 5.5**).

Historically, under-ice-shelf environments were thought to be food-sparse yet space-plentiful, with low densities of a few colonist species (Griffiths et al., 2021). However, it is now known, principally through studies utilising borehole-enabled seafloor imagery and sediment sample collections, that some benthic assemblages under ice shelves can be dense and complex (e.g., Riddle et al., 2007; Kim, 2019). If competition for any resource was anticipated in an environmental setting of seemingly little food and much space, exploitation competition (for scarce food) might have been more expected than contest competition. However, from the limited imagery that has been obtained from sub-ice-shelf seafloor environments and reported on (e.g., Post et al., 2014), it would appear that substrata typically viewed as "hard" and colonisable, such as dropstones (Ziegler et al., 2017) and boulders (Griffiths et al., 2021), also seem rare; thus, space for colonisation by encrusting species (lithophiles) is potentially at a premium in the under-ice-shelf habitat, hence competed for. From the current study on sub-glacial substrata from the eastern Weddell Sea, it is now evident that even when much finer-grained suitable hard substrata are available under ice shelves, such as biologically-generated skeletal fragments (Barnes et al., 2021a; and this study), encrusting biota can be both abundant and species-rich, and much spatial contest competition can transpire.

In the under-ice-shelf environments investigated in the current study, bryozoans, specifically cheilostomes, were both the major spatial competitors and the main spatial resource (hard substrata) being competed for, i.e., as dead fragments of erect bryozoans – the cheilostomes re-purposed, following death, as platforms for new life. This type of ecosystem structuring, whereby organisms use the skeletal remains of others as living space (i.e., "taphonomic feedback"; Kidwell and Jablonski, 1983), is also reflected in

coral reef systems, where coral is the primary substratum and competitor for this space (e.g., Buss and Jackson, 1979); otherwise, coral reefs and under-ice-shelf benthic habitats appear considerably contrasting.

Food availability, and quality, are important to the structuring of marine benthic assemblages (Svensson and Marshall, 2015; Campanyà-Llovet et al., 2017), as is space in all habitats, not least for access to food (Kellner and Asner, 2014). It has been speculated by Barnes et al. (2021a) that food might be so limited under ice shelves that spatial competitors with feeding (planktotrophic) larvae may struggle to survive and colonise space there. Indeed, most of the competitors for space identified in the present study were those with exclusively yolk-feeding (lecithotrophic) larvae. This apparent dominance of larval form could be because lecithotrophic larvae are less sensitive to a potentially food-poor/inconsistent water column, whereas planktotrophic larvae must feed in the water column to achieve the size and maturity required for settlement (and subsequent metamorphosis to colony development). In addition, lecithotrophic larvae are generally thought to have lower dispersal capabilities than planktotrophic larvae, so presumably would mostly settle closer to their origin, providing appropriate substratum is available, such as the cheilostome bryozoan fragments in this study. Nonetheless, clearly an adequate enough or adequately consistent food supply has been present and/or delivered under Ekström Ice Shelf, at least to the sites sampled, to also support adult planktotrophic life there over thousands of years (Barnes et al., 2021a).

While Antarctica's open continental shelf hosts some of Earth's most naturally disturbed environments (Gutt and Starmans, 2001), the seafloor underneath ice shelves comparatively represents a disturbance minimum and a potential refuge from natural (and potentially anthropogenic) disturbance, in part owing to the existence and persistence of the floating ice shelf above, and additionally evidenced by lifespans, under Ekström Ice

Shelf, of almost 6,000 years (Barnes et al., 2021a). These two systems, either side of the ice-shelf front, therefore, present as profoundly different settings for competitors and competition. McKinney (1995) found that in environmental conditions of strong fossilisation (warm shallow seas), competition for space between the two major bryozoan clades remained relatively constant over a 100 Ma time span, with cheilostomes (consistently) competitively outperforming cyclostomes, with a mean win rate of 66.5% across time. However, evidence from current habitats across Earth's wider spectrum of environmental conditions indicates competition between these clades, and the competitive success of one over another, can be much more variable (Barnes and Dick, 2000). If under-ice-shelf environments are as extreme as being long-enduring disturbance minima, hence also potentially echoing conditions of calmer geological time, the expectation was to find extreme interclade results, which is precisely what was found in this study; cheilostomes winning, on average, ~90% of spatial contests against cyclostomes (**Figure 5.6**).

Ice losses are one of the most striking and rapid responses to global climate change (Turner and Comiso, 2017; Parkinson, 2019). Although ice-shelf dynamics have proven complex, and sea ice losses in some regions have been matched by gains in others, it seems reasonable to deduce that marine (and terrestrial) icescapes, and hence associated habitats such as those explored in this study, must be under considerable threat from GHG-emissions-driven global warming (IPCC, 2019; Gilbert and Kittel, 2021). With ice-shelf retreat or collapse, there is a potential for the disturbance regime of the previously overlain continental shelf to significantly alter – rapidly transitioning from an extremely low- to high-disturbance environment. In response, the nature and dynamics of competition may change, which would have implications for both assemblage structure and broader habitat functions and services that are yet to be fully realised.

5.7 Conclusions

Rare borehole-derived collections of sub-ice-shelf seabed substrata and stereo microscopy methodologies have provided not just the first evidence of competition from a distinct and mainly unexplored environment, but also from a habitat that has persisted for thousands of years, and, therefore, potentially of exceptionally low disturbance. Due to the ubiquity of bryozoans, sub-ice-shelf findings could be compared with existing global datasets, and although sampling is limited, it appears that spatial competition under Ekström Ice Shelf is not only very different from that of open-water polar areas but also remarkably similar, in several traits, to non-polar marine benthic environments. Whether such findings extend to or are more widely representative of the sub-ice-shelf habitats fringing Dronning Maud Land, East Antarctica, and elsewhere in this vast ecosystem, is yet to be confirmed. Nonetheless, the results of this study further indicate the potential utility of bryozoans as indicators of environmental differences. The findings also offer a precedent that perhaps in a permanently ice-covered and minimally-disturbed seafloor environment, spatial competition among the benthos can be intense and severe, unique in nature, and be dominated by a particular faunal clade.

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Chapter 6 | Conclusions

Respecting the aims and objectives of the thesis (as indicated in Chapter 1), this thesis has captured the complexities of rarely studied Antarctic marine communities, in particular benthic assemblages and their potential responses to a changing climate and marine icescape. Varied data types and extensive datasets, including digital, have been analysed to produce, for example, taxonomic and functional group structures required for explorations and statistical analyses conducted in the research chapters and to test current conceptual understanding of resource competition (in this instance, the resource being colonisable space). The thesis has highlighted novel findings whilst further revealing important knowledge gaps. Key findings of each research chapter are provided below.

6.1 Key Findings

6.1.1 Structure of Megabenthic Assemblages – Larsen C Ice Shelf Polynya

The study of the seabed habitat and structure of megabenthic assemblages of the Larsen C Polynya, western Weddell Sea, encompassed four study continental shelf sites of varying proximity to Larsen C Ice Shelf. The research revealed that although sites were potentially in the path of transiting icebergs (steered by the Weddell Gyre, see Vernet et al., 2019, and constituting a major source of physical disturbance when contact with the seafloor is made, e.g., Gutt and Starmans, 2001; Gutt and Piepenberg, 2003), faunal density nevertheless generally increased with distance seaward from the ice-shelf front. Furthermore, due to the study partly encompassing a functional group approach, a surrogate for overall faunal density trends was able to be identified: deposit-feeding crawlers (all holothurians). Leveraging of such a surrogate could reduce imagery analysis

timeframes, plus the visual characteristics of holothurians present them as ideal candidates for the development of automated appraisal tools (Li et al., 2021).

Contrary to faunal density, biodiversity (richness) did not exhibit a significant pattern with distance from the ice shelf and was most variable at the two sites closest to the ice-shelf edge – this variability potentially highlighting biological sensitivities to environmental differences and influences, e.g., prevailing substratum type and oceanic temperature. The site closest to Jason Peninsula was dominated by poorly-sorted coarse-grained substrata and had notably low faunal richness and densities, while the Bawden Ice Rise site, despite being further south, experienced warmer oceanic temperatures (Hutchinson et al., 2020), was protected from potential ice scour (Han et al., 2019), and had high richness and densities. The two ice-shelf front sites were also the most compositionally dissimilar.

Although primary production correlated with distance seaward from the ice shelf, which may influence, for example, benthic faunal distributions and densities, ice-shelf proximity did not directly emerge as a significant potential driver of assemblage structure. However, when considering historical sea-ice and ice-shelf cover together as composite ice cover, this variable did emerge as a significant potential influencer of composition differences – the consideration of multiple ice cover types (where applicable), which act in a similar way (e.g., inhibiting photosynthetic primary production), would perhaps be beneficial to other studies endeavouring to unravel biophysical relationships.

In addition, the study newly uncovered faunistic legacies of chemotrophic activity southward of the Jason Peninsula, which unlike those observed further north along the eastern Antarctic Peninsula (e.g., Domack et al., 2005; Niemann et al., 2009), presented in areas with no historical ice-shelf cover (also see Batchelor et al., 2022) – enduring ice-

cover speculated to be conducive to chemotrophic ecosystems (Domack et al., 2005). The seabed below the polynya was also host to small circular/elliptic depressions, akin to those observed by Gutt et al. (2010) in a nearby area of the western Weddell Sea, their origin posited as potentially biological (e.g., feeding marks/pits or nursery areas for fish) or geological (e.g., cold seep sources).

Overall, the research conducted in Chapter 3, (in part) enabled by the opening of the Larsen C Polynya and suitable leads in pack ice (Dowdeswell et al., 2019, 2020), has afforded the first comprehensive community analysis of the megabenthos residing next to the evolving Larsen C Ice Shelf, including structuring (i.e., composition and densities) and potential environmental drivers. The study found biologically-diverse, heterogeneous and complex seafloor habitats close to an ice-shelf front and provides new ecological baselines (by morphotaxa and higher-level functional group groupings) that can be utilised in monitoring and forecasting southern high-latitude benthic ecosystem responses to climate-forced environmental change, including ice-shelf retreat along the eastern Antarctic Peninsula, and which are also required to inform ocean conservation and management. The research also contributes to knowledge of seabed habitats and assemblages abutting the dynamic floating perimeter of the Antarctic Ice Sheet, which, to date, have seldom been investigated – this despite, ice shelves constituting >14,000 km of Antarctica's coastline (Drewry et al., 1982; Dowdeswell and Bamber, 2007).

6.1.2 Function of Zoobenthic Assemblages – Carbon Storage Across a Southern Polar Gradient (Scotia Arc)

The study of the blue carbon-associated function of zoobenthic assemblages across a southern polar gradient included four continental/island shelf study areas dispersed along the Scotia Arc, and representative of a transition from cool to seasonally-surface-freezing

marine waters. Acquisition of zoobenthic specimens and adoption of a functional group approach (similar to Chapter 3) enabled estimations of the amount of carbon held by each functional group per study area to be computed, which initially revealed mean carbon content of functional groups to vary depending on area – something to consider for future blue carbon studies. Zoobenthic carbon storage, when principally based on the epi-zoobenthos, was estimated for the two study areas south of the Antarctic Circumpolar Current to be around six times higher than for the northernmost areas situated in warmer and potentially more disturbed waters essentially free of modern-day ice cover. Nonetheless, at each study area, zoobenthic carbon storage exhibited a positive relationship with morphotaxa richness, faunal density, and density of Vulnerable Marine Ecosystem (VME; see CCAMLR, 2009 and 2019, and FAO, 2009) indicator taxa (VME indicators constituting ~50% of all zoobenthic taxa observed in the study). Furthermore, VME taxa were also found to be important faunal contributors to carbon storage (at most study sites). In addition, differences in the functional groups most contributing to carbon storage were observed between (and within) study areas, suggesting that "collective protection" may best safeguard benthic carbon storage functioning.

When investigating the influence of various environmental variables, sea-ice cover was the single variable with the highest correlation with zoobenthic assemblage and carbon storage by (functional groups) structures, and carbon storage (as a single response variable) – the latter two findings suggesting that the function of carbon storage is potentially influenced by an environmental variable expected to alter considerably with climate change (Rogers et al., 2020). In addition, boulders or dropstones (relatively coarse hard substrata) tended to host more diverse assemblages and higher faunal densities (as observed by Ziegler et al., 2017), and greater carbon storage. Such physical seabed

features are also expected to increase in prevalence with ice-shelf retreat and increased iceberg generation as they can constitute a part of ice-rafted debris.

Overall, the research conducted in Chapter 4 has highlighted the potentially significant role of Antarctic continental shelf habitats and residing communities (marine living resources) as natural carbon sinks – the carbon stored in open-shelf epi-zoobenthos alone equating to an estimative drawdown of ~0.5 billion tonnes of atmospheric carbon dioxide. The study contributes to building the knowledge base around high-latitude blue carbon estates, and can also support decision-making, by various actors, within the region and associated environs, regarding, for example, marine conservation prioritisation and climate-considerate spatial planning.

6.1.3 Behaviour of Macrobenthic Assemblages – Sub-Ice-Shelf Spatial Competition

The study of the behaviour of encrusting macrobenthos on seabed substrata obtained from locations beneath Ekström Ice Shelf, eastern Weddell Sea, East Antarctica, afforded the first known evidence of competition for resources transpiring under Antarctica's ice shelves – a vast yet minimally-explored environment extending around 1.6 million km^2 (Clarke and Johnstone, 2003), where, in particular, very little is known about constituent seabed habitats and communities (Kim, 2019; Barnes et al., 2021; Griffiths et al., 2021).

In endeavouring to test the existing conceptual understanding of resource competition in such an understudied environment, competition for space, as carried out by macrobenthic organisms, was found to be (perhaps unexpectedly) prevalent underneath the ice shelf. The nature of such competition was able to be determined by means of stereo microscopy and a series of corresponding spatial competition measures was calculated for the sub-ice-shelf environment, permitting comparison with global

datasets. A finding of particular note was that the nature of sub-ice-shelf competition was discernibly different to that of the open-water polar continental shelf, presenting as higher in intensity, severity and complexity, and more-over resembling that of temperate and tropical seabed environments. In addition, the competitive dominance of a particular bryozoan clade was remarkably high in the sub-ice-shelf samples, essentially reflecting expectations (also posited in this research) for seabed environments of minimal disturbance.

Overall, the research conducted in Chapter 5 has provided novel insights into encrusting macrobenthic assemblages of a persistently dark and long-thought depauperate sub-glacial environment, an environment anticipated to be reduced or even forfeited as a consequence of climate-forced warming (e.g., Gilbert and Kittel, 2021; Naughten et al., 2023). The study constitutes the first analysis of competition of any kind under an ice shelf, hence helps with narrowing associated and significant knowledge gaps, and also suggests that the sub-ice-shelf environment may be more hospitable and supporting of marine life than previously thought – a supposition that can be further explored. The findings and data generated also serve as a new ecological baseline for future monitoring and temporal studies in the eastern Weddell Sea region, especially of its sub-ice-shelf benthic habitats (Gutt et al., 2022; Lowther et al., 2022).

6.2 Future Perspectives

Discovery of the Antarctic benthos is certainly an ongoing process. Much of the continental shelf around Antarctica is yet to be ecologically explored and sampled, and novel and significant ecological findings continue to present themselves, for example, the recent discovery of exceptionally productive seabed habitats and an extensive icefish breeding colony of global significance in the Filchner Trough, southern Weddell Sea

(Purser et al., 2022), an area which currently experiences heavy perennial sea-ice cover (Pineda-Metz et al., 2019). In particular, very little is known about or documented for the benthos of the spatially-vast sub-ice-shelf seabed environment (i.e., continental shelf overlain by "permanent" ice cover), which is vulnerable to future warming (Gilbert and Kittel, 2021); however, recent findings (e.g., Barnes et al., 2021 and Chapter 5 of this thesis) continue to challenge expectations and long-held assumptions, including how far under ice shelves sessile suspension feeders can persist (Griffiths et al., 2021).

As access to and sampling of Antarctic marine environments improves with technological advancements in data collection/capture apparatuses (e.g., submersibles and associated payloads), and, in the future, with potential ice-cover loss, it can be envisaged that bentho-ecological knowledge gaps will narrow, and, in addition, the closing of such knowledge gaps accelerated with expedited data (seafloor imagery) analysis by, for example, moves to higher-level ecological appraisals (e.g., employing functional groups), use of proxies/surrogates (for the wider fauna), and automation (e.g., Marini et al., 2022). Given the spatial extent of the marine region (millions of km^2), knowledge (and sampling) gaps may, however, not be reconciled before impacts of climate change have transpired (or are in motion), as exemplified by areas of the Larsen Ice Shelf System, western Weddell Sea, West Antarctica (e.g., Domack et al., 2005; Gutt et al., 2011, 2013; Fillinger et al., 2013). However, for some areas, such as around Ekström Ice Shelf, eastern Weddell Sea, East Antarctica, climate change impacts are yet to be evidenced; hence, such areas could serve as living laboratories for examining/monitoring benthic biota response to environmental modifications (e.g., marine icescape alterations), including those brought about by climate change (Gutt et al., 2022; Lowther et al., 2022).

As seabed habitats, especially of the Antarctic continental shelf, are becoming increasingly recognised for their, in some cases growing, contribution to biologically-facilitated carbon storage, and prospective sequestration (Peck et al., 2010; Alurralde et al., 2019; Barnes et al., 2020), interest in their role as potential high-latitude/polar nature-based contributors to climate change mitigation is also mounting (e.g., Morley et al., 2022; Zwerschke et al., 2022; Sands et al., 2023). However, consideration of such an ecological function (or ecosystem service) has yet to be reflected in marine conservation measures and spatial planning within the region, including in a precautionary way. Blue carbon studies could influence regional decision-making (i.e., by CCAMLR), including prioritising for protection areas exhibiting (or anticipated to exhibit) both high biodiversity and carbon storage, which could contribute to alleviating the entangled biodiversity and climate crises, as advocated for by Pörtner et al. (2023) (plus see IPCC 2022, 2023; Siegert et al., 2023). In addition, emerging seabed habitats, such as those exposed by glacial retreat (Barnes et al., 2021; Zwerschke et al., 2022), could be monitored to see how zoobenthic assemblages and carbon storage function develop through time.

While the blue carbon focus (and remit) of the current research was principally epi-zoobenthic carbon storage, it would be of value to also consider in-faunal carbon storage – although associated field data collection methods (e.g., sediment coring; Pineda-Metz and Gerdes, 2018; Zwerschke et al., 2022) would be more intrusive, and additional mini-Agassiz trawls (or equivalent) potentially required for acquisition of further representative faunal specimens. Additionally, it would perhaps be of further added value to determine the amount of organic carbon stored in corresponding seafloor sediments – typically ascertained using sediment core samples. In Antarctic fjords, for example, infaunal carbon storage and organic carbon stored in the sediment have recently been

estimated to be equivalent to and ten times greater than epibenthic carbon storage, respectively – such findings leveraging ash-free dry mass calculations and potentially providing a more comprehensive evaluation of seabed carbon storage (Zwerschke et al., 2022).

Research on sub-ice-shelf benthic habitats/assemblages is very limited, with access to the respective environment still presenting as the major barrier to exploration and sampling. However, access challenges may also be alleviated by wider employment and enhanced capabilities of autonomous underwater vehicles and remotely operated vehicles. Thus, future research opportunities regarding the sub-ice-shelf seafloor environment (of ~1.6 million km^2) are potentially vast and diverse. Furthermore, recent discoveries continue to heighten interest and challenge preceding assumptions, such as the unexpected richness and longevity of sub-ice-shelf benthic life (Barnes et al., 2021) and the existence and nature of competition for space (Chapter 5 of this thesis), and inspire questions, including, for example, around whether sub-ice-shelf habitats act as refugia for seabed biota, and, if so, which biota (and on what timescales), as well as the ecological consequences of the potential loss of these habitats, e.g., through disintegration or collapse of ice shelf above, and if alterations in the behaviour of component sub-ice-shelf assemblages could be used to indicate environmental changes as yet undetected or as first response.

6.3 Concluding Remarks

This thesis has contributed to furthering the knowledge and enhancing the understanding of contemporary Antarctic continental shelf benthic assemblages in terms of their structure, function and behaviour, within the context of a warming world and anticipated changes to overlying marine icescapes. The various connected biotic aspects examined,

all likely to alter in response to environmental modifications, and outputs of corresponding studies have also facilitated delivery of new evidence bases, including novel ecological baselines, which can help support conservation and management measures directly within the six study areas encompassed, and in Antarctica's seas more generally.

6.4 References

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Appendix A: Supplementary Material

A1 – Supplementary Material to Chapter 3

Supplementary information, figures and tables for: Antarctic Seabed Assemblages in an Ice-Shelf-Adjacent Polynya, Western Weddell Sea.

Frinault, B.A.V., et al. (2022). *Biology*, **11**, 1705.

https://doi.org/10.3390/biology11121705

Methods regarding phytodetritus cover

The degree of phytodetritus cover was scored on a scale of 1-5 (1 being the lowest cover and 5 the highest). The scale was custom-developed for the study area (and time) and verified to be operational by two independent appraisers who analysed the same test set of still frames and scored them identically for phytodetritus cover.

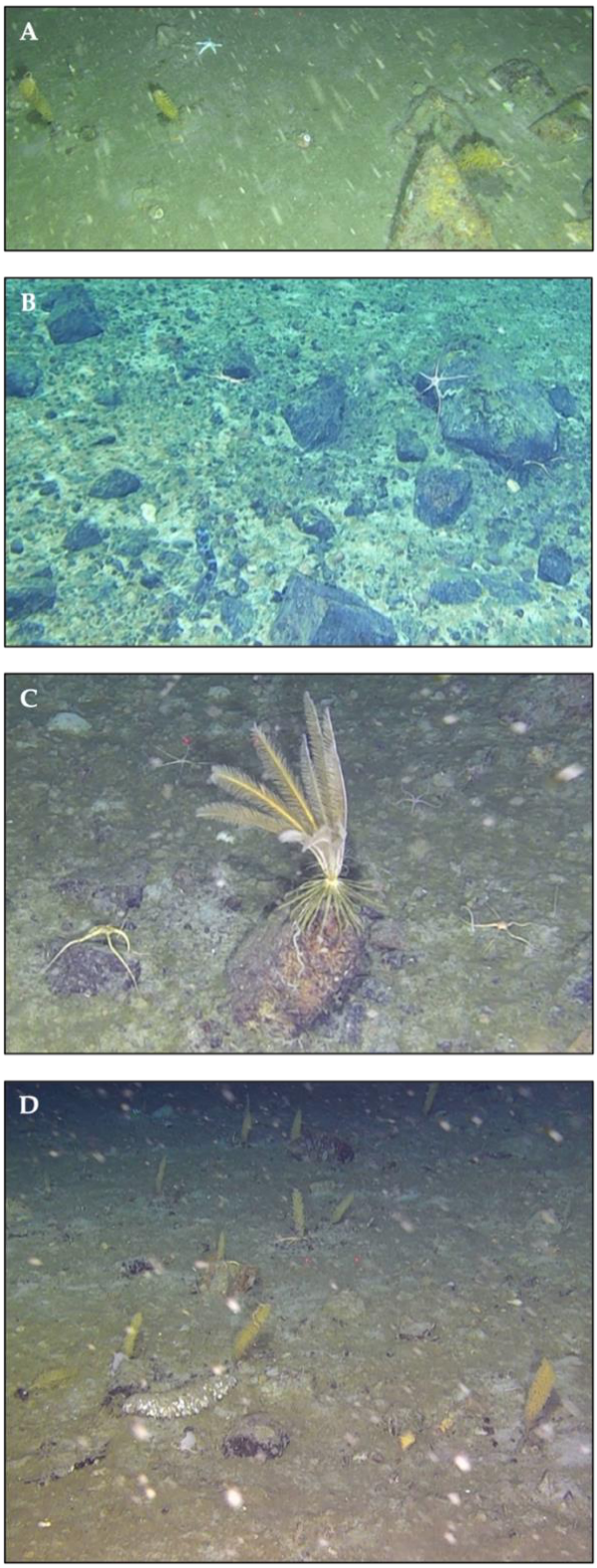


Figure S3.1: Example imagery and megabenthic communities observed at the Larsen C Polynya study sites, LCP1-4, western Weddell Sea, Antarctica: (**A**) LCP1, (**B**) LCP2, (**C**) LCP3, and (**D**) LCP4.

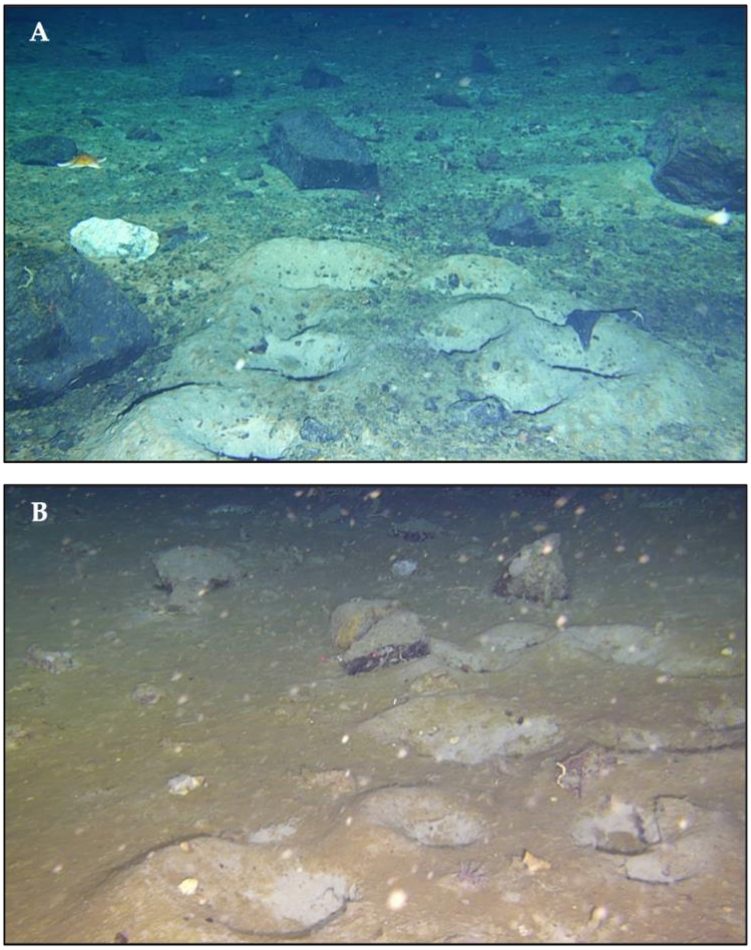


Figure S3.2: Cluster of depressions in the seabed close to the Larsen C Ice Shelf, at study sites (**A**) LCP2 and (**B**) LCP4, of ~299 and ~349 m water depth, respectively.

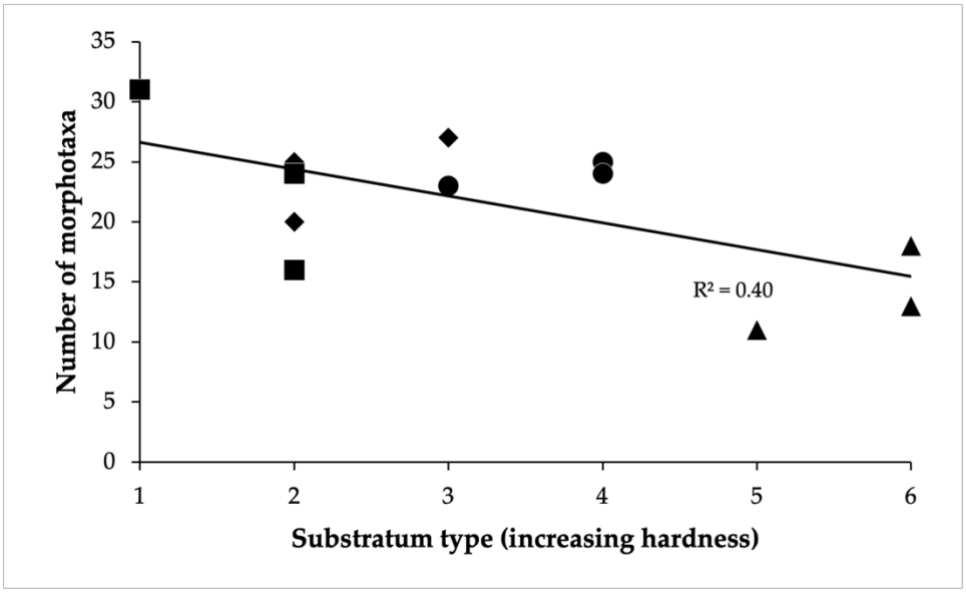


Figure S3.3: Morphotaxa richness with substratum type (increasing hardness) for standardised 100 m^2 samples across Larsen C Polynya study sites, LCP1-4, and showing a weak (inverse) relationship. Sites are (left to right) LCP4 = squares, LCP1 = diamonds, LCP3 = circles, and LCP2 = triangles.

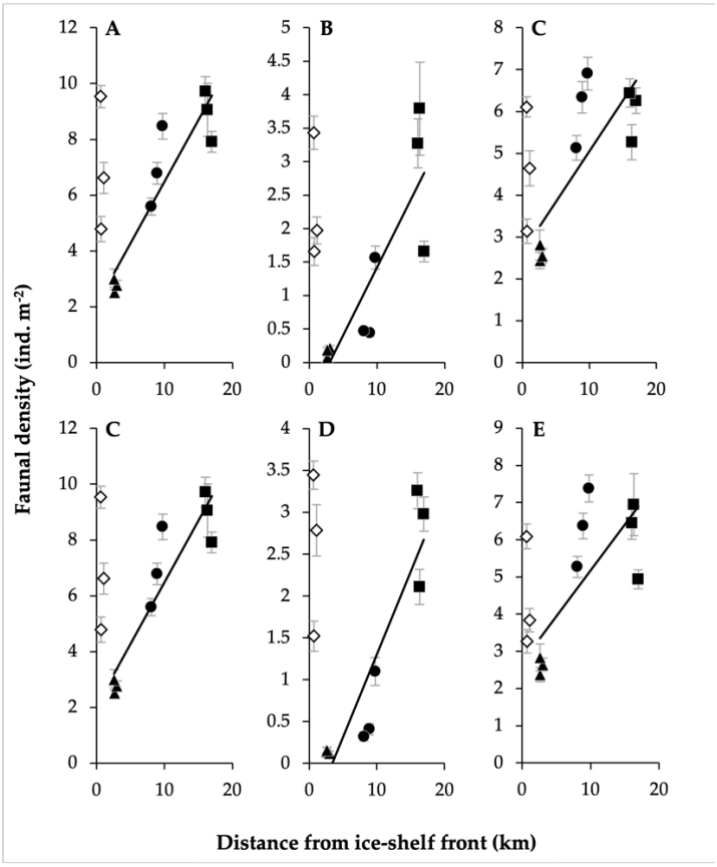


Figure S3.4: Exploration of functional groups pioneer sessile suspension feeders and hard sessile predator/scavengers as potential surrogates for the overall faunal density trend[a]. Mean densities (ind. m^{-2}) (± SE) with distance from the ice-shelf front (km) of: (**A**) overall fauna; (**B**) pioneer sessile suspension feeders; (**C**) overall fauna excluding pioneer sessile suspension feeders; (**D**) overall fauna; (**E**) hard sessile predator/scavengers; and (**F**) overall fauna excluding hard sessile predator/scavengers. Site LCP1 = diamonds, LCP2 = triangles, LCP3 = circles, and LCP4 = squares.

[a]The overall faunal pattern remains reasonably intact when data of either functional group are removed; however, the two functional groups appear to closely match one another in terms of their individual density pattern, and their densities influence overall faunal densities. In contrast, the deposit-feeding crawlers group (**Figure 3.6** in the main text) presents densities that do not influence overall faunal densities while reflecting the pattern (hence selected as the strongest surrogacy candidate).

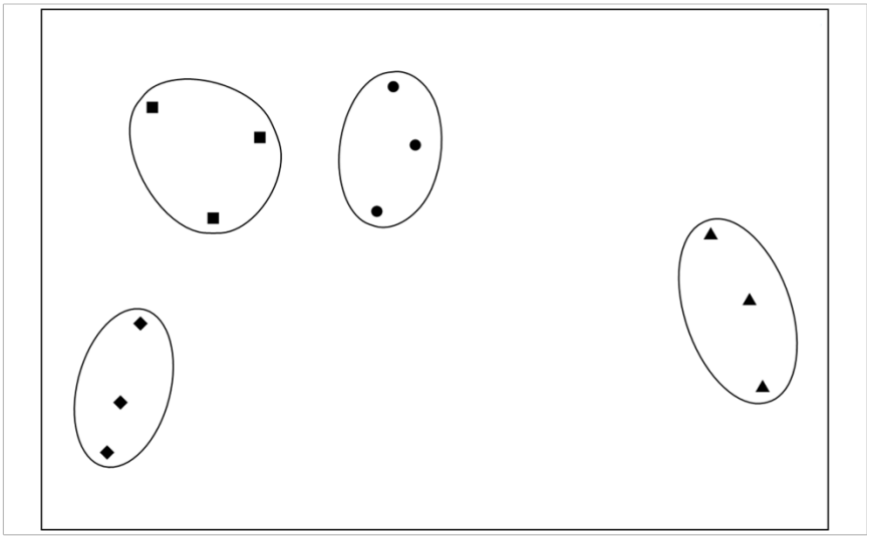


Figure S3.5: Non-metric multidimensional scaling (nMDS) ordination of Larsen C Polynya samples based on Bray-Curtis similarities calculated from fourth-root transformed morphotaxa density data (2D Stress= 0.05). Symbols for site samples (from left to right) are LCP1 = diamonds, LCP4 = squares, LCP3 = circles, and LCP2 = triangles. Ellipses around samples = significant groupings identified by a SIMPROF test during hierarchical cluster analysis.

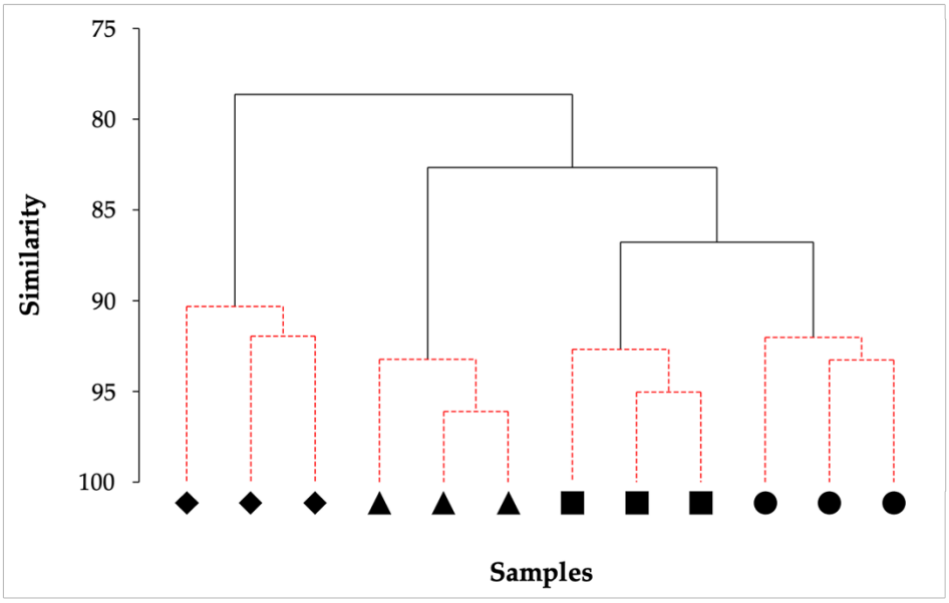


Figure S3.6: Dendrogram from hierarchical agglomerative clustering of Larsen C Polynya samples using group-average linking of Bray-Curtis similarities calculated from functional group densities data. Similarity profiles (SIMPROF) testing applied to determine significance of divisions (at $p < 0.05$) with black continuous lines indicating significant clusters and red hashed lines indicating non-significant clusters. Site LCP1 = diamonds, LCP2 = triangles, LCP3 = circles, and LCP4 = squares.

Table S3.1: Distances (m) between Larsen C Polynya study sites LCP1-4. Calculated using Vector Analysis Tools in QGIS v3.16.6.

Site	LCP1	LCP2	LCP3	LCP4
LCP1	0	57,490	75,377	60,879
LCP2	57,490	0	19,192	14,650
LCP3	75,377	19,192	0	17,167
LCP4	60,879	14,650	17,167	0

Table S3.2: Larsen C Polynya substratum types. Hardness scale[a].

Dominant substratum 1	Dominant substratum 2	Hardness scale
Soft sediment	Mixed	**1**
Mixed	Soft sediment	**2**
Mixed	Boulder	**3**
Assorted hard	Mixed	**4**
Assorted hard	Boulder/mixed	**5**
Assorted hard	Boulder	**6**

[a]Soft sediment (predominantly fine-grained sediment, i.e., mud/sand); mixed (patches of both soft and hard sediment); boulder (dominant feature in frame); and assorted hard (sediment of various coarse grain-sizes, i.e., pebbles to boulder).

Table S3.3: Range of environmental variables[a-e] prepared and examined to discern how sites differ in terms of environmental context. Presented are variables that displayed variation between sites, with variables showing high correlation (or anticorrelation) (r ≥95% [or ≤-95%]) with another identified by ✓. Variables used in statistical analyses are presented (**in bold**) and include variables used as a proxy for respective correlates.

Data sources	**GIS**	**ROV**	**Imagery**		**Remote Sensing[b,c]**					**CTD[d,e]**					
Environmental variables[a]	**Distance from ice shelf**	**Depth**	**Substratum**	**Phytodetritus**	Mean daily NPP	Mean peak NPP	**Sea ice**	Years ice-shelf-free	Mean ice cover[f]	Silicic acid	**Nitrate**	**Phosphate**	**Salinity**	Oxygen	**Temp**
Distance from ice shelf					✓	✓									
Depth															
Substratum															
Phytodetritus															
Mean daily NPP	✓										✓				
Mean peak NPP	✓														
Sea ice								✓		✓					
Years as ice-shelf-free							✓								
Mean ice cover[f]															
Silicic acid							✓								
Nitrate					✓										
Phosphate															
Salinity															
Oxygen															✓
Temp														✓	

[a]Distance from ice shelf = distance of sample from the ice-shelf front at time of sampling (m); Depth = mean depth of sample (m); Substratum = substratum type hardness of sample by dominating substratum types (as per Table S2); Phytodetritus = degree of phytodetritus cover (1 to 5; 1 = lowest, 5 = highest); Mean daily NPP = mean daily net primary production over the period 1997-2018 (mg C m^{-2} d^{-1}); Mean peak NPP = mean net peak primary production over the period 1997-2018 (mg C m^{-2} d^{-1}); Sea ice = mean monthly sea-ice concentration (SIC) over the period 1997-2018 (%); Number of years ice-shelf-free = number of years not covered by ice shelf

for the period 1963-2018; Mean ice cover = composite mean monthly ice cover (incorporating both ice-shelf cover and sea-ice concentration data) for the period 1997-2018 (%) (not used in the main study); Silicic acid = Log [Silicic acid] (μM); Nitrate = Log [Nitrate] (μM); Phosphate = Log [Phosphate] (μM); Salinity = Salinity (PSU); Oxygen = Log [Oxygen] (μM); Temp = bottom water temperature (°C).

Correlations: Distance from ice shelf with mean daily NPP and mean peak NPP; nitrate with mean daily NPP; sea ice with silicic acid and years ice-shelf-free; and temp with oxygen (represented in the study as "water physico-chemistry", and indicating LCP1 to be situated in warmer and less oxygenated waters than LCP2-4).

[b]Mean daily NPP and mean peak NPP were determined from data generated as per procedures described in Arrigo, K.R.; van Dijken, G.L.; Bushinsky, S. Primary production in the Southern Ocean, 1997–2006. *J. Geophys. Res.* **2008**, 113, doi:10.1029/2007jc004551 and Arrigo, K.R.; van Dijken, G.L.; Strong, A.L. Environmental controls of marine productivity hot spots around Antarctica. *J. Geophys. Res. Oceans* **2015**, 120, 5545-5565, doi:10.1002/2015jc010888.

[c]Sea-ice concentration and number of years ice-shelf-free (and mean ice cover) were based on data obtained as per methods described in Christie, F.D.W.; Benham, T.J.; Batchelor, C.L.; Rack, W.; Montelli, A.; Dowdeswell, J.A. Antarctic ice-shelf advance driven by anomalous atmospheric and sea-ice circulation. *Nat. Geosci.* **2022**, 15, 356-362, doi:10.1038/s41561-022-00938-x.

[d]Nitrate, silicic acid, and phosphate concentrations were acquired as per methodologies described in Flynn, R.F.; Bornman, T.G.; Burger, J.M.; Smith, S.; Spence, K.A.M.; Fawcett, S.E. Summertime productivity and carbon export potential in the Weddell Sea, with a focus on the waters adjacent to Larsen C Ice Shelf. *Biogeosciences* **2021**, 18, 6031-6059, doi:10.5194/bg-18-6031-2021.

[e]Salinity and temperature measurements, and oxygen concentrations were obtained as per methods described in Hutchinson, K.; Deshayes, J.; Sallee, J.B.; Dowdeswell, J.A.; Lavergne, C.; Ansorge, I.; Luyt, H.; Henry, T.; Fawcett, S.E. Water Mass Characteristics and Distribution Adjacent to Larsen C Ice Shelf, Antarctica. *J. Geophys. Res. Oceans* **2020**, 125, doi:10.1029/2019jc015855.

[f]Mean ice cover: To take into consideration both types of ice cover, i.e., sea-ice and ice-shelf cover, a composite variable: "mean ice cover" (%), was computed using SIC (%) and historical ice-shelf cover data. Mean ice cover was calculated (for each site) for the 1997-2018 period and wherein ice-shelf cover corresponded to 100% ice cover. Although not used in the main paper, when mean ice cover was trialled in BEST analysis, the measure was found to best correlate (along with substratum) with benthic assemblage composition differences.

Table S3.4: Similarity percentages (SIMPER) analysis displaying percentage contributions of benthic morphotaxa responsible for within-site (LCP1-4) similarities. Cut-off where cumulative percentage contribution reaches 50%. Overall average similarities (%): LCP1 samples = 71.57; LCP2 samples = 69.82; LCP3 samples = 70.94; LCP4 samples = 74.3.

Benthic morphotaxa	Av. dens. (ind. m^{-2})	Av. sim. (%)	Sim./SD	Contrib. (%)	Cum. contrib. (%)
LCP1					
Bottlebrush/bushy corals - (e.g., *Thouarella*)	1.22	8.57	12.36	11.98	11.98
Encrusting lithophilic organisms	1.16	8.19	14.63	11.44	23.42
Ophiuroidea	0.96	6.77	11.59	9.47	32.89
Echinoid 1 - *Sterechinus antarcticus*	0.74	5.25	14.08	7.34	40.23
Asteroidea	0.65	4.76	13.01	6.66	46.89
Holothurian 1 - *Pseudostichopus mollis*	0.62	4.42	13.17	6.18	53.06
LCP2					
Ophiuroidea	1.16	15.17	19.34	21.72	21.72
Encrusting lithophilic organisms	0.61	7.55	7.35	10.81	32.53
Scleractinian cup corals (e.g., Flabellidae)	0.58	7.38	35.84	10.57	43.1
Asteroidea	0.55	7.22	40.61	10.34	53.44
LCP3					
Ophiuroidea	1.44	11.67	117.16	16.45	16.45
Encrusting lithophilic organisms	0.88	6.55	33.04	9.23	25.68
Holothurian 1 - *Pseudostichopus mollis*	0.72	5.8	102.97	8.18	33.86
Bottlebrush/bushy corals - (e.g., *Thouarella*)	0.71	5.22	31.09	7.35	41.21
Asteroidea	0.64	4.96	17.34	7	48.21
Scleractinian cup corals (e.g., Flabellidae)	0.64	4.95	21.11	6.97	55.18
LCP4					
Bottlebrush/bushy corals - (e.g., *Thouarella*)	1.26	8.63	102.99	11.62	11.62
Ophiuroidea	1.18	8.34	26.47	11.22	22.84
Encrusting lithophilic organisms	1.21	8.24	9.8	11.1	33.93
Holothurian 1 - *Pseudostichopus mollis*	0.77	5.09	7.59	6.85	40.78
Asteroidea	0.65	4.59	24.28	6.18	46.96

Ascidian 1 - *Pyura* spp.	0.6	3.96	8.91	5.33	52.29

Av. dens. = average density, Av. sim. = average similarity, Sim./SD = similarity/standard deviation, Contrib. = contribution, Cum. contrib. = cumulative contribution.

Table S3.5: Similarity percentages (SIMPER) analysis displaying percentage contributions of benthic morphotaxa responsible for dissimilarities between sites (LCP1-4). Cut-off where cumulative percentage contribution reaches 50%. Overall average dissimilarities (%): LCP1 and LCP2 = 61.20; LCP1 and LCP3 = 47.36; LCP1 and LCP4 = 41.56; LCP2 and LCP3 = 49.23; LCP2 and LCP4 = 56.90; LCP3 and LCP4 = 38.72.

Benthic morphotaxa	Av. dens. (ind. m^{-2})	Av. dens. (ind. m^{-2})	Av. diss. (%)	Diss./SD	Contrib. (%)	Cum. contrib. (%)
Sites closest to ice-shelf front	**LCP1**	**LCP2**				
Bottlebrush/bushy corals (e.g., *Thouarella*)	1.22	0	5.88	14.53	9.61	9.61
Encrusting lithophilic organisms	1.16	0.61	2.63	7.49	4.3	13.91
Gymnolaemate bryozoans	0.53	0	2.55	15.63	4.16	18.07
Echinoid 1 - *Sterechinus antarcticus*	0.74	0.28	2.2	11.11	3.59	21.66
Ascidian 1 - *Pyura* spp.	0.43	0	2.13	2.9	3.48	25.14
Echinoid 3 - Spatangoida	0.43	0	2.1	5.07	3.43	28.57
Holothurian 2 - *Peniagone vignoni*	0	0.42	2.03	6.71	3.31	31.88
Echinoid 2 - Ctenocidaridae	0.41	0	1.97	21.44	3.23	35.11
Holothurian 1 - *Pseudostichopus mollis*	0.62	0.23	1.86	1.96	3.04	38.15
Demosponge – *Phakellia*	0.38	0	1.79	7.85	2.92	41.07
Perciformes - Bathydraconidae	0.33	0	1.58	7.31	2.58	43.65
Demosponge 2	0.33	0	1.52	1.23	2.48	46.12
Whip corals	0.29	0	1.49	1.33	2.44	48.56
Decapod shrimps	0.31	0	1.48	20.73	2.42	50.98
Sites at ~400 m depth	**LCP1**	**LCP3**				
Echinoid 1 - *Sterechinus antarcticus*	0.74	0.21	2.08	3.24	4.4	4.4
Bottlebrush/bushy corals (e.g., *Thouarella*)	1.22	0.71	2.01	3.25	4.24	8.64
Ophiuroidea	0.96	1.44	1.91	4.36	4.03	12.66
Echinoid 3 - Spatangoida	0.43	0	1.72	5.36	3.63	16.29
Echinoid 2 - Ctenocidaridae	0.41	0	1.62	17.49	3.42	19.72
Demosponge – *Phakellia*	0.38	0	1.47	6.95	3.1	22.82

Stalked crinoids (e.g., *Dumetocrinus antarcticus*)	0	0.33	1.33	5.95	2.8	25.62
Eucarid malacostracans	0	0.33	1.32	8.56	2.78	28.4
Perciformes - Bathydraconidae	0.33	0	1.29	7.62	2.73	31.14
Demosponge 2	0.33	0	1.25	1.22	2.65	33.78
Demosponge 1	0.31	0	1.21	21.14	2.56	36.35
Sea pen 2 - *Umbellula* spp.	0	0.3	1.2	7.78	2.54	38.89
Stenolaemate bryozoans	0.29	0	1.12	1.28	2.37	41.26
Encrusting lithophilic organisms	1.16	0.88	1.09	1.74	2.31	43.57
Unstalked crinoids (e.g., *Promachocrinus kerguelensis*)	0.2	0.45	1.01	1.46	2.13	45.7
Hexactinellid 1 - *Chonelasma*	0	0.25	1	1.28	2.11	47.81
Hexactinellida	0.24	0	0.94	1.32	2	49.8
Ascidian 1 - *Pyura* spp.	0.43	0.22	0.94	1.33	1.99	51.79
	LCP1	**LCP4**				
Echinoid 1 - *Sterechinus antarcticus*	0.74	0	2.71	17.89	6.52	6.52
Eucarid malacostracans	0	0.46	1.69	6.58	4.08	10.6
Hydroid 1	0.11	0.55	1.65	2.32	3.98	14.57
Echinoid 3 - Spatangoida	0.43	0.09	1.23	2.23	2.95	17.53
Perciformes - Bathydraconidae	0.33	0	1.2	7.6	2.88	20.41
Echinoid 2 - Ctenocidaridae	0.41	0.09	1.14	2.29	2.74	23.14
Nudibranchia	0	0.31	1.13	8.57	2.73	25.87
Demosponge 1	0.31	0	1.12	18.91	2.7	28.57
Demosponge 2	0.33	0.13	1.06	1.22	2.56	31.13
Stenolaemate bryozoans	0.29	0	1.04	1.27	2.51	33.64
Demosponge – *Phakellia*	0.38	0.1	1.01	1.7	2.44	36.08
Gymnolaemate bryozoans	0.53	0.26	0.97	1.34	2.33	38.41
Soft coral 1 - Nephtheidae	0.1	0.36	0.93	1.73	2.25	40.65
Sabelleria	0.09	0.32	0.85	1.55	2.05	42.7
Sea pen 1	0	0.23	0.84	1.33	2.02	44.73
Ophiuroidea	0.96	1.18	0.83	2.41	2.01	46.73

Unstalked crinoids (e.g., *Promachocrinus kerguelensis*)	0.2	0.42	0.81	1.32	1.95	48.68
Holothurian 3 - *Bathyplotes gourdoni*	0.23	0	0.8	1.31	1.93	50.61
	LCP2	**LCP3**				
Bottlebrush/bushy corals (e.g., *Thouarella*)	0	0.71	3.63	7.57	7.38	7.38
Decapod shrimps	0	0.51	2.6	19.4	5.28	12.66
Holothurian 1 - *Pseudostichopus mollis*	0.23	0.72	2.5	2.57	5.09	17.75
Holothurian 2 - *Peniagone vignoni*	0.42	0	2.14	7.74	4.35	22.09
Gymnolaemate bryozoans	0	0.3	1.55	8.46	3.15	25.24
Whip corals	0	0.29	1.46	21.9	2.96	28.2
Ophiuroidea	1.16	1.44	1.4	8.15	2.84	31.05
Encrusting lithophilic organisms	0.61	0.88	1.39	1.92	2.82	33.87
Holothurian 3 - *Bathyplotes gourdoni*	0	0.26	1.3	1.33	2.65	36.52
Hexactinellid 1 - *Chonelasma*	0	0.25	1.29	1.29	2.62	39.14
Demospongiae	0	0.25	1.26	1.33	2.56	41.7
Unstalked crinoids (e.g., *Promachocrinus kerguelensis*)	0.22	0.45	1.18	1.28	2.4	44.1
Ascidian 1 - *Pyura* spp.	0	0.22	1.14	1.33	2.31	46.41
Hydrozoan 1 - Rhodaliidae	0.22	0	1.09	1.28	2.22	48.63
Brisingids	0.21	0	1.08	1.33	2.2	50.83
Sites at <350 m depth	**LCP2**	**LCP4**				
Bottlebrush/bushy corals (e.g., *Thouarella*)	0	1.26	5.81	45.29	10.22	10.22
Ascidian 1 - *Pyura* spp.	0	0.6	2.8	6.84	4.93	15.15
Encrusting lithophilic organisms	0.61	1.21	2.8	5.77	4.93	20.07
Hydroid 1	0	0.55	2.55	9.01	4.48	24.56
Holothurian 1 - *Pseudostichopus mollis*	0.23	0.77	2.5	2.56	4.38	28.94
Holothurian 2 - *Peniagone vignoni*	0.42	0	1.94	7.46	3.41	32.35
Whip corals	0	0.39	1.81	4.7	3.18	35.52
Soft coral 1 - Nephtheidae	0	0.36	1.64	8.27	2.88	38.4

Hexactinellida	0	0.33	1.55	17.21	2.72	41.12
Sabelleria	0	0.32	1.47	9.45	2.58	43.7
Echinoid 1 - *Sterechinus antarcticus*	0.28	0	1.31	9.46	2.3	46
Gymnolaemate bryozoans	0	0.26	1.23	1.3	2.15	48.16
Decapod shrimps	0	0.25	1.12	1.32	1.97	50.13
Sites furthest from ice-shelf front	**LCP3**	**LCP4**				
Bottlebrush/bushy corals (e.g., *Thouarella*)	0.71	1.26	2.09	4.18	5.39	5.39
Hydroid 1	0.12	0.55	1.66	2.24	4.27	9.67
Ascidian 1 - *Pyura* spp.	0.22	0.6	1.47	2.21	3.79	13.46
Hexactinellida	0	0.33	1.28	17.82	3.3	16.76
Stalked crinoids (e.g., *Dumetocrinus antarcticus*)	0.33	0	1.28	6.3	3.3	20.07
Encrusting lithophilic organisms	0.88	1.21	1.27	2	3.29	23.36
Sabelleria	0	0.32	1.21	9.99	3.13	26.48
Decapod shrimps	0.51	0.25	1.02	1.28	2.62	29.11
Holothurian 3 - *Bathyplotes gourdoni*	0.26	0	0.98	1.33	2.54	31.65
Ophiuroidea	1.44	1.18	0.97	7.28	2.5	34.15
Hexactinellid 1 - *Chonelasma*	0.25	0	0.96	1.29	2.49	36.64
Scleractinian cup corals (e.g., Flabellidae)	0.64	0.4	0.93	3.06	2.41	39.05
Sea pen 1	0	0.23	0.88	1.33	2.27	41.32
Anemone 1	0.15	0.21	0.83	1.35	2.14	43.45
Echinoid 1 - *Sterechinus antarcticus*	0.21	0	0.82	1.31	2.11	45.56
Nudibranchia	0.09	0.31	0.81	1.52	2.1	47.66
Actiniaria/Corallimorpharia/Ceriantharia	0.22	0.4	0.79	1.23	2.04	49.7
Ascidian 2	0.18	0	0.71	1.33	1.85	51.55

Av. dens. = average density, Av. diss. = average dissimilarity, Diss./SD = dissimilarity/standard deviation, Contrib. = contribution, Cum. contrib. = cumulative contribution.

A2 – Supplementary Material to Chapter 4

Supplementary figures and tables for: Variability in Zoobenthic Blue Carbon across a Southern Polar Gradient.

Frinault B.A.V. and Barnes D.K.A. (2024). *Mar. Environ. Res.*, **199**, 106621.

https://doi.org/10.1016/j.marenvres.2024.106621

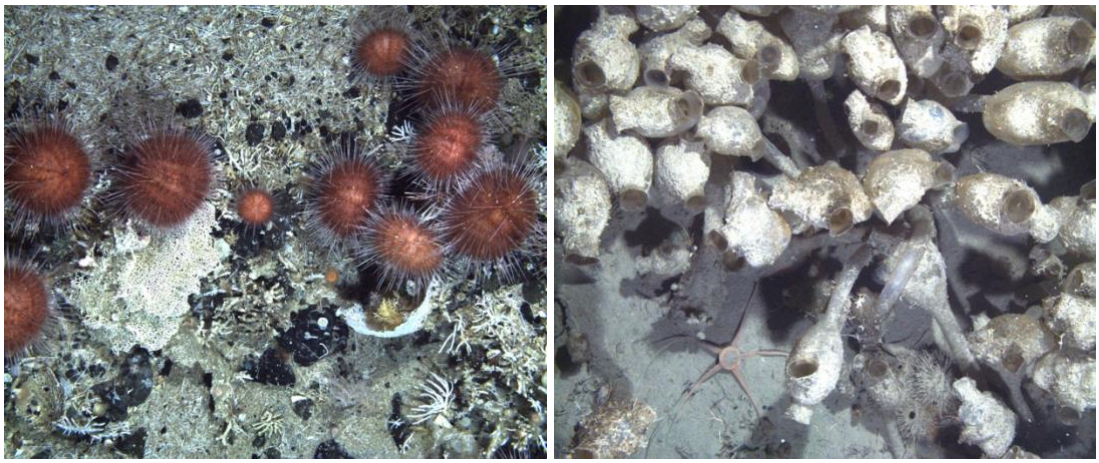


Figure S4.1: Example continental/island shelf images captured by the Shelf Underwater Camera System (SUCS) developed by the British Antarctic Survey Antarctic Marine Engineering Team.

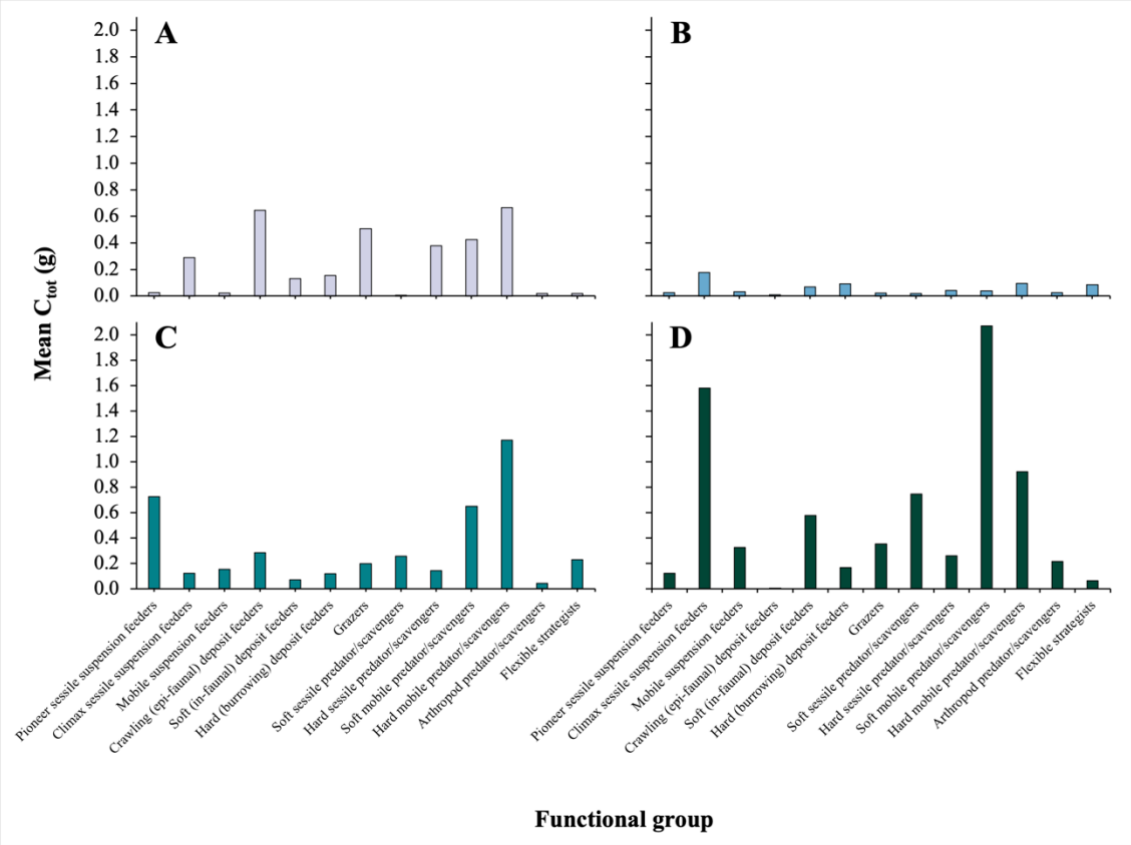


Figure S4.2: Mean total carbon content (C_{tot}; g) of functional groups for four continental/island shelf study areas: (**A**) South Patagonia, specifically the shelf of the Falkland Islands/Islas Malvinas; (**B**) South Georgia; (**C**) Marian Cove of King George Island; and (**D**) an area of the western Antarctic Peninsula near Marguerite Bay.

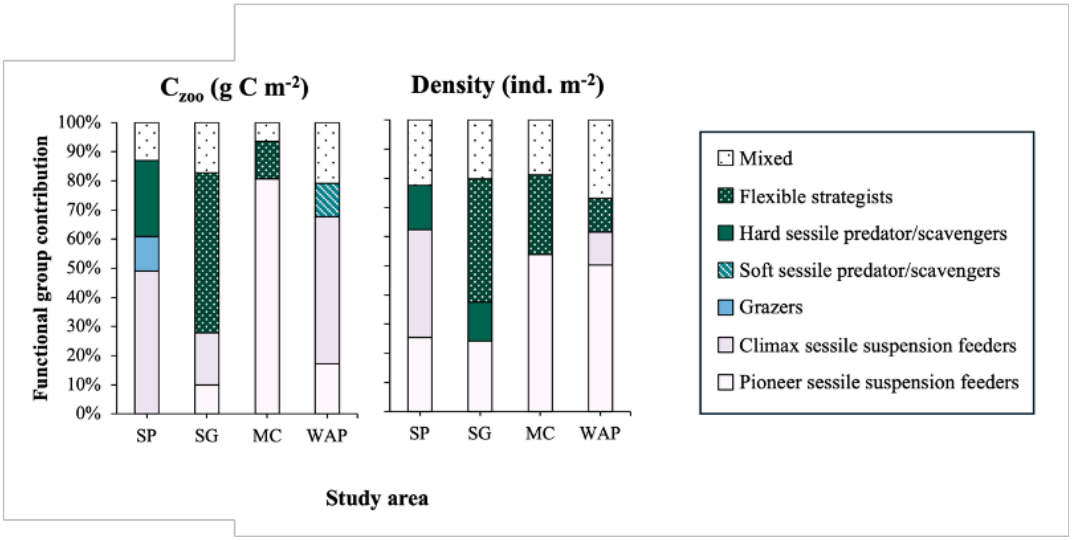


Figure S4.3: Average functional group contribution (%) to zoobenthic carbon storage (C_{zoo}; g C m^{-2}) and faunal density (ind. m^{-2}) for continental/island shelf study areas SP (South Patagonia, specifically the shelf of the Falkland Islands/Islas Malvinas), SG (South Georgia), MC (Marian Cove of King George Island), and WAP (an area of the western Antarctic Peninsula westward of Marguerite Bay and Adelaide Island). Individual functional groups are shown where their contribution was ≥ 10%. Otherwise, groups were pooled with others whose contributions were also < 10% and designated as the "mixed" group.

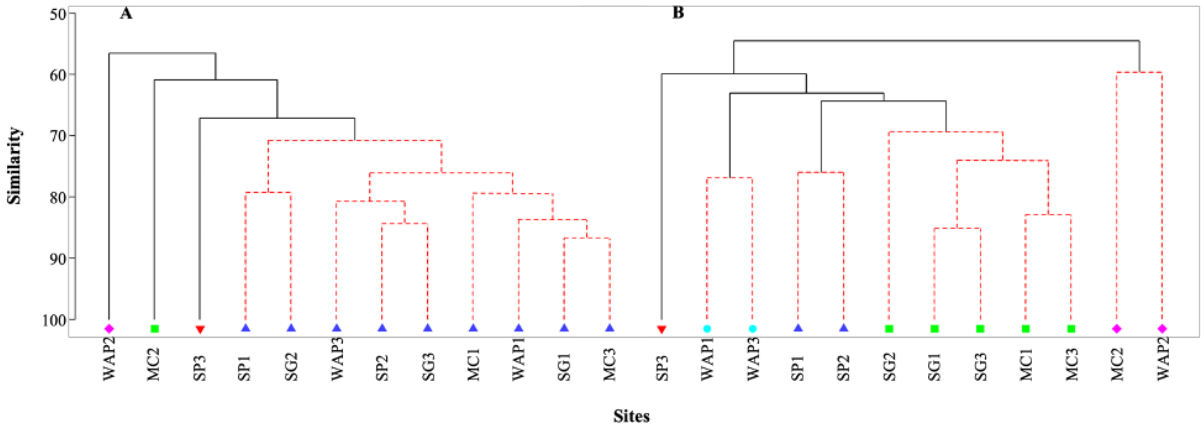


Figure S4.4: Dendrograms resulting from hierarchical agglomerative cluster (HAC) analysis (with a similarity profile [SIMPROF] test) for (**A**) site-level assemblage (structured by functional groups) data and (**B**) site-level carbon storage (by functional groups) data. The HAC analysis was based on Bray-Curtis similarities and group-average linking utilized. Black continuous lines indicate significant clusters, identified by the SIMPROF test, and red dashed lines indicate non-significant clusters.

Table S4.1. Environmental variables used to discern how Scotia Arc study areas and sites differ environmentally. Presented are environmental variables that displayed variation between study areas and sites, with variables showing high correlation (r ≥95%) identified by ✓. Variables used in statistical analyses are presented (**in bold**) and include variables used as a proxy for respective correlates.

Data source	**SUCS**	**Imagery**		**Remote Sensing**					**CTD**				
Environmental variable	**Depth**	**Substratum**	**Rugosity**	Mean SIC	**Mean no. of days sea-ice covered**	Mean daily NPP	**Mean peak NPP**	Mean daily SST	**Near seafloor temperature**	**Salinity**	**Oxygen**	**Chlorophyll-*a***	**Turbidity**
Depth													
Substratum													
Rugosity													
Mean SIC					✓								
Mean no. of days sea-ice covered				✓									
Mean daily NPP							✓						
Mean peak NPP						✓							
Mean daily SST									✓				
Near seafloor temperature								✓					
Salinity													
Oxygen													
Chlorophyll-*a*													
Turbidity													

Table 7: **Table S4.2**: Environmental context of Scotia Arc study areas.

Environmental variable	SP	SG	MC	WAP
Near-seafloor temperature (°C)	7.4 (± 0.1)	2.9 (± 0.1)	0.1 (± 0.2)	1.3 (± 0.1)
Salinity (PSU)	33.4 (± 1.2)	34.1 (± 0.2)	34.3 (± 0.1)	34.7 (± 0.0)
Dissolved oxygen (μmol L^{-1})	277.9 (± 15.1)	249.5 (± 45.4)	346.6 (± 19.8)	177.8 (± 6.3)
Chlorophyll-a (μg L^{-1})	0.21 (± 0.1)	0.04 (± <0.1)	0.03 (± <0.1)	0.02 (± <0.1)
Turbidity (beam transmittance; %)	93.8 (± 2.3)	94.3 (± 3.7)	94.7 (± 2.1)	97.9 (± 0.3)
SIC (%)	0	0	10.1	39.8 (± 1.4)
Daily NPP	383.7 (± 134.3)	345.6 (± 38.61)	300.3 (± 0.2)	389.3 (±36.5)
Peak NPP	1,126.8 (± 548.4)	1,023.5 (± 114.7)	520.4 (± 0.9)	1,019.4 (± 158.0)
Sea surface temperature (°C)	5.8 (±0.4)	1.7 (±0.1)	-0.2 (±0.0)	-0.8 (±0.0)

Means (± 1 SD) are provided for each environmental variable. MC sea-ice data all within one grid cell.

Table S4.3: Similarity percentages (SIMPER) results for assemblage structure (structured by functional groups). Functional groups are ordered according to their average contribution to similarity/dissimilarity within and between groups as defined by hierarchical agglomerative cluster (HAC) analysis with a similarity profile (SIMPROF) test.

Average similarity	Functional group	Av. dens.	Av. sim.	Contrib. (%)	Cum. contrib. (%)
Group D = 75.6	Pioneer ssf	2.31	13.93	18.43	18.43
	Flexible strat	2.03	11.74	15.53	33.96
	Climax ssf	1.7	10.04	13.28	47.24
	Hard sessile pred/scav	1.41	7.91	10.46	57.71

Groups A-C = <2 samples in each group

Average dissimilarity	Functional group	Av. dens.	Av. dens.	Av. diss.	Contrib. (%)	Cum. contrib. (%)
Groups D & C = 32.9	Pioneer ssf	2.31	0.97	5.15	15.65	15.65
	Climax ssf	1.7	0.59	4.26	12.95	28.6
	Mobile sf	0.81	0	3.17	9.63	38.23
	Flexible strat	2.03	1.46	3.13	9.51	47.74
	Grazer	0.93	1.48	3.09	9.4	57.14
Groups D & B = 39.2	Flexible strat	2.03	0	8.21	20.94	20.94
	Soft (in-faunal) df	0.37	1.93	6.49	16.56	37.51
	Hard sessile pred/scav	1.41	0	5.69	14.52	52.03
Groups C & B = 38.5	Pioneer ssf	0.97	2.53	7.06	18.33	18.33
	Flexible strat	1.46	0	6.58	17.07	35.4
	Hard sessile pred/scav	1.35	0	6.1	15.83	51.23
Groups D & A = 44.2	Df crawler	0.26	1.99	7.34	16.6	16.6
	Climax ssf	1.7	0	7.01	15.86	32.46

	Hard sessile pred/scav	1.41	0	5.84	13.22	45.68
	Flexible strat	2.03	1.21	3.82	8.64	54.32
Groups C & A = 38.6	Df crawler	0	1.99	9.21	23.84	23.84
	Grazer	1.48	0	6.88	17.8	41.64
	Hard sessile pred/scav	1.35	0	6.28	16.24	57.88
Groups B & A = 42.2	Df crawler	0	1.99	9.57	22.67	22.67
	Flexible strat	0	1.21	5.85	13.85	36.52
	Soft (in-faunal) df	1.93	0.92	4.85	11.49	48.01
	Climax ssf	0.98	0	4.73	11.21	59.22

Av. dens. = average density (ind. m^{-2}), Av. sim. = average similarity, Av. diss. = average dissimilarity, Contrib. (%) = contribution, and Cum. contrib. (%) = cumulative contribution. Group A = WAP2; Group B = MC2; Group C = SP3; and Group D = SP1-2, SG1-3; MC1, MC3, WAP1, and WAP3. df = deposit feeders; pred/scav = predator/scavengers; sf = suspension feeders; ssf = sessile suspension feeders; and strat = strategists.

Table S4.4: Similarity percentages (SIMPER) results for carbon storage (by functional group) structure. Functional groups are ordered according to their average contribution to similarity/dissimilarity within and between groups as defined by hierarchical agglomerative cluster (HAC) analysis with a similarity profile (SIMPROF) test.

Average similarity	Functional group	Av. dens.	Av. sim.	Contrib. (%)	Cum. contrib. (%)
Group C = 76.0	Hard sessile pred/scav	1.23	16.53	21.76	21.76
	Climax ssf	1.36	13.77	18.13	39.89
	Hard mobile pred/scav	0.89	10.5	13.82	53.71
Groups A = <2 samples in group					
Group D = 74.2	Flexible strat	1.45	16.46	22.19	22.19
	Pioneer ssf	1.45	11.5	15.5	37.69
	Climax ssf	0.91	10.06	13.57	51.26
Group E = 59.7	Pioneer ssf	1.65	13.69	22.94	22.94
	Soft (in-faunal) df	0.9	11.34	19.01	41.95
	Hard mobile pred/scav	0.84	10.96	18.37	60.31
Group B = 76.9	Climax ssf	2.41	18	23.4	23.4
	Pioneer ssf	1.68	9.71	12.62	36.02
	Soft sessile pred/scav	1.54	9.3	12.09	48.1
	Hard sessile pred/scav	1.14	8.63	11.22	59.32

Average dissimilarity	Functional group	Av. dens.	Av. dens.	Av. diss.	Contrib. (%)	Cum. contrib. (%)
Groups C & A = 35.8	Climax ssf	1.36	0.44	6.73	18.83	18.83
	Shelled df	0	0.58	4.5	12.58	31.41
	Grazer	0.68	1.25	4.48	12.52	43.93

	Soft (in-faunal) df	0	0.53	4.11	11.49	55.42
Groups C & D = 35.7	Flexible strat	0.37	1.45	7.59	21.25	21.25
	Pioneer ssf	0.73	1.45	4.89	13.68	34.93
	Hard sessile pred/scav	1.23	0.63	4.16	11.65	46.58
	Climax ssf	1.36	0.91	3.43	9.6	56.18
Groups A & D = 40.4	Pioneer ssf	0.39	1.45	6.72	16.66	16.66
	Grazer	1.25	0.31	6.45	15.98	32.64
	Flexible strat	0.55	1.45	6.12	15.16	47.8
	Climax ssf	0.44	0.91	3.22	7.97	55.77
Groups C & E = 54.7	Hard sessile pred/scav	1.23	0	9.11	16.66	16.66
	Climax ssf	1.36	0.29	7.72	14.13	30.79
	Pioneer ssf	0.73	1.65	6.9	12.62	43.41
	Soft (in-faunal) df	0	0.9	6.71	12.27	55.68
Groups A & E = 46.4	Pioneer ssf	0.39	1.65	9.06	19.52	19.52
	Grazer	1.25	0.17	7.92	17.06	36.58
	Hard sessile pred/scav	1.06	0	7.7	16.59	53.18
Groups D & E = 41.7	Flexible strat	1.45	0.31	7.56	18.11	18.11
	Pioneer ssf	1.45	1.65	5.41	12.96	31.08
	Soft (in-faunal) df	0.25	0.9	4.42	10.59	41.67
	Hard sessile pred/scav	0.63	0	4.22	10.11	51.78
Groups C & B = 38.1	Soft sessile pred/scav	0.26	1.54	6.59	17.29	17.29
	Climax ssf	1.36	2.41	5.61	14.71	31.99

	Pioneer ssf	0.73	1.68	5.06	13.28	45.27
	Soft mobile pred/scav	0.3	1.02	3.82	10.01	55.28
Groups A & B = 43.8	Climax ssf	0.44	2.41	10	22.84	22.84
	Pioneer ssf	0.39	1.68	6.64	15.17	38.01
	Soft sessile pred/scav	0.37	1.54	5.89	13.45	51.46
Groups D & B = 36.4	Climax ssf	0.91	2.41	7.17	19.71	19.71
	Soft sessile pred/scav	0.57	1.54	4.65	12.78	32.48
	Grazer	0.31	1.22	4.42	12.13	44.61
	Pioneer ssf	1.45	1.68	3.69	10.14	54.76
Groups E & B = 44.8	Climax ssf	0.29	2.41	10.58	23.6	23.6
	Hard sessile pred/scav	0	1.14	5.67	12.66	36.26
	Grazer	0.17	1.22	5.34	11.92	48.18
	Soft sessile pred/scav	0.71	1.54	4.09	9.13	57.32

Av. dens. = average density (g C m^{-2}), Av. sim. = average similarity, Av. diss. = average dissimilarity, Contrib. (%) = contribution, and Cum. contrib. (%) = cumulative contribution. Group A = SP3; Group B = WAP1 and WAP3; Group C = SP1-2; Group D = SG1-3, MC1 and MC3; and Group E = MC2 and WAP2. df = deposit feeders; pred/scav = predator/scavengers; sf = suspension feeders; ssf = sessile suspension feeders; and strat = strategists.

A3 – Supplementary Material to Chapter 5

Supplementary figures and tables for: Spatial competition in a global disturbance minimum; the seabed under an Antarctic ice shelf.

Frinault, B.A.V., et al. (2023). *Sci. Tot. Environ.*, **903**, 166157.

https://doi.org/10.1016/j.scitotenv.2023.166157

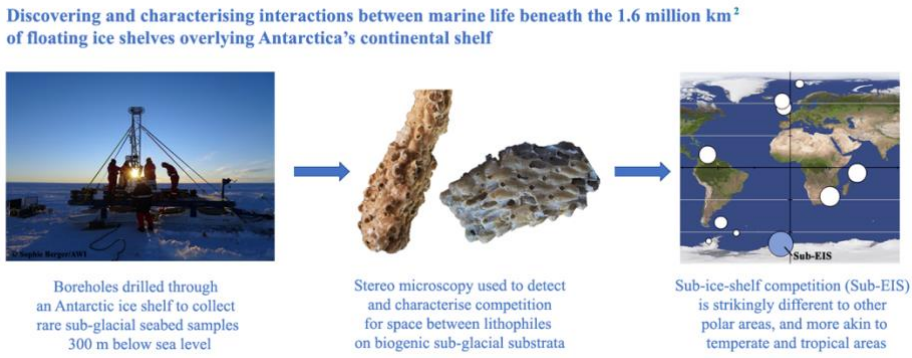


Figure S5.1: Graphical abstract of published research paper corresponding to Chapter 5.

Appendix B: Copies of Published Research Papers

Frinault, B.A.V. et al. (2022). Antarctic Seabed Assemblages in an Ice-Shelf-Adjacent Polynya, Western Weddell Sea. *Biology*, **11**, 1705. https://doi.org/10.3390/biology11121705.

Frinault, B.A.V., Barnes, D.K.A. (2024). Variability in Zoobenthic Blue Carbon Storage across a Southern Polar Gradient. *Mar. Environ. Res.*, **199**, 106621. https://doi.org/10.1016/j.marenvres.2024.106621.

Frinault, B.A.V. et al. (2023). Spatial competition in a global disturbance minimum; the seabed under an Antarctic ice shelf. *Sci. Tot. Environ.*, **903**, 166157. https://doi.org/10.1016/j.scitotenv.2023.166157.

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Article

Antarctic Seabed Assemblages in an Ice-Shelf-Adjacent Polynya, Western Weddell Sea

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Simple Summary: One-third of the Antarctic continental shelf is covered by ice shelves, floating extensions of the Antarctic Ice Sheet. Marine life beneath and bordering ice shelves is rarely investigated, yet likely to be highly impacted by climate change. As ice shelves retreat, marine environments transition into new open-water spaces, with potential for primary production and consequent food-fall to the seafloor. How Antarctic seabed assemblages (benthos) develop in such emerging spaces is influenced by neighboring and oceanographically-connected communities; thus, closing knowledge-gaps of benthic biodiversity near ice shelves underpins understanding of future ecosystem change. This study examined seafloor assemblages, and environmental differences, in a region that has experienced ice-shelf retreat, in a polynya adjacent to a marine margin at the forefront of climate change: the ice-shelf front. The study area, located in the Weddell Sea, is seldom accessible, and lies within a proposed international marine protected area. The study found a physically- and biologically-diverse seabed, complexity in potential environmental influences, and evidence of increasing megafaunal densities with increasing distance from an ice-shelf front. This research provides insights into seafloor habitats and inhabitants close to an evolving marine margin, and establishes ecological baselines from which biological responses to climate change can be evaluated to inform marine management.

Abstract: Ice shelves cover ~1.6 million km^2 of the Antarctic continental shelf and are sensitive indicators of climate change. With ice-shelf retreat, aphotic marine environments transform into new open-water spaces of photo-induced primary production and associated organic matter export to the benthos. Predicting how Antarctic seafloor assemblages may develop following ice-shelf loss requires knowledge of assemblages bordering the ice-shelf margins, which are relatively undocumented. This study investigated seafloor assemblages, by taxa and functional groups, in a coastal polynya adjacent to the Larsen C Ice Shelf front, western Weddell Sea. The study area is rarely accessed, at the frontline of climate change, and located within a CCAMLR-proposed international marine protected area. Four sites, ~1 to 16 km from the ice-shelf front, were explored for megabenthic assemblages, and potential environmental drivers of assemblage structures were assessed. Faunal density increased with distance from the ice shelf, with epifaunal deposit-feeders a surrogate for overall density trends. Faunal richness did not exhibit a significant pattern with distance from the ice shelf and was most variable at sites closest to the ice-shelf front. Faunal assemblages significantly differed in composition among sites, and those nearest to the ice shelf were the most dissimilar; however, ice-shelf proximity did not emerge as a significant driver of assemblage structure. Overall,

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the study found a biologically-diverse and complex seafloor environment close to an ice-shelf front and provides ecological baselines for monitoring benthic ecosystem responses to environmental change, supporting marine management.

Keywords: climate change; ice shelf; continental shelf; coastal polynya; benthic assemblages; benthic biodiversity; functional groups; Larsen C Ice Shelf; Antarctica; Weddell Sea

1. Introduction

Previously long-constant Southern Ocean ecosystems are in transition, with climate change considered the greatest influencer [1,2]. Despite being geographically remote, and partially protected oceanographically by the Antarctic Circumpolar Current (ACC) for ~34 million years [3,4], the cold-water coastal seas of Antarctica are undergoing profound transformations, some of which are climate-linked [5,6]. These environmental transitions are perhaps most conspicuously evidenced by changes in the marine cryosphere (icescape), including areas of sea-ice decline, glacier recession, large iceberg calving and ice-shelf retreat and collapse, particularly in the Antarctic Peninsula and West Antarctic Ice Sheet regions [7–13]. Such ice losses are "blue-ing" the Southern Ocean, potentially opening up areas to new or enhanced primary production, and will likely have wide-ranging implications for Antarctica's varied marine ecosystems, living resources, and ecosystem services over different spatial and temporal scales [6,14–17].

The majority (~95%) of Antarctica's known marine biodiversity is seafloor-dwelling, i.e., benthic [18]. Benthos is a key component of the Southern Ocean ecosystem and food web [19], and is becoming increasingly recognized for its role in ocean health and carbon capture, storage and sequestration [20–23]. Antarctic seabed life (e.g., sponges, corals, brittle stars and feather stars) has evolved in partial isolation, afforded by the ACC (and its role as a barrier to meridional exchange), and relative constancy of physical conditions [1], punctuated by the seaward advance of the Antarctic Ice Sheet (AIS) during glaciations. Where such ice sheet extensions occur as grounded ice, much seafloor life is erased off the continental shelf. In contrast, the warmer interglacial periods are characterized by a comparatively much retreated AIS, and bring intense seasonality of light, sea-ice cover and food availability, and disturbance. Consequently, Southern Ocean seafloor biota is unlike any other, with very high levels of endemism—some taxa having undergone extensive evolutionary radiations (e.g., sea spiders and notothenioid fish) [1,24]. In comparison, other taxa are notably rare or absent (perhaps yet to be detected), such as durophagous (shell-crushing) predators (e.g., crabs and sharks; [25]). Furthermore, many benthic taxa possess specific adaptations and traits, exemplified by antifreeze glycoproteins [24], slow growth and development, and great longevity [1,26]. How such specialized biota and the communities they make up will respond to ongoing and anticipated changes in the Antarctic environment, including to a rapidly changing marine icescape, is, however, not yet clear [6,27–29].

Approximately one-third of Antarctica's extensive (~4.6 million km^2) and deep (mean depth > 450 m) continental shelf is overlain by a unique environment: ice shelves [26]. Ice shelves are the floating extensions of the AIS, often hundreds of meters thick and hundreds of km wide, and inhibit the flow of inland grounded ice into the ocean [13,30–32]. The marine cavities beneath ice shelves (i.e., sub-ice-shelf; between the grounding line and the ice-shelf front) experience aphotic conditions, some for thousands of years, and are arguably the least biologically-explored large-environment on Earth, in part due to challenges of access [33]. Benthic life beneath ice shelves has generally been posited as increasingly depauperate with increasing distance into the cavity [26,34]. This is hypothesized, in part, because sub-ice-shelf benthic communities, in particular the primary consumers, are considered as having some dependency on food supplies laterally advected under the ice shelf from open-water areas, although chemotrophic communities may also be present [35].

However, examples of sessile suspension feeders (e.g., sponges and bryozoans) have been observed as far as 260 km landward of an ice-shelf front, this being in addition to mobile scavengers and predators (e.g., [33,34,36–38]). These faunal observations suggest that such marine spaces are potentially more habitable than previously long-thought.

The remaining two-thirds of Antarctica's continental shelf (~3 million km^2) can be viewed as an "open-water" system, typically with regimes of seasonal sea-ice cover (extended winter sea-surface freezes and summer melts) and primary productivity (phytoplankton blooms) [1]; however, some open-water shelf areas, for example, in the Weddell Sea embayment, can be dominated by multi-year sea ice [39]. Although extensive sampling and knowledge gaps remain [40,41], far more is known about Antarctic open-water continental shelf communities. In this respect, rich and abundant benthic communities have been documented in some areas [42], as well as, more recently, expansive breeding colonies of icefish [43], while in other areas, communities shaped by intense disturbance from iceberg scouring or ploughing [44], and nearby glacier retreat [45] or rapid ice-shelf collapse [35].

Ice-related seafloor disturbance is a major driver of Antarctic shelf community patterns, and the severity and impact of such disturbances can differ over spatial scales, and temporally. For example, while iceberg scouring or ploughing of the seabed can be catastrophic to benthos at local scales, it can also, over time, promote higher regional diversity as mosaics of different faunal successional stages emerge across the seafloor [46–50]. A transfer from an ice-shelf-covered to open-water state, and vice versa, can also represent a disturbance [51], with energy dynamics considerably changing through the introduction of, for example, seasonal fluxes of light, and new occurrences of localized photosynthetic primary productivity [52,53]. Such changes can have implications for depositional and trophic regimes of benthic habitats, hence the structure of resident biotic communities [37,54]. Abrupt ice-shelf retreats, such as those associated with the 2002 disintegration of Larsen B Ice Shelf, eastern Antarctic Peninsula [55], can result in a forfeiture of some species living under the ice shelf, potentially accustomed to sub-ice-shelf environmental conditions. However, such environmental transitions can also create new opportunities for colonization of the seafloor and initiation of recruitment and community successional processes [56].

Following ice-related disturbance, (re)colonization of the Antarctic continental shelf can involve some predictable taxa and assemblage dynamics and, depth-depending, take from just several to hundreds of years for mature communities to (re)establish [46,48,57]. Faunal colonization, recruitment, and succession processes have been predominantly studied in the shallows near established research stations using settlement panels and SCUBA-based photographic surveys (e.g., [4,45,58,59]), and in deeper shelf waters using underwater cameras, towed collection apparatus and sediment cores (e.g., [60–62]). In such studies, the density and composition of proximate, or oceanographically-connected, communities are recognized as important to colonization and recovery patterns. However, temporal investigations of benthic-community dynamics following the retreat of an ice shelf above remain relatively rare, yet nevertheless include, for example, pivotal studies by Fillinger et al. [56] and Gutt et al. [54] at the Larsen Ice Shelf System, eastern Antarctic Peninsula—a region where pronounced ice-shelf loss has been observed over the satellite observation era [9,13,63].

Over the last 50 years, considerable ice-shelf loss has occurred in Antarctica, which is predicted to continue in a warming world. Indeed, a recent study by Gilbert and Kittel [64] has suggested that within this century, one-seventh to over one-third of Antarctica's ice shelves are at risk of destabilization and potential collapse if the global mean atmospheric temperature reaches 1.5 to 4 °C above pre-industrial temperature, respectively. Furthermore, Gilbert and Kittel [64] also identified Larsen C Ice Shelf, once neighbored to the north by the now-collapsed Larsen A and B Ice Shelves, as one of the most at-risk and vulnerable ice shelves in Antarctica. With such future ice-shelf losses projected, it can be anticipated that there will be intensification in disruption to continental shelf environments, ecosystems, and associated biotic communities, particularly near to and underneath

ice shelves, with potential implications for their structure, functioning and carbon sink capacity [20,21,23,44,65].

As a center of ice-shelf loss, and with the regional benthos well-studied by Antarctic standards (e.g., [35,54,56,66–69]), the eastern Antarctic Peninsula is a key region for studying how seafloor communities develop, over time, in response to a transition from once ice-shelf-covered to open-water coastal conditions. The current study explored four continental shelf sites adjacent to the Larsen C Ice Shelf front (a border between sub-ice-shelf and open-water shelf habitats), in an area falling within a proposed marine protected area (MPA): the Weddell Sea MPA (WS-MPA), under consideration by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) [70,71]. All study sites were within an occasionally-present coastal polynya and situated at various distances seaward from the ice-shelf edge, with two sites covered by ice shelf in recent-time. The study aimed to: (1) compare ice-shelf-adjacent benthic habitats and assemblages; (2) determine whether density and richness of benthos alter with distance from an ice-shelf front (and with substratum type), and subsequently discern potential functional group surrogates of the patterns observed (note, a surrogate is herein defined as a taxon that serves as a proxy for wider faunal patterns while not driving them); and (3) identify potential environmental drivers of assemblage structures discerned. A broader goal of the research was to increase understanding of the nature and variability of seabed habitats and life at the ice-shelf margins in areas at the cusp of environmental change. As such, the study provides an ecological baseline of benthic megafaunal structure from which change can be assessed and contributes to the wider understanding of the impact of a changing icescape on the benthos of the Antarctic continental shelf.

2. Materials and Methods

2.1. Study Area and Sites

The Weddell Sea lies within the Atlantic sector of the Southern Ocean. It is a coastal sea bordered by the Antarctic continent, including the Antarctic Peninsula, and the Scotia Arc, and is characterized by a broad and deep continental shelf (maximal depths exceeding 1 km), vast ice shelves, perennially-heavy sea-ice cover [26,39,72], and the presence of the strong cyclonic Weddell Gyre; the latter implicated in the northward transit of icebergs and sea ice along the eastern Antarctic Peninsula [73].

The study area is situated on the inner continental shelf of the western Weddell Sea adjacent to the northeast sector of the Larsen C Ice Shelf (maximum width ~200 km and thickness of ice front ~200 m) [63,74], between Jason Peninsula and Bawden Ice Rise (Figure 1). It is within CCAMLR Statistical Subarea 48.5 and MPA Planning Domain 3, and proposed WS-MPA [70,71]. Associated fieldwork was carried out in January and February 2019 (austral summer 2018/19) aboard the South African polar supply and research vessel *SA Agulhas II* (IMO: 9577135), as part of the Weddell Sea Expedition 2019 data collection program [75]. At the time of sampling, study sites were located within the intermittent and wind-driven Larsen C Ice Shelf Polynya (LCP), averaging, when present, an open-water area of ~4700 km^2 for 128 days per annum (pa), with phytoplankton blooms for 69 days pa [74]; the area is otherwise covered in first- to multi-year sea ice up to 5 m thick [39]. Benthic megafaunal assemblages were investigated at four sites, LCP1-4 (Table 1), situated at various distances from the nearest ice-shelf front, i.e., coastline (ranging from <1 to ~16 km, and labeled accordingly, with LCP1 being closest to the ice shelf and LCP4 farthest away). The sites were located on either side of the glacially-deepened Jason Trough [76–78]. LCP1 was the most southerly site, close to Bawden Ice Rise, and LCP2-4 were located north of Jason Trough, near Cape Framnes at the tip of Jason Peninsula. Sites were 15 to 75 km apart (Table S1), with LCP1 (the Bawden Ice Rise site) situated between ~57 to 75 km south of the Jason Peninsula sites, the latter all within ~19 km of each other. Sites were of depths ranging from ~300 to 400 m. At the time of sampling, a large tabular iceberg (A-68) was pivoting towards the study zone (see Figure 6A in Dowdeswell et al. [39]), in part shielding the area from the influx of sea ice and enabling vessel access.

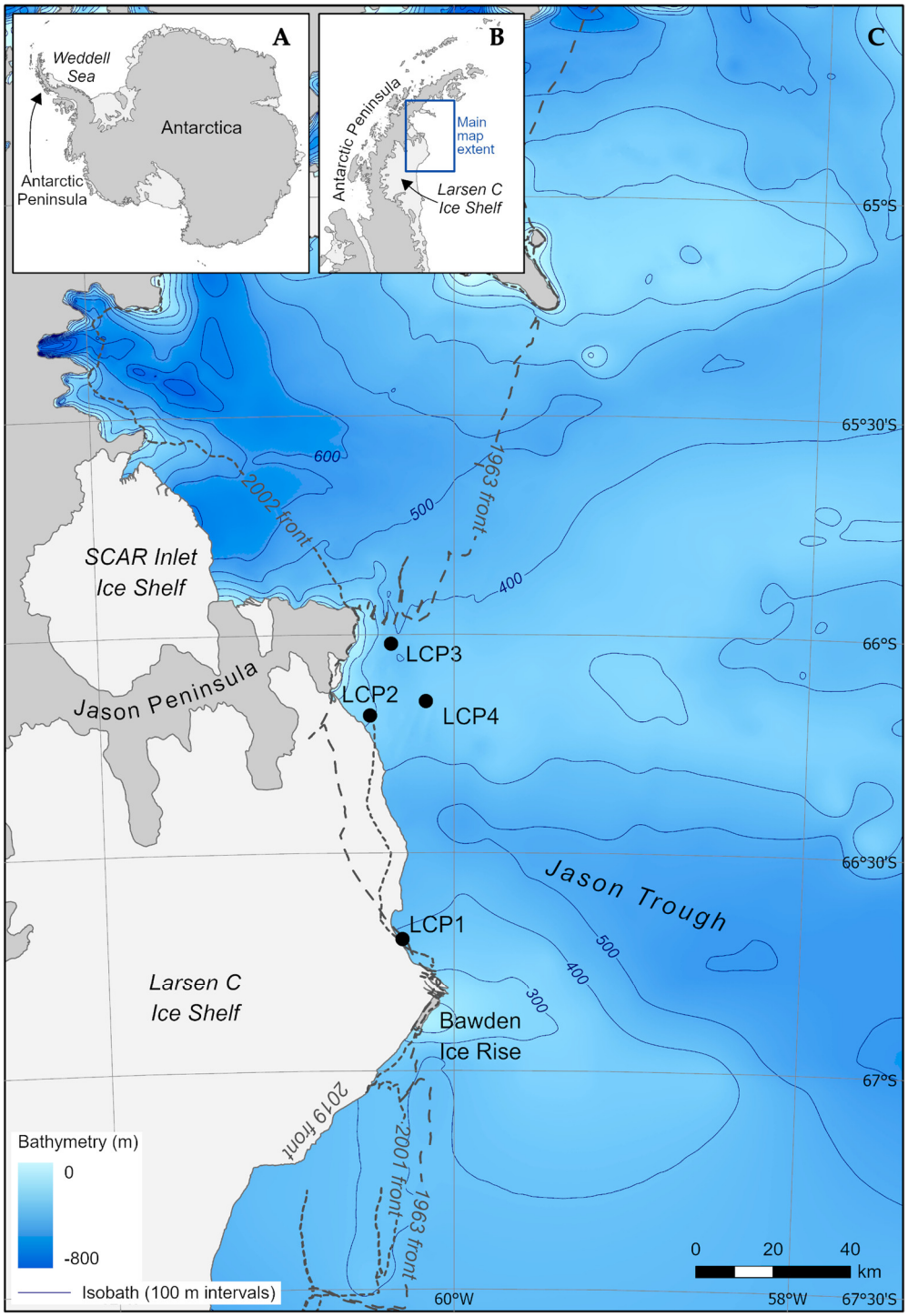


Figure 1. Study zone and sites. Inset (**A**) Antarctica indicating the Antarctic Peninsula and Weddell Sea; inset (**B**) Antarctic Peninsula indicating Larsen C Ice Shelf and the extent of the main map; and (**C**) main map of western Weddell Sea study area, showing the modern-day (2019) ice front and the locations of continental shelf study sites, LCP1-4 (black circles), investigated for benthic megafaunal assemblages. Light gray indicates ice shelves and darker gray indicates ice-covered land/grounded ice. Bathymetry is from the International Bathymetry Chart of the Southern Ocean v2 [79], with 100 m contours. The ice-shelf fronts are from Cook and Vaughan [9], Cook et al. [80] and Christie et al. [81].

Table 1. Western Weddell Sea continental shelf study sites, LCP1-4, investigated for benthic megafaunal assemblages, including date(s) sampled (seafloor imagery collection), position in decimal degrees latitude (°S) and longitude (°W), and water depth (m) (all means across associated seafloor imagery), and distance from the ice-shelf front at the time of sampling (m).

Site	Date(s) Sampled	Latitude (°S)	Longitude (°W)	Water Depth (m) [1]	Distance from Ice-Shelf Front (m) [2]
LCP1—Bawden Ice Rise	21–22 January 2019	−66.6975	−60.2981	397	777
LCP2—Jason Peninsula	20 January 2019	−66.1868	−60.4742	299	2752
LCP3—Jason Peninsula	14 January 2019	−66.0219	−60.3526	400	9024
LCP4—Jason Peninsula	23 January 2019	−66.1544	−60.1594	349	16,459

[1] Measured during sampling by high-precision acoustic positioning system (Section 2.3). [2] Calculated following sampling using Vector Analysis Tools in QGIS v3.16.6.

2.2. Collation of Environmental Data Used in the Study

To discern how sites differed environmentally, and to help identify environmental variables potentially responsible for structuring megabenthic assemblages, various environmental datasets (remotely sensed, collected in situ and seafloor-imagery-derived) were used.

Ice-shelf cover and ice-shelf front proximity. The distance of each site from the nearest ice-shelf front, at the time of sampling, was calculated using Vector Analysis Tools in QGIS (see Table 1), and employed in the same way as distance from a coastline (or glacier front) is utilized (e.g., [42,82,83]). Historical areal extent and ice-shelf front positions of Larsen C (and its environs), available from 1963 onwards (with annual observations from 2009), were obtained from several published satellite-based datasets [9,80,81,84–87]. These datasets were used to estimate for each site for the 1963–2018 observation period, the number of years ice-shelf covered (or open water), the number of years since last covered by ice shelf, and when ice-shelf retreats occurred.

Sea-ice concentration. Mean monthly sea-ice concentration (SIC; %) data, spanning 1979 to 2019 and derived from Nimbus-7 SMMR and DMSP SSM/I-SSMIS passive microwave observations [88], were obtained from the US National Snow and Ice Data Center. These records have a grid cell resolution of 25 × 25-km^2 and were processed in the same manner as described by Christie et al. [13]. Using this data, mean SIC was calculated for each site for the 1997–2018 period, complementing available primary production data.

Primary productivity. Mean daily net primary production (NPP; mg C m^{-2} day^{-1}) data, spanning 1997 to 2018, were generated following the methods of Arrigo et al. [74,89]. From such data, both mean daily NPP and mean peak NPP were calculated for each site for the 1997–2018 period.

Oceanography. Oceanographical data were acquired by deployment of a CTD (conductivity-temperature-depth) system (Sea-Bird Scientific SBE 911plus), which included auxiliary sensors (e.g., oxygen and photosynthetically active radiation; PAR) and a rosette of 24 12-L Niskin bottles enabling collection of water samples (see Hutchinson et al. [90] and Flynn et al. [91]). The CTD was deployed from the sea surface to within 10 m of the seafloor at 19 stations in the study area. Measurements of temperature, salinity (from conductivity), and dissolved oxygen (to which a correction was applied, see [90]) were obtained, and from associated water samples, an array of nutrient concentrations determined (see [91]). For each site, data from the nearest CTD station were used, and associated measurements depth-matched wherever possible to the imagery; otherwise, the bottom-most measurements were utilized. CTD variables that varied negligibly between sites, including, for example, turbidity and PAR, were not included in further analyses, with those remaining given in Table S3.

Substratum and phytodetritus. Both substratum type (hardness) and level of phytodetritus cover were determined during seafloor imagery analysis (Section 2.5).

2.3. Seafloor Imagery Collection

At each site, three seafloor video-transects were conducted using a remotely operated vehicle (ROV) (EGI GP-50 Work Class; Eclipse Group Inc., Annapolis, MD, USA) (piloted by Eclipse Group Inc. and supported by Deep Ocean Search Ltd. and Ocean In-finity Inc.) equipped with a high-definition (HD) 1080i/29.97 fps color video camera (DSP&L HD Zoom SeaCam; DeepSea Inc., San Diego, CA, USA); the camera was forward-facing and angled obliquely towards the seabed. The ROV was fitted with two red parallel scaling lasers (DSP&L Micro SeaLaser; DeepSea Inc.), 10 cm apart, and six lights (DSP&L LED SeaLite; DeepSea Inc.). During dives, the three-dimensional position (i.e., latitude, longitude and depth) of the ROV was provided by a high-precision acoustic positioning system (Kongsberg HiPAP 502; Kongsberg, Norway). Videos were time-stamped, enabling the pairing of observations with positional data. Mean transect length was 847 m and depth within transects varied by <15 m.

2.4. Post-Processing of Collected Imagery

Raw transect videos (three per study site, 12 in total) were de-interlaced in HandBrake 1.3.3 (www.handbrake.fr, accessed on 15 June 2022), an open-source video transcoder. Frames were extracted from re-encoded videos every 20 s to avoid spatial overlap between successive frames. Frames not viable for analysis (e.g., too high above the seafloor, significantly obscured by sediment kick-up and/or laser points non-discernible) were discarded, the mean discard rate being ~25%. A 250 m sample was taken from each transect for analysis (and standardized to 100 m^2 for richness calculations). Examples of seafloor imagery from the study are provided in Figure S1.

2.5. Frame Analysis and Assignments

As per Jones et al. [92], video frame appraisal methodologies were identical to those of still photographs. Frames were analyzed using the web-based imagery annotation tool BIIGLE 2.0 (www.biigle.de, accessed on 15 June 2022) [93]. Analysis was restricted to the lower-half of each frame (below the laser points), and frames were examined in random order. For each frame, all discernible epibenthic megafauna were annotated (hence counted) and identified to the highest taxonomic resolution possible or assigned a practicable morphotaxon/operational taxonomic unit (with taxonomic specialists and literature consulted, as appropriate, during the appraisal process). Substratum type was categorized as soft (i.e., mud or sand), assorted hard (varied coarse grain sizes from pebble to boulder (with soft sediment interstices)), boulder, or mixed sediment; the latter a ~50:50 mixture of soft and hard sediment. At sample-level, where frames became aggregated, substratum type assignment was based on the two most dominant substratum categories and then converted to a scale of "hardness" from 1–6 (1 being the softest substratum and 6 the hardest) (Table S2). The level of phytodetritus cover (indicated by a greenish layer on the seafloor) was recorded on a scale of 1–5 (1 being the lowest cover and 5 the highest). Laser points were marked and used to calculate the width of the field of view at the laser line, enabling computation of the seafloor area analyzed (mean of 2.2 m^2 per frame). To provide further ecological context to the megabenthic diversity observed, and also to potentially identify ecological proxies to facilitate future monitoring, a functional group (one of 14; see Table 2), based on functional traits of feeding-strategy, mobility, and "skeletisation", was ascribed to each morphotaxon; groups being adapted from Barnes and Sands [94] and Barnes et al. [95]. For each frame and sample, epibenthic megafauna and functional group counts were converted into densities, i.e., individuals per m^2 (ind. m^{-2}).

Table 2. Functional group categories (based on [94,95]) and example taxa discerned in Larsen C Ice Shelf Polynya (current study).

Functional Group	Example Taxa
Deposit-feeding crawlers (epifaunal)	Holothurians
Soft infaunal deposit-feeders	None discerned
Hard burrowing deposit-feeders	Irregular echinoids
Flexible strategists	Ophiuroids
Grazers	Regular echinoids
Soft sessile predator/scavengers [1]	Pennatulaceans, soft corals, anemones (actiniarians), hydroids
Hard sessile predator/scavengers [1]	Scleractinian corals, calcaxonian whips, hydrocorals
Soft mobile predator/scavengers	Nemerteans, nudibranchs, octopi
Hard mobile predator/scavengers	Fish, gastropods, asteroids
Arthropod predator/scavengers	Pycnogonids, decapod shrimps
Pioneer sessile suspension feeders	Encrusting bryozoans, ascidians, some polychaetes
Climax sessile suspension feeders	Demosponges, hexactinellids, brachiopods, some bryozoans
Sedentary suspension feeders	None discerned
Mobile suspension feeders	Crinoids

[1] Can also be considered as "active and passive filter feeders" (see [96,97]).

2.6. Statistical Analyses to Explore Biotic Differences and Potential Environmental Drivers

Statistical analysis comprised calculations of univariate indices, including the total number of morphotaxa (richness), as well as the application of multivariate statistical techniques in PRIMER v7 [98] with PERMANOVA+ add-on [99].

Prior to multivariate analysis, and adopting established procedures (see [98,100]; and references therein), environmental variables that displayed right-skewed distributions were log-transformed, and collinearity between variables was assessed using Draftsman plots. Of those variables that were highly correlated (or anticorrelated) ($r \geq 95\%$ (or $\leq -95\%$)), one variable was retained, acting as a proxy for the other(s) (Table S3). The remaining environmental variables were normalized to provide a common (dimensionless) scale for analysis. The megafaunal density data were fourth-root transformed to give more weight to rarer taxa and less weight to more dominant taxa [101].

The Bray–Curtis similarity coefficient [102] was used to evaluate compositional similarities of faunal assemblages within and between sites (based on the transformed faunal data), generating a resemblance matrix. Hierarchical (group-average) agglomerative clustering (HAC) analysis [103], based on Bray–Curtis similarities, was performed with a similarity profile (SIMPROF) test to visualize and assess the structure of the biological data, clustering the data into groups previously undefined and allowing for significant clusters to be identified [104]. The similarity percentages (SIMPER) routine [105] was employed to: (i) quantify the contribution of each morphotaxon to the average compositional similarity of samples within the SIMPROF-defined groups (in this case, groups = sites), i.e., identifying morphotaxa "typifying" groups; and (ii) quantify the contribution of each morphotaxon to the average compositional dissimilarity between groups, i.e., identifying morphotaxa "discriminating" among groups. Additionally, and also using Bray–Curtis similarities, a non-metric multidimensional scaling (nMDS) ordination [106] was used to visualize the compositional similarity of samples.

For the normalized environmental data, a resemblance matrix, based on Euclidean distance, was generated and used in a principal component analysis (PCA) [107]. The PCA was undertaken to visualize patterns in the environmental data across sites (and samples) and provide a preliminary indication of which variables may be influencing assemblage structures. In addition, the BEST (Bio-Env) routine, employing the Spearman's rank correlation coefficient and including a global BEST test (999 random permutations) [104,108], was used to identify which subset of environmental variables best matched (or "explained") the observed biotic patterns (i.e., assemblage structures), and to test the statistical significance of the match. Note, the procedure uses biological resemblance and normalized-environmental data matrices (and applies Euclidean distance to the latter during the process).

The statistical processes were also conducted for the functional group-based classification.

3. Results

3.1. Seafloor Habitat of the Study Area—Observations and Features

Across and within the study sites, the seafloor varied considerably in terms of rugosity (roughness) and dominant substratum type. Expanses of poorly-sorted coarse-grained (pebbles to boulders) substratum were particularly prominent at site LCP2, closest to Jason Peninsula. Such material appeared similar to that observed northward along the Larsen A Ice Shelf front [109]; indeed, the angularity and separateness of the boulders, in particular, suggested presence of supraglacially-derived ice-rafted debris [77].

Recent iceberg-scouring, such as that observed by Gutt and Piepenburg [49] and Gutt et al. [54] via ROV, was not evident in the imagery, although relatively wide and deep furrows were observed in the seabed at the two shallower sites, LCP2 and LCP4 (both <350 m deep).

Phytodetritus cover of the seafloor, indicative of potential "food banks" [110,111], was heaviest at the sites farthest offshore (i.e., LCP3 and LCP4), with lighter cover observed at the sites closest to the ice shelf, LCP1 and LCP2 (both within 3 km of Larsen C).

Circular/elliptic seabed depressions (~10 to 25 cm in diameter) were observed at each study site. These depressions appeared individually and in clusters, with more and larger clusters observed at the shallower sites, LCP2 and LCP4.

Very similar to the documented video-derived observations of Domack et al. [35] and Niemann et al. [112] of the continental shelf of the Larsen B embayment, potential chemotrophic habitats were observed. Such habitats presented as shallow indentations in the seabed (~0.75 to 2.5 m across) with soft sediment within (i.e., mud/sand), and were occasionally edged by bedrock. These habitats are likely inactive or low-activity cold seeps, evidenced by a faunistic legacy of *Calyptogena*-like shells and weedy worm-tubes (possibly Siboglinidae; see [113]), and the occurrence of potential bacterial mats within or around the features. Such chemotrophic habitats were observed at sites with the most contrasting ice-shelf-cover history, LCP1 and LCP4 (see Section 3.2), although further examples may have been camouflaged across the study area by sedimentation.

Across the study sites, biota, and associated functional groups, were, at times, highly variable in terms of abundance, diversity and composition—indicating a degree of faunal patchiness. Some areas could be depauperate, with little or no perceptible biota, or comparatively dominated by a particular taxon or functional group (e.g., corals and ophiuroids). In contrast, other areas could host multiple encrusting fauna (e.g., ascidians, sponges and pioneering bryozoans) on hard substratum (mainly larger rocks and boulders). Giant predatory and suspension-feeding asteroids, e.g., *Perknaster* sp. and brisingids, respectively, were observed in higher numbers at LCP2, the latter consistently on large boulders (potentially glacial dropstones). Instances of commensalism were evident throughout much of the study area, including, for example, crinoids and ophiuroids on top of corals or large sponges [114].

3.2. Environmental Differences Determined from Remotely-Sensed Data

Ice-shelf cover and ice-shelf front proximity. Observations of changing areal extent of Larsen C throughout the satellite era revealed varying degrees of ice-shelf cover over the study sites. Specifically, it was found that LCP1 and LCP2 had intermittently been covered by ice shelf in the observation period (1963–2018), consistent with the natural advance and calving of small icebergs along this particular stretch of the Larsen C front through time [9,13]. LCP1 and LCP2 were last ice-shelf-covered around 2009 and 2003, i.e., 10 and 16 years prior to sampling, respectively. It was observed that LCP1 had experienced (at least) two retreats, remained in close proximity (<1 to ~3 km) to the Larsen C ice-shelf front, and was ice-shelf-covered for (at least) two separate periods totaling 23 years (of the 56 years of observations). LCP2 also experienced two retreats and was covered for two distinct periods (totaling 7 years), and was proximate to Larsen C from the 1990s onwards. In contrast, LCP3 and LCP4 were free of ice-shelf cover throughout the observation period [13], and possibly for longer [115]. LCP3 was, in certain years, notably close to the Larsen B

Ice Shelf margin (e.g., in 1968, 1986, and 1993), whereas LCP4 was comparatively (and consistently) distant from any ice-shelf fronts.

Sea-ice concentration. Mean monthly SIC (±1 SD), for the 1997–2018 period, was lowest at LCP1 (65.1% (±22.7)) and highest at LCP2-4 (69.6% (±25.7)). The low SIC values observed are indicative of the presence of the polynya.

Primary productivity. Mean daily NPP and mean peak NPP, for the 1997–2018 period, were highest at LCP4 and showed a significant increase with increasing distance from the ice-shelf front (regression-associated ANOVAs, R^2 = 0.93 and 0.94, F = 129.37 and 152.16, respectively, with both p-values < 0.001). For LCP1-4, the mean daily NPP values (±1 SD) were 123.5 (±202.8), 165.9 (±226.4), 199.4 (±245.2), and 243.8 (±309.3) mg C m^{-2} d^{-1}, respectively, and mean peak NPP values (±1 SD) 264.5 (±329.7), 372.6 (±207.7), 435.4 (± 309.5), and 791.7 (±552.9) mg C m^{-2} d^{-1}, respectively.

3.3. Megafaunal Richness: Accumulation with Area, and Pattern with Ice-Shelf Proximity and Substratum Hardness

Overall, a total of 98 morphotaxa from 23 classes of 10 phyla were observed across the study zone.

The relationship between richness and area surveyed was examined at each site and compared to determine if megafaunal richness accumulated differently across sites. As expected, faunal richness increased from the area of a single frame to a sample (mean 165.7 m^2), the latter peaking at 32 morphotaxa (Figure 2). The lowest intercept and most gradual slope (indicative of richness accumulation) were at LCP2, equating to half the level of richness observed at LCP1 and LCP4 (the sites closest to and farthest from the ice-shelf edge, respectively). LCP1 and LCP4 were not significantly different in terms of richness accumulation (p > 0.2), while all other pairwise comparisons indicated slopes to be significantly different.

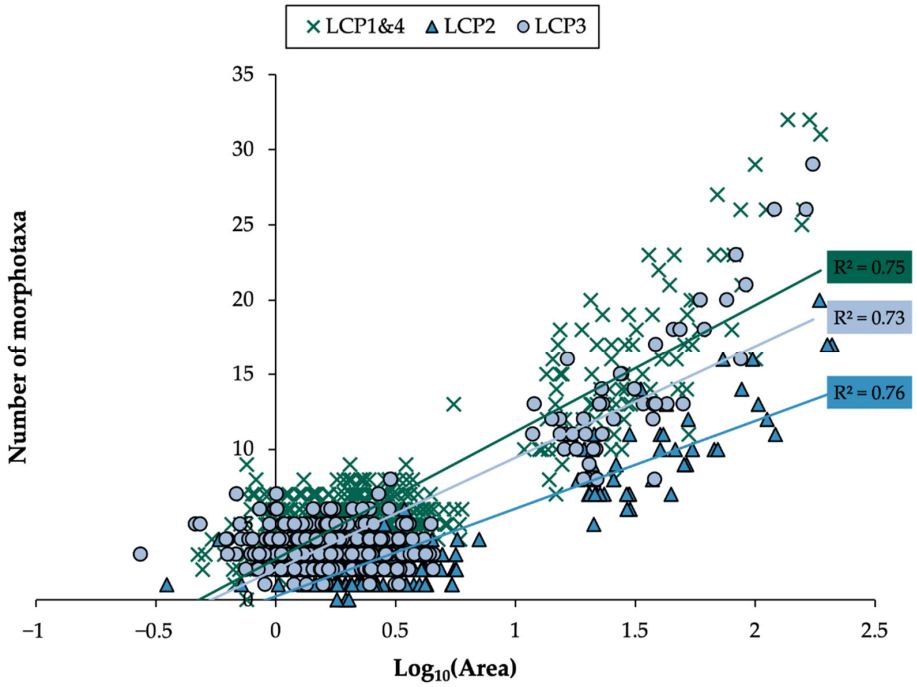


Figure 2. Ice-shelf-adjacent sites accumulate faunal richness differently. Morphotaxa richness with area surveyed for sites LCP1-4 (note, slopes for LCP1 and LCP4 were not significantly different from each other, p > 0.2, therefore, datasets pooled). Significantly different slopes are shown (p-values for differences between slopes all <0.01). For regression lines, F-values = 1546.39, 767.44, and 930.35, for LCP1 and LCP4 combined, LCP2, and LCP3, respectively, with p-values all <0.001.

Larger areas increasingly accumulated the less abundant and rarer morphotaxa (e.g., particular sponges, asteroids, anthozoans, ascidians, and brachiopods), including "singletons" (morphotaxa that only appeared once), and this mainly drove the increased richness observed at LCP1 and LCP4, with different taxa contributing to the morphotaxa count of each site.

When comparing standardized 100 m^2 samples (three per site), the lowest richness was observed in an LCP2 sample and the highest in an LCP4 sample, with 11 and 31 morphotaxa recorded, respectively. An LCP1 sample exhibited the second-highest richness at 27 different morphotaxa. The richness of LCP4 samples was varied, with the value of one sample being almost double of another (16 and 31), whereas the richness of LCP3 samples was noticeably more uniform (23, 24 and 25). Marked variability in richness was found at the sites closest to the ice-shelf front, with richness more than doubling from the poorest to richest sample (11 and 27).

In terms of a relationship with proximity to the ice shelf, richness did not significantly alter with increasing distance from the ice-shelf front (regression-associated ANOVA, $F = 1.0$, $p = 0.33$). However, when LCP1 samples were excluded from the exploration, as they were located within a different water mass (see [90]), the relationship became more robust although remained non-significant (R^2 value = 0.4, and regression-associated ANOVA, $F = 4.6$, $p = 0.06$).

Overall, a weak (inverse) relationship was observed between richness and "hardness" of substratum (Figure S2, $F = 6.59$, $p = 0.03$), although richness did halve from predominantly soft-sedimented (with incidences of mixed) substratum through to assorted hard sediment-boulder fields.

3.4. Megafaunal Density and Pattern with Ice-Shelf Proximity and Substratum Hardness

Across samples, mean benthic megafaunal density varied by nearly an order of magnitude, from 2.5 to 9.7 ind. m^{-2} (see y-axis of Figure 3). The lowest densities were typically found at LCP2 (all three samples observed to be faunally depauperate) and the highest densities generally at LCP4; although, at LCP1, closest to the ice-shelf edge, faunal densities could also be high, although more variable. When considered together, the two sites nearest to the ice shelf were more variable in terms of faunal density than the two sites farthest away.

With increasing distance from the ice-shelf front, it was observed that density generally increased (regression-associated ANOVA, $R^2 = 0.35$, $F = 5.39$, $p = 0.04$). To control for water mass differences, this trend was also explored without LCP1, where it became more significant (Figure 3, regression-associated ANOVA, $F = 43.3$, $p < 0.01$).

The general relationship of increased faunal density from the ice-shelf front to farther offshore was principally caused by increases in densities of bottlebrush corals (e.g., Primnoidae, including *Thouarella* spp.), ophiuroids (e.g., *Ophionotus*) and encrusting lithophilic fauna (e.g., pioneering bryozoans, ascidians and sponges). Bottlebrush corals and encrusting fauna mainly drove the high variability in density and occasionally high values at LCP1.

The nature of the substratum also appeared to influence faunal densities, with faunal density significantly decreasing with increasing substrate hardness (Figure 4, regression-associated ANOVA, $F = 13.7$, $p < 0.01$). The lowest density values were observed in the samples categorized as having the "hardest" substratum type. This trend was principally driven by decreased densities across the majority of faunal groups at LCP2 (closest to Jason Peninsula), but particularly in encrusting suspension feeders, and the apparent absence of certain taxa, including bottlebrush corals (see Section 3.6).

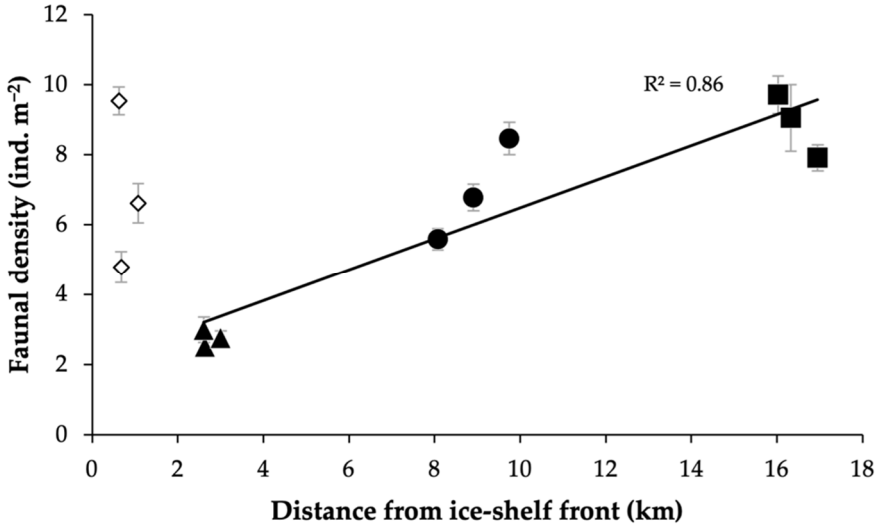


Figure 3. Megafaunal density generally increases with distance from the ice shelf. Mean benthic megafaunal density (ind. m^{-2}) (±SE) of each sample (three per site) with distance from the ice-shelf front (km). Mean density (±SE) calculated for each sample using associated frames (minimum of 44 frames per data point). Site LCP1 = diamonds, LCP2 = triangles, LCP3 = circles, and LCP4 = squares. Symbols filled in white excluded from regression statistics (hence trend-line generation) (owing to water mass differences, see [90]).

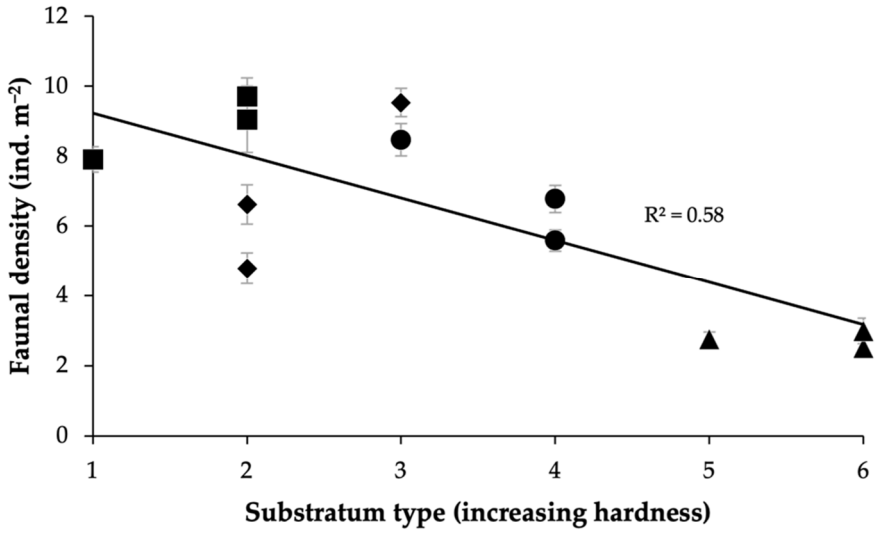


Figure 4. Megafaunal density generally decreases with increasing hardness of the substratum. Mean faunal densities (ind. m^{-2}) (± SE) of samples with substratum type (scale of increasing hardness from left to right), where 1 = soft-sediment: mixed; 2 = mixed: soft-sediment; 3 = mixed: boulder; 4 = assorted hard: mixed; 5 = assorted hard: boulder/mixed; and 6 = assorted hard: boulder. Site LCP1 = diamonds, LCP2 = triangles, LCP3 = circles, and LCP4 = squares.

3.5. Functional Group Richness and Density Patterns with Ice-Shelf Proximity and Substratum Hardness, and Potential Surrogacy of Wider Faunal Patterns

Of the 14 functional groups (Table 2), 12 were represented by the fauna discerned in the imagery. Whether such functional groups reflected taxonomic patterns in richness and overall density was assessed.

With respect to richness, functional group richness, like morphotaxa richness, did not significantly change with increasing distance from the ice-shelf front, including when removing groups represented by singletons (both p-values > 0.3). However, in contrast,

functional group richness did not exhibit a relationship with substratum hardness, including when removing singleton groups (both p-values > 0.7).

As with taxonomic groups, the density of some functional groups altered with distance from the ice shelf. Deposit-feeding crawlers (all holothurians), pioneer sessile suspension feeders (primarily encrusting lithophiles) and hard sessile predator/scavengers (principally bottlebrush corals) all showed similar patterns to the overall faunal trend (Figure 5A–C); this including high densities at LCP1 (cf. Figure 3). In contrast, grazers and hard deposit-feeders (both groups predominantly echinoids) showed high densities at LCP1 and no trend with increased distance away from the ice shelf (Figure 5D,E). Some fauna, such as soft sessile predator/scavengers (primarily anemones), increased in density with distance from the ice shelf (Figure 5F) and did not display high densities at LCP1 (hence, differed from the overall faunal pattern).

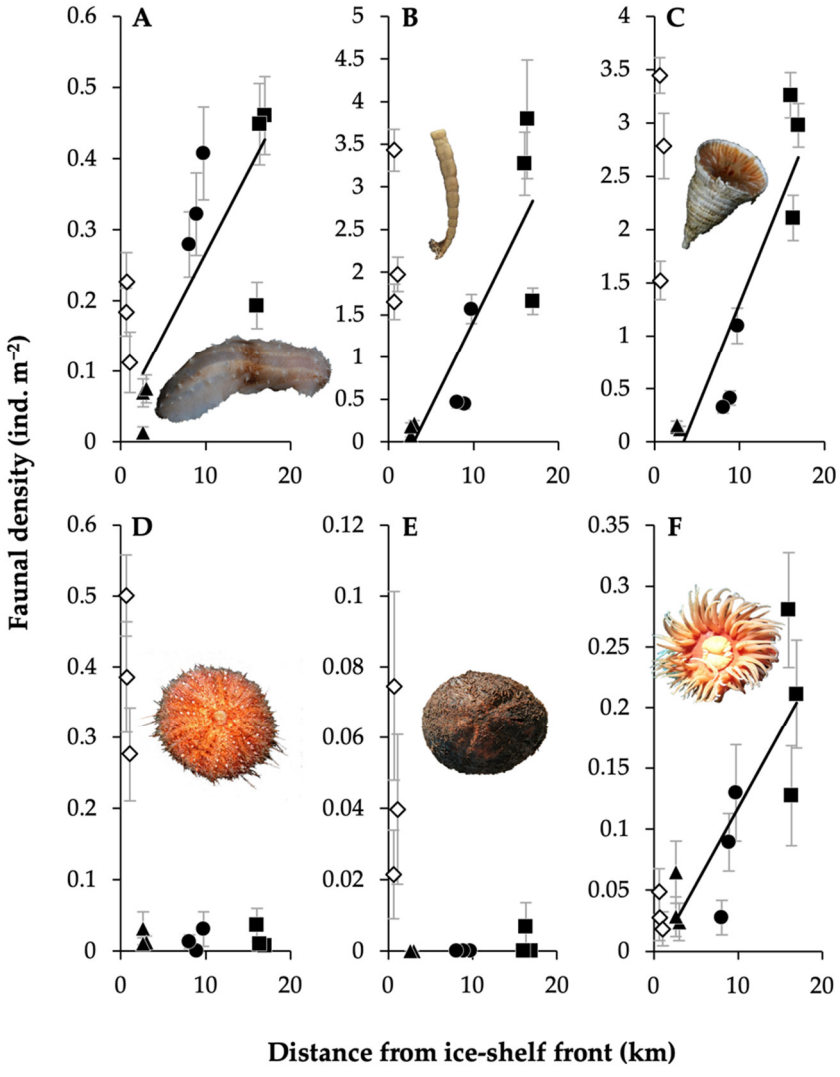


Figure 5. Functional group densities can alter differently relative to ice-shelf proximity. Mean functional group densities (ind. m^{-2}) (±SE) of samples with distance from the ice-shelf front (km), with an example taxon for each group (images provided by D.K.A.B.): (**A**) deposit-feeding crawlers; (**B**) pioneer sessile suspension feeders; (**C**) hard sessile predator/scavengers; (**D**) grazers; (**E**) hard deposit-feeders; and (**F**) soft sessile predator/scavengers. Site LCP1 = diamonds, LCP2 = triangles, LCP3 = circles, and LCP4 = squares; white-filled symbols indicate (due to water mass disparities, see [90]) data not included in trend-line generation. R^2 values for (**A**–**C**,**F**) = 0.63, 0.85, 0.74 and 0.70, respectively, and regression statistics indicated all associated p-values $\leq$ 0.01.

With regard to substratum type, deposit-feeding crawlers, hard sessile predator/scavengers, and pioneer sessile suspension feeders, like the overall fauna pattern, decreased in density with increased substratum hardness (regression-associated ANOVAs, F = 7.4, 19.88 and 11.64, p = 0.02, 0.001 and 0.007, respectively). Whereas other functional groups (and component taxa), e.g., climax suspension feeders, flexible strategists (all ophiuroids), sedentary suspension feeders (all crinoids), and mobile hard predator/scavengers (principally asteroids and notothenioid fish) did not show clear trends with substratum hardness (p-values > 0.1).

On exploring whether any functional groups could be considered a proxy (surrogate) for the wider faunal patterns observed, e.g., in density, deposit-feeding crawlers appeared to be the strongest surrogacy candidate (Figure 6; and see Figure S3 for pioneer sessile suspension feeders and hard sessile predator/scavengers). The functional group individually reflected the density pattern, and when removed from the broader dataset, the pattern remained, supporting that deposit-feeding crawlers did not drive the trend. Furthermore, and as above-mentioned, the density-trend of deposit-feeding crawlers with substratum type also reflected that of the overall fauna.

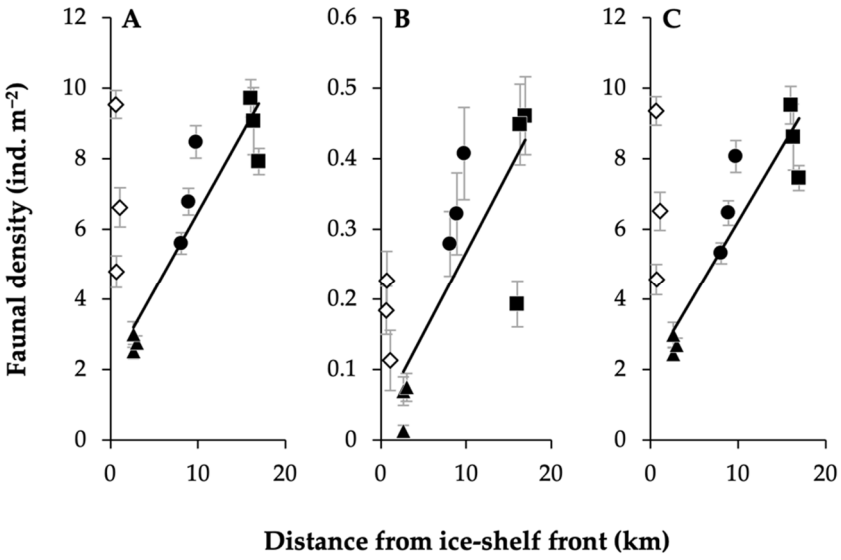


Figure 6. Deposit-feeding crawlers as an effective surrogate of the overall faunal density trend observed with distance from the ice shelf. Mean densities (ind. m^{-2}) (±SE) with distance from the ice-shelf front (km) of: (**A**) overall fauna; (**B**) deposit-feeding crawlers; and (**C**) overall fauna excluding deposit-feeding crawlers. Site LCP1 = diamonds, LCP2 = triangles, LCP3 = circles, and LCP4 = squares; white-filled symbols indicate data not included in trend-line generation (because of water mass differences, see [90]). R^2 values for (**A**–**C**) = 0.86, 0.63 and 0.85, respectively. Regression statistics for C presented a p-value of ≤0.001.

3.6. Megafaunal Assemblage Composition

The nMDS ordination of megafaunal assemblages of samples showed a robust two-dimensional representation of non-metric multidimensional space (stress 0.05, Figure S4). This analysis revealed that the sites closest to the ice shelf were not compositionally homogeneous, in fact LCP1 and LCP2 had the most dissimilar assemblages (61.2% dissimilarity) of any two sites. The highest Bray–Curtis similarities were observed from intra-site comparisons (highest = 77.6% at LCP4) and the lowest from inter-site comparisons (lowest = 35.6% between LCP1 and LCP2). The key morphotaxa found to be driving similarity between samples within sites were ophiuroids (particularly for LCP2 and LCP3), encrusting lithophiles and bottlebrush corals (Table S4). Key morphotaxa driving dissimilarity between sites included bottlebrush corals, particularly when comparing LCP2 samples with others (although not key for LCP1 and LCP4 dissimilarity), *Sterechinus antarcticus* (as

well as other echinoid species), principally when comparing LCP1 with offshore sites, and, in some site comparisons, encrusting lithophilic organisms and *Pyura* sp. (potentially *Pyura bouvetensis*) (see Table S5).

The differences between LCP2 samples and those of other sites appeared to be driven by absences and much lower densities of various taxa, although LCP2 was the only site in which the holothurian *Peniagone vignoni* was observed. Notably, LCP1 had higher densities of echinoids (of at least three different morphospecies). At LCP4, an athecate hydroid species occurred in higher densities than at other sites. Compared to LCP3, LCP4 had more bottlebrush corals, the aforementioned hydroid species, and the *Pyura* sp. In general, LCP3 and LCP4 had higher densities of holothurians (of differing species), particularly those (visually) identified as *Pseudostichopus mollis*.

HAC analysis with a SIMPROF test identified four distinct groupings among samples, corresponding to the four individual sites (Figure 7). Further examination of the HAC dendrogram showed that LCP2 samples were compositionally more distinct from those of the other sites; this was followed by LCP1, and then LCP3 and LCP4. The results of this analysis were reflected in the nMDS findings showing that the sites closest to the ice-shelf front were the most compositionally dissimilar.

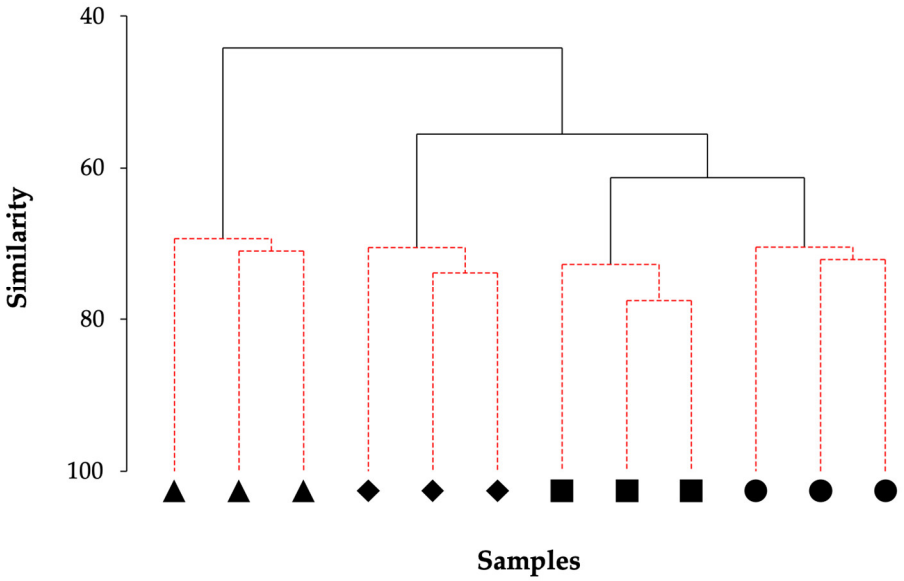


Figure 7. Clustering of samples corresponds with respective study site. Dendrogram resulting from hierarchical cluster analysis of samples from Larsen C study sites (based on Bray–Curtis similarities and using group-average linking). Black continuous lines indicate significant clusters, identified by a SIMPROF test, and red dashed lines indicate non-significant clusters. Site LCP1 = diamonds, LCP2 = triangles, LCP3 = circles, and LCP4 = squares.

When HAC (plus SIMPROF) analysis was performed for functional groups, results were similar to that of the morphotaxa in that the samples were again clustered by their respective study site (Figure S5).

3.7. Environmental Differences between Study Sites

A range of environmental variables (15 in total and 9 following correlation analysis, see Table S3) was examined to discern how sites differed in terms of environmental context. The PCA and associated ordination (Figure 8) showed that the first two principal components accounted for >85% of the environmental variability (52.9% and 32.4%, respectively). The first principal component explained environmental differences among samples due to sea-ice cover, nitrate, salinity, and water physico-chemistry (represented by temperature and correlation with oxygen concentration) (Eigenvectors = 0.45, 0.43, 0.39, and −0.38, respectively). The second principal component further showed the factors of substratum

type, distance from the ice-shelf front, depth, and phosphate (Eigenvectors = −0.55, 0.38, 0.38 and −0.38, respectively).

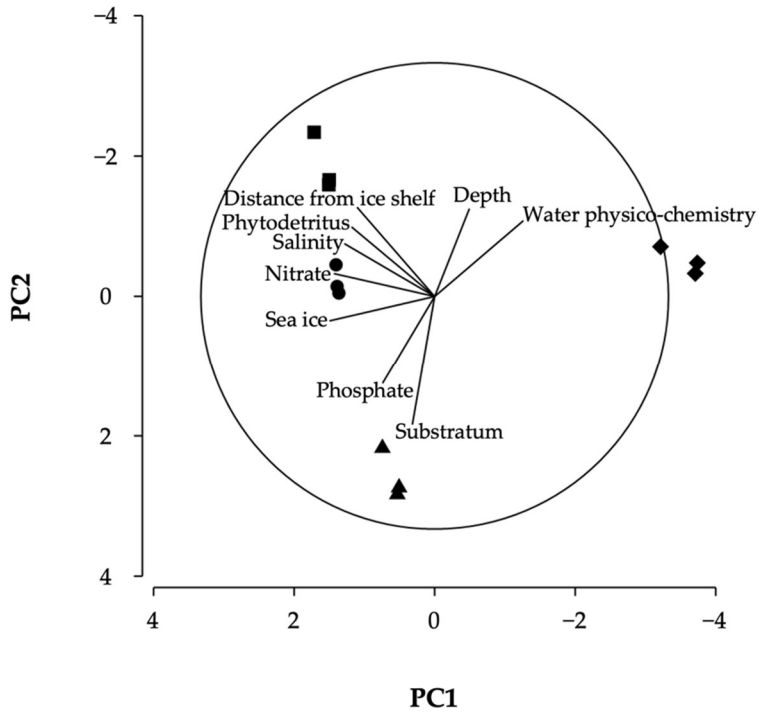


Figure 8. Differences in the environmental setting of sites (and samples). PCA ordination showing spatial variation in environmental variables among the 12 samples. Site LCP1 = diamonds, LCP2 = triangles, LCP3 = circles, and LCP4 = squares. PC = Principal Component.

Overall, the PCA indicated the importance of measuring a range of environmental variables when studying multiple sites, as water physio-chemistry appeared the most influential in differentiating LCP1 from the other sites (hence, separation in Figure 3), substratum at LCP2, and distance from the ice shelf and phytodetritus cover at LCP3 and LCP4.

3.8. Environmental Influences on Megafaunal Assemblage Composition Differences

Having established environmental differences among sites, BEST analysis was performed to determine which variables correlated with, and hence could be potentially influencing, megabenthic assemblage compositional differences in space. The results showed that specific combinations of environmental variables were more likely to be underpinning faunal differences.

The BEST analysis indicated that a subset of three environmental variables most highly correlated with (or "best explained") the variation in faunal assemblage structure (Rho correlation = 0.93, $p < 0.01$). This subset included mean depth, water physico-chemistry and substratum hardness. The single variable showing the highest Rho correlation (0.77) was substratum type, considered a local-scale variable.

When comparing BEST analysis results of all faunal grouping methods, i.e., morphotaxa, class and functional groups, the most highly correlated subsets of potential explanatory variables each included water physico-chemistry and substratum hardness (Rho correlations for the latter two faunal groupings = 0.87 and 0.93, respectively, with associated p-values < 0.01). As such, there appears to be some consistency in which environmental variables emerged as potential key drivers of the biotic variation observed, irrespective of whether the benthic biodiversity was classified by taxonomic levels or functional groups.

4. Discussion

The Southern Ocean can be characterized by relative constancy [1] and also sharp marine environmental gradients, the latter exemplified by conditions either side of the Polar Front (the strongest jet of the ACC) [116], the continental shelf break (the terminus of grounded ice in glaciations) [72,117,118], the marginal sea-ice zone and the ice-shelf front [119]. With ocean and atmospheric warming, Antarctic icescapes and associated marine ecosystems are expected to change, with implications for biota [2,6]. While there have been various studies of biological response to Antarctic glacier retreat (e.g., [45,120–122]), few have covered life underneath ice shelves (see [33,34,38]) and even fewer on what shapes biodiversity, and how it develops, in areas that have recently experienced ice-shelf loss [54,56,68]. The current study investigated megabenthic biodiversity (richness, density and composition) and potential environmental drivers at a key Antarctic marine frontier that is arguably one of the most sensitive to climate change, the ice-shelf edge. Furthermore, the respective study area sits entirely within the constraints of an important and characteristic Antarctic marine feature, a coastal polynya [74,123]. The seafloor biology where these two systems co-occur is little known [124], and yet, potentially representative of how seabed communities may develop in new areas of open water as Antarctic ice shelves retreat in a warming world.

The present study found a trend in the overall density of megafauna with increasing distance from the ice-shelf front; however, perhaps surprisingly, not in richness (biodiversity). When individual taxa and functional groups were explored, some groups were found to reflect the overall density trend (i.e., could potentially be used as proxies), some contrasted, and some showed no clear pattern. Substratum type appeared to strongly influence megafaunal density, although it did not appear to exert the same impact on richness. Distance from the ice-shelf edge, which, in the confines of the study, correlated with the remotely-sensed primary-production-related variables, did not emerge as a significant environmental driver of assemblage composition. Instead, different environmental variables appeared to be important locally at each study site. Compared to offshore sites, assemblages closest to the ice-shelf front could be expected to be more similar to each other (having had less time in terms of environmental exposure to diverge), yet they were actually the most dissimilar. Overall, results suggested that a study zone, where a polynya abuts the ice shelf, can be a complex coastal environment, both physically and biologically.

Large-scale alterations in faunal richness have been widely observed across geological time [125] and space, e.g., latitude [126,127], with pronounced hemispherical asymmetry [1,128] due to the Antarctic Ocean being anomalously highly biodiverse [18,26]. Various reasons for changes to faunal richness across scales have been presented, including energy availability [129] and species turnover [130]. Given that the number of species encountered generally increases with the size of area surveyed (e.g., Figure 2), it is important to evaluate richness levels within comparable area sizes (i.e., standardized samples), for example, when comparing findings, such as the current study's, with those of other regions. In the case of the present study, investigating continental shelf assemblages proximate to Larsen C, morphotaxa richness increased (at each site) with the size of area examined, however, less rapidly than, for example, at Ryder Bay (western Antarctic Peninsula) [21], around the island of South Georgia [94], and in the Barents Sea (Arctic) [131] (Figure 9, using associated datasets).

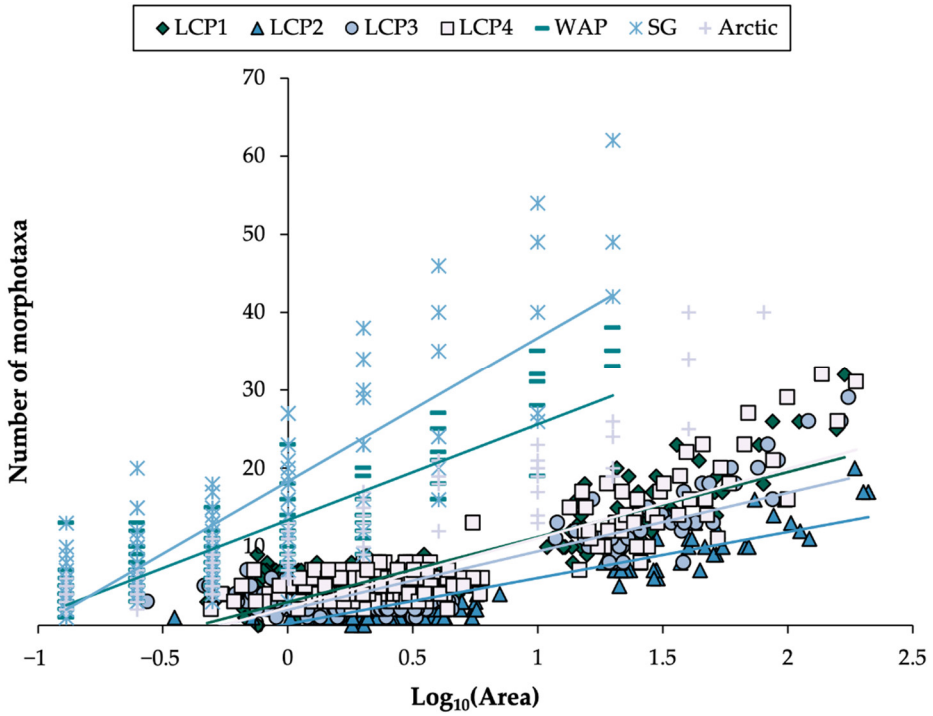


Figure 9. Geographical regions accumulate faunal richness differently. Morphotaxa richness with area examined for Larsen C Polynya study sites, LCP1-4, compared to photographic studies from Ryder Bay (western Antarctic Peninsula, WAP), around the island of South Georgia Island (SG) and the Barents Sea (labeled here as "Arctic") (sources of external datasets used are provided in the text).

Potentially having experienced greater historic disturbance (e.g., from iceberg scouring), Antarctica's coastal open-water shelf areas can harbor a great array of habitat types and niches, and hence resident biota, including those associated with different successional stages. As such, it was envisaged that a positive richness gradient would be observed with increasing distance from the ice-shelf front (i.e., farther offshore). However, within the study confines, no significant increase (or change) in faunal richness was discerned (including when examining Jason Peninsula sites exclusively). Furthermore, richness values were particularly variable at the sites closest to the ice-shelf front. Similarly, Grange and Smith [132] found no increase in richness with distance from western Antarctic Peninsula glacier termini, whereas Kim et al. [83] found the greatest richness at a location farthest from a glacier front in Marian Cove, King George Island. The results of the current study could be due to several reasons, including: (1) the nature of the seabed environment close to the ice-shelf front being similarly (or more) variable to that of open shelf farther away (e.g., reflected in the different prevailing substratum types); and, alternatively or additionally, (2) the principal environmental influences driving biodiversity patterns are site-specific, i.e., differ according to the site (Figure 8; and as found by Post et al. [133] with regard to rugosity), and are more influential than ice-shelf-edge proximity (and respective correlates, i.e., mean daily and mean peak NPP). However, examining biodiversity differences using richness alone can obscure underlying variances and changes [134] and is better evaluated in coordination with other measures such as density and faunal composition.

Biota responses to major environmental gradients can be reflected in faunal density in both space and time. In the polar regions, this can be exemplified by (re)colonization of seafloor on ecological timescales in response to ice scour, glacier retreat and ice-shelf collapse [44,54,56,132,135], and by (re)colonization of the continental shelf on evolutionary timescales following the recession of the AIS and associated grounded ice (e.g., following the Last Glacial Maximum ~20,000 years ago) [136,137]. Significant changes in the density of benthos can occur from the abyssal plain through continental slope to continental shelf [118], i.e., spatially, and over time, for example, in association with food-fall [111,138].

However, some studies have shown that faunal abundance does not always directly reflect observed phytodetritus fall and cover of the seafloor [139,140]. The present study found that faunal density generally increased with increasing distance offshore. This result is in some contrast to the findings of Grange and Smith [132], which showed lower densities on the open-water continental shelf compared to study locations at glacial termini, albeit on a larger spatial scale. However, in the current study, the Bawden Ice Rise site (LCP1), closest to the ice shelf and with the greatest ice-shelf cover over the observation period, had some of the highest faunal densities observed in the study area. These high densities may have been driven by the site experiencing different water mass conditions (see Figures 3 and 8, and [90]); in particular, water temperatures were higher, possibly influencing the occurrence and growth of taxa (e.g., see [27]) and/or parts of the site being serviced by bottom currents rich in organic matter.

Additionally, the seafloor (hence benthos) at LCP1 may have been more protected from ice-mediated disturbance than the Jason Peninsula sites due to being more consistently ice-shelf-covered, and for a more extended period, at least within the satellite era. Furthermore, when open water, LCP1 may have been afforded further protection from disturbance by Bawden Ice Rise and associated shallow seafloor, known to constrain iceberg-flow into and within the area [141]. Nonetheless, it is notable that farther north on the western Weddell Sea continental shelf, it has been observed that in just a few years of areas becoming ice-shelf-free, density and biomass of benthos can increase considerably, i.e., in response to new exposure to open-water conditions and associated food regime changes [54,56].

The site with the lowest faunal densities was LCP2, closest to Jason Peninsula. Such density values may be explained in reference to the aerial/satellite imagery that showed the site had often been proximate to the ice-shelf edge and had undergone ice-shelf advance and retreat (at least twice) in recent-time. Additionally, the site is at a water depth within reach of modern iceberg keels in an area of iceberg transit (conditions also particularly pertinent to LCP4 and potentially explaining the faunal patchiness observed there). Hence, the respective site may have been especially subject to disturbance such as scouring and the deposition of ice-rafted debris (associated with calving-front dynamics, ice-shelf basal melt, and transiting icebergs) [142,143].

Although all sites in the study occurred within a polynya, and therefore an area of potentially elevated primary production and related organic matter export to the seabed [74,144], megafaunal density values were not necessarily as high as those recorded for other open-water continental shelf areas (e.g., [42]; and see Table VI of Post et al. [124]). The lower faunal densities observed could be related to the fact that the polynya only occurs intermittently, and the study area is otherwise covered in heavy year-round sea ice. Furthermore, there is a contrasting seasonality of sea-ice cover in the polynya compared to other Southern Ocean areas—sea-ice cover in the polynya being at a maximum during the austral summer (when phytoplankton blooms are typically most productive) as opposed to winter. Such aspects may compromise primary production potential, and thus associated organic matter flux to the Antarctic seabed.

Biological patterns were not only explored by looking at the megafaunal assemblage as a whole, but also through the 12 functional groups represented by the fauna detected (Table 2; Figure 5). Such an approach has advantages in examining the functionality of biodiversity and also potentially helping reduce imagery appraisal times. In the study, specific taxa and functional groups, e.g., anemones and hydroids—both components of the soft sessile predator/scavengers group, showed significant density increases as distance from the ice shelf increased. Some taxa, e.g., echinoids of grazing and deposit-feeding types, showed exceptionally high densities at the Bawden Ice Rise site (LCP1), and low densities (or absences) elsewhere, while others, e.g., climax suspension feeders, showed no discernible trends. It could be predicted that pioneer species would be of higher density in more-recently ice-shelf-uncovered areas and climax species in more established areas (i.e., those that have been uncovered for longer) [48,49]. However, the study found high pioneer densities at LCP4, free of ice-shelf cover during and potentially before the satellite

era, and LCP1, the site most consistently ice-shelf-covered and still situated very close to the ice-shelf edge. In addition, pioneer suspension feeders displayed a significant positive density relationship with distance from the ice-shelf edge, particularly when the Jason Peninsula sites were considered exclusively. Climax suspension feeders, e.g., sponges and bryozoans, did not show a trend with distance from the ice shelf, and interestingly, the highest densities were found within an LCP1 sample, challenging the assumption that climax suspension feeders would be more prevalent in areas farther from the ice shelf where primary production may be higher. Additionally, it could also be predicted that grazers would be better represented in seabed spaces featuring more hard substratum (hence potential attached food sources), and deposit-feeders in soft-sedimented areas [1]. While this was not the case for grazers in this study, densities of epifaunal deposit-feeders did increase with increasing substratum softness.

Partitioning faunal density and richness into various taxonomic levels, or by function, permits further insight into how different elements of biodiversity respond to environmental conditions. Finding appropriate surrogacy, or indicators, can also help simplify ecosystem monitoring, accelerate data processing and results-delivery, and thus enhance the timeliness of informing marine management, which is particularly important for rapidly changing environments. Suitable surrogates should reflect the overall biotic pattern of interest while not driving it. In the present study, deposit-feeding crawlers, all of which were holothurians, were found to be the strongest surrogacy candidate for overall megafaunal density (Figure 6). Although preliminary, this finding could be especially advantageous for imagery-based seafloor assessments given that holothurians are relatively easy to detect and identify due to their visual characteristics and mobility, making them also potentially ideal candidates for the development of automated appraisal and monitoring tools (e.g., [145]). Nevertheless, it remains important to continue testing proposed surrogates. For example, gastropods have been used as indicators of latitudinal trends in the reproductive strategy of benthic invertebrates, i.e., Thorson's rule [146], yet when exploring this rule in echinoderms [147], quite different patterns were uncovered; rather than brooding becoming a more dominant reproductive strategy with increasing latitude, lecithotrophy (non-feeding larvae) became more common. Additionally, in Southern Ocean seabed conservation and management, taxa considered representative of Vulnerable Marine Ecosystems (VMEs) [148,149] can be employed to pinpoint and designate VMEs. While such taxa are invaluable tools, it is not yet fully known whether all are true indicators of VMEs and/or are vulnerable themselves (see [4,56,59]).

Ordination techniques, such as nMDS, can help reveal underlying structural differences in biodiversity at various scales, for example, between islands and seamounts [150], along fjords [132], and across depths [118]. Given that offshore sites were considered more likely to have experienced historic disturbance, hence display differing successional/colonization stages, such sites were expected to be the most compositionally dissimilar (within and between respective sites). The nMDS visualization, however, revealed two particular aspects of note. Firstly, variability, in terms of assemblage composition, was similar within sites irrespective of distance from the ice-shelf edge, and secondly, sites closest to the ice shelf were the most compositionally dissimilar. A potential explanation is that the ice-shelf margin is a similarly (or more) variable continental seabed environment to that of offshore. This variability at the ice front may be due to the differing retreat-advance dynamics of the ice shelf, and the varying degrees (and nature) of sediment loading and stochasticity of release, which will impact the seafloor in terms of disturbance and substratum make-up, hence benthic assemblage structures.

One of the striking biological differences between Jason Peninsula site LCP2 and other sites was that it did not appear to host calcaxonian corals, despite the availability of plentiful hard surfaces, i.e., attachment points. However, the distribution of such biota is also thought to be strongly influenced by water depth, coincident iceberg scouring, and the flow of organic matter [151], so these factors may play an important role around this part of the Larsen C Ice Shelf margin. Furthermore, LCP2 was also the only site observed to host

elasipod holothurians, which could indicate a food-poor habitat as the taxon is considered well-adapted to food scarcity [140]. Larsen-marginal habitat differences appear complex, perhaps even enigmatic. Nevertheless, the underlying drivers of assemblage differences are ultimately environmental, with various biota elements responding differently.

A priori considerations that ice-shelf proximity may be a major influencer of megafaunal assemblage composition were not directly supported by the BEST analysis findings of this study. However, such a factor (as aforementioned) could be linked to other environmental variables such as prevailing substratum type. As found in other polar locations and farther afield (e.g., [124,132,152–154]), substratum type and depth were also found to be important drivers of faunal composition, although the impact of depth is not always clear in the Antarctic owing to wide bathymetric ranges of many benthic species [136]. Given that areas exhibiting hard substratum are expected to be more heavily colonized and display characteristic taxa [153,154], the substratum results of the present study were somewhat counterintuitive. For instance, the "hardest" site, LCP2, had notably low faunal densities, including very few encrusting lithophiles, and corals appeared unrepresented. It is thus likely that further factors were influential at LCP2, including, for example, potentially organic-poor (oligotrophic) bottom currents coming from beneath the ice shelf, as described by Dayton and Oliver [155] for an area on the west flank of the McMurdo Sound, next to Ross Ice Shelf. Alternatively, the substratum at LCP2 (as per above) was indicative of a more frequently disturbed environment in relation to ice-shelf processes and dynamics; hence faunal assemblage components and densities are reflective.

In the polar seas, sea-ice cover (concentration, timing and duration) is a key influencer of seabed biodiversity dynamics, in part through associated impacts on light penetration, primary production, and flux of particulate organic matter to the seafloor [156,157]. However, in this study, sea-ice cover was not significantly coincident with differences in assemblage structure. This result may be because sea-ice cover (on its own) did not sufficiently differentiate between all of the sites and/or the associated variable did not account for periods of ice-shelf cover. Water physico-chemistry was also found to be important in influencing faunal composition. This variable notably included ocean temperature, considered highly likely to be impacted by climate change, with implications for biotic communities, in particular those of coastal habitats and habitats at continental shelf depths [6]. As an assortment of variables, i.e., depth, substratum type and water physico-chemistry, were the best explanatory set of environmental factors, this supports the view that the Antarctic continental shelf is a complex environment. Exploration of further variables/parameters, in particular those related to biological interactions such as predation and competition, may provide additional, potentially important, ecological insights, particularly in the case of likely alterations to benthic assemblages in response to environmental change. Furthermore, extending studies to other ice-shelf-adjacent polynyas (e.g., those pinpointed in [74]) would help determine if there is a degree of commonality (or not) among polynyas in terms of benthic assemblage structuring and drivers, and, together with the present study, additionally offer a collective ecological baseline for conservation and management purposes.

5. Conclusions

This study explored benthic assemblages of four western Weddell Sea continental shelf sites, all within an ice-shelf-adjacent coastal polynya, and two of which have recently experienced ice-shelf retreat. The research revealed distinct faunal patterns in density (but not in richness), and identified a taxonomic and functional group (deposit-feeding crawlers (all holothurians)) that could potentially be a surrogate for the wider megafauna, hence contributing to simplifying, and potentially expediting, future marine environmental monitoring efforts. Distance from the ice shelf was not identified as a key driver of assemblage composition; however, results evidenced that at the ice-shelf front, habitats and assemblages can be very different across space. The study further showed that different environmental variables were potentially important in structuring benthic assemblages at

each study site (e.g., water physico-chemistry at LCP1), emphasizing the complexity of Antarctic continental shelf environments, particularly those at the edge of ice shelves.

The current findings provide an indication of how seabed communities may develop along the eastern Antarctic Peninsula as further ice-shelf cover is lost, and narrow biological knowledge gaps of a very rarely accessed and distinctive area within a CCAMLR-proposed MPA.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/biology11121705/s1, Figure S1. Example imagery and megabenthic communities observed at the Larsen C Polynya study sites, LCP1-4, western Weddell Sea, Antarctica; Figure S2. Morphotaxa richness with substratum type (increasing hardness) for standardized 100 m^2 samples across Larsen C Polynya (LCP) study sites, LCP1-4; Figure S3. Exploration of functional groups pioneer sessile suspension feeders and hard sessile predator/scavengers as potential surrogates for the overall faunal density trend; Figure S4. Non-metric multidimensional scaling (nMDS) ordination of Larsen C Polynya samples based on Bray–Curtis similarities calculated from fourth-root transformed morphotaxa density data (2D Stress = 0.05); Figure S5. Dendrogram from hierarchical agglomerative clustering (HAC) of Larsen C Polynya samples using group-average linking of Bray–Curtis similarities calculated from functional group densities data. Similarity profiles (SIMPROF) testing applied to determine significance of divisions (at $p < 0.05$); Table S1. Distances (m) between Larsen C Polynya study sites LCP1-4. Calculated using Vector Analysis Tools in QGIS v3.16.6; Table S2. Larsen C Polynya substratum types. Hardness scale; Table S3. Environmental variables considered in the study and correlations $\geq$ 95% observed; Table S4. Similarity percentages (SIMPER) analysis displaying percentage contributions of benthic morphotaxa responsible for within-site (LCP1-4) similarities. Cut-off where cumulative percentage contribution reaches 50%; Table S5. Similarity percentages (SIMPER) analysis displaying percentage contributions of benthic morphotaxa responsible for dissimilarities between sites (LCP1-4). Cut-off where cumulative percentage contribution reaches 50%.

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Variability in zoobenthic blue carbon storage across a southern polar gradient

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ABSTRACT

The seabed of the Antarctic continental shelf hosts most of Antarctica's known species, including taxa considered indicative of vulnerable marine ecosystems (VMEs). Nonetheless, the potential impact of climatic and environmental change, including marine icescape transition, on Antarctic shelf zoobenthos, and their blue carbon-associated function, is still poorly characterised. To help narrow knowledge gaps, four continental shelf study areas, spanning a southern polar gradient, were investigated for zoobenthic (principally epi-faunal) carbon storage (a component of blue carbon), and potential environmental influences, employing a functional group approach. Zoobenthic carbon storage was highest at the two southernmost study areas (with a mean estimate of 41.6 versus 7.2 g C m^{-2}) and, at each study area, increased with morphotaxa richness, overall faunal density, and VME indicator density. Functional group mean carbon content varied with study area, as did each group's percentage contribution to carbon storage and faunal density. Of the environmental variables explored, sea-ice cover and primary production, both likely to be strongly impacted by climate change, featured in variable subsets most highly correlating with assemblage and carbon storage (by functional groups) structures. The study findings can underpin biodiversity- and climate-considerate marine spatial planning and conservation measures in the Southern Ocean.

1. Introduction

This century sees the tercentenary of the Industrial Revolution, and over the corresponding period, atmospheric levels of greenhouse gases (GHGs) have been rising. The atmospheric concentration of the most ubiquitous GHG, carbon dioxide (CO_2), has increased from around 280 parts per million (ppm) in 1750, i.e., pre-industrial-era, to a 2022 average of ~417 ppm; this rise being particularly significant in the last 75 years and mainly from intensities of fossil-fuel combustion, cement production, and deforestation, i.e., anthropogenic (Friedlingstein et al., 2023; IPCC, 2023). The cumulative effect of GHG emissions is global climate change, including warming, the impacts of which are increasingly experienced across the world and considered intertwined with the biodiversity crisis (IPCC, 2022, 2023; Pörtner et al., 2023; Siegert et al., 2023). To reduce levels of atmospheric CO_2, societal efforts centre on minimising emissions at source (i.e., decarbonisation methodologies) and large-scale CO_2 capture; the captured CO_2 later used in further processes or potentially placed in long-term geological storage, e.g., within depleted oil and gas reservoirs of continental shelves – legacies of hydrocarbon extraction (Holloway and Burnard, 2009; Luo et al., 2023). In parallel, protection and capacity enhancement of natural carbon sinks, including, for example, the living resources/biomass of various marine ecosystems such as those present along tropical and temperate shorelines (e.g., McLeod et al., 2011; Greiner et al., 2013; Howard et al., 2014; Song et al., 2023) and on high-latitude/polar continental shelves (e.g., Gogarty et al., 2020; Cavanagh et al., 2021; Bax et al., 2022), are also being pursued.

The vast ocean network, constituting >70% of the world's surface, plays a major role in mitigating climate change by helping regulate atmospheric levels of CO_2, the oceans collectively absorbing ~26% of anthropogenic CO_2 emissions (Friedlingstein et al., 2023) and the Southern Ocean, representing ~10% of the ocean network, disproportionately accounting for around one-quarter of total oceanic uptake of atmospheric CO_2 (Arrigo et al., 2008). Marine biodiversity can help support this process through "blue carbon", a component of which can be defined as the carbon captured and stored by marine life, i.e., the carbon within living marine biomass (Barnes, 2018). Blue carbon is also considered a marine ecosystem service benefitting humankind (Grant

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et al., 2013; Rogers et al., 2020; Cavanagh et al., 2021). Marine primary producers, such as phytoplankton and macroalgae, initially capture CO_2 via photosynthesis, and thereafter, carbon is exported/transferred within associated and conjugated ecosystems (Cavan and Hill, 2022), being stored across the marine food web over diverse timespans and spatial scales, eventually leading to its sequestration within seabed sediments (Barnes, 2018).

In the polar regions, biological carbon pathways (and fates) are yet to be fully understood (Cartapanis et al., 2016; Henley et al., 2020; Sands et al., 2023); however, at high-temperate, sub-polar and polar latitudes, marine food webs can be based on macroalgae (e.g., kelp; see Vilas et al., 2020) and phytoplankton (microalgae), and at the very highest latitudes of the Southern Ocean and its constituent seas, phytoplankton dominate primary production (Deppeler and Davidson, 2017). In the cold surface waters of the Antarctic, where atmospheric CO_2 more readily dissolves (Arrigo et al., 2008), huge seasonal (austral spring and summer) accumulations (blooms) of phytoplankton capture CO_2, incorporating it into the biological carbon cycle and initiating pathways for carbon storage in the Antarctic marine food web, including in the zoobenthos (seafloor-dwelling animals), by which an estimated 12–18% of Southern Ocean primary production is consumed (Barnes, 2017, Fi g. 8 in Henley et al., 2020). The seafloor is also where the majority of Antarctica's known biodiversity resides (De Broyer et al., 2014) and where taxa considered indicative of vulnerable marine ecosystems (VMEs), as defined by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR; CCAMLR, 2009), have been observed (CCAMLR, 2019; Lockhart and Hocevar, 2021). The presence of VME indicator taxa can strengthen justification for the adoption of proposed regional protection frameworks, such as Marine Protected Areas (MPAs) (Lockhart and Hocevar, 2021), and some VME indicators, e.g., corals, owing to their carbonate skeletons, are particularly proficient at storing carbon (and enhancing sequestration, i.e., long-term storage potential) (Barnes, 2018) whilst some are also important habitat providers/ecosystem engineers (Miller et al., 2012); hence, can help amplify carbon storage through associated inhabitants.

Similar to terrestrial forests and coastal wetlands (Howard et al., 2014; Mildrexler et al., 2020), marine biodiversity can be important in capturing, storing and facilitating sequestration of carbon. Carbon that might otherwise be broken down and recycled by the microbial loop is taken up and bound into tissues (and skeletons) of marine biota (Barnes, 2018). Benthic habitats, including, for example, their biological/zoobenthic communities (and component assemblages), i.e., the fauna living on (epi-faunal) and within (in-faunal) the seabed, can function as carbon sinks, accumulating and immobilising carbon (see Peck et al., 2010; Alurralde et al., 2019; Barnes et al., 2020). Zoobenthic assemblages, in terms of their composition, are known to be shaped by various combinations of environmental variables, such as ice cover, substratum type and physical/chemical features of the seabed (e.g., Domack et al., 2005; Isla et al., 2006; Niemann et al., 2009; Clark et al., 2017; Post et al., 2017; Ziegler et al., 2017; Almond et al., 2021). Alterations in such variables may impact the structure and function (including performance) of assemblages. Disentangling bio-physical relationships can be helpful for predictions regarding biological responses to environmental change (Cummings et al., 2018). To discern benthic community/assemblage structure epi-zoobenthos (the epifaunal component of zoobenthos) can be sampled/surveyed by relatively non-destructive means, e.g., via seafloor imaging techniques, whereas in-fauna are generally sampled by (more intrusive) sediment cores and grabs (Pineda-Metz and Gerdes, 2018). Although in-faunal organisms do not fall within the remit of the current study, they can account for ~50% of the carbon stored in the benthos (when epifauna and infauna are both considered), for example, of Antarctic fjords (Zwerschke et al., 2022).

Studies assessing high-latitude benthic blue carbon, including within the context of ecosystem services and nature-based solutions to moderating climate change, are growing yet still relatively rare. Furthermore, such studies are primarily conducted within exclusive economic zones or performed in consideration of unilateral marine protection zones (e.g., Barnes et al., 2019, 2021a; Bax et al., 2022); this opposed to, for example, internationally-shared waters or areas beyond national jurisdiction. If left undisturbed, these seabed ecosystems may continue functioning as carbon sinks and store carbon delivered to them through the food web (Sands et al., 2023). However, given ongoing and anticipated environmental shifts in high-latitude marine environments brought about by climate change and direct human impacts associated with the Anthropocene (Steffen et al., 2011), Antarctic seafloor habitats, their component communities/assemblages, and their associated functions and services may alter in response or indeed be at risk (Rogers et al., 2020; Cavanagh et al., 2021; Gutt et al., 2021).

Over the past few decades, carbon storage in polar zoobenthic communities has garnered attention in both hemispheres. Several investigations have now employed blue-carbon-oriented "functional groups" – a faunal grouping method in which fauna are grouped based on functional traits considered important in benthic blue carbon pathways (see Barnes and Sands, 2017). For example, studies in the Barents Sea, where carbon storage capacities, also referred to as "carbon standing stocks", of sedimented continental shelf assemblages were assessed (Souster et al., 2020, 2024), and in deglaciating fjords of the western Antarctic Peninsula, where blue carbon of emerging coastal benthic ecosystems was evaluated (Barnes et al., 2020; Zwerschke et al., 2022). Emergent polar marine habitats experiencing losses of overlying ice (e.g., sea ice, glaciers and ice shelves) are, in particular, regarded as potentially large-scale negative feedbacks on climate change (Peck et al., 2010; Morley et al., 2022; Zwerschke et al., 2022; Sands et al., 2023).

Antarctic seabed biodiversity, having developed in relative constancy of physical conditions and partial isolation due to the presence of the Antarctic Circumpolar Current (ACC) (Arntz et al., 1994), is likely vulnerable to climate change and associated environmental alterations (Rogers et al., 2020; Gutt et al., 2021; Casado et al., 2023). Nevertheless, considerable knowledge gaps exist around how high-latitude zoobenthic communities, and their carbon storage function, may alter in a warming world and as marine icescapes modify (however, see Barnes, 2017; Pineda-Metz et al., 2020). In respect, this study aims to discern how zoobenthic carbon storage varies across a southern polar gradient and examines zoobenthic (principally epi-zoobenthic) assemblages of four continental/island shelf study areas, all connected by the Scotia Arc, and representative of a transition from cool to seasonally-surface-freezing marine waters. The study includes the following objectives: (i) to ascertain whether zoobenthic carbon storage variance aligns with biodiversity measures (richness) and faunal density; (ii) to determine if VME indicator taxa substantially contribute to zoobenthic carbon storage; (iii) to explore functional groups' contributions to zoobenthic carbon storage; and, finally, (iv) to identify potential environmental drivers of zoobenthic carbon storage, including whether dropstones, physical features of the seabed, exhibit a discernible influence. The wider aims of this study include furthering the knowledge base of very high-latitude blue carbon estates in a warming world with anticipated marine icescape transformation, and providing an indication of the zoobenthic carbon storage capacity of the southern high-latitude/polar region. The study is also conducted in view of underpinning marine spatial planning and supporting conservation measures, present and future.

2. Materials and methods

2.1. Scotia Arc study areas and sites

Situated in the southern South Atlantic Ocean and Atlantic sector of the Southern Ocean, the four study areas, collectively making up the "study region", lie within the latitudinal and longitudinal ranges of ~53–67°S and ~37–71°W, respectively (Fig. 1A; Table 1). The study areas are ~760 to 2200 km apart and are connected by the underwater ridge and island system of the Scotia Arc, which links the Terra del Fuego region of South America to the Antarctic Peninsula and semi-

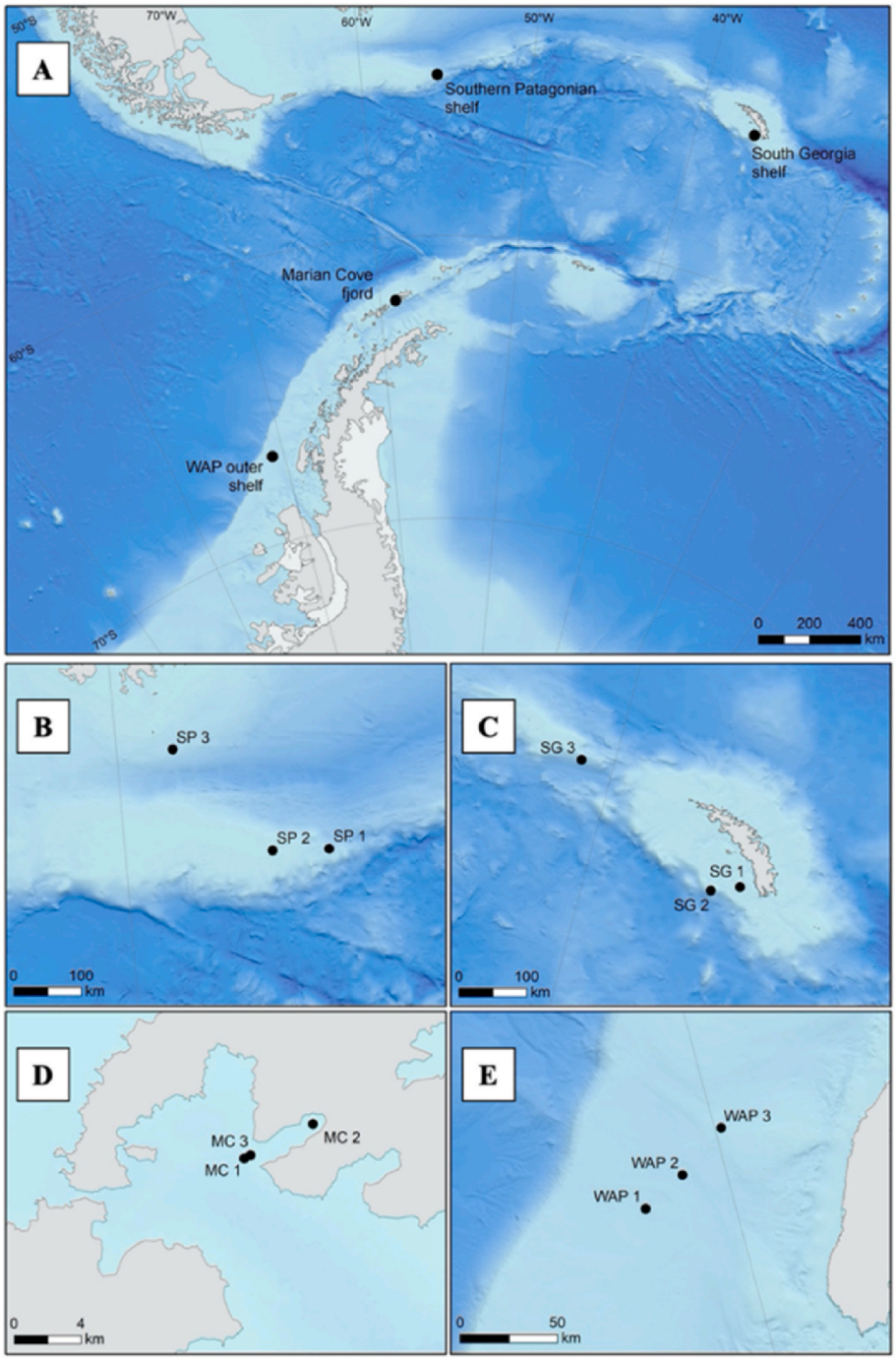


Fig. 1. Southern South Atlantic and Antarctic study areas and respective sites where benthic imagery was captured by the bespoke Shelf Underwater Camera System (SUCS). (**A**) Location of study areas in the wider context of the southern South Atlantic Ocean and Atlantic sector of the Southern Ocean, including the southern Patagonian shelf, South Georgia shelf, Marian Cove fjord (of King George Island), and the western Antarctic Peninsula (WAP) outer continental shelf; (**B**) Southern Patagonian shelf sites SP1-3; (**C**) South Georgia island shelf sites SG1-3; (**D**) Marian Cove fjord sites MC1-3; and (**E**) WAP outer continental shelf sites WAP1-3. White areas of the main map denote ice shelves, and grey areas of all maps represent land or ice-covered land/grounded ice (as appropriate). The bathymetry data is from the International Bathymetry Chart of the Southern Ocean v2 (Dorschel et al., 2022), with 100 m contours.

encloses the Scotia Sea. The northernmost study area falls within the southern South Atlantic Ocean and is situated on the southeast Patagonian shelf and the western side of the North Scotia Ridge. The most easterly study area is the shelf around the island of South Georgia, positioned south of the Polar Front, the strongest jet of the ACC, at a cusp between sub-Antarctic and Antarctic waters. Following the Scotia Arc clockwise from South Georgia toward higher latitudes leads to the third study area, Marian Cove (a relatively enclosed fjord basin) of King George Island – the largest island of the South Shetland Islands. This archipelago is at the southern boundary of the Drake Passage, and the study area is separated from the South Scotia Ridge and the Antarctic Peninsula by the Bransfield Strait. The fourth and most southerly study area is some 760 km from King George Island, situated west of Marguerite Bay and Adelaide Island on the outer continental shelf of the western Antarctic Peninsula in the Bellingshausen Sea, and falls within the Antarctic Circle. The study areas of the Scotia Arc study region are herein referred to as SP for southeast Patagonia, SG for South Georgia, MC for Marian Cove and WAP for the western Antarctic Peninsula.

Table 1
Southern South Atlantic and Antarctic study areas and sites, including latitude (∘S), longitude (∘W) and water depth (m) (all means across associated benthic imagery), and habitat type.

Study area	Site	Latitude[a]	Longitude[a]	Depth[a]	Habitat type
Southern Patagonian shelf	SP1	−54.4949	−55.5205	610	Shelf bank
	SP2	−54.4997	−56.7649	109	
	SP3	−53.1558	−58.8065	572	
South Georgia shelf	SG1	−54.8735	−36.5875	166	Shelf bank
	SG2	−55.0314	−37.1792	236	
	SG3	−53.7746	−40.6700	678	
Marian Cove (of King George Island)	MC1	−62.2200	−58.8159	205	Fjord
	MC2	−62.2031	−58.7313	83	
	MC3	−62.2174	−58.8065	62	
WAP outer continental shelf	WAP1	−66.9342	−71.0422	479	Trough
	WAP2	−66.7882	−70.4847	620	
	WAP3	−66.6648	−69.9220	358	

[a] Recorded during collection of benthic imagery by an underwater acoustic positioning system – all depths fall within the depth range of the Antarctic continental shelf (Clarke et al., 2004).

Each Scotia Arc study area was represented by three continental/island shelf sites (Fig. 1B–E; Table 1) with associated field datasets acquired during various ship-based, chiefly Royal Research Ship RRS *James Clark Ross*, scientific expeditions occurring during austral summers spanning 2009–2020. The southeast Patagonian shelf sites include two at the shallow seamount Burdwood Bank (~18,000 km^2 in area) lying ~200 km south of the Falkland Islands (Islas Malvinas); the sites correspond to SP1 and SP2 and are of ~610 and 110 m water depth, respectively. The third site, SP3 (~570 m depth), lies south of Beauchêne Island – the southernmost and most remote island of the Falkland archipelago at >60 km from East Falkland. At South Georgia, two sites are situated on the island's southern shelf, SG1 (at ~170 m depth) mid-shelf and SG2 (~240 m depth) at the shelf break, while SG3 (~680 m depth) is located on the western shelf of the island. At King George Island, the specific area of focus is Marian Cove fjord, bordered by the Weaver and Barton Peninsulas and situated within Maxwell Bay. With regard to Marian Cove sites, MC1 (at ~200 m depth) sits just outside the fjord (at the entrance), while MC2 (~80 m depth) lies deep within and is closest to the glacier terminus, and MC3 (~60 m depth) is located on the sill of the cove. On the outer continental shelf of the WAP, all three sites, WAP1-3, are situated westward of Marguerite Bay and Adelaide Island, with a depth range of ~360–620 m.

2.2. Environmental data collection

To determine how study sites and/or areas differed environmentally and to help identify environmental variables potentially responsible for biological structuring, various environmental datasets, collected in situ (during seabed imagery collection campaigns), remotely sensed and imagery-analysis-derived, were utilised.

In situ oceanographical data were acquired for each site (during corresponding imagery acquisition efforts) by deploying a Conductivity-Temperature-Depth system (CTD) fitted with auxiliary sensors. The CTD was cast from the sea surface to within ~10 m of the seabed, obtaining near-seafloor temperature (°C), salinity (Practical Salinity Unit; PSU), dissolved oxygen (O_2; μmol L^{-1}), chlorophyll-a (μg L^{-1}) and turbidity (beam transmittance; %) measurements.

Daily sea-ice concentration (SIC; %) data, spanning October 1978 to December 2021, and derived from passive microwave observations, were obtained from the US National Snow and Ice Data Center (NSIDC) (in conjunction with the US National Oceanic and Atmospheric Administration; NOAA). The dataset used was the NOAA/NSIDC Climate Data Record of Passive Microwave Sea Ice Concentration, Version 4 (G02202) (Meier et al., 2021), with a 25 by 25 km grid cell resolution. These records were used to calculate mean SIC for each site and area for the 14-year period prior to respective imagery collection (see section 2.3 regarding the latter), the period complementing available primary production data. As per Cummings et al. (2021), a year was considered as being from July through to June. In addition, the mean number of days sea-ice-covered per year was also computed for each site and area for the same period, with ≥85% sea-ice concentration/cover considered sea-ice-covered (as per Souster et al., 2020). For the purpose of the study, study sites were defined as "sea-ice sites" when the mean number of days of sea-ice-covered per year was at least 40.

Daily net primary production (NPP; mg C m^{-2} day^{-1}) data, spanning September 1997 to July 2019, were generated following the methods of Arrigo et al. (2008, 2015). From such data, mean daily NPP and mean peak NPP were calculated for each site and area for the 14-year period prior to respective imagery collection.

Daily sea surface temperature (SST; °C) data, spanning September 1981 to March 2022, were obtained from NOAA. The dataset used was the NOAA 1/4° Daily Optimum Interpolation Sea Surface Temperature dataset (Huang et al., 2020). From such data, mean daily SST was calculated for each site and area for the 14-year period prior to respective imagery collection, again the period complementing available primary production data.

Substratum type and rugosity of each image were determined during seafloor imagery analysis (section 2.4), and corresponding (mode-based) assignments assigned to each site.

2.3. Continental shelf imagery collection

Seabed imagery (for example images see Fig. S1) was acquired for each study site using the Shelf Underwater Camera System (SUCS; developed by the British Antarctic Survey Antarctic Marine Engineering Team). SUCS comprises a high-resolution still camera, lights, and a real-time ultra-short baseline positioning beacon, all mounted on a tethered (fibre-optic multimode cable) tripod, which can adjust for slope (see Barnes et al., 2020; Zwerschke et al., 2022). The camera was positioned perpendicular to the seabed at the same pre-set distance to capture images with a known field of view (area), enabling faunal density calculations. Images were captured when the tripod was at rest and spaced ~5 m apart to avoid spatial overlap. Typically, 20 images (replicates) were taken per site; hence, 60 per study area and ~240 across the Scotia Arc region.

2.4. Imagery analysis and functional group and VME indicator assignments

Each seafloor image collected was analysed for discernible zoobenthic macro- and mega-fauna using the web-based imagery annotation software BIIGLE 2.0 (www.biigle.de; Langenkämper et al., 2017). For each image, the number of different morphotaxa (morphotaxa richness) was recorded, and counts of individual functional groups (see Table 2; adapted from Barnes and Sands, 2017; Frinault et al., 2022) were conducted; hence, functional group richness was also recorded. Functional groups were based on mobility, feeding strategy and skeletal support (see Barnes and Sands, 2017) and included three suspension-feeding groups, three deposit-feeding groups, a flexible feeding strategy group (typified in the study by ophiuroids), a grazing group and five predating/scavenging groups. The number of taxa considered indicative of VMEs, as per CCAMLR (2009), was also determined (referred to herein as VME indicator taxa or simply VME taxa). As the area of each image was known, taxonomic group, functional group, and VME taxa counts could be converted into corresponding densities, i.e., individuals per m^2 (ind. m^{-2}) – standardisation permitting direct comparisons.

Additionally, for each image, substratum type was categorised as mud/fine sand, coarse sand, fine pebbles, coarse pebbles, cobbles, boulders/bedrock, or biogenic. The seven categories (principally of

Table 2
Functional groups based on Barnes and Sands (2017) and Frinault et al. (2022), with example taxa discerned in this study.

Functional group	Example taxa
Pioneer sessile suspension feeders	Ascidians, encrusting bryozoans, some tubicolous polychaetes
Climax sessile suspension feeders	Brachiopods, some erect bryozoans, poriferans (of classes Demospongiae and Hexactinellida)
Sedentary/mobile suspension feeders	Crinoids, some holothurians
Crawling (epi-faunal) deposit feeders	Holothurians
Soft (in-faunal) deposit feeders	Echiurans, some polychaetes, sipunculans
Hard (burrowing) deposit feeders	Bivalves, irregular echinoids, scaphopods
Flexible strategists	Ophiuroids
Grazers	Regular echinoids, gastropods
Soft sessile predator/ scavengers	Actiniarians, hydroids, pennatulaceans, soft corals, staurozoans
Hard sessile predator/ scavengers	Calcaxonian whips, hydrocorals, scleractinians
Soft mobile predator/ scavengers	Octopi, nemerteans, nudibranchs
Hard mobile predator/ scavengers	Asteroids, fish, some gastropods
Arthropod predator/ scavengers	Amphipods, decapod shrimps, pycnogonids

increasing sediment grain size) were based on the modified Udden-Wentworth sediment classification scheme (Blair and McPherson, 1999) and categorisations by Barnes et al. (2019) and Souster et al. (2020). Further to substratum categorisation, an image was also defined as a "dropstone image" if a dropstone or boulder was present at least three sediment-size classes larger than proximate substrata (for more information regarding glacial dropstones, see Ziegler et al., 2017; Post et al., 2020) in order to assess if such features had any influence on zoobenthic carbon storage and other biological variables in the study region. Finally, rugosity, the small-scale roughness of the seabed, was graded by measuring the "shadow length" of substrata (again following Barnes et al., 2019; Souster et al., 2020). The seven categories (of increasing rugosity) included <1 mm (i.e., smooth), 1–10 mm, >10–20 mm, >20–30 mm, >30–40 mm, >40–50 mm and ≥50 mm (i.e., rough).

2.5. Zoobenthos – acquisition and carbon content analysis, and zoobenthic carbon storage estimations

Zoobenthic specimens were collected in the vicinity of SUCS deployments (and oceanographical data collections) using Agassiz or mini-Agassiz trawls. Specimens were washed and morphologically-identified prior to storage, with the carbon contents of identified taxa later determined and used to calculate the mean carbon content of each functional group for each study area. The total number of specimens used in such calculations varied from 84 to 102 per study area. For three study areas, zoobenthic carbon content data of associated specimens were acquired from previous studies, which employed identical methodologies (Barnes, 2017; Barnes and Sands, 2017; Bax, *pers. comms.*), and for Marian Cove, the carbon content of respective zoobenthos was determined as part of this study, with associated methods reported below.

The carbon content of Marian Cove zoobenthic specimens was determined following standardised methods (see Barnes, 2017; Barnes and Sands, 2017; Barnes et al., 2019; Souster et al., 2020), facilitating direct comparability. Specimens were first washed with deionised water (Millipore Elix® Type 2) and placed into pre-etched and pre-weighed aluminium weighing boats for the duration of the analysis; a specimen was divided between more boats as necessary. Specimens were then dried for 12–24 h in a drying oven (Genlab OV/125/F/DIG) at 70 °C until constant mass achieved and subsequently incinerated for 12 h in a muffle furnace (Carbolite ESF 12/10) at 480 °C and reweighed – the tissue mass, equivalent to ash-free dry mass (AFDM), having been burnt off and skeletal mass isolated. The organic carbon content of a specimen, C_{org}, was calculated as 50% of AFDM, while the inorganic carbon content, C_{inorg}, was computed as 12% of the residual skeletal mass; however, if a specimen was siliceous (e.g., a Hexactinellid sponge), C_{inorg} was calculated as 1% of the residual skeletal mass (as per Barnes and Sands, 2017). A specimen's total carbon content, C_{tot}, i.e., g of C held, was obtained by summing the corresponding values of C_{org} and C_{inorg}.

Using C_{tot} of all corresponding specimens, the mean C_{tot} of each functional group was computed for each study area – note, the mean C_{tot} a functional group will be influenced by which specimens are (able to be) collected. To estimate zoobenthic carbon storage per m^2 (C_{zoo}; g C m^{-2}), functional group densities, determined during section 2.4 procedures, were multiplied by respective values for mean C_{tot}. Around 20 separate C_{zoo} values were generated per study site, thus 60 for each study area.

2.6. Statistical analyses

Differences in C_{zoo} and faunal density among study areas were tested using non-parametric (Kruskal Wallis) tests (with Dunn's post-hoc tests) as associated data did not meet the assumptions of Analysis of Variance (ANOVA), even after transformation. The relationship between C_{zoo} and various biological variables (i.e., richness and density) was explored via linear regression.

In advance of multivariate analyses, performed in PRIMER v7 (Clarke and Gorley, 2015) with PERMANOVA + add-on (Anderson et al., 2008), and following established procedures (Clarke et al., 2014; Clarke and Gorley, 2015), all environmental/abiotic variables were assessed for collinearity (via Draftsman plots and an accompanying correlation matrix). For variables exhibiting a high correlation coefficient, r ≥ 95%, a single variable was retained as a proxy for the other (Table S1); the remaining variables were then normalised onto a common dimensionless scale for analysis. Biological data, i.e., functional group densities (assemblage structure) and C_{zoo} values split by functional group (carbon storage structure), were fourth-root transformed, permitting rarer/less numerically dominant groups to have some influence in subsequent similarity calculations (Clarke and Green, 1988).

The similarity between study sites' biological structuring was investigated using the Bray-Curtis similarity coefficient (which generates a resemblance matrix; Bray and Curtis, 1957), followed by hierarchical agglomerative cluster (HAC) analysis (based on the resemblance matrix; Everitt, 1980), with a similarity profile (SIMPROF) test (Clarke et al., 2008), and the similarity percentages (SIMPER) procedure (see Clarke, 1993).

The BEST (Bio-Env) routine, employing the Spearman's rank correlation coefficient, was used to identify which subset of environmental variables (Table S1) best matched, or "explained", the biological structuring observed, accompanied by a global BEST test (999 random permutations) to determine the statistical significance of the match (Clarke et al., 2008; Clarke and Ainsworth, 1993). The BEST routine uses biological resemblance and normalised-environmental data matrices (and applies Euclidean distance to the latter during the process). Total C_{zoo} was also explored as a single response variable, with the corresponding resemblance matrix being based on Euclidean distance (Clarke and Gorley, 2015).

In addition, Wilcoxon matched-pair signed-rank tests were used to compare the means of several biological variables of dropstone images and randomly-selected non-dropstone images (paired from the same study site).

3. Results

3.1. Environmental differences of study areas

In terms of CTD-derived environmental (i.e., in situ oceanographical) differences, and for SP, SG, MC and WAP collectively, mean (±1 SD) near-seafloor temperature (°C) ranged from 0.1 (±0.2) to 7.4 (±0.1); salinity (PSU) from 33.4 (±1.2) to 34.7 (±0.0); dissolved oxygen (μmol L^{-1}) from 177.8 (±6.3) to 346.6 (±19.8); chlorophyll-a (μg L^{-1}) from 0.02 (±<0.1) to 0.21 (±0.1); and turbidity (beam transmittance; %) from 93.8 (±2.3) to 97.9 (±0.3).

From remotely-sensed data, it was found that mean (±1 SD) SIC (%) for the 14-year period prior to respective imagery collection ranged from 0 (for SP) and 39.8 (±1.4) (for WAP). The mean (±1 SD) number of days per annum sea-ice-covered (days) varied from 0 (for SP and SG) to 117.4 (±7.4) (for WAP).

Mean daily and peak NPP for the 14-year period prior to respective imagery collection were highest at WAP and SP, respectively. For SP, SG, MC and WAP collectively, mean (±1 SD) daily NPP values (mg C m^{-2} d^{-1}) ranged from 300.3 (±0.2) to 389.3 (±36.5), and mean (±1 SD) peak NPP values (mg C m^{-2} d^{-1}) from 520.4 (±0.9) to 1126.8 (±548.4).

Mean (±1 SD) sea surface temperature (°C) for the 14-year period prior to respective imagery collection ranged from 5.8 (±0.4) (for SP) to −0.8 (±0.0) (for WAP).

Study area-specific means of environmental data can be found in Table S2.

Regarding imagery-informed environmental differences, the finest sedimented (i.e., mud/fine sand) and smoothest seabed (i.e., lowest rugosity) was observed at sites MC2, WAP2 and WAP3. The site with the coarsest sediment (largest grain size) and highest rugosity was SP3, which featured boulders. Coarse pebbles were observed at SG3 and WAP3.

3.2. Zoobenthos of the Scotia Arc imagery

Over 9400 individual fauna were detected across the Scotia Arc imagery, with all functional groups (Table 2) being represented. Overall, images were dominated by pioneer sessile suspension feeders (e.g., ascidians and encrusting bryozoans) and mobile flexible-feeding ophiuroids. Specifically, 39.4% of individuals belonged to the pioneer sessile suspension feeder group, 25.7% to the flexible feeding strategy group, 11.9% to the climax sessile suspension feeder group, which included, for example, demosponges, and 7.3% to the soft sessile predator/scavenger group (exemplified by sea anemones and hydroids) – the remaining individuals were distributed across the nine other functional groups. In addition, 46.8% of all zoobenthic taxa observed were classified as VME taxa, i.e., >4400 individuals.

3.3. Zoobenthic carbon storage across study areas

A zoobenthic specimen of the Scotia Arc study region held, on average, 0.3 g of carbon (with a standard deviation of ±0.6). When looking at the mean (±1 SD) C_{tot} of individual functional groups across all study areas, 0.001 (±0.0007) g was the lowest value calculated (the responsible functional group type being crawling deposit feeders – i.e., holothurians) and 2.1 (±2.3) g the highest (the responsible functional group types being soft mobile predator/scavengers) (see Fig. S2). The mean C_{tot} of a particular functional group varied between the four study areas. Considering all respective specimens, mean C_{tot} was lowest for SG (which bisects the ACC), followed by SP and MC, and highest for WAP.

At site level, means (plus standard deviations) for zoobenthic carbon storage ranged from 2.4 (±2.5) g C m^{-2} at SP1 to 76.0 (±39.4) g C m^{-2} at WAP3. At study area level, means for zoobenthic carbon storage were 8.2 (±8.9), 6.2 (±5.1), 38.6 (±28.8), and 44.6 (±57.9) g C m^{-2} for SP, SG, MC, and WAP, respectively, i.e., the two polar study areas south of the ACC exhibited higher mean carbon storage values compared to the other two areas, collectively averaging 41.6 (±45.6) and 7.2 (±7.3) g C m^{-2}, respectively. Kruskal Wallis tests indicated that all study areas significantly differed in terms of carbon storage except the two lower-latitude areas, SP and SG (Table 3).

3.4. Zoobenthic carbon storage and morphotaxa and functional group richness

An objective of the current study was to investigate relationships between marine biological carbon storage and biodiversity measures (morphotaxa and functional group richness). For all study areas, statistically significant positive relationships were found between zoobenthic carbon storage and morphotaxa richness; however, some relationships appeared stronger than others, in particular, those of SP and WAP (see Fig. 2A) – the most northerly and southerly areas, respectively. Thus, it appeared that greater carbon storage function, within the study region, generally aligned with higher biodiversity (richness). In addition, the carbon-morphotaxa richness relationships of the study areas were all statistically significantly different.

Significant positive relationships were also found between C_{zoo} and functional group richness (Fig. 2B); however, these relationships were not as strong as those observed for C_{zoo} and morphotaxa richness. WAP exhibited the strongest relationship of all areas. Nonetheless, almost all carbon-functional group richness relationships were statistically significantly different, with the relationship of SP and SG the exception (i.e., not significantly different).

3.5. Faunal density and zoobenthic carbon storage

In terms of seabed macro- and mega-faunal densities, WAP exhibited the highest image level faunal density value, 484.9 ind. m^{-2}, and also the highest estimated zoobenthic carbon storage value, 297.5 g C m^{-2} (Fig. 3). When examining lowest faunal densities, some images had no discernible fauna, i.e., faunal densities of zero (including imagery of sites SG2, WAP1 and WAP2). The lowest density greater than zero was observed in an SP1 image at 2.5 ind. m^{-2}. At site level, the highest mean faunal density was 255.1 (±88.4) ind. m^{-2} at WAP3, and the lowest was 12.8 (±2.4) ind. m^{-2} at SP1 – the former aligning with the highest average for carbon storage and the latter aligning with the lowest average for carbon storage (see 3.3). Kruskal Wallis tests indicated that SP statistically significantly differed from all other study areas in terms of faunal density, while SG and MC, SG and WAP, and MC and WAP did not significantly differ (see bottom row of Table 3).

For all study areas, significant positive relationships were found between zoobenthic carbon storage and faunal density, and carbon-faunal density relationships were all statistically significantly different (Fig. 3). Generally, C_{zoo} exhibited a stronger relationship with faunal density than with morphotaxa and functional group richness; the exception being WAP, where the carbon-morphotaxa richness relationship appeared the strongest of the relationships examined.

3.6. VME taxa and zoobenthic carbon storage

VME taxa contributed at least 53% to zoobenthic carbon storage at eight (out of 12) study sites. In the SP study area, VME taxa contributed 81, 87 and 31% at sites SP1-3, respectively; hence, VME taxa contribution to zoobenthic carbon storage was highest at the two Burdwood Bank sites, corresponding with previous observations (Bax, *pers. comms.*). For the SG study area, SG3 (situated on the western shelf) exhibited the highest VME taxa contribution at 56%, while contributions at SG1 and SG2 (both on the southern shelf) were lower at 23 and 7%, respectively. In MC, VME taxa contributions to zoobenthic carbon storage were high across study sites at 53, 82 and 66% for MC1-3, respectively. Finally, VME taxa contributed 86, 31 and 64% at WAP1-3, respectively. Overall, WAP1 (the southernmost site of the study) displayed the highest site-level VME taxa contribution to zoobenthic

Table 3
P-values (with Bonferroni correction) resulting from Kruskal-Wallis tests between Scotia Arc study areas for zoobenthic carbon storage (C_{zoo}; g C m^{-2}) and faunal density (ind. m^{-2}). Regarding continental/island shelf study areas: SP = South Patagonia (specifically the shelf of the Falkland Islands/Islas Malvinas); SG = South Georgia; MC = Marian Cove (of King George Island); and WAP = western Antarctic Peninsula (westward of Marguerite Bay and Adelaide Island). Significant p-values are shown in bold and asterisked.

	SP vs SG	SP vs MC	SP vs WAP	SG vs MC	SG vs WAP	MC vs WAP
C_{zoo}	$p > 0.05$	**$p < 0.001$****	**$p < 0.001$****	**$p < 0.001$****	**$p < 0.001$****	**$p = 0.049$***
Faunal density	***p < 0.001*****	***p < 0.001*****	***p < 0.001*****	*p > 0.05*	*p > 0.05*	*p > 0.05*

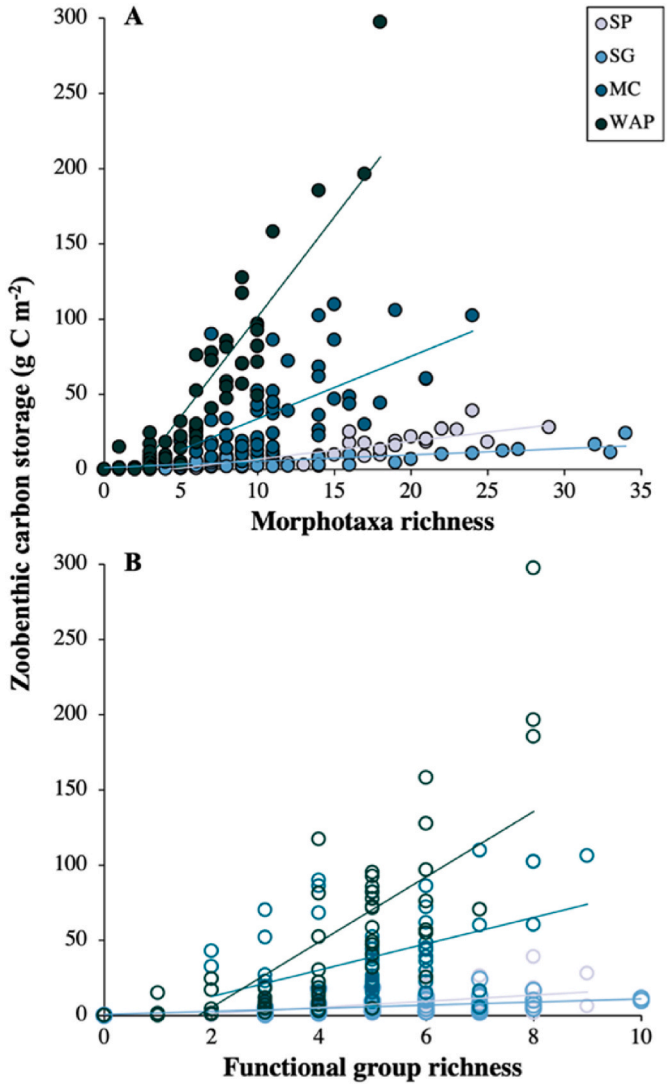


Fig. 2. Carbon storage by zoobenthos (C_{zoo}; g C m^{-2}) versus faunal richness for (**A**) morphotaxa richness and (**B**) functional group richness. R^2 for (**A**): SP = 0.82; SG = 0.42; MC = 0.35; and WAP = 0.82. R^2 for (**B**): SP = 0.19; SG = 0.21; MC = 0.19; and WAP = 0.53. Regarding continental/island shelf study areas: SP = South Patagonia (specifically the shelf of the Falkland Islands/Islas Malvinas); SG = South Georgia; MC = Marian Cove (of King George Island); and WAP = western Antarctic Peninsula (westward of Marguerite Bay and Adelaide Island). For C_{zoo} versus morphotaxa richness, all slopes were statistically significantly different (p-values all <0.001). For C_{zoo} versus functional group richness, all slopes were significantly different (p-values all <0.001, bar SP versus MC, where the p-value was 0.004) except for SP versus SG, where the p-value was non-significant. Regression-associated ANOVA results for C_{zoo} versus morphotaxa richness: F = 258.33, 39.85, 31.69, and 267.30 for SP, SG, MC, and WAP, respectively, and p-values all <0.001, and for C_{zoo} versus functional group richness: F = 12.84, 13.33, 15.76, and 78.87 for SP, SG, MC, and WAP, respectively, and p-values all <0.001.

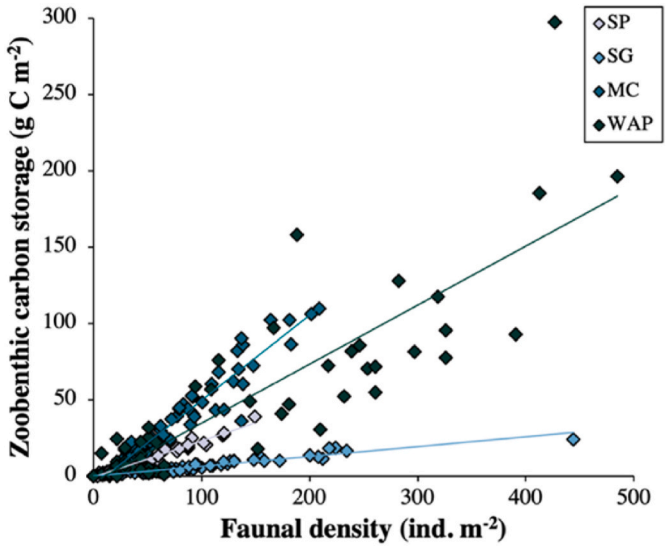


Fig. 3. Carbon storage by zoobenthos (C_{zoo}; g C m^{-2}) versus faunal density (ind. m^{-2}). R^2: SP = 0.97; SG = 0.92; MC = 0.92; and WAP = 0.75. Regarding continental/island shelf study areas: SP = South Patagonia (specifically the shelf of the Falkland Islands/Islas Malvinas); SG = South Georgia; MC = Marian Cove (of King George Island); and WAP = western Antarctic Peninsula (westward of Marguerite Bay and Adelaide Island). All slopes were statistically significantly different (p-values all <0.001). Regression-associated ANOVA results for C_{zoo} versus fauna density: F = 1874.79, 672.35, 639.96, and 172.68 for SP, SG, MC, and WAP, respectively, and p-values all <0.001.

carbon storage of all sites, and SG2 the lowest.

In addition, the relationship between zoobenthic carbon storage and VME taxa density was also examined for each study area (Fig. 4). All carbon-VME density relationships were positive and significant and significantly differed from one another. Compared to carbon and complete faunal density relationships (Fig. 3), the carbon-VME density relationships displayed slightly lower R^2 and less significant p-values for SP and MC, and a much lower R^2 and less significant p-value for SG; however, a higher R^2 and more significant p-value for WAP.

3.7. Functional group contributions to zoobenthic carbon storage and faunal density

Overall, nine functional groups were found to be substantial contributors (i.e., ≥10%) to zoobenthic carbon storage at site level (Fig. 5), the exceptions being sedentary/mobile suspension feeders and all deposit-feeding groups. At area level, six functional groups were substantial contributors (see Fig. S3), including pioneer sessile suspension feeders, climax sessile suspension feeders, grazers, soft and hard sessile predator/scavengers, and flexible strategists. No individual functional group was found to be a substantial contributor to zoobenthic carbon storage at all 12 sites, and similarly, no individual group was found to be a major contributor in all four study areas.

Functional groups which contributed most substantially to the zoobenthic carbon stored at each study area (Fig. S3) included climax sessile suspension feeders at both SP and WAP (49.0 and 50.5%, respectively),

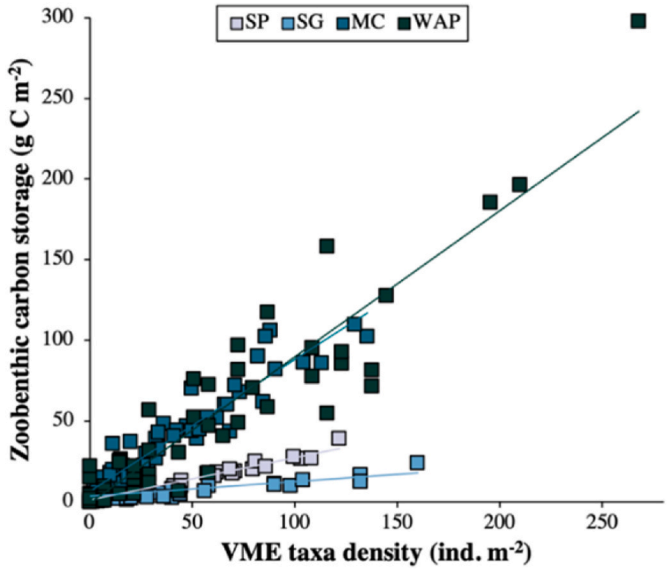


Fig. 4. Zoobenthic carbon storage (C_{zoo}; g C m^{-2}) versus density of Vulnerable Marine Ecosystem (VME) indicator taxa (ind. m^{-2}). R^2: SP = 0.96; SG = 0.40; MC = 0.90; and WAP = 0.87. Regarding continental/island shelf areas: SP = South Patagonia (specifically the shelf of the Falkland Islands/Islas Malvinas); SG = South Georgia; MC = Marian Cove (of King George Island); and WAP = western Antarctic Peninsula (westward of Marguerite Bay and Adelaide Island). All slopes were statistically significantly different (p-values all <0.001). Regression-associated ANOVA results for C_{zoo} versus VME taxa density: F = 1289.91, 37.17, 498.79, and 404.72 for SP, SG, MC, and WAP, respectively, and p-values all <0.001.

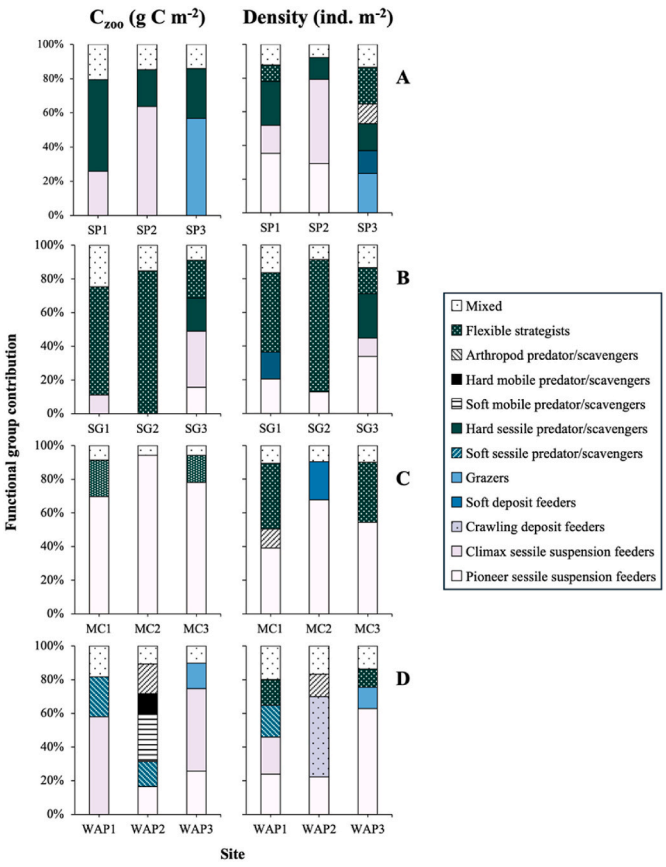


Fig. 5. Average functional group contribution (%) to zoobenthic carbon storage (C_{zoo}; g C m^{-2}) and faunal density (ind. m^{-2}) for continental/island shelf study sites of (**A**) South Patagonia (specifically the shelf of the Falkland Islands/Islas Malvinas), (**B**) South Georgia, (**C**) Marian Cove (of King George Island), and (**D**) the western Antarctic Peninsula (westward of Marguerite Bay and Adelaide Island). Individual functional groups are shown where their contribution was ≥10%. Otherwise, groups were pooled with others whose contributions were also <10% and designated as the "mixed" group.

flexible strategists (i.e., ophiuroids) at SG (54.9%), and pioneer sessile suspensions feeders at MC (80.7%). Other substantial contributors to zoobenthic carbon storage included hard sessile predator/scavengers and grazers at SP, climax sessile suspension feeders and pioneer sessile suspension feeders at SG, flexible strategists at MC, and pioneer sessile suspension feeders and soft sessile predator/scavengers at WAP. The "mixed" group, which included functional groups that individually contributed <10% to zoobenthic carbon storage, also substantially contributed in three out of four study areas (ranging from 13.1 to 20.8%), the exception being MC (at 6.4%).

At a more granular level (i.e., site level; Fig. 5), different combinations of functional groups substantially contributed to zoobenthic carbon storage. For example, functional groups substantially contributing at SP sites included hard sessile predator/scavengers at SP1-3 (53.6, 21.7, and 29.8%, respectively), climax sessile suspension feeders at SP1 and SP2 (25.9 and 63.7%, respectively), and grazers (made up of grazing gastropod molluscs), rather than climax sessile suspension feeders, at SP3 (56.7%). At SG1, flexible strategists (64.3%) and climax sessile suspension feeders (11.1%) were substantial contributors, as well as the mixed group (24.6%). At SG2, flexible strategists were the dominant carbon storage contributors (84.8%), the remaining contributors all within the mixed group (15.2%). At SG3, four individual functional groups substantially contributed to zoobenthic carbon storage: flexible strategists (22.5%; as observed at SG1 and SG2), climax sessile suspension feeders (33.2%; and consistent with SG1), and, in addition, hard sessile predator/scavengers (19.8%) and pioneer sessile suspension feeders (15.7%). The most considerable contribution to zoobenthic carbon storage at MC1-3 was from the pioneer sessile suspension feeders functional group (with a percentage contribution range of 69.7–94.2%), and, at MC1 and MC3, a substantial contribution was also observed from flexible strategists (21.8 and 16.0%, respectively). The mixed group did not contribute substantially at any MC site (all ≤8.5%). At both WAP1 and WAP3, climax sessile suspension feeders were the major contributor to carbon storage (at 58.0 and 48.9%, respectively), although not at WAP2. Site WAP2 appeared to be the most complex with respect to major contributor make-up, with five functional groups substantially contributing to zoobenthic carbon; groups included soft sessile predator/scavengers (in common with WAP1), pioneer sessile suspension feeders (in common with WAP3) and, additionally (and contrary to WAP1 and WAP3), soft mobile predator/scavengers (27.9%), arthropod predator/scavengers (17.5%), and hard mobile predator/scavengers (12.4%).

Across the study region, at both study area and site level, functional group (percentage) contributions to zoobenthic carbon storage differed from respective contributions to faunal density (see Fig. 5 and S3, respectively). For example, at area level, some functional groups had greater contributions to C_{zoo} than density, e.g., climax sessile suspension feeders at SP, SG and WAP, grazers and hard sessile predator/scavengers at SP, flexible strategists at SG, pioneer sessile suspension feeders at MC, and soft sessile predator/scavengers at WAP. Conversely, some functional groups had smaller contributions to C_{zoo} than density, including pioneer sessile suspension feeders at SP, SG, and WAP, soft sessile predator/scavengers at SG, and hard sessile predator/scavengers at MC and WAP (the two south of 60°S polar areas). This observation was similarly the case for site-level functional group percentage contributions (Fig. 5), where some functional groups contributed greatly to C_{zoo} and not faunal density, and vice versa.

3.8. Assemblage and zoobenthic carbon storage structures and potential environmental drivers

With regard to assemblage structure (by functional groups), HAC analysis (with SIMPROF) identified four distinct groupings among the 12 sites (Fig. S4A). WAP2, MC2 and SP3 were each compositionally distinct (hence, each their own group), while the remaining nine sites formed one group (with an average similarity of 75.6% and with pioneer sessile suspension feeders, flexible strategists and climax sessile suspension feeders being the top functional groups contributing to similarity [according to SIMPER]). WAP2 and the group comprising the nine sites were the most compositionally dissimilar (with an average dissimilarity of >44% – principally due to an abundance of crawling deposit feeders and a lack of climax sessile suspension feeders and hard sessile predator/scavengers at WAP2). For more details, see Table S3.

Regarding carbon storage (by functional group) structure, HAC analysis (with SIMPROF) identified six distinct groupings among sites (Fig. S4B). MC2 and WAP2 constituted one group, which had the lowest average similarity at 59.7%, SP3 was compositionally distinct in its own right (hence, its own group), WAP1 and WAP3 formed another group, SP1 and SP2 another, and SG1-3, MC1 and MC3 the final group (with an average similarity of 74.2%). The MC2 and WAP2 group (both polar sites) and the SP1-2 group (the northernmost sites) were the most compositionally dissimilar (with an average dissimilarity of 54.7%). For the SP1-2 group and the MC2 and WAP2 group, dissimilarities were principally driven by hard sessile predator/scavengers, climax sessile suspensions feeders, pioneer sessile suspension feeders, and in-faunal deposit feeders. For more details, see Table S4.

BEST analyses indicated that a subset of four environmental variables most highly correlated with the variation in faunal assemblage structure (by functional groups) (Rho correlation = 0.34, p-value <0.01). The subset comprised sea-ice cover, peak NPP, turbidity, and substratum.

For the carbon storage by functional group data, a subset of three environmental variables was identified as the most highly correlating (Rho correlation = 0.41, p-value <0.01). The subset included sea-ice cover, peak NPP, and temperature.

Sea-ice cover was the single variable with the highest correlation with assemblage and carbon storage by functional groups structures (Rho correlations all >0.32), and sea-ice cover and peak NPP were encompassed in all optimal subsets of environmental variables. The subsets, therefore, included a mixture of remotely sensed and local-scale environmental variables.

Additionally, when examining zoobenthic carbon storage as a single response variable, sea-ice cover was both the single variable with the highest correlation and the optimal subset (Rho correlation = 0.26, p-value <0.01).

3.9. Influence of dropstones

The influence of dropstones and boulders (relatively raised physical seabed features) on zoobenthic carbon storage and other biological variables was also examined. All dropstones observed were of boulder grain sizes (i.e., >256 mm; Blair and McPherson, 1999). Dropstone images, although relatively rare, representing just 3% of the Scotia Arc imagery analysed, displayed higher values (means) than non-dropstone images for all biological variables explored, i.e., morphotaxa and functional group richness, zoobenthic carbon storage and faunal density; however, Wilcoxon matched-pair signed-rank tests revealed these differences to be statistically non-significant (Table 4) – perhaps due to the limited sample size. SP1, SP2, SG3, MC1-3, and WAP3 each presented paired samples.

Table 4
Results of Wilcoxon matched-pair signed-rank tests for various biological variables of dropstone images and non-dropstone images of Scotia Arc continental/island shelf study areas. "N" indicates sample size (i.e., number of images) and the biological variables examined included morphotaxa and functional group richness, zoobenthic carbon storage (C_{zoo}; g C m^{-2}), and faunal density (ind. m^{-2}).

	Dropstone images $\bar{x}$ (±1 SD) N = 7	Non-dropstone images $\bar{x}$ (±1 SD) N = 7	Wilcoxon matched-pair test results
Morphotaxa richness	18.9 (±7.5)	11.3 (±5.3)	**p = 0.06**
Functional group richness	6.0 (±1.3)	5.0 (±1.3)	**p = 0.07**
Zoobenthic carbon storage	61.1 (±66.1)	30.1 (±44.1)	**p = 0.06**
Faunal density	191.8 (±190.3)	84.1 (±94.0)	**p = 0.09**

4. Discussion

The Scotia Arc study region, which encompasses the southern South Atlantic Ocean and Atlantic sector of the Southern Ocean, is a collective hotspot of climate change, high-latitude biodiversity, and ecosystem services; however, not, as of yet, protection (Rogers et al., 2020; Cavanagh et al., 2021). Much of the study region falls within a proposed network of marine protected areas (MPAs under consideration by CCAMLR (Brooks et al., 2020). Building evidence bases, such as those concerning biodiversity and blue carbon (as an ecosystem service), and VME taxa presence and their contributions to the former, is vital in supporting MPA designations; the current study contributes to such evidence bases. Additionally a recent review, supported by the Intergovernmental Panel on Climate Change, has recommended a synergistic approach to alleviating the biodiversity and climate crises (i.e., Pörtner et al., 2023). Although such an approach is seemingly yet to be implemented in polar waters, evidence is building, including from this study, with regard to high-latitude benthic biodiversity supporting carbon storage, and potentially climate change mitigation (Morley et al., 2022; Zwerschke et al., 2022; Sands et al., 2023).

4.1. Variation in zoobenthic carbon storage

Reflecting the complex and patchy nature of southern high-latitude continental/island shelf habitats, zoobenthic carbon storage was here found to vary within and between study sites and study areas – i.e., over different spatial scales. Nonetheless, when comparing the combined average for carbon storage by zoobenthic assemblages of the two southernmost study areas with that of the two northernmost areas, the former was six times greater than that of the latter. This considerable difference in ecosystem function could be for several reasons, including, for example, the two areas south of the ACC being comparatively less disturbed, naturally and/or anthropogenically; both areas experience periods of sea-ice cover, which can afford protection from various physical disturbances such as iceberg scouring (Smale et al., 2008; Clark et al., 2017). In addition, some sites, such as WAP1-2 of the Bellingshausen Sea, are also situated at depths beyond the reach of many modern iceberg keels (Dowdeswell and Bamber, 2007); thus, should evade most ice scouring. This attribute, however, is not shared by WAP3 (the respective site exhibiting the highest zoobenthic carbon storage and faunal density values), which is at a depth of 358 m, and hence, at greater risk of experiencing iceberg-mediated disturbance. Nevertheless, areas with more constant environmental conditions (e.g., deprived of or with minimal disturbance) could promote the development/advancement of benthic communities to later (more complex) successional stages (Teixidó et al., 2007) with potentially positive implications for carbon storage capacity (Barnes et al., 2020). Furthermore, in (seasonally) sea-ice covered areas, sympagic (ice-affiliated) primary production can also be taking place, with the organic matter produced principally reaching and consumed by the benthos (Cautain et al., 2022).

4.2. Extrapolating zoobenthic carbon storage to the antarctic continental shelf

In blue carbon studies, findings are occasionally extrapolated to a wider region/environment (e.g., Barnes et al., 2019, 2020; Sands et al., 2023). For the current study, an extrapolation is made for the Antarctic continental shelf, which is deep (up to 1000 m) and extensive, constituting an area of 4.6 million km^2 (Clarke and Johnston, 2003). However, as around one-third of the Antarctic continental shelf is overlain by ice shelves, floating seaward extensions of the Antarctic Ice Sheet, and very little is known about or documented for the benthic assemblages residing beneath ice shelves, for example, compositional, functional or behavioural traits (see Barnes et al., 2021b; Griffiths et al., 2021; Frinault et al., 2023), this study's extrapolation extends the ice-shelf-free continental shelf only. Based on mean zoobenthic carbon storage from MC and WAP data (south of the ACC), it is therefore estimated that ~125 million tonnes of carbon could be stored on the open-water continental shelf by epi-zoobenthic assemblages alone. This estimate, although conjectural, is equivalent to a CO_2 drawdown of 458 million tonnes, which, for contextualisation purposes only, is a greater amount than the CO_2 (including equivalents) estimated to have been emitted by the United Kingdom in 2022 (DESNZ, 2023). If in-faunal benthic carbon storage were to be included in the appraisal, the amount of carbon stored in Antarctic open shelf benthos, and equivalent GHG drawdown, is potentially considerably higher (e.g., see Zwerschke et al., 2022). Such extrapolations should, nonetheless, be treated with caution, especially in Antarctica, given the innate heterogeneous and patchy nature of its seabed habitats and communities – some areas of the continental shelf appear depauperate while others are highly abundant and biodiverse (Post et al., 2017; Almond et al., 2021; Brasier et al., 2021). Although, in this study, the highest latitude areas of interest already displayed the highest estimated zoobenthic carbon storage values per unit area, it is thought that the capacity of Antarctica's continental shelf to store carbon will, in the absence of disturbance, e.g., from fishery activities, increase with loss of ice cover – potentially acting as a negative feedback on climate change (Peck et al., 2010; Barnes et al., 2020; Morley et al., 2022; Zwerschke et al., 2022; Sands et al., 2023).

4.3. Zoobenthic carbon storage aligns with richness and faunal density

The climate change crisis is considered intertwined with the dilapidation of ecosystems, and the ongoing biodiversity crisis, hence, the degradation or forfeiture of associated functions (IPCC, 2022, 2023; Pörtner et al., 2023; Siegert et al., 2023). Marine ecosystems that can be identified as assisting with moderating climate change (e.g., through their carbon storage capacity), by virtue of hosting diverse biological communities, could be prioritised for protection in marine spatial planning to help address these entangled issues. A key objective of the current study, therefore, was to ascertain whether zoobenthic carbon storage variance aligns with biodiversity measures (richness), and also faunal density. For all study areas, zoobenthic carbon storage increased with richness (biodiversity), particularly morphotaxa richness. Thus, species-rich or carbon-rich areas could be priority areas for protection (permitting both bio/ecological elements to be protected simultaneously). For each area, zoobenthic carbon storage also exhibited a particularly strong relationship with density. Such an alignment has been observed elsewhere, including in the Barents Sea, in the northern hemisphere (Souster et al., 2020), and on the South Georgia shelf (see Fig. 2 of Barnes and Sands, 2017), and potentially indicates that ecosystem monitoring and MPA efficacy evaluations could be supported by higher-level data.

4.4. VME taxa prevalent and major contributors to zoobenthic carbon storage

In the Southern Ocean, seabed conservation and management tools include an array of benthic taxa classified by CCAMLR as VME indicators (CCAMLR, 2009; FAO, 2009). While the approach can be important for decision-making, e.g., regarding CCAMLR MPA design and designation, it is not yet fully known whether all such taxa indicate VMEs or, indeed, are vulnerable themselves (see Dayton et al., 2013, 2016; Fillinger et al., 2013). However, advances are being made to better characterise the vulnerability of these taxa based on morphology (Gros et al., 2023). The current study importantly has shown that VME indicator taxa are both prevalent components of benthic assemblages observed, particularly those assemblages of Burdwood Bank (and polar site WAP1), and major contributors to zoobenthic carbon storage in all study areas explored (although not uniformly so). This finding is of further interest as VME taxa are also often habitat formers/providers (correspondingly termed ecosystem engineers); hence, a co-benefit resulting from their presence (and protection) is the elevation of biodiversity levels and attendant functions (Buhl-Mortensen et al., 2010). In addition, as VME density-carbon relationships were similar to faunal density-carbon relationships, this may be potentially useful information for CCAMLR (or other regional management organisations) which exclusively (or particularly) monitor VME taxa. Such findings concerning VME taxa could be leveraged in marine spatial planning and protection prioritisation decisions in (and beyond) the study region.

4.5. A functional group approach for benthic assemblage analysis under environmental change

Several investigations, across both hemispheres, have employed a functional group approach to characterising benthic community structures and functions, for example, via grouping taxa by feeding mode (e.g., Jansen et al., 2020; Thyrring and Peck, 2021). A functional group approach has varied advantages, such as enabling the functionality of biodiversity to be examined and vastly reducing imagery appraisal times – the latter a renowned bottleneck between the acquisition of seabed images/video and desired outputs (Bowden et al., 2020), and ever more critical given the rate of environmental change, particularly, for example, in West Antarctica. Notably, in this study, different and multiple functional groups were major contributors to zoobenthic carbon storage across study areas (and sites). This finding indicates that, as at South Georgia (Barnes and Sands, 2017), all functional groups should be considered in view of protecting the carbon storage function of the benthos and benthic habitats. When comparing which groups majorly contributed at sites, MC1 and MC3 were the most similar – of all the sites, these sites were the closest in distance (<1 km) and situated within a relatively enclosed fjord basin.

4.6. Biological patterns and their environmental context, including sea-ice incidence

Consideration of the environment in which organisms live and habitats persist provides the opportunity to detect bio-environmental relationships (e.g., Cummings et al., 2018; Gutt et al., 2019) – helpful for understanding and predicting the effects of environmental change. In the current study, environmental data, of various spatial and temporal scales, were derived from in situ measurements, remote sensing and imagery, providing a contemporary environmental context to biological observations in the Scotia Arc study region. However, some of the environmental variables considered, and found to be coincident with zoobenthic carbon storage, are expected to be modified by climate change (Rogers et al., 2020), for example, long-projected sea-ice decline (Fox-Kemper et al., 2021). In the polar seas, sea-ice cover, including concentration, extent, timing and duration (the latter two features also referred to as "seasonality"), is regarded as a key environmental influencer of seabed habitat biodiversity and functionality (Lohrer et al., 2013; Clark et al., 2017; Pineda-Metz et al., 2020). Nonetheless, sea-ice cover (as well as other types of ice cover, e.g., ice shelf; Gilbert and Kittel, 2021) will likely be reduced due to the impacts of climate change

(depending on timescale, and societal action to mitigate [Pörtner et al., 2023]), with implications for marine community structuring and associated ecosystem services (Rogers et al., 2020; Cavanagh et al., 2021). Given the current climatic situation, it is particularly notable when environmental variables likely to modify with climate change are identified as potential drivers of contemporary biological patterns.

Greater zoobenthic carbon storage might be expected in areas void of extensive sea-ice cover, given potentially greater access by benthic fauna to primary-production-derived food, hence, for example, higher faunal densities (Smith et al., 2006; Lohrer et al., 2013). In this study, however, the opposite was observed (for both carbon storage and faunal density). Furthermore, when comparing southern (this study) and northern (Arctic; Souster et al., 2020) high-latitude study regions, C_{zoo} significantly differed between sea-ice-covered and non-sea-ice-covered sites (Fig. 6). For both of the polar regions, sites that experience sea-ice cover exhibited higher C_{zoo} values on average than sites that do not; however, for both sea-ice-cover conditions, the Antarctic study region had greater zoobenthic carbon storage means than the Arctic (though with large standard deviations). Again, this finding could be related to disparities in disturbance regime, where sites covered by sea ice are more shielded from disturbance than those that are not. This observation is similar to that of Frinault et al. (2022) at the Larsen C Ice Shelf front, in that biological variations (faunal densities) did not meet expectations based on ice-cover regime. The Antarctic observations are further interesting as the Bellingshausen Sea (where the sea-ice sites of the current study are situated) is considered a warm polar sea region, and the Weddell Sea (which hosts the Larsen C) is a cold polar sea region (of significance for bottom water formation; Meredith, 2013; Zhou et al., 2023). Thus, irrespective of being a warm or cold southern high-latitude marine region, similar unexpected density relationships appeared with sea-ice incidence. Whether the findings are related to sea ice in terms of sympagic primary production, and affiliated food-falls to the benthos, may also be important to determine (see Cautain et al., 2022).

4.7. Dropstones as potential islands of zoobenthic carbon storage

Dropstones are considered important physical seabed features, sometimes referred to as "islands", offering hard substrata/surfaces for benthic colonisation across swathes of soft/fine sediment (Ziegler et al., 2017), as well as providing platforms for elevation of suspension-feeding fauna into passing bottom currents in search of sustenance, as exemplified below the Filchner-Ronne Ice Shelf, southern Weddell Sea

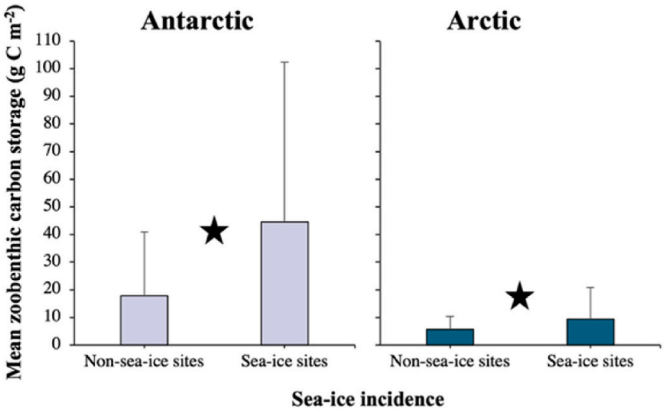


Fig. 6. Mean zoobenthic carbon storage (C_{zoo}; g C m^{-2}) of non-sea-ice and sea-ice sites for Antarctic and Arctic regions. Sea-ice sites correspond to those with a mean annual sea-ice cover of >10%. Data for the Antarctic are from this study, and for the Barents Sea (Arctic), from Souster et al. (2020). A black star indicates a statistically significant difference between non-sea-ice and sea-ice sites ($t = -3.480$ and -4.225 for the Antarctic and Arctic, respectively, with both p-values <0.001).

(Griffiths et al., 2021). In the present study, dropstones were relatively rare, constituting just a few percent of the seabed surface analysed, echoing findings of Post et al. (2020) for the Sabrina continental shelf, East Antarctica, where dropstones (in particular) accounted for <1% of the seafloor surface examined. Similar to results of Ziegler et al. (2017), for fjords of the western Antarctic Peninsula, the current study also found that dropstones generally supported higher morphotaxa richness and faunal densities and, in addition, zoobenthic carbon storage. Although in this study (as observed in others), dropstones were of low occurrence, given their association with ice-rafted debris, including of supraglacial provenance, it may be anticipated that dropstones will become more prevalent as icescapes transform in a warming world, especially in areas undergoing ice-shelf retreat and experiencing increased iceberg generation and transit. In consequence, respective areas may also eventually experience enhanced biodiversity (richness) and faunal densities, and, potentially, increased zoobenthic carbon storage, although other environmental factors (and changes to them) will also shape benthic community structure and function (Rogers et al., 2020).

4.8. Protection of benthic biodiversity aligns with safeguarding of zoobenthic carbon storage

Antarctica, its surrounding seas, and hence marine ecosystems and associated components, are currently under the protection of the Antarctic Treaty (due for renegotiation by 2048; Rogers et al., 2020) and attendant conventions, including those prohibiting mineral exploration (and exploitation), whaling and sealing, and restricting fishing activities, including pertaining to Antarctic krill, *Euphausia superba* – a key species of the Southern Ocean food web (Trathan and Hill, 2016; Rogers et al., 2020). Nonetheless, no convention presently exists directly addressing the safeguarding of Antarctic benthos (which includes most of Antarctica's known species), thus related functions. Nevertheless, as climate change intensifies and further ice-cover loss is experienced, the Southern Ocean and the Antarctic continental shelf will become more accessible; thus, novel challenges may be presented regarding the protection and endurance of benthic blue carbon estates of this southern high-latitude region. Further protections could be placed on blue carbon and possibly in a way that benefits international stakeholders – for example, via sharing the value of carbon stored by benthic or other marine habitats of the region between Antarctic Treaty nations, e.g., for incorporation into corresponding nationally determined contributions (as appropriate, and as per the 2015 Paris Agreement; UNFCCC, 2023). Given that benthic carbon storage and biodiversity have been shown to align, protecting blue carbon habitats and ecosystems could support both climate change mitigation and the safeguarding of biodiversity, and hence contribute to alleviating the associated crises.

5. Conclusions

Exploring four distinct continental shelf areas, all connected by the Scotia Arc, has provided an indication of how zoobenthic carbon storage capacity can vary along a southern polar gradient, with seabed habitats of the southernmost areas, i.e., those south of the ACC, currently supporting greater carbon storage (with a sixfold higher storage average presented). This exploration has also revealed that high-latitude zoobenthic carbon storage consistently aligned with faunal richness and density, as well as density of VME indicator taxa – the former finding supporting that the protection of benthic biodiversity could be complementary to the protection of benthic blue carbon (and vice versa), and the lattermost finding confirming that VME indicators can be important contributors to benthic blue carbon. Functional group contributions to carbon storage were also found to vary within and between study areas, advocating the notion of "collective protection" of high-latitude and polar benthic assemblages to best support their carbon storage function. In addition, and although other variables are likely

influential, zoobenthic blue carbon, in the confines of this study, appeared coincident with sea-ice cover – an environmental variable sensitive to ocean and atmospheric warming.

The current study has provided contemporary estimates of benthic blue carbon in terms of principally (epi-)zoobenthic carbon storage, as well as ecological and environmental baselines, and supports the protection of the benthos as a whole when considering, by example, the protection and endurance of their carbon storage function. Furthermore, findings may also contribute to evidence bases supporting high-latitude marine conservation measures and climate-considerate marine spatial planning.

CRediT authorship contribution statement

Bétina A.V. Frinault: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **David K.A. Barnes:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

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

Data availability

The imagery analysed for this study can be found at the UK Polar Data Centre.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106621.

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Spatial competition in a global disturbance minimum; the seabed under an Antarctic ice shelf

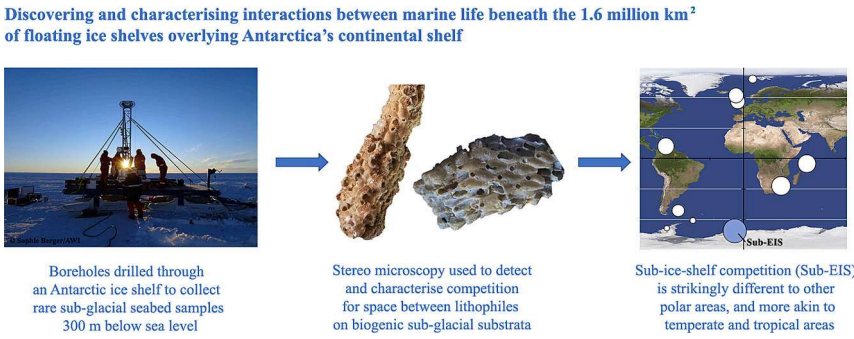
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HIGHLIGHTS

- Life in vast sub-ice-shelf habitats among Earth's least known and least disturbed.
- Boreholes through Ekström Ice Shelf allow unique access to sub-glacial benthos.
- Seabed samples provide first evidence of competition for space under ice shelves.
- Sub-ice-shelf spatial competition complex and globally-high in intensity and severity.
- Implications for ecosystem response to climate-induced environmental change.

GRAPHICAL ABSTRACT



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ABSTRACT

The marine habitat beneath Antarctica's ice shelves spans ~1.6 million km^2, and life in this vast and extreme environment is among Earth's least accessible, least disturbed and least known, yet likely to be impacted by climate-forced warming and environmental change. Although competition among biota is a fundamental structuring force of ecological communities, hence ecosystem functions and services, nothing was known of competition for resources under ice shelves, until this study. Boreholes drilled through a ~ 200 m thick ice shelf enabled collections of novel sub-ice-shelf seabed sediment which contained fragments of biogenic substrata rich in encrusting (lithophilic) macrobenthos, principally bryozoans – a globally-ubiquitous phylum sensitive to environmental change. Analysis of sub-glacial biogenic substrata, by stereo microscopy, provided first evidence of spatial contest competition, enabling generation of a new range of competition measures for the sub-ice-shelf benthic space. Measures were compared with those of global open-water datasets traversing polar, temperate and tropical latitudes (and encompassing both hemispheres). Spatial competition in sub-ice-shelf samples was found to be higher in intensity and severity than all other global means. The likelihood of sub-ice-shelf competition being intraspecific was three times lower than for open-sea polar continental shelf areas, and competition complexity, in terms of the number of different types of competitor pairings, was two-fold higher. As posited for

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an enduring disturbance minimum, a specific bryozoan clade was especially competitively dominant in sub-ice-shelf samples compared with both contemporary and fossil assemblage records. Overall, spatial competition under an Antarctic ice shelf, as characterised by bryozoan interactions, was strikingly different from that of open-sea polar continental shelf sites, and more closely resembled tropical and temperate latitudes. This study represents the first analysis of sub-ice-shelf macrobenthic spatial competition and provides a new ecological baseline for exploring, monitoring and comparing ecosystem response to environmental change in a warming world.

1. Introduction

With anthropogenic greenhouse gas (GHG) emissions at unprecedented levels and atmospheric carbon dioxide concentrations still rising (Friedlingstein et al., 2022), one of the most significant, and perhaps most conspicuous, changes to a warming world is the shrinking of the cryosphere (icescape) (Turner and Comiso, 2017; IPCC, 2019; Parkinson, 2019; Rogers et al., 2020).

In the southern polar region, ice shelves are the floating extensions of the Antarctic Ice Sheet, dominate most of the Antarctic coastline, fringing ~75 % (Rignot et al., 2013), and overlie one-third of Antarctica's continental shelf (Clarke and Johnstone, 2003). The under-ice-shelf marine environment is aphotic and vast, ~1.6 million km^2 (Clarke and Johnstone, 2003), and, mainly on account of challenges of access, one of the least known habitats on Earth (Barnes et al., 2021b; Griffiths et al., 2021), as well as one vulnerable to GHG-induced global warming (Miles et al., 2017; Lai et al., 2020; Gilbert and Kittel, 2021). Furthermore, the seabed underneath ice shelves is ostensibly among the least disturbed marine surface habitats on the planet (Barnes, 2017).

In Antarctica, episodic retreats and collapses of ice shelves at their outer marine termini, calving fronts, constitute a major source of icebergs (Bigg, 2015). Such icebergs can cause disturbance by colliding with the seafloor of the open-water polar continental shelf (Gutt, 2001). These collisions, referred to as "ice scours" or "iceberg ploughmarks", can be ubiquitous across the shallower shelf of the seasonal sea ice zone and occur to maximum depths of 650 m (Dowdeswell and Bamber, 2007), and are considered one of the most catastrophic natural disturbance events to benthic marine systems (Gutt and Starmans, 2001). In contrast, the expansive seafloor underneath ice shelves is relatively undisturbed, the presence of (permanent) ice shelf above affording it protection from ice-mediated disturbance, in some instances over millennia timescales. Thus, in terms of natural disturbance, Antarctica's continental shelf comprises some of the most and least disturbed seabed habitats on Earth (Gutt and Starmans, 2001; Barnes, 2017), with the under-ice-shelf environment representing a rare example of a disturbance minimum for life.

Sampling the environment under ice shelves is challenging and costly, and thus collections of sub-ice-shelf biological samples, are a rarity, constraining our understanding of this vast space. Boreholes hot-water-drilled through ice shelves, however, are an essential method for accessing and enabling the sampling/surveying of sub-ice-shelf marine ecosystems, and various sampling devices can be passed through them into the water column and to the seafloor below. Such access holes, created through less than ten Antarctic ice shelves to date (see Gong et al., 2019), have facilitated some remarkable ecological discoveries, including those related to the underlying seabed habitat and its biotic components. For example, cameras passed down boreholes in the Ross, Amery and McMurdo Ice Shelves uncovered a surprising abundance and variety of seabed-dwelling life – generally unexpected considering the lack of in situ photo-induced primary production, i.e., potential food sources (Pawlowski et al., 2005; Riddle et al., 2007; Kim, 2019). More recently, borehole cameras through Filchner-Ronne Ice Shelf revealed colonisation of hard substrata (a boulder in the particular example) by primary consumers, including suspension-feeding sponges, is possible hundreds of km from the ice-shelf front, and considerable distances from light and open water (Griffiths et al., 2021). Furthermore, physical seafloor samples obtained via sediment grabber and corers dropped through boreholes in the Ekström Ice Shelf, eastern Weddell Sea (Kuhn et al., 2019), provided evidence of benthic life spanning circa 5800 years as well as an unprecedented richness in bryozoan species exceeding even that of the open-sea continental shelf (Barnes et al., 2021b), such assemblages and novel observations of interactions between individual biota/colonies being the basis of the current study.

Competition is a fundamental component and structuring force of communities (Dayton, 1971; Turner and Todd, 1994; Lomolino et al., 2004), hence influences associated ecosystem services. However, the nature of any competition under ice shelves was, until the current study, unknown or unreported. Borehole-derived samples of the lithophilic benthos residing under the Ekström Ice Shelf recently revealed that both cheilostome and cyclostome encrusting bryozoans are represented (Barnes et al., 2021b). Hence, the corresponding samples and their colonisers can be harnessed to discern whether competition, particularly spatial competition, actually occurs under Antarctic ice shelves and, if so, evaluate whether it resembles open-sea polar competition, as well as where it may fit in a more global context. This research, therefore, not only helps narrow a significant knowledge gap but also provides new baseline information for future ecological monitoring and projected long-term Antarctic studies (see Gutt et al., 2022; Lowther et al., 2022). Furthermore, a rare and novel opportunity is provided in that polar latitude data can, in this instance, be decoupled from high disturbance. As the study area has been relatively unaffected by climate change thus far (e.g., especially compared to much of the Antarctic Peninsula) (Gutt et al., 2022), gaining knowledge of the interactions between the contemporary assemblage constituents is particularly valuable as future temporal change can be more confidently attributed to climate/environmental change.

Previously, Barnes and Neutel (2016) demonstrated high-latitude (polar) spatial competition to be extremely hierarchical and suggested that without disturbance, superior competitors would monopolise space. Such monopolisation should, therefore, eventually lead to most spatial competition being intraspecific (i.e., between members of the same species), hence more tie/stand-off outcomes between competitors (as competitively matched) rather than more "severe" definitive win-losses. In addition, polar substrata from continental-shelf depths have indicated low colonisation levels (Barnes and Kuklinski, 2010). Thus, it was first hypothesised that the intensity and severity of sub-ice-shelf spatial competition, being of a very high-latitude environment of minimal disturbance, would be globally low and mainly comprise intraspecific encounters between the strongest competitor(s). Hence, the second hypothesis was that the complexity of spatial competition under ice shelves would also be low, with little diversity in pairwise competitive encounters due to the majority of spatial competition involving the most dominant competitor(s). Finally, McKinney et al. (1998) previously showed that during and following a massive disturbance event (i.e., mass extinction), cyclostomes dominated over cheilostomes, but then cheilostomes recovered to dominate over cyclostomes across calmer geological time. Thus, it was also predicted that cheilostomes would be especially competitively dominant under ice shelves, given that the sub-ice-shelf seafloor environment is anticipated to be a long-standing disturbance minimum.

2. Materials and methods

2.1. Study area and sites

In January 2018 (austral summer 2017/18), as part of the Sub-Ekström Ice Shelf-Observations (Sub-EIS-Obs) Project (Kuhn and Gaedicke, 2015; Kuhn et al., 2019), seafloor material was collected from two continental shelf sites, EIS-2 and EIS-3, underneath the Ekström Ice Shelf, eastern Weddell Sea, Dronning Maud Land, East Antarctica (Fig. 1, Table S1); the wider environs of particular interest for long-term systematic ecological studies related to the impacts of climate and environmental change (see Gutt et al., 2022; Lowther et al., 2022). Sites EIS-2 and EIS-3 were ~ 19.6 km apart, the distance determined using Vector Analysis Tools in QGIS v3.22.9. The site closest to the ice-shelf edge/front, EIS-2, was at 250 m water depth in a 58 m high sub-ice-shelf cavity and ~ 3.4 km from seasonally-open water. The second site, EIS-3, was at 300 m water depth in a 110 m high sub-ice-shelf cavity and ~ 9.6 km from seasonally-open water. Both sites, being sub-ice-shelf (and set back from the ice-shelf calving front), are protected from iceberg-mediated disturbance; indeed, seaward of Ekström's ice-shelf front transiting/drifting icebergs scour and rework the sediment of the adjacent open continental shelf (Oetting et al., 2022 and see Fig. 7 within).

2.2. Collection of physical samples (seabed substrata)

The sub-glacial seafloor samples of this study (corresponding to one sample per site) were brought up from a depth of 250–300 m to the ice-shelf surface through hot water drill (bore)holes (the ice shelf being ~190 m thick at each location) and were obtained from the seabed surface sediment layer (up to 5 cm depth) using a Wippermann grabber (Wippermann GmbH, Germany) at EIS-2 and JLU vibrocorer (Justus Liebig University, Germany) at EIS-3 (Kuhn et al., 2019; Gong et al., 2019; Kuhn et al., 2021). Dead bryozoan fragments (skeletons), i.e., the seabed substrata examined in this study, constituted 9.7 and 8.95 % of

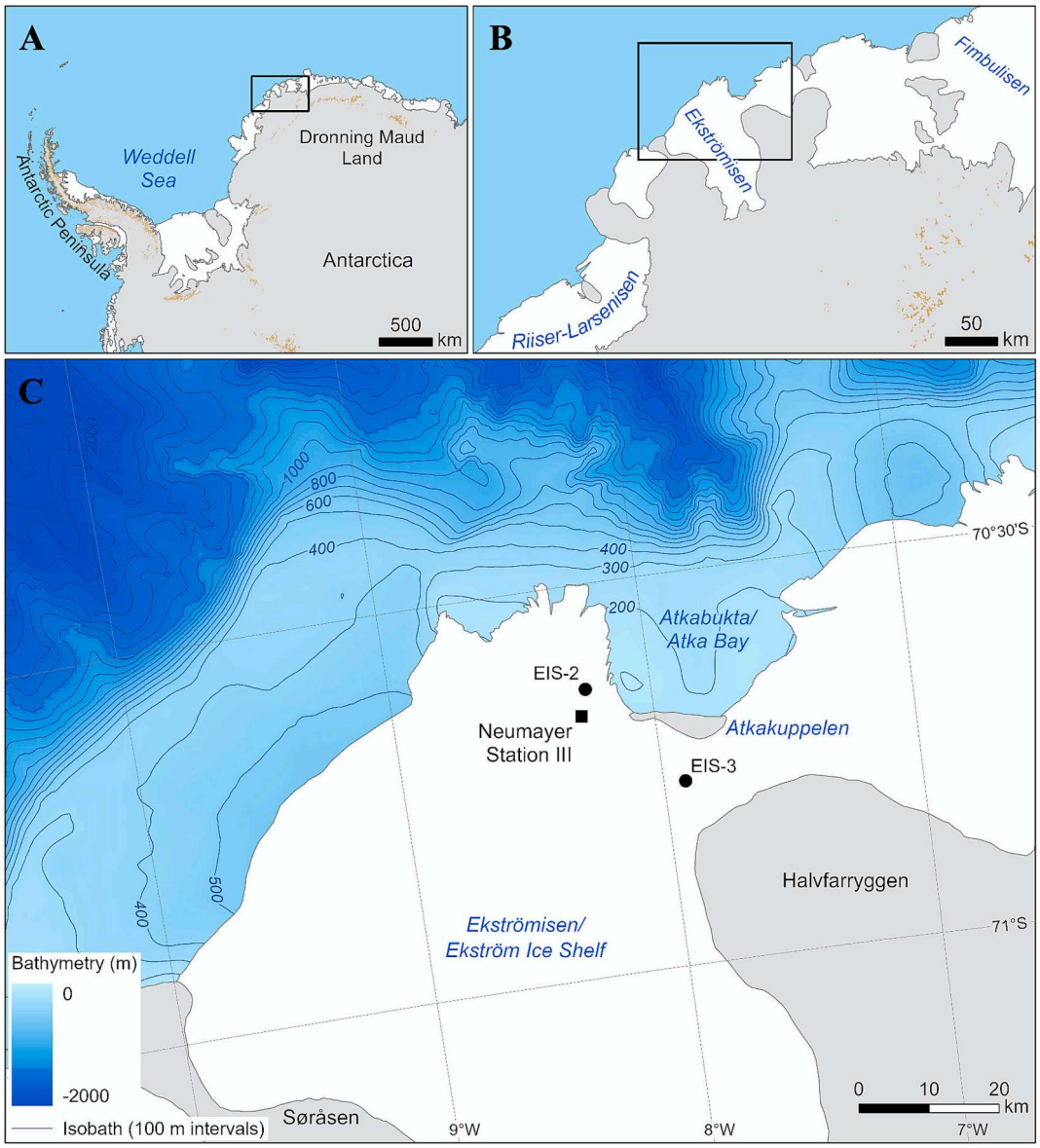


Fig. 1. East Antarctic Southern Ocean study zone and sites. White indicates ice shelves, and grey indicates ice-covered land/grounded ice. (A) Weddell Sea region indicating the Antarctic Peninsula, Dronning Maud Land and general location of Ekström Ice Shelf and environs; (B) Ekström Ice Shelf (Ekströmisen) and neighbouring ice shelves off Dronning Maud Land with extent of main map indicated; and (C) main map showing locations of borehole study sites, EIS-2 and EIS-3 (black circles), where underlying seafloor substrata, investigated for macrobenthic spatial competition, was collected, and with position of nearby Neumayer III research station shown (black square). Bathymetry is from the International Bathymetry Chart of the Southern Ocean v2 (Dorschel et al., 2022), with 100 m contours.

the seafloor sediment samples of EIS-2 and EIS-3, respectively (see Barnes et al., 2021b).

2.3. Stereo microscopy for analysis of spatial competition

Spatial contest competition between encrusting colonists (predominantly bryozoans) on the isolated bryozoan fragments (158 and 166 for EIS-2 and EIS-3, respectively; 324 total) was examined using stereo microscopes (Leica M165 FC and S8 APO; Leica Microsystem (UK) Ltd., UK), with example images provided in Fig. 2. Each fragment was analysed following the same procedure. For each fragment, the surface area was calculated (cm^2), and all colonies, i.e., potential competitors, residing on the fragment were counted (enabling calculations of colony density, i.e., number of colonies cm^{-2}). Each colony was identified to the highest taxonomic resolution possible, predominantly to species level, using Hayward (1995) and proceeding primary literature. Colonised fragments were further inspected for competitive interactions between colonies, determined whereby the growth boundaries of colonies physically met, with at least 5 % of their perimeter being affected (as per Barnes and Kuklinski, 2004) and signs/indications that both colonies were alive at the time of the interaction, i.e., detection of defensive responses in colony morphology such as the formation of protective spines on newer zooids at the growth edge (e.g., Seroy and Grünbaum, 2018; Liow et al., 2019). Following established criteria, for every competitive encounter, the outcome was classified as either a tie/stand-off or a win-loss; a tie being, for example, where the growth of colonies ceased along the contact margin or reciprocal overgrowth occurred, and a win-loss where a colony overgrew another to cover the apertures of its zooids (Stebbing, 1973; Buss and Jackson, 1979; Barnes and Kuklinski, 2004; Liow et al., 2016). The outcome for each competing colony was also logged (as a tie, win or loss). In addition, for all competitive interactions, the lowest taxonomic divergence point of the competing colonists, i.e., kingdom, phyla, class, family, genus or species, or different colonies of the same species, was also recorded. All data pertaining to microscopy studies were recorded in Microsoft Excel (Microsoft Corp, USA).

2.4. Spatial competition measures explored

Data generated from stereo microscopy analyses were subsequently used to calculate a series of differing spatial competition measures for both EIS-2 and EIS-3 samples. The measures and their associated calculations (based on literature-derived definitions; see Barnes and Neutel, 2016; Barnes et al., 2021a, and summarised in Table S2) were: Density – the number of competitive encounters divided by the total substratum surface area examined; Intensity – the number of competitive encounters divided by the total number of colonies observed, i.e., the probability of a given colony experiencing competition; Severity – the number of competitive encounters resulting in a definitive (win-loss) outcome divided by the total number of colonies, i.e., the probability of a colony being involved in severe competition; Identity – the number of intraspecific encounters (encounters between colonies/individuals of the same species) divided by the total number of competitive encounters, i.e., the probability of a competitive encounter being intraspecific; Dominance – the number of competitive encounters involving the most frequent competitor divided by the total number of competitive encounters; Complexity – the number of different pairwise competitive encounter types (e.g., Competitor A versus B is one type); and Taxonomic spread – the proportion of competitive encounters falling within each of seven categories based on the lowest taxonomic divergence of the respective combatting competitors. The categories included competitors being of the same species (i.e., the most taxonomically similar category and constituting intraspecific competition) to being from different species, genera, families, classes, phyla and kingdoms (the latter being the most taxonomically divergent category). The taxonomic divergence of competitors provides a further way to examine complexity of competition.

2.5. Global open-sea bryozoan assemblage datasets

To determine where sub-ice-shelf competition fits in a more global context, competition measures for EIS-2 and EIS-3 were compared with those obtained/calculated from available and comparable global open-sea bryozoan assemblage datasets (Barnes and Kuklinski, 2010; Barnes and Neutel, 2016); it is, however, acknowledged that comparisons are constrained in power due to the scarcity of sub-ice-shelf samples necessitating comparisons of single measures with means from elsewhere. The comparison datasets encompassed a latitudinal range of 5 to 78° across the two hemispheres and were classified as either tropical,

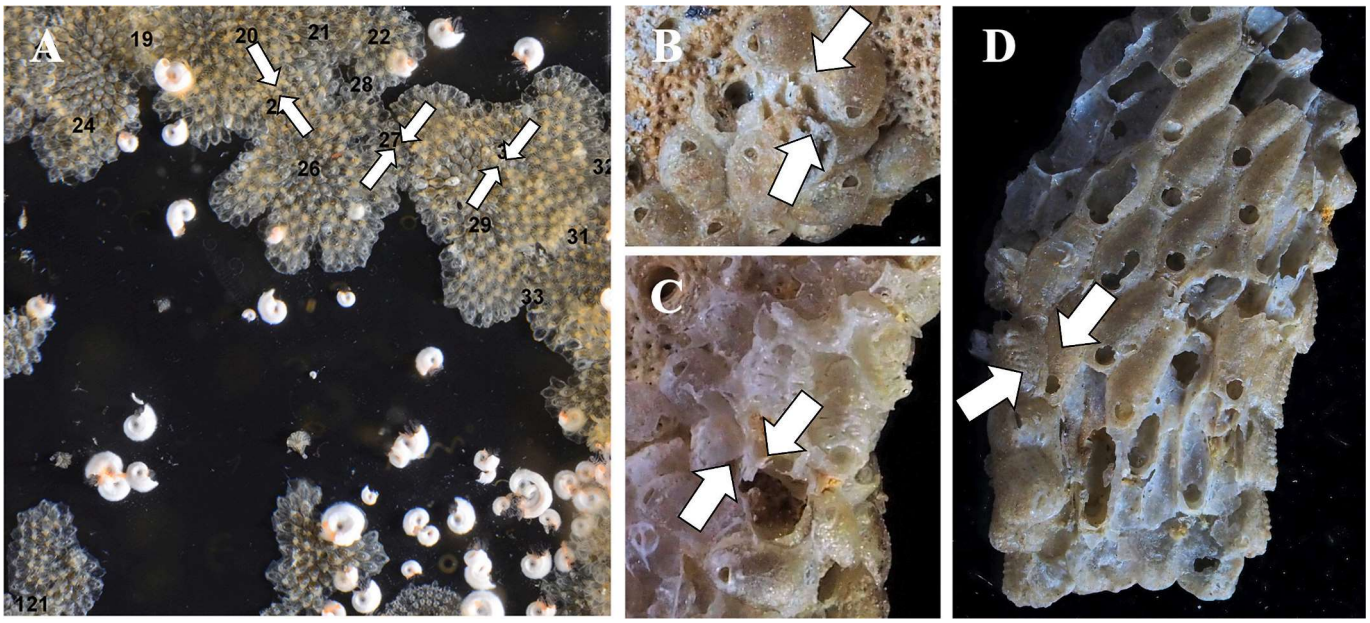


Fig. 2. Example images showing spatial competition between bryozoan colonies (indicated by white arrows): (A) on a settlement panel from Antarctic shallow waters (15 m depth) (Barnes et al., 2021a) and (B-D) on bryozoan fragments of sub-ice-shelf sediment samples (this study), whereby (B) shows colonies of the same species competing for space (intraspecific competition), and (C-D) depict colonies of different species competing for space (interspecific competition).

temperate or polar, defined here as ≤30, >30 to <60 and ≥ 60°N/S, respectively. All datasets focused on encrusting bryozoan assemblages of island or continental shelf systems and employed comparable methods for analysing colonisation and competition. Substrata were abiotic, ranged from pebble to boulder grain sizes (with surface areas of ~2 to 500 cm^2) and collected via SCUBA, Agassiz trawls or dredging techniques. Datasets were based on multiple samples from multiple locations within a sampling area, the exception being the eastern Weddell Sea dataset (Barnes and Kuklinski, 2010), which comprised four individual samples from four locations (and only used for the competition intensity comparison). For more information regarding comparison datasets, see Barnes and Kuklinski (2010) and Barnes and Neutel (2016).

2.6. Interclade spatial competition

The relative competitive success of the two major bryozoan clades, cheilostomes (Gymnolaemata) and cyclostomes (Stenolaemata), was investigated by determining the percentage win rate of cheilostomes against cyclostomes for EIS-2 and EIS-3 using all competitive encounters in which the two clades met. Sub-ice-shelf win rates were then compared to those of literature data, encompassing fossil and recent assemblages. These assembled data span >100 million years before present and global space, i.e., across varying latitudes. The fossil assemblage data was compiled by McKinney (1995) and those of global living bryozoans by Barnes and Dick (2000). The probability of the sub-ice-shelf cheilostome win-rate observation was also calculated.

3. Results

The surface area of sub-glacial substrata (fragments) ranged from 0.2 to 7.2 cm^2, with a mean area of 0.8 cm^2. Of the 158 and 166 fragments microscopically examined from EIS-2 and EIS-3 seafloor sediment samples, 39 and 48 % were found to be colonised by encrusting macrobenthos, respectively. The colonists were identified as predominantly cheilostome, followed by cyclostome bryozoans, with occasional tube-building serpulid polychaetes. Colony density for EIS-2 and EIS-3 substrata was ~1.3 and 1.6 colonies cm^{-2}, respectively. Spatial contest competition was detected on 47 and 30 % of colonised substrata for EIS-2 and EIS-3, respectively, with up to 21 competitive interactions being observed on a single fragment. Competition density for the EIS-2 and EIS-3 samples was ~0.54 and ~0.79 competitive encounters cm^{-2}, corresponding to 5443 and 7875 competitive encounters m^{-2}, respectively. Regarding colonists, cheilostomes were the most speciose taxon, the major occupiers of space on fragments, and were involved in most competitive interactions; for EIS-2, cheilostomes were involved in ~92 % of all pairwise encounters (>94 % when bryozoan-bryozoan encounters considered exclusively), and for EIS-3, cheilostomes were involved in 100 % of the encounters.

3.1. Intensity, severity and identity of spatial competition

The intensity of competition on sub-ice-shelf samples was ~41 and 49 % for EIS-2 and EIS-3, respectively. Sub-ice-shelf intensity values were high relative to global levels (Fig. 3A), and, in particular, very high compared to other polar data from similar depths and region, i.e., the eastern Weddell Sea open-shelf dataset; the mean intensities were 5 % and 15 % for the eastern Weddell Sea shelf and the collective polar region, respectively, therefore sub-ice-shelf competition intensity was nine and three times higher, respectively.

The severity of sub-ice-shelf competition was ~31 and 39 % for EIS-2 and EIS-3, respectively. Sub-ice-shelf severity values were also high relative to global levels and outside corresponding 95 % confidence intervals (Fig. 3B). Competition severity under the ice shelf was much higher than that observed for other polar data; the mean severity of polar data being 12.5 %, hence sub-ice-shelf values almost three times higher (similar in difference to competition intensity).

Regarding competition identity, i.e., the proportion of intraspecific encounters, sites EIS-2 and EIS-3 presented very similar values at 19.4 and 18.7 %, respectively. Sub-ice-shelf identity values also markedly differed from that of open-water polar data (Fig. 3C), the mean intraspecificity of competition for other polar data being >45.5 %, equivalent to greater than a twofold difference. Sub-ice-shelf identity values were more similar to those observed for non-polar environments.

3.2. Complexity of spatial competition

Two initial aspects of competition complexity were investigated: the numerical dominance in encounters by the most frequent single competitor, i.e., the proportion of competitive encounters involving the most common competitor, and the number of different pairwise competitor combinations discerned (Fig. 4).

The numerical dominance by a single competitor at EIS-2 and EIS-3 was 26.4 and 42.9 %, respectively (Fig. 4A). Such under-ice-shelf dominance levels were found to be more comparable with that of equivalent competition in tropical and temperate samples (with means of 39.5 and ~ 49 %, respectively), and around or less than half that previously recorded for polar regions, the collective polar mean being ~85 %, and the Antarctic specific mean 94 %. The species most frequently involved in competitive interactions were cheilostomes *Microporella stenoporta* for EIS-2 and *Lacerna watersi* for EIS-3.

Regarding how many types of competitive encounters were present, sub-ice-shelf samples presented 43 and 31 different types for EIS-2 and EIS-3, respectively (Fig. 4B). The EIS-3 value was more similar to those of lower-latitude and Arctic samples, with the mean number of encounter types for temperate and tropical regions being ~30 and for the Arctic 28, whereas EIS-2 exhibited a particularly high diversity in pairwise competitive encounter types compared to anywhere else. Both

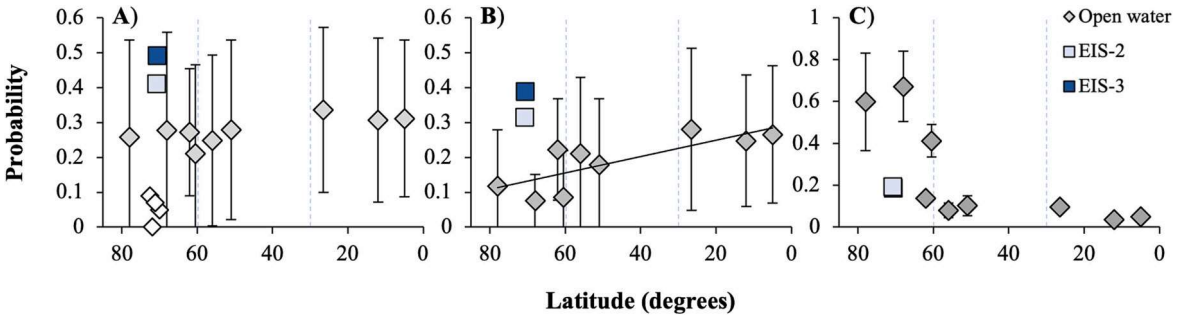


Fig. 3. Spatial competition on marine substrata from under an Antarctic ice shelf and comparison with competition across different latitudes. Including: (A) Intensity; (B) Severity (with regression line); and (C) Identity. Sub-Ekström Ice Shelf (EIS) data are shown as individual samples (with light and dark blue squares for sites EIS-2 and EIS-3, respectively). Open-water data are shown as means with standard deviations for the shallows (grey diamonds, calculated using data from Barnes and Neutel, 2016) and as individual samples for ~120–650 m shelf depths (white diamonds, computed utilising data from Barnes and Kuklinski, 2010). Regression-associated ANOVA indicated a significant inverse relationship between latitude and competition severity ($R^2 = 0.61$, $F = 10.99$ and $p = 0.01$).

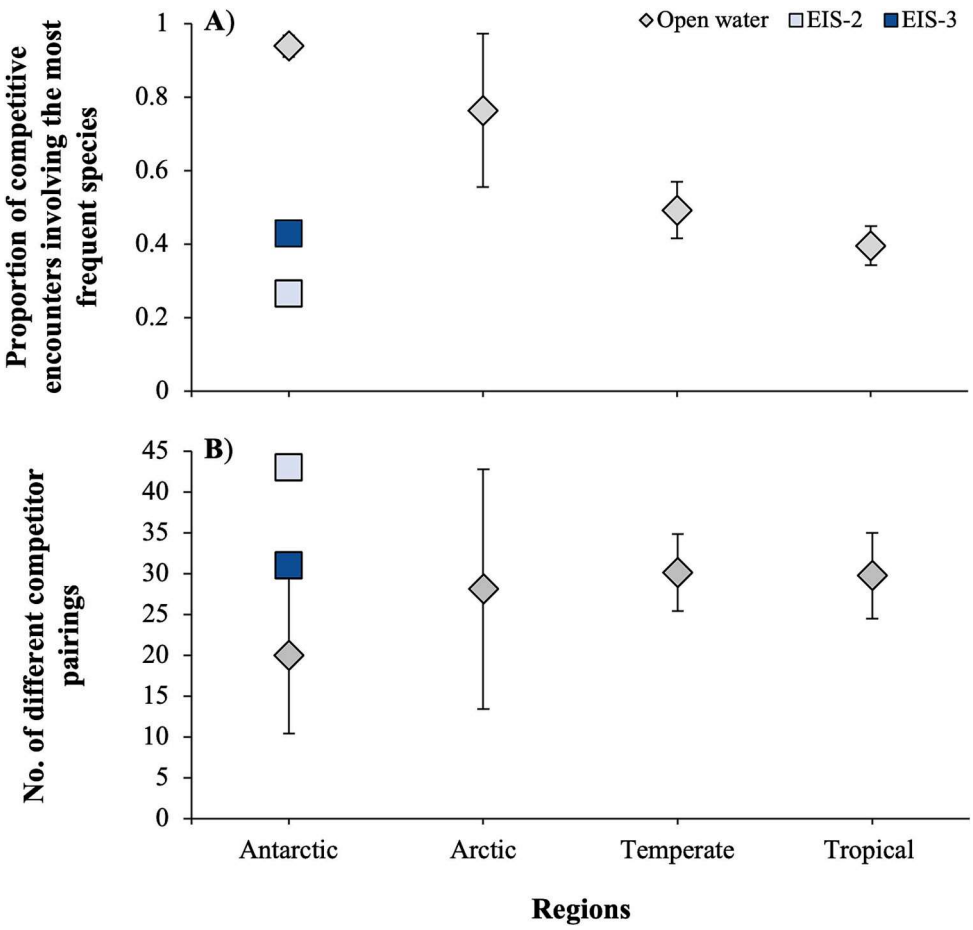


Fig. 4. Complexity of spatial competition on marine substrata from under an Antarctic ice shelf and comparison with competition complexity of Antarctic, Arctic, temperate and tropical regions. Including: (**A**) Numerical dominance of the most frequent competitor in interactions; and (**B**) Variety of pairwise competitive encounter types. Sub-Ekström-Ice-Shelf (EIS) data are shown as individual samples (squares – light and dark blue for sites EIS-2 and EIS-3, respectively). Open-water data are shown as means with standard deviations for the shallows (grey diamonds, calculated using datasets from Barnes and Neutel, 2016).

under-ice-shelf samples exhibited a greater variety of encounter types (at least >50 % more) than the open-water Antarctic region, which had a mean of 20 types.

3.3. Taxonomic difference between competitors for space

As a broader way of realising complexity of competition, the frequencies of the taxonomic divergences (taxonomic spread) of competitors were explored for the sub-ice-shelf samples and subsequently compared with those calculated from available global datasets (Fig. 5).

For EIS-2 and EIS-3, the taxonomic difference between competitors varied from within species (intraspecific), e.g., *Lacerna watersi*, to between representatives of different phyla, i.e., Bryozoa and Annelida (Fig. 5A). However, the most common spatial competitive encounters found on sub-Ekström-Ice-Shelf samples (i.e., dead bryozoan fragments) were between competitors belonging to different families (of the same class, phyla and kingdom) at >45 and 55 % of all encounters for EIS-2 and EIS3, respectively. The mean proportions of competition being interfamilial for tropical, temperate and polar regions were 72, 68 and 32.7 %, correspondingly, i.e., the sub-ice-shelf findings sitting between that of lower-latitude and polar regions (Fig. 5A,B). Under-ice-shelf patterns of spatial competition also showed comparatively moderate levels of intraspecific competition with a mean >18.4 % (Fig. 5A), whereas means for tropical, temperate and polar regions were ~4, ~10 and >55 %, respectively, i.e., again, the sub-ice-shelf findings lying between lower latitude and polar, however, in this case, more towards tropical and temperate regions.

3.4. Interclade spatial competition

The win rate between the two most abundant marine bryozoan clades: cheilostomes (all of class Gymnolaemata) and cyclostomes (all of class Stenolaemata), was established for each sub-ice-shelf sample. At both under-Ekström-Ice-Shelf sites, cheilostomes were competitively superior and exhibited very high win rates against cyclostomes, at 92.9 % for EIS-2 and 86.2 % for EIS-3 (Fig. 6).

When comparing sub-ice-shelf cheilostome win rates with those of present-day living assemblages and fossil assemblages, the sub-ice-shelf samples interestingly displayed not only two of the three highest win rates against cyclostomes in present-time but also when the fossil record was considered (Fig. 6); the mean win rate for fossil assemblages being 66.5 % across time. The probability of two of the three highest win rates occurring in the sub-ice-shelf samples (out of all 33 samples) is <0.006 (i.e., <1 %).

4. Discussion

Competition for resources, including space, food and mates, is a common and fundamental component of populations and communities across global ecosystems (Lomolino et al., 2004; Schemske et al., 2009). However, to the authors' knowledge, before this study, competition for any resource had not been described for the vast environment under the Antarctic ice shelves. Indeed, prior to recent discoveries that complex, rich and abundant life can occur on the seabed underlying ice shelves (Kim, 2019; Barnes et al., 2021b), the sheer presence of competition in this permanently dark, historically-assumed food-scarce (Clarke and Johnstone, 2003) habitat may have been a surprise. The results of the current study, however, not only show for the first time that competition

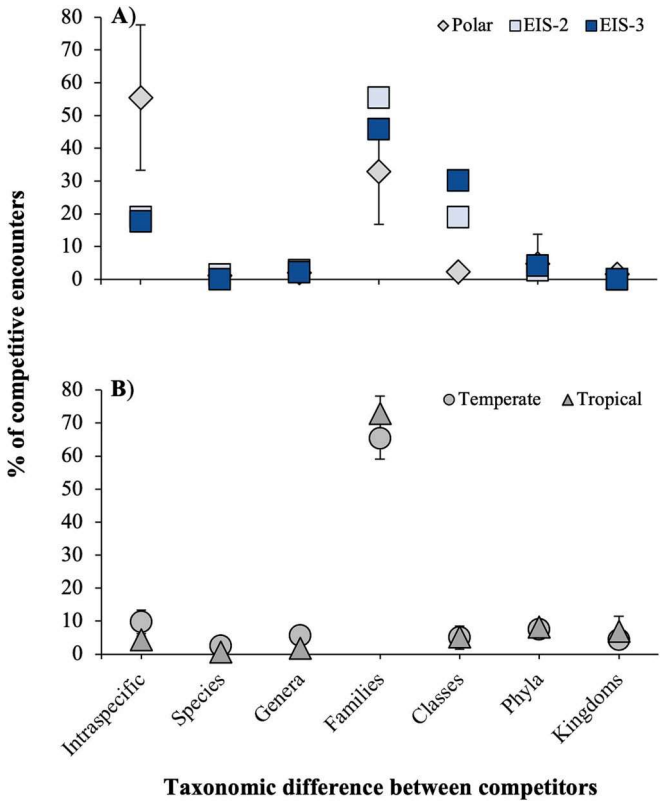


Fig. 5. Taxonomic difference between competitors for space on marine substrata from under an ice shelf and comparison with different regions. Including: (A) polar – sub-ice-shelf and open water; and (B) temperate and tropical. Sub-Ekström Ice Shelf (EIS) data are shown as individual samples (with light and dark blue squares for sites EIS-2 and EIS-3, respectively). Open-water data are shown as means with standard deviations for the shallows (calculated utilising data from Barnes and Neutel, 2016) with symbols for polar, temperate and tropical regions being diamonds, triangles and circles, respectively.

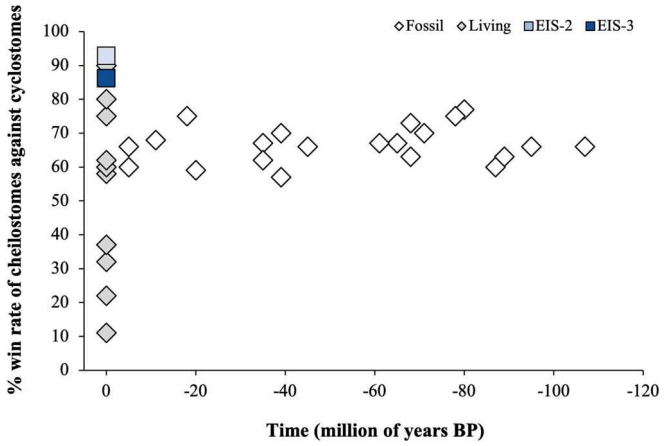


Fig. 6. Outcomes of spatial competition between two major marine bryozoan clades: Cheilostomatida and Cyclostomatida, in terms of cheilostome win rates (%) over cyclostomes, on marine substrata from under an Antarctic ice shelf, Ekström Ice Shelf (EIS), and comparison with win rates of open-water global living and fossil assemblages (i.e., present and before present, BP) (Barnes and Dick, 2000 and references therein).

is present, indeed prevalent below an ice shelf (Ekström Ice Shelf, Dronning Maud Land), but also that the nature of such sub-ice-shelf competition is quite different from any previously reported from open-water polar latitudes.

Sub-ice-shelf spatial competition was not of globally-low intensity or severity as initially hypothesised. Instead, both measures were high under Ekström Ice Shelf relative to those of the global marine data, and particularly compared to other polar data from open-water areas of the seasonal sea ice zone (Fig. 3A,B). If present, under-ice-shelf competition was expected to be principally intraspecific, as observed elsewhere in polar seas; however, this was not supported – just 18–19 % of competitive encounters were intraspecific compared to a non-sub-ice-shelf polar mean of ~46 % (Fig. 3C). The second hypothesis that competition complexity under an ice shelf would be low (as in other polar areas) was also not supported; sub-ice-shelf samples displayed higher complexity levels than all other global datasets (Fig. 4A,B), and the taxonomic divergence of competitors was predominantly at the family (followed by class) level rather than at the intraspecific level (Fig. 5). The expectation, based on McKinney et al. (1998), that cheilostome bryozoans would be extremely competitively dominant over cyclostomes in such a disturbance minimum as under an ice shelf was, however, supported by the results of the study (Fig. 6). Nonetheless, in all the measures of spatial competition explored, sub-ice-shelf competition bore most resemblance to lower-latitude (non-polar) rather than open-sea high-latitude (polar) competition. In respect, the nature of competition for resources in one of Earth's least known, and perhaps least disturbed habitats appears (according to the current study) to be atypical and has a distinctive mix of attributes compared to similar assemblages elsewhere (e.g., Karlson and Jackson, 1981; Quinn, 1982; Russ, 1982; Chornesky, 1989).

Competition for resources can frequently occur between competitors of differing taxonomic relatedness, as extreme as belonging to different kingdoms (Hochberg and Lawton, 1990) or phyla (Brown and Davidson, 1979). These extremes in competitor relatedness are common in the marine environment and often involve humans as competitors (Diamond, 1987), e.g., for fish stocks (Östman et al., 2013; Hansson et al., 2018) or space via coastal development/re-assignment (Richards and Friess, 2015) – such competition for such resources having considerable ramifications for society and nature's near future. Taxonomic relatedness of spatial competitors is not randomly spread in terms of frequency, and on the seabed, competition appears to be most commonly interfamilial (between members of different families) for reasons yet to be clarified. However, polar coastal shelf competition is predominantly intraspecific (Barnes et al., 2014; Barnes and Neutel, 2016), except seemingly under ice shelves (this study). The current study explored how competitive encounters were distributed across a competitor-relatedness spectrum in an environment unlike any other investigated to date – the seabed underneath an ice shelf. The spread of competitive encounters for space across the competitor-relatedness spectrum was similar for both sub-ice-shelf sites; however, the overall pattern differed from that of other global data (Fig. 5).

Historically, under-ice-shelf environments were thought to be food-sparse yet space-plentiful, with low densities of a few colonist species (Griffiths et al., 2021). However, it is now known, principally through studies utilising borehole-enabled seafloor imagery and sediment sample collections, that some benthic assemblages under ice shelves can be dense and complex (e.g., Riddle et al., 2007; Kim, 2019). If competition for any resource was anticipated in an environmental setting of seemingly little food and much space, exploitation competition (for scarce food) might have been more expected than contest competition. However, from the limited imagery that has been obtained from sub-ice-shelf seafloor environments and reported on (e.g., Post et al., 2014), it would appear that substrata typically viewed as "hard" and colonisable, such as dropstones (Ziegler et al., 2017) and boulders (Griffiths et al., 2021), also seem rare; thus, space for colonisation by encrusting species (lithophiles) is potentially at a premium in the under-ice-shelf habitat, hence competed for. From the current study on sub-glacial substrata from the eastern Weddell Sea, it is now evident that even when much finer-grained suitable hard substrata are available under ice shelves, such as biologically-generated skeletal fragments (Barnes et al., 2021b; and this

study), encrusting biota can be both abundant and species-rich, and much spatial contest competition can transpire.

In the under-ice-shelf environments investigated in the current study, bryozoans, specifically cheilostomes, were both the major spatial competitors and the main spatial resource (hard substrata) being competed for, i.e., as dead fragments of erect bryozoans – the cheilostomes re-purposed, following death, as platforms for new life. This type of ecosystem structuring, whereby organisms use the skeletal remains of others as living space (i.e., "taphonomic feedback"; Kidwell and Jablonski, 1983), is also reflected in coral reef systems, where coral is the primary substratum and competitor for this space (e.g., Buss and Jackson, 1979); otherwise, coral reefs and under-ice-shelf benthic habitats appear considerably contrasting.

Food availability, and quality, are important to the structuring of marine benthic assemblages (Svensson and Marshall, 2015; Campanyà-Llovet et al., 2017), as is space in all habitats, not least for access to food (Kellner and Asner, 2014). It has been speculated by Barnes et al. (2021b) that food might be so limited under ice shelves that spatial competitors with feeding (planktotrophic) larvae may struggle to survive and colonise space there. Indeed, most of the competitors for space identified in the present study were those with exclusively yolk-feeding (lecithotrophic) larvae. This apparent dominance of larval form could be because lecithotrophic larvae are less sensitive to a potentially food-poor/−inconsistent water column, whereas planktotrophic larvae must feed in the water column to achieve the size and maturity required for settlement (and subsequent metamorphosis to colony development). In addition, lecithotrophic larvae are generally thought to have lower dispersal capabilities than planktotrophic larvae, so presumably would mostly settle closer to their origin, providing appropriate substratum is available, such as the cheilostome bryozoan fragments in this study. Nonetheless, clearly an adequate enough or adequately consistent food supply has been present and/or delivered under Ekström Ice Shelf, at least to the sites sampled, to also support adult planktotrophic life there over thousands of years (Barnes et al., 2021b).

While Antarctica's open continental shelf hosts some of Earth's most naturally disturbed environments (Gutt and Starmans, 2001), the seafloor underneath ice shelves comparatively represents a disturbance minimum and a potential refuge from natural (and potentially anthropogenic) disturbance, in part owing to the existence and persistence of the floating ice shelf above, and additionally evidenced by lifespans, under Ekström Ice Shelf, of almost 6000 years (Barnes et al., 2021b). These two systems, either side of the ice-shelf front, therefore, present as profoundly different settings for competitors and competition. McKinney (1995) found that in environmental conditions of strong fossilisation (warm shallow seas), competition for space between the two major bryozoan clades remained relatively constant over a 100 Ma time span, with cheilostomes (consistently) competitively outperforming cyclostomes, with a mean win rate of 66.5 % across time. However, evidence from current habitats across Earth's wider spectrum of environmental conditions indicates competition between these clades, and the competitive success of one over another, can be much more variable (Barnes and Dick, 2000). If under-ice-shelf environments are as extreme as being long-enduring disturbance minima, hence also potentially echoing conditions of calmer geological time, the expectation was to find extreme interclade results, which is precisely what was found in this study; cheilostomes winning, on average, ~90 % of spatial contests against cyclostomes (Fig. 6).

Marine ice losses are one of the most striking and rapid responses to global climate change (Turner and Comiso, 2017; Parkinson, 2019). Although ice-shelf dynamics have proven complex, and sea ice losses in some regions have been matched by gains in others, it seems reasonable to deduce that marine (and terrestrial) icescapes, and hence associated habitats such as those explored in this study, must be under considerable threat from GHG-emissions-driven global warming (IPCC, 2019; Gilbert and Kittel, 2021). With ice-shelf retreat or collapse, there is a potential for the disturbance regime of the previously overlain continental shelf to significantly alter – rapidly transitioning from an extremely low- to high-disturbance environment. In response, the nature and dynamics of competition may change, which would have implications for both assemblage structure and broader habitat functions and services that are yet to be fully realised.

5. Conclusions

Rare borehole-derived collections of sub-ice-shelf seabed substrata and stereo microscopy methodologies have provided not just the first evidence of competition from a distinct and mainly unexplored environment, but also from a habitat that has persisted for thousands of years, and, therefore, potentially of exceptionally low disturbance. Due to the ubiquity of bryozoans, sub-ice-shelf findings could be compared with existing global datasets, and although sampling is limited, it appears that spatial competition under Ekström Ice Shelf is not only very different from that of open-water polar areas but also remarkably similar, in several traits, to non-polar marine benthic environments. Whether such findings extend to or are more widely representative of the sub-ice-shelf habitats fringing Dronning Maud Land, East Antarctica, and elsewhere in this vast ecosystem, is yet to be confirmed. Nonetheless, the results of this study further indicate the potential utility of bryozoans as indicators of environmental differences. The findings also offer a precedent that perhaps in a permanently ice-covered and minimally-disturbed seafloor environment, spatial competition among the benthos can be intense and severe, unique in nature, and be dominated by a particular faunal clade.

CRediT authorship contribution statement

Bétina A.V. Frinault: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. **David K.A. Barnes:** Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Validation, Writing – review & editing. **Boris K. Biskaborn:** Resources, Writing – review & editing. **Raphael Gromig:** Resources, Writing – review & editing. **Claus-Dieter Hillenbrand:** Resources, Writing – review & editing. **Johann P. Klages:** Resources, Writing – review & editing. **Nikola Koglin:** Resources, Writing – review & editing. **Gerhard Kuhn:** Resources, Writing – review & editing.

Declaration of competing interest

The authors declare no competing interest.

Data availability

Data are available upon reasonable request.

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Appendix A. Supplementary data

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