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- **MASTER THESIS PROJECT** -

Traits and Drivers: An integrative approach to benthos dynamics on the continental shelf off the Antarctic Peninsula

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Abstract

The Western Antarctic Peninsula is undergoing rapid environmental change in response to climate forcing. The current study collected high precision underwater imagery of epibenthos to investigate biological differences between inner (Marian Cove fjord) and outer (Marguerite Trough) continental shelf benthic assemblages and to identify key environmental drivers. The fjord exhibited significantly higher benthic mega and macrofaunal densities, reflecting productive and diverse ecosystems. Both taxonomic and functional richness increased with distance from the (retreating) glacier terminus within the study fjord and were generally higher in the inner compared to the outer shelf. Furthermore, benthic assemblages transitioned from stress-tolerant taxa near the glacier to more mature communities resembling those of the outer shelf as habitat age (exposure since glacial retreat) increased and environmental conditions became more constant. Overall, suspension feeders numerically dominated along the study shelf, underscoring their role in pelagic-benthic coupling and importance in carbon pathways within polar marine ecosystems. Temperature emerged as a primary predictor for multiple functional groups in the fjord, whilst hard-bottom substrate was a significant driver on the outer shelf. These findings emphasize the complex interplay between environmental conditions and benthic functional structure in this physically and biologically dynamic region.

Key words: **Benthic assemblages, Functional traits, Continental shelf, West Antarctic Peninsula**

Resumen

La Península Antártica Occidental está experimentando un rápido cambio ambiental. El presente estudio recopiló imágenes submarinas de alta precisión del epibentos para investigar las diferencias biológicas entre los ensambles bentónicos de la plataforma continental interna (fiordo Marian Cove) y externa (Marguerite Trough) e identificar los principales impulsores ambientales. El fiordo exhibió densidades significativamente más altas de mega y macrofauna bentónica, reflejando ecosistemas productivos y diversos. Tanto la riqueza taxonómica como funcional aumentaron con la distancia del glaciar (en retroceso) dentro del fiordo estudiado y fueron generalmente más altas en la plataforma interna en comparación con la externa. Además, los ensamblajes bentónicos transitaron de taxones tolerantes al estrés cerca del glaciar a comunidades más maduras similares a las de la plataforma externa a medida que aumentó la edad del hábitat (exposición desde el retroceso glacial) y se estabilizaron las condiciones ambientales. En general, los suspensívoros dominaron numéricamente ambos ambientes, resaltando su papel en el acoplamiento pelágico-bentónico e importancia en las vías del carbono dentro de los ecosistemas marinos polares. La temperatura fue un predictor de las abundancias de múltiples grupos funcionales en el fiordo, mientras que el sustrato duro fue un predictor significativo en la plataforma externa. Estos hallazgos enfatizan la compleja interacción entre las condiciones ambientales y la estructura funcional bentónica en esta región física y biológicamente dinámica.

Palabras clave: **Ensamblaje bentónico, Rasgos funcionales, Plataforma continental, Península Antártica Occidental**

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Glossary

- **Alpha-diversity**: species richness within a single habitat or sampling site. It's a measure of the fauna variety locally.
- **Assemblage**: subunit of a larger community. It's a collection of species that occur in a particular place and time.
- **Bentho-pelagic coupling**: interconnectedness between the seafloor (benthos) and the water column above (pelagos). It emphasizes how bottom-dwelling organisms (benthos) influence and modify the physical and biological properties of the water column (e.g., nutrient cycling and resuspension of sediment).
- **Beta-diversity**: variation in species composition between different communities (e.g., comparison of the species makeup of the benthos between two different sites along the Antarctic coastline).
- **Community**: group of populations of different species that co-exist and interact within a specific habitat.
- **Epifaunal benthos**: Fraction of seabed organisms (fauna) living on the surface of the sediment.
- **Infaunal benthos**: Fraction of the seabed organisms (fauna) living buried within the sediment.
- **Macro- and mega-benthos**: larger-sized organisms (>3mm) easily visible in underwater imagery and video surveys. They can be readily distinguished with the naked eye or through basic sampling techniques.
- **Pelago-benthic coupling**: influence of the water column (pelagos) on the seafloor (benthos). It describes how processes from the water column affect the benthic environment (e.g., the settling of organic matter or the sinking of dead organisms).
- **Rugosity:** physical complexity of the seafloor. A highly rugose seabed would be very uneven, with features like rocks, crevices, and overhangs. Rugosity plays an important role in providing habitat for various benthic organisms.

1. Introduction

1.1 The Southernmost continent on Earth: Antarctica

Antarctica is a vast, icy continent surrounded by the Southern Ocean and divided into East Antarctica and West Antarctica (Jun et al., 2020). The ice sheet, and its seaward extension of ice shelves, expanded during glaciations (90ky of each 100ky) and receded during interglacial periods, relatively warmer intervals such as the current Holocene (Chorley et al., 2023). At its outermost boundary, the Southern Ocean is demarked by the Antarctic Polar Front (APF) – the strongest jet of the powerful and semi-isolating Antarctic Circumpolar Current (ACC) – and the Subantarctic Front (Ward et al., 2002; Derkani et al., 2021). Over much shorter 'ecological' time periods, the Southern Ocean also oscillates between millions of km^2 of sea surface freezing in winter and predominantly open water, studded by roaming icebergs in summer (Barnes et al., 2018). This seasonality is accompanied by water temperature varying from ~-2°C to ~+2°C (Barnes et al., 2006). Despite extreme light regimes due to high latitude, most physicochemical variables such as temperature, dissolved oxygen and salinity, have been relatively constant for considerable time scales (Isla 2023; Peck et al., 2006).

1.2 Antarctic benthos

The Southern Ocean floor supports rich and abundant benthos. Unlike the charismatic megafauna in the water column and sea surface, the benthos comprise many thousands of species (including most of Antarctica's endemics). A significant portion remains undescribed, hinting at the immensity of biodiversity concealed beneath the icy waters (SCARMarBIN, scarmarbin.be).

This benthos is dominated by invertebrates, boasting a richness and abundance as high or higher than any non-coral reef environments in warmer waters (Peck 2018; Krasnobaev et al., 2020). Sponges, for instance, are particularly abundant macroinvertebrates (McClintock et al., 2005) providing a haven for other organisms to colonize their surfaces and interiors (epibionts and endobionts) while also being a food source for predators.

Perhaps the most striking feature of the Antarctic benthos is its high level of endemism. Ascidians, for example, are estimated to have 25-51% of species unique to the Southern Ocean (Avila & Angulo-Preckler, 2021). The exceptional level of endemism in the region likely stems from both historical and contemporary factors. The opening of the Drake Passage and Tasmanian gateways during the Miocene initiated a process of isolation that led to the development of the ACC into its modern-like characteristics (Evangelinos et al., 2024). This large-geophysical scale barrier, combined with polar frontal systems that form the poleward boundary (Hay et al., 2005), has fostered long-term physical constancy and smaller-scale regional isolation (e.g., outlying archipelagos and semi-enclosed seas) (Barnes & Conlan, 2006). The persistent extreme conditions have also led fauna to slow growth rates during larval stages and a condensed reproductive season compared to their warmer-water counterparts (Webb et al., 2020).

Antarctic benthos have a dynamic interplay with the water column above (pelagos), a connection known as bentho-pelagic coupling (such as feeding mainly on pelagic food and many benthos having pelagic larvae) (Ingels et al., 2018). The terms "bentho-pelagic" and "pelago-benthic'' differentiate the direction of this synergy. Bentho-pelagic coupling, sometimes referred to as "upward" coupling, highlights how benthos can influence or modify the pelagos, whilst pelago-benthic coupling, or "downward" coupling, emphasizes the pelagos influencing the benthos, such as the settling of organic matter from the water column, especially that of carbon (Smith et al., 2006). The sinking of diatom aggregates and faecal pellets are examples of efficient pelagic-benthic coupling that facilitates carbon pathways from the surface water column down to the seabed (Bax et al., 2020). Eventually, benthic organisms act as carbon stores, also known as blue carbon, immobilizing carbon in the short-term compared to the long-term carbon accumulation in the seafloor. As long lived consumers within the food web, when the benthic organisms die some of this "blue carbon" can get buried in the seabed, once this burial gets below the oxygenated zone it can become sequestered for millenia (Bergagna et al., 2024). Seasonally ice-free shores of the Antarctic Peninsula, are estimated to hold around 253,000 tonnes of carbon buried at a depth of 20 m with a potential to sequester roughly 4,500 tonnes of carbon annually (Morley et al., 2022). This represents an important contribution to the global carbon cycle.

Abiotic factors, such as particle concentration and sediment grain size, can influence the variety of life forms on the seabed and their ecological roles; and vice versa (Jungblut et al., 2020). The functional diversity of the benthos, meaning specific roles and traits of different species (e.g., feeding types, mobility, and habitat preferences), can determine how efficiently they capture and store this carbon (Barnes & Sands, 2017). For instance, deposit and filter feeders play a critical role in transporting organic matter from the water column to the seabed. Studies have shown that functional diversity can be a stronger predictor of ecosystem functioning than simply species richness (Beauchard et al., 2023; Gagic et al., 2015). While the ideal method remains under discussion, the focus on functional redundancy – the ability of a diverse community to maintain ecosystem functions even if some species are lost – makes studying functional groups a promising avenue for future Antarctic benthos research (Nasir et al., 2024).

Some of the earliest accounts of the richness and diversity of benthic communities relied on traditional techniques, initially SCUBA diving, and in easily accessible areas where permanent coastal scientific research stations and field camps were established (Piazza et al., 2020). Later on, the surveys were augmented in critical ways with the deployment of Van Veen grabs, Agassiz Trawls, epibenthic sledges and innovative techniques such as box cores, multicores, and non-invasive methods based on optical imagery (Frinault & Barnes, 2024; Braeckman et al., 2021; Pineda-Metz & Gerdes, 2018). The diversity of apparatus, collection sites and scientific disciplines examining Antarctic benthic samples has significantly enhanced the understanding of both deep-sea and coastal benthic ecosystems along the continental shelf.

1.3 The vast Antarctic continental shelf

The Antarctic continental shelf, encompassing roughly 11% of global shelf area, is weighed down by a massive ice sheet, consequently it is unusually deep, ranging from 500 to 800 meters (Linse et al., 2006). Accurately mapping the Antarctic seafloor, particularly depressions and troughs, is crucial for understanding how fast glaciers flow and melt. These features can be highways for warm Circumpolar Deep Water (CDW) to reach the ice shelf, accelerating melting and ice loss (Thomas et al., 2023; Etourneau et al., 2019; Dinniman et al., 2018). Furthermore, oceanic exchanges across the continental shelves of Antarctica play an important role in biological systems and the mass balance of ice sheets (Rignot et al., 2019; St-Laurent et al., 2013).

The Antarctic Ice Sheet, for instance, has been a major contributor to sea level rise over the past four decades (Rignot et al., 2024). The West Antarctic Peninsula (WAP), a sector of the West Antarctic Ice Sheet (WAIS) with glaciers that terminate in fjords, has exhibited threshold behavior in response to atmospheric and ocean warming, as demonstrated by the Antarctic Buttressing Model Intercomparison Project (ABUMIP), which found that WAIS could contribute 1.91–5.08 meters to sea-level rise due to marine ice-sheet instability over 500-year simulations (Chambers et al., 2021).

Inner shelf waterbody: Fjord

Fjords linked to continental shelves, such as those found in Greenland and the WAP, are key regulators between tidewater glaciers and continental shelf waters, displaying intricate patterns of overturning circulations and horizontal recirculations mainly influenced by water mass transformation at the fjord's entrance, variability on the continental shelf, and atmospheric conditions (Zhao et al., 2021).

Along the WAP, fjords can show a fairly varied benthic abundance, biomass and biodiversity, owing to diverse weak meltwater influences, minimal sedimentation disturbance, and rich food inputs (Grange & Smith, 2013; Zwerschke et al., 2021). What’s more, WAP fjords are habitat and foraging grounds for Antarctic krill and top predators, such as baleen whales, underscoring the urgent need for deeper knowledge about their structure, dynamics, and climate sensitivity (Barnes et al., 2020).

Benthic ecosystems, however, have been extensively studied in only a few fjordic systems across the WAP. Potter Cove, for instance, hosts a high density and biomass of filter feeder species that derive their energy mainly from benthic primary production (micro- and macro-algae) (Rodriguez et al., 2022). Another well-described fjord is South Bay, where fauna such as sea stars, crustaceans, bivalves and sponges exhibit clear depth zonation patterns along with corresponding substrate features (Rovelli et al., 2022).

Despite the efforts to characterize these assemblages, the marine terminating glacier, like most along the WAP, is rapidly retreating and the resulting massive sedimentation has driven drastic shifts in biota assemblages (Sahade et al., 2015; Braeckman et al., 2024) revealing in some cases a non-linear, rapid, intense, and heterogeneous response (Henley et al., 2019). This may ultimately favor the settlement of specialized benthic organisms adapted to these dynamic conditions, making some fjords habitats suited for resilient species (Garza et al., 2023).

Outer shelf ecosystem: Trough

As fjords are to the coast, another distinctive environment widely found further from shore across the Antarctic continental shelf are the troughs.

During late Cenozoic glaciations, the expansion of ice sheets across the Antarctic continental shelves resulted in the erosion of major shelf troughs (Post et al., 2020). These work as underwater highways, guiding dense, cold water eddies offshore in a chain-like pattern (Gaul et al., 2024) and also channeling the upwelled nutrient-rich CDW –the warm saline water of the ACC– to the base of glaciers (Tamsitt et al., 2021; Etourneau et al., 2019). Across the southern extension of the ACC, many troughs are particularly effective at delivering warm water toward ice shelves in the Amundsen and Bellingshausen Seas (Schulze et al., 2021).

At this point, the troughs become a link with other geographical-oceanographic features such as fjords. Interestingly, when upwelling modified CDW (mCDW) unevenly supplies heat and nutrients, leads to the heterogeneous nature of WAP primary production within the coastal fjords (Cassarino et al., 2020). The mechanisms underlying the heat exchanges have been identified to occur through a meridional melt-driven flow within the trough, the interaction of the mean flow with the topography, as well as eddy-like features through Rossby wave-topography interactions (Brearley et al., 2019; St-Laurent et al., 2013).

In West Antarctica, several troughs play crucial roles in shaping oceanographic and geological features. Extending across the Bellingshausen and Amundsen Seas, the most prominent include Marguerite, Belgica, Getz-Dotson and Pine Island Trough; whereas in the eastern part of the AP, including the Weddell Sea, troughs like Vega, Robertson, Jason, Kenyon and the Ronne and Filchner are prominent features (Gales et al., 2013; Dotto et al., 2020; Batchelor et al., 2022). Among those previously mentioned, Filchner Trough and Marguerite Trough are likely the most extensively researched in terms of deep benthic communities. The Filchner Trough is a conduit for ice shelf water from underneath the Filchner-Rønne Ice Shelf towards the continental slope (Humbert et al., 2022). Studies have documented a predominantly deposit-feeding, epifauna-dominated community (mainly Holothurians), with a relatively low number of taxa, high epifaunal abundance, and low infaunal abundance and biomass (e.g., polychaetes) (Pineda-Metz et al., 2019). Whereas in Marguerite Trough, the largest trough in central WAP which runs from the shelf break at about 66.5°S to George VI Ice Shelf in Marguerite Bay (Moffat & Meredith, 2018), recent benthic work has shown soft coral, hydroid, bryozoan, and poriferan with climax sessile suspension feeders being the most dominant (Nasir et al., 2023).

1.4 West Antarctic Peninsula as a case study

The WAP continental shelf, which spans approximately 130 km in width, is a region of complex bathymetry featuring shallow plateaus, and deep depressions with mean depths of 400 m and maximum up to 1600 m (Moffat et al., 2008). This shelf can be broadly divided into two distinct regions: the Bransfield Strait and the central WAP (Moffat & Meredith et al., 2018). The influences of the warm Bellingshausen Sea to the south and the cold Weddell Sea water flowing into the Bransfield Strait to the north create strong along-shore hydrographic gradients that affect the spatial pattern of glacier retreat and are associated with various physical and biochemical changes along the shelf (Wang et al., 2022).

Amidst those changes, the highly dynamic sea ice cycle along the WAP leads to varying light, nutrient, and grazing conditions, across fine spatial and temporal scales, resulting in highly heterogeneous production concentrated in biological hotspots (Pan et al., 2023; Cassarino et al., 2020) including important benthic ecosystems.

The rich diversity of macro- and megafauna encompass echinoderms such as brittle stars, holothurians, sea urchins, asteroids and crinoids, as well as abundant sponges, sea spiders, ascidians, polychaetes, bivalves, gastropods, brachiopods, bryozoans and sipunculan worms amongst many other types (Henley et al., 2019). Collectively, these seafloor dwellers influence the overall ecosystem structure and functioning along the WAP by facilitating biogeochemical cycling, storing and potentially sequestering carbon from the water column above (Tait et al., 2024; Henley et al., 2019). Specially in shallow benthic environments (e.g., coastal and near-shore regions), this process is greatly supported by macroalgae and their epiphytes, which, when associated with rocky substrates (Morley et al., 2022), can serve as important year-round carbon sources (Braeckman et al., 2019; Pasotti et al., 2015). Since the mid-twentieth century, however, the WAP has experienced some of the most rapid rates of sea surface temperature rise globally, associated with rapid retreats of sea ice, surface ocean warming and a shortening of the sea ice season (Antoni et al., 2024; Moffat & Meredith 2018). Interlinked processes have been suggested to underlie this warming, including stratospheric ozone depletion, local sea-ice loss, increased westerly winds, and changes in the strength and location of atmospheric teleconnections between low and high latitudes (Turner et al., 2016).

Concurrent with the complex causes and their associated mechanisms, regional warming has led to a wide range of consequences including reduced cold winters, sea level rise, and increased snow/rainfall (Rogers et al., 2020; Wang et al., 2022; Morales et al., 2024). These cumulative changes are more prominent in shallow coastal waters, where marine-terminating glaciers have rapidly retreated over the past fifty years (Ahn et al., 2021), alongside certain areas experiencing water temperatures forecasted for the year 2100 (Cárdenas et al., 2018). According to Cook et al. (2016), the strongest retreats have mainly occurred in the central/southern WAP where intrusions of warm, deep water from offshore can penetrate across the shelf and undercut the marine termini of the glaciers. Across the northern WAP, westerly winds drive warm and moist air, thinning the coastal ice shelves and increasing meltwater discharge from surface runoff and ablation (Rignot et al., 2004).

The main concern tackled in a wealth of studies, and the focus of the current research, is the rapidity and magnitude of these changes which may surpass the ability of biological systems to adapt, resulting in profound impacts on the regional ecosystem and its biodiversity such as shifts in species distribution, the proliferation of opportunistic species, the decline of less-competitive species, alterations in biological niches, and the risk of potential introduction, establishment and spread of invasive species (Morales et al., 2024; Dulière al., 2022; Hughes et al., 2020).

Processes following glacial retreat can impact marine inhabitants, particularly seabed communities whose structure is strongly influenced by ice dynamics along the WAP (Henley et al., 2019), both direct- or indirectly. Directly, glacial retreats and subsequent iceberg scouring, create a fragmented mosaic of benthic assemblages at various stages of recovery across polar seabed substrates (Campana et al., 2020). Early studies revealed that areas frequently disturbed often see the eradication of most sessile organisms, allowing pioneer species to thrive on the affected substrate, thus showing a continual natural cycle of destruction and recovery (Gutt et al., 1996).

Alternatively to this primary succession process, glacial retreat may indirectly affect benthos through the tightly complex bentho-pelgaic coupling. Longer phytoplankton blooms and alterations in disturbance regimes (Antoni et al., 2024; Morley et al., 2022) could ultimately trigger responses throughout the food chain, as suggested by studies on the Potter Cove food web (Marina et al., 2018) as well as other cascade effects associated with primary production, organic matter flux to the seafloor and provision of the food bank (Ingels et al., 2020).

In a region transitioning from a cold-dry polar-type to a warm-humid sub-Antarctic-type climate and rapidly increasing human activity (Rodriguez et al., 2022), the need for sound baseline information about benthic community structure and composition to detect and quantify changes is a well-recognized priority (Gutt et al., 2020; Piazza et al., 2019).

Research question & objectives

This study aims to understand *how benthic assemblages vary between inner and outer shelf environments along the West Antarctic Peninsula, and what are the underlying relationships between biotic composition and environmental drivers*. Coastal environments of the WAP have been patchily investigated, particularly areas close to scientific stations (Nasir et al., 2024; Grange & Smith, 2013). The present study seeks to expand the temporal and spatial knowledge of benthic dynamics from coastal regions to the deeper continental shelf. To underpin this goal the detailed objectives are:

i. Describe the faunistic composition of benthic assemblages along a spatial gradient (e.g., comparing fjord with trough), based on *a priori*-defined functional relevant groups.

ii. Analyse relationships between the biotic assemblage composition and their potential environmental drivers.

Given their role in Vulnerable Marine Ecosystems (VMEs) – characterized by fragile, long-lived epibenthic organisms susceptible to disturbance (Almond et al., 2021; Clarke et al., 2016a) – Antarctic benthos is likely to be ideal models for assessing ecosystem function and its response to changing environmental conditions in the Antarctic Peninsula (Gros et al., 2023).

Hypothesis Testing

Based on the research objectives, the hypotheses for this master's thesis are:

Hi. *Benthic assemblage density*

Given the documented higher abundance of fjordic assemblages along the WAP compared to adjacent shelf areas (Grange & Smith, 2013), benthic assemblages in the study fjord will have higher densities than those in open continental shelf such as Marguerite Trough.

Hii. *Benthic assemblage richness*

Species richness is typically depressed with youth and environmental stress, such as near retreating glacier termini (Sahade et al., 2015). Other factors being equal taxonomic and functional richness will increase away from glacier terminus within a fjord (e.g., Moon et al., 2015), and decrease from inner to outer shelf (Grange & Smith 2013).

Hiii. *Benthic composition*

Species composition and associated functional traits on the Antarctic continental shelf are structured by habitat age and environmental gradients, (Kaiser et al. 2013; Post et al. 2011). Assemblages are expected to transition from pioneer, mobile, and sediment-tolerant taxa near the glacier terminus (Sahade et al., 2015) to more mature assemblages resembling those found on the outer shelf as habitat age increases and environmental conditions become more constant.

2. Methodology

2.1 Study area and data collection

Within the WAP, two representative soft-sediment study sites were selected for their comparable area, based on photo coverage, number of sampling sites, and distance from furthest sites. Both were then sampled with consistent linear transects, similar in intensity, instrumentation, and protocol to capture all major habitat types.

The study area encompasses ten stations distributed across the following regions:

i. **Marian Cove (MC)** in King George Island; a fjord located in the south of the South Shetland Islands (SSI), the southwestern Bransfield Strait. Five sampling stations (MC1-MC5) were identified along a cove transect; MC5 is near the tidewater glacier terminus, whilst MC1 lies at the mouth of the cove towards Maxwell Bay (Figure 1).

ii. **Marguerite Trough (MT)**; in the Transitional Zonal Water with Bellingshausen Sea and CDW influence. The cross-trough section included five sampling stations (MT1-MT5) distributed about 70–100 km from the western part of Adelaide Island, West Antarctica (Figure 1).

Considering latitudinal differences and variations in bathymetry, topography, and proximity to shore, both regions exhibit distinct features. Marguerite Trough represents an open shelf environment, the shallower Marian Cove is semi-enclosed with fjord characteristics and is directly influenced by its nearby tidewater glacier. In contrast, Marguerite Trough is hundreds of km from retreating glaciers although it harbors extensive relict subglacial meltwater channels on the Antarctic inner shelf (Gales et al., 2013).

These disparities likely lead to differences in exposure to currents, storms, and iceberg scour. Throughout this study, the terms "inner shelf" and "outer shelf" will denote Marian Cove and Marguerite Trough, respectively.

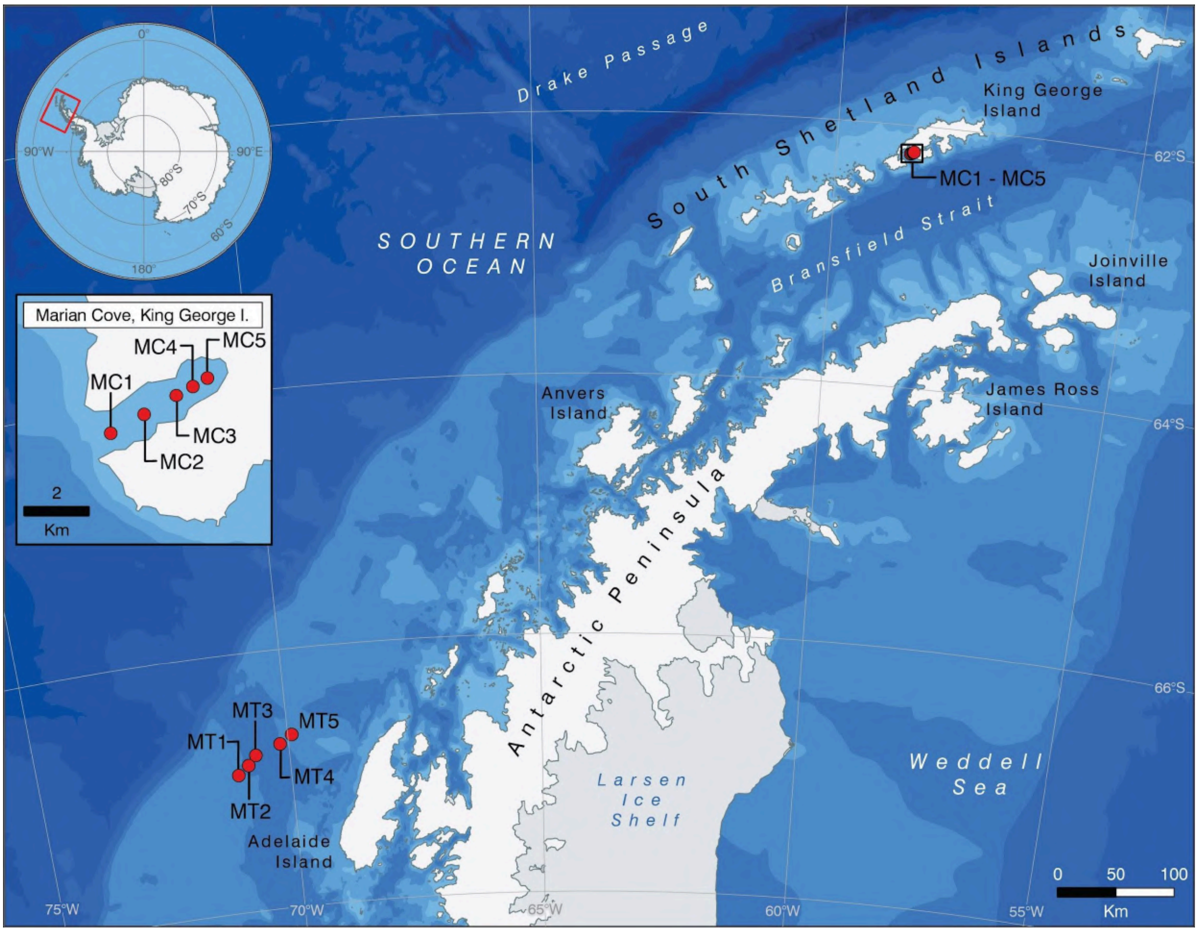


Figure 1. Geographic location of the study area. Seabed imagery and oceanographic measurements were conducted northeast of King George Island, with sampling stations labeled in Marian Cove as MC1, MC2, MC3, MC4, and MC5, and in Marguerite Trough as MT1, MT2, MT3, MT4, and MT5. The georeferenced positions of these sites are based on Garza et al. (2023) [MC1-5] and Nasir et al. (2024) [MT1-5].

Physical setting

Marian Cove. King George Island (KGI) is a large island of the SSI archipelago in West Antarctica, separated from the AP by the Bransfield Strait and from South America by the waters of the Drake Passage (Llanillo et al. 2019)(Figure 2). Marian Cove, a tributary embayment of Maxwell Bay on the southwestern side of KGI, stretches approximately 4.5 km in length, with a width of up to 1.5 km and reaching a maximum depth of ~110 m (Kim et al. 2021). Dominated by mixed semi-diurnal tides, the ice-free summer cove boasts gravel beaches of varying slopes. Snowmelt and glacier calving fill the cove from December to March with icebergs and meltwater. Tidal and wind forces redistribute sediments, with wind patterns influencing supraglacial meltwater particle deposition (Ko et al., 2023).

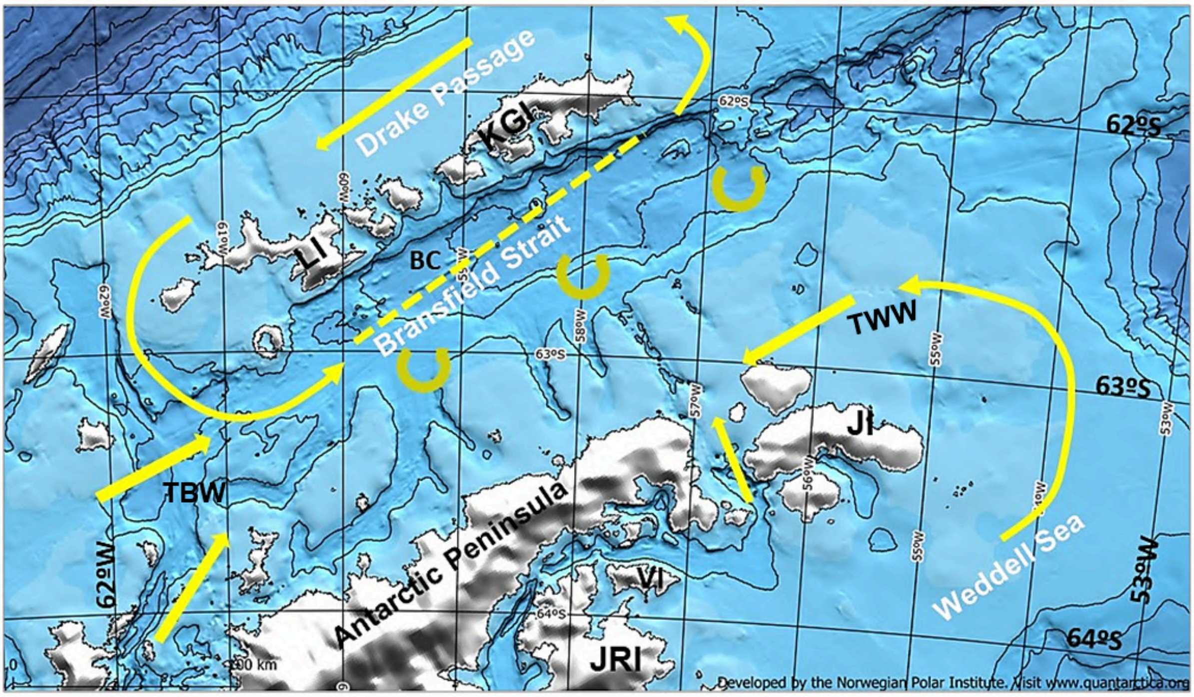


Figure 2. Schematic of mean surface circulation in Bransfield Strait, South Shetlands Archipelago and western Antarctic Peninsula. The approximate positions of the anticyclonic eddy field in the Bransfield Strait and the Bransfield Current (dotted line, BC) are based on Sangrà et al. (2017). Arrow sizes do not represent the water current magnitudes; arrow size differences are due to software auto-production. LI, KGI, JI, JRI, TWW, TBW stand for Livingston, King George, Joinville and James Ross islands, Transitional Zonal Waters with Bellingshausen Sea and Weddell Sea influence, respectively. Background bathymetry based on the International Bathymetric Chart of the Southern Ocean IBCSO (Arndt et al., 2013). Bathymetry isolines represent 500 m water depth increments. This figure was produced using the QGIS software (https://www.qgis.org/en/site/) and Quantarctica, from the Norwegian Polar Institute (https://www.npolar.no/quantarctica/) packages (Matsuoka et al., 2021).

Marguerite Trough. Deep glacially carved canyon linking the shelf break to Marguerite Bay, deepens relatively gently from the shelf break, where it is roughly 550 m deep, to the mouth of Marguerite Bay, where it extends to around 900 m deep (Brearley et al., 2019). Subsequently, it undergoes a rapid deepening to a maximum depth of 1600 meters just off the northern coast of Alexander Island (Moffat et al., 2009). Within the WAP, Marguerite Trough serves as a crucial pathway for warm CDW to reach the AP shelf. This warm water is transported by currents and eddies, impacting coastal dynamics and contributing to the melting of ice shelves whilst it is also a well-known region of marginal sea ice (Dinniman et al., 2011; Couto et al., 2016).

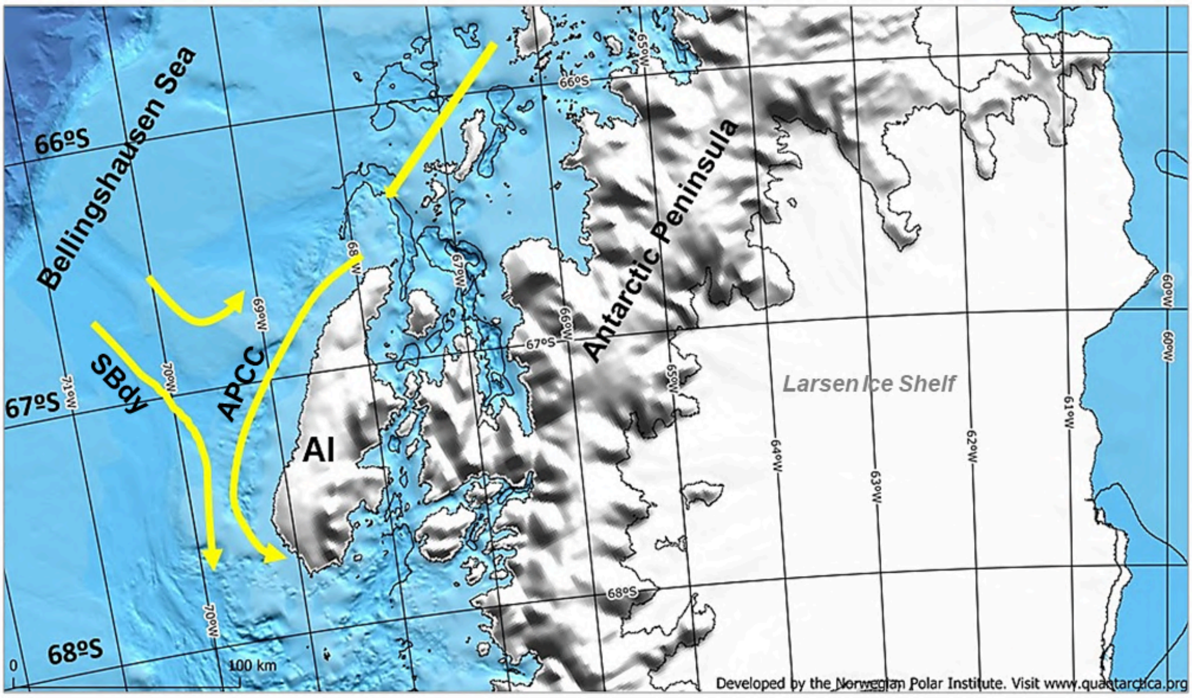


Figure 3. Schematic of mean surface circulation in the western coast of Adelaide Island. The approximate positions of the flow patterns are based on Dinniman & Klinck (2004) and Moffat et al. (2018). Arrow sizes do not represent the water current magnitudes; arrow size differences are due to software auto-production. AI, APCC, SBdy stand for Adelaide Island, Antarctic Peninsula Coastal Current and Southern ACC Boundary, respectively. Background bathymetry was based on the International Bathymetric Chart of the Southern Ocean IBCSO (Arndt et al., 2013). Bathymetry isolines represent 500 m water depth increments. This figure was produced using QGIS software (https://www.qgis.org/en/site/) and Quantarctica, from the Norwegian Polar Institute (https://www.npolar.no/quantarctica/) packages (Matsuoka et al., 2021).

Photographic Survey

The benthic fauna at the 10 stations was non-invasively surveyed using seabed images (SBI) captured by a fibre optic, high resolution Shallow Underwater (drop) Camera System (SUCS) across water depths ranging from 68 to 620 m (Table 1). Each station had photo-transects of about 80 m length. The SUCS, equipped with a downward-facing CCTV live-view imaging system, was designed with a tripod for stability along with weights to steady itself and allowed the lander to settle perpendicular to the seabed (Figure S1 Supplementary Information). Two controllable light sources provided the necessary illumination for clear image capture. The SBI images were captured in 10MB JPG format, ensuring HD documentation of the benthic environment.

Fieldwork campaigns and data collection were conducted aboard the RRS James Clark Ross (JR17001-JR19003) during austral summer expeditions, spanning the period 2017-2020 (Table 1).

Table 1. Summary of image data collected for each region. A total of 100 Seabed Imagery (SBI) samples were taken, comprising 5 stations per region, each with 10 replicates.

Region	Year	Station	Latitude	Longitude	Mean Depth (m) (n=10)
Marian Cove	2017-2020	MC1	62° 13.0488′ S	58° 47.3532′ W	93.68 ± 1.86
		MC2	62° 12.7416′ S	58° 46.2276′ W	105.79 ± 4.92
		MC3	62° 12.4782′ S	58° 44.9742′ W	99.17 ± 8.12
		MC4	62° 12.3222′ S	58° 44.4810′ W	104.89 ± 8.41
		MC5	62° 12.2148′ S	58° 43.8606′ W	76.49 ± 7.62
Marguerite Trough	2017	MT1	66° 56.0994′ S	71° 2.58540′ W	479.2 ± 1.46
		MT2	66° 51.9930′ S	70° 49.5978′ W	509.2 ± 1.68
		MT3	66° 47.7000′ S	70° 39.6000′ W	619.0 ± 0.54
		MT4	66° 43.7412′ S	70° 9.92160′ W	500.5 ± 0.88
		MT5	66° 39.8844′ S	69° 55.2348′ W	359.0 ± 0.24

2.2 Image analysis

Each SBI covered a physical area of 405.7 mm x 340.6 mm, which is approximately 0.1382 m^2. The digital resolution of each image was 2448 x 2050 pixels, totaling 5,018,400 pixels. This resolution accurately represented the physical seabed area, with each pixel corresponding to ~$2.75 \times 10^{-8} m^2$ of the seabed. For analysis, 100 images (10 replicates per station) were processed using Adobe Photoshop v24.1 software.

In regions with limited accessibility, such as Antarctica, taxonomic uncertainty and a lack of resources, mainly identification keys, pose challenges for species identification. To overcome this, all unique macro and mega-organisms (>3mm) were classified as Taxonomic Units (TUs) or morphospecies. In the case of colonial organisms, each colony was treated as one individual in the image. Despite resolution constraints limiting the size of identifiable organisms in the images, the classification scheme aligned with previous studies in the WAP (e.g., Nasir et al., 2024), facilitating direct comparisons with existing literature and reducing uncertainty. Moreover, organism identification relied on consultation with multiple reputable sources (e.g., Scientific Committee on Antarctic Research- Marine Biodiversity Information Network; SCAR-MarBIN), including primary literature and underwent cross-referencing to ensure accuracy.

2.3 Defining Habitat Heterogeneity

Habitat heterogeneity and environmental characterization were assessed using a wide range of descriptors based on their ecological significance to benthic and Antarctic studies (Fabri-Ruiz et al., 2021) and subdivided into the following categories: (i) *physical habitat* (ii) *chemical environment* (iii) *food resources* and (iv) *geography*. Together, the selected descriptors effectively capture some primary characteristics of TUs or functional groups (see Table S1. Supplementary Information). To acquire the data, an extensive suite of sources were compiled ranging from spatial data (e.g., distance from features, coordinates), seafloor data (derived from SBI), and both physical and chemical oceanographic data (Table 2). The latter was gathered concurrently with the SBI surveys by means of CTD casted from the sea surface to within ~10 m of the seabed.

Univariate statistics. Environmental differences across both regions were evaluated using one-way ANOVA or the non-parametric Kruskal-Wallis test depending on data distribution. Assumptions of normality (Shapiro-Wilk test) and homoscedasticity (Levene's test) were firstly checked. Post-hoc comparisons were conducted using the non-parametric Mann-Whitney U test and statistically significant differences were considered when $p<0.05$.

Multivariate statistics. Descriptive statistics were employed to develop supervised models aimed at predicting the response variable, namely benthic imagery observations, as a function of environmental predictors derived from the environmental descriptors (refer to 2.5 section). These models were designed to predict the abundance of functional groups observed from seafloor imagery and provide insights into the complex relationships between environmental parameters and benthic functional biodiversity.

Table 2. Inventory of environmental descriptors. Summary of parameters based on their ecological significance to the benthos and the study area along with the methods for acquiring those data.

Environmental descriptor		Gear / Source	Units/classification
Physical habitat	Depth	CTD (*)	Metres (m)
	Seafloor temperature	CTD (*)	Celsius (°C)
	Substrate nature	Spatial Extrapolation: dominant type covering 75% of the seabed image (mud, sand, pebbles, or boulders)	Soft bottom (mud and sand), Hard-soft bottom (mud and fine or coarse pebbles), Hard-rocky bottom (boulder field)
	Slope	Angle of the seabed between consecutive pictures	Degrees (°)
	Roughness/rugosity	Approximate maximum difference in height between two areas of seabed in the picture, from shadow length	Centimetres (cm)
Chemical environment	Dissolved Oxygen concentration (DO)	Sea-Bird SBE 43 Dissolved Oxygen Sensor (*)	Micromoles per litre, (µmol/L)
	Salinity	Derived from CTD conductivity (*)	Practical Salinity Units (PSU)
	Turbidity	Transmissometer: percentage of light detected at a distance of 1 cm away from its source (*)	Transmission
Food Resources	Chlorophyll-a concentration	Fluorometer (*)	Micrograms per litre, (µg/L)
Geography	Distance to the (glacier) Antarctic continent	Rectilinear transect from each station GPS point to the glacier terminus at the head of the fjord (MC) or to the continent (MT) in QGIS.	Kilometre (km)

(*) In situ oceanographical data collected at the same locations as the photographic surveys, allowing for the acquisition of environmental data concurrently with the SBI.

2.4 Benthic data and treatment

The identified organisms comprised a raw dataset of 45 TUs (Table 3) that were aggregated into two methods of visualization based on Barnes & Sands (2017). One method grouped TUs solely by taxonomy, while the other categorized TUs based on functional traits selected *a priori* due to their discernibility from images, aligning with past categorizations of

Antarctic benthic communities (Gutt et al., 1996). Each TU was evaluated for its feeding type, including suspension feeders, deposit feeders, grazers, and scavengers-predators. Additionally, certain TUs underwent further functional classification based on their position in the substrate (epifauna or infauna), mobility (mobile or sessile) and skeletalization (soft-bodied, hard-bodied, jointed-legged, shelled). In the case of sessile suspension feeders, a further distinction was made between 'pioneer' and 'climax' groups, denoting their occurrence during early and late succession stages following habitat disturbance, such as ice scouring, respectively. Through the aggregation of TUs sharing these traits, a total of 13 distinct functional groups were identified (Table 3).

Table 3. Functional group classification on the study area. Criteria based and modified from Barnes and Sands (2017). Sessile suspension feeders were classified into 'pioneer' and 'climax' based on early and late succession after habitat disturbance (e.g., ice scouring) respectively (Gutt et al., 1996).

Functional group-trait		Taxonomic Unit (TU)
Feeding mechanism	Mobility and skeletisation	
Suspension feeders	Pioneer sessile	Polychaete annelids, bryozoan (Gymnolaemate, Stenolaemate), ascidian chordates (Colonial, Solitary), Priapulans
	Climax sessile	Demospongiae, Poriferans, Erect gymnolaemate bryozoans, Articulate brachiopod
	Sedentary	Echinoderm (Crinoid, Basket star)
	Mobile	Suspension feeding malacostracan crustaceans, Ophiuroid echinoderm
Deposit feeders	Epifaunal	Holothuroid echinoderm
	Infaunal soft-bodied	Deposit feeding polychaetes, Sipunculans, Echiurans
	Infaunal shelled	Molluscs (Scaphopod, Bivalve), Burrowing echinoid echinoderms
Grazers		Molluscs (Polyplacophora, Gastropod), Regular echinoid echinoderm
Scavenger/predator	Soft-bodied, sessile	Cnidarians (Soft coral anthozoan, Actinaria anthozoan, Seapen anthozoan, Hydroid), Ctenophore
	Hard-bodied, sessile	Scleractinaria anthozoa cnidarian, Octocoral
	Soft-bodied, mobile	Errant polychaetes, Nemerteans, Turbellarian platyhelminthes, Octopus, Molluscs
	Hard-bodied, mobile	Asteroid echinoderm, Predatory gastropod molluscs, Pisces chordata
	Jointed legged, mobile	Pycnogonid chelicerate, Isopod, Spider crab, Hermit crab, Shrimp Crab/lobster, Generalist ophiuroids, Amphipod

To assess the completeness of TUs inventories in each region, species accumulation curves were plotted based on the deterministic exact method which provides a precise estimate of species richness accumulation in small datasets without relying on random permutations (Thompson & Withers, 2003). Specifically, whether the curves reached asymptotic values or continued to accumulate was examined. Accumulation curves (observed value) exhibited almost plateaus, indicating that TU inventories were nearly complete (Figure S2. Supplementary Information). The biodiversity analyses subsequently conducted should be meaningful.

Biodiversity measures. The diversity at the local scale was estimated by quantifying the density of 13 functional groups at each station. This involved counting organisms along an 80-meter photo-transect, representing an area of 1.382 m^2. Regional densities for the four feeding-based groups were then calculated based on the total area covered by the 50 images (6.91 m^2). Additionally, alpha-biodiversity metrics were computed (Table 4), encompassing the two fundamental components of diversity: richness, which reflects the variety of functional groups present, and evenness, which measures the relative abundance distribution among functional groups. The Simpson index was also included to assess species dominance and complement the functional assemblage description.

Table 4. Local biodiversity patterns. Estimation of alpha indices in each region.

α-index	Description	Formula	Range of Values
Species richness (S)	Quantifies the compositional differences in species abundances between habitats.	$S = N \sim N$=number of species	S≥0
Shannon-Wiener diversity (H’)	Measures the diversity and evenness of species abundance between habitats (Shannon, 1948).	$H' =- \sum_{i=1}^{S} p_i ln\,(p_i) \sim p_i = \frac{n_i}{N}$	0≤H’≤5
Pielou’s Evenness (J’)	Estimates the evenness of species abundance between habitats (Pielou, 1966).	$J' = \frac{H'}{ln\,(S)}$	0≤J’≤1
Simpson (D) index	Estimates the dominance and diversity of species abundance between habitats (Simpson, 1949)	$D = 1 - \sum_{i=1}^{S} (p_i)^2$ $\sim p_i = \frac{n_i}{N}$	0≤D≤1

To determine if there were significant differences in diversity indices among stations, homoscedasticity and the normal distribution were tested using the Bartlett's test and the Shapiro-Wilk's test, respectively. Due to the non-parametric nature of the data, differences between stations were evaluated using the non-parametric Kruskal-Wallis test followed by Nemenyi's non-parametric all-pairs comparison test. Significance was assumed at 0.05.

Local comparisons of benthic assemblage structure across the stations were assessed through multivariate statistics. The abundance raw dataset was previously 2th-root transformed to normalize and stabilize the variance, reducing the influence of extreme values and making the distribution more symmetrical. Thereafter, compositional dissimilarity among benthic communities across the different stations was calculated using the Bray-Curtis Index (Bray & Curtis, 1957). This (dis)similarity matrix was later employed to perform a nested one-way PERMANOVA (Anderson, 2017) and SIMPER analyses (Clarke & Warwick, 1994) to test for differences in abundance among stations and identify key functional groups driving differences between stations, respectively. Generally, the contributions to the difference between the sample units are relativized so that the average contributions of all species sum to 1 (Bakker, 2023). In the study, this dissimilarity was estimated by setting a cut-off level around 50% whilst the three functional groups that contributed the most to the differentiation were identified by their individual contribution based on cumulative percentage (cumulative contribution of this and all previous functional groups in list).

In a further step, to test hypotheses regarding regional differences between the benthic assemblages, a range of beta-diversity indices were computed (Table 5). For this purpose, imputation of abundance data was performed to ensure complete matrices, particularly important for Bray-Curtis and Jaccard dissimilarity indices, which require complete data matrices to accurately calculate dissimilarity values.

The environmental and benthic data treatment were conducted and plotted in Python and R Statistical Software (v4.1.0; R Core Team, 2021) using vegan (Oksanen et al., 2017), BiodiversityR (Kindt & Coe, 2005), pairwiseAdonis (Arbizu, 2017), dplyr (Wickham & Francois, 2015), betapart (Baselga & Orme, 2012), ggplot2 (Wickham, 2016) and tidyr (Wickham & Henry, 2020) packages.

Table 5. Regional biodiversity patterns. Beta indices estimated per region.

β-index name	Description	Range of Values
Bray-Curtis Dissimilarity	Quantifies the compositional differences in species abundances between habitats (Dai et al., 2020)	0≤Bray-Curtis≤1
Jaccard Dissimilarity	Measures the similarity in species presence-absence patterns between habitats (Medeiros et al., 2020)	0≤Jaccard≤1
Bootstrap species richness estimator	Estimates species richness along with its uncertainty using a non-parametric resampling technique (Hughes et al., 2021)	Dependent on sample data
Jackknife 2 species richness estimator	Estimates species richness along with its uncertainty using a leave-one-out resampling technique (Hughes et al., 2021)	Dependent on sample data

2.5 Environmental data and treatment

Due to the numerical response, low sample sizes and few predictors, multiple regression analyses were performed to model the benthic abundances using the environmental descriptors as predictors. Generalized Linear Models (GLM; Hardin & Hilbe, 2012) were applied as a parametric model method, which is a statistically robust method, used frequently to model species occurrences and distributions (Deregibus et al., 2023; Leps et al., 2015; Reiss et al., 2014). Kernel density estimates (KDE plots; Figure S3) revealed a predominantly right-skewed distribution in the abundance data, evident by the median exceeding the mean. The Gamma distribution is a natural choice for such data because it excels at modeling right-skewed, positive-valued counts where variance increases with the mean (Zhang & Zhang, 2022). To account for this skewness, Gamma Regression Models (GRMs) were employed and fitted with the default, canonical link function for the Gamma distribution (Amin et al., 2018). The link function is the reciprocal of the response variable ($\frac{1}{abundance}$). This analysis was conducted using a custom R function for automated stepwise model selection (auto_glm from the MASS package; Ripley et al., 2012).

Full GLM Construction. GLMs were built including all environmental descriptors; the physicochemical, food resources and geographical. When considering the main effects of each predictor, the number of possible combinations was 2^{12}= 4096 because each predictor could either be included or excluded from the model independently, resulting in 2 choices for each of the 12 predictors. Since these combinations could be applied to each of the 13 dependent variables, the total number of models for a single region amounted to 4,096 * 13 = 53,248. The study encompassed two sampling regions, and therefore, the total number of models across both locations reached 53,248 * 2 = 106,496.

To better meet the various assumptions and calibrate subsequent GLMs analyses, collinear predictors were initially checked in each region using pairwise Spearman's rank correlation test (collinearity was assumed for $|\rho| \geq 0.7$; see Dormann et al., 2012). In Marian Cove, due to the very high collinearity of salinity, oxygen and chlorophyll-a with most of the predictors and hard-soft bottom with soft bottom (Table S2 Supplementary Information), simultaneous use of several descriptors would have violated the multiple regressions' assumptions. Similarly, in Marguerite Trough temperature and salinity showed high collinearity of chlorophyll-a and depth (Table S2 Supplementary Information). These predictors were therefore removed along with uninformative constant predictors that did not offer explanatory variability, such as hardy-rocky bottom in Marian Cove and turbidity and distance to glacier in Marguerite Trough.

Despite the statistical constraints, each functional group (response variable) fulfilled a broader range of relevant predictors (Table 6).

Table 6. Model data input. Environmental drivers of benthic assemblages analyzed for each region, with functional groups as the response variable and a set of environmental variables as predictors.

Response variable (abundance)	Predictor		
	Marian Cove	Marguerite Trough	
Pioneer sessile suspension feeders	Depth	Depth	*Physical habitat*
Climax sessile suspension feeders	Soft bottom	Soft bottom	
Sedentary suspension feeders	-	Hard-soft bottom	
Mobile suspension feeders	-	Hard-rocky bottom	
Epifaunal deposit feeders	Seafloor temperature	-	
Infaunal soft-bodied			
Infaunal shelled deposit feeders	Slope	Slope	
Grazers	Roughness/rugosity	Roughness/rugosity	
Soft-bodied, sessile scavenger/predator	Turbidity	DO concentration	*Chemical environment*
Hard-bodied, sessile scavenger/predators			
Soft-bodied, mobile scavenger/predators	-	Chlorophyll-a concentration	*Food resources*
Hard-bodied, mobile scavenger/predators	Distance to the glacier	-	*Geography*
Jointed legged, mobile scavenger/predators			

Model selection procedure. Model selection was based on the Akaike information criterion coefficient (AICc), the small-sample (second-order) bias adjusted AIC (Akaike Information Criterion; Burnham & Anderson, 2001). A backward elimination was applied (Braeckman et al., 2021) with a maximum of 50 iterations set by default, pruning the models while minimizing the AICc to find the most parsimonious model that adequately describes the data. Calculations were done using a modified version of the R function stepAIC (originally included in the MASS package; Ripley et al., 2012).

Model Fit Assessment. The simplified models (hereafter referred to as reduced models) were checked for overall model significance (assesses the goodness of fit of the model) through the χ^2test and deviance. The later was computed as Explained Deviance (%) = $\frac{Null\ deviance-Residual\ deviance}{Null\ deviance}*100$ to represent the percentage of deviance in the response variable explained by the model's predictor (fixed effects). For predictor-specific significances, Wald tests (Wald, 1943) were performed while significance levels were lowered with the Bonferroni method to prevent inflation of Type I error rates (i.e., 0.05 divided by the number of comparisons) (Lee & Lee, 2018; Negishi et al., 2019).

3. Results

In the study region of the WAP, variability of physico-chemical descriptors and benthic patterns were shown between Marian Cove and Marguerite Trough. The following sections delve into these trends, highlighting the contrasts between inner- and outer shelf environments and their influence on benthic fauna.

3.1 Marian Cove fjord

Defining Habitat Heterogeneity within fjord

The surveyed area extended from MC1, in the outer cove (4.3 km away from the glacier terminus) to MC5, closer to the glacier in the inner cove (0.8 km away from the glacier terminus). The proximity of each station to the glacier front within the fjord was reflected in their environmental conditions.

Along this gradient, both MC1 and MC5 were shallower than stations in the middle of the fjord (Table 7). During the survey, the temperature remained relatively stable, consistently dipping below -1°C. However, sea temperature was higher near the mouth of the fjord, likely due to mixing with warmer oceanic waters. Conversely, temperature decreased with depth and inwards, likely influenced by glacial meltwater.

Table 7. Marian Cove environmental summary. Average environmental parameters (Mean ± SD, n=10).

	Environmental descriptor						
	Physical habitat		*Chemical environment*			*Food resources*	*Geography*
	Mean Depth (m)	Mean Temp (°C)	Mean Salinity (PSU)	Mean DO (µmol/L)	Turbidity (transmission)	Chla (µg/L)	Glacier distance (km)
MC1	93.68 ± 1.86	-1.049 ± 0.001	34.1808 ± 0	302.804 ± 0.043	95.4325± 0	0.035 ± 0	4.3
MC2	105.79 ± 4.92	-1.072 ± 0.001	34.1842 ± 0	302.615 ± 0.001	95.7451± 0	0.0318 ± 0	3.1
MC3	99.17 ± 8.12	-1.735 ± 0.031	34.27 ± 0.01	311.832 ± 0.016	95.1459± 0	0.006 ± 0.002	1.8
MC4	104.89 ± 8.41	-1.770 ± 0.013	34.285 ± 0.01	312.501 ± 0.008	91.1334± 0	0.004 ± 0.001	1.5
MC5	76.49 ± 7.62	-1.104 ± 0.013	34.176 ± 0	301.275 ± 0.050	95.9275± 0	0.148 ± 0	0.8

The chemical parameters remained relatively uniform across the cove, even though waters ~2 km away from glacier terminus (MC3 and MC4) were slightly more oxygenated, saltier and clearer accompanied by low momentaneous chlorophyll-a concentrations, indicative of phytoplankton abundance when taking the SBI. This environmental descriptor ranged from a low of 0.004 µg/L at MC4 to a high of 0.148 µg/L at MC5, reflecting minor fluctuations along the gradient (Table 7).

The seabed morphology in Marian Cove displayed variations in substrate composition, slope, and terrain complexity (Figure 4). Substrate composition predominantly consisted of soft, muddy sediment, except in the inner cove where it exhibited a mixture of soft and hard substrates, including fine and coarse pebbles likely from terrigenous sources (glacial-derived supply). The stations near the tidewater glacier terminus featured steeper terrain (gray shaded in Figure 4), consistent with their proximity to the glacier where the land slopes downwards sharply into the fjord and this might in turn, facilitate the transport and accumulation of pebbles. The terrain gradually becomes less steep when moving towards the cove's mouth (MC1 and MC2; Figure 4) along with a varied rugosity, reflecting a more uneven seabed (Figure 4).

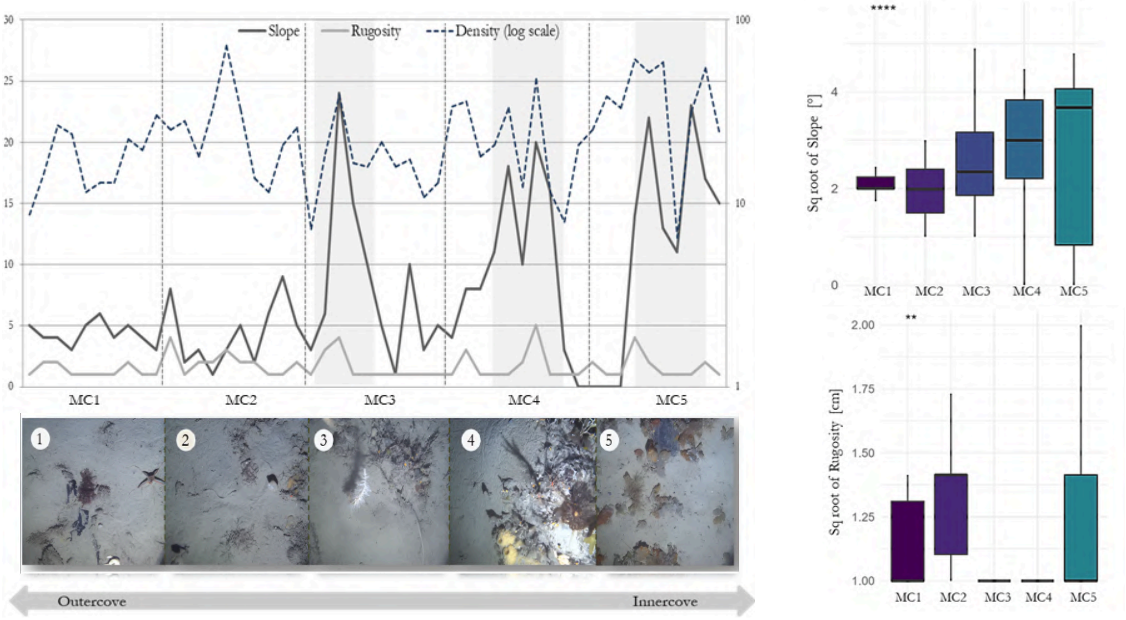


Figure 4. Seabed morphology in Marian Cove. Examples of soft bottom substrates with varied rugosity and slope types: MC1. Rugisty 2cm, slope 4°; MC2. Rugisty 2cm, slope 1°; MC3. Rugisty 4cm, slope 24°; MC4. Rugisty 5cm, slope 20° and MC5. Rugisty 4cm, slope 14°. The steepest slopes are shaded in gray.

Diversity and composition of benthic assemblage within fjord

Along the soft-bottom fjord, a total of 1887 individuals were recorded (273 ind/m^2, 7% unidentified), with suspension feeders dominating the assemblage at 68% (166 ind/m^2), followed by deposit feeders at 19% (46 ind/m^2), scavenger-predators at 12% (29 ind/m^2), while the number of grazers was almost negligible (Figure 5).

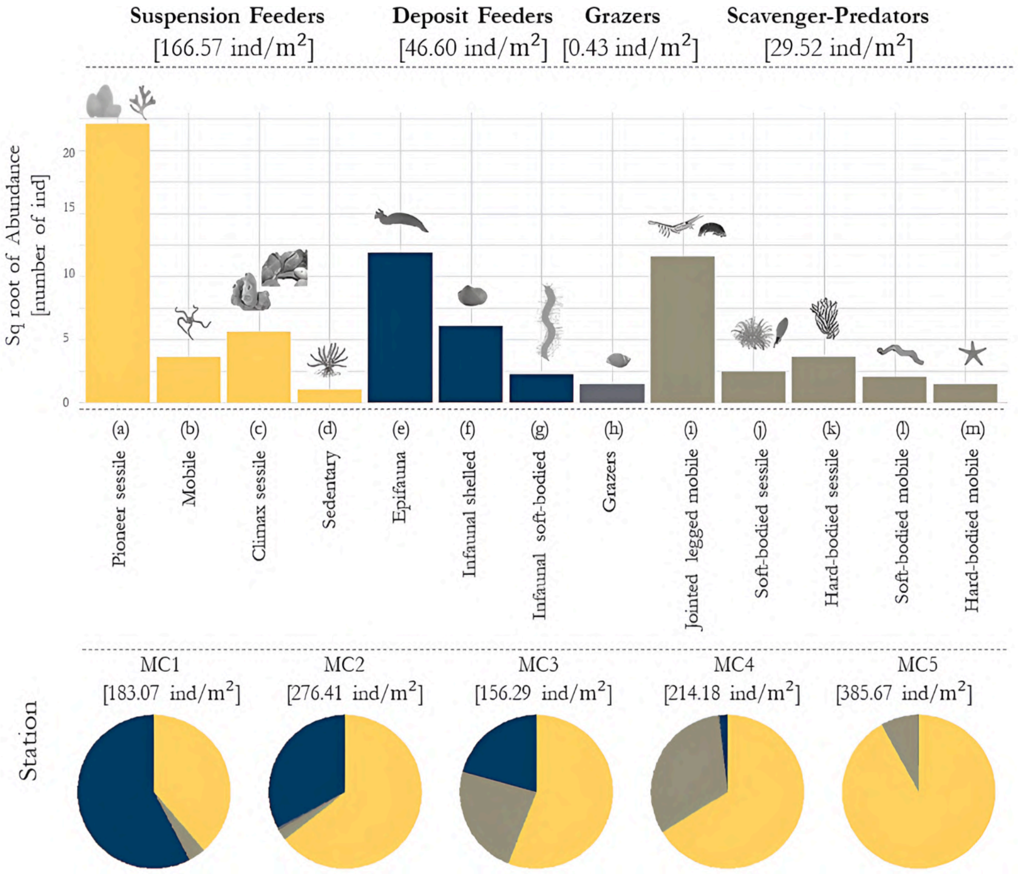
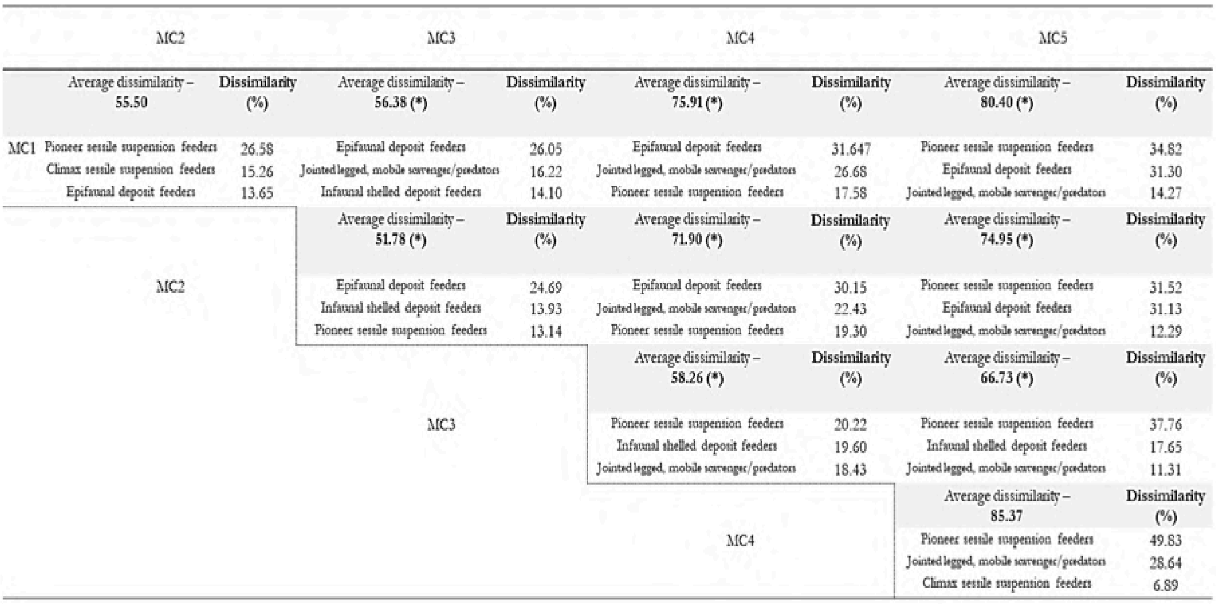


Figure 5. Benthic assemblages in Marian Cove. Functional groups and their main associated taxonomic units: (a) Solitary ascidian and gymnolaemate bryozoan; (b) Ophiuroid echinoderm, (c) Demospongiae, poriferans and articulate brachiopod; (d) Crinoid echinoderm,; (e) Holothuroid echinoderm; (f) Bivalve molluscs; (g) Deposit feeding polychaetes (h) Gastropod mollusc; (i) Shrimp malacostracan and amphipod; (j) Actinaria anthozoan and ctenophore; (k) Octocoral; (l) Errant polychaetes; (m) Asteroid echinoderm.

A total of 60% among the identified biota were pioneer sessile suspension feeders, composed mainly by ascidians (in terms of numbers of individuals), colonial gymnolaemate bryozoans and to a lesser extent, polychaete annelids (Figure S4. Supplementary Information). Demosponges (poriferans) and articulate brachiopods were numerous among climax sessile organisms, representing the second most abundant functional group of suspension feeders. Within deposit feeders, epifaunal organisms were most numerous (predominantly holothuroids), followed by shelled infauna (mainly bivalves), and soft-bodied infauna with deposit-feeding polychaetes as the most prevalent taxa (Figure 5). Among scavenger-predators, mobile jointed-legged taxa such as (decapod) shrimps and amphipods, were widely represented, constituting the most abundant macrozoobenthos. Similarly, hard-bodied organisms, especially octocorals were also numerous (Figure 5). Lastly, grazers were the functional group with few identified specimens, except for gastropod mollusks observed at 2 out of the 5 sampled stations.

Taken together, alpha-diversity metrics and SIMPER/PERMANOVA, significant differences were observed across fjord stations, indicating a heterogeneous benthic biological assemblage. The coastal station, MC5 (closest to the glacier terminus), although denser (Figure 5), had significantly lower richness and diversity (Figure S5. Supplementary Information), with pioneer sessile suspension feeders largely dominated it. This was also reflected in the low Pielou index, implying uneven distribution with high densities of only a few groups. Conversely, station MC3 (in the middle of the fjord) was the least dense (Figure 5), however, it displayed significantly higher values of alpha-diversity metrics (Figure S5 Supplementary Information). For instance, shelled infauna (bivalve mollusks) were solely registered herein, explaining, on average, up to 20% of dissimilarities with the rest of the stations (Table 8). Further examination with the SIMPER test revealed homogeneity of some assemblages, especially areas closer to the glacier terminus (MC4 and MC5) and those further at the mouth of the cove (MC1 and MC2) where major groups showed no statistical differences. The overall major contributors in the fjord were pioneer sessile suspension feeders and epifaunal deposit feeders which accounted for an average dissimilarity ranging from 20% to 50% across stations (Table 8).

Table 8. Functional groups contributing to dissimilarity between stations in Marian Cove. Differences according to the percentage similarity analysis (SIMPER). Average dissimilarity is expressed as the sum of the three groups contributing the most to the percentage of dissimilarity (in bold) while dissimilarity is a percentage of contribution based on cumulative percentage. PAIRWISE analysis (in brackets) after 999 permutations. Significantly differences: (*) p < 0.05, (.) p < 0.01.



	MC2		MC3		MC4		MC5	
	Average dissimilarity – **55.50**	**Dissimilarity (%)**	Average dissimilarity – **56.38 (*)**	**Dissimilarity (%)**	Average dissimilarity – **75.91 (*)**	**Dissimilarity (%)**	Average dissimilarity – **80.40 (*)**	**Dissimilarity (%)**
MC1	Pioneer sessile suspension feeders	26.58	Epifaunal deposit feeders	26.05	Epifaunal deposit feeders	31.647	Pioneer sessile suspension feeders	34.82
	Climax sessile suspension feeders	15.26	Jointed legged, mobile scavenger/predators	16.22	Jointed legged, mobile scavenger/predators	26.68	Epifaunal deposit feeders	31.30
	Epifaunal deposit feeders	13.65	Infaunal shelled deposit feeders	14.10	Pioneer sessile suspension feeders	17.58	Jointed legged, mobile scavenger/predators	14.27
			Average dissimilarity – **51.78 (*)**	**Dissimilarity (%)**	Average dissimilarity – **71.90 (*)**	**Dissimilarity (%)**	Average dissimilarity – **74.95 (*)**	**Dissimilarity (%)**
MC2			Epifaunal deposit feeders	24.69	Epifaunal deposit feeders	30.15	Pioneer sessile suspension feeders	31.52
			Infaunal shelled deposit feeders	13.93	Jointed legged, mobile scavenger/predators	22.43	Epifaunal deposit feeders	31.13
			Pioneer sessile suspension feeders	13.14	Pioneer sessile suspension feeders	19.30	Jointed legged, mobile scavenger/predators	12.29
					Average dissimilarity – **58.26 (*)**	**Dissimilarity (%)**	Average dissimilarity – **66.73 (*)**	**Dissimilarity (%)**
MC3					Pioneer sessile suspension feeders	20.22	Pioneer sessile suspension feeders	37.76
					Infaunal shelled deposit feeders	19.60	Infaunal shelled deposit feeders	17.65
					Jointed legged, mobile scavenger/predators	18.43	Jointed legged, mobile scavenger/predators	11.31
							Average dissimilarity – **85.37**	**Dissimilarity (%)**
MC4							Pioneer sessile suspension feeders	49.83
							Jointed legged, mobile scavenger/predators	28.64
							Climax sessile suspension feeders	6.89

The beta-diversity indices supported the previously inferred patterns of functional composition (Table 9). While most of the dominant groups might influence the specific richness estimates, the moderate value of Bray-Curtis index indicated a noticeable difference in the group's composition across the cove while the even higher Jaccard index suggested a greater difference in group's presence/absence (Table 9). This aligned with the pioneer suspension feeders' dominance near the glacier and the presence of some groups such as shelled infauna (deposit feeders) and soft-bodied, sessile (scavenger-predator) only in MC3. Equally, the richness estimators agreed with the observed biodiversity variations, perhaps attributed to environmental conditions across the cove.

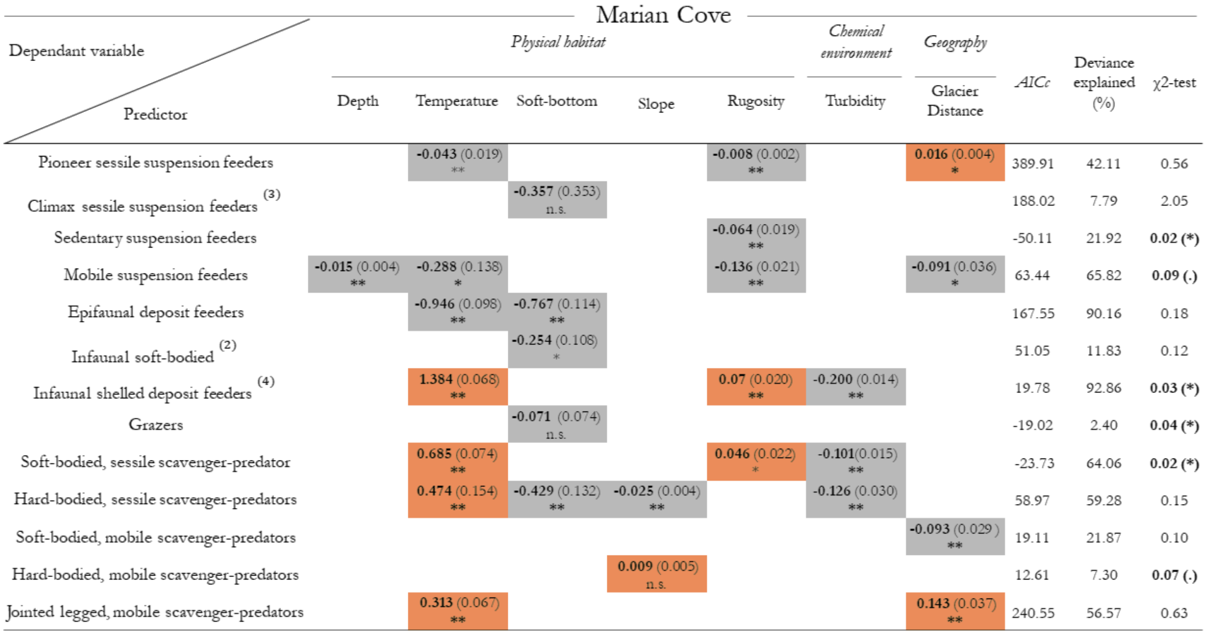
Table 9. Local diversity metric values (± standard deviation) in Marian Cove. Differences according to β-index estimators.

Dissimilarity		Species richness estimator	
Bray-Curtis	Jaccard	Bootstrap	Jackknife 2
0.6	0.73	9.36±2.01	39.64±0.48

Influence of Habitat Heterogeneity on the inner shelf functional benthic assemblage

The stepwise GLM regression procedures emphasized the importance of certain predictors (e.g., temperature and glacier distance) for specific functional groups and the varying degree of model fit across different dependent variables. Overall, models explained between 7% and 92% of the deviance in the abundance distribution, even though a few reduced models were not significant (Table 10). The Bonferroni adjustment for false positives reduction applied to the initial models ($P< 0.05/7$), generally led to a reduction in the number of predictors for functional groups with multiple predictors and lowered predictor-specific significance levels.

Table 10. Effects of environmental predictors relative to functional groups in Marian Cove. Positive and negative predictor effects on response variables are shown in bold with standard errors (SEs) in orange and gray, respectively. Bonferroni-corrected significance levels are indicated by asterisks: * $p < 0.05$, ** $p < 0.006$. Model coefficients and overall significance are bolded. Superscripts on response variables denote the number of multiple comparisons adjusted by the Bonferroni method. (n.s.) indicates non-significance.



	Marian Cove									
Dependant variable	*Physical habitat*					*Chemical environment*	*Geography*			
Predictor	Depth	Temperature	Soft-bottom	Slope	Rugosity	Turbidity	Glacier Distance	*AICc*	Deviance explained (%)	χ2-test
Pioneer sessile suspension feeders		**-0.043** (0.019) **			**-0.008** (0.002) **		**0.016** (0.004) *	389.91	42.11	0.56
Climax sessile suspension feeders $^{(3)}$			**-0.357** (0.353) n.s.					188.02	7.79	2.05
Sedentary suspension feeders					**-0.064** (0.019) **			-50.11	21.92	**0.02 (*)**
Mobile suspension feeders	**-0.015** (0.004) **	**-0.288** (0.138) *			**-0.136** (0.021) **		**-0.091** (0.036) *	63.44	65.82	**0.09 (.)**
Epifaunal deposit feeders		**-0.946** (0.098) **	**-0.767** (0.114) **					167.55	90.16	0.18
Infaunal soft-bodied $^{(2)}$			**-0.254** (0.108) *					51.05	11.83	0.12
Infaunal shelled deposit feeders $^{(4)}$		**1.384** (0.068) **			**0.07** (0.020) **	**-0.200** (0.014) **		19.78	92.86	**0.03 (*)**
Grazers			**-0.071** (0.074) n.s.					-19.02	2.40	**0.04 (*)**
Soft-bodied, sessile scavenger-predator		**0.685** (0.074) **			**0.046** (0.022) *	**-0.101**(0.015) **		-23.73	64.06	**0.02 (*)**
Hard-bodied, sessile scavenger-predators		**0.474** (0.154) **	**-0.429** (0.132) **	**-0.025** (0.004) **		**-0.126** (0.030) **		58.97	59.28	0.15
Soft-bodied, mobile scavenger-predators							**-0.093** (0.029) **	19.11	21.87	0.10
Hard-bodied, mobile scavenger-predators				**0.009** (0.005) n.s.				12.61	7.30	**0.07 (.)**
Jointed legged, mobile scavenger-predators		**0.313** (0.067) **					**0.143** (0.037) **	240.55	56.57	0.63

Given the reciprocal relationship between predictor coefficients and abundance, the magnitude of responses to environmental factors varied among functional groups. In the case of suspension feeders, an increase in temperature near the seabed and substrate complexity were associated with higher abundances, especially that of climax and mobile. Pioneer and mobile showed a set of predictors explaining around 42% and 65% of the deviance in their abundance. Glacier distance showed minimal influence, with a slightly positive effect on pioneer abundance, potentially linked to their prevalence at stations MC4 and MC5. Temperature emerged as a strong predictor for deposit feeders, with opposing effects on epi- and infauna. Higher temperatures and soft bottoms were associated with higher epifaunal abundances, agreeing with the conditions met in the outercove stations. Conversely, lower temperatures and areas with less seabed rugosity, as seen in MC3, promote higher infaunal and sessile soft bodied scavenger-predators abundances. Generally, lower temperatures strongly correlated with higher abundance of many scavenger-predator groups whilst it explained a high proportion of abundance deviance along with other predictors such as turbidity and glacier distance.

3.2. Marguerite Trough

Defining Habitat Heterogeneity within trough

Marian Cove stations varied in their orientation within the fjord (mouth vs. head), all Marguerite Trough stations (MT1-MT5) were positioned roughly 100 km away from the continent and exhibited a wider depth range (359 meters at MT5 to 619 meters at MT3) compared to Marian Cove's shallower depths. This suggests a more uniform environment throughout the trough, in terms of all being open coastal and similar in distance from coast and environmental gradients. The seafloor temperatures during the survey ranged from 1.16°C to 1.37°C, which is significantly higher than the -1°C average observed in Marian Cove. These warmer conditions concomitantly resulted in lower DO levels. Chlorophyll-a concentrations when taking the SBI, decreased gradually when moving northeast (MT5) where levels were broadly similar to MT1 and to trends off the mouth of Marian Cove.

Table 11. Marguerite Trough environmental summary. Average environmental parameters (Mean ± SD, n=10).

	Environmental descriptor						
	Physical habitat		*Chemical environment*			*Food resources*	*Geography*
	Mean Depth (m)	Mean Temp (°C)	Mean Salinity (PSU)	Mean DO (µmol/L)	Turbidity (transmission)	Chla (µg/L)	Glacier distance (km)
MT1	479.2 ± 1.46	1.3342 ± 0	34.7171 ± 0	171.0913 ± 0	99± 0	0.0269 ± 0	100
MT2	509.2 ± 1.68	1.3368 ± 0	34.7138 ± 0	172.7251 ± 0	99± 0	0.0179 ± 0	100
MT3	619.0 ± 0.54	1.1572 ± 0	34.7226 ± 0	186.1565 ± 0	99± 0	0.0124 ± 0	100
MT4	500.5 ± 0.88	1.1653 ± 0	34.7239 ± 0	188.111 ± 0	99 ± 0	0.0094 ± 0	100
MT5	359.0 ± 0.24	1.37 ± 0	34.7144 ± 0	176.1363 ± 0	99 ± 0	0.0286 ± 0	100

In terms of topography, the steepest slope was observed at the furthest southwest (gray shaded in Figure 6), while the northern sites transitioned to a nearly flat terrain. This was accompanied by a generally smooth seabed along the cross section, evidenced by low mean values (bottom right, Figure 6) and 58% soft bottom. However, the complexity of the seabed increased towards shallower depths (MT5), coinciding with a shift in substrate to hard-rocky boulder field and higher benthic density (blue dashed line, Figure 6).

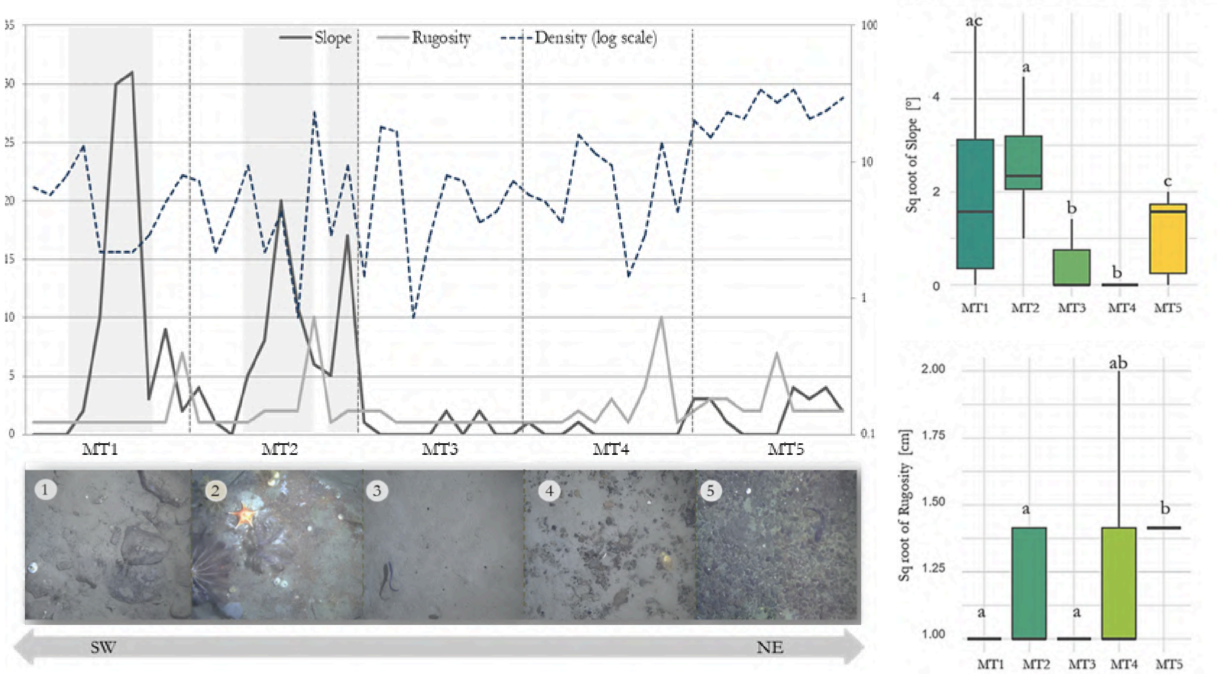


Figure 6. Seabed morphology in Marguerite Trough. Examples of substrates with varied rugosity and slope types: 1. hard soft bottom, rugosity 7cm, slope 2°; 2. hard rocky bottom, rugosity 10cm, slope 6°; 3. soft bottom, rugosity 1cm, slope 0°; 4. hard soft bottom, rugosity 1cm, slope 0° and 5. hard rocky bottom, rugosity 2cm, slope 0°. The steepest slopes are shaded in gray.

Diversity and composition of benthic assemblage within trough

The benthic abundance in Marguerite Trough was typically half that of the fjord (Figure S4. Supplementary Information). A total of 752 individuals were recorded (103 ind/m^2), with 5% remaining unidentified. The denser functional group in terms of "feeding habit", mirroring that in Marian Cove, were suspension feeders (Figure 7), representing 50% of the assemblage (51 ind/m^2), followed by grazers at 30% (31 ind/m^2), scavenger-predators at 11% (11 ind/m^2), and deposit feeders with only 8% of the total abundance (8 ind/m^2).

Among suspension feeders, the most represented were pioneer sessiles, with polychaete annelids and ascidians standing out as the main TUs. Similar to in the fjord, demosponges (poriferans) were a highly represented group within climax sessiles. Regionally, suspension feeders were denser at MT5 (Figure S5. Supplementary Information), however in proportion, grazers outnumbered these locally (Figure 7). In particular gastropod molluscs constituted 23% of the benthic assemblage in the region, followed by regular echinoid echinoderms (*e.g, Sterechinus neumayeri*).

While overall scavenger-predator density was much lower than observed in the study fjord, most subgroups shared comparable values. Shrimps were primarily identified, with some amphipods and pycnogonid chelicerates making up nearly 4% of the total abundance. Similarly, actinarian anthozoan cnidarians (soft-bodied, sessile) were also prevalent in this functional group.

In a smaller proportion, epifaunal deposit feeders, mainly mobile holothuroidea of the Elasipodida order (recognizable by its characteristic tentacles) and the species *Elpidia glacialis* were identified. Unlike in the fjord, no infaunal soft-bodied organisms (e.g., deposit-feeding polychaetes, sipunculans, and echiurans) were recorded in this region (Figure 7) only infaunal shelled (*e.g.*, *Limopsis marionensis*).

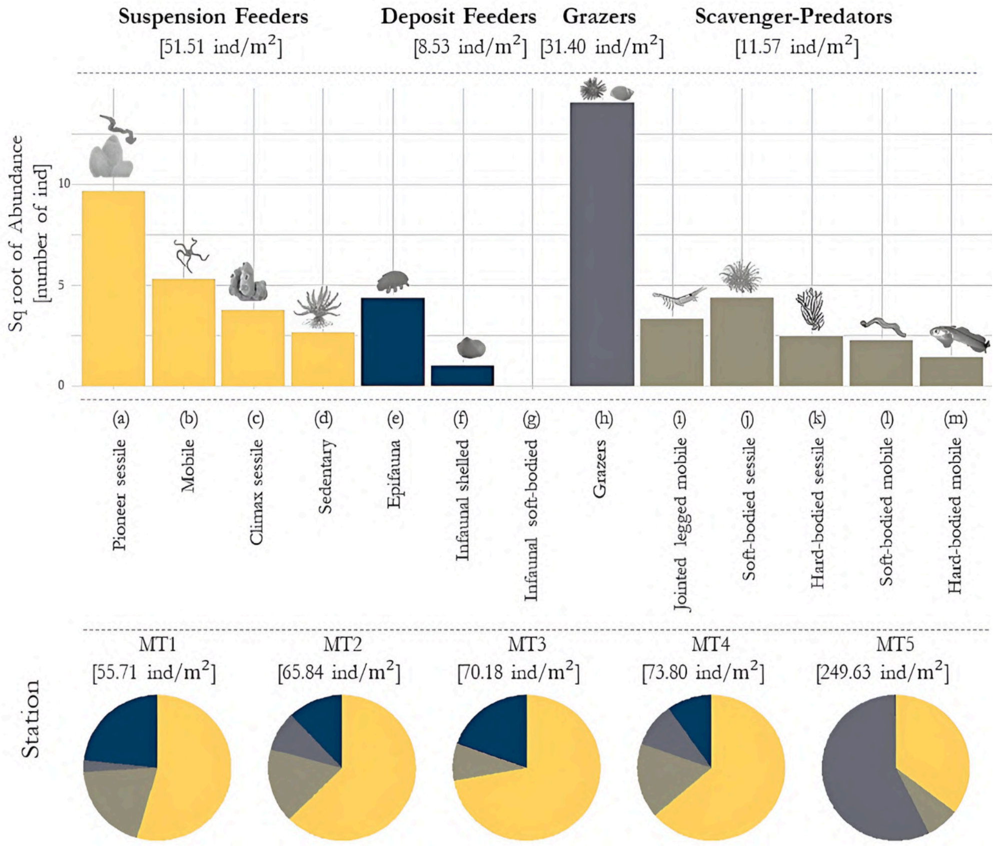


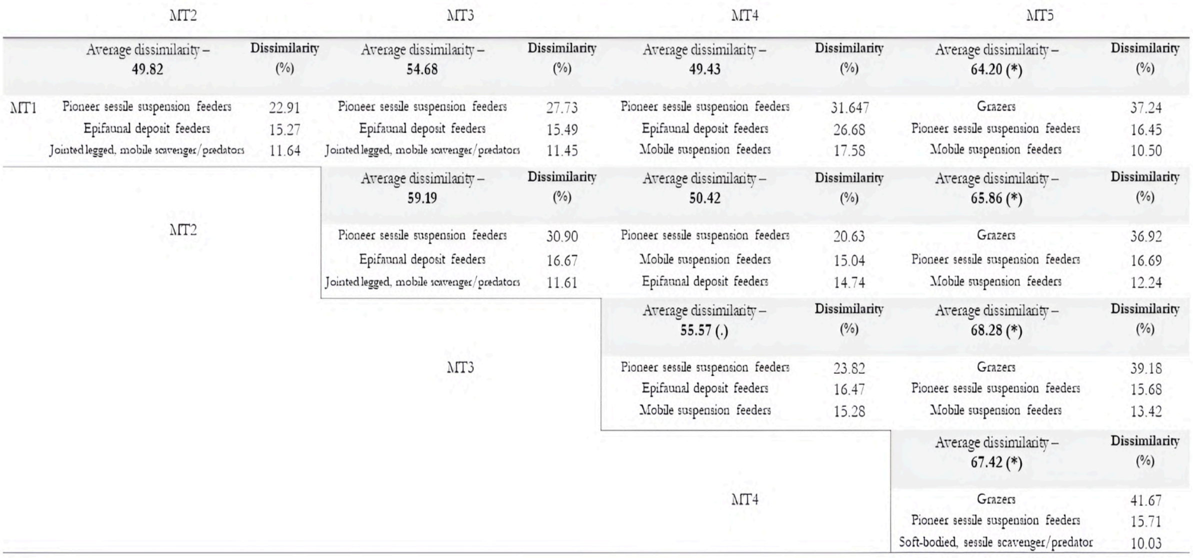
Figure 7. Benthic assemblages in Marguerite Trough. Functional groups and their main associated taxonomic units: (a). Polychaete annelids and solitary ascidians; (b). Ophiuroid echinoderms, (c). Demosponge, poriferans; (d). Crinoid echinoderms; (e). Holothuroid echinoderms; (f). Bivalve molluscs; (g) Not registered; (h). Gastropod mollusc and regular echinoid echinoderms; (i). Shrimp malacostracans; (j). Actinarian anthozoan; (k). Octocorals; (l). Errant polychaetes; (m). Pisces.

In contrast to the high heterogeneity across stations in Marian Cove (fjord), the overall benthic assemblage composition and distribution of functional groups in Marguerite Trough were similar (Fig. S5 Supplementary Information). For example, Pielou's evenness was slightly higher (~20%) compared to Marian Cove. These values along with minor statistical differences between stations, suggests a more uniform functional composition along the trough transect.

The SIMPER analysis further supported the relatively homogenous distribution of functional groups across stations with no statistically significant dissimilarities (Table 12). The shallowest and northernmost station MT5 stood out as it displayed the highest density and most contrasting biodiversity metric values compared to the rest of the sample stations, especially the least diverse and, taxon-poor MT2 and MT3 (Figure S5. Supplementary

Information). Conversely, the lowest density in the southernmost MT1 was compensated by a relatively even distribution of groups, reflected by its high Pielou's evenness index (Figure S5. Supplementary Information).

Table 12. Functional groups contributing to dissimilarity between stations in Marguerite Trough. Differences according to the percentage similarity analysis (SIMPER). Average dissimilarity expressed as the sum of the three groups contributing the most to the percentage of dissimilarity (in bold) while dissimilarity as a percentage of contribution based on cumulative percentage. PAIRWISE analysis (in brackets) after 999 permutations. Significantly differences: (*) p < 0.05, (.) p < 0.01.



	MT2		MT3		MT4		MT5	
	Average dissimilarity – **49.82**	**Dissimilarity** (%)	Average dissimilarity – **54.68**	**Dissimilarity** (%)	Average dissimilarity – **49.43**	**Dissimilarity** (%)	Average dissimilarity – **64.20 (*)**	**Dissimilarity** (%)
MT1	Pioneer sessile suspension feeders	22.91	Pioneer sessile suspension feeders	27.73	Pioneer sessile suspension feeders	31.647	Grazers	37.24
	Epifaunal deposit feeders	15.27	Epifaunal deposit feeders	15.49	Epifaunal deposit feeders	26.68	Pioneer sessile suspension feeders	16.45
	Jointed legged, mobile scavenger/predators	11.64	Jointed legged, mobile scavenger/predators	11.45	Mobile suspension feeders	17.58	Mobile suspension feeders	10.50
			Average dissimilarity – **59.19**	**Dissimilarity** (%)	Average dissimilarity – **50.42**	**Dissimilarity** (%)	Average dissimilarity – **65.86 (*)**	**Dissimilarity** (%)
MT2			Pioneer sessile suspension feeders	30.90	Pioneer sessile suspension feeders	20.63	Grazers	36.92
			Epifaunal deposit feeders	16.67	Mobile suspension feeders	15.04	Pioneer sessile suspension feeders	16.69
			Jointed legged, mobile scavenger/predators	11.61	Epifaunal deposit feeders	14.74	Mobile suspension feeders	12.24
					Average dissimilarity – **55.57 (.)**	**Dissimilarity** (%)	Average dissimilarity – **68.28 (*)**	**Dissimilarity** (%)
MT3					Pioneer sessile suspension feeders	23.82	Grazers	39.18
					Epifaunal deposit feeders	16.47	Pioneer sessile suspension feeders	15.68
					Mobile suspension feeders	15.28	Mobile suspension feeders	13.42
							Average dissimilarity – **67.42 (*)**	**Dissimilarity** (%)
MT4							Grazers	41.67
							Pioneer sessile suspension feeders	15.71
							Soft-bodied, sessile scavenger/predator	10.03

A closer examination of the benthic composition across stations revealed that grazers outnumbered their abundance in MT5 with no presence in MT3 (Figure 7 and Figure S5. Supplementary Information), specifically regular echinoid echinoderms and gastropod molluscs. This functional group solely contributed to nearly half of the observed dissimilarities with the other stations (Table 12). Furthermore, suspension feeders such as pioneer sessile and mobile were significantly more abundant at MT5, collectively summing to 55% of the dissimilarities between some stations (Table 12). To a lesser extent, a gradient of scavenger-predators distribution was observed across the trough. While those which were mobile jointed-legged contributed to dissimilarity between southernmost stations (MT1, MT2, and MT3), those which were soft-bodied drove dissimilarity between the northern stations (MT4 and MT5) in roughly the same proportion.

The beta diversity patterns suggested a more spatially variable distribution of functional groups within Marguerite Trough than Marian Cove (Table 13). The lower species richness estimators imply lower overall species richness in Marguerite Trough than found at Marian Cove.

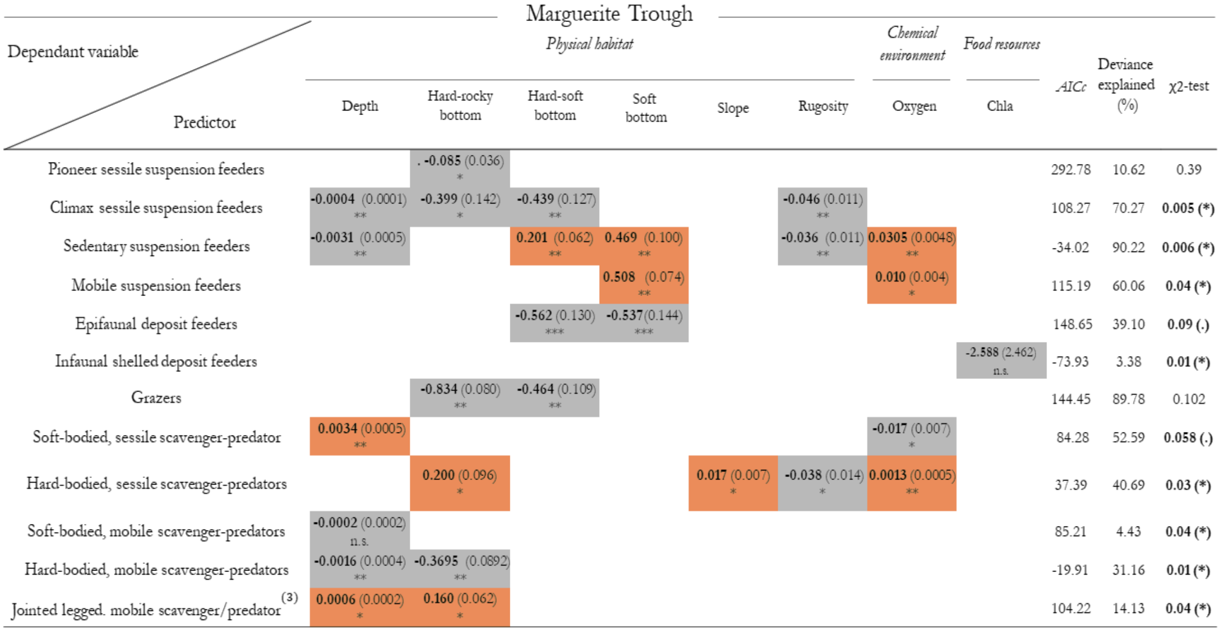
Table 13. Local diversity metric values (± standard deviation) in Marguerite Trough. Differences according to β-index estimators.

Dissimilarity		Species richness estimator	
Bray-Curtis	Jaccard	Bootstrap	Jackknife 2
0.71	0.81	6.98±1.6	23.92±0.27

Influence of Habitat Heterogeneity on the outer shelf functional benthic assemblage

The distribution and abundance of macrobenthos strongly correlated with seafloor-based predictors, particularly different types of substrates. The Bonferroni adjustment for false positives reduction applied to the initial models (P <0.05/8), lowered predictor-specific significance levels even though it did not necessarily lead to a reduction in the number of predictors for functional groups with multiple predictors.

Table 12. Effects of environmental predictors relative to functional groups in Marguerite Trough. Positive and negative predictor effects on response variables are shown in bold with standard errors (SEs) in orange and gray, respectively. Bonferroni-corrected significance levels are indicated by asterisks: * p < 0.05, ** p < 0.006. Model coefficients and overall significance are bolded. Superscripts on response variables denote the number of multiple comparisons adjusted by the Bonferroni method. (n.s.) indicates non-significance.



Dependant variable / Predictor	Marguerite Trough										
	Physical habitat						*Chemical environment*	*Food resources*			
	Depth	Hard-rocky bottom	Hard-soft bottom	Soft bottom	Slope	Rugosity	Oxygen	Chla	*AICc*	Deviance explained (%)	χ2-test
Pioneer sessile suspension feeders		. **-0.085** (0.036) *							292.78	10.62	0.39
Climax sessile suspension feeders	**-0.0004** (0.0001) **	**-0.399** (0.142) *	**-0.439** (0.127) **			**-0.046** (0.011) **			108.27	70.27	**0.005 (*)**
Sedentary suspension feeders	**-0.0031** (0.0005) **		**0.201** (0.062) **	**0.469** (0.100) **		**-0.036** (0.011) **	**0.0305** (0.0048) **		-34.02	90.22	**0.006 (*)**
Mobile suspension feeders				**0.508** (0.074) **			**0.010** (0.004) *		115.19	60.06	**0.04 (*)**
Epifaunal deposit feeders			**-0.562** (0.130) ***	**-0.537** (0.144) ***					148.65	39.10	**0.09 (.)**
Infaunal shelled deposit feeders								**-2.588** (2.462) n.s.	-73.93	3.38	**0.01 (*)**
Grazers		**-0.834** (0.080) **	**-0.464** (0.109) **						144.45	89.78	0.102
Soft-bodied, sessile scavenger-predator	**0.0034** (0.0005) **						**-0.017** (0.007) *		84.28	52.59	**0.058 (.)**
Hard-bodied, sessile scavenger-predators		**0.200** (0.096) *			**0.017** (0.007) *	**-0.038** (0.014) *	**0.0013** (0.0005) **		37.39	40.69	**0.03 (*)**
Soft-bodied, mobile scavenger-predators	**-0.0002** (0.0002) n.s.								85.21	4.43	**0.04 (*)**
Hard-bodied, mobile scavenger-predators	**-0.0016** (0.0004) **	**-0.3695** (0.0892) **							-19.91	31.16	**0.01 (*)**
Jointed legged. mobile scavenger/predator$^{(3)}$	**0.0006** (0.0002) *	**0.160** (0.062) *							104.22	14.13	**0.04 (*)**

Depth, slope, dissolved oxygen, and rugosity also influenced abundance, but to a lesser extent and with varying effects across functional groups, reflecting distinct ecological adaptations. Conversely to Marian Cove, most of the models were significant and some predictors explained a high fraction of the abundances' deviance, particularly those of suspension feeders and grazers. The moderate negative effect of hard substrates on climax abundance as well as the moderate positive effect of soft substrates on sedentary and mobile suspension feeders, imply a higher abundance and perhaps, their preference for hard bottoms. Together with other predictors, these models explained a high proportion of the deviance of the gamma data distributions.

Similarly, the high density of grazers at the shallow, rocky station MT5 corresponded with their strong preference for hard substrates, as indicated by the reduced model explaining nearly 90% of their abundance variation. Epifauna deposit feeders, in contrast, were predicted to thrive on softer substrates.

4. Discussion

Fjords are key emergent environments along the WAP, where blue carbon and species-rich habitats develop after glacier retreats (Barnes et al., 2020). New surveys along such fjords, are revealing their climate mitigation importance (Zwerschke et al., 2022). The current study is one of the few to compare the fjords with other distinct regional habitats. The results reported here supported Hypothesis 1, and aligned with Grange & Smith (2013), in which benthic assemblages in a fjord environment exhibited significantly higher density compared to adjacent shelf areas. This would be consistent with productive and diverse communities within fjord environments (e.g., Grange & Smith 2013; Zwerschke et al 2022). Hypothesis 2 was also supported as taxonomic and functional richness increased away from the glacier terminus in Marian Cove, as found by Moon et al. (2015), and also was higher on the inner compared to outer shelf (Grange & Smith 2013). Although some regional studies have found depressed richness on fjord floors, the richest biological assemblages tend to occur on steep fjord walls making them difficult to survey for (and thus report from) research ships unless they are ROV/AUV equipped (Barnes et al., 2023). While the study fjord in the present work displayed greater environmental heterogeneity, leading to an increase in within-station diversity (alpha diversity), some metrics in the trough transect trended in the opposite direction. One potential explanation is that the methodologies used might not have fully captured the diversity patterns in the trough. This would be unsurprising considering how sparsely they are sampled in time and space, yet they are physically changing quickly (Cook et al., 2016). Ideally, a wide range of apparatus and techniques would be used to survey biodiversity, but given that multiple sites and replicates are also needed to be robust, this is difficult to realize as Southern Ocean ship time is scarce, expensive in time and manpower and often limited in itineraries by other logistics commitments. Imaging techniques (aligned with corresponding environmental information captured using seabed mapping, CTD, physico-chemistry), especially with the advent of high resolution, digital, live view equipment is aiding ecological characterization of fjord biota (Gros et al 2023, Jansen et al 2023). Finally, our results seem to be aligned with Hypothesis 3 as assemblages transitioned from environmental stress tolerant-taxa near the glacier terminus (e.g., of sedimentation see Sahade et al., 2015) to more mature assemblages resembling those found on the outer shelf as habitat age increases and environmental conditions become more constant (at fjord mouths). Considering the mentioned caveats, the following sections review the benthic assemblages associated with different shelf environments.

4.1. Inner shelf: benthic diversity gradients in a glacial fjord

Marian Cove is primarily fed by glacial meltwater originating from the land-terminating Fourcade Glacier to the northeast (Jones et al., 2023). High sedimentation rates, freshwater dilution, and temperature fluctuations caused by the glacier's proximity are among the well-documented disturbances affecting Marian Cove and adjacent fjords during active calving summers (Kim et al., 2023; Ko et al., 2023; Deregibus et al., 2017). The benthic diversity-density patterns in Marian Cove can be interpreted through the lens of the classical successional model Intermediate Disturbance Hypothesis (IDH; Huston 1979) which suggests that diversity is typically maximized at intermediate levels of disturbance. Some work in coastal West Antarctic peninsula has supported the relevance of this hypothesis regionally (Robinson et al., 2021). In the current study context, the transect from the glacier terminus towards the fjord mouth is likely to reflect a spatial gradient of potential disturbance. Our observations registered a peak of richness and diversity midway between the glacier terminus and fjord mouth, likely due to a complex balance of environmental factors. Similar findings were reported in Adelaide Island (WAP), where intermediate ice scour disturbance was coincident with peak benthic biodiversity (Robinson et al., 2021) as well as in some Arctic fjords (Udalov et al., 2021). Moreover, the spatial gradient can be temporally dynamic, as tempo of benthic colonization usually covaries with the period of exposure of the seabed after deglaciation (Lagger et al., 2021). The lower diversity in the fjord's extremities, accompanied by a shift in the assemblage composition (distribution and dominance of certain traits and taxa), corroborates further an IDH driven trend. In the inner-cove, suspension feeders prevailed whereas in the outer-cove, deposit feeders were more prevalent. This was surprising given that many suspension feeders might be expected to have problems managing abiotic sedimentation load, but it is possible this was outweighed by food quality or quantity. Meltwater inputs at the grounding line of marine-terminating glaciers can drive upward fluxes of macro- and micronutrients through shelf sediment resuspension (Jones et al., 2023) that can be later capitalized by some suspension feeders. On its opposite, recent geochemical evidence, coincidentally with the period surveyed, reported enhanced depth-integrated phytoplankton productivity (Jones et al., 2023; Mo et al., 2023) and past sediment Total Organic Carbon (TOC) content in the outer-cove relative to the inner section (Zwerschke et al., 2022). This higher productivity in the water column as well as in the sediments in the outer cove, can support the observed assemblage of slow-moving surface deposit feeders (holothuroidea and infaunal spionid polychaetes *Aurospio* sp. n), sedentary and mobile suspension feeders (crinoids and ophiuroids) and some scavengers-predators (errant polychaetes and shrimps). Energy for these feeding guilds becomes available only after it settles on the seabed (deposit feeders) or passes through the foodweb of other organisms (scavengers and predators), as documented in Weddell Sea benthic communities (Pineda-Metz et al., 2020). The deposit-feeder dominated area ultimately has the potential to store carbon through deposition of organic matter upon death and subsequently get buried into the sediment (influenced in complex ways by infauna, see Braeckman et al., 2024). Based on the models, soft substrate seemed to promote epifauna and infauna deposit feeders abundance. However, lower temperatures may boost higher epifaunal abundance, the opposite effects are expected on shelled infauna. Moreover, sessile groups with diverse feeding mechanisms and skeletisation (climax suspension feeders, hard-body scavengers and infaunal deposit feeders) were found in the stations away from the glacier. This might be due to the nature of the soft sediment. The poorly sorted muddy sediments in Marian Cove are interspersed with sand, gravel, and rock fragments transported by glacial processes (Yoon et al., 2004). Despite the lack of direct grain size measurements, gravel was reported to be a suitable substrate for diverse sessile fauna in ice-distal sites (Moon et al., 2015). Conversely, the influx of high sediment loads in the inner cove can reduce net primary production due to light limitation (Ferreira et al., 2020) and macronutrient uptake inhibition (Holding et al., 2019). While macronutrient exchange at the sediment-water interface in Marian Cove likely occurs both vertically and horizontally, the cove's narrow and shallow geometry, coupled with strong wind events, would drive relatively rapid flushing of the cove (Jones et al., 2023). As a consequence, the particle flux and chemistry in the inner cove –characterized by lower productivity and lower TOC– may only support the observed poorer benthic assemblage. The absence or scarcity of deposit feeders and grazers under these conditions depresses diversity and increases the apparent dominance of a few disturbance-tolerant taxa and traits (as found in Potter Cove by Sahade et al., 2015). This is exemplified by the widespread occurrence of suspension feeders such as bryozoans and solitary ascidians near glacier termini. The ability to disperse by pelagic larvae (including Serpulidae spp., *Molgula pedunculata*, and *Cnemidocarpa verrucosa*) allows rapid post-disturbance (e.g. glacial-retreat) colonization (Almond et al., 2022; Zwerschke et al., 2022). Additional adaptations of some pioneer taxa include rapid growth rates and early maturity for reproduction, which can later become a substrate for other fauna (Kim et al., 2021; Arntz et al., 2005). Moreover, roughened seabeds - positively correlated with the abundance of pioneers- offer increased surface area, complex flow and habitats, and hard surface attachment sites (Kostylev et al., 2005). This can ultimately promote the settlement and growth of many pioneer species (see Barnes & Conlan 2006; Zwerschke et al 2021) as well as serve as food supply to the scavengers and carnivores that form the rest of the benthic food web. A notable pattern emerged with higher densities of scavengers and predators associated with high abundance of suspension feeder transects near the glacier. These top predators feed on both planktonic and benthic suspension feeders and in some cases, can cope well with the low oxygen concentration on the seafloor as well as the sediment rain (Alurralde et al., 2019). The suspension-scavenger coupling was further supported by model results, which linked scavenger abundance to lower temperatures, proximity to glaciers, and increased turbidity.

The observed benthic patchiness, specially at small (within transects among adjacent seabed photos) or intermediate (region) spatial scales, provides the opportunity for heightened diversity through the coexistence of different functional groups and traits in a mosaic-like pattern (Barnes & Conlan, 2006). Yet, the degree to which successional colonization enhances regional diversity can be difficult to establish. While habitat heterogeneity can potentially buffer against frequent disturbance (Moon et al., 2015), a consensus among researchers is that disturbance can adversely impact seabed assemblages (Gutt et al., 2001). Sahade et al. (2015) reached a similar conclusion based on a record over a two-decade of faunal impoverishment, linked to high sedimentation rates. Traditionally, Antarctic benthic organisms have been characterized by narrow physiological temperature tolerances (Peck, 2006). Consistent with threshold tolerance, Torre et al. (2012) experimentally demonstrated varying sensitivities to sedimentation among several filter-feeding regional species. In the current study, both temperature and turbidity significantly correlated with benthic abundances. Temperature, a key abiotic factor for the development of organisms, was negatively correlated with organism types incapable of escaping thermal stress such as infauna and sessile scavengers. Elevated temperatures accelerate metabolic rates and oxygen consumption, while reducing larval dispersal and survival (e.g., premature hatching, accelerated larval development) (Gillooly et al., 2001).

4.2. Outer shelf: depth and hard substrate as drivers of functional diversity in Marguerite Trough

Latitude, whilst not itself an environmental factor, reflects some basic ecosystem properties such as day length, average light energy, temperature and thus has influence on production (Arntz et al., 2005). Unlike the more variable conditions found in the shallower coastal fjord, the overall stability of Marguerite Trough (MT) as an open marine environment was coincident with less patchy distribution of functional groups. At these depths, with high oxygen levels and limited annual food availability (Nasir et al., 2024), the higher abundance of macro- and megafauna in terms of feeding modality (suspension/filter feeder) and mobility (sessile) might be due to higher loads of suspended particles close to the seabed, suggesting increased near-bottom currents and the presence of a strong benthic nepheloid layer (BNL). Käß et al. (2021) also observed the same macrobenthic pattern across the deep Fram Strait in the Arctic Ocean. Overall, detritivore feeding strategies dominated the benthic assemblage (in terms of number of individuals), suggesting the availability of organic matter, sedimentation rates, and favourable water column dynamics. Summer phytoplankton blooms provide the main primary food source along the WAP shelf, with phytodetritus accumulating on the seabed as a 'food bank' (Smith et al., 2006). The presence of mobile invertebrates (e.g., polychaete worms, numerous ophiuroids and crinoids) and fish predators along the trough, appeared to utilize epibenthic or pelagic food resources such as zooplankton. Despite seasonal fluctuations in phytoplankton production, Mincks et al. (2008) noted a substantial inertia in benthic–pelagic coupling, whereby sediment ecosystems integrate long-term variability in production processes in the water column above. At the surveyed depths, where there is typically a sharp reduction of vertical exports from photosynthetic production at the surface (Weston et al., 2013), Isla et al. (2006) identified that bottom current velocity can control sediment deposition, potentially structuring macrobenthic faunal assemblages. The water current velocity near the seabed benefits filter-feeding over deposit-feeding species as it can actively redistribute sediments and organic matter across the shelf, promoting a more homogenous distribution of particles and energy (e.g., labile OC fractions). Indeed Souster et al. (2020) found mean bottom velocity the biggest single environmental correlate of biomass and carbon stored in zoobenthos in Barent Sea soft sediment environments. Spring-neap tidal currents increase turbulence at the Weddell seabed- water interface (Isla et al., 2006), so it can be hypothesized that the tidal regime in Marguerite Trough likely contributes to sediment resuspension and nutrient cycling above the seafloor. A key vector tightly linked to tides, are the small spinning vortices—known as eddies—containing shelf water and periodically generated from instabilities that derive from the horizontal shear of the flow. Brearley et al. (2019) demonstrated that intense eddy activity on the northern bank of the Marguerite Trough facilitates the transport of heat and nutrients, enabling the intrusion of Upper Circumpolar Deep Water (UCDW) into the trough's bottom waters. These resuspended nutrients can be later utilized by suspension/filter feeders (sponges) and some deposit feeders as well (*Limopsis marionensis*). The sub-ice-shelf silty muds potentially formed through a combination of meltwater-derived sedimentation and tidal pumping (Kilfeather et al., 2011), further underscore the influence of hydrodynamic processes on sediment dynamics and the occurrence of certain traits. Although the abundance of deposit-detritivore feeders was low, but elpidiid holothurians were found a few kms north from the trough digesting particular sedimentary components, including bacteria and their exudates between Nov and Mar, concurrently with peaks in microbial biomass (Mincks et al., 2008). Besides nutrients availability, the area within the trough surveyed in the current work included hard substrate types especially noticeable around 350 m depth, and higher number of corresponding sessile suspension feeders and grazers living on that habitat. Previous studies have also documented high species richness of Antarctic continental shelf echinoderms (e.g., the omnivorous species *Sterechinus neumayeri*), especially between 100 and 1,000 m depth along the Antarctic Peninsula, Weddell Sea, and East Antarctica (Fabri-Ruiz et al., 2020). According to Kilfeather et al. (2011), the melt out of sediment from the base of the ice shelf and/or from icebergs deliver coarse particles to the seafloor. Stable anchoring points and increased habitat complexity offered by pebbles, large and small rocks dropped by icebergs and removed from the continent by glacial erosion, likely provides favorable conditions for the establishment and growth of sessile assemblages, even near the shelf break (Nasir et al., 2024) as well as promote filter-feeding organism (Käß et al., 2021). Souster et al. (2020) similarly found suspension feeder inhabited boulders around a shelf break trough in the high Arctic. The type of substrate may not only have a role on influencing the functional groups distribution but also acts as a key factor in zoobenthic carbon storage, suggesting that rocky bottoms store more carbon compared to soft substrates (Barnes & Sands 2017; Morley et al., 2022). Of note, biotic substrates (such as shells) along the rocky field appeared to provide additional sites for attachment and therefore new ecological niches for sessile species (Figure S6. Supplementary Information). This ectosymbiosis – i.e., sessile life on biotic substrate, whatever the nature of the relationship: mutualism, commensalism, or parasitism– can enhance species richness and abundance within sessile communities without altering overall diversity (Hétérier et al., 2008). Cidaroids (echinoids), widely registered in the rocky station, often serve as hosts for a variety of epibionts in the Antarctic deep sea (Hétérier et al., 2008).

Overall, organisms in this environment can capitalize on quite different food sources, either sediment-derived nutrients or exploit epibenthic and pelagic food sources, such as zooplankton. The presence of dropstones and boulders, creating habitat heterogeneity, can also enhance biodiversity, particularly among sessile benthic fauna. Nonetheless, further studies on links between functional traits and biochemical fluxes at the sediment–water interface are needed to understand in detail how and which species and macrofauna assemblages affect biochemical fluxes at the sediment–water interface.

5. Concluding remarks

Our knowledge of trends in diversity and faunal composition along the continental shelf settings has grown steadily during the last two decades, particularly on West Antarctic shelf benthos (e.g., Kaiser et al 2013). However, the factors underlying any biological differences between outer and inner shelves or on- *versus* offshore, are often unclear, complex and require clarification (e.g., Rogers et al 2020). In the current study example, the fjord showed almost two-fold greater benthic macro- and megafaunal richness and density than the outer shelf. In the frame of proposed (but yet to be designated) as Marine Protected Areas, we corroborated the fjords as important hotspots of benthic abundance and biodiversity. Nevertheless, global change impacts —such as change in iceberg scouring and massive sediment loads derived from glacier retreats— have been documented and even projected as a powerful negative feedback on climate change (e.g., blue carbon pathway to sequestration) in coastal zones on the AP (Zwerschke et al., 2022). In the present study, the functional analysis proved to be successful in assessment of functional variation of macro- and megafauna in response to processes related to pelago-benthic coupling (e.g., food input to– and its availability for the benthos). These processes, however, can be highly climate sensitive environmental parameters (e.g., glacial retreat).

In the context of rapid climate change along the AP, the 'light touch' and lower expertise requirement to using functional grouping or ecological traits could provide a fundamental basis to aid monitoring changes, in particular, to tackle the concern of climate-induced environmental forcing. By achieving this, we would be able to understand the occurrence and predict shifts in benthic functioning in response to future climate scenarios in a changing AP.

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7. Supplementary Information

Figure S1. British Antarctic Survey's Shallow Underwater Camera System (SUCS). Photo credit: David Barnes (Bridges et. al, 2021).

Table S1. Relationship between environmental descriptors and benthos in polar regions.

Environmental driver	Processes related to polar marine benthos	Reference
Depth	Acts as an important buffer against iceberg impacts.	Morales et al., 2024
	Regulates benthic food input by modifying particle residence time in the water column, affecting the quantity and quality of organic matter available to benthos.	Jumars & Wheatcroft, 1989 Pineda-Metz et al., 2019
Temperature	Influences metabolic rates of benthic organisms, affecting their growth, reproduction, and distribution.	Peck, 2020
Substrate nature	Dropstones serve as crucial stepping stones for dispersal and connectivity of those communities relying on hard substrates.	Post et al., 2016 Almond et al., 2021
	Coarse substrates are preferred by filter or suspension feeders due to enhanced attachment surface and elevated positions, facilitating capture success rates.	Muschenheim, 1987
	Fine, siltier sediments provide food resources for deposit feeders (both facultative and obligate).	Gutt, 1990
	Availability of hard substrates (stones and boulders) influences sessile epibenthic biota recruitment success.	Gray & Elliott 2009 Gutt et al., 2019

Seabed Slope (inclination of the substrate)	Acts as an important buffer against iceberg impacts.	Alley et al., 2023 Morales et al., 2024
	Influence distribution of benthic fauna	Jerosch et al., 2015
Rugosity (roughness)	Higher rugosity creates complex habitats with various microhabitats, promoting colonization and population growth of species.	Kostylev et al., 2005
	Irregular surfaces provide more attachment points for settling larvae and juveniles, promoting colonization and population growth of various species.	Hills et al., 1999
	Influences food resource accessibility, with higher rugosity potentially harboring more food due to increased surface area and organic matter retention.	
Distance to the (glacier) Antarctic continent	Topography of the shelf influences benthos-pelagos interconnectivity, affecting benthic distribution patterns and transport/deposition of suspended particles. E.g,. increased turbidity due to higher freshwater flux; sedimentation rates decline towards fjord mouth in Arctic fjords as well rise of labile organic-carbon content in sediments.	Jungblut et al., 2020 González et al., 2011 Grange & Smith, 2013
Chlorophyll-a concentration	Boosts energy input and food availability for filter-feeding benthic species, such as sponges, bryozoans, and some mollusks.	Braeckman et al., 2024
	Alters light availability for benthic primary producers (macroalgae and seagrasses) affecting their growth and distribution. E.g., annual growth performance of the erect bryozoan *Cellarinella watersi* at Signy was related to the length of annual nanophytoplankton bloom.	Barnes, 1995 Jerosch, K. et al., 2019
Oxygen concentration	Influences metabolic processes and survival of benthic organisms.	Peck, 2020
Sea Water Salinity	Affects osmoregulation and physiological functions of benthic organisms.	Rakusa-Suszczewski & McWhinnie, 1976
Turbidity	Used as a proxy for sedimentation	Tait, 2019
	Reduces availability of rocky substrates for settlement of consumers and primary producers.	Khim et al., 2007
	Mineral discharge reduces available food for suspension feeders and in the extreme scenario, can clog their feeding appendages.	Krzeminska & Kuklinski, 2018 Valdivia et al., 2020
	Increases light attenuation rate with depth, affecting primary producers' vertical stress gradient in the glacier's nearby.	Braeckman et al., 2024

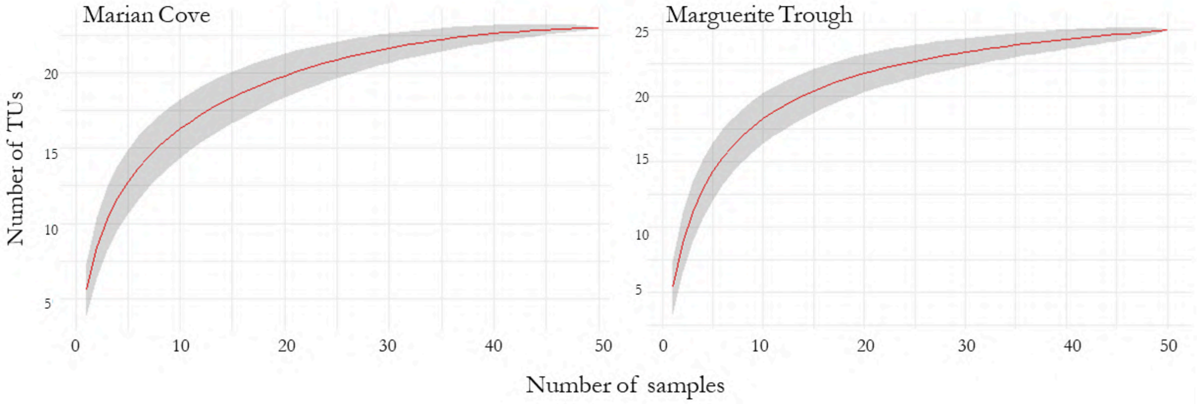


Figure S2. Effect of sampling effort on the number of Taxonomic Units (TUs). Species accumulation curves comparing observed data (solid red line) for replicates (n=10) taken at 5 stations in Marian Cove (left) and Marguerite Trough (right). Confidence intervals around the accumulation curve (shaded areas) represent the variability in species richness estimates.

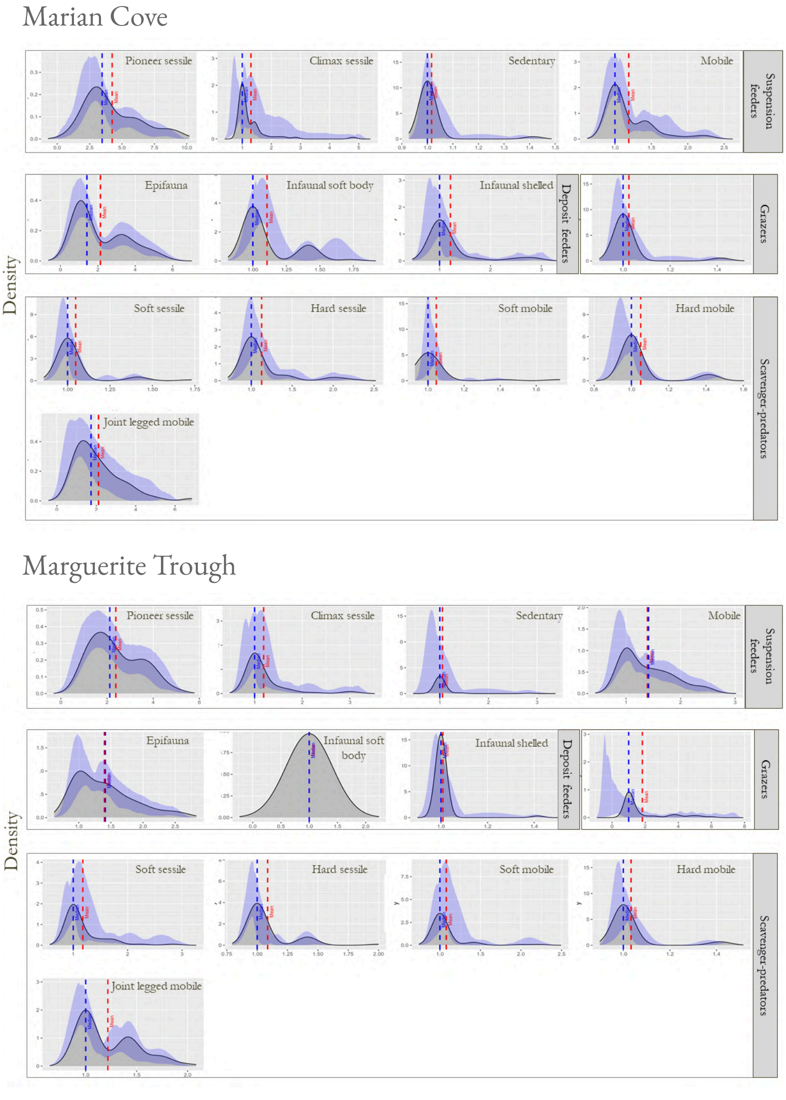


Figure S3. Distribution of benthic macro- and megafauna abundance. Kernel density plots visualize the distribution of square root-transformed abundance data for Marian Cove (top panel) and Marguerite Trough (bottom panel). The red dashed line indicates the mean, and the blue dashed line represents the median. The shaded light purple area represents the 95% confidence band, estimated using bootstrapping techniques.

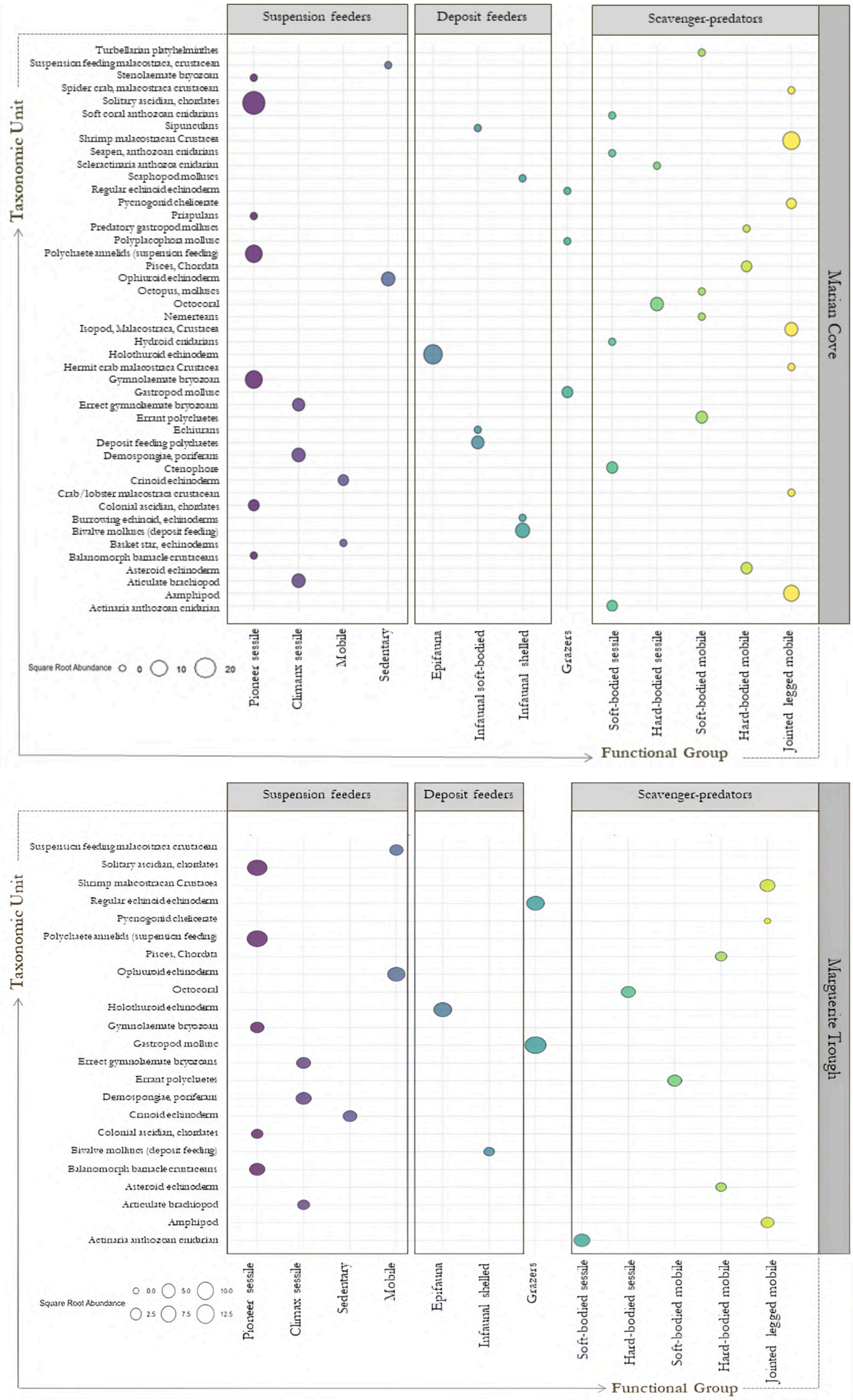


Figure S4. Regional benthic assemblage. Taxonomic composition and functional groups in Marian Cove (top panel) and Marguerite Trough (bottom panel). Of note, no infaunal soft-bodied were found in Marguerite Trough, reflecting an overall lower taxonomic-functional richness and abundance.

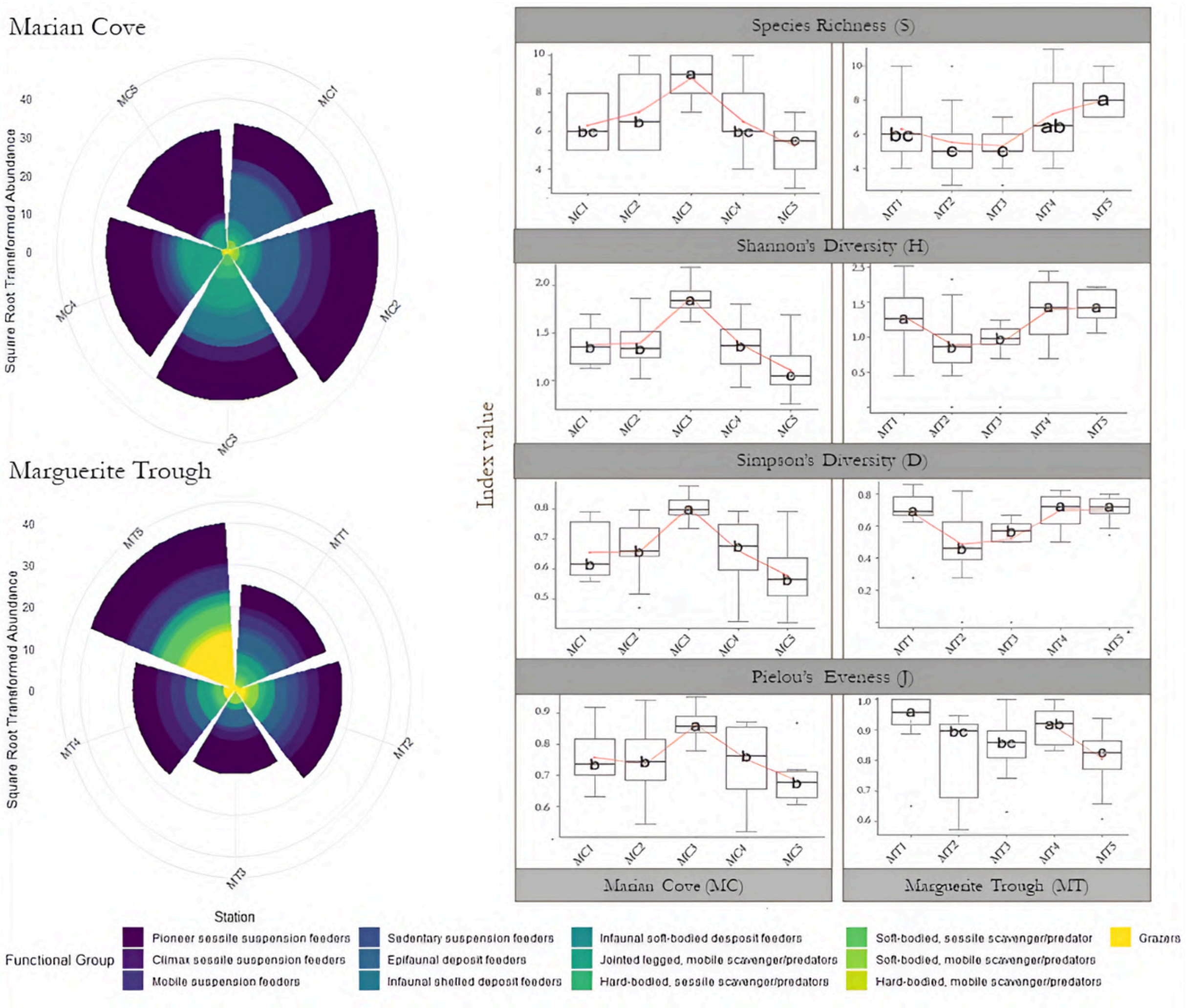
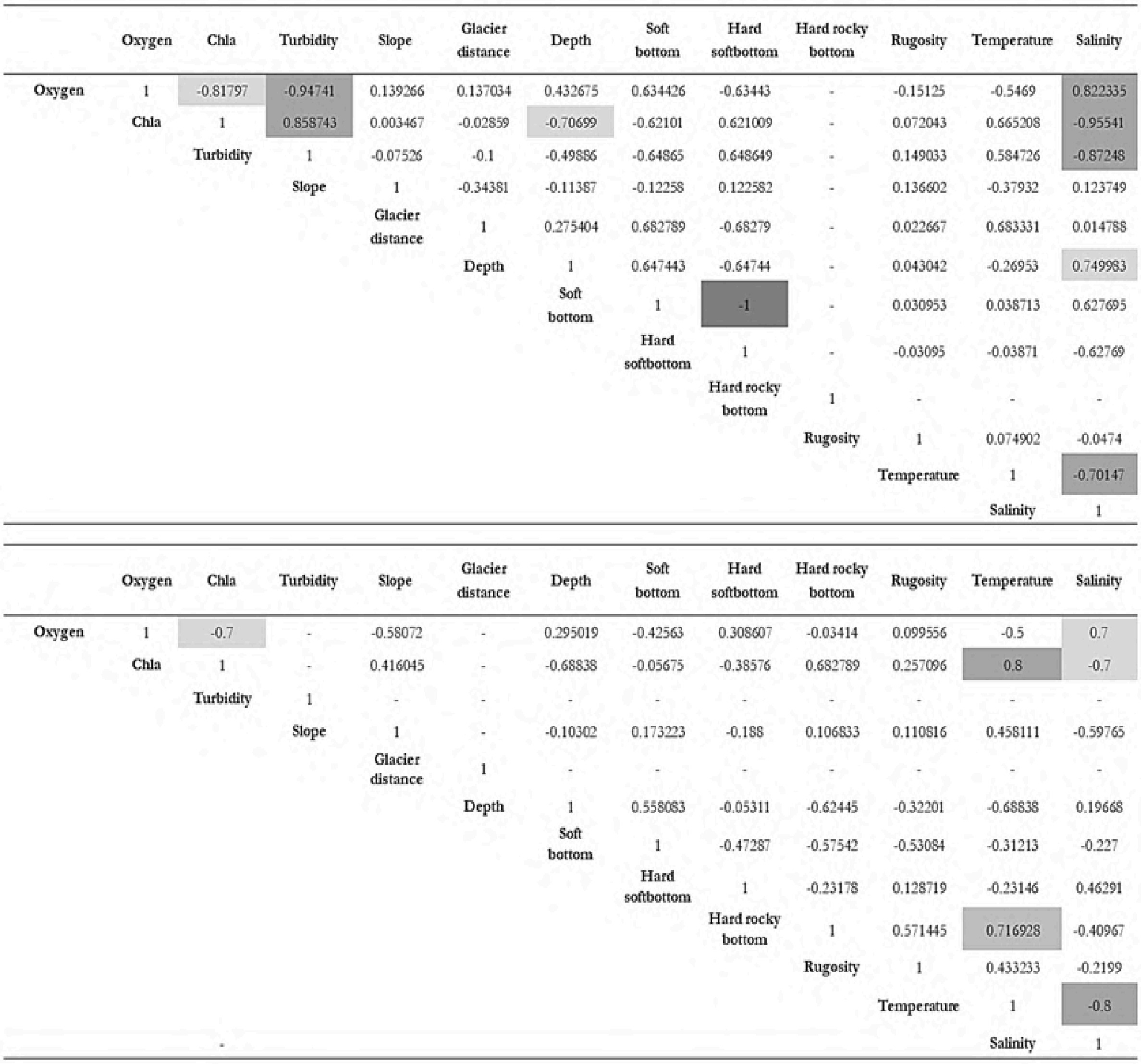


Figure S5. Benthic biodiversity comparison between stations in Marian Cove (top) and Marguerite Trough (bottom). Left: Benthic composition of functional groups per station. Right: Alpha-biodiversity metrics per station.

Table S2. Collinearity of predictors. Spearman rank correlation coefficients (ρ) showing collinearity of the predictors in Marian Cove (top) and Marguerite Trough (bottom). The presence of high collinearity ($\rho \geq 0.7$) is highlighted in gray.



	Oxygen	Chla	Turbidity	Slope	Glacier distance	Depth	Soft bottom	Hard softbottom	Hard rocky bottom	Rugosity	Temperature	Salinity
Oxygen	1	-0.81797	-0.94741	0.139266	0.137034	0.432675	0.634426	-0.63443	-	-0.15125	-0.5469	0.822335
Chla		1	0.858743	0.003467	-0.02859	-0.70699	-0.62101	0.621009	-	0.072043	0.665208	-0.95541
Turbidity			1	-0.07526	-0.1	-0.49886	-0.64865	0.648649	-	0.149033	0.584726	-0.87248
Slope				1	-0.34381	-0.11387	-0.12258	0.122582	-	0.136602	-0.37932	0.123749
Glacier distance					1	0.275404	0.682789	-0.68279	-	0.022667	0.683331	0.014788
Depth						1	0.647443	-0.64744	-	0.043042	-0.26953	0.749983
Soft bottom							1	-1	-	0.030953	0.038713	0.627695
Hard softbottom								1	-	-0.03095	-0.03871	-0.62769
Hard rocky bottom									1	-	-	-
Rugosity										1	0.074902	-0.0474
Temperature											1	-0.70147
Salinity												1

	Oxygen	Chla	Turbidity	Slope	Glacier distance	Depth	Soft bottom	Hard softbottom	Hard rocky bottom	Rugosity	Temperature	Salinity
Oxygen	1	-0.7	-	-0.58072	-	0.295019	-0.42563	0.308607	-0.03414	0.099556	-0.5	0.7
Chla		1	-	0.416045	-	-0.68838	-0.05675	-0.38576	0.682789	0.257096	0.8	-0.7
Turbidity			1	-	-	-	-	-	-	-	-	-
Slope				1	-	-0.10302	0.173223	-0.188	0.106833	0.110816	0.458111	-0.59765
Glacier distance					1	-	-	-	-	-	-	-
Depth						1	0.558083	-0.05311	-0.62445	-0.32201	-0.68838	0.19668
Soft bottom							1	-0.47287	-0.57542	-0.53084	-0.31213	-0.227
Hard softbottom								1	-0.23178	0.128719	-0.23146	0.46291
Hard rocky bottom									1	0.571445	0.716928	-0.40967
Rugosity										1	0.433233	-0.2199
Temperature											1	-0.8
Salinity												1

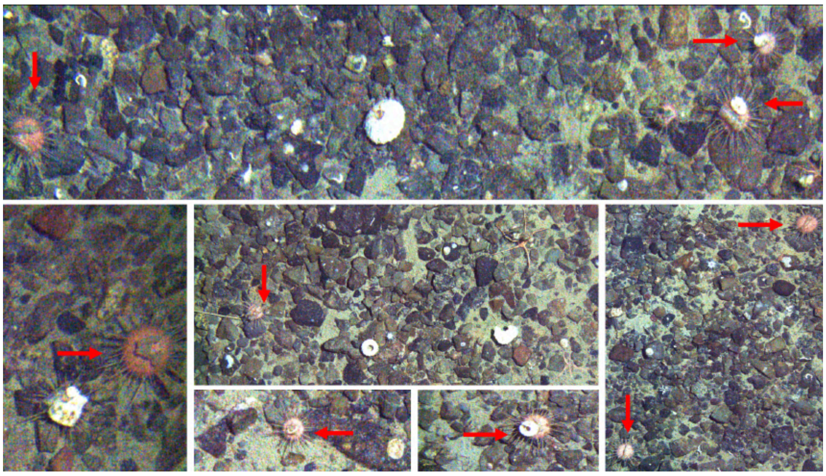


Figure S6. Ectosymbiosis in Marguerite Trough. Sessile life on biotic substrate, whatever the nature of the relationship: mutualism, commensalism, or parasitism. Cidaroids often serve as hosts for a variety of epibionts in the Antarctic deep sea. Of note, this was exclusively observed in areas with rocky substrate.

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