Environmental parameters

Parameters	S5	S7	S9	S13	S15	S23	S29	S32
Depth (m)	600	332	3000	461	488	290	405	3000
OC (%)	0.56	0.26	0.54	0.02	0.41	0.91	0.40	0.15
OM (%)	0.96	0.45	0.93	0.03	0.71	1.57	0.69	0.27
Sand (%)	12.14	88.57	2.53	84.68	64.68	22.38	52.98	37.13
Silt (%)	76.26	15.76	81.71	9.32	6.12	16.10	37.59	47.67
Clay (%)	11.60	6.40	15.76	6.00	29.20	61.52	9.44	15.20

Station	Biomass Average (g	SD
S5	0.53	0.53
S7	22.09	18.60
S13	49.37	33.47
S15	173.18	61.20
S23	624.65	145.49
S29	1210.19	157.41
S32	499.03	158.52

Present- Absent data

	Stn 5	Stn 7	Stn 9	Stn 13	Stn 15	Stn 23	Stn 29	Stn 32
Ophiomastus serratus	-	-	-	+	-	-	-	-
Amphiura (Amphiura) lym	-	+	-	+	-	-	-	-
Amphiura belgicae	-	+	-	-	-	-	-	-
Ophiura flexibilis	-	+	-	-	-	-	-	-
Ophiura crassa	-	-	-	+	-	+	-	+
Ophiacantha antarctica	-	-	-	-	-	-	+	-
Ophioplinthus tumescens	-	-	-	+	-	-	-	-
Ophiosabine vivipara	-	-	-	+	-	-	-	-
Ophiomastus meridionalis	-	-	-	+	-	+	-	-
Ophiomastus perforatus	-	-	-	-	-	+	-	-
Ophiacantha cosmica	-	-	-	-	-	+	-	-
Ophiomastus primula	-	-	-	+	-	+	-	-
Nacella kerguelenensis	-	-	-	+	+	+	-	-
Cancellariidae (unidentifie	-	-	-	+	-	-	-	-
Pareuthria sp.	-	-	-	-	-	+	-	-
Cyclostrema sp.	-	-	-	-	+	-	-	-
Microdiscula sp.	-	-	-	-	+	-	-	-
Limopsis sp.	-	-	-	-	+	-	-	-
Cyamiidae (unidentified)	-	-	-	-	+	-	-	-
Magellania joubini	-	-	-	-	+	+	-	-
Aerothyris maquarensis	-	-	-	-	+	+	-	-
Aerothyris kerguelensis	-	-	-	-	+	-	-	-
Ampelisca sp.	-	-	-	-	-	+	-	-
Epimeria sp.	-	+	-	-	-	-	-	-
Eusirus sp.	-	+	-	-	-	-	+	-
Alexandrella chione	-	-	-	-	+	+	-	-
Epimera (Subepimeria) io	-	-	-	-	+	-	-	-
Epimera (Epimeriella) ma	-	-	-	-	-	+	-	-
Alexandrella mixta	-	-	-	-	-	+	-	-
Epimera (Drakepimeria)	-	-	-	-	-	+	-	-
Notoproctus sp.	-	+	-	-	-	-	-	-
Lumbrineris magalhaensis	-	-	-	-	-	+	-	-
Scalibregma inflatum	-	-	-	-	-	+	+	-
Glycera kerguelensis	+	-	-	+	-	-	-	-
Glycera sp.	-	-	-	-	-	-	+	-
Notomastus sp.	-	-	-	+	-	-	-	-
Syllis cornuta	-	-	-	+	-	+	-	-
Syllis sp.	-	-	-	-	-	+	-	-
Mystides notialis	-	-	-	-	-	+	-	-
Nereis sp.	-	-	-	-	-	+	-	-
Phyllodoce madeirensis	-	-	-	-	-	+	-	-
Lacydonia oculata	-	-	-	-	-	+	-	-
Scoletoma tetraura	-	-	-	-	-	+	-	-
Capitella capitata	-	-	-	-	-	-	+	-
Nephtys ferruginea	-	-	-	-	-	-	+	-
Ninoe falklandica	+	-	-	-	-	-	-	-
Symplectoscyphus vanhoe	-	+	-	-	-	-	-	-
Symplectoscyphus sp.	-	-	-	+	-	-	-	-
Filaguria sp.	-	-	-	-	-	+	-	-
Margaretta sp.	-	-	-	-	-	+	-	-
Caberea sp.	-	-	-	-	-	+	-	-
Rossella antarctica	-	-	-	-	+	+	+	+
Achelia hoekii	-	+	-	-	-	-	-	-
Nymphon inornatum	-	-	-	+	-	-	-	-
Nymphon sp. 1	-	-	-	-	-	+	-	-
Nymphon sp. 2	-	-	-	-	-	+	-	-
Austrodecus sp.	-	+	-	-	-	+	-	-

Total meiobenthic abundance

Stations	Abundance (Indv. 1	SD
5	170	10
7	114	11
9	24	4
13	254	33
15	258	8
23	521	17
29	251	41
32	247	16

% contribution in vertical distribution

Stations	0-1	1-2	2-5	5-10	10-15	15-30
5	31.18	25.29	17.65	11.18	9.41	5.29
9	20.83	25	20.83	16.67	16.67	0
15	39.53	26.36	15.89	10.08	5.81	2.33
23	31.29	25.14	14.22	14.38	10.75	4.22
29	36.33	38.33	9	13.3	2.14	0.9
32	43.72	18.63	18.62	8.91	5.26	4.86

Nematode present absent data

Nematode Species	S 5	S 7	S 9	S 13	S 15	S 23	S 29	S 32
Acantholaimus quintus	+	+	-	+	-	-	-	+
Actinonema chitwoodi	-	-	-	+	-	-	-	-
Actinonema pachydermatum	+	-	-	+	-	+	-	-
Adoncholaimus thalassophygas	-	-	-	-	+	-	-	-
Aegialoalaimus tenuis	-	-	-	-	-	+	-	-
Anoplostoma tenuisetum	-	-	-	-	+	+	-	-
Anticoma acuminata	+	-	-	+	-	+	+	-
Araeolaimus elegans	-	-	-	-	+	-	-	-
Atrochromadora microlaima	-	-	-	-	-	-	+	-
Bathylaimus filicaudatus	+	-	-	-	-	+	-	+
Calyptronema acuminatum	-	-	-	-	-	-	-	+
Cervonema tenuicaudatum	-	-	-	-	-	-	+	-
Chromadora nudicapitata	-	+	-	+	-	-	-	-
Chromadorina cervix	-	-	-	+	-	-	-	+
Comesoma arenae	+	-	-	+	+	+	-	-
Comesoma hermani	+	-	-	-	+	-	-	+
Comesomoides sp.	-	-	-	-	-	+	-	-
Curvolaimus filiformis	-	+	-	-	-	-	-	-
Daptonema sp.	+	-	-	-	-	+	-	-
Deontolaimus longicauda	-	-	-	-	-	-	-	+
Desmodora greenpatchi	-	+	-	-	-	-	-	-
Desmodora scaldensis	+	+-	-	+	+	+	-	-
Desmodora tenuicauda	+	+	-	-	-	+	-	-
Desmodorella sanguinea	+	+	-		+	+	-	-
Desmodorella tenuispiculum	+	+	-	+	+	+	-	-
Desmoscolex sp.	+	+	-	+	+	+-	+	+
Dichromadora antarctica	-	-	-	-	-	-	+	-
Dorylaimopsis punctata	+	+	-	+	-	+	-	+
Elzalia sp.	-	-	-	-	-	-	+	-
Enoplolaimus longicaudatus	+	-	-	-	-	+	+-	-
Epacanthion filicaudatum	-	+	-	-	-	-	-	-
Greeffiella sp.	-	-	-	-	+	-	-	+
Halalaimus ciliocaudatus	-	+	-	+	+	+	+	-
Halalaimus filicaudatus	-	-	-	+	-	-	-	-
Halalaimus gracilis	-	+	-	+	+	-	+	-
Haliplectus dorsali	-	-	-	+	-	-	-	-
Haliplectus wheeleri	+	-	-	+	-	+	-	-
Hopperia macramphida	-	+	-	+	-	-	+	-
Laimella longicauda	-	-	-	-	-	-	-	+
Leptolaimus antarcticus	+	-	-	-	-	+	+	-
Litinium longicaudatum	-	+	-	-	-	-	-	-
Litinium sp.	-	-	-	-	-	-	-	+
Marylynnia complexa	-	-	-	-	-	-	+	-
Metacomesoma cyatholaimoides	+	-	-	-	-	-	-	+
Metadasynemoides sp.	-	-	-	-	+	-	-	-
Metalinhomoeus setosus	-	-	-	-	-	+	-	-
Micoletzkyia sp.	-	-	-	-	-	-	+	-
Microlaimus acuticaudatus	-	-	-	-	-	-	-	+
Monoposthia costata	+	-	-	-	-	+	+	+
Neochromadora tecta	-	-	-	-	-	-	-	+
Nudora campbelli	-	-	-	-	-	-	+	-
Oxystomina filicaudata	+	-	-	-	-	+	-	-
Paragnomoxyala sp.	-	-	-	-	-	-	+	-
Paramarylynnia sp.	-	-	-	-	-	-	+	-
Pareurystomina scilloniensis	-	-	-	-	-	+	-	-
Parodontophora quadristicha	-	+	-	-	-	-	-	-
Phanoderma sp.	-	-	-	+	-	-	-	-
Pierrickia vitielloi	+	-	-	-	-	+	-	+
Pselionema detriticola	+	-	-	+	-	+	+	-
Pselionema minutum	-	-	-	-	-	-	+	-
Pseudolella sp.	-	-	-	-	+	-	-	-
Rhabdocoma sp.	+	-	-	-	-	+	-	+
Rhinema longispicula	-	-	-	-	-	-	+	-
Sabatieria celtica	-	+	-	+	-	-	+	-
Sabatieria challengerensis	+	+	-	+	+	+	+	-
Sabatieria conicauda	+	+	-	+-	-	-	+	+
Sabatieria conicoseta	-	+	-	+	-	+		-
Sabatieria lyonessa	+	+	-	+	-	+	+	+
Sabatieria minuta	-	-	-	+	-	-	-	-
Sabatieria mortenseni	+	+	-	+	-	-	-	+
Sabatieria pisinna	-	-	-	+	-	-	+	-
Sabatieria praedatrix	+	+	-	+	+	+-	+	+
Sabatieria pulchra	+	+	-	+	-	+	+	-
Sabatieria punctata	+	+	-	+	-	+	+	+
Sphaerolaimus arcospiculum	-	+	-	-	-	-	-	-
Spilophorella euxina	-	-	-	-	+	+	+	-
Terschellingia longicaudata	+	-	-	-	-	-	-	+
Thalassomonhystera parva	-	-	-	-	-	-	+	-
Theristus sp.	-	-	-	+	-	-	-	-
Thoracostoma coronatum	-	+	-	-	-	-	-	-
Trefusia longicauda	-	-	-	-	-	-	-	+
Tricoma (Quadricoma) scanica	+	+	-	-	+	+	+	+
Vasostoma spiratum	+	-	-	-	+	-	-	+
Viscosia glabra	-	-	-	+	-	-	+	+
Viscosia viscosa	-	-	-	+	-	-	+	-
Wieseria longicauda	-	-	-	-	-	+	-	-

Continental Shelf Research 263 (2023) 105043



Contents lists available at ScienceDirect

Continental Shelf Research

journal homepage: www.elsevier.com/locate/csr





Unraveling the functional diversity of macrobenthic community from Prydz Bay, Indian sector of the Southern Ocean

Snigdha Bhaumik [a], Sumit Mandal [a,*], Sarat Chandra Tripathy [b]

[a] Marine Ecology Laboratory, Department of Life Sciences, Presidency University, 86/1, College Street, Kolkata, 700073, India
[b] ESSO-National Centre for Polar and Ocean Research, Ministry of Earth Sciences, Headland Sada, Vasco-da-Gama, Goa, 403804, India

ARTICLE INFO

Keywords:
Southern Ocean
Prydz Bay
Macrobenthos
Abundance
Biomass
Biological trait analysis

ABSTRACT

Antarctic marine ecosystems show rich macrobenthic diversity with a high level of endemism and biomass which is under the threat of global climate change. Till date, information regarding the structure of macrobenthic communities from Prydz Bay is extremely meagre. The present study investigates the spatial pattern of macrobenthic communities, and their response to environmental factors from Prydz Bay complemented with trait-based functional diversity patterns. Samples were collected from 8 stations during the 11th Indian scientific expedition to the Southern Ocean. A total of 57 species of macrobenthos belonging to 8 phyla and 33 families were identified. The macrobenthic communities were dominated by families, Lumbrineridae, Glyceridae, Ophiuridae, and Epimeriidae. Macrobenthos abundance in the study area ranged from 0 to 1592 indv.m^{-2}, whereas biomass ranged from 0 to 1210.2 g m^{-2}. CLUSTER analysis divided the entire macrobenthic community into four groups based on 13.5% similarity. SIMPER analysis delineated species *Nacella kerguenlensis* and *Rossella antarctica* as the main contributors for establishing similarity in macrobenthic community composition across the groups. Canonical correspondence analysis (CCA) showed environmental variables like clay %, depth, and sediment total organic carbon as the governing factors in structuring the composition of macrobenthic species. Biological trait analysis (BTA) was performed to visualize the functional diversity of the total macrobenthic population based on morphological and ecological characteristics. A total of 23 traits in 6 categories were used to assess the functional diversity of the study area. The most widespread trait categories were epifaunal environmental position, motile locomotion strategy, sexual brooder and spawner, burrowing living habitat, predatory and detritivore feeding strategies. Investigating the functional diversity of macrobenthic assemblages using BTA represents a novel step towards evaluating the ecological status of the benthic realm of Prydz Bay. RLQ approach in combination with fourth-corner analysis was used to evaluate the relationships among biological traits, macrobenthic species and environmental parameters.The RLQ analysis revealed the positive association of tube dwelling and burrowing polychaetes with silty substratum, and the sessile organisms were found to be negatively correlated with the presence of carnivores/predators. The present study gives a comprehensive understanding about the macrobenthic community structure along with biological trait categories from Prydz Bay.

1. Introduction

In recent years climate change in the Southern Ocean has wreaked havoc on its ecosystem. Last decade onwards, the Southern Ocean, especially the West Antarctic Peninsula, recorded maximum global warming rates over the entire planet (Clarke et al., 2005; Aronson et al., 2009). Due to such incessant warming, the oceans surrounding Antarctica are experiencing rapid fluctuations in sea ice coverage, collapsing of ice shelves, melting of the glacier, and changes in salinity and seawater temperature (Gutt et al., 2015), which leads to hydrographic and ecosystem instability (Gutt et al., 2015; Sahade et al., 2015). The Antarctic cryosphere, particularly the East Antarctic Ice Sheet (EAIS) is massively responsible for regulating global climate structure (White et al., 2009; Crespin et al., 2014; Mackintosh et al., 2014). According to polar researchers, Antarctic marine ecosystems have been significantly affected by these recent trends in global warming. Alteration in benthic assemblage composition (Smith et al., 2008), phytoplankton biomass reduction (Stammerjohn et al., 2008; Montes-Hugo et al., 2009), habitat loss of euphausiid juveniles due to sea-ice melting (Fraser and Hofmann, 2003), discrepancy in physiological

* Corresponding author.
E-mail address: sumit.dbs@presiuniv.ac.in (S. Mandal).

https://doi.org/10.1016/j.csr.2023.105043
Received 14 February 2023; Received in revised form 29 May 2023; Accepted 4 June 2023
Available online 15 June 2023
0278-4343/© 2023 Elsevier Ltd. All rights reserved.

function like growth and feeding rates (Peck et al., 2006), geographical distributional modification resulting in concomitant species invasion from lower latitudes (Thatje, 2005; Walther et al., 2009) have already been observed as a consequence of climate change in Antarctica.

Research over the past few decades revealed that most of the Antarctica's species richness occurs on its shelves and seafloor, characterized by unusually rich macrobenthic biodiversity with a high degree of endemism (Clarke, 2008), extreme sensitivity (Peck et al., 2006) and nominal anthropogenic impact (Gutt et al., 2004, 2013; Knox, 2006; Sirenko, 2009). It was observed that Antarctic macrobenthos showcase extreme variation in biomass, where epifaunal suspension feeders exhibit almost double the biomass of infaunal deposit feeders (Gallardo, 1987; Linse et al., 2013; Liu et al., 2020; Mou et al., 2022). The Antarctic macrobenthic communities have been known to play a gargantuan role in marine ecosystem functioning especially in energy flow, mineral cycling, and benthic-pelagic coupling (Brey and Gerdes, 1998). A resurgence of interest has been mounting up in recent years to unveil and predict the shifts in macrobenthic community structure from these areas (Allan et al., 2013; Gutt et al., 2015). This is because the Southern Ocean, especially the seafloor, has already started showing signals of climate change (Constable et al., 2014) and is under the continuous threat of climate change-mediated global warming (Turner et al., 2014).

The Prydz Bay has relatively stable and unique hydrographic characteristics (Barbara et al., 2010; Liang et al., 2016; Gong et al., 2018). According to the researchers, biogeochemical nutrient cycling is enhanced by these stable environmental features, which make Prydz Bay an active hub for rich biodiversity (Ma et al., 2020). Unlike other Southern Ocean seas, the Prydz Bay has an extensive continental shelf, drastic shelf breaks with massive water depth variation, and complex terrains with patchy sediment deposition due to differential hydrographic dynamics and glacier sediment deposition (Williams et al., 2016; Gong et al., 2018). The area, thickness, range, formation as well as melting time of the sea ice are significant factors that affect the Prydz Bay coastal marine ecosystems (Li et al., 2023). The natural, as well as geographical uniqueness, makes this bay an ideal site for predicting changes in macrobenthic community structure due to environmental perturbations instigated by climate change.

A plethora of studies have been conducted on macrobenthic diversity assemblage from multiple regions of the Antarctic continental shelf except Prydz Bay, which is comparatively less explored than other regions of the Southern Ocean. Literature exhibits that the Ross Sea had a higher abundance of polychaetes and bivalves (Gambi and Bussotti, 1999; Rehm et al., 2011). South Shetland waters were dominated by sponges, ascidians, and polychaetes (Sáiz-Salinas et al., 1997), whereas the South-eastern Weddell Sea had a higher abundance of sponges, holothurians, asteroids, polychaetes (Gerdes et al., 1992). Other areas like the Amundsen Sea, West Antarctic peninsula, and shallow Terre Aselie (<100 m deep) were mainly dominated by echinoderms (Linse et al., 2013), polychaetes (Glover et al., 2008) and holothuroids (Gutt et al., 2007), respectively. It has been speculated that the advent of cooler bottom waters is the driving force behind the variation in dominant macrobenthic species composition over different seas and coasts in Antarctica (Gutt et al., 2007). Furthermore, few studies have been reported on environmental parameters, sediment chemistry, glacier retreat, and hydrographic dynamics from Prydz Bay (Pasotti et al., 2015; Wang et al., 2016; Ma et al., 2020), howbeit; information about the benthic community structure is meagre (Stark, 2000; Liu et al., 2020; Mou et al., 2022). Studies related to macrobenthos in Prydz Bay are restricted only to macrobenthic biomass composition, description of new species, and taxonomic studies (O'Loughlin and VandenSpiegel, 2010; Moles et al., 2015; O'Loughlin et al., 2020). A study conducted by Constable (1991) revealed the dominance of fauna like ascidians and sponges while studying the impact of bottom trawling on the benthic biota of Prydz Bay. Between the years 1977–1986 a major survey was undertaken by the Biological Investigations of Marine Antarctic Systems in Prydz Bay on all living entities like fishes, birds, mammals, krill except macrobenthic community structure (Gowing, 1995).

To date, only two works are available on the macrobenthic community structure from Prydz Bay (Liu et al., 2020; Mou et al., 2022). However, both of these studies sampled depth ranges <700 m, which impedes to depict the overall macrobenthic diversity structure of the bay, considering the presence of an extremely steep continental shelf increased drastically from 600 m to >3000 m. The present study aimed to unveil the macrobenthic community structure from the continental shelf of Prydz Bay by covering the wider variation in the depth of collected samples (290 m–3000 m) and complemented with Biological Traits Analysis (BTA) approach. BTA has gathered substantial attention recently due to its holistic approach in delineating the ecosystem functioning of a community (Chevene et al., 1994; Dolédec et al., 2006). A wide series of trait categories like body size, environmental position, living habitat, mobility pattern, and reproductive strategy (Bremner et al., 2003, 2006) are investigated to reveal the functional diversity pattern of the macrobenthic community from this area. In general, members of different macrobenthic taxa share several biological traits, which make BTA a valuable tool to determine the dominant traits represented in a particular habitat or environmental condition (Bhowmik and Mandal, 2021). BTA advocates the theory of environmental filters which recognize a subsection of the entire species assemblage with distinct functional traits prevalent in a specific environmental condition (Keddy, 1992). The BTA approach undertaken in the present study is thus vital to unriddle the patterns of biological trait variation of macrobenthic communities from Prydz Bay in the context of changing environmental parameters. Moreover, with the advancement of statistical analysis, another multivariate ordination method (RLQ) in combination with fourth-corner analysis has gained considerable attention among ecological researchers due to its robustness in evaluating the relationships among traits, species and environmental parameters (Dolédec et al., 1996; Legendre et al., 1997; Dray and Legendre, 2008; Piló et al., 2016; Wouters et al., 2018; Hu et al., 2019). The RLQ analysis is efficacious in constructing models which can envisage the effects of environmental alterations and anthropogenic perturbation on ecosystems (Dray and Legendre, 2008). Furthermore, this approach presents as an effective biomonitoring tool and can be implemented for conservation practices in future (Dolédec et al., 1999).

Against this backdrop, the present study endeavours to unravel the following questions: (I) what is the macrobenthic community composition and how do trait modalities of microbenthic community structure alter in Prydz Bay? and (II) how do environmental parameters govern the structure of macrobenthic community assemblages in Prydz Bay? The current study will provide a better understanding of the intricate dynamics of macrobenthic biodiversity patterns, species distribution patterns, and functional traits in the milieu of accelerated climate change.

2. Materials and methods

2.1. Survey area

The Prydz Bay is the largest embayment located within the Indian sector of the Southern Ocean, east Antarctica (Smith et al., 1984; Passchier et al., 2003; Liu et al., 2020) and is the third largest bay in Antarctica (Ma et al., 2020). The position of Prydz Bay lies approximately between 67°45′–69°30′S and 66°–79°E (Fricker et al., 2001; Borchers et al., 2011; Liang et al., 2016). This bay is located at the eastern end of the Amery Ice Shelf, having an area of $8.0 \times 104\ km^2$ (Ma et al., 2020). The Prydz Bay has a unique geographical location, with the southern end being in contact with the Amery Ice Shelf and the northern part extending to a vast continental shelf. The eastern side of the extended bay immerging towards the continental shelf is called the Four Ladies bank whereas the western part of the continental shelf surrounding the bay is the Frame Bank. The Pyrdz channel having an average depth greater than 500 m, aids in nutrient exchange and is a

zone with unique environmental characteristics (Barbara et al., 2010). Additionally, input from dense water and prevailing winds drives Antarctic Slope Current to the, north-flowing along the slope of 66°S. These features along with being surrounded from three sides create a relatively stable environment, particularly at the mouth of the bay (Liang et al., 2016; Gong et al., 2018). According to Clarke and Johnston (2003) the continental shelf edge of Prydz Bay is approximately 1000 m. The transition terrain or shelf break site between the channel and the continental shelf is extremely steep, and depth increases drastically from 600 m to >3000 m. Continuous scouring by ice shelves and enormous continental ice masses causes more deepening of the continental shelf. During winter, the entire Prydz Bay is frozen, and drift ice extends nearly 60°S up to 2 m ice thickness. It partially melts in summer, resulting in varied drift ice-covered areas (Taylor et al., 1997).

2.2. Sampling methodology

Macrobenthic samples were collected at eight stations in the Prydz Bay (Fig. 1) during the 11th Indian Scientific expedition to the Southern Ocean during January to March 2020, onboard *S.A. Agulhas*. The sampling stations were all within the continental shelf area and named in the order as Stn-5, 7, 9, 15, 19, 23, 29, and 32 (Fig. 1). At each station, sediment samples were collected using a 0.25 m^2 box corer (50 cm × 50 cm × 65 cm). Sub-sampling was performed using a PVC hand corer of 12 cm internal diameter. Collected samples were *in-situ* sieved through a 0.5 mm mesh, transferred to marked zipper bags, and fixed immediately in 10% buffered formaldehyde solution. On transportation to the laboratory, the organisms were subsequently processed, sorted, and enumerated. Macrobenthic species were identified up to the lowest taxonomic level following standard literature (Fauvel, 1953; Fell, 1961; Hartman, 1966; Day, 1967; Fauchald and Jumars, 1979; Hartman, 1991; Child, 1994; Linse, 2002; d'Acoz and Verheye, 2017; Emig, 2017; Florence and Atkinson, 2018). Numerical data obtained were converted to individuals m^{-2}. Taxon names were cross-checked against the World Register of Marine Species (http://marinespecies.org/) and Register of Antarctic Marine Species database (http://www.marinespecies.org). Similarly, the biomass of each station was obtained by taking the wet weight of all specimens from each station and expressed in g m^{-2}. Separate sediment samples were also collected for analysis of chief environmental parameters. Organic matter and total organic carbon content was analyzed using chromic acid digestion by wet oxidation method followed by titration with 0.2 N ammonium ferrous sulphate (Wakeel and Riley, 1957). Sediment texture analysis (percentage composition of sand, silt, and clay) was determined following the sieve and pipette method (Folk, 1968).

2.3. Data analysis

The Plymouth Routines in Multivariate Ecological Research (PRIMER) v.6 software (Clarke and Gorley, 2001; Clarke et al., 2008) aided with an add-on package of permutational multivariate analysis of variance (PERMANOVA) (Anderson et al., 2008) was used to perform univariate and multivariate analysis. Bray-Curtis similarity index was calculated using square root transformed macrobenthic abundance data. Hierarchical aggregation clustering (CLUSTER) was constructed based on Bray-Curtis similarity index. SIMPROF test for similarity profile using 0.05 level of significance with a default of 1000 permutations for mean similarity profile and 999 permutations for simulated profile was done for detecting the significant difference in macrobenthic diversity similarity among the groups. Similarity of percentage (SIMPER) analysis was subsequently used to identify the characteristic species that are responsible for contributing to intra-group similarity as well as species responsible for the dissimilarity between groups. Principal Component Analysis (PCA) was performed on normalized data to visualize the environmental parameters that characterize the study area. A two-way PERMANOVA was conducted to examine the significant difference in total macrobenthic abundance across the studied stations. This analysis was performed with seven factors using "stations" as the fixed factor. The correlation between macrobenthic communities and environmental parameters were investigated using distance-based linear modeling (DistLM) and visualized by distance-based redundancy analysis (dbRDA) to generate an ordination plot (Anderson et al., 2008). The DistLM employed the AICc model selection criteria that use a stepwise selection procedure to permit the fitting of best explanatory environmental factors and to model the macrobenthic community data (Bray Curtis resemblance matrix) against normalized environmental variables. The following indices were used to determine the overall diversity of microbenthic assemblages from various stations of Prydz Bay: Margalef's species richness (d) (Sanders, 1968), Pielou's evenness (J′) (Pielou, 1969), Shannon diversity (H′) (Shannon and Weaver, 1949) and Simpson index (1-λ′) (Simpson, 1949). Canonical correspondence analysis (CCA) (Ter Braak, 1986) was used to evaluate the relationship of individual species with various computed environmental factors using the Multivariate Statistical Package (MVSP) version 3.1 (Kovach, 1998). Identified macrobenthic species' biological trait database was developed for the Biological Trait Analysis (BTA). Trait categories were selected based on previous work and methods described in Bhowmik and Mandal (2021), Bremner et al. (2006), Hu et al. (2019), Piló et al. (2016). Information required to formulate the biological traits database for total macrobenthic species identified from Prydz Bay were mined from various books (Fauvel, 1953; Day, 1967; Giese and Pierse, 1977; Fauchald and Jumars, 1979; Hartman, 1991), published literatures

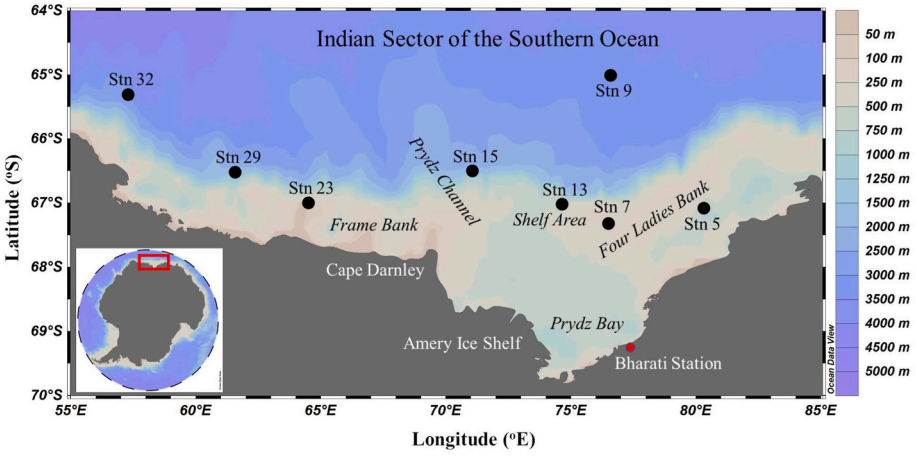


Fig. 1. Map showing the sampling locations in the Prydz Bay region.

(Bremner et al., 2003, 2006; Schüller, 2007; Egres et al., 2019; Liu et al., 2020; Bhowmik and Mandal, 2021), websites like Polytraits (Faulwetter et al., 2014), Encyclopedia of Life (Parr et al., 2014) and Biological Traits Information Catalogue (BIOTIC) (Marshall et al., 2006). For cases where traits information was unavailable for individual genera or species, traits data for different species belonging to the same family were used to extract traits. Fuzzy coding principles (Chevene et al., 1994) were applied to score each trait for each individual taxon. Based on affinity towards each trait, a scale ranging from 0 to 3 score has been denoted. Obligate and total affinity traits were scored a 3, whereas non-affinity traits were scored 0. Individuals showing two or more types of traits for a single trait category were marked 1 or 2 according to the affinity towards each trait involved in the life history of the individual species.

2.4. RLQ and fourth-corner analysis

A combination of the RLQ multivariate technique (Dolédec et al., 1996) and the fourth-corner method (Dray et al., 2014; Legendre et al., 1997) was employed to examine the relationship between environmental factors and species trait modalities in relation to the RLQ axis. Prior to analysis, three distinct tables, namely L (species distribution across samples: sites in rows and species in columns), R (environmental parameters of samples: sites in rows and environmental variables in columns), and Q (species traits: species in rows and traits in columns) were constructed. Each of these tables was analyzed separately in order to perform the RLQ analysis. Correspondence analysis (CA) and principal component analysis (PCA) were applied to table L and Q respectively (Dray et al., 2014) whereas, for table R, Hill-Smith analysis (Dray, 2013) was employed. The RLQ analysis can alone provide an overview of the global relationship among these three metrics. However, when combined with the fourth-corner analysis, it can provide insights into the significance of these bivariate associations. The Monte-Carlo test was conducted with 49,999 random permutations of model 2 (to test the null hypothesis: taxon densities with fixed traits are unrelated to environmental parameters) and model 4 (taxon densities with fixed

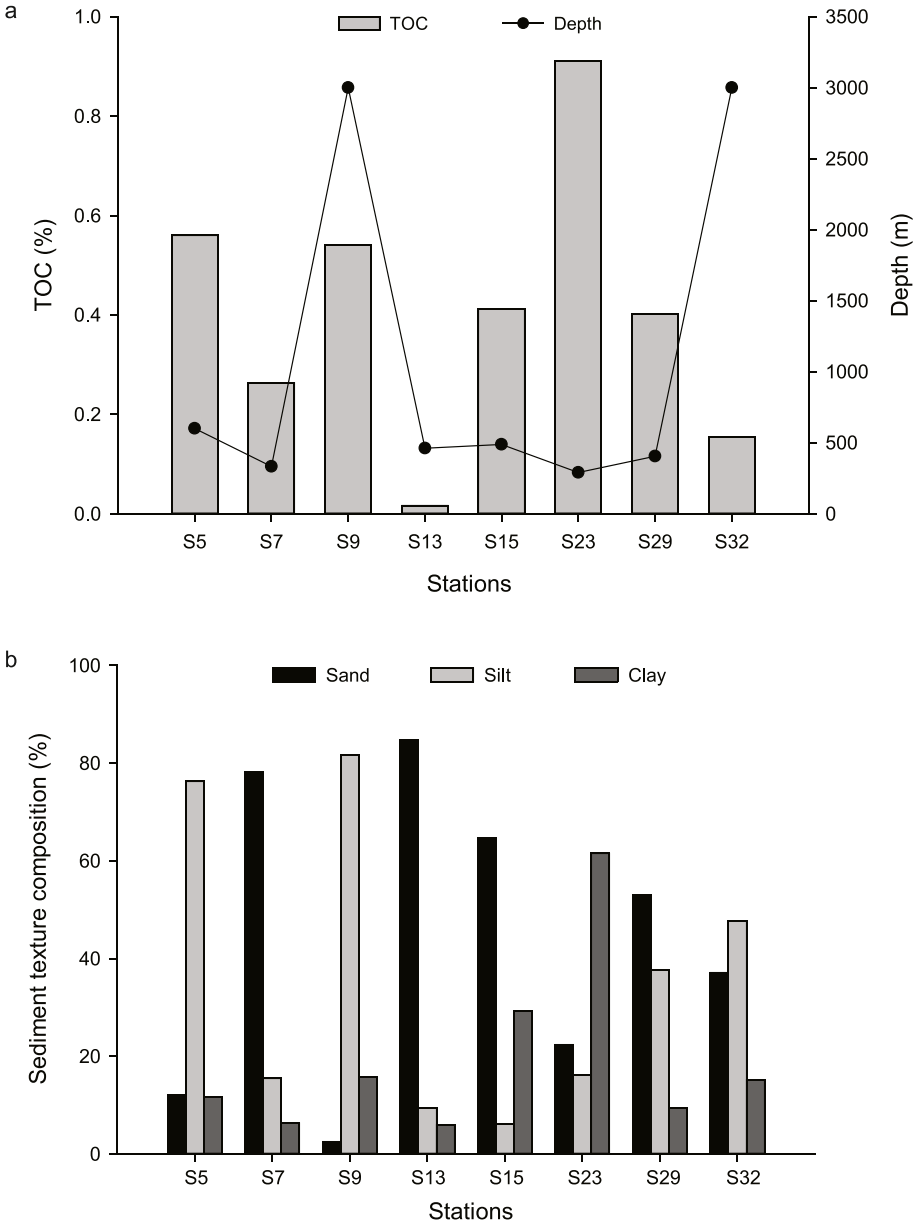


Fig. 2. a. Spatial variation of TOC and depth of studied stations in Prydz Bay; b. Sediment texture (sand %, silt %, clay %) composition of studied stations in Prydz Bay.

environmental factors are not influenced by species traits), and the p-value was adjusted accordingly. The RLQ/fourth-corner combined analysis was performed using the "ade4" package (Dray and Dufour, 2007) in R software (version 4.0.1).

3. Results

3.1. Environmental conditions

A suite of environmental parameters such as depth, sediment texture, organic carbon, and organic matter were measured at each of the 8 stations in Prydz Bay (Fig. 2). The average water depth was 1072 m, ranging from 290 to 3000 m. The shallowest sampling point was at station 23, while the deepest were station 9 and 32 (Fig. 2a). Sediment texture analysis revealed sand and silt (sandy silt and silty sand) as the main component of sediment types in the studied region. Sand was dominant in stations 7, 13, 15, and 29, whereas silt was dominant in stations 5, 9, and 32. Station 23 was the only exceptional that showed clay sediment texture (Fig. 2b). Total organic carbon percentage (TOC %) content at each station ranged from 0.01% to 0.91% (Fig. 2a). Similarly, organic matter content (OM %) ranged from 0.02% to 1.56%. Station 13 showed the lowest TOC % and OM % of all the stations, while station 23 showed the maximum TOC % and OM % content.

3.2. Taxonomic composition and distribution pattern

A total of 57 macrobenthic species belonging to 8 phyla and 33 families was recorded during the faunistic surveillance. Polychaetes (16 species), echinoderms (12 species) and arthropods (12 species) were the most prevalent groups comprising 70% of the total species obtained. The remaining species included mollusca (4 species), pycnogonida (4 species), bryozoa (3 species), cnidaria (2 species), and porifera (1 species). The macrobenthic communities of Prydz Bay were dominated by families like Lumbrineridae, Glyceridae, Ophiuridae, Epimeriidae, Nymphonidae and Terebratellidae. Station 23 was the most speciose with thirty documented microbenthic species, however; no species were recorded at Station 9. Stations 32, 13, and 7 were dominated by echinoderms, whereas stations 5 and 29 showed a higher prevalence of polychaetes, which contributes about 50% of the total macrobenthic species. Correspondingly, station 23 had polychaetes and arthropods in

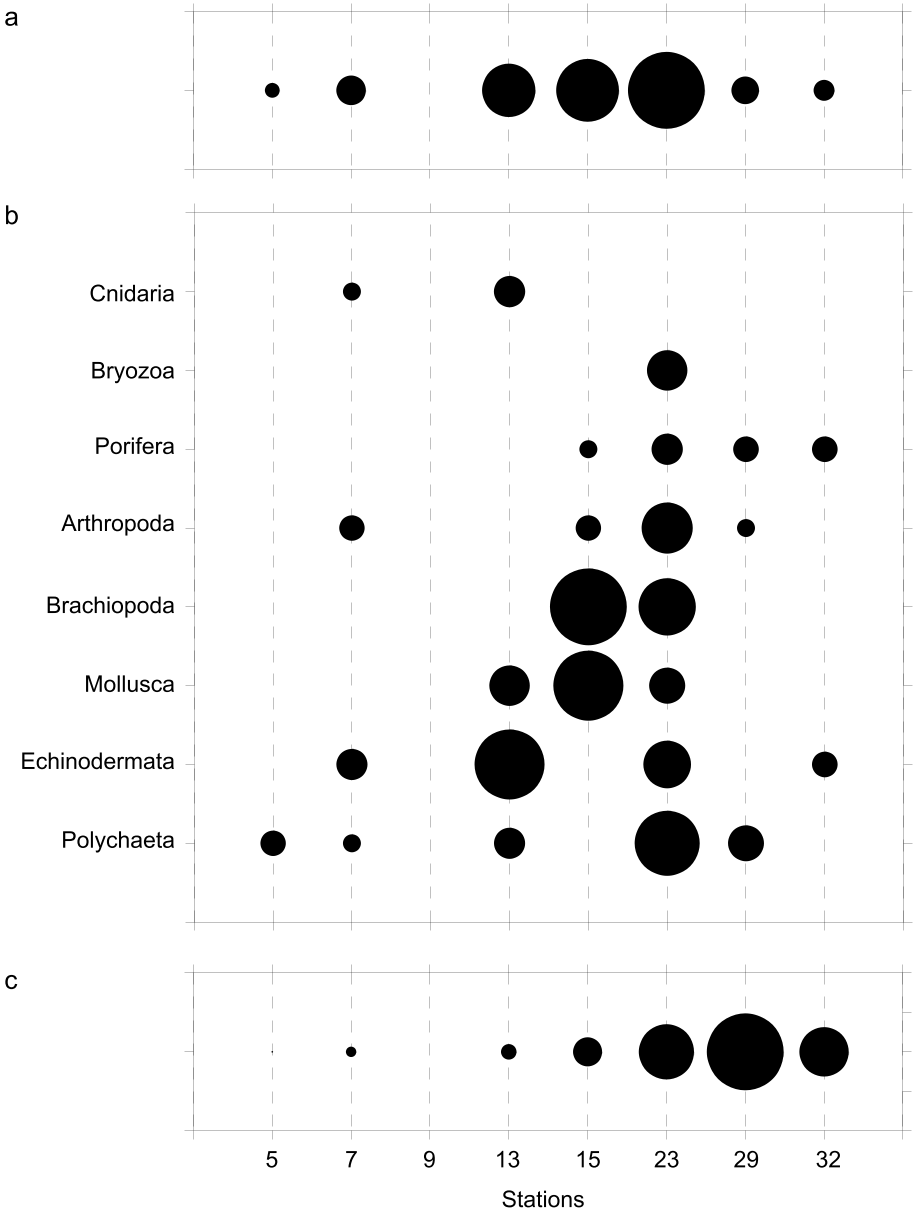


Fig. 3. a. Station-wise variation in the abundance of macrobenthic communities from Prydz Bay. The maximum symbol diameter corresponds to 1592 indv. m^{-2}; b. Spatial variation of taxa-wise macrobenthic abundance from studied stations of Prydz Bay. The maximum symbol diameter corresponds to 530 indv. m^{-2}; c. Spatial distribution pattern of macrobenthic biomass from studied stations of Prydz Bay. The maximum symbol diameter corresponds to 1210 g m^{-2}. All data were scaled using the square-root function.

equal proportion, while station 15 had a complete preponderance of molluscs.

3.3. Abundance and biomass distribution of macrobenthic community

Macrobenthic abundance in the studied stations ranged from 0 to 1592 indv.m^{-2}, with an average abundance of 505 indv.m^{-2}. The highest abundance was observed at station 23 and lowest at station 9. Station 23 was followed by station 15 with 1062 indv.m^{-2} and station 13 with 767 indv.m^{-2}. Extremely low species abundance with 59 indv.m^{-2} was observed in station 5 (Fig. 3a). Spatial variation of taxa-wise macrobenthic abundance from each of the studied station was also assessed. The average abundance of echinoderms (117.5 indv.m^{-2}) and polychaetes (84.25 indv.m^{-2}) were the highest, attributing 26.9% and 25.5% of the total average abundance, respectively (Fig. 3b). The average biomass obtained from all the stations was 322.2 g m^{-2} with a range of 0–1210.2 g m^{-2} (Fig. 3c). Sponges had the highest average proportion (304.2 g m^{-2}), contributing about 94% of the total biomass obtained cumulatively for all stations. Station 29 showed the highest biomass due to the occurrence of a large number of glass sponge *Rossella antarctica* (Fig. 3c). However, station 13 showed the highest biomass (49.4 g m^{-2}) among all stations when sponge biomass was not considered.

3.4. Statistical analysis

Univariate and multivariate analysis revealed a distinct spatial variation in the microbenthic community structure. To understand the effect of crucial abiotic factors, Principal Components Analysis (PCA) was done taking six environmental variables. The PCA detected a distinct habitat difference among sampled stations with reference to environmental parameters (Fig. 4). Results portrayed the association of stations 7, 13, and 15 with higher sand % while higher values of silt % characterized at stations 5, 9, and 32. The TOC % did not display any distinct association with any station. The PERMANOVA analysis revealed a significant spatial variation in macrobenthic abundance ($F = 3.4751$, $p = 0.001$) across the studied stations. Diversity indices based on macrobenthic abundance are shown in Table 1. Margalef's species richness (d) was recorded as highest for station 23 (4.07) and lowest for station 32 (0.21). Pielou's evenness index (J′) ranged from 0.88 (station 15) to 1 (stations 5, 7, and 32). Shannon–Wiener index (H′ log$_e$) was observed to be lowest in station 5 and station 32 (0.69 in each), whereas it showed maximum values for station 23 (3.24). Similar results were obtained for Simpson's index where diversity ranged from 0.50 to 0.95 in stations 32 and 23 correspondingly. Diversity indices concluded station 23 as the most diverse station both in terms of richness and evenness. DistLM portrayed that 6 abiotic variables were related to the variation in macrofaunal community structure from Prydz Bay, even though all variables were not significant. Variables such as TOC, silt, and clay showed the highest correlations ($p < 0.05$) with macrofaunal assemblages. In dbRDA ordination diagram, the best explanatory model depicted silt to structure the macrobenthic assemblages of station 29 whereas depth characterized the macrobenthos of both station 13 and 32 (Fig. 5a). CLUSTER analysis of the Bray-Curtis similarity matrix based on square root transformed macrobenthic abundance data delineated 4 different groups at 13.5% similarity (SIMPROF test $p < 0.05$) (Fig. 5b). According to SIMPER analysis, *Nacella kerguenlensis* and *Rossella antarctica* were the main contributors in the formation of the group 1 and 2, respectively. *Nacella kerguenlensis* made the highest contribution of 32.72% in the formation of Group 1 (average similarity: 19.55%), whereas *Rossella antarctica* contributed 6.72% and 100% in the formation of both Group 1 (average similarity: 19.55%) and Group 2 (average similarity: 28.03%) respectively (Table 2). The ordination plot resulting from Canonical Correspondence Analysis (CCA) biplot of 57 macrobenthic taxa (Table 3) represented 80.96% cumulative percentage in five axes. A total of 5 environmental parameters were used to explain the species biplot. According to CCA, out of the 5 environmental variables clay % and total organic carbon (TOC %) are the most significant governing factors in regulating the composition of macrobenthic species in Prydz Bay. Clay % and TOC % influenced Axis 1, whereas Axis 2 was driven by the rest 3 variables (depth, sand %, and clay %). CCA species biplot of 57 macrobenthic species revealed taxon belonging to phylum Brachiopoda and Mollusca showed great affinity towards clay % and TOC % of the sediment (Fig. 6). Subsurface and surface deposit feeding macrobenthic species like *Aerothris maquarensis*, *Magellania joubini*, *Alexandrella chione* were seen to be associated with clayey sediment substratum, however; *Aerothyris kerguelensis, Cyclostrema* sp., *Microdiscula* sp., *Limopsis* sp. and *Subepimeria iota* showed a positive correlation with TOC %. Subsequently, polychaetes like *Glycera* sp., *Capitella capitata,* and *Nephtys ferruginea* showed affinity towards the percentage of silt in sediment. Detritivores and carnivorous echinoderms belonging family Ophiuridae like *Ophiura crassa*, *Ophiura meredionalis*, *Ophiomastus primula,* along with glass sponge *Rossella antarctica* and polychaeta *Syllis* sp. showed positive correlation with water depth. *Amphiura lymani* was the only species influenced by the sand percentage of sediment substratum. Finally, *Amphiura belgicae*, *Ophiura flexibilis*, *Notoproctus* sp., *Epimeria* sp. 2, *Symplectoscyphus vanhoefeni* did not show a correlation with any environmental parameters.

Table 1
Spatial variation in macrobenthic community indices. S = Total number of species, N = Total population density, d = Species richness (Margalef's), J′ = Pielou's evenness, H′ (loge) = Shannon index, 1-λ′ = Simpson index.

Station	S	N	d	J'	H' (loge)	1-λ′
Stn 5	2	58	0.25	1.00	0.69	0.51
Stn 7	8	232	1.29	1.00	2.08	0.88
Stn 13	13	762	1.81	0.94	2.41	0.90
Stn 15	11	1058	1.44	0.88	2.10	0.84
Stn 23	31	1582	4.07	0.94	3.24	0.95
Stn 29	6	204	0.94	0.97	1.75	0.82
Stn 32	2	118	0.21	1.00	0.69	0.50

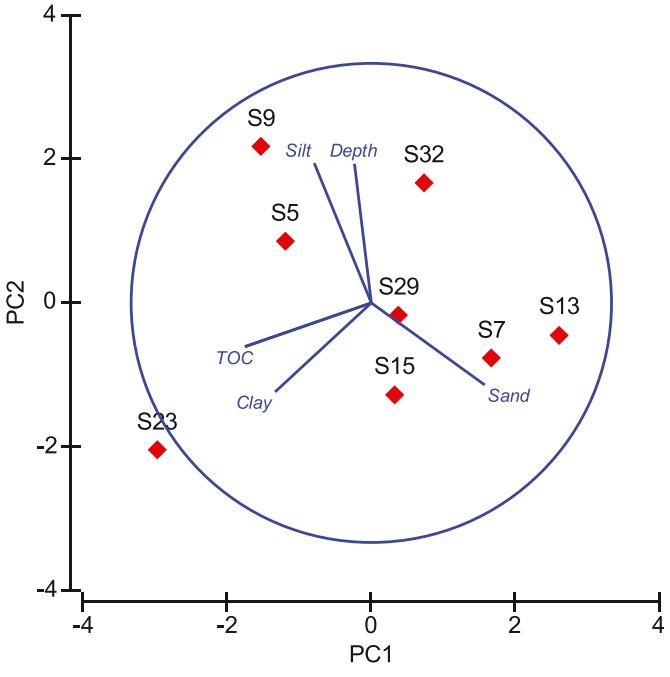


Fig. 4. PCA ordinations depicting the correlation of environmental parameters with various sampled stations.

3.5. Biological Trait Analysis

Biological Trait Analysis (BTA) of macrobenthic assemblages was

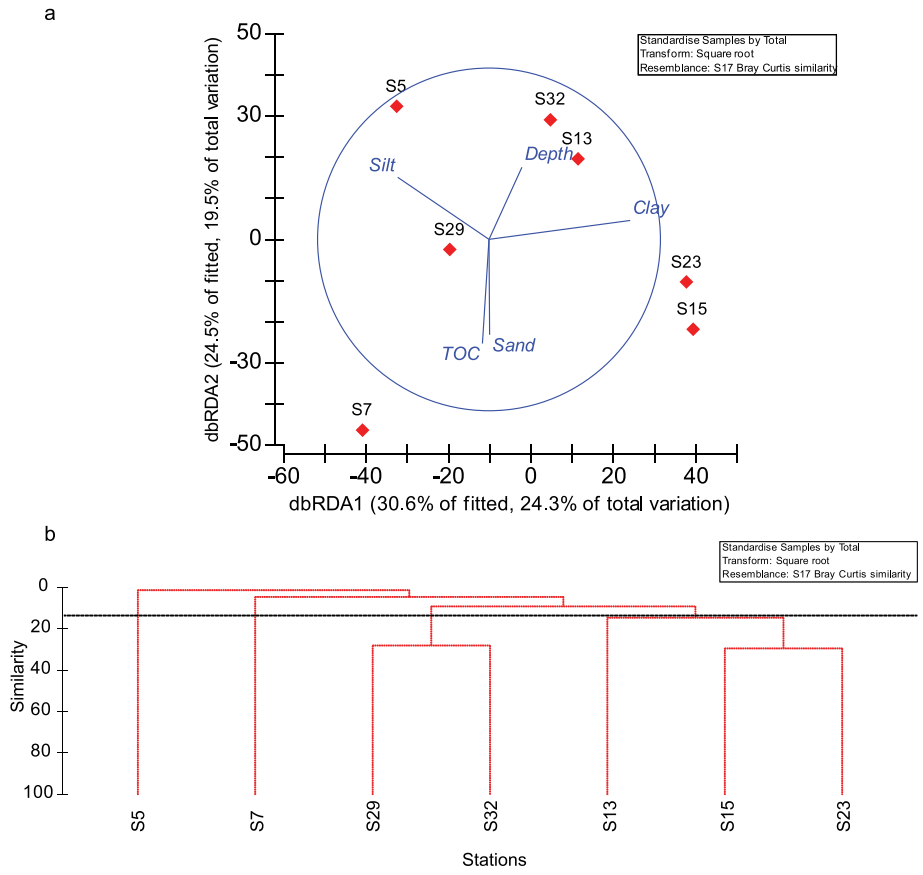


Fig. 5. a. Distance-based redundancy analysis (dbRDA) ordination plot of fitted environmental variables illustrating macrobenthic community patterns in Prydz Bay; b. Cluster plot based on Bray–Curtis similarity coefficient of macrobenthic assemblages.

Table 2
SIMPER similarins in Prydz Bay.

Group	Species	Average Abundance (individual m^{-2})	Average similarity (%)	Contribution rate (%)	Cumulative percentage (%)
1 (Average similarity: 19.55 %)	*Nacella kerguelenensis*	2.89	6.40	32.72	32.72
	Magellania joubini	3.04	2.65	13.57	46.29
	Aerothyris maquarensis	1.87	2.17	11.08	57.37
	Ophiura crassa	2.25	1.79	9.16	66.53
	Rossella antarctica	1.34	1.31	6.72	73.24
	Limopsis sp.	1.41	1.07	5.49	78.74
	Alexandrella chione	1.00	1.07	5.49	84.23
	Ophiomastus meridionalis	1.10	1.03	5.26	89.49
	Ophiomastus primula	1.58	1.03	5.26	94.74
2 (Average similarity: 28.03 %)	*Rossella antarctica*	6.22	28.03	100	100

applied to visualize the functional diversity of the total macrobenthic population of Prydz Bay based on morphological and ecological characteristics. A total of 23 traits in 6 categories were used to distinguish the functional diversity between each station sampled in Prydz Bay (Table 4). The most widespread trait categories obtained in all stations were epifaunal (environmental position), motile (Locomotion strategy), sexual reproduction (brooder and spawner), burrowing (living habitat), predatory and detritivore (feeding strategies). In the case of Body Size (BS) trait, 'Small' (<3 cm) and 'Medium' (3–6 cm) sized animals were prevalent in all the stations except station 7, which showed a dominance of 'Large' trait due to presence of large-sized ophiuroids and pycnogonids (Fig. 7a). Epifaunal trait under the trait category 'Environment Position' (EP) was dominant in most of the stations except station 5 and 29 which showed higher 'In-faunal' trait due to the prevalence of tube-dwelling and burrowing polychaetes (Fig. 7b). Similarly, the trait category 'Living Habitat' (LH) was dominated by 'Free-living' and 'Crawling' traits. 'Tube dwelling' and 'Burrowing' traits were least observed but prominent only in stations having higher echinoderm and polychaete abundance (Fig. 7c). 'Motile' trait was dominant in most of the stations, however; stations 15, 23 and 32 showed higher 'Sessile' trait, due to the presence of a greater abundance of poriferans, cnidarians, brachiopods and bryozoans (Fig. 7d). Carnivores/predator and scavengers/detritivore traits were most common under the trait category 'Feeding Strategy'. Contrastingly, station 15 showed a higher percentage of the 'Suspension feeding' (SF) trait due to a higher preponderance of molluscs and brachiopods. Stations 23, 29, and 32 also showed a good proportion of 'SF' trait (32.38%, 22.52%, and 42.85%, respectively). Sub-surface deposit feeders (SSDF) and surface deposit feeders (SDF)

Table 3
Spatial variation (presence/absence) of macrobenthic species along with their CCA and RLQ code.

	Stn 5	Stn 7	Stn 9	Stn 13	Stn 15	Stn 23	Stn 29	Stn 32	CCA code	RLQ code
Ophiomastus serratus	−	−	−	+	−	−	−	−	1	Opse
Amphiura (Amphiura) lymani	−	+	−	+	−	−	−	−	2	Amly
Amphiura belgicae	−	+	−	−	−	−	−	−	3	Ambe
Ophiura flexibilis	−	+	−	−	−	−	−	−	4	Opfl
Ophiura crassa	−	−	−	+	−	+	−	+	5	Opcr
Ophiacantha antarctica	−	−	−	−	−	−	+	−	6	Opan
Ophioplinthus tumescens	−	−	−	+	−	−	−	−	7	Optu
Ophiosabine vivipara	−	−	−	+	−	−	−	−	8	Opvi
Ophiomastus meridionalis	−	−	−	+	−	+	−	−	9	Opme
Ophiomastus perforatus	−	−	−	−	−	+	−	−	10	Oppe
Ophiacantha cosmica	−	−	−	−	−	+	−	−	11	Opco
Ophiomastus primula	−	−	−	+	−	+	−	−	12	Oppr
Nacella kerguelenensis	−	−	−	+	+	+	−	−	13	Nake
Cancellariidae (unidentified)	−	−	−	+	−	−	−	−	14	CaU
Pareuthria sp.	−	−	−	−	−	+	−	−	15	PaS
Cyclostrema sp.	−	−	−	−	+	−	−	−	16	CyS
Microdiscula sp.	−	−	−	−	+	−	−	−	17	MiS
Limopsis sp.	−	−	−	−	+	−	−	−	18	LiS
Cyamiidae (unidentified)	−	−	−	−	+	−	−	−	19	CyU
Magellania joubini	−	−	−	−	+	+	−	−	20	Majo
Aerothyris maquarensis	−	−	−	−	+	+	−	−	21	Aema
Aerothyris kerguelensis	−	−	−	−	+	−	−	−	22	Aeke
Ampelisca sp.	−	−	−	−	−	+	−	−	23	AmS
Epimeria sp.	−	+	−	−	−	−	−	−	24	EpS
Eusirus sp.	−	+	−	−	−	−	+	−	25	EuS
Alexandrella chione	−	−	−	−	+	+	−	−	26	Alch
Epimera (Subepimeria) iota	−	−	−	−	+	−	−	−	27	Epio
Epimera (Epimeriella) macronyx	−	−	−	−	−	+	−	−	28	Epma
Alexandrella mixta	−	−	−	−	−	+	−	−	29	Almi
Epimera (Drakepimeria) sp.	−	−	−	−	−	+	−	−	30	EpDS
Notoproctus sp.	−	+	−	−	−	−	−	−	31	NotS
Lumbrineris magalhaensis	−	−	−	−	−	+	−	−	32	Luma
Scalibregma inflatum	−	−	−	−	−	+	+	−	33	Scin
Glycera kerguelensis	+	−	−	+	−	−	−	−	34	Glke
Glycera sp.	−	−	−	−	−	−	+	−	35	GlS
Notomastus sp.	−	−	−	+	−	−	−	−	36	NoS
Syllis cornuta	−	−	−	+	−	+	−	−	37	Syco
Syllis sp.	−	−	−	−	−	+	−	−	38	SyS
Mystides notialis	−	−	−	−	−	+	−	−	39	Myno
Nereis sp.	−	−	−	−	−	+	−	−	40	NeS
Phyllodoce madeirensis	−	−	−	−	−	+	−	−	41	Phma
Lacydonia oculata	−	−	−	−	−	+	−	−	42	Laoc
Scoletoma tetraura	−	−	−	−	−	+	−	−	43	Scte
Capitella capitata	−	−	−	−	−	−	+	−	44	Caca
Nephtys ferruginea	−	−	−	−	−	−	+	−	45	Nefe
Ninoe falklandica	+	−	−	−	−	−	−	−	46	Nifa
Symplectoscyphus vanhoeffeni	−	+	−	−	−	−	−	−	47	Syva
Symplectoscyphus sp.	−	−	−	+	−	−	−	−	48	SymS
Filaguria sp.	−	−	−	−	−	+	−	−	49	FiS
Margaretta sp.	−	−	−	−	−	+	−	−	50	MaS
Caberea sp.	−	−	−	−	−	+	−	−	51	CaS
Rossella antarctica	−	−	−	−	+	+	+	+	52	Roan
Achelia hoekii	−	+	−	−	−	−	−	−	53	Acho
Nymphon inornatum	−	−	−	+	−	−	−	−	54	Nyin
Nymphon sp. 1	−	−	−	−	−	+	−	−	55	NyS1
Nymphon sp. 2	−	−	−	−	−	+	−	−	56	NyS2
Austrodecus sp.	−	+	−	−	−	+	−	−	57	AuS

were seen only in stations 5, 7, 23, and 29, which had a higher abundance of polychaetes, amphipods, and amphiurid echinoderms (Fig. 7e). 'Reproductive Strategy' (RS) trait category showed inclination towards sexual (spawner and brooder) traits. Sexual spawners were the principal trait modality at stations with a higher abundance of molluscs and polychaetes (like stations 5 and 15), howbeit; in a few stations like 7 and 13, sexual brooders were dominant due to a higher abundance of echinoderms and arthropods. Asexual trait had higher preponderance in stations with higher dominance of poriferan, cnidarian and bryozoan taxa (Fig. 7f).

The RLQ analysis has displayed some correlation amongst the metrics (Table 5). Subsequently, forth corner analysis was performed, using the 138 associations possible at a significance level of $\alpha = 0.05$. Only 3 associations were found to be significant (1 negative and 2 positive) following Dray and Legendre (2008) approach. No significant association was obtained when p values were adjusted for multiple testing. On combining both RLQ and fourth corner analysis, the global test did not display any significant relationships between environmental parameters and species distribution (model 2, p value = 0.94670) as well as not between species distribution and species traits (model 4, p value = 0.15868). The first RLQ axis accounts for 52.47% of the total variation while the second RLQ axis represents 26.72% (Table 5). Axis 1 and axis 2 together encompass the most important associations between environmental parameters, traits, and macrobenthic species composition. The positive part of axis 1 and negative part of axis 2 have unveiled that deposit feeders are positively associated with the TOC content of the

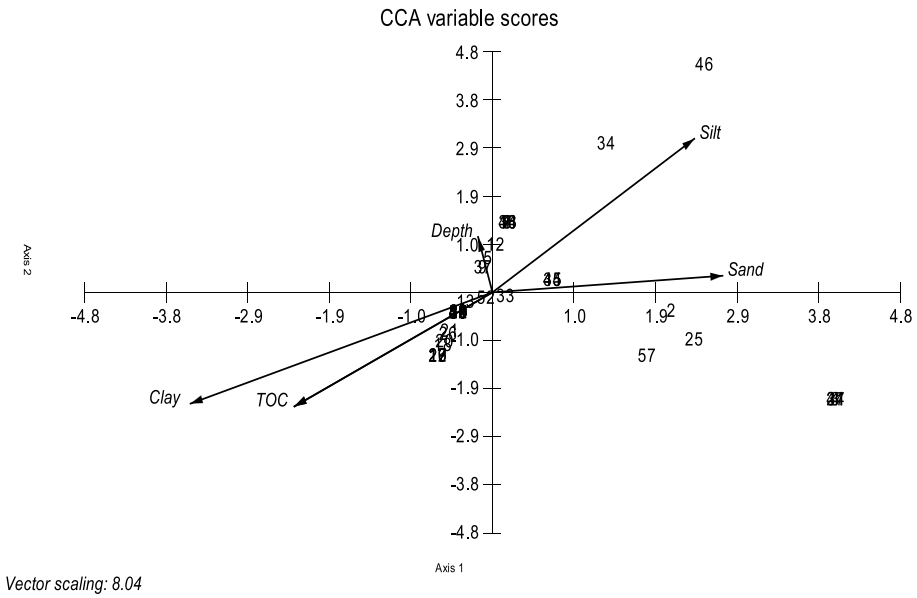


Fig. 6. Canonical correspondence analysis (CCA) ordination for macrobenthic species and environmental variables. The environmental variables (Water depth, sand %, silt %, clay %, Total Organic Carbon) are indicated by arrows. Species codes are given in Table 3.

Table 4
List of biological traits, abbreviations and categories used to describe macrobenthic assemblages.

Trait (Abbreviations)	Categories
Body size (BS)	1.Small (SM) (<3 cm)
	2.Medium (ME) (3–6 cm)
	3.Large (LA) (>6 cm)
Environmental position (EP)	1.Infaunal (IN)
	2.Epifaunal (EP)
	3.Symbiotic (SY)
Living habitat (LH)	1.Tube dweller (TU)
	2.Burrower (BU)
	3.Free swimmer (FS)
	4.Crawler (CR)
	5.Attached (AT)
Motility (M)	1.Motile (MO)
	2.Discretely motile (DM)
	3.Sessile (SE)
Feeding strategy (F)	1.Sub surface deposit feeder (SSDF)
	2.Surface deposit feeder (SDF)
	3.Suspension feeder (SF)
	4.Scavenger/Detritivore (SCA/DET)
	5.Carnivore/Predator (CAR/PRE)
	6.Omnivore (OM)
Reproductive strategy (RS)	1.Asexual (A)
	2.Sexual-Brooder (SB)
	3.Sexual-Spawner (SS)

sediment (Fig. 8a, b). The positive part of both the axis reveals that motile tube dwelling and burrowing polychaetes are positively associated with silty substratum (Fig. 8a and b). Scavenger and detritivore ophiuroids of genus *Ophiomastus* and *Ophioplinthus* dominate in sandy sediments and mostly occupy the negative part of axis 1 and positive part of axis 2 (Fig. 8a, b, c). Interestingly, the RLQ analysis displays trait modalities carnivorous/predators positioned at the positive part of both the axis are negatively associated with the presence of sessile biological trait occupying the negative part of both the axis (Fig. 8b). Discretely motile molluscs of genus *Nacella*, *Microdiscula* and *Pareuthria* are positioned at the negative part of axis 1 and positive part of axis 2 (Fig. 8b and c).

4. Discussion

4.1. Environmental parameters

Sediment texture and organic carbon distribution in sediments are important parameters for analysing the mechanism involved in various depositional facets of periglacial habitats (Asthana et al., 2013). These environmental factors are known to influence and regulate the distribution pattern of macrobenthic communities in marine ecosystems worldwide (Nanami et al., 2005; Veiga et al., 2017; Bhowmik and Mandal, 2021; Wang et al., 2021; Mou et al., 2022). The disturbance caused by abrasion from icebergs and the action of sea ice are one of the prime reasons for causing large variations in macrobenthic abundance, biomass, and species distribution from shallow waters surrounding the Antarctic continental shelf (Gutt et al., 2004). In our study, gradients in environmental descriptors were observed for total organic carbon and sediment texture. The sediment texture parameters revealed spatial variation across the bay. Stations near the mouth of Prydz Bay (Stn-7, 13, and 15) exhibited higher fractions of sand, while the stations in deeper continental shelves (Stn-5, 9, and 32) displayed a high percentage of silt in the sediment. The geographical structure, hydrological current, and circulation pattern prevalent provide insights concerning the variation of sediment patterns observed across the study stations. Strong westward wind drift along with the west coastal current produces a clockwise circulation of surface water which results in a higher sand percentage in stations near the mouth and west of the bay (Smith et al., 1984; Guo et al., 2019). The prevalence of high-velocity currents near Four ladies bank on the eastward side of the bay produces finer sedimentation, mainly dominated by silt (Hodgkinson, 1991; Liu et al., 2020). Total Organic Carbon (TOC) content were relatively lower (<1%) in all studied stations, and ranged from 0.01 to 0.9%. TOC was observed to be higher in stations situated towards the western part of the bay than on the eastern side. This can be explained by the presence of the Prydz Bay Gyre (PBG) (Smith and Tréguer, 1994), which is the main component of water circulation predominant in the bay. The PGB traps water in the deeper sections of the bay for a comparatively longer duration, especially in the middle and western regions, which provide more time for the settlement of organic matter on the seafloor. TOC was observed to be dominant in stations with higher silt and clay fraction (Stn-5, 9, and 23), which evidently indicates their affinity to adhere with finer particles. Concurrently, the lowest TOC was observed for station 13,

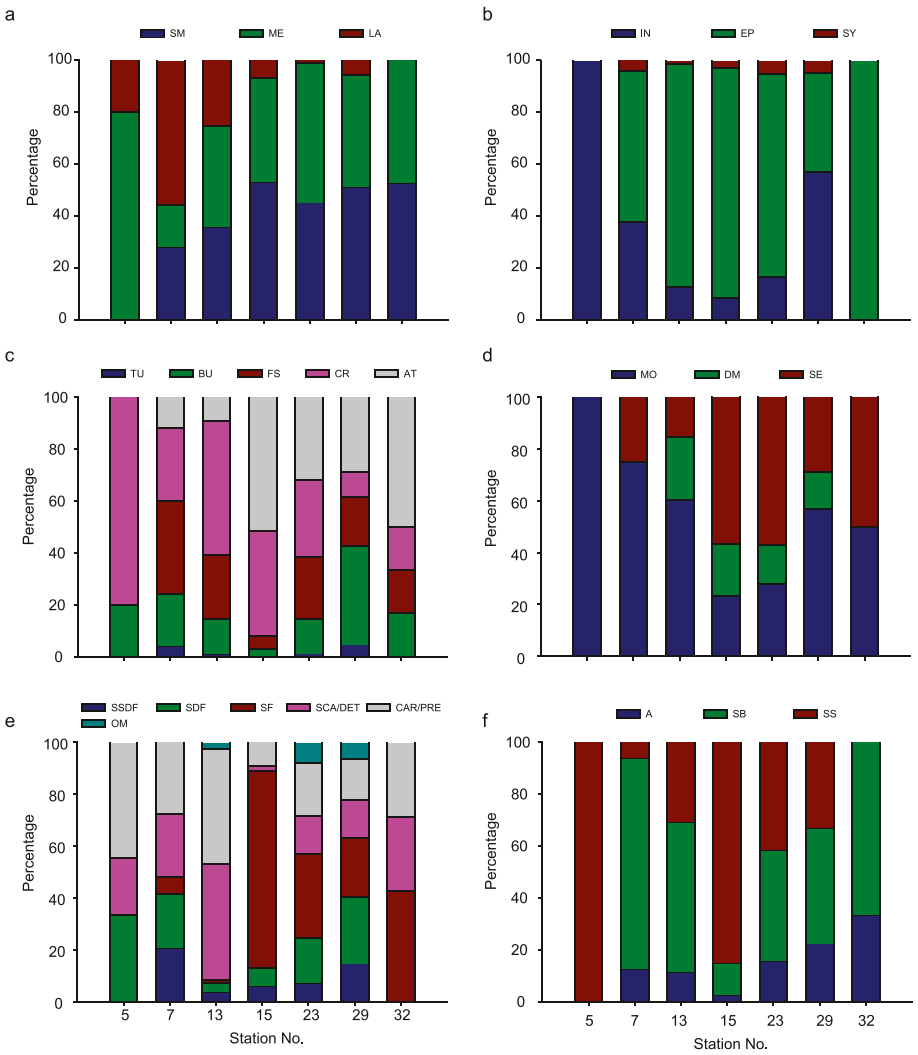


Fig. 7. Percentage of trait categories for macrobenthic assemblages at different stations. a = Body size, b = Environmental position, c = Living habitat, d = Mobility, e = Feeding strategy, f = Reproductive strategy. The abbreviations are available in Table 4.

Table 5
RLQ results. Individual R-L-Q separate analysis and RLQ analysis.

Separated analysis	Axis 1 eigenvalue (Variance %)	Axis 2 eigenvalue (Variance %)
R/Hill-Smith	3.93 (65.56)	1.53 (25.44)
L/CA	0.84 (22.98)	0.79 (21.48)
Q/PCA	5.95 (25.87)	3.70 (16.07)
RLQ Analysis	**Axis 1**	**Axis 2**
Eigenvalues	1.26	0.64
Variance %	52.47	26.72
R/RLQ Variance	1.84	1.25
Variance %	28.98	26.41
Q/RLQ Variance	1.81	1.66
Variance %	28.42	35.01
L/RLQ Variance	0.34	0.39
Variance %	5.27	8.17

which had one of the highest sand contents (84.63%). These observations are in agreement with the findings of Choudhary et al. (2018), which revealed the distribution pattern of TOC is directly proportional to the silt and clay content of the sediment, whereas it is negatively correlated with the fraction of sand content in the sediment. The same authors have also postulated that the TOC and organic matter were mostly associated with finer sediments due to their affinity to adsorb on the larger surface area. Station 23, the shallowest of all stations, located in front of Cape Darnley, close to the Amery Ice Shelf, displayed maximum clay and organic carbon content, as organically rich matters and clayey terrestrial debris are deposited through continuous melting of the ice sheet from the Amery Ice shelf. It is established that sediments on Cape Darnley, Frame Bank, and near the Amery Ice Shelf are influenced by a large amount of organic matter-rich ice-rafted inputs (Huang et al., 2022). Contrastingly, it was observed that station 32, the deepest station positioned on the extreme western side of the bay, showed low values of TOC and organic matter despite having higher silt content. This dissimilarity in observation indicates a correlation between TOC and water depth. A decrease in organic matter content with depth has been reported from several deep-sea regions around the globe (Sweeney et al., 2000; Arnaud et al., 2001; Ingole, 2003; Huang et al., 2022). The Prydz Bay has a wide depth variation ranging from shallow coastal regions to extremely deep continental shelves. The shelf break site is extremely steep, and depth drastically increases from 600 m to >3000 m (Clarke and Johnston, 2003). Depth may therefore play a crucial role in structuring the macrobenthic community of Prydz Bay as numerous biotic and abiotic factors alter with water depth which has been established for the deep sea macrobenthic studies (Arnaud et al., 2001; Pavithran et al., 2009; Cummings et al., 2010).

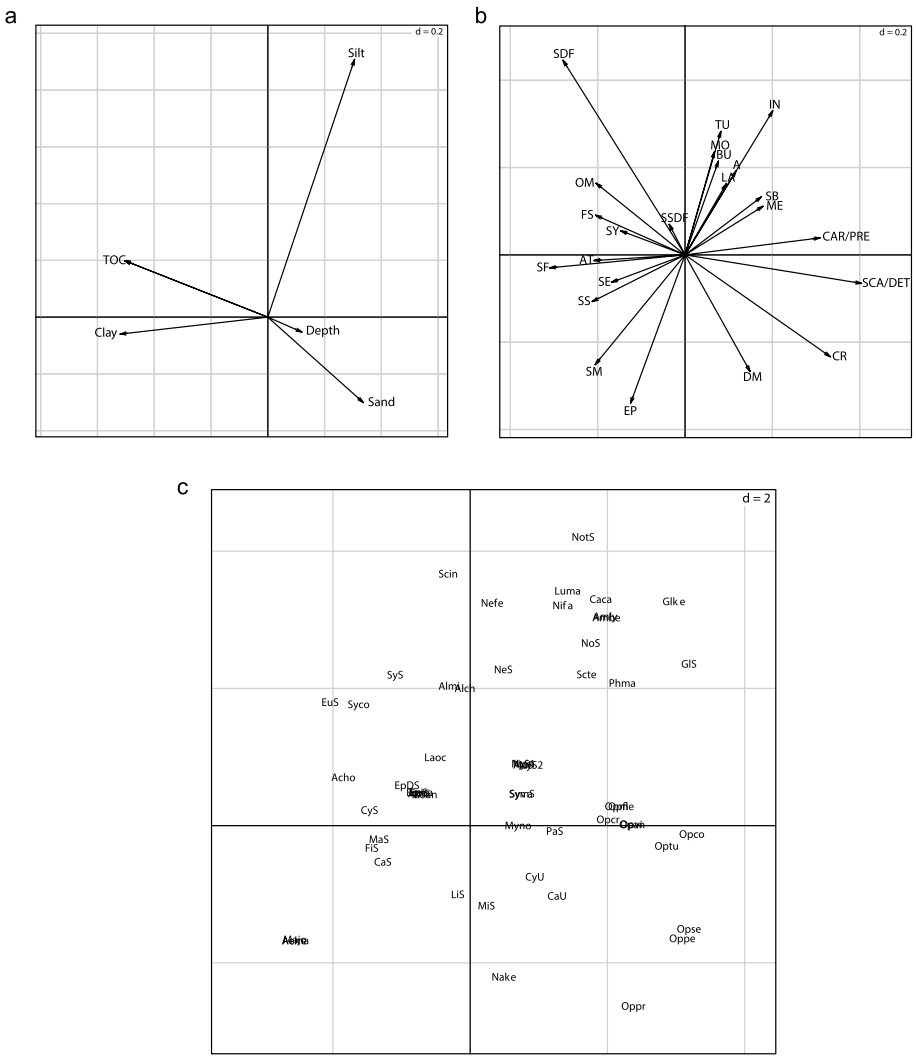


Fig. 8. a. RLQ diagram as defined by the 1st and 2nd axes with the projection of environmental variables (TOC – Total organic carbon); b. RLQ diagram as defined by the 1st and 2nd axes with the projection of trait categories (see Table 4 for the abbreviations of trait categories); c. RLQ diagram as defined by the 1st and 2nd axes with the projection of species (see Table 3 for respective RLQ codes of species). The d value in the upper right corner is the scale of the graph given by a grid.

4.2. Macrobenthic assemblages

In the Southern Ocean, delineating the macrobenthic species assemblages and the processes that regulate their diversity is a challenging endeavour due to several hindrances that cause inconsistencies during macrobenthos samplings like limited access, extreme patchiness, freezing temperatures, and deep continental shelves. Macrobenthic community structure is affected by a plethora of environmental factors, including seasonal water temperature, depth, pH, salinity, sediment texture, and organic matter content (Veiga et al., 2017; Bhowmik and Mandal, 2021; Wang et al., 2021). However, the correlation between macrobenthic community structure and environmental entities in different regions of the Southern Ocean still remains elusive (Gambi and Bussotti, 1999; Choudhury and Brandt, 2007; Kröger and Rowden, 2008). The microbenthic community composition in Prydz Bay is particularly dominated by species-rich in polychaetes, echinoderms, amphipods, and pycnogonids but with lower representation from groups like poriferans and cnidarians. The present study displays similar patterns of microbenthic composition, which is in accordance with the previous studies undertaken at Prydz Bay (Liu et al., 2020; Mou et al., 2022). However, the distribution pattern and species composition of macrobenthos from Prydz Bay were observed to be quite different from the adjacent seas like the Ross, Amundsen, and Weddell Seas, which are relatively much explored areas around the Antarctic continental shelf of Southern Ocean (SO). In contrast to the Prydz Bay, the Amundsen Sea is comparatively richer in bryozoans, decapods, and echinoderms (Linse et al., 2013), and the Ross Sea is dominated by polychaetes, crustaceans, and bivalves (Gambi and Bussotti, 1999), howbeit the south-eastern Weddell Sea showed a higher representation of sponges, holothuroids, asteroids and polychaetes (Gerdes et al., 1992). This variable dominance of macrobenthic species composition along the Antarctic continental shelf may be associated with the emergence of colder Antarctic bottom water, which is absent in the Amundsen Sea and other sea areas around the Antarctic continental shelf (Olbers et al., 1992; Gutt et al., 2007). In the present investigation, polychaetes are found to be the most diverse and numerically dominant taxa at Prydz Bay. Stations nearer to the Antarctic coasts with higher silt and clay content showed a greater preponderance of polychaetes. It is a well-established fact that polychaetes dominate intertidal mudflats and coasts as they prefer higher saline zones than any other macrobenthic taxa (Alongi, 1989; Glover et al., 2008; Liu et al., 2020).

Compared to the other seas of the Antarctic continental shelf, macrobenthic species diversity, abundance, and biomass in the Prydz Bay were found to be similar to the Ross Sea. The abundance of macrobenthos in Prydz Bay (0–1592 indv.m^{-2}) was much lower when compared to the south-eastern Weddell Sea (131–12,846 indv.m^{-2}) and

South Shetland waters (160–4380 indv.m^{-2}) (Gerdes et al., 1992; Sáiz-Salinas et al., 1997). In the present study, species abundance and diversity are much higher than the macrobenthic abundance obtained from the Amundsen Sea ($2.50 \times 10^{-3} - 0.40$ indv.m^{-2}) (Linse et al., 2013). The macrobenthic abundance of the Ross Ice shelf (250–1040 indv.m^{-2}) (Gambi and Bussotti, 1999) was similar to the values obtained from Prydz Bay. Previous studies at Prydz bay using grab (Liu et al., 2020) and trawled samples (Mou et al., 2022) showed a much lower macrobenthic abundance of 0–592 indv.m^{-2} and $1 \times 10^{-3} - 0.24$ indv. m^{-2} respectively. Likewise, the biomass obtained in the present study (0–1210 g m^{-2}) shows similar values to the previous study undertaken by Liu et al. (2020) (0–1155.5 g m^{-2}) but is much higher than the biomass recorded by Mou et al., (2022) ($9.32 \times 10^{-3} - 17.7$ g m^{-2}) from Prydz Bay. The maximum values of species richness, average abundance, and average biomass were found at the Prydz Channel and the Four Ladies Bank (Stn-13, 15, and 23) where polychaetes, arthropods, and echinoderms dominated. The Prydz Channel, most of which is greater than 500 m deep stations is the main channel for exchange of material between the inner and outer sections of the bay (Barbara et al., 2010; Kun et al., 2020). This makes the area near Prydz Channel conducive to accumulate food particles (Glud et al., 2013; Leduc et al., 2016), improves nutrient utilization and biogeochemical cycling, and creates a stable environment as mirrored by in higher macrobenthic abundance (Smith et al., 1984; Vaz and Lennon, 1996). Harsh and complex environments outside the bay in addition to abrupt depth variation, creates a zone of lower nutrient utilization and recycling. This causes a lower abundance of macrobenthos in these regions, as portrayed by stations 5, 9, and 32, with a much lower abundance as compared to other stations of the bay. Station 23, the shallowest station located in front of the Amery Ice shelf, exhibited the maximum macrobenthic abundance and TOC content of all stations. Furthermore, Shannon, Margalef's, and Pielou biotic indices conjointly showed a higher diversity of station 23 both in richness and evenness. This indicates a possibility of a positive correlation of macrobenthic abundance with TOC. Furthermore, DistLM depicted that TOC, silt, and clay had the highest correlations ($p < 0.05$) with macrofaunal assemblages. These results are in agreement with the works of Wu and Shin (1997) which postulated that the crucial drivers affecting the abundance of soft bottom macrobenthic communities are majorly driven by sediment texture and organic matter content. Furthermore, as the amount and quality of organic matter is known to decrease with depth, our findings also displayed a decrease in abundance and biomass in deeper regions of the bay as portrayed by Stn-5, 9 and 32.

The presence of Antarctic Circumpolar Current, along with specific geographical and environmental conditions in the SO produce a highly discrete and patchy distribution pattern of macrobenthic assemblage (Thrush et al., 2006; Lin et al., 2016; Liu et al., 2019). The degree of the geographical isolation of the Southern Ocean is much higher when compared to the Arctic Ocean, thereby exhibiting greater macrobenthic species endemicity (Grebmeier et al., 2006). The macrobenthic community in Prydz Bay is no exception and portrays a highly dispersed patchy distribution pattern (Liu et al., 2020). In the present study, the macrobenthic communities of the Prydz Bay are roughly divided into mainly two groups. Further, SIMPER analysis revealed Group 1 (Stn-13, 15, and 23) had an average species similarity of 19.55%, and was mainly distributed near the mouth of the Prydz Bay with molluscs, brachiopods, and echinoderms as he dominant taxon. Species *Nacella kerguenlensis* and *Magellania joubini* contributed to 46.29% of the total similarity. The glass sponge *Rossella antarctica* monopolized in Group 2 with 28.03% of average similarity. Results of the present study have indicated a relative correlation between macrobenthic community and environmental parameters. In the canonical correspondence analysis (CCA), the species biplot depicts that environmental parameter like clay %, depth, and total organic carbon (TOC %) are the most important factor in structuring the microbenthic community of Prydz Bay. Deposit-feeding molluscs are known to favour sediments with rich organic matter and also dominate fine clayey and silty sediments (Liu et al., 2020). They significantly contribute to increasing the overall productivity of the entire ecosystem by utilizing suspended organic matter (Rosenberg, 2001; Newell, 2004; Tillin et al., 2006). Stations 23 and 29 were observed to be dominated by higher proportions of carnivorous and detritivorous polychaetes. According to Liu et al. (2020), the disintegration and melting of ice shelves and icebergs of the Amery ice shelf contribute to the input of rich organic matter that favors the survival of carnivorous and detritivorous feeding guilds. Similarly, polychaetes of a few genera, like *Glycera* sp., *Capitella capitata* and *Nephtys ferruginea* showed affinity towards percentage of silt in sediment. Detritivorous and carnivorous echinoderms belonging to the family Ophiuridae, like *Ophiura crassa*, *Ophiura meredionalis*, *Ophiomastus primula* showed preference towards depth as these feeding strategies require deeper organically rich sediment beds for easier scavenging. According to dbRDA ordination plot the structure of macrobenthic assemblages of station 13 and 32 (mostly dominated by echinoderms) were characterized by the depth of these stations. It is reported among Antarctic echinoderms that reduced illumination in deep sea regions promotes predation of sessile organisms like sponges especially belonging to species *Rosella racovitzae* and *Tetilla leptoderma* (McClintock, 1994). According to Cummings et al. (2010), sand %, silt %, depth, and the sediment chlorophyll *a* to pheophytin ratio, were the most important factors regulating the macrobenthic community structure from the Northwest Ross Sea continental shelf.

4.3. Biological trait analysis

Biological Trait Analysis from polar marine ecosystems is a challenging endeavour due to lack of detailed and accurate trait information (Tyler et al., 2012), especially for the microbenthic community. For the first time, BTA approach has been applied to any macrobenthic study from SO, to address the plausible changes in benthic ecosystem functioning in response to environmental gradients (Paganelli et al., 2012; van der Linden et al., 2012; Munari, 2013). According to Bremner et al. (2006) sediment grain size is the key environmental factor that regulates the body size trait. As depicted in our study, overall 'small' and 'medium' size microbenthic organisms dominated the Prydz Bay, which indicates a continuously perturbed environment. The 'small' body size trait permits organisms to become more specialized in diversified elements of environmental mosaics (Hutchinson and MacArthur, 1959). 'Large' body size trait was only prevalent in station 7 due to the presence of large-sized carnivorous ophiuroids and pycnogonids. Interestingly, the percentage of sand was much higher than all other stations sampled at Prydz Bay. Apart from body size, the rate of mobility is remarkably affected by the granulometry of the habitat. The living habitat (LH) trait was mostly dominated by burrowers that require soft penetrable substratum to build successful burrows for their habitat (Bhowmik and Mandal, 2021). As the entire study stretch of Prydz Bay is mostly silty, the prevalence of burrowers like Lumbrineridae, Glyceridae is justified. According to RLQ analysis prevalence of tube dwelling and burrowing polychaetes were found to be positively associated with silty substratum. Burrowers can act as sediment re-worker through the suspension of finer particulate matter into overlying water. Burrowing by macrobenthic organisms increase the oxygen content at the sediment-water interface, thereby acting as a molecular sieve (Aller, 1983; Bremner et al., 2006; Constable, 1999). Additionally, burrows also provide a microenvironment which enhances nutrient recycling and organic matter decomposition. Mobility is a crucial trait that affects food capture methods and also defines the trophic relationship in the benthic community (Sigala et al., 2012). Interestingly, RLQ analysis portrayed that presence of sessile organisms was found to be negatively correlated with the presence of carnivores/predators in the habitat. According to Hunt and Scheibling (1997), an increase in macrobenthic predators can hinder the recruitment of sessile organisms in a habitat. It can be inferred from this hypothesis that the predatory effect might have played a critical role in suppressing the sessile macrobenthic population throughout the bay. In our study, BTA showed a higher fraction of

carnivorous and detritivores feeding traits for most of the stations. According to Liu et al. (2020), the input of organically rich sediments from adjacent Amery Ice Shelf and glaciers favours the existence of predatory and scavenging modes of feeding traits in Prydz Bay. The prevalence of carnivores is said to indicate healthier sediment quality and concomitantly allows species with a wide range of feeding modes to flourish (Hu et al., 2019). Apart from carnivores and/or detritivores a more comprehensive and detailed analysis revealed that stations near the mouth of the Prydz Bay represented by stations 15, 13 and 7 had a greater composition of suspension-feeding echinoderms-molluscs. However, other stations had higher deposit-feeding polychaete-arthropod composition. Areas of Ross Sea with finer biogenic sediments like silt and clay harboured a high abundance of surface and sub-surface deposit feeders like polychaetes and crustaceans (Gambi and Bussotti, 1999), which is in agreement with our findings. Suspension feeders were observed to prefer areas with coarser sediments (sand), as finer sediments can disrupt their feeding apparatus (Constable, 1991). The dominance of suspension feeders depends on the amount of particulate organic matter in the sediment. However, deposit feeders tend to be higher in locations where particles are deposited in sediment or suspended in the water column (Peterson and Skilleter, 1994; Bock and Miller, 1996). The Antarctic macrobenthos are well adapted to face cold isolation, like extreme seasonal and interannual variations in temperature and food availability. This helped them to evolve characteristics like stenothermia, extended generation time, late maturity age and brooding as predominant reproductive strategy (Barnes et al., 2006; Pörtner et al., 2007). In this context, our present investigation displays 'sexual brooding' as the most dominant reproductive strategy prevalent in Prydz Bay. 'Sexual spawning' was observed to be dominant in station 15 which had a lower predatory species composition compared to other stations.

Though BTA is effective in unraveling the functionality of macrobenthic assemblages, however, due to lack of precise information on traits, BTA may sometimes fail to depict the fine scale species level trait differentiation. Many macrobenthic species present in the same and/or similar habitat have similar traits which might lead to functional redundancy in a community. Substitution of such species may produce very little or no effect on ecosystem processes (Rosenfeld, 2002). Functional redundancy of macrobenthic assemblages is found to be higher in Prydz Bay as it is said to be more prevalent in naturally perturbed ecosystems having endemic species with long-term intrinsic adaptations (Piló et al., 2016). To elucidate the mechanisms that underpin the functional diversity of macrobenthic community assemblages from Prydz Bay, an extensive, systematic, reliable and robust trait database is extremely crucial. Furthermore, long-term spatio-temporal BTA studies are required to determine the specific environmental factors that regulate trait categories in a fragile and ecologically important polar marine ecosystem like Prydz Bay.

5. Conclusion

Macrobenthic community structure from Prydz Bay has been studied by selecting 8 stations of different depth regime. A total of 57 macrobenthic species were documented, along with comprehensive information on their community pattern, distribution, and spatial variation along the Prydz Bay, East Antarctica. The macrobenthic community composition in Prydz Bay was found to be particularly dominated by species-rich in polychaetes, echinoderms, amphipods, and pycnogonids. The environmental parameters like clay %, depth, and total organic carbon (TOC %) were found to be the key factors in structuring the macrobenthic community of the Prydz Bay. In this study characterization of macrobenthic assemblages using BTA is the first attempt towards enriching our understanding about the macrobenthic community structure and evaluating the ecological status of Prydz Bay's benthic realm. The most widespread trait categories obtained were epifaunal (environmental position), motile (locomotion strategy), brooder and spawner (reproductive strategy), burrowing (living habitat), predatory and detritivore (feeding strategies). Complementation of taxonomic as well as functional attributes is crucial to unriddle the patterns of trait variation in the context of changing environmental parameters at the Southern Ocean. Hence, long-term spatio-temporal monitoring with additional trait categories is necessary to understand the macrobenthic ecosystem functioning more accurately and their changes due to climate change-mediated perturbed environmental factors in coming years.

Declaration of competing interest

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

Data availability

Data will be made available on request.

Acknowledgments

The authors wish to express their gratitude to the Vice Chancellor, Presidency University for providing facilities and encouragement to carry out the above research work. We are also grateful to the Director, NCPOR, Ministry of Earth Sciences, Goa, for his encouragement and for permitting S.M. to participate in the 11th Indian Scientific Expedition to the Southern Ocean (ISESO). We are grateful to one and all members of ISESO who helped onboard during the collection of samples. This work is supported by grants awarded to S.M. from NCPOR (NCPOR/2019/PACER-POP/BS-09 dated 05.07.2019) under the Pacer Outreach Program (POP) under the Polar Science And Cryosphere Programme (PACER) initiative. The authors would also like to express their appreciation to the members of the Marine Ecology Laboratory for their time-to-time help and excellent teamwork. This is NCPOR contribution number J-12/2023-24.

References

Allan, E., Froneman, P., Durgadoo, J., McQuaid, C., Ansorge, I., Richoux, N., 2013. Critical indirect effects of climate change on sub-Antarctic ecosystem functioning. Ecol. Evol. 3 (9), 2994–3004.
Aller, R.C., 1983. The importance of the diffusive permeability of animal burrow linings in determining marine sediment chemistry. J. Mar. Res. 41 (2), 299–322.
Alongi, D.M., 1989. Ecology of tropical soft-bottom benthos: a review with emphasis on emerging concepts. Rev. Biol. Trop. 37, 85–100.
Anderson, M., Gorley, R., Clarke, K.P., 2008. For PRIMER: Guide to Software and Statistical Methods. Primer-e, Plymouth, UK, p. 32.
Arnaud, P.M., Troncoso, J.S., Ramos, A., 2001. Species diversity and assemblages of macrobenthic Mollusca from the South Shetland islands and Bransfield Strait (Antarctica). Polar Biol. 24 (2), 105–112.
Aronson, R.B., Moody, R.M., Ivany, L.C., Blake, D.B., Werner, J.E., Glass, A., 2009. Climate change and trophic response of the Antarctic bottom fauna. PLoS One 4 (2), e4385.
Asthana, R., Shrivastava, P.K., Beg, M.J., Swain, A.K., Dharwadkar, A., Roy, S.K., Srivastava, H.B., 2013. Sedimentary processes in two different polar periglacial environments: examples from Schirmacher Oasis and Larsemann Hills, East Antarctica. Geol. Soc. Spec. Publ. 381 (1), 411–427.
Barbara, L., Crosta, X., Massé, G., Ther, O., 2010. Deglacial environments in eastern Prydz Bay, East Antarctica. Quat. Sci. Rev. 29 (19–20), 2731–2740.
Barnes, D.K., Hodgson, D., Convey, P., Allen, C., Clarke, A., 2006. Incursion and excursion of Antarctic biota: past, present and future. Global Ecol. Biogeogr. 15, 121–142.
Bhowmik, M., Mandal, S., 2021. Do seasonal dynamics influence traits and composition of macrobenthic assemblages of Sundarbans Estuarine System, India? Oceanologia 63 (1), 80–98.
Bock, M.J., Miller, D.C., 1996. Fluid flow and suspended particulates as determinants polychaete feeding behavior. J. Mar. Res. 54 (3), 565–588.
Borchers, A., Voigt, I., Kuhn, G., Diekmann, B., 2011. Mineralogy of glaciomarine sediments from the Prydz Bay-Kerguelen region: relation to modern depositional environments. Antarct. Sci. 23 (2), 164–179.
Bremner, J., Rogers, S., Frid, C., 2003. Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. Mar. Ecol. Prog. Ser. 254, 11–25.

Bremner, J., Rogers, S., Frid, C., 2006. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecol. Indicat. 6 (3), 609–622.
Brey, T., Gerdes, D., 1998. High Antarctic microbenthic community production. J. Exp. Mar. Biol. Ecol. 231 (2), 191–200.
Chevene, F., Doleadec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of long- term ecological data. Freshw. Biol. 31 (3), 295–309.
Child, C.A., 1994. Antarctic and Subantarctic Pycnogonida: Ammotheidae and Austrodecidae. American Geophysical Union.
Choudhary, S., Nayak, G., Tiwari, A.K., Khare, N., 2018. Sediment composition and its effect on the productivity in larsemann hills, East Antarctica. Arabian J. Geosci. 11 (15), 1–17.
Choudhury, M., Brandt, A., 2007. Composition and distribution of benthic isopod (Crustacea, Malacostraca) families off the Victoria-Land Coast (Ross Sea, Antarctica). Polar Biol. 30 (11), 1431–1437.
Clarke, A., 2008. Antarctic marine benthic diversity: patterns and processes. J. Exp. Mar. Biol. Ecol. 366 (1–2), 48–55.
Clarke, K., Gorley, R., 2001. Primer v5: User Manual/Tutorial, Primer E: Plymouth. Plymouth Marine Laboratory, Plymouth, UK.
Clarke, A., Johnston, N.M., 2003. Antarctic marine benthic diversity. Oceanogr. Mar. Biol. 41, 47–114.
Clarke, A., Barnes, D.K., Hodgson, D.A., 2005. How isolated is Antarctica? Trends Ecol. Evol. 20 (1), 1–3.
Clarke, K.R., Somerfield, P.J., Gorley, R.N., 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. J. Exp. Mar. Biol. Ecol. 366 (1–2), 56–69.
Constable, A., 1991. Potential impacts of bottom trawling on benthic communities in Prydz Bay, Antarctica. In: CCAMLR Select Sci. Papers SC-CAMLR-X/BG/19 8, pp. 403–410.
Constable, A.J., 1999. Ecology of benthic macro-invertebrates in soft-sediment environments: a review of progress towards quantitative models and predictions. Aust. J. Ecol. 24, 452–476.
Constable, A.J., Melbourne-Thomas, J., Corney, S.P., Arrigo, K.R., Barbraud, C., Barnes, D.K., Bindoff, N.L., Boyd, P.W., Brandt, A., Costa, D.P., Davidson, A.T., 2014. Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota. Global Change Biol. 20 (10), 3004–3025.
Crespin, J., Yam, R., Crosta, X., Massé, G., Schmidt, S., Campagne, P., Shemesh, A., 2014. Holocene glacial discharge fluctuations and recent instability in East Antarctica. Earth Planet Sci. Lett. 394, 38–47.
Cummings, V.J., Thrush, S.F., Chiantore, M., Hewitt, J.E., Cattaneo-Vietti, R., 2010. Macrobenthic communities of the north-western Ross Sea shelf: links to depth, sediment characteristics and latitude. Antarct. Sci. 22 (6), 793–804.
d'Acoz, C.D.U., Verheye, M.L., 2017. Epimeria of the Southern Ocean with notes on their relatives (Crustacea, Amphipoda, Eusiroidea). Eur. J. Taxon. 359, 1–553.
Day, J.H., 1967. A Monograph on the Polychaeta of Southern Africa. Part I (Errantia) and II (Sedentaria). Trustees of the British Museum (Natural History).
Dolédec, S., Chessel, D., Ter Braak, C.J., Champely, S., 1996. Matching species traits to environmental variables: a new three-table ordination method. Environ. Ecol. Stat. 3 (2), 143–166.
Dolédec, S., Statzner, B., Bournard, M., 1999. Species traits for future biomonitoring across ecoregions: patterns along a humanimpacted river. Freshw. Biol. 42 (4), 737–758.
Dolédec, S., Phillips, N., Scarsbrook, M., Riley, R.H., Townsend, C.R., 2006. Comparison of structural and functional approaches to determining land use effects on grassland stream invertebrate communities. J. N. Am. Benthol. Soc. 25 (1), 44–60.
Dray, S., 2013. A Tutorial to Perform Fourth-Corner and RLQ Analyses in R.
Dray, S., Dufour, A.B., 2007. The ade4 package: implementing the duality diagram for ecologists. J. Stat. Software 22, 1–20.
Dray, S., Legendre, P., 2008. Testing the species traits-environment relationships: the fourth-corner problem revisited. Ecology 89, 3400–3412.
Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S., ter Braak, C.J. F., 2014. Combining the fourthcorner and the RLQ methods for assessing trait responses to environmental variation. Ecology 95 (1), 14–21.
Egres, A.G., Hatje, V., Miranda, D.A., Gallucci, F., Barros, F., 2019. Functional response of tropical estuarine benthic assemblages to perturbation by Polycyclic Aromatic Hydrocarbons. Ecol. Indicat. 96, 229–240.
Emig, C.C., 2017. Atlas of antarctic and sub-antarctic Brachiopoda. Carnets Géol. 3, 1–97.
Fauchald, K., Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Annu. Rev. 7, 193–284.
Faulwetter, M.S., Markantonatou, M.V., Pavloudi, M.C., Papageorgiou, N., Keklikoglou, M.K., Chatzinikolaou, E., Pafilis, E., Chatzigeorgiou, M.G., Vasileiadou, M.K., Dailianis, T., 2014. Polytraits: a database on biological traits of marine polychaetes. Biodivers. Data J. 2, e1024.
Fauvel, P., 1953. Annelida Polychaeta. The Fauna of India, Including Pakistan, Ceylon, Burma and Malaya, pp. 1–507.
Fell, H.B., 1961. The fauna of the Ross Sea. Part 1. Ophiuroidea. N. Z. Dep. Sci. Ind. Res. Bull. 142, 1–118.
Florence, W.K., Atkinson, L.J., 2018. Phylum Bryozoa in: Field Guide to the Ofshore Marine Invertebrates of South Africa. Malachite Marketing and Media, pp. 227–243.
Folk, R.L., 1968. Petrology of sedimentary rocks: Hemphill's. Austin. Texas 170, 85.
Fraser, W.R., Hofmann, E.E., 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. Mar. Ecol. Prog. Ser. 265, 1–15.
Fricker, H., Popov, S., Allison, I., Young, N., 2001. Distribution of marine ice under the Amery Ice Shelf, East Antarctica. Geophys. Res. Lett. 28 (11), 2241–2244.
Gallardo, V., 1987. The sublittoral macrofaunal benthos of the Antarctic shelf. Environ. Int. 13 (1), 71–81.
Gambi, M., Bussotti, S., 1999. Composition, abundance and stratification of soft-bottom macrobenthos from selected areas of the Ross Sea shelf (Antarctica). Polar Biol. 21 (6), 347–354.
Gerdes, D., Klages, M., Arntz, W., Herman, R., Galéron, J., Hain, S., 1992. Quantitative investigations on macrobenthos communities of the southeastern Weddell Sea shelf based on multibox corer samples. Polar Biol. 12 (2), 291–301.
Giese, A., Pierse, J., 1977. Reproduction of Marine Invertebrates Volume IV: Molluscs: Gastropods and Cephalopods. Academic Press, p. 369.
Glover, A.G., Smith, C.R., Mincks, S.L., Sumida, P.Y., Thurber, A.R., 2008. Macrofaunal abundance and composition on the West Antarctic Peninsula continental shelf: evidence for a sediment 'food bank'and similarities to deep-sea habitats. Deep Sea Res. Part II Top. Stud. Oceanogr. 55 (22–23), 2491–2501.
Glud, R.N., Wenzhofer, F., Middelboe, M., Oguri, K., Turnewitsch, R., Canfield, D.E., Kitazato, H., 2013. High rates of microbial carbon turnover in sediments in the deepest oceanic trench on Earth. Nat. Geosci. 6, 284–288.
Gong, Z., Liang, Y., Wang, M., Jiang, Y., Yang, Q., Xia, J., Zhou, X., You, S., Gao, C., Wang, J., 2018. Viral diversity and its relationship with environmental factors at the surface and deep sea of Prydz Bay, Antarctica. Front. Microbiol. 9, 2981.
Gowing, M.M., 1995. Antarctic investigations-Southern ocean ecology: the BIOMASS perspective edited by Sayed Z. El-Sayed. Bioscience 45 (4), 291.
Grebmeier, J.M., Overland, J.E., Moore, S.E., Farley, E.V., Carmack, E.C., Cooper, L.W., Frey, K.E., Helle, J.H., McLaughlin, F.A., McNutt, S.L., 2006. A major ecosystem shift in the northern Bering Sea. Science 311 (5766), 1461–1464.
Guo, G., Shi, J., Gao, L., Tamura, T., Williams, G.D., 2019. Reduced sea ice production due to upwelled oceanic heat flux in Prydz Bay, East Antarctica. Geophys. Res. Lett. 46 (9), 4782–4789.
Gutt, J., Sirenko, B.I., Smirnov, I.S., Arntz, W.E., 2004. How many macrozoobenthic species might inhabit the Antarctic shelf? Antarct. Sci. 16 (1), 11.
Gutt, J., Koubbi, P., Eléaume, M., 2007. Mega-epibenthic diversity off Terre Adélie (Antarctica) in relation to disturbance. Polar Biol. 30 (10), 1323–1329.
Gutt, J., Griffiths, H.J., Jones, C.D., 2013. Circumpolar overview and spatial heterogeneity of Antarctic macrobenthic communities. Mar. Biodivers. 43 (4), 481–487.
Gutt, J., Bertler, N., Bracegirdle, T.J., Buschmann, A., Comiso, J., Hosie, G., Isla, E., Schloss, I.R., Smith, C.R., Tournadre, J., 2015. The Southern Ocean ecosystem under multiple climate change stresses- an integrated circumpolar assessment. Global Change Biol. 21 (4), 1434–1453.
Hartman, O., 1966. Polychaeta Myzostomidae and Sedentaria of Antarctica. Antarct. Res. 7, 1–158.
Hartman, O., 1991. Polychaeta errantia of Antarctica. American geophysical union. Hodgkinson, R.
Hodgkinson, R., 1991. Current meter moorings in the region of Prydz Bay, Antarctica, 1986. Antarctic Division, Department of the Arts, Sport, the Environment, Tourism and Territories., n.d..
Hu, C., Dong, J., Gao, L., Yang, X., Wang, Z., Zhang, X., 2019. Macrobenthos functional trait responses to heavy metal pollution gradients in a temperate lagoon. Environ. Pollut. 253, 1107–1116.
Huang, D., Wang, J., Tian, P., Niu, W., 2022. The distribution and controlling factors of meiofaunal community in Prydz Bay, Antarctica. Deep Sea Res. Part II Top. Stud. Oceanogr. 202, 105107.
Hunt, H.L., Scheibling, R.E., 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. Mar. Ecol. Prog. Ser. 155, 269–301.
Hutchinson, G.E., MacArthur, R.H., 1959. A theoretical ecological model of size distributions among species of animals. Am. Nat. 93, 117–125.
Ingole, B., 2003. Macrobenthic abundance in the vicinity of spreading ridge environment in Central Indian Ocean. Curr. Sci. 328–333.
Keddy, P.A., 1992. Assembly and response rules: two goals for predictive community ecology. J. Veg. Sci. 3 (2), 157–164.
Knox, G.A., 2006. Biology of the Southern Ocean. CRC press.
Kovach, W.L., 1998. MVSP–multivariate Statistical Package for Windows, Ver 3.0. Kovach computing services, Pentraeth.
Kröger, K., Rowden, A.A., 2008. Polychaete assemblages of the northwestern Ross Sea shelf: worming out the environmental drivers of Antarctic macrobenthic assemblage composition. Polar Biol. 31 (8), 971–989.
Kun, L., Heshan, L., Xuebao, H., Yaqin, H., Zhong, L., Junhui, L., Jianfeng, M., Shuyi, Z., Jianjun, W., Jun, S., 2020. Macrobenthic communities on the continental shelf of the Prydz bay, East Antarctica. Acta Oceanol. Sin. 39, 38–48.
Leduc, D., Rowden, A.A., Glud, R.N., Wenzhofer, F., Kitazato, H., Clark, M.R., 2016. Comparison between infaunal communities of the deep floor and edge of the Tonga Trench: possible effects of differences in organic matter supply. Deep-Sea Res., Part I. 116, 264–275.
Legendre, P., Galzin, R., Harmelin-Vivien, M.L., 1997. Relating behavior to habitat: solutions to the fourth corner problem. Ecology 78 (2), 547–562.
Li, N., Lei, R., Heil, P., Cheng, B., Ding, M., Tian, Z., Li, B., 2023. Seasonal and interannual variability of the landfast ice mass balance between 2009 and 2018 in Prydz Bay, East Antarctica. Cryosphere 17 (2), 917–937.
Liang, Y., Bai, X., Jiang, Y., Wang, M., He, J., McMinn, A., 2016. Distribution of marine viruses and their potential hosts in Prydz Bay and adjacent Southern Ocean, Antarctic. Polar Biol. 39 (2), 365–378.
Lin, H., Wang, J., Liu, K., He, X., Lin, J., Huang, Y., Zhang, S., Mou, J., Zheng, C., Wang, Y., 2016. Benthic macrofaunal production for a typical shelf–slope–basin region in the western Arctic Ocean. Continent. Shelf Res. 113, 30–37.
Linse, K., 2002. The Shelled Magellanic Mollusca: with Special Reference to Biogeographic Relations in the Southern Ocean. A.R.G Gantner Verlag KG.

Linse, K., Griffiths, H.J., Barnes, D.K., Brandt, A., Davey, N., David, B., De Grave, S., Eléaume, M., Glover, A.G., Hemery, L.G., Mah, C., 2013. The macro-and megabenthic fauna on the continental shelf of the eastern Amundsen Sea, Antarctica. Continent. Shelf Res. 68, 80–90.
Liu, K., Lin, H., He, X., Huang, Y., Li, Z., Lin, J., Mou, J., Zhang, S., Lin, L., Wang, J., Sun, J., 2019. Functional trait composition and diversity patterns of marine macrobenthos across the Arctic Bering Sea. Ecol. Indicat. 102, 673–685.
Liu, K., Lin, H., He, X., Huang, Y., Li, Z., Lin, J., Mou, J., Zhang, S., Wang, J., Sun, J., 2020. Macrobenthic communities on the continental shelf of the Prydz Bay, East Antarctica. Acta Oceanol. Sin. 39 (2), 38–48.
Ma, J., Song, J., Li, X., Yuan, H., Li, N., Duan, L., Wang, Q., 2020. The change of nutrient situation in the Prydz Bay waters along longitude 73° E, Antarctica, in the context of global environmental change. Mar. Pollut. Bull. 154, 111071.
Mackintosh, A.N., Verleyen, E., O'Brien, P.E., White, D.A., Jones, R.S., McKay, R., Dunbar, R., Gore, D.B., Fink, D., Post, A.L., 2014. Retreat history of the East Antarctic Ice Sheet since the last glacial maximum. Quat. Sci. Rev. 100, 10–30.
Marshall, C., Tyler-Walters, H., Langmead, O., Jackson, E., Lear, D., Somerfield, P., 2006. BIOTIC- Biological Traits Information Catalogue. Marine life information network.
McClintock, J.B., 1994. Trophic biology of Antarctic shallow-water echinoderms. Mar. Ecol. Prog. Ser. 111 (1), 191–202.
Moles, J., Figuerola, B., Campanya-Llovet, N., Monleón-Getino, T., Taboada, S., Avila, C., 2015. Distribution patterns in antarctic and Subantarctic echinoderms. Polar Biol. 38 (6), 799–813.
Montes-Hugo, M., Doney, S.C., Ducklow, H.W., Fraser, W., Martinson, D., Stammerjohn, S.E., Schofield, O., 2009. Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. Science 323 (5920), 1470–1473.
Mou, J., Liu, K., Huang, Y., He, X., Zhang, S., Wang, J., Lin, J., Lin, H., Liu, W., 2022. The macro-and megabenthic fauna on the continental shelf of Prydz Bay, east Antarctica. Deep Sea Res. Part II Top. Stud. Oceanogr. 198, 105052.
Munari, C., 2013. Benthic community and biological trait composition in respect to artificial coastal defence structures: a study case in the northern Adriatic Sea. Mar. Environ. Res. 90, 47–54.
Nanami, A., Saito, H., Akita, T., Motomatsu, K.I., Kuwahara, H., 2005. Spatial distribution and assemblage structure of macrobenthic invertebrates in a brackish lake in relation to environmental variables. Estuar. Coast Shelf Sci. 63 (1–2), 167–176.
Newell, R.I., 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. J. Shellfish Res. 23 (1), 51–62.
Olbers, D., Gouretsky, V., Seiss, G., Schröter, J., 1992. Hydrographic Atlas of the Southern Ocean. Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany.
O'Loughlin, P.M., VandenSpiegel, D., 2010. A revision of Antarctic and some Indo-Pacific apodid sea cucumbers (Echinodermata: Holothuroidea: Apodida). Mem. Mus. Vic. 67 (1).
O'Loughlin, P.M., Bardsley, T.M., O'Hara, T.D., 2020. A Preliminary Analysis of Diversity and Distribution of Holothurioidea from Prydz Bay and the MacRobertson Shelf, eastern Antarctica, Echinoderms through Time. CRC Press, pp. 549–555.
Paganelli, D., Marchini, A., Occhipinti-Ambrogi, A., 2012. Functional structure of marine benthic assemblages using Biological traits analysis (BTA): a study along the emilia-Romagna coastline (Italy, north-west adriatic Sea). Estuar. Coast Shelf Sci. 96, 245–256.
Parr, C.S., Wilson, M.N., Leary, M.P., Schulz, K.S., Lans, M.K., Walley, M.L., Hammock, J. A., Goddard, M.A., Rice, M.J., Studer, M.M., 2014. The encyclopedia of life v2: providing global access to knowledge about life on earth. Biodivers. Data J. 2, e1079.
Pasotti, F., Manini, E., Giovannelli, D., Wölfl, A.C., Monien, D., Verleyen, E., Braeckman, U., Abele, D., Vanreusel, A., 2015. Antarctic shallow water benthos in an area of recent rapid glacier retreat. Mar. Ecol. 36 (3), 716–733.
Passchier, S., O'Brien, P., Damuth, J., Januszczak, N., Handwerger, D., Whitehead, J.M., 2003. Pliocene–pleistocene glaciomarine sedimentation in eastern Prydz Bay and development of the Prydz trough-mouth fan, ODP Sites 1166 and 1167, East Antarctica. Mar. Geol. 199 (3–4), 279–305.
Pavithran, S., Ingole, B.S., Nanajkar, M., Raghukumar, C., Nath, B.N., Valsangkar, A.B., 2009. Composition of macrobenthos from the central Indian ocean Basin. J. Earth Syst. Sci. 118 (6), 689–700.
Peck, L.S., Clarke, A., Chapman, A.L., 2006. Metabolism and development of pelagic larvae of Antarctic gastropods with mixed reproductive strategies. Mar. Ecol. Prog. Ser. 318, 213–220.
Peterson, C.H., Skilleter, G.A., 1994. Control of foraging behaviour of individuals within an ecosystem context: the clam *Macoma balthica*, flow environment, and siphon cropping fishes. Oecologia 100 (3), 256–267.
Pielou, E.C., 1969. An Introduction to Mathematical ecology. An Introduction to Mathematical ecology.
Piló, D., Ben-Hamadou, R., Pereira, F., Carriço, A., Pereira, P., Corzo, A., Gaspar, M., Carvalho, S., 2016. How functional traits of estuarine macrobenthic assemblages respond to metal contamination? Ecol. Indicat. 71, 645–659.
Pörtner, H.O., Peck, L., Somero, G., 2007. Thermal limits and adaptation in marine Antarctic ectotherms: an integrative view. Philos. Trans. R. Soc. Lond. B Biol. Sci. 362 (1488), 2233–2258.
Rehm, P., Hooke, R.A., Thatje, S., 2011. Macrofaunal communities on the continental shelf off victoria land, Ross Sea, Antarctica. Antarct. Sci. 23 (5), 449–455.
Rosenberg, R., 2001. Marine benthic faunal successional stages and related sedimentary activity. Sci. Mar. 65 (S2), 107–119.
Rosenfeld, J.S., 2002. Functional redundancy in ecology and conservation. Oikos 98 (1), 156–162.
Sahade, R., Lagger, C., Torre, L., Momo, F., Monien, P., Schloss, I., Barnes, D.K., Servetto, N., Tarantelli, S., Tatián, M., Zamboni, N., 2015. Climate change and glacier retreat drive shifts in an Antarctic benthic ecosystem. Sci. Adv. 1 (10), e1500050.
Sáiz-Salinas, J., Ramos, A., García, F., Troncoso, J., San Martin, G., Sanz, C., Palacin, C., 1997. Quantitative analysis of macrobenthic soft-bottom assemblages in South Shetland waters (Antarctica). Polar Biol. 17 (4), 393–400.
Sanders, H.L., 1968. Marine benthic diversity: a comparative study. Am. Nat. 102, 243–282.
Schüller, M, 2007. Biodiversity and Zoogeography of the Polychaeta (Annelida) in the deep Weddell Sea (Southern Ocean, Antarctica) and adjacent deep-sea basins. Dissertation zur Erlangung des Grades eines Doktors der Naturwissenschaften der Fakultät für Biologie und Biotechnologie, Ruhr-Universität Bochum.
Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication. University of Illinois Press, Urbana, p. 96.
Sigala, K., Reizopoulou, S., Basset, A., Nicolaidou, A., 2012. Functional diversity in three Mediterranean transitional water ecosystems. Estuar. Coast Shelf Sci. 110, 202–209.
Simpson, E.H., 1949. Measurement of diversity. Nature 163 (4148), 688.
Sirenko, B., 2009. Main differences in macrobenthos and benthic communities of the Arctic and Antarctic, as illustrated by comparison of the Laptev and Weddell Sea faunas. Russ. J. Mar. Biol. 35, 445–453.
Smith, N., Tréguer, P., 1994. Physical and chemical oceanography in the vicinity of Prydz Bay, Antarctica. In: Southern Ocean Ecology: The BIOMASS Perspective, pp. 25–45.
Smith, N.R., Zhaoqian, D., Kerry, K.R., Wright, S., 1984. Water masses and circulation in the region of Prydz Bay, Antarctica. Deep-Sea Res. I: Oceanogr. Res. Pap. 31 (9), 1121–1147.
Smith, C.R., De Leo, F.C., Bernardino, A.F., Sweetman, A.K., Arbizu, P.M., 2008. Abyssal food limitation, ecosystem structure and climate change. Trends Ecol. Evol. 23 (9), 518–528.
Stammerjohn, S.E., Martinson, D.G., Smith, R.C., Iannuzzi, R.A., 2008. Sea ice in the western Antarctic Peninsula region: Spatio-temporal variability from ecological and climate change perspectives. Deep Sea Res. Part II Top. Stud. Oceanogr. 55 (18–19), 2041–2058.
Stark, J.S., 2000. The distribution and abundance of soft-sediment macrobenthos around Casey Station, East Antarctica. Polar Biol. 23 (12), 840–850.
Sweeney, C., Hansell, D.A., Carlson, C.A., Codispoti, L.A., Gordon, L.I., Marra, J., Millero, F.J., Smith, W.O., Takahashi, T., 2000. Biogeochemical regimes, net community production and carbon export in the Ross Sea, Antarctica. Deep Sea Res. Part II Top. Stud. Oceanogr. 47 (15-16), 3369–3394.
Taylor, F., McMinn, A., Franklin, D., 1997. Distribution of diatoms in surface sediments of Prydz Bay, Antarctica. Mar. Micropaleontol. 32 (3–4), 209–229.
Ter Braak, C.J., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67, 1167–1179.
Thatje, S., 2005. The future fate of the Antarctic marine biota? Trends Ecol. Evol. 20 (8), 418–419.
Thrush, S., Dayton, P., Cattaneo-Vietti, R., Chiantore, M., Cummings, V., Andrew, N., Hawes, I., Kim, S., Kvitek, R., Schwarz, A.M., 2006. Broad-scale factors influencing the biodiversity of coastal benthic communities of the Ross Sea. Deep-Sea Res. II: Top. Stud. Oceanogr. 53 (8–10), 959–971.
Tillin, H., Hiddink, J.G., Jennings, S., Kaiser, M., 2006. Chronic bottom trawling alters the 872 functional composition of benthic invertebrate communities on a sea-basin scale. Mar. Ecol. Prog. Ser. 318, 31–45.
Turner, J., Barrand, N.E., Bracegirdle, T.J., Convey, P., Hodgson, D.A., Jarvis, M., Jenkins, A., Marshall, G., Meredith, M.P., Roscoe, H., 2014. Antarctic climate change and the environment: an update. Polar Rec. 50 (3), 237–259.
Tyler, E.H., Somerfield, P.J., Berghe, E.V., Bremner, J., Jackson, E., Langmead, O., Palomares, M.L.D., Webb, T.J., 2012. Extensive gaps and biases in our knowledge of a well-known fauna: implications for integrating biological traits into macroecology. Global Ecol. Biogeogr. 21 (9), 922–934.
van der Linden, P., Patrício, J., Marchini, A., Cid, N., Neto, J.M., Marques, J.C., 2012. A biological trait approach to assess the functional composition of subtidal benthic communities in an estuarine ecosystem. Ecol. Indicat. 20, 121–133.
Vaz, R.A.N., Lennon, G.W., 1996. Physical oceanography of the Prydz Bay region of antarctic waters. Deep-Sea Res. I: Oceanogr. Res. Pap. 43 (5), 603–641.
Veiga, P., Redondo, W., Sousa-Pinto, I., Rubal, M., 2017. Relationship between structure of macrobenthic assemblages and environmental variables in shallow sublittoral soft bottoms. Mar. Environ. Res. 129, 396–407.
Wakeel, S.K., Riley, J.P., 1957. Determination of organic carbon in the marine muds. J. Cons. Int. Explor. Mer. 22 (2), 180–183.
Walther, G.R., Roques, A., Hulme, P.E., Sykes, M.T., Pysek, P., Kuhn, I., Zobel, M., Bacher, S., Botta-Dukat, Z., Bugmann, H., Czucz, B., Dauber, J., Hickler, T., Jarosyk, V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V.E., Reineking, B., Robinet, C., Semenchenko, V., Solarz, W., Thuiller, W., Vila, M., Vohland, K., Settele, J., 2009. Alien species in a warmer world: risks and opportunities. Trends Ecol. Evol. 24 (12), 686–693.
Wang, H., Chen, Z., Wang, K., Liu, H., Tang, Z., Huang, Y., 2016. Characteristics of heavy minerals and grain size of surface sediments on the continental shelf of Prydz Bay: implications for sediment provenance. Antarct. Sci. 28 (2), 103–114.
Wang, Y., Liu, J.J., Liu, W., Feng, Q., Li, B.L., Lu, H., Wang, S., 2021. Spatial variation in macrobenthic assemblages and their relationship with environmental factors in the upstream and midstream regions of the Heihe River Basin, China. Environ. Monit. Assess. 193 (2), 1–22.
White, D.A., Bennike, O., Berg, S., Harley, S.L., Fink, D., Kiernan, K., McConnell, A., Wagner, B., 2009. Geomorphology and glacial history of Rauer group, East Antarctica. Quat. Res. 72 (1), 80–90.

Williams, G.D., Herraiz-Borreguero, L., Roquet, F., Tamura, T., Ohshima, K.I., Fukamachi, Y., Fraser, A.D., Gao, L., Chen, H., McMahon, C.R., Harcourt, R., 2016. The suppression of Antarctic bottom water formation by melting ice shelves in Prydz Bay. Nat. Commun. 7 (1), 12577.

Wouters, J.M., Gusmao, J.B., Mattos, G., Lana, P., 2018. Polychaete functional diversity in shallow habitats: shelter from the storm. J. Sea Res. 135, 18–30.

Wu, R., Shin, P., 1997. Sediment characteristics and colonization of soft-bottom benthos: a field manipulation experiment. Mar. Biol. 128 (3), 475–487.

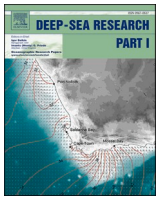
Deep–Sea Research I 199 (2023) 104109



Contents lists available at ScienceDirect

Deep-Sea Research Part I

journal homepage: www.elsevier.com/locate/dsri





Unveiling the meiobenthic community structure of Prydz Bay, Antarctica during austral summer

Soumya Subhra Baishnab [a], Ahmed Shahir [a], Sumit Mandal [a,*], Sarat Chandra Tripathy [b]

[a] Marine Ecology Laboratory, Department of Life Sciences, Presidency University, 86/1, College Street, Kolkata 700073, India
[b] ESSO-National Centre for Polar and Ocean Research, Ministry of Earth Sciences, Headland Sada, Vasco-da-Gama, Goa - 403804, India

ARTICLE INFO

Keywords:
Southern Ocean
Prydz Bay
Meiobenthos
Nematoda
Abundance
Biological Trait Analysis

ABSTRACT

Meiobenthos are bottom-dwelling aquatic invertebrates having a size range of 63–500 μm. They play a pivotal role in ecosystem functioning, biogeochemical and trophic nutrient cycling. Due to the presence of Antarctic Circumpolar Current and steep gradient in nutrients and temperature, many taxa of the Southern Ocean (SO) show diverse biodiversity patterns in comparison to other deep sea areas of the world. Over the years, several Indian SO Expeditions have been carried out in the Indian sector of SO (ISSO), but this is a pioneer attempt to unveil the meiobenthic community structure and their functional diversity pattern from Prydz Bay (Indian sector of Southern Ocean), Antarctica. Meiobenthic community structures were investigated in eight different sampling sites along with their vertical profiling from the Prydz Bay during the austral summer 2020. Total meiofaunal abundance ranged from 24 to 521 indv. 10 cm^{-2}, with the highest abundance recorded at station 23 and the lowest at station 9. A total of 9 meiobenthic taxa were found from this eco-region, with the highest percentage being the free-living marine nematodes as metazoan taxa. A total of 86 free-living nematode species were identified, where *Sabatieria* was the most common genus and represented by eleven species. Several univariate and multivariate analyses deciphered a distinct spatial variation in the meiobenthic community structure. Sediment texture and depth were the most significant environmental variables in shaping nematode assemblages. Biological Trait Analysis was performed using a total of 24 traits in 5 categories to unravel the functional diversity of free-living marine nematodes. The most dominant morphotypes were slender body shape, conical tail shape, dotted cuticle pattern, and non-selective deposit feeders with colonizing abilities of 2 (c–p score 2, in a scale from 1 to 5). Maturity Index (MI) and Index of Trophic Diversity (ITD) were highest in stations 15 and 32, respectively. RLQ approach with fourth-corner analysis was used to decipher the relationship between traits and environmental parameters. The RLQ analysis revealed the positive association of non-selective deposit feeder and slender body-shaped nematodes with higher water depth. The characterization of meiobenthic (especially nematode) communities in the context of taxonomic and functional attributes could help to evaluate the ecological status of ISSO. Further long term monitoring is also needed to get a comprehensive idea about their role in benthic ecosystem functioning in the milieu of global climate change.

1. Introduction

Marine habitats, including ocean margins and the deep sea, represent the largest continuous habitat for a wide variety of marine phyla, constituting one of the largest ecosystems on the planet (Thistle, 2003). Ocean margins, also known as the continental shelf, are transitional zones between the oceans and continents. They harbor a diverse array of faunal communities and account for a major chunk of the global benthic carbon mineralization (Middelburg et al., 1997; Wenzhöfer and Glud, 2002; Włodarska-Kowalczuk et al., 2019). Organic matter inputs from the upper water column sustain the diversity, abundance, and persistence of benthic assemblages on the ocean floor. Benthic ecosystems have greater marine biodiversity than pelagic ones (Gray, 1997).

Among the benthic fauna, the abundance and diversity of the meiobenthos exceed that of the macro and the megafauna (Krishnapriya et al., 2018). In marine habitats, meiobenthic organisms are closely associated with other components of the benthic ecosystem (including microfauna and macrofauna) and perform a range of ecosystem services (Baldrighi et al., 2013). They play a pivotal role in the global biogeochemical cycles and detrital food webs and act as the principal energy

* Corresponding author.
E-mail address: sumit.dbs@presiuniv.ac.in (S. Mandal).

https://doi.org/10.1016/j.dsr.2023.104109
Received 10 April 2023; Received in revised form 10 July 2023; Accepted 13 July 2023
Available online 20 July 2023
0967-0637/© 2023 Elsevier Ltd. All rights reserved.

provision to higher trophic level consumers such as macrobenthic animals like crab, shrimp, and juvenile demersal fishes (Liqi, 2003; Azovsky et al., 2020; Ingels et al., 2020; Stark et al., 2020; Xiaoshou et al., 2020; Leasi et al., 2021). Thus, meiobenthic organisms act as an integral part in the benthic food web (Schmid-Araya et al., 2016; Schratzberger and Ingels, 2018). Furthermore, they serve as key players in bio-mineralization of detrital matter and enhance nutrient regeneration (Coull, 1999; Nascimento et al., 2012). Several studies have suggested that meiobenthic organisms can mediate ecosystem processes with little or no macrobenthic organisms (Schratzberger and Somerfield, 2020). Due to their high abundance and diversity, widespread distribution, rapid generation time, fast metabolic rates, and vital contribution to ecosystem functioning, meiobenthic organisms are important ecological indicators for gauging the impact of climate change and anthropogenic perturbations (Zeppilli et al., 2015). They are also used as excellent models and proxies to investigate general ecological hypotheses and theories (Jessup et al., 2004; Nascimento et al., 2011, 2012; Bonaglia et al., 2014).

Meiobenthic organisms have ubiquitous distribution and are found in and on soft sediments of aquatic ecosystems ranging from polar, temperate, subtropical, and tropical eco-regions. Their abundance, distribution pattern, morphological and functional diversity are known to be affected by several abiotic factors, including temperature, salinity, hydrodynamic processes, sediment granulometry, oxygen, and food availability (Ingels et al., 2011; Lizhe et al., 2012; Ngo et al., 2013; Zeppilli et al., 2013; Górska et al., 2014; Pusceddu et al., 2014), and also, by biotic factors like predation and competition (Tita et al., 2000; Danovaro et al., 2007; Nascimento et al., 2011; Braeckman et al., 2013; Boldina et al., 2014). Meiobenthos represents the most abundant and diverse biocenosis in the marine realm in comparison to other benthic components, encompassing nearly 24 of the 35 major metazoan phyla and a few protozoan phyla (e.g. Sarcomastigophora: Order Foraminifera) (Giere, 2009; Zeppilli et al., 2015). Free-living nematodes are among the most numerically dominant and species-rich groups among all marine meiobenthic taxa (Lambshead and Boucher, 2003). In recent decades, marine ecosystem functioning has been investigated by analyzing free-living marine nematode communities (Jax, 2005; Edwards et al., 2014). Ecosystem functioning is an amalgam of physical, geochemical, and biological processes carried out within an ecosystem, served by each individual or in combination (Jax, 2005; Edwards et al., 2014). It is well established that higher functional biodiversity represents a stable and resilient ecosystem. Ecological indices, such as the Maturity Index (MI) and the Index of Tropic Diversity (ITD), based on functional diversity and community structure of free-living marine nematodes, provide useful information about ecosystem health. Due to this, the identification of organisms up to the species level, complemented by their functional diversity patterns or biological traits, are necessary to monitor the health of an ecosystem (Radwell and Brown, 2008).

Biological traits are the characteristic features that define any species in the context of their ecological roles (Diaz and Cabido, 2001). Biological trait analysis (BTA) is used to assess the functional diversity of any assemblages based on multiple traits or characteristics (Bremner et al., 2003, 2006). The traditional morpho-taxonomic descriptions of nematode communities and their abundance pattern may not provide a comprehensive picture of their contribution to ecosystem functioning and autecological role, as closely related species may differ in their functional roles (Maurer, 2000). Free-living marine nematode communities have numerous morphological characteristics which are considered to play important ecological roles: body shape (important adaptive feature to different sedimentary environments, Soetaert et al., 2002; Vanaverbeke et al., 2003, 2004a), tail shape (crucial for locomotion, reproduction, and sediment retention, Thistle and Sherman, 1985; Thistle et al., 1995), cuticle morphology (a protective covering of the body to avoid intoxication of organisms through diffusion, Soetaert et al., 2002) and buccal morphology (a proxy to assess trophic relationships, Wieser, 1953). Moreover, ecological traits such as life history strategy (Bongers, 1990) provide valuable information about their habitat disturbances and stages of ecological succession. To date, functional diversity and spatiotemporal variations of free-living marine nematode assemblage in response to environmental settings remain poorly resolved, especially for polar benthos.

In the age of the Anthropocene, global warming, freshening, increased sedimentation, and acidification wreaked havoc polar ecosystems. Global climate change has a generally negative effect on meiofauna, with far-reaching consequences on benthic food webs. However, some meiofaunal species can be favoured by the extreme conditions induced by global climate change, owing to their remarkable physiological adaptations. Antarctic marine ecosystems are jeopardized by such climatic fluctuations (Moline et al., 2004; Barnes and Peck, 2008). Studies of Antarctic meiofauna (one of the highest diverse groups in the SO) have been limited to the Ross Sea, Weddell Sea, Drake Passage, and Antarctic Peninsula, with few in other areas, especially in East Antarctica (Fabiano and Danovaro, 1999; Veit-Köhler et al., 2011; Kaiser et al., 2013; Rose et al., 2015; Zeppilli et al., 2015; Stark et al., 2020). However, the ISSO is poorly explored in the context of distribution and governing factors of the meiobenthic community structure from the Prydz Bay (Ingole and Singh, 2010; Huang et al., 2022).

Prydz Bay lies in the ISSO that receives active deposition of sediments from the East Antarctic Ice Sheet through the Lambert Glacier System (Vaz and Lennon, 1996; Kun et al., 2020). It has a large continental shelf and significant variations in water depth due to shelf breaks and complex terrain. The Bay's unique natural and geographical features make it a useful site for studying the effects of global climate change in structuring polar meiobenthic communities. Due to the influence of sea ice melting, temperature, and solar radiation, zooplankton predation, the seasonal and spatial variations of primary productivity and chlorophyll *a* production in Prydz Bay is high (Zhang et al., 2014). The Bay's topography and currents make it a particularly useful location for studying the structure and function of both benthic and pelagic ecosystems (Kun et al., 2020). However, assessment of meiobenthic community structure along with biological trait analysis has never been attempted from Prydz Bay.

Against this backdrop, the present study is a novel attempt to assess the taxonomic and functional diversity of the meiobenthic community from the Prydz Bay region with the aim to establish monitoring baseline data that can help researchers in assessing the impact of global climate change in the future. Our study seeks to address the following ecological questions: (i) what is the meiobenthic community composition, and how do trait modalities of meiobenthic community structure alter in the Prydz Bay? (ii) how do environmental parameters govern the structuring of meiobenthic community assemblages in Prydz Bay? The current study seeks to foster a better understanding of the intricate dynamics of meiobenthic community composition, biodiversity pattern, species distribution, functional traits, and ecosystem processes in the era of rapid climate change.

2. Materials and methods

2.1. Study area

To study the meiobenthic community structure, samples were collected from eight stations along the continental shelves of the Prydz Bay (Fig. 1) during the 11th Indian scientific expedition to the Southern Ocean, on board *S. A. Agulhas.* The Prydz Bay is the third largest bay of Antarctica, having an area of 8.0 × 104 km^2 (Ma et al., 2020). This pristine bay is the largest embayment located within the ISSO, East Antarctica (Smith et al., 1984; Passchier et al., 2003). The Prydz bay is located at the eastern end of the Amery Ice Shelf between 67°45′–69°30′S and 66°–79°E (Fricker et al., 2001; Borchers et al., 2011). The southernmost end of the Prydz Bay is connected with the Amery Ice Shelf, whereas the northernmost end is extended to the

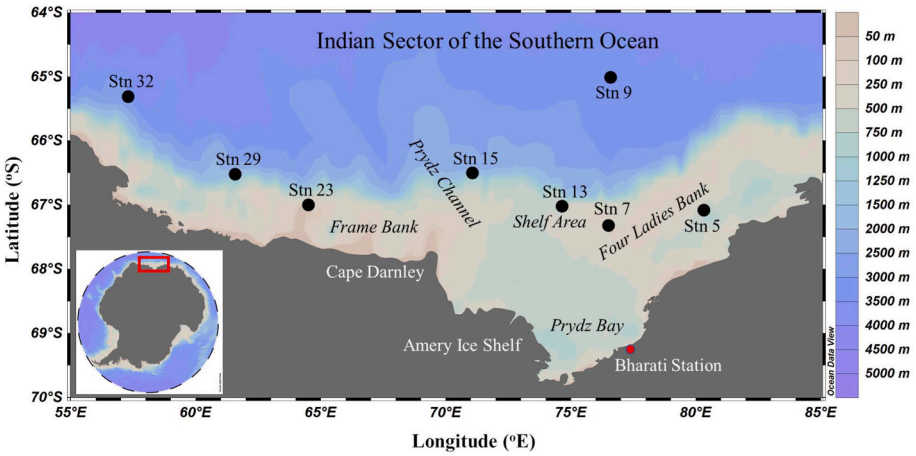


Fig. 1. Geographic location of the sampling stations in the Prydz Bay region.

continental shelf edge. In the context of physiography, this bay is characterized by an 800m deep depression at the central part, which is trenched by the Svenner Channel to the east and Prydz Channel to the west. This bay is surrounded by the Four Ladies Banks to the northeast and Fram Bank to the north-west end. The banks form partial barriers to deep-water exchange between the bay and the deep ocean (Barbara et al., 2010). The whole Prydz Bay becomes frozen, and drifting ice extends close to 60°S up to 2m ice thickness during the winter season. This area melts partially in summer, and some drifting ice-covered areas develop (Taylor et al., 1997).

2.2. Sample collection

Sediment samples were collected from each station by using a 0.25 m^2 box corer (50 cm × 50 cm × 65 cm). Due to time limitations, the box corer was deployed at each station only once. From each box core sample, further sub-samples were taken using a hand-held acrylic corer having an internal diameter of 7.5 cm. Each core sample for meiofauna analysis was sliced in situ into 0–1, 1–2, 2–5, 5–10, 10–15, and 15–30 cm sections. Another core was also collected from each station for sediment texture analysis (percentage composition) following the sieve and pipette method (Folk, 1968). Furthermore, organic carbon was estimated by the wet oxidation method using chromic acid digestion followed by titration with 0.2 N ferrous ammonium sulphate solutions (El Wakeel and Riley, 1957).

For analyses of the meiofaunal community, the samples were fixed immediately in 4% buffered formalin (Danovaro et al., 2004), stained with Rose Bengal (0.5 g l^{-1}) and transported to the laboratory for further processing and analysis. Preserved samples were then washed through 500 and 63 μm sieves to separate macro and meiofaunal organisms, respectively (Pfannkuche and Thiel, 1988). Sediments retained on the 63 μm mesh were subjected to a floatation technique (Armenteros et al., 2008) in order to extract the meiofauna. All the meiofauna were identified up to higher taxon and enumerated under a stereo-zoom microscope (Olympus SZX7), and the density was expressed in individuals 10 cm^{-2} ±SD. After enumeration, all the free-living nematode specimens were picked and mounted over glass slides following the formalin–ethanol–glycerol technique (Seinhorst, 1959). Further identification up to the species level was carried out under a compound microscope equipped with a camera (Nikon Eclipse Ci) using standard literature (Platt and Warwick, 1983, 1988; Warwick et al., 1998; Huang and Guo, 2022) and the NeMys online database (Bezerra et al., 2019).

2.3. Biological trait analysis

For the Biological Trait Analysis of the nematode community, five different trait categories were selected: four morphological (adult body shape, tail shape, cuticle morphology, and feeding guild or buccal cavity structure) and one ecological (c-p value or life-history strategy) (Table 1). According to Soetaert et al. (2002), three body shape types of adult nematodes were documented-stout, slender, and long/thin. On the basis of tail shape and size, nematodes were classified into four tail shape categories following the classification of Thistle et al. (1995)-short/round, elongated/filiform, conical, and clavate. Nematode species were categorized into four groups based on their cuticle morphology: smooth, striated, covered with dots, and ornamented (Soetaert et al., 2002). On account of their buccal morphology, feeding guilds of each free-living marine nematode species were allocated as per Wieser (1953) classification: 1A-selective deposit feeders, 1B-non selective deposit feeders, 2A-epistrate feeders, and 2B-carnivorous/omnivorous. Each nematode species was classified under one of the five c-p (colonizer-persister) categories by using the literature of Bongers et al. (1991, 1995): 1-colonisers (opportunistic species; r-strategists); 2-tolerant to stress; 3-intermediate; 4-highly sensitive to stress; and 5-persisters (k-strategists).

Table 1
List of biological traits and categories used to describe nematode assemblages.

Biological traits	Categories
(A) Body shape	(i) Stout (ST) (ii) Slender (SL) (iii) Long/thin (LT)
(B) Tail shape	(i) Short/round (SR) (ii) Elongate/filiform (EF) (iii) Conical (CO) (iv) Clavate (CL)
(C) Cuticle morphology	(i) Smooth (SM) (ii) Striated (STR) (iii) Covered with dots (CD) (iv) Ornamented (OR)
(D) Life-history strategy (c-p score)	(i) Extreme colonizer (c-p 1) (ii) Colonizer (c-p 2) (iii) Intermediary (c-p 3) (iv) Persister (c-p 4) (v) Extreme rsister (c-p 5)
(E) Feeding guild	(i) Selective deposit feeders (1A) (ii) Non-selective deposit feeders (1B) (iii) Epistrate feeders (2A) (iv) Predators (2B)

2.4. Data analysis

Several univariate and multivariate analyses were performed by using Plymouth Routines In Multivariate Ecological Research (PRIMER) v.6 software (Clarke and Gorley, 2001; Clarke et al., 2008) aided with an add-on package of Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson et al., 2008). Principal component analysis (PCA) was performed to identify essential environmental variables that characterize the study area. Bray-Curtis similarity index was calculated using square root transformed free-living marine nematode abundance data of the Prydz Bay. Using the Bray-Curtis similarity index, hierarchical aggregation clustering (CLUSTER) was constructed. A SIMPROF (similarity profile) test was done to detect the significantly different stations using the default of 1000 permutations for the mean similarity profile and 999 permutations for the simulated profile with a significance level of 0.05. Furthermore, the similarity of percentage (SIMPER) analysis was conducted to identify the percentage contribution of major nematode species responsible for the total similarity and dissimilarity between groups. The following biotic indices were also analyzed based on nematode species composition: Shannon–Wiener diversity (H' loge), Margalef's species richness (d), Pielou's evenness (J'), and Simpson index ($1 - \lambda'$). Canonical Correspondence Analysis (CCA) (Ter Braak, 1986) was performed in order to visualize the shape of nematode species composition with different environmental variables using the Multi-Variate Statistical Package (MVSP) program (version 3.1) (Kovach, 1998).

Based on free-living marine nematode community structure, two different functional diversity measures, namely the Maturity Index (MI) (Bongers, 1990) and the Index of Trophic Diversity (ITD) (Heip et al., 1985) were analyzed to report the community descriptors. MI was calculated as $MI = \sum v(i) * f(i) / \sum f(i)$, where v(i) is the c-p value of taxon i and f(i) is the frequency of taxon i. Colonizer –persister or c-p value is assigned to each nematode genus based on their colonizing ability, ranging from 1 (rapid colonizer, and highly tolerable to stress: r strategies) to 5 (poor colonizer and highly susceptible to stress: persister or k strategies) (Bongers, 1990).ITD was calculated as $ITD = \sum \theta_i^2$, where θ_i is the abundance of the i^{th} trophic guild. Free-living marine nematodes were assigned to 4 trophic guilds, following Wieser (1953) classification (Table 1).

Another multivariate technique RLQ (Dolédec et al., 1996) with combination of the fourth-corner method (Legendre et al., 1997; Dray et al., 2014) was conducted to record the relationship between environmental factors and species trait modalities in relation to RLQ axis. Three separate tables L (species distribution across samples: sites in rows and species in columns), R (environmental variables of samples: sites in rows and environmental variables in columns) and Q (species traits: species in rows and traits in columns) were constructed prior to the analysis. Each of the tables needs to be analyzed separately to perform the RLQ analysis. Correspondence analysis (CA) and principal component analysis (PCA) were applied to table L and Q, respectively (Dray et al., 2014), whereas, for table R, Hill Smith analysis (Dray, 2013) was conducted. RLQ analysis alone can give insights on the global visual summary of the relationship among these three metrics; however, in combination with fourth-corner analysis; it can depict the significance of these bivariate associations. Additionally, the Monte-Carlo test was run with 49999 random permutations of model 2 (to test the null hypothesis: taxon densities with fixed traits are unrelated to environmental parameters) and model 4 (taxon densities with fixed environmental factors are not influenced by species traits), with subsequent adjustment of p-value (Benjamini and Hochberg, 1995; Dray, 2013). The RLQ/fourth-corner combined analysis was performed using the "ade4" package (Dray and Dufour, 2007) available in R software (version 4.0.1). This approach has gained significant attention among ecological researchers due to its robustness in evaluating the relationship among environmental parameters, traits, and species (Piló et al., 2016; Wouters et al., 2018; Hu et al., 2019). The RLQ analysis is efficient in constructing models which can reveal the impacts of environmental alterations and anthropogenic perturbation on ecosystems (Dray and Legendre, 2008).

3. Results

3.1. Environmental parameters

Environmental factors such as depth, sediment texture, organic carbon, and organic matter were measured at each of the 8 stations in Prydz Bay. Significant differences in the sediment factors were observed among the sediment of each sampling station. Water depth of the stations ranged from 290 (station 23) to 3000 m (stations 9 and 32). Sediment texture analysis revealed sand and silt (sandy silt and silty sand) were the major sediment types in the studied stations. Sand was the dominant sediment type in stations 7, 15, and 29, whereas silt was the main principal component in stations 5 and 9. In contrast with others, clay was the main sediment type in station 23 (Fig. 2a). In our studied stations, Total Organic Carbon content (TOC) ranged from 0.016% to 0.910%, with stations 23 and 13 having the highest and lowest TOC%, respectively (Fig. 2b).

3.2. Meiobenthic community structure

The abundance of meiofauna ranged from 24 ± 4.24 to 521 ± 16.97 indv.10 cm^{-2}. The highest meiofaunal abundance was found at station 23 and the lowest at station 9 (Fig. 3a). A total of nine major meiofaunal taxa were found in this eco-region, namely Foraminifera, Tintinnina, Kinorhyncha, Ostracoda, Copepoda (Harpacticoida), Nematoda, Aracnida, Bivalvia, polychaete juveniles (Fig. 3b). Nematodes were the most dominant metazoan taxa followed by harpacticoid copepoda. The vertical profile of meiofaunal composition suggested that the top 2 cm of the sediment harboured nearly 60% of the total meiofaunal community. From our study, it can be depicted that nearly 70% of total meiobenthic organisms were restricted in the upper 5 cm sediment, and 90–95% of the total meiobenthic community were present in the upper 10 cm layer, although few organisms were present up to 30 cm depth (Fig. 4).

3.3. Nematode assemblage

A total of 86 species belonging to 66 genera, 28 families and 7 orders were identified from the 7 sampling stations (Table 2). No representative of nematodes had been recorded from station 9. Araeolaimida was the most dominant nematode order followed by Desmoscolecida, howbeit the order Monhysterida had poor representation. Among 28 nematode families, Comesomatidae was the most diverse and dominant, represented by 10 genera, followed by Desmoscolecidae with 3 genera. A few other major nematode families were Chromadoridae, Desmodoridae, and Ceramonematidae represented by 8, 3, and 2 genera, respectively. Families like Aegialoalaimidae, Anticomidae, Anoplostomatidae, Camacolaimidae, Diplopeltidae, Leptolaimidae, Microlaimidae, Monhysteridae, Sphaerolaimidae, Trityloididae were only represented by a single genus per family. *Sabatieria* was the most common genus represented by 11 species, among which *Sabatieria challengerensis* was the most dominant, followed by *S. praedatrix*. The second abundant nematode genus was *Desmoscolex,* and the third was *Tricoma* (*Quadricoma*). A few other important nematode genera were *Pselionema*, *Halalaimus* and *Desmodora*.

3.4. Statistical analysis

From the results of univariate and multivariate analysis, a distinct spatial variation in the meiobenthic community structure was observed. Principal Components Analysis (PCA) was performed to understand the dominant sediment factors in each study station (Fig. 2c). The PCA result showed distinct habitat differences among the 8 studied stations in the context of environmental parameters. According to PCA analysis,

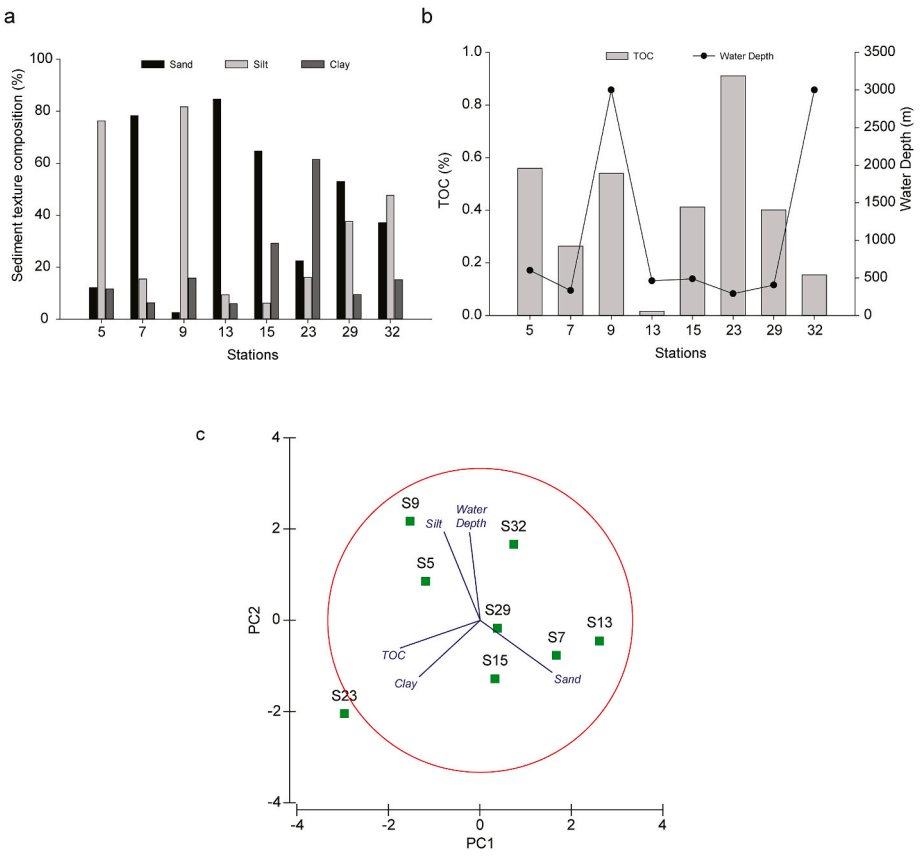


Fig. 2. a. Spatial variation of sediment texture of studied stations in Prydz Bay, b. Spatial variation of TOC, and water depth of studied stations in Prydz Bay, c. PCA ordinations depicting the correlation of environmental parameters with various sampled stations.

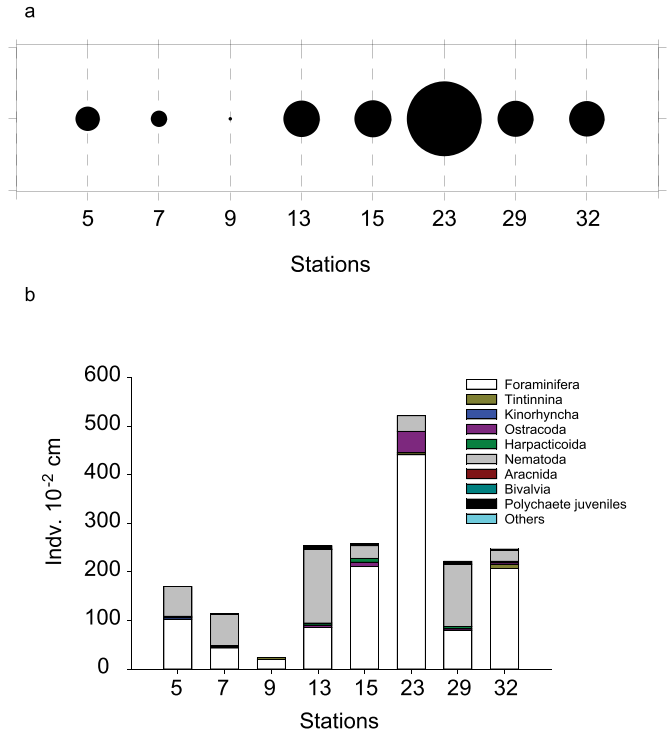


Fig. 3a. Spatial variation of meiobenthic density in the Prydz Bay region. The maximum symbol diameter corresponds to 521 indv. 10 cm^{-2}, b. Spatial variation of meiobenthic community structure in Prydz Bay.

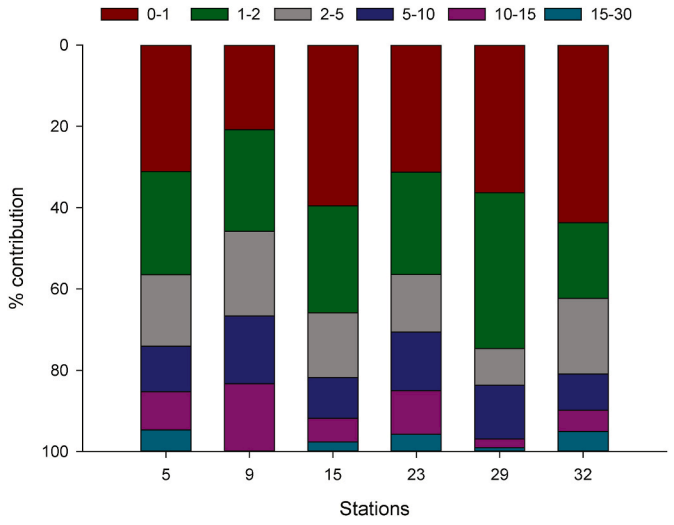


Fig. 4. Vertical profile of relative abundance percentage of meiobenthic community in the Prydz Bay region.

stations 7, 15, and 29 were associated with higher sand%, while stations 5 and 9 were related to higher values of silt%. The TOC did not display any distinct association with any station. The PERMANOVA analysis revealed a significant spatial variation in free-living marine nematode abundance ($p = 0.001$) across the sampling stations. Diversity indices based on free-living marine nematode abundance are shown in Table 3. Margalef's species richness (d) was recorded as highest for station 23 (6.91) and lowest for station 15 (3.93). Pielou's evenness index (J′) ranged from 0.84 (station 32) to 0.94 (station15). Shannon–Wiener

Table 2
List of free-living marine nematode species recorded at different stations along with CCA codes and RLQ codes.

Nematode Species	CCA code	RLQ code	S 5	S 7	S 9	S 13	S 15	S 23	S 29	S 32
Acantholaimus quintus	1	Acqu	+	+	−	+	−	−	−	+
Actinonema chitwoodi	2	Acch	−	−	−	+	−	−	−	−
Actinonema pachydermatum	3	Acpa	+	−	−	+	−	+	−	−
Adoncholaimus thalassophygas	4	Adth	−	−	−	−	+	−	−	−
Aegialoalaimus tenuis	5	Aete	−	−	−	−	−	+	−	−
Anoplostoma tenuisetum	6	Ante	−	−	−	−	+	+	−	−
Anticoma acuminata	7	Anac	+	−	−	+	−	+	+	−
Araeolaimus elegans	8	Arel	−	−	−	−	+	−	−	−
Atrochromadora microlaima	9	Atmi	−	−	−	−	−	−	+	−
Bathylaimus filicaudatus	10	Bafi	+	−	−	−	−	+	−	+
Calyptronema acuminatum	11	Caac	−	−	−	−	−	−	−	+
Cervonema tenuicaudatum	12	Cete	−	−	−	−	−	−	+	−
Chromadora nudicapitata	13	Chnu	−	+	−	+	−	−	−	−
Chromadorina cervix	14	Chce	−	−	−	+	−	−	−	+
Comesoma arenae	15	Coar	+	−	−	+	+	+	−	−
Comesoma hermani	16	Cohe	+	−	−	−	+	−	−	+
Comesomoides sp.	17	CoS	−	−	−	−	−	+	−	−
Curvolaimus filiformis	18	Cufi	−	+	−	−	−	−	−	−
Daptonema sp.	19	DaS	+	−	−	−	−	+	−	−
Deontolaimus longicauda	20	Delo	−	−	−	−	−	−	−	+
Desmodora greenpatchi	21	Degr	−	+	−	−	−	−	−	−
Desmodora scaldensis	22	Desc	+	+-	−	+	+	+	−	−
Desmodora tenuicauda	23	Dete	+	+	−	−	−	+	−	−
Desmodorella sanguinea	24	Desa	+	+	−		+	+	−	−
Desmodorella tenuispiculum	25	Dest	+	+	−	+	+	+	−	−
Desmoscolex sp.	26	DeS	+	+	−	+	+	+-	+	+
Dichromadora antarctica	27	Dian	−	−	−	−	−	−	+	−
Dorylaimopsis punctata	28	Dopu	+	+	−	+	−	+	−	+
Elzalia sp.	29	ElS	−	−	−	−	−	−	+	−
Enoplolaimus longicaudatus	30	Enlo	+	−	−	−	−	+	+-	−
Epacanthion filicaudatum	31	Epfi	−	+	−	−	−	−	−	−
Greeffiella sp.	32	GrS	−	−	−	−	+	−	−	+
Halalaimus ciliocaudatus	33	Haci	−	+	−	+	+	+	+	−
Halalaimus filicaudatus	34	Hafi	−	−	−	+	−	−	−	−
Halalaimus gracilis	35	Hagr	−	+	−	+	+	−	+	−
Haliplectus dorsali	36	Hado	−	−	−	+	−	−	−	−
Haliplectus wheeleri	37	Hawh	+	−	−	+	−	+	−	−
Hopperia macramphida	38	Homa	−	+	−	+	−	−	+	−
Laimella longicauda	39	Lalo	−	−	−	−	−	−	−	+
Leptolaimus antarcticus	40	Lean	+	−	−	−	−	+	+	−
Litinium longicaudatum	41	Lilo	−	+	−	−	−	−	−	−
Litinium sp.	42	LiS	−	−	−	−	−	−	−	+
Marylynnia complexa	43	Maco	−	−	−	−	−	−	+	−
Metacomesoma cyatholaimoides	44	Mecy	+	−	−	−	−	−	−	+
Metadasynemoides sp.	45	MeS	−	−	−	−	+	−	−	−
Metalinhomoeus setosus	46	Mese	−	−	−	−	−	+	−	−
Micoletzkyia sp.	47	MiS	−	−	−	−	−	−	+	−
Microlaimus acuticaudatus	48	Miac	−	−	−	−	−	−	−	+
Monoposthia costata	49	Moco	+	−	−	−	−	+	+	+
Neochromadora tecta	50	Nete	−	−	−	−	−	−	−	+
Nudora campbelli	51	Nuca	−	−	−	−	−	−	+	−
Oxystomina filicaudata	52	Oxfi	+	−	−	−	−	+	−	−
Paragnomoxyala sp.	53	PaS	−	−	−	−	−	−	+	−
Paramarylynnia sp.	54	ParS	−	−	−	−	−	−	+	−
Pareurystomina scilloniensis	55	Paqu	−	−	−	−	−	+	−	−
Parodontophora quadristicha	56	Prqu	−	+	−	−	−	−	−	−
Phanoderma sp.	57	PhS	−	−	−	+	−	−	−	−
Pierrickia vitielloi	58	Pivi	+	−	−	−	−	+	−	+
Pselionema detriticola	59	Psde	+	−	−	+	−	+	+	−
Pselionema minutum	60	Psmi	−	−	−	−	−	−	+	−
Pseudolella sp.	61	PsS	−	−	−	−	+	−	−	−
Rhabdocoma sp.	62	RhS	+	−	−	−	−	+	−	+
Rhinema longispicula	63	Rhlo	−	−	−	−	−	−	+	−
Sabatieria celtica	64	Sace	−	+	−	+	−	−	+	−
Sabatieria challengerensis	65	Sach	+	+	−	+	+	+	+	−
Sabatieria conicauda	66	Saco	+	+	−	+-	−	−	+	+
Sabatieria conicoseta	67	Sacs	−	+	−	+	−	+		−
Sabatieria lyonessa	68	Saly	+	+	−	+	−	+	+	+
Sabatieria minuta	69	Sami	−	−	−	+	−	−	−	−
Sabatieria mortenseni	70	Samo	+	+	−	+	−	−	−	+
Sabatieria pisinna	71	Sapi	−	−	−	+	−	−	+	−
Sabatieria praedatrix	72	Sapr	+	+	−	+	+	+-	+	+
Sabatieria pulchra	73	Sapu	+	+	−	+	−	+	+	−
Sabatieria punctata	74	Sapn	+	+	−	+	−	+	+	+

(*continued on next page*)

Table 2 (*continued*)

Nematode Species	CCA code	RLQ code	S 5	S 7	S 9	S 13	S 15	S 23	S 29	S 32
Sphaerolaimus arcospiculum	75	Spar	–	+	–	–	–	–	–	–
Spilophorella euxina	76	Speu	–	–	–	–	+	+	+	–
Terschellingia longicaudata	77	Telo	+	–	–	–	–	–	–	+
Thalassomonhystera parva	78	Thpa	–	–	–	–	–	–	+	–
Theristus sp.	79	ThS	–	–	–	+	–	–	–	–
Thoracostoma coronatum	80	Thco	–	+	–	–	–	–	–	–
Trefusia longicauda	81	Trlo	–	–	–	–	–	–	–	+
Tricoma (Quadricoma) scanica	82	Trsc	+	+	–	–	+	+	+	+
Vasostoma spiratum	83	Vasp	+	–	–	–	+	–	–	+
Viscosia glabra	84	Vigl	–	–	–	+	–	–	+	+
Viscosia viscosa	85	Vivi	–	–	–	+	–	–	+	–
Wieseria longicauda	86	Wilo	–	–	–	–	–	+	–	–

Table 3
Spatial variation in nemato-faunal community indices. S = Total number of species, N = Total population density, d = Species richness (Margalef's), J ' = Pielou's evenness, H′ (loge) = Shannon index, 1-λ' = Simpson index.

Station	S	N	d	J'	H'(loge)	1-λ′
S 5	32	234	5.68	0.88	3.05	0.95
S 7	28	250	4.89	0.91	3.04	0.94
S 13	33	581	5.03	0.94	3.28	0.96
S 15	19	98	3.93	0.94	2.77	0.94
S 23	34	119	6.91	0.91	3.22	0.96
S 29	33	599	5.00	0.89	3.11	0.95
S 32	27	86	5.84	0.84	2.76	0.91

index (H′ loge) was observed to be lowest in station 32 (2.76), whereas it showed maximum values for station 23 (3.22). Similar results were obtained for Simpson's index, where diversity ranged from 0.91 in station 32 to 0.96 for stations 13 and 23. The diversity analysis indicated that station 23 is the most diverse station both in terms of richness and evenness.

CLUSTER analysis of the Bray-Curtis similarity matrix based on square root transformed free-living marine nematode abundance data delineated 5 clustersat 52% similarity (SIMPROF test $p < 0.05$) (Fig. 5). According to SIMPER analysis, *Desmoscolex* sp. was the main contributor in the formation of both groups 1 and 2. In case of group 1 (average similarity 52.68%), *Desmscolex* sp. made the highest contribution (10.13%), followed by *Sabatieria praedatrix* (9%) and *S. challengerensis* (8.76%). In case of group 2 (average similarity 72.80%) *Desmscolex* sp. made the highest contribution (7.65%), followed by *S. praedatrix* (6.9%) and *S. challengerensis* (6.84%) (Table 4). CCA biplot based on free-living

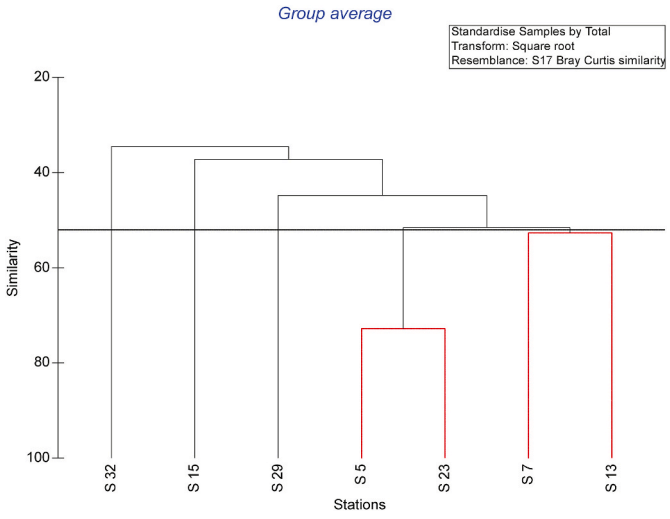


Fig. 5. Cluster plot based on Bray–Curtis similarity coefficient of free-living marine nematode species.

nematode assemblage deciphered the relationship of nematode species with several environmental factors (Fig. 6). Sediment texture, depth, and TOC% play the most crucial role in structuring the nematode communities. Nematodes like *Sabatieria pisinna*, *Chromadora nudicapitata,* and *Viscosia viscosa* were associated with sandy sediment type. *Leptolaimus antarcticus*, *Sabatieria mortenseni* showed their preference for silty sediment texture. Nematode like *Oxystomina filicaudata*, *Monoposthia costata*, *Daptonema* sp. and *Anoplastoma tenuisetum* were profited by high clay percentage. *Actinonema chitwoodi* and *Pselionema detriticola* were benefitted by depth. TOC content gave advantage to *Enoplolaimus longicaudatus*, *Spilophorella euxina*, *Sabatieria conicauda*.

3.5. Biological trait analysis

Biological Trait Analysis (BTA) of free-living marine nematode assemblages was applied to portray the functional diversity of the total nematode population of Prydz Bay based on morphological and ecological characteristics. A total of 24 traits in 5 categories were used to distinguish the functional diversity of nematode species sampled in each station of Prydz Bay (Supplementary Table S1). The most widespread trait categories obtained in all stations were slender (Body shape) (Fig. 7a), conical (tail shape) (Fig. 7b), covered with dots (cuticle morphology) (Fig. 7c), c-p 2 (c-p value) (Fig. 7d) and non-selective deposit feeders (feeding guild) (Fig. 7e). In context of body shape category, slender-bodied nematodes were the most dominant in our studied stations. In the "tail shape" category, "conical" tail shape was most prevalent, followed by "clavate" tail shape. Related to "cuticle morphology", most of the nematodes had cuticle "covered with dots", followed by "striated" cuticle. Nematodes with c-p value 2 were most prominent in all study stations, whereas nematodes with c-p value 3 and 4 were present in all stations with average abundance. Nematodes with c-p value 1 and c-p value 5 were only present in station 29 and station 7, respectively. The Maturity Index was highest in station 15 and lowest in station 5, respectively (Fig. 8a). Under the trait category "feeding guild", "non-selective deposit feeders" were most dominant in all study stations. The Index of Trophic Diversity was highest at station 32 and lowest in station 15 among all studied stations (Fig. 8b).

The RLQ analysis portrayed some correlation between the metrics (Table 5). Correspondingly, fourth corner analysis was performed among the 120 possible associations at a significance level of $\alpha = 0.1$, and only 2 significant associations (1 negative and 1 positive) had been noticed following Dray and Legendre (2008) approach. When p values were adjusted for multiple testing, there was no significant association. Subsequently, RLQ in combination with fourth corner analysis, the global test did not show any significant relationships between species distribution and environmental parameters (model 2, p value = 0.92728) as well as between species distribution and species traits (model 4, p value = 0.48592). The first RLQ axis represents the 60.40% of the total variation, while the second RLQ axis represents 23.74% (Table 5), encompassing the most important associations between traits, environment parameters, and responsible species composition. Positive

Table 4
SIMPER similarity analysis based on the free living marine nematode community composition of Prydz Bay region.

Group	Species	Average Abundance (individual. 10 cm^{-2})	Average similarity (%)	Contribution rate (%)	Cum. Percentage
Group- 1	*Desmoscolex* sp.	2.80	5.34	10.13	10.13
Average similarity 52.68%	*Sabatieria praedatrix*	2.55	4.74	9.00	19.13
	Sabatieria challengerensis	3.17	4.61	8.76	27.89
	Sabatieria punctata	2.11	3.93	7.47	35.35
	Sabatieria lyonessa	2.13	3.85	7.31	42.66
	Sabatieria pulchra	1.92	3.67	6.97	49.64
	Desmodora scaldensis	1.90	3.50	6.64	56.28
	Desmodorella tenuispiculum	1.89	3.46	6.57	62.85
	Halalaimus gracilis	1.46	2.66	5.06	67.91
	Sabatieria conicauda	1.70	2.54	4.82	72.73
	Dorylaimopsis punctata	1.35	2.45	4.65	77.38
	Acantholaimus quintus	1.66	2.12	4.02	81.40
	Chromadora nudicapitata	1.22	1.97	3.73	85.14
	Hopperia macramphida	1.22	1.97	3.73	88.87
	Halalaimus ciliocaudatus	1.33	1.73	3.29	92.16
Group -2	*Desmoscolex* sp.	3.02	5.57	7.65	7.65
Average similarity 72.80%	*Sabatieria praedatrix*	2.76	5.02	6.9	14.54
	Tricoma (Quadricoma) scanica	2.79	4.98	6.84	21.38
	Pselionema detriticola	2.51	4.35	5.97	27.36
	Sabatieria lyonessa	2.43	4.35	5.97	33.33
	Sabatieria punctata	2.30	4.31	5.92	39.25
	Desmodora tenuicauda	2.16	3.94	5.41	44.66
	Desmodora scaldensis	2.3	3.55	4.88	49.54
	Monoposthia costata	1.95	3.55	4.88	54.41
	Desmodorella tenuispiculum	1.78	3.32	4.56	58.97
	Rhabdocoma sp.	1.59	3.05	4.19	63.16
	Sabatieria challengerensis	2.52	3.05	4.19	67.35
	Sabatieria pulchra	1.88	3.05	4.19	71.54
	Haliplectus wheeleri	1.51	2.49	3.42	74.96
	Desmodorella sanguinea	1.21	2.17	2.99	77.94
	Enoplolaimus longicaudatus	1.21	2.17	2.99	80.93
	Actinonema pachydermatum	1.11	1.78	2.44	83.37
	Anticoma acuminata	1.11	1.78	2.44	85.81
	Daptonema sp.	1.11	1.78	2.44	88.25
	Leptolaimus antarcticus	1.38	1.78	2.44	90.68

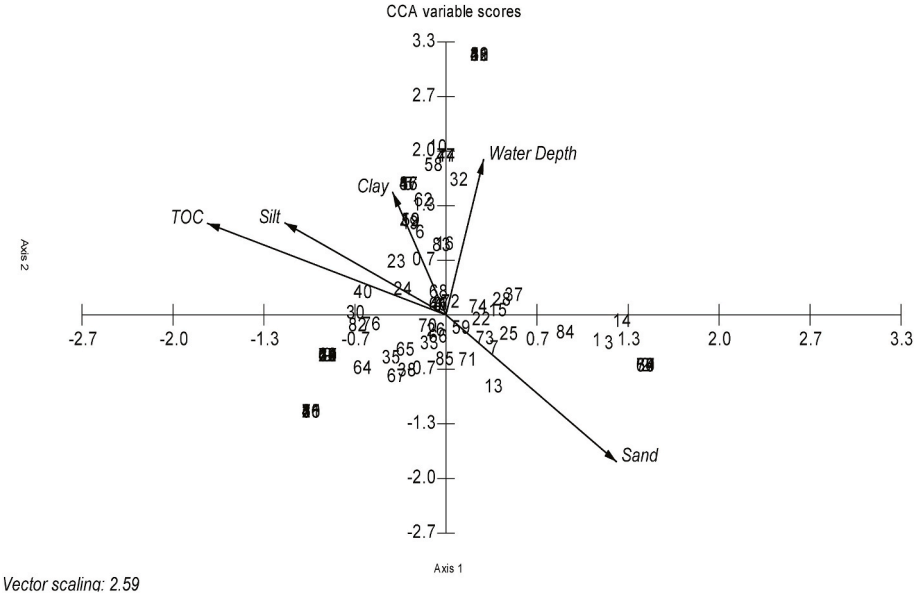


Fig. 6. Canonical correspondence analysis (CCA) ordination for free-living marine nematode species and environmental variables. The environmental variables (Water depth, sand %, silt %, clay %, TOC) are indicated by arrows. Species codes are given in Table 2.

parts of both axis-1 and axis-2 have revealed that slender body shape nematodes and nematodes with punctated cuticle morphology are closely associated with water depth. Negative part of axis-1 and positive part of axis-2 highlighted the preference of short-round tail-shaped nematode towards sandy sediment texture. Positive part of axis-1 and the negative part of axis 2 represent the association of colonizer nematodes (c-p 2) with sediments having higher silt and clay percentage (Fig. 9 a,b). Nonselective deposit feeder nematodes (1B) such as *Sabatieria mortenseni, Sabatieria pisinna, Sabatieria pulchra, Sabatieria punctata* are positioned at the positive part of both the axis (Fig. 9 b,c).

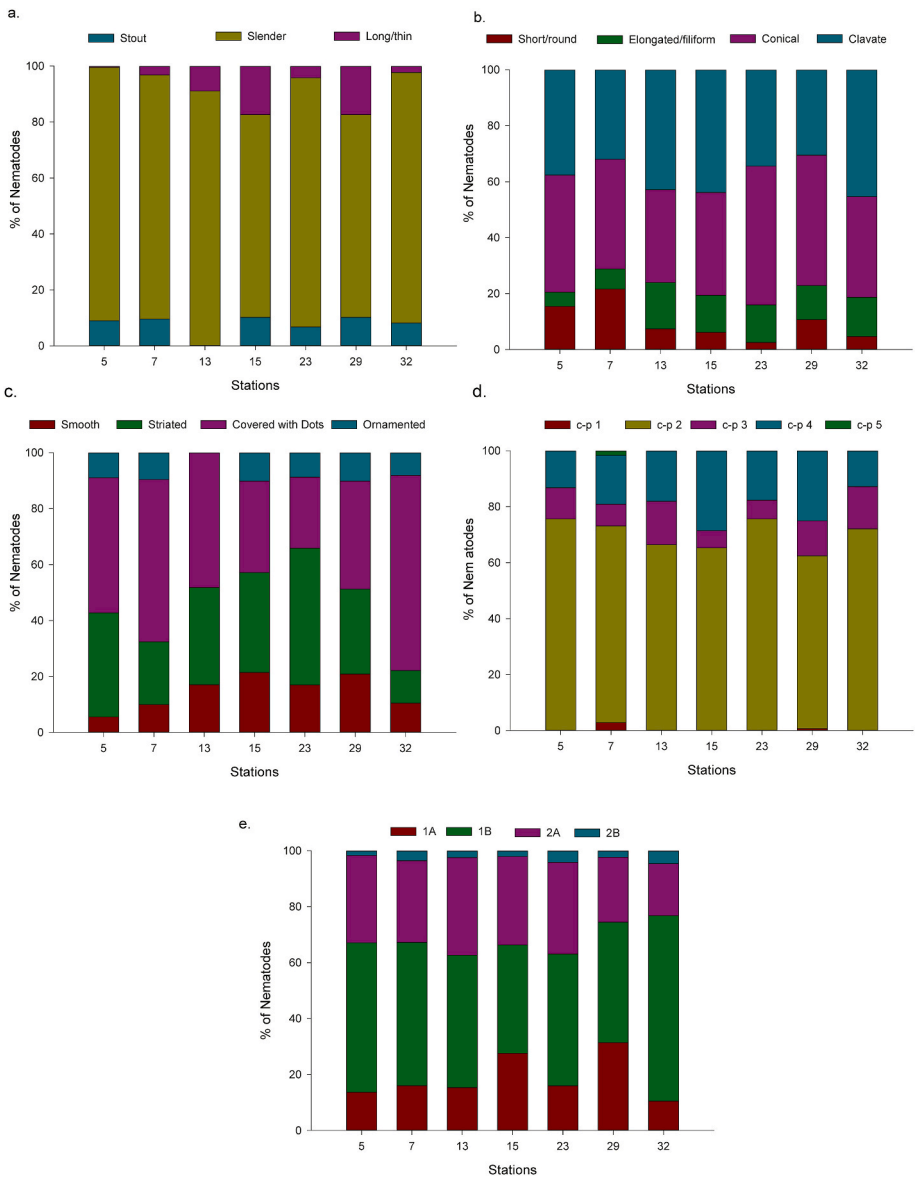


Fig. 7. Percentage of trait categories for free living marine nematode assemblages at different sampling stations percentage of trait categories for meiobenthic assemblages at different stations. a = Body size, b = Tail shape, c = cuticle morphology, d = c-p value, e = feeding guild.

4. Discussion

4.1. Environmental parameters

In a marine ecosystem, biotic components are heavily influenced by several physical, chemical, and biological components (Zeppilli et al., 2015; Xiaoshou et al., 2020; Ghosh and Mandal, 2021). In our study, the environmental factors (sediment texture and TOC %) portrayed a clear spatial variation. The sand percentage was found to be higher in the sediments of stations 7, 13, and 15, situated near the mouth of Prydz Bay, whereas a higher silt percentage is observed in the stations of deeper continental shelves (Station 5and 32) and deep sea station (Station 9). Stations near the mouth and west of the bay showed higher sand percentage because of a clockwise circulation of surface water produced by strong westward wind drift along with the west coastal current (Smith et al., 1984; Guo et al., 2019). Silt is dominated near the Four ladies bank on the eastward side of the bay because the prevalence of high-velocity currents leads to the production of finer sediments (Liu et al., 2020). Total organic carbon (TOC) percentage was less than 1% in all studied stations, with a range of 0.016–0.9%. Due to the presence of the Prydz Bay Gyre (PBG), the main component of water circulation predominant in the bay, higher TOC was observed in the western part stations of the bay than the eastern side (Smith and Tréguer, 1994). Water is trapped for an extended period of time in the deeper sections of the bay, mainly in the middle and western part of the bay due to PBG, which allows more settlement of organic matter on the seafloor in this region of the bay. High TOC content was documented from the stations having higher silt and clay fraction (stations 5, 9, and 23). This observation clearly depicts the affinity of organic carbon to adhere to finer sediment particles. Simultaneously, station 13, which had one of the highest sand contents (84.63%) showed the lowest TOC. According to Choudhary et al. (2018), the distribution pattern of TOC has a direct correlation with the silt and clay content of the sediment while having a negative correlation with the fraction of sand. Our study portrayed similar kinds of observations. Due to the availability of a larger surface area for adhesion, TOC% has a close association with finer sediment (Choudhary et al., 2018).

Maximum clay and organic carbon content were documented from the shallowest station 23. Due to continuous sea ice abrasion from the Amery Ice shelf, rich organic matter and clayey terrestrial debris are

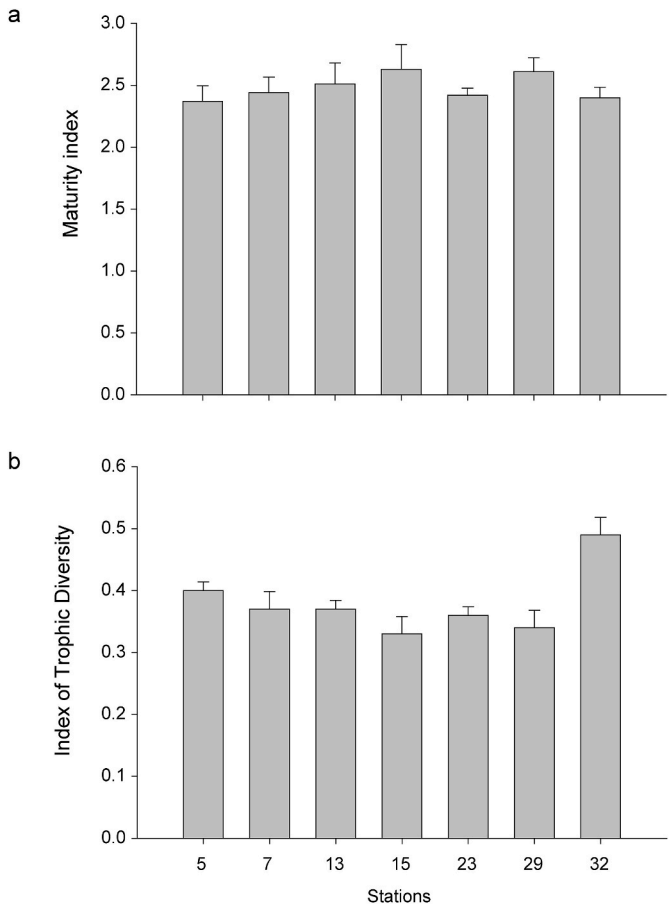


Fig. 8. Free living marine nematode a) Maturity Index and b) Index of Trophic Diversity in each samples stations of Prydz Bay.

Table 5
RLQ results. Individual R-L-Q separate analysis and RLQ analysis.

Separated analysis	Axis 1 eigenvalue (Variance %)	Axis 2 eigenvalue (Variance %)
R/Hill-Smith	3.62 (60.40)	1.42 (23.74)
L/CA	0.33 (25.13)	0.30 (22.73)
Q/PCA	5.76 (28.78)	2.88 (14.38)

RLQ Analysis	Axis 1	Axis 2
Eigenvalues	0.24	0.05
Variance %	75.74	16.31
R/RLQ Variance	1.83	1.26
Variance %	40.69	35.86
Q/RLQ Variance	1.79	1.88
Variance %	39.78	53.51
L/RLQ Variance	0.15	0.10
Variance %	3.33	2.85

deposited in this area. Station 32, one of the deepest stations, is situated at the western end of the bay and exhibited low TOC and organic matter (OM) despite showing silt dominance. This heterogeneous observation depicted a correlation between TOC and water depth. In several deep-sea regions, total organic carbon is inversely proportional to water depth. A wide depth variation ranging from shallow coastal regions to extremely deep continental shelves is present in the Prydz Bay. In general, the shelf break site is extremely steep, and the depth drastically increases from 600m to greater than 3000m (Clarke and Johnston, 2003). Several biotic and abiotic factors are associated with water depth; therefore, water depth also plays a crucial role in structuring the meiobenthic community of the Prydz Bay.

4.2. Meiobenthic assemblage

In a polar ecosystem, unveiling the meiobenthic species diversity and their community structure is a formidable task. Studies have suggested that Antarctic meiofaunal community structure depends on several environmental factors, such as water depth, grain size, organic matter content, the actions of sea ice, and abrasion from icebergs (Ingole and Singh, 2010; Veit-Köhler et al., 2011; Hauquier et al., 2015; Rose et al., 2015; Brannock et al., 2018; Azovsky et al., 2020; Liu et al., 2020; Stark et al., 2020; Huang et al., 2022). In several studied areas of the SO (such as Kapp Norvegia, Halley Bay, and Larsen Area), meiobenthic abundance ranged from 500 to 5100 indv.10 cm^{-2} (Herman and Dahms, 1992; Vanhove et al., 1995; Fabiano and Danovaro, 1999; Raes et al., 2010; Stark et al., 2020) with limited information available from the Prydz Bay (but see Ingole and Singh 2010; Huang et al., 2022). From the nearshore waters of Prydz Bay, Ingole and Singh (2010) documented the meiobenthic abundance with a range of 119–319 indv. 10 cm^{-2}. In our study, total meiobenthic abundance showed spatial variation having range of 24–521 indv. 10 cm^{-2}. Food availability plays a crucial role in structuring the meiobenthic communities (Rose et al., 2015; Veit-Köhler et al., 2018). Input of organic matter influences the meiobenthic abundance and their community structure (Vanhove et al., 2000). Station 23, with higher organic matter exhibits higher meiobenthic abundance. Due to the reduction of amount and quality of organic matter with depth, the abundance of meiobenthic organisms is lower in deeper regions (Tietjen, 1992; Vanhove et al., 2004; Rose et al., 2015). In our study, lower meiobenthic abundance (24 indv. 10 cm^{-2}) was recorded from the deep-sea station 9. A similar result has been reported by Huang et al. (2022), where the lowest meiobenthic abundance was 23 indv. 10 cm^{-2} in the deep sea area of the Prydz Bay. Heterogeneity in meiobenthic abundance in stations with similar depths might have occurred due to the differences in food supply (Ingole and Singh, 2010). Station 32 (with the highest depth in bay area), displayed comparatively higher meiobenthic abundance than station 9. A gradual reduction of chlorophyll and primary productivity from the south to the north part of the Prydz Bay (Fan et al., 2013; Huang et al., 2022) results in higher meiobenthic abundance in bay and self area than deep sea area. In the present study, comparatively higher meiobenthic abundance has been observed in the continental shelf area of the bay (station 23), which is in accordance with Huang et al. (2022).

The present study shows that the top 2 cm of the sediment harbored nearly 60% of the total meiofaunal community. Due to more favourable conditions like lower compactness and higher food supply, surface layers (mainly the upper 2 cm) always harbor higher meiobenthic abundance than the layers beneath (Ingole and Singh, 2010). Downward movement of phytoplankton by the dominance of organic matter promotes the respiratory activities of the meiobenthic organisms and enhances the meiofaunal abundance in the surface layer of the sediment (Veit-Köhler et al., 2011; Lins et al., 2014).

From all the studied stations, 9 major meiobenthic taxa were recorded with an average of 5 taxa per station. Because of their high adaptation rate, free-living nematodes are the most dominant metazoan taxa followed by harpacticoid copepods. In case of nematode assemblages, a total of 66 nematode genera were documented from Prydz Bay. These results are quite closer to the study of Ingole and Singh (2010). According to them, nematode was the most dominant metazoan taxa, and *Sabatieria* was the most common nematode genus. Our study also documented the *Sabatieria* as the most common and abundant nematode genus. Studies suggest that several species of *Sabatieria* are associated with finer sediment texture (Moreno et al., 2008; Alves et al., 2014) and organic matter deposition (Hourston et al., 2009). They are specially adapted to reduce their mobility and respiration rate in hypoxic conditions.

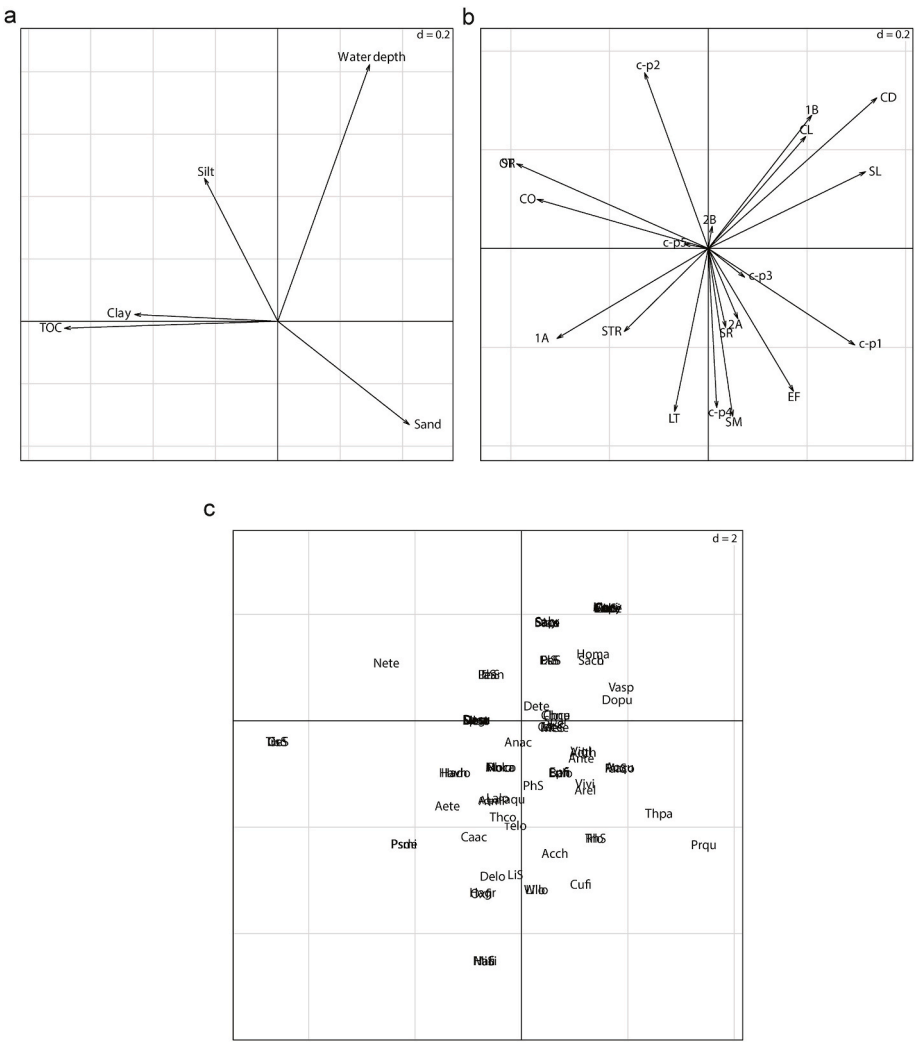


Fig. 9. a. RLQ diagram as defined by the 1st and 2nd axes with the projection of environmental variables (TOC- Total organic carbon), b.RLQ diagram as defined by the 1st and 2nd axes with the projection of trait categories (see Table 1 for the abbreviations of trait categories), c. RLQ diagram as defined by the 1st and 2nd axes with the projection of species (see Table 2 for respective RLQ codes of species). The d value in the upper right corner is the scale of the graph given by a grid.

4.3. Biological trait analysis

Nematode functional diversity is indicative of ecosystem maturity and health. Biological Trait Analysis on free-living marine nematode community depicts how each trait is associated with environmental conditions. For free-living `marine nematodes four trait categories are based purely on morphological features (i.e., body shape, feeding guild, cuticle morphology, and tail shape), and one is associated with physiological and developmental features (i.e., life strategy or c-p value). Variations in the relative contribution of trait percentages across stations likely reflect ecological adaptations of nematode species to the habitat environment.

Nematode body shape is associated with food availability and sediment biogeochemical condition (Soetaert et al., 2002; Vanaverbeke et al., 2004b; Losi et al., 2013). A strong dominance of slender body shape was observed in station 5 and station 23 as an adaptation to higher TOC% and silt/clay fraction of the sediment. The majority of stout bodied nematodes are represented by Desmoscolids while the paucity of other stout bodied genera may be attributed to the higher depth of our sampling stations. Nematodes with slender body sizes showed a clear dominance pattern in all sampling stations. According to Schratzberger et al. (2007), nematodes with slender body types are closely associated with higher clay and silt percentage, as mirrored in our findings. RLQ analysis also revealed that nematode with slender body shape is closely associated with water depth. In changing oxygen concentrations (due to depth variation) and coarser sediments, body elongation is an adaptive feature to help in higher epidermal uptake of oxygen as well as organic matter (Jensen, 1987; Singh and Ingole, 2016). Elongated body size is considered an adaptive feature of nematodes in response to increasing depth (Soetaert et al., 2002).

Tail shape may bring useful ecological information for the interpretation of trait composition patterns. The elongated/filiform tail shape was well-represented in silty sediments (stations 7, 29, and 32). Nematodes with elongated or filiform tail act as burrowing species pushing the sediment particles to create their space within the sediment to enhance their locomotion. For the other habitats where particle size is coarse (sandy) or the substrate is non-sedimentary, the interstitial strategy should be more important and shorter round and clavate tail shapes seem to have higher adaptive benefits. The preference of nematode with short and round tail towards sandy sediment texture was also depicted in RLQ analysis. A significant number of clavate and conical tails were observed at all sampling stations in our study. According to several authors, these tail-shaped nematodes generally have been associated with coarse sediment texture (Schratzberger et al., 2007; Armenteros et al., 2009).

Chromadorids and Desmoscolids are mostly with punctated and ornamented cuticles and have ubiquitous distribution in all depths (Venekey et al., 2019). The genus *Sabatieria* and *Tricoma* showed high

abundance in silty sediments. Six orders of chromadorids dominated the studied stations: Chromadorida, Desmodorida, Monhysterida, Plectida, Araeolaimida, and Desmoscolecida. An important fraction of nematodes from deep water sediments had a cuticle with wide body annules and longitudinal ridges as mirrored by relatively high dominance of the family Ceramonematidae, Monoposthidae and Chromadoridae in our study. This adaptive feature pointed to a phylogenetic signature which indicates a particular family inhabiting deep-waters and bearing a cuticle with wide body annules and longitudinal ridges (Decraemer, 1976). This information suggested a phylogenetic signature from a specific family that resides in deep waters and has a cuticle characterized by broad body rings and longitudinal ridges. However, there is no clear connection between the habitat and the type of cuticle (Armenteros et al., 2019). Our findings suggest the dominance of punctated/annulated types that likely reflect a phylogenetic signature instead of ecological adaptations to the environment.

Life strategy characterization revealed a dominance of colonizers and persisters (c-p 2 followed by c-p 4). Dominance of opportunistic taxa like, *Sabatieria* (c-p 2), *Desmoscolex, Tricoma* (*Quadricoma*) (c-p 4) were recorded from all the sampling stations. *Sabatieria* and *Halalaimus*are considered as "opportunistic" species and are indicators of enriched but disturbed habitats. They are successfully adapted to hypoxic conditions by reducing their mobility and respiration rate, which sequentially decreases their oxygen demand (Warwick and Price, 1979). Studies revealed an increase of c-p value along with an increase in grain size (Semprucci et al., 2018). Our findings correspond with these patterns as nematodes with c-p value 4, such as *Desmoscolex, Tricoma (Quadricoma)*, *Halalaimus* were dominated in the stations with high sand percentage. However, the anomalous abundance of c-p1 nematodes in station 7 coupled with low TOC and high sand percentage point towards recent disturbance of the sampling site. Highest value of MI was reported in station 15, due to the higher abundance of persister (c-p 4) nematodes in this station.

Trophic groups in marine habitats give an indication of the food sources used by the nematodes. The presence of all four feeding types of nematodes indicated a complex environment at Prydz Bay. Free-living marine nematode assemblage was dominated by non selective deposit feeder nematodes (1B) in our studied stations. A similar result was also reported by Schratzberger et al. (2007) and Vijay et al. (2017). Habitats where detritus sediments constitute the main source of food were characterized by clay-silt type sediment texture (stations 15 and 23) and showed the dominance of deposit-feeding nematodes. Dominance of deposit feeders and cosmopolitan genera (e.g., *Sabatieria*, *Tricoma*) in deep sediments suggest high microbial activity in these stations. Abundance of selective and non-selective deposit feeders were found to be associated with shallower depths and showed an increment in abundance as we moved from the eastern to the western stations (Stations 23, 29, and 32). The westward trend in high abundance is exhibited in spite of variability in TOC% and clay content among stations, asserting the dominance of the current regime and water depth in structuring the feeding guild over TOC and texture. The stations situated at the mouth of the bay (13 and 15) supported a large proportion of epigrowth feeders (*Chromadora, Desmodora, Desmoscolex*), those are able to feed on biofilm growing on sand grains, macro-algae thallus or coral rubble. These stations are characterized by coarser sediment types and variable TOC and are positioned near the vortex of the Prydz Bay gyre that facilitates epigrowth formations. Many species behave as opportunistic feeders which may change feeding strategies in response to available food (Moens and Vincx, 1997). Due to this reason, abundance of non selective deposit feeders and index of trophic diversity values were recorded higher in station 32 (station with highest depth in continental shelf region).

BTA added a new aspect in biodiversity study over solely taxonomical information. Subsequently, our understanding of the ecological gradients present within an ecosystem was further improved. In addition with dominant species, low-abundance species also contributed to ecosystem functioning. In stressful environmental conditions, nematode species with different biological traits respond differently and corroborate resilience to community structure.

5. Conclusion

Our study depicted the systematic description of biodiversity patterns and vertical profiling of meiobenthic assemblages, with a special accentuate on free-living nematodes from the pristine eco region of Prydz Bay. Contribution of different environmental factors in structuring the meiobenthic community structure was also unraveled in our study. The present study reveals the diverse morpho-functional and ecological traits characterized by heterogeneous niches and microhabitats that lead to the development of a wide range of adaptations in free-living marine nematodes. Finally, our work may represent a significant baseline study of meiobenthic organisms with their functional diversity, which can act as a roadmap for future researchers and environmental policymakers. Furthermore, long-term spatio-temporal studies on meiobenthic organisms with biological trait analysis are necessary for a comprehensive understanding of their community structure in the milieu of climate change and anthropogenic stressors mediated global changes.

Declaration of competing interest

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

Data availability

Data will be made available on request.

Acknowledgments

The authors wish to express their gratitude to the Vice Chancellor, Presidency University for providing facilities and encouragement to carry out the above research work. We are also grateful to the Director, NCPOR, Ministry of Earth Sciences, Goa, for his encouragement and for permitting S.M. to participate in the 11th Indian Scientific Expedition to the Southern Ocean (ISESO). We are grateful to one and all members of ISESO who helped onboard during the collection of samples. This work is supported by grants awarded to S.M. from NCPOR (NCPOR/2019/PACER-POP/BS-09 dated 05.07.2019) under the Pacer Outreach Program (POP) under the Polar Science And Cryosphere Programme (PACER) initiative. The data in this paper is part of a doctoral thesis of SSB to be submitted in partial fulfillment of the requirements of a degree of Doctor of Philosophy from Presidency University, Kolkata. The authors would also like to express their appreciation to the members of the Marine Ecology Laboratory for their time-to-time help and excellent teamwork. This is NCPOR contribution number J-17/2023-24.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2023.104109.

References

Alves, A.S., Veríssimo, H., Costa, M.J., Marques, J.C., 2014. Taxonomic resolution and Biological Traits Analysis (BTA) approaches in estuarine free living nematodes. Estuar. Coast Shelf Sci. 138, 69–78.

Anderson, M., Gorley, R., Clarke, K.P., 2008. For PRIMER: Guide to Software and Statistical Methods. Primer-e, Plymouth, UK, p. 32.

Armenteros, M., Pérez-García, J.A., Marzo-Pérez, D., Rodríguez-García, P., 2019. The influential role of the habitat on the diversity patterns of free-living aquatic nematode assemblages in the Cuban archipelago. Diversity 11 (9), 166.

Armenteros, M., Perez-Garcıa, J.A., Perez-Angulo, A., Williams, J.P., 2008. Efficiency of extraction of meiofauna from sandy and muddy marine sediments. Rev. Invest. Mar. 29 (2), 113–118.
Armenteros, M., Ruiz-Abierno, A., Fernández-Garcés, R., Pérez-García, J.A., Díaz-Asencio, L., Vincx, M., Decraemer, W., 2009. Biodiversity patterns of free-living marine nematodes in a tropical bay: Cienfuegos, Caribbean Sea. Estuar. Coast Shelf Sci. 85 (2), 179–189.
Azovsky, A.I., Chertoprud, E.S., Garlitska, L.A., Mazei, Y.A., Tikhonenkov, D.V., 2020. Does size really matter in biogeography? Patterns and drivers of global distribution of marine micro and meiofauna. J. Biogeogr. 1–13.
Baldrighi, E., Aliani, S., Conversi, A., Lavaleye, M., Borghini, M., Manini, E., 2013. From microbes to macrofauna: an integrated study of deep benthic communities and their response to environmental variables along the Malta Escarpment (Ionian Sea). Sci. Mar. 77 (4), 625–639.
Barbara, L., Crosta, X., Massé, G., Ther, O., 2010. Deglacial environments in eastern Prydz bay, east Antarctica. Quat. Sci. Rev. 29 (19–20), 2731–2740.
Barnes, D.K., Peck, L.S., 2008. Vulnerability of Antarctic shelf biodiversity to predicted regional warming. Clim. Res. 37 (2–3), 149–163.
Benjamini, Y., Hochberg, Y., 1995. Controlling the False Discovery rate: a Practical and Powerful approach to multiple testing. J. R. Stat. Soc. Ser. B Methodol. 57, 289–300.
Bezerra, T.N., Decraemer, W., Eisendle-Flöckner, U., Hodda, M., Holovachov, O., Leduc, D., Miljutin, D., Mokievsky, V., Peña Santiago, R., Sharma, J., Smol, N., Tchesunov, A., Venekey, V., Zeng, Z., Vanreusel, A., 2019. NeMys: World database of nematodes. http://nemys.ugent.be. (Accessed 18 January 2022).
Boldina, I., Beninger, P.G., Le Coz, M., 2014. Effect of long-term mechanical perturbation on intertidal soft-bottom meiofaunal community spatial structure. J. Sea Res. 85, 85–91.
Bonaglia, S., Nascimento, F.J.A., Bartoli, M., Klawonn, I., Brüchert, V., 2014. Meiofauna increases bacterial denitrification in marine sediments. Nat. Commun. 5, 5133.
Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83, 14–19.
Bongers, T., Alkemade, R., Yeates, G.W., 1991. Interpretation of disturbanceinduced maturity decrease in marine nematode assemblages by means of the Maturity Index. Mar. Ecol. Prog. Ser. 76, 135–142.
Bongers, T., de Goede, R.G.M., Korthals, G.W., Yeates, G.W., 1995. Proposed changes of c-p classification for nematodes. Russ. J. Nematol. 3, 61–62.
Borchers, A., Voigt, I., Kuhn, G., Diekmann, B., 2011. Mineralogy of glaciomarine sediments from the Prydz Bay-Kerguelen region: relation to modern depositional environments. Antarct. Sci. 23 (2), 164–179.
Braeckman, U., Vanaverbeke, J., Vincx, M., van Oevelen, D., Soetaert, K., 2013. Meiofauna metabolism in suboxic sediments: currently overestimated. PLoS One 8 (3), e59289.
Brannock, P.M., Learman, D.R., Mahon, A.R., Santos, S.R., Halanych, K.M., 2018. Meiobenthic community composition and biodiversity along a 5500 km transect of Western Antarctica: a metabarcoding analysis. Mar. Ecol. Prog. Ser. 603, 47–60.
Bremner, J., Rogers, S.I., Frid, C.L.J., 2003. Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. Mar. Ecol. Prog. Ser. 254, 11–25.
Bremner, J., Rogers, S.I., Frid, C.L.J., 2006. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecol. Indic. 6, 609–622.
Choudhary, S., Nayak, G., Tiwari, A.K., Khare, N., 2018. Sediment composition and its effect on the productivity in larsemann hills, East Antarctica. Arab. J. Geosci. 11 (15), 1–17.
Clarke, A., Johnston, N.M., 2003. Antarctic marine benthic diversity. Oceanogr. Mar. Biol. 41, 47–114.
Clarke, K., Gorley, R., 2001. Primer V5: User Manual/Tutorial, Primer E: Plymouth. Plymouth Marine Laboratory, Plymouth, UK.
Clarke, K.R., Somerfield, P.J., Gorley, R.N., 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. J. Exp. Mar. Biol. Ecol. 366 (1–2), 56–69.
Coull, B.C., 1999. Role of meiobenthos in estuarine soft-bottom habitats. Austral. J. Ecol. 24, 327–343.
Danovaro, R., Gambi, C., Mirto, S., Sandulli, R., Ceccherelli, V.U., 2004. Meiofauna. Biol. Mar. Mediterr. 11, 55–97.
Danovaro, R., Scopa, M., Gambi, C., Fraschetti, S., 2007. Trophic importance of subtidal metazoan meiofauna: evidence from in situ exclusion experiments on soft and rocky substrates. Mar. Biol. 152, 339–350.
Decraemer, W., 1976. The cuticular structure in *Desmoscolex* with description of *D. spinosus*sp. n. and redescription of *D. michaelseni* Steiner, 1916 (Nematoda: Desmoscolecida). Biol. Jaarb. Dodonaea 44, 123–134.
Diaz, S., Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol. Evol. 16, 646–655.
Dolédec, S., Chessel, D., ter Braak, C.J.F., Champely, S., 1996. Matching species traits to environmental variables: a new three-table ordination method. Environ. Ecol. Stat. 3 (2), 143–166.
Dray, S., 2013. A Tutorial to Perform Fourth-Corner and RLQ Analyses in R.
Dray, S., Dufour, A.B., 2007. The ade4 package: implementing the duality diagram for ecologists. J. Stat. Softw. 22, 1–20.
Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S., ter Braak, C.J. F., 2014. Combining the fourth corner and the RLQ methods for assessing trait responses to environmental variation. Ecology 95 (1), 14–21.
Dray, S., Legendre, P., 2008. Testing the species traits—environment relationships: the fourth-corner problem revisited. Ecology 89, 3400–3412.
Edwards, D.P., Tobias, J.A., Sheil, D., Meijaard, E., Laurance, W.F., 2014. Maintaining ecosystem function and services in logged tropical forests. Trends Ecol. Evol. 29, 511–520.
El Wakeel, S.K., Riley, J.P., 1957. Determination of organic carbon in the marine muds. J. Cons. Int. Explor. Mer. 22 (2), 180–183.
Fabiano, M., Danovaro, R., 1999. Meiofauna distribution and mesoscale variability in two sites of the Ross Sea (Antarctica) with contrasting food supply. Polar Biol. 22, 115–123.
Fan, Z., Zhongyong, G., Heng, S., 2013. Advances in carbon-cycle research for Prydz bay, the Antarctica. Chin. J. Polar Reas. 25, 284–293.
Folk, R.L., 1968. Petrology of sedimentary rocks: Hemphill's. Austin. Texas 170, 85.
Fricker, H., Popov, S., Allison, I., Young, N., 2001. Distribution of marine ice under the Amery ice shelf, east Antarctica. Geophys. Res. Lett. 28 (11), 2241–2244.
Ghosh, M., Mandal, S., 2021. Disentangling the effect of seasonal dynamics on meiobenthic community structure from river Matla of sundarbans estuarine System, India. Front. Mar. Sci. 8, 671372.
Giere, O., 2009. Meiobenthology. The Microscopic Motile Fauna of Aquatic Sediments, second ed. Springer-Verlag, Berlin.
Górska, B., Grzelak, K., Kotwicki, L., Hasemann, C., Schewe, I., Soltwedel, T., Włodarska-Kowalczuk, M., 2014. Bathymetric variations in vertical distribution patterns of meiofauna in the surface sediments of the deep Arctic ocean (HAUSGARTEN, Fram strait). Deep-Sea Res. Part I Oceanogr. Res. Pap. 91, 36–49.
Gray, J.S., 1997. Marine biodiversity: patterns, threats and conservation needs. Biodiverse. Conserv. 6 (1), 153–175.
Guo, G., Shi, J., Gao, L., Tamura, T., Williams, G.D., 2019. Reduced sea ice production due to upwelled oceanic heat flux in Prydz Bay, East Antarctica. Geophys. Res. Lett. 46 (9), 4782–4789.
Hauquier, F., Dur' an Suja, L., Gutt, J., Veit-Köhler, G., Vanreusel, A., 2015. Different oceanographic regimes in the vicinity of the Antarctic peninsula reflected in benthic nematode communities. PLoS One 10, e0137527.
Heip, C.H., Vincx, M., Vranken, G., 1985. The ecology of marine Nematoda. Oceanogr. Mar. Biol. 23, 399–489.
Herman, R.L., Dahms, H.U., 1992. Meiofauna communities along a depth transect off Halley bay (Weddell Sea-Antarctica). Polar Biol. 12, 313–320.
Hourston, M., Potter, I.C., Warwick, R.M., Valesini, F.J., Clarke, K.R., 2009. Spatial and seasonal variations in the ecological characteristics of the free-living nematode assemblages in a large microtidal estuary. Estuar. Coast Shelf Sci. 82, 309–322.
Hu, C., Dong, J., Gao, L., Yang, X., Wang, Z., Zhang, X., 2019. Macrobenthos functional trait responses to heavy metal pollution gradients in a temperate lagoon. Environ. Pollut. 253, 1107–1116.
Huang, D., Wang, J., Tian, P., Niu, W., 2022. The distribution and controlling factors of meiofaunal community in Prydz Bay, Antarctica. Deep Sea Res. Part II Top. Stud. Oceanogr. 202.
Huang, Y., Guo, Y., 2022. Free-living Marine Nematodes from the East China Sea. Springer.
Ingels, J., Tchesunov, A.V., Vanreusel, A., 2011. Meiofauna in the Gollum channels and the whittard canyon, Celtic margin—how local environmental conditions shape nematode structure and function. PLoS One 6 (5), e20094.
Ingels, J., Vanreusel, A., Pape, E., Pasotti, F., Macheriotou, L., Arbizu, P.M., Sørensen, M. V., Edgcomb, V.P., Sharma, J., Sanchez, N., Homoky, W.B., Woulds, C., Leduc, D., Gooday, A.J., Pawlowski, J., Dolan, J.R., Schratzberger, M., Gollner, S., Schoenle, A., Arndt, H., Zeppilli, D., 2020. Ecological variables for deep-ocean monitoring must include microbiota and meiofauna for effective conservation. Nat. Ecol. Evol. 5, 21–29.
Ingole, B., Singh, R., 2010. Biodiversity and community structure of free-living marine nematodes from the Larsemann Ice Shelf, East Antarctica. Curr. Sci. 99, 1413–1419.
Jax, K., 2005. Function and "functioning" in ecology: what does it mean? Oikos 111, 641–648.
Jensen, P., 1987. Differences in microhabitat, abundance, biomass and body size between oxybiotic and thiobiotic free-living marine nematodes. Oecologia 71, 564–567.
Jessup, C.M., Kassen, R., Forde, S.E., Kerr, B., Buckling, A., Rainey, P.B., Bohannan, B.J. M., 2004. Big questions, small worlds: microbial model systems in ecology. Trends Ecol. Evol. 19, 189–197.
Kaiser, S., Brandão, S.N., Brix, S., Barnes, D.K.A., Bowden, D.A., Ingels, J., Leese, F., Schiaparelli, S., Arango, C.P., Badhe, R., Bax, N., Blazewicz-Paszkowycz, M., Brandt, A., Brenke, N., Catarino, A.I., David, B., De Ridder, C., Dubois, P., Ellingsen, K.E., Glover, A.G., Griffiths, H.J., Gutt, J., Halanych, K.M., Havermans, C., Held, C., Janussen, D., Lörz, A.-N., Pearce, D.A., Pierrat, B., Riehl, T., Rose, A., Sands, C.J., Soler-Membrives, A., Schüller, M., Strugnell, J.M., Vanreusel, A., Veit-Köhler, G., Wilson, N.G., Yasuhara, M., 2013. Patterns, processes and vulnerability of Southern Ocean benthos: a decadal leap in knowledge and understanding. Mar. Biol. 160, 2295–2317.
Kovach, W.L., 1998. MVSP–multivariate Statistical Package for Windows, Ver 3.0. Kovach computing services, Pentraeth.
Krishnapriya, P.P., Minu, M., Nandan, S.B., 2018. Composition and distribution of meiobenthos in Arctic Kongsfjord (Svalbard) with reference to carbon potential of selected fauna. Indian J. Mar. Sci. 47 (3), 613–622.
Kun, L., Heshan, L., Xuebao, H., Yaqin, H., Zhong, L., Junhui, L., Jianfeng, M., Shuyi, Z., Jianjun, W., Jun, S., 2020. Macrobenthic communities on the continental shelf of the Prydz bay, East Antarctica. Acta Oceanol. Sin. 39, 38–48.
Lambshead, P., Boucher, G., 2003. Marine nematode deep sea biodiversity – hyperdiverse or hype? J. Biogeogr. 30, 475–485.
Leasi, F., Sevigny, J.L., Hassett, B.T., 2021. Meiofauna as a valuable bioindicator of climate change in the polar regions. Ecol. Indicat. 121, 107133.
Legendre, P., Galzin, R., Harmelin-Vivien, M.L., 1997. Relating behavior to habitat: solutions to the fourth corner problem. Ecology 78 (2), 547–562.

Lins, L., Guilini, K., Veit-Köhler, G., Hauquier, F., Alves, R.M.S., Esteves, A.M., Vanreusel, A., 2014. The link between meiofauna and surface productivity in the Southern Ocean. Deep-Sea Res. Part II. 108, 60–68.
Liqi, C., 2003. Marine Environment and Air-Sea Interaction in the Arctic Region. China Ocean Press, Beijing, pp. 1–339 (in Chinese).
Liu, K., Lin, H., He, X., Huang, Y., Li, Z., Lin, J., Mou, J., Zhang, S., Wang, J., Sun, J., 2020. Macrobenthic communities on the continental shelf of the Prydz bay, east Antarctica. Acta Oceanol. Sin. 39 (2), 38–48.
Lizhe, C., Sujing, F., Jie, Y., Xiping, Z., 2012. Distribution of meiofaunal abundance in relation to environmental factors in Beibu Gulf, South China Sea. Acta Oceanol. Sin. 31, 92–103.
Losi, V., Moreno, M., Gaozza, L., Vezzulli, L., Fabiano, M., Albertelli, G., 2013. Nematode biomass and allometric attributes as indicators of environmental quality in a Mediterranean harbour (Ligurian Sea, Italy). Ecol. Indic. 30, 80–89.
Ma, J., Song, J., Li, X., Yuan, H., Li, N., Duan, L., Wang, Q., 2020. The change of nutrient situation in the Prydz Bay waters along longitude 73° E, Antarctica, in the context of global environmental change. Mar. Pollut. Bull. 154, 111071.
Maurer, D., 2000. The dark side of the taxonomic sufficiency (TS). Mar. Pollut. Bull. 40, 98–101.
Middelburg, J.J., Soetaert, K., Herman, P.M., 1997. Empirical relationships for use in global diagenetic models. Deep-Sea Res. Part I Oceanogr. Res. Pap. 44, 327–344.
Moens, T., Vincx, M., 1997. Observations on the feeding ecology of estuarine nematodes. J. Mar. Biol. Assoc. 77 (1), 211–227.
Moline, M.A., Claustre, H., Frazer, T.K., Schofield, O., Vernet, M., 2004. Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend. Glob. Change Biol. 10 (12), 1973–1980.
Moreno, M., Ferrero, T.J., Gallizia, I., Vezzulli, L., Albertelli, G., Fabiano, M., 2008. An assessment of the spatial heterogeneity of environmental disturbance within an enclosed harbor through the analysis of meiofauna and nematode assemblages. Estuar. Coast Shelf Sci. 77, 565–576.
Nascimento, F.J.A., Karlson, A.M.L., Näslund, J., Elmgren, R., 2011. Diversity of larger consumers enhances interference competition effects on smaller competitors. Oecologia 166, 337–347.
Nascimento, F.J.A., Näslund, J., Elmgren, R., 2012. Meiofauna enhances organic matter mineralization in soft sediment ecosystems. Limnol. Oceanogr. 57 (1), 338–346.
Ngo, X.Q., Smol, N., Cah, V.A., 2013. The meiofauna distribution in correlation with environmental characteristics in 5 Mekong estuaries. Vietnam. Cah. Biol. Mar. 54, 71–83.
Passchier, S., O'Brien, P., Damuth, J., Januszczak, N., Handwerger, D., Whitehead, J.M., 2003. Pliocene–pleistocene glaciomarine sedimentation in eastern Prydz bay and development of the Prydz trough-mouth fan, ODP sites 1166 and 1167, east Antarctica. Mar. Geol. 199 (3–4), 279–305.
Pfannkuche, O., Thiel, H., 1988. Sample processing. In: Higgins, R.P., Thiel, H.n((Eds.), Introduction to the Study of Meiofauna. Smithsonian Institute Press, pp. 134–145.
Piló, D., Ben-Hamadou, R., Pereira, F., Carriço, A., Pereira, P., Corzo, A., Gaspar, M.B., Carvalho, S., 2016. How functional traits of estuarine macrobenthic assemblages respond to metal contamination? Ecol. Indicat. 71, 645–659.
Platt, H.M., Warwick, R.M., 1983. Free living marine nematodes. In: Part I. British Enoplids. Synopses of the British Fauna No 28. Cambridge University Press.
Platt, H.M., Warwick, R.M., 1988. Free living marine nematodes. In: Part II. British Chromadorids. Synopses of the British Fauna No 38. E.J Brill. Dr. W. Backhuys for the Linnean Society of London and the Estuarine and Brackish-water Sciences Association.
Pusceddu, A., Gambi, C., Corinaldesi, C., Scopa, M., Danovaro, R., 2014. Relationships between meiofaunal biodiversity and prokaryotic heterotrophic production in different tropical habitats and oceanic regions. PLoS One 9, e91056.
Radwell, A.J., Brown, A.V., 2008. Benthic meiofauna assemblage structure of headwater streams: density and distribution of taxa relative to substrate size. Aquat. Ecol. 42, 405–414.
Raes, M., Rose, A., Vanreusel, A., 2010. Response of nematode communities after largescale ice-shelf collapse events in the Antarctic Larsen area. Glob. Change Biol. 16, 1618–1631.
Rose, A., Ingels, J., Raes, M., Vanreusel, A., Arbizu, P.M., 2015. Long-term iceshelfcovered meiobenthic communities of the Antarctic continental shelf resemble those of the deep sea. Mar. Biodivers. 45, 743–762.
Schmid-Araya, J.M., Schmid, P.E., Tod, S.P., Esteban, G.F., 2016. Trophic positioning of meiofauna revealed by stable isotopes and food web analyses. Ecology 97, 3099–3109.
Schratzberger, M., Ingels, J., 2018. Meiofauna matters: the roles of meiofauna in benthic ecosystems. J. Exp. Mar. Biol. Ecol. 502, 12–25.
Schratzberger, M., Somerfield, P.J., 2020. Effects of widespread human disturbances in the marine environment suggest a new agenda for meiofauna research is needed. Sci. Total Environ. 728, 138435.
Schratzberger, M., Warr, K., Rogers, S.I., 2007. Functional diversity of nematode communities in the southwestern North Sea. Mar. Environ. Res. 63, 368–389.
Seinhorst, J.W., 1959. A rapid method for the transfer of nematodes from fixative to anhydrous glycerine. Nematologica 4, 67–69.
Semprucci, F., Cesaroni, L., Guidi, L., Balsamo, M., 2018. Do the morphological and functional traits of free-living marine nematodes mirror taxonomical diversity? Mar. Environ. Res. 135, 114–122.
Singh, R., Ingole, B.S., 2016. Structure and function of nematode communities across the Indian western continental margin and its oxygen minimum zone. Biogeosciences 13, 191–209.
Smith, N., Tréguer, P., 1994. Physical and chemical oceanography in the vicinity of Prydz Bay, Antarctica. In: Southern Ocean Ecology: the BIOMASS Perspective, pp. 25–45.
Smith, N.R., Zhaoqian, D., Kerry, K.R., Wright, S., 1984. Water masses and circulation in the region of Prydz Bay, Antarctica. Deep-Sea Res. I: Oceanogr. Res. Pap. 31 (9), 1121–1147.
Soetaert, K., Muthumbi, A., Heip, C., 2002. Size and shape of ocean margin nematodes: morphological diversity and depth-related patterns. Mar. Ecol. Prog. Ser. 242, 179–193.
Stark, J.S., Mohammad, M., Mcminn, A., Ingels, J., 2020. Diversity, abundance, spatial variation, and human impacts in marine meiobenthic nematode and copepod communities at Casey station, east Antarctica. Front. Mar. Sci. 7, 480.
Taylor, F., McMinn, A., Franklin, D., 1997. Distribution of diatoms in surface sediments of Prydz Bay, Antarctica. Mar. Micropaleontol. 32 (3–4), 209–229.
Ter Braak, C.J., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67, 1167–1179.
Thistle, D., 2003. The deep-sea floor: anoverview. Ecosystems of the deep oceans 5.
Thistle, D., Lambshead, P.J.D., Sherman, K.M., 1995. Nematode tail-shape groups respond to environmental differences in the deep sea. Vie Milieu 45, 107–115.
Thistle, D., Sherman, K.M., 1985. The nematode fauna of a deep-sea site exposed to strong near-bottom currents. Deep-Sea Res. Part I Oceanogr. Res. Pap. 32, 1077–1088.
Tietjen, J.H., 1992. Abundance and biomass of metazoan meiobenthos in the deep sea. In: Rowe, G.T., Pariente, V. (Eds.), Deep-sea Food Chains and the Global Carbon Cycle. Kluwer Academic Publishers, pp. 45–62.
Tita, G., Desrosiers, G., Vincx, M., Nozais, C., 2000. Predation and sediment disturbance effects of the intertidal polychaete *Nereis virens* (Sars) on associated meiofaunal assemblages. J. Exp. Mar. Biol. Ecol. 243 (2), 261–282.
Vanaverbeke, J., Soetaert, K., Vincx, M., 2004a. Changes in morphometric characteristics of nematode communities during a spring phytoplankton bloom deposition. Mar. Ecol. Prog. Ser. 273, 139–146.
Vanaverbeke, J., Steyaert, M., Soetaert, K., Rousseau, V., Van Gansbeke, D., Parent, J.Y., Vincx, M., 2004b. Changes in structural and functional diversity of nematode communities during a spring phytoplankton bloom in the southern North Sea. J. Sea Res. 52 (4), 281–292.
Vanaverbeke, J., Steyaert, M., Vanreusel, A., Vincx, M., 2003. Nematode biomass spectra as descriptors of functional changes to human and natural impact. Mar. Ecol. Prog. Ser. 249, 17–157.
Vanhove, S., Beghyn, M., Van Gansbeke, Bullough, L.W., Vincx, M., 2000. A seasonally varying biotope at Signy Island, Antarctic: implications for meiofaunal structure. Mar. Ecol. Prog. Ser. 202, 13–25.
Vanhove, S., Vermeeren, H., Vanreusel, A., 2004. Meiofauna towards the South Sandwich trench (750-6300m), focus on nematodes. Deep-Sea Res. Part II 51, 1665–1687.
Vanhove, S., Wittoeck, J., Desmet, G., Van den Berghe, B., Herman, R.L., Bak, R.P.M., Nieuwland, G., Vosjan, J.H., Boldrin, A., Rabitti, S., Vincx, M., 1995. Deep-sea meiofauna communities in Antarctica: structural analysis and relation with the environment. Mar. Ecol. Prog. Ser. 127, 65–76.
Vaz, R.A.N., Lennon, G.W., 1996. Physical oceanography of the Prydz bay region of antarctic waters. Deep-Sea Res. Part I Oceanogr. Res. Pap. 43, 603–641.
Veit-Köhler, G., Durst, S., Schuckenbrock, J., Hauquier, F., Suja, L.D., Dorschel, B., Vanreusel, A., Arbizu, P.M., 2018. Oceanographic and topographic conditions structure benthic meiofauna communities in the Weddell Sea, Bransfield strait and Drake passage (Antarctic). Prog. Oceanogr. 162, 240–256.
Veit-Köhler, G., Guilini, K., Peeken, I., Sachs, O., Sauter, E.J., Würzberg, L., 2011. Antarctic deep-sea meiofauna and bacteria react to the deposition of particulate organic matter after a phytoplankton bloom. Deep-Sea Res. Part II. 58, 1983–1995.
Venekey, V., Gheller, P.F., Kandratavicius, N., Cunha, B.P., Vilas-Boas, A.C., Fonseca, G., Maria, T.F., 2019. The state of the art of Chromadoridae (Nematoda, Chromadorida): a historical review, diagnoses and comments about valid and dubious genera and a list of valid species. Zootaxa 4578 (1), 1–67.
Vijay, A., Bijoy Nandan, S., Krishnan, K.P., 2017. Functional trait analysis of meiobenthic nematodes in the Arctic Kongsfjord. J. Aquat. Biol. Fish 5, 65–78.
Warwick, R.M., Platt, H.M., Somerfield, P.J., 1998. Free-living marine nematodes. In: Part III. British Monohysterids. Synopsis of British Fauna (New Series) No. 53. Field Studies Council.
Warwick, R.M., Price, R., 1979. Ecological and metabolic studies on freeliving marine nematodes from an estuarine mud-flat. Estuar. Coast Shelf Sci. 9, 257–271.
Wenzhöfer, F., Glud, R.N., 2002. Benthic carbon mineralization in the Atlantic: a synthesis based on in situ data from the last decade. Deep-Sea Res. I: Oceanogr. 49 (7), 1255–1279.
Wieser, W., 1953. Die BeziehungzwischenMundhöhlengestalt, Ernährungswiese und 1000 Vorkommenbeifreilebendenmarinen Nematoden. Ark. fürZool. 4, 439–484.
Włodarska-Kowalczuk, M., Mazurkiewicz, M., Górska, B., Michel, L.N., Jankowska, E., Zaborska, A., 2019. Organic carbon origin, benthic faunal consumption, and burial in sediments of Northern Atlantic and Arctic Fjords (60–81 N). J. Geophys. Res. Biogeosci. 124 (12), 3737–3751.
Wouters, J.M., Gusmao, J.B., Mattos, G., Lana, P., 2018. Polychaete functional diversity in shallow habitats: shelter from the storm. J. Sea Res. 135, 18–30.
Xiaoshou, L., Xiaoxiao, W., Lu, W., Zhinan, Z., 2020. A preliminary study of intertidal meiofauna in Fildes Peninsula, Antarctica. Chin. J. Polar Reas. 32, 281–289.

Zeppilli, D., Bongiorni, L., Cattaneo, A., Danovaro, R., Serrão Santos, R., 2013. Meiofauna assemblages of the condor seamount (north east Atlantic ocean) and adjacent deep-sea sediments. Deep Sea Res. Part II 98, 87–100.
Zeppilli, D., Sarrazin, J., Leduc, D., Arbizu, P.M., Fontaneto, D., Fontanier, C., Gooday, A. J., Kristensen, R.M., Ivanenko, V.N., Sørensen, M.V., Vanreusel, A., 2015. Is the meiofauna a good indicator for climate change and anthropogenic impacts? Mar. Biodivers. 45 (3), 505–535.
Zhang, H., Han, Z., Zhao, J., Yu, P., Hu, C., Sun, W., Yang, D., Zhu, G., Lu, B., Peter, H.U., Vetter, W., 2014. Phytoplankton and chlorophyll a relationships with ENSO in Prydz bay, east Antarctica. Sci. China Earth Sci. 57, 3073–3083.