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RESEARCH

Effects of an Adélie penguin colony on coastal meiofaunal assemblages of the Ross Sea (Antarctica)

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Abstract

Factors shaping biodiversity and functioning of coastal ecosystems in Antarctica are still largely unknown due to the overlap of multiple physical and bio-ecological forcings. Here, we investigated three coastal areas of the Ross Sea (Antarctica) across a coast-offshore transect (25–140 m depth), including an area located in front of the longest-dwelling penguin colony of the Adélie Cove Bay and other two areas, Camp Icarus Bay and Rod Bay, far from the penguin colony. The deposition of the penguin guano determined an extraordinary accumulation of organic matter in coastal sediments (6.9 ± 0.6 mgC g^{-1}), among the highest values reported worldwide so far, which cause apparent detrimental effects on meiofaunal biodiversity, in terms of richness of taxa and nematode species. Meiofaunal abundance showed a wide spatial variability among bays and depths (range: 252 ± 103 to 5961 ± 659 ind. 10 cm^{-2}) with lower abundance and biomass at shallow stations. Here, we found a limited food availability possibly associated with the occurrence of the ice-scouring along the coast. Overall, 17 meiofaunal higher taxa were identified and the richness of taxa reached the highest values at 140 m depth in all the three bays investigated. Nematodes were characterized by a high diversity with 100 species identified. A relevant number of exclusive nematode species was observed in each bay and only 16 species were common at all sampling areas. The huge variability of biodiversity among the investigated areas was apparently related to a combination of biological (food availability and trophic interactions) and physical (ice-scouring) factors generating a mosaic of different assemblages. The combination of these factors determined a high turnover (beta) diversity (up to 100% of turnover for meiofaunal rare taxa and 81% for nematode species), which is likely a key driver for the high regional biodiversity observed in the coastal Antarctic sediments.

Keywords Meiofauna · Biodiversity · Rare taxa · Nematode species · Ross Sea

Introduction

Coastal Antarctic ecosystems show a very high variability due to several over-imposing factors that make it very difficult to predict the patterns of local biodiversity and even enucleate the main drivers shaping community structure (Almond et al. 2021). Habitat complexity and substrate heterogeneity are extremely high in Antarctica and are characterized by relevant spatial variability across different depths and areas/bays (Convey and Peck 2019). It has long been recognized that ice is an important factor influencing the structure and functions of coastal communities both for the physical effects and the role played in regulating biological rhythms and food availability (Peck 2018).

The occurrence of iceberg scouring is increasing rapidly due to the reduction of winter fast ice in the shallow seafloor experiencing warming (Smale et al. 2008; Robinson et al.

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2021). Typically, ice scours are limited to ca. 500 m depth and are identified among the key factors driving the biodiversity patterns of the Antarctic seafloor (Barnes and Tarling 2017; Robinson et al. 2021). However, dramatic changes in the abundance and diversity of fauna due to seafloor erosion caused by ice scouring have been documented at depths of less than 30 m (Lee et al. 2001; Brown et al. 2004; Barnes and Souster 2011; Pasotti et al. 2015).

Current theory argues that most Antarctic taxa are constrained by food limitation (Michel et al. 2019). Food supply in Antarctic sediments changes seasonally and can sustain an abundant benthic community in bloom periods (Smith et al. 2006; Veit-Koehler et al. 2011). The quantity and quality of phytodetritus deposition to the marine sediments may fuel the benthic biota and largely define their success in terms of abundance and biodiversity, which can reach values like those reported in highly productive coastal areas (Arrigo et al. 2008; Glover et al. 2008; Fonseca et al. 2017). Seabirds and especially penguins, whose colonies range from hundreds to thousands of individuals (Espejo et al. 2017), can provide a relevant input of organic nutrients through their guano deposition on to the sediments (Bokhorst et al. 2019; Wang et al. 2020; De La Peña-Lastra 2021; Almela et al. 2022). The presence of guano provides a fertilizing effect in the coastal waters not only for its high content of nutrients (Shatova et al. 2016), but also for its high content of iron, but also for Penguins, in fact, they are also considered a relevant vector in iron cycling since their guano is seen as a significant contributor to the iron requirements of primary productivity in the Southern Ocean (Belyaev et al. 2023; García-Veira et al. 2024). In the Ross Sea region, several colonies of Adélie penguins (*Pygoscelis adeliae*) have been documented as permanent members of the Antarctic fauna (Emslie et al. 2021), and their guano determines the accumulation of organic matter at levels higher than in highly marine productive areas worldwide (Bueno et al. 2018).

Meiofaunal assemblages show a wide spatial variability in coastal Antarctic sediments and their assemblage composition and diversity are still poorly understood (Danovaro et al. 1999; Vanhove et al. 2000; Petti et al. 2006; Pasotti et al. 2014). Available information indicates that meiofaunal taxa are very sensitive to the high variability of food inputs and environmental conditions (Vanhove et al. 1998; Skowronski and Corbisier 2002; Pasotti et al. 2012) and can recolonize benthic habitats rapidly after the occurrence of a disturbance (Lee et al. 2001; Rose et al. 2015).

The Adélie Cove Bay hosts one of the largest permanent colonies of *Pygoscelis adeliae* in the Ross Sea (Harris et al. 2015) and no studies have been conducted yet to investigate the response of the benthic fauna to the organic enrichment associated with the guano deposition along a coast-to-offshore transect up to 140 m depth. In the present study, we tested the effects of the presence of the penguin colony and related guano deposition on meiofaunal assemblages in Adélie Cove Bay. Two additional bays with no visible penguin rookeries, Camp Icarus Bay and Rod Bay, were used as controls. In particular, we analyzed meiofaunal abundance, biomass, alpha diversity (at both the taxon and nematode species levels) and beta (turnover) diversity, as well as their potential drivers (i.e., sedimentary grain size, depth, concentration, availability, and quality of organic matter).

The results obtained here will contribute to expanding our understanding of Antarctic benthic biodiversity patterns, identifying and offering cues to investigate understudied drivers (e.g., ice scouring).

Materials and methods

Study area and sampling strategy

In the austral summer of 2015, during the 30th Antarctic Expedition of the Italian Research Program (PNRA), sediment samples were collected in Terra Nova Bay (Ross Sea; Fig. 1). Sampling activities were carried out using the M/V "Malippo," and sediment samples were collected through a Van Veen grab (surface ca 0.2 m^2) in three bays: Adélie Cove (which hosts a permanent and large penguin colony, hereafter defined AC), Camp Icarus Bay (hereafter defined CI), and Rod Bay (hereafter defined RB). This grab model equipped with two doors on the top size allowed the collection of undisturbed sediments using a plexiglass corer (internal diameter: 3.6 cm) inserted into the central part of the grab. This sampling device was efficiently used in previous Antarctic expeditions (Semprucci et al. 2021; Munari et al. 2022). In each bay, 3 stations were selected at increasing water depth (i.e., 25, 70, and 140 m; Supplementary Table S1) and 3 independent samplings were carried out for each station.

Adélie Cove is a small and V-shaped bay separated from the open sea by a 12- to 15-m deep sill forming a barrier to inflow and outflow (Semprucci et al. 2021), characterized by the presence of the longest dwelling penguin colony (Adélie penguin) of *Pygoscelis adeliae*, one of the two penguin species that breed in Antarctica and relatively abundant along these coasts (Olmastroni et al. 2020; Gao et al. 2022). Camp Icarus and Rod Bays are located a few km from Adélie Cove Bay and were not colonized by penguin populations at the time of this study.

From each station, replicated sediment samples were collected using plexiglass corers (internal diameter: 3.6 cm) to analyze meiofaunal abundance, biomass, and diversity. Overall, 27 sediment cores were collected (9 corers for each bay, three corers for each depth) and were preserved at − 20 °C until all analyses were performed in the laboratory. In the same Antarctic expedition, additional 27 sediment

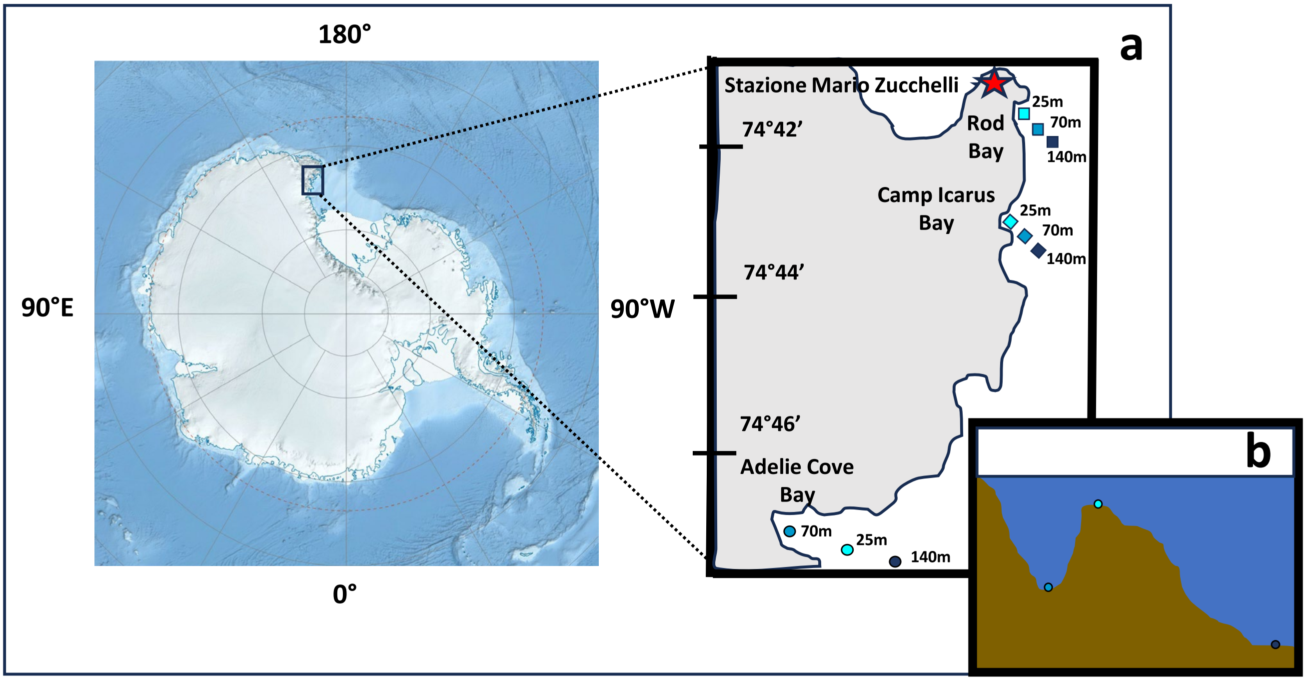

Fig. 1 Location of the sampling stations in the Ross Sea. Reported are **a** the bathymetric transect investigated in Adélie Cove Bay, Camp Icarus Bay, and Rod Bay, respectively, and **b** the details of the bathymetric profile of the coast-offshore transect in front of the Adélie Cove Bay

samples were collected to analyze sedimentary grain size, the biochemical composition of the organic matter (protein, carbohydrate, and lipid concentrations) and total phytopigments concentration. These data, including biopolymeric C concentrations (i.e., used as a proxy of trophic status; sensu Pusceddu et al. 2009), were published previously by Munari et al. (2022) and summarized in Supplemental Table S1. In the present study, we also calculated the ratio between protein and carbohydrate (PRT/CHO) concentrations to define the organic matter quality according to Danovaro (2010).

Meiofaunal abundance, biomass, and diversity

For meiofaunal analyses, each sediment sample was treated with ultrasound (for 1 min 3 times, with 30-s intervals) to detach organisms from the grain particle surface and then, sieved through a 500-µm and a 20-µm mesh net to retain the smallest organisms. The fraction remaining on the latter sieve was re-suspended and centrifuged three times with Ludox HS40 diluted with water to a final density of 1.18 gcm^{-3} (Danovaro 2010). All specimens from three independent replicates per station were counted and sorted by taxa, under a stereomicroscope and after staining with Rose Bengal (0.5 gL^{-1}) and stored in ethanol at 70%. Meiofaunal taxa representing $< 1\%$ of the total abundance were defined as rare taxa (Bianchelli et al. 2010). Meiofaunal biomass was assessed by bio-volumetric measurements of all retrieved specimens. Nematode biomass was calculated from their bio-volume, using the formula: $V = L \times W^2 \times 0.063 \times 10^{-5}$, in which body length, L, and width, W, are expressed in µm. Body volumes of all other taxa were derived from measurements of body length (L, in mm) and width (W, in mm), using the formula $V = L \times W^2 \times C$, where C is a dimensionless factor (specific for each meiofaunal taxon) used to convert $L \times W^2$ to body volume, according to models relating body dimensions and volume (Feller and Warwick 1988). Each body volume was multiplied by an average density of 1.13 gcm^{-3} to obtain the biomass (µg dry weight: µg wet weight = 0.25; Danovaro 2010) with carbon content 40% of the dry weight (Feller and Warwick 1988). We estimated the richness of meiofaunal taxa as the sum of taxa encountered in the three replicated sediment samples for each station.

Nematode diversity

One hundred specimens (or all the retrieved nematodes if < 100 per sample) were randomly picked up from the three replicates per station and were mounted on permanent slides using the formalin-ethanol-glycerol technique. Nematodes were identified to the species level or morphotypes (sensu De Mesel et al. 2006) according to Platt and Warwick (1983, 1988), Warwick et al. (1998), and the NeMys database (Nemys 2024). To standardize nematode diversity, the expected species number [ES(X)] (Hurlbert 1971) for a theoretical sample of 51 specimens, ES (51), was selected according to previous investigations (Gambi et al. 2014; Gambi and Danovaro 2016). Species evenness was measured using Pielou's index (J, Pielou 1975). We also estimated the number of exclusive species of nematodes as the number of species exclusively encountered in each bay and station. Each nematode species was assigned to one of the following 4 trophic groups, based on the buccal morphology: (1A) selective (bacterial) feeders: No buccal cavity or a fine tubular one; (1B) non-selective deposit feeders: Large but unarmed buccal cavity; (2A) epistrate or epi-growth (diatom) feeders: Buccal cavity with scraping teeth; and (2B) predators/omnivores: Buccal cavity with large jaws. The nematode life strategy was estimated as the Maturity Index (MI), calculated according to the weighted mean of the individual genus scores: $MI = \Sigma\, \nu\, (i)\, f\, (i)$, where ν is the c-p value (colonizers-persisters) of genus i as given in the Appendix of Bongers et al. (1991) and f (i) is the frequency of that genus. The colonizer-persister scale is composed of five classes: 1–5; the colonizers receive a low value (c-p = 1/2), while the persisters are allocated to c-p = 4/5.

Analysis of turnover diversity

SIMPER analyses were performed to assess the turnover (beta) diversity as a percentage of dissimilarity in meiofaunal assemblages' composition and nematode species within each bay among depths and among different bays at the same depth. A ranked matrix of Bray–Curtis similarities, constructed on previously presence/absence transformed data for (i) meiofaunal higher taxa, (ii) meiofaunal rare taxa, and (iii) nematode species assemblages, was used as input for the SIMPER tests (Clarke and Gorley 2015).

Drivers of meiofaunal patterns

To identify the potential drivers (depth, grain size, food availability, and quality) of meiofaunal and nematode variables, non-parametric multivariate multiple regression analyses based on Euclidean distances were carried out, using the routine DistLM, the forward selection procedure and R^2 as the selection criterion (McArdle and Anderson 2001). The forward selection of the predictor variables was carried out with tests by permutation. P values were obtained using 999 permutations of the raw data for the marginal tests (test of individual variables), whereas, for all the conditional tests, the routine used 999 permutations of residuals under a reduced model. To run this test, meiofaunal and nematode variables were used, separately, as dependent variables, whereas grain size, depth, total phytopigments (as a proxy of fresh algal inputs), biopolymeric C (as a proxy of potentially bioavailable fraction of the organic matter), and the ratio between protein and carbohydrate concentrations (PRT/CHO, as a proxy of the quality of the organic matter) were used as potential explanatory variables. The DistLM analyses were performed using the routines included in the PRIMER v7 and PERMANOVA software (Clarke and Gorley 2015; Anderson 2017).

Statistical analyses

Due to the high variability of the environmental and trophic conditions along the bathymetric (and coast to offshore) gradients in the investigated area, we tested for differences in total meiofaunal abundance, biomass, richness of taxa, and community composition (both higher and rare taxa) and nematode diversity (including species and trophic composition) among stations of different bays at similar depth and among stations along the bathymetric gradient within each bay. To do this, we used two-way distance-based permutational analyses of variance (PERMANOVA) based on unrestricted permutations of the raw data. The analyses were carried out using different bays and depths (fixed selected) (3 levels for bay: Adélie Cove Bay, Camp Icarus Bay, and Rod Bay and 3 levels for depth: 25 m, 70 m, and 140 m), respectively, as the main sources of variance. For meiofaunal taxa and nematode species composition, all analyses were carried out on Bray–Curtis similarity matrices of transformed data (as presence/absence), using 999 permutations of the residuals under a reduced model. The same approach described above was carried out for meiofaunal abundance, biomass, and number of taxa and nematode ES(51), J and Maturity Index using Euclidean distance matrices commonly used for faunal variables (Alves et al. 2015). For all analyses, when significant effects of the considered factors were observed, pair-wise tests were also carried out, to ascertain where (bay and depth) the significant differences were observed. Because of the restricted number of unique permutations in the pair-wise tests, *p* values were obtained from Monte Carlo samplings (Anderson and Robinson 2003). Meiofaunal taxa and nematode species composition in different bays and depths were also used as inputs for the shade plots to visualize the spatial distribution of each taxon and species. The PERMANOVA analyses and Shadow plots were performed using the routines included in the PRIMER v7 and PERMANOVA software (Clarke and Gorley 2015; Anderson 2017).

Results

Grain size and food availability

Data on grain size and sedimentary biochemical composition of organic matter previously published by Munari et al. (2022) are summarized in Supplemental Table S1. Briefly, sediment grain size was dominated by sand (> 81%) in all sampling stations, except at 70 m depth in Rod Bay where the gravel fraction accounted for 56%. The highest concentrations of total phytopigments (126.9 ± 23.9 μg g^{-1}) and biopolymeric C (6.9 ± 0.6 mgC g^{-1}) were observed in the closest station to the coast facing the Adélie Cove Bay (at 70 m depth). When examining the coast-to-offshore transects of Camp Icarus Bay and Rod Bay, both total phytopigment and biopolymeric C concentrations were highest at the deepest stations (140 m depth). Conversely, the highest protein-to-carbohydrate ratio (3.0) was observed at the depth of 25 m facing Rod Bay. Protein-to-carbohydrate ratio values decreased along the coast-offshore transects in Adélie Cove Bay and Rod Bay while the ratio increased with the increasing depth in Camp Icarus Bay.

Meiofaunal abundance, biomass, and diversity

Meiofaunal abundance ranged from 252 ± 103 (at 25 m in the Adélie Cove Bay) to 5961 ± 659 ind. 10 cm^{-2} (at 140 m depth in Camp Icarus Bay) and showed a wide variability among sampling areas and depths (Fig. 2a). Typically, meiofaunal abundance was significantly higher at 70 and 140 m depths than at shallower depths (25 m; Table S2) in all three bays. Meiofaunal biomass ranged from 51 ± 28 (at 25 m in Adélie Cove Bay) to 2003 ± 467 μgC 10 cm^{-2} (at 140 m in Camp Icarus Bay) and showed the same spatial pattern reported for abundance (Fig. 2b; Table S2).

Overall, 17 taxa were identified: Nematodes, copepods, acaridans, amphipods, bivalves, cladocerans, gastropods, isopods, larvae of crustaceans, loriciferans, oligochaetes, ostracods, polychaetes, priapulids, sipunculids, tanaidaceans, and gastrotrichs. The richness of meiofaunal higher taxa in each sampling station (as the sum of the overall number of taxa of three replicates) ranged from 4 to 12 groups with the highest values at 140 m depth in all investigated bays (Fig. 2c; Table S2).

Nematodes were the dominant taxon (accounting for 92–100% of total meiofaunal abundance) at all sampling stations, followed by copepods (including their nauplii 0–7%) and ostracods (0–1%) (Fig. 3a). All other taxa were rare since they accounted for < 1% of the total meiofaunal abundance (Fig. 3b). The shade plots allow us to show the different spatial patterns of each taxon in the three bays at 25, 70 and 140 m depths (Fig S1a, b).

The composition of meiofaunal assemblages both at higher and rare taxa varied significantly among depths and different bays (Table S2).

The turnover diversity, expressed as dissimilarity in higher taxa composition ranged from 47 to 53% within Camp Icarus Bay, from 37 to 45% within the Rod Bay and from 29 to 49% within the Adélie Cove Bay, respectively (Table 1). However, the dissimilarity in rare taxa composition was higher than that in higher taxa ranging from 68 to 92% within Camp Icarus Bay, from 61 to 93% within Rod Bay and from 61 to 100% within the Adélie Cove Bay, respectively (Table 1).

Nematode diversity and composition

Overall, 100 putative species of nematodes were identified in the three bays. The results of PERMANOVA analyses revealed that nematode diversity expressed as ES(51) varied significantly among the bays with higher values in Camp Icarus Bay than in Adélie Cove and Rod Bays (Fig. 4a; Table S4). Significant differences occurred also among sampling depths with higher diversity at 140 m depth than at shallower depths. The evenness changed accordingly and varied significantly across depths and bays (Fig S2; Table S3).

Each area showed a relevant number of exclusive species: 20 in Adélie Cove Bay, 22 in Camp Icarus Bay, and 15 in Rod Bay. Among all identified nematode species, only 16 species were common in the three bays, and some of them dominated the nematode assemblage but with different relative importance (Table 2; Fig S3).

The results of PERMANOVA analyses showed that nematode assemblage composition varied significantly among sampling depths and bays and pair-wise tests revealed that nematode species composition changed significantly among bays at all sampling depths (Table S3).

The trophic structure of nematode assemblages is reported in Fig. 4b. The non-selective deposit feeders were the dominant trophic group (46–92% of the nematode assemblages in all bays), whereas the selective deposit feeders accounted for 7–25% increasing at 140 m depth. The epistrate feeders accounted for 7 to 68%, while predators were less abundant and contributed 1–12% to nematode assemblages. The results of PERMANOVA analysis showed a significant interaction between the factors bay and depth on the nematode trophic structure (Table S4). Pair-wise tests revealed significant differences in trophic composition among Adélie Cove Bay, Camp Icarus Bay, and Rod Bay and the three sampling depths indicating that differences in nematode trophic composition between bays depended on depth and differences between depths depended on bay.

The SIMPER analysis showed a high nematode turnover diversity among bays and sampling depths (56–81%; Table 1) with high values at all sampling depths and slightly higher values in Adélie Cove Bay (60–81%).

The Maturity Index varied significantly among sampling depths and bays with the highest values at 140 m depth and in Camp Icarus Bay (Fig. 4c, Table S3). The lowest Maturity Index of nematode assemblages was observed at 70 m depth in Adélie Cove Bay.

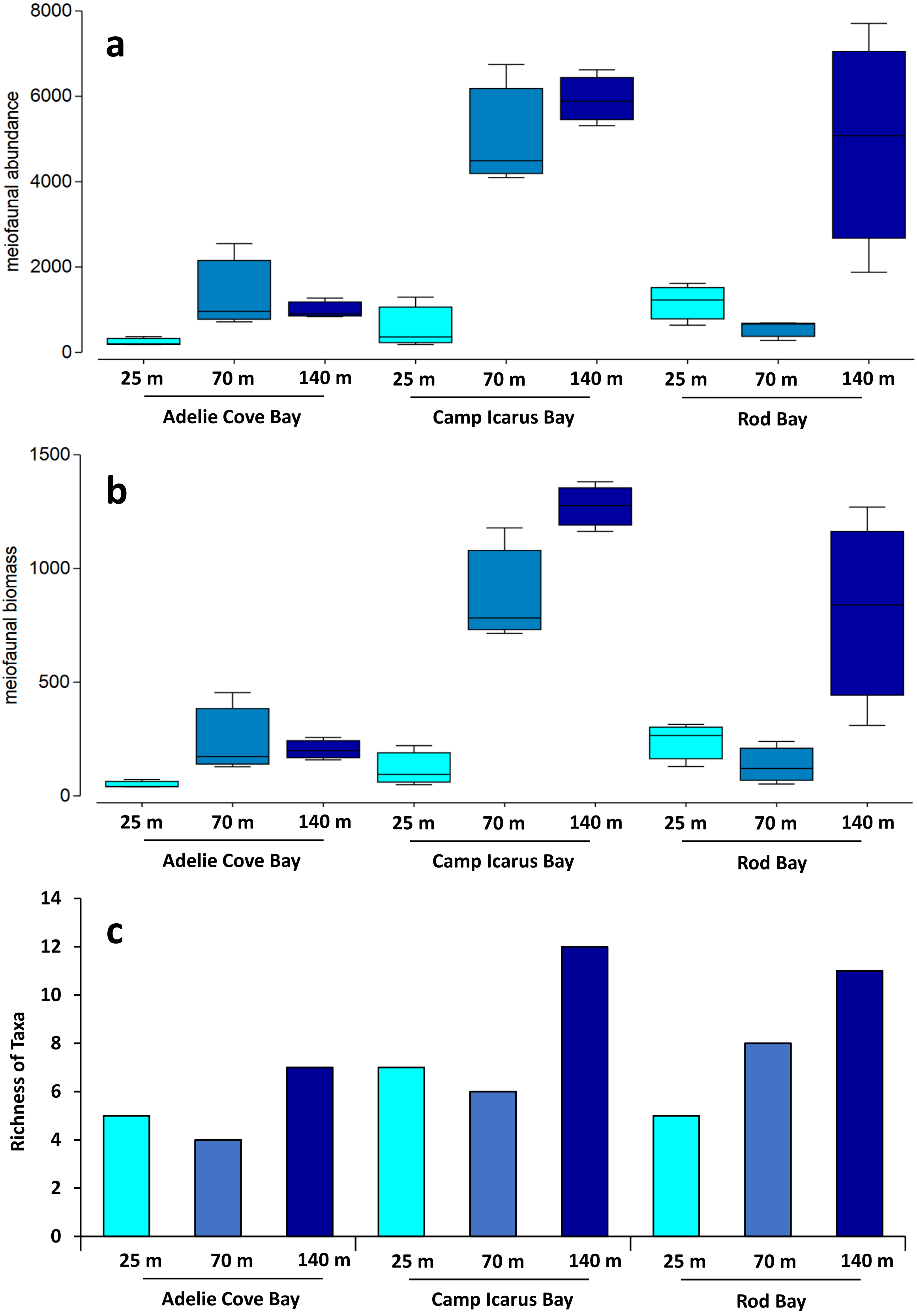

Fig. 2 Spatial distribution of meiofaunal assemblages in the three investigated bays of the Ross Sea. Reported are **a** abundance, **b** biomass, and **c** diversity (as richness of higher taxa) at 25 m, 70 m, and 140 m in Adélie Cove Bay, Camp Icarus Bay, and Rod Bay

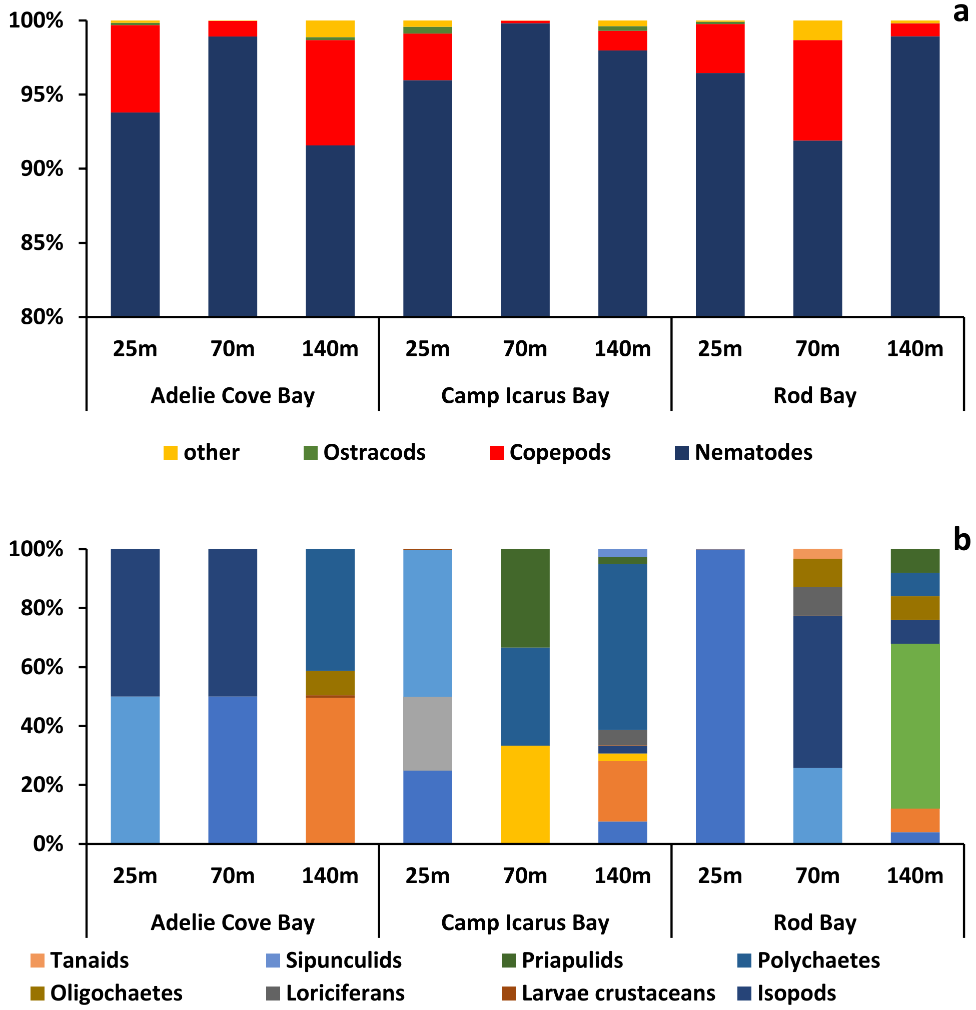

Fig. 3 Meiofaunal composition in the three investigated bays of the Ross Sea. Reported are **a** the most abundant taxa and **b** rare taxa (< 1%) at 25 m, 70 m, and 140 m in Adélie Cove Bay, Camp Icarus Bay, and Rod Bay

Drivers of meiofaunal assemblages

The results of the DistLM analyses are reported in Table 3. The analyses revealed that depth influenced the spatial distribution of meiofaunal abundance (31%), biomass (33%), and diversity (as richness of taxa (34%), taxa composition (17%), nematode diversity (44%), and species composition (21%)). Biopolymeric C mainly explained the spatial variability of meiofaunal biomass (13%), nematode diversity (as ES(51) (17%)) and Maturity Index (31%). Total phytopigments mainly accounted for 36% of the total variance of nematodes evenness. Grain size composition explained only the spatial distribution of nematode species composition (12%).

Discussion

Effects of the penguin colony on meiofauna

Coastal Antarctic areas are subjected to a strong seasonality and the combined effects of physical disturbance and biological interactions (Convey and Peck 2019; Braeckman et al. 2021). Here, due to the lack of rivers, terrestrial inputs of nutrients are extremely limited (McMinn et al. 1995), however, penguin colonies, such as in Adélie Cove Bay, can represent a major source of nutrients and provide a strong organic enrichment of marine sediments. In our study, this was evident as we found a huge accumulation of organic matter (up to ca. 7 mg g^{-1} of biopolymeric C) in Adélie Cove Bay at 70 m depth, a site of enhanced and focused bio-deposition also due to the particular "U" shape of the sea bottom (Fig. 1 for details). Such an organic accumulation in the sediments in front of the penguin colonies determined hyper-eutrophic conditions with the highest values of biopolymeric C ever reported for coastal areas (Pusceddu et al. 2009). Also, the other bays investigated (e.g., Camp Icarus Bay and Rod Bay located 3–5 km north of Adélie Cove Bay) were characterized by very high sediment organic matter concentrations, with a preferential accumulation at 140-m depth, indicating that primary production processes were also important (as evident from the high concentrations of total phytopigments).

Table 1 Turnover diversity carried out on meiofaunal all and rare higher taxa and nematode species composition determined in the three investigated bays of the Ross Sea at different sampling depths. Reported is the percentage of dissimilarity (output of the SIMPER analysis)

			Meiofaunal Composition		
			All taxa	Rare taxa	Nematode Species
25 m			%	%	%
Adélie Cove Bay	vs	Camp Icarus Bay	36	55	60
Adélie Cove Bay	vs	Rod Bay	30	72	57
Rod Bay	vs	Camp Icarus Bay ay	32	49	61
70 m					
Adélie Cove Bay	vs	Camp Icarus Bay	31	100	76
Adélie Cove Bay	vs	Rod Bay	36	95	75
Rod Bay	vs	Camp Icarus Bay	39	91	63
140 m					
Adélie Cove Bay	vs	Camp Icarus Bay ay	39	59	63
Adélie Cove Bay	vs	Rod Bay	32	50	63
Rod Bay	vs	Camp Icarus Bay	35	52	64
Adélie Cove Bay					
25 m	vs	70 m	29	93	60
25 m	vs	140 m	38	71	81
70 m	vs	140 m	49	100	71
Camp Icarus Bay					
25 m	vs	70 m	53	92	59
25 m	vs	140 m	50	68	70
70 m	vs	140 m	47	76	56
Rod Bay					
25 m	vs	70 m	37	93	59
25 m	vs	140 m	37	61	71
70 m	vs	140 m	45	75	73

Likely due to the large food availability, meiofaunal abundance, biomass, and diversity were high, especially offshore Camp Icarus Bay and Rod Bay, although they exhibited different spatial patterns along the bathymetric gradients. In Adélie Cove Bay, meiofaunal abundance and biomass were characterized by the highest values at 70 m depth where the greatest organic enrichment due to the bio-deposition from the penguin colony and from primary production processes, was also observed. However, in the deepest stations of the two bays used as control, meiofaunal abundance and biomass were generally even higher than in Adélie Cove Bay, except for the Rod Bay station at depth of 70 m (see below). The meiofaunal abundances reported in Rod Bay and Camp Icarus Bay (Fig. 2a) were, indeed, 6–7 times higher than the abundances reported in other previously investigated sites of the Southern Ocean at similar depths (at Prydz Bay on average: 899 ind 10 cm^{-2}, Huang et al. 2022). In particular, the values reported here are among the highest ever reported at high latitudes according to previous studies (Pasotti et al. 2012). These findings suggest that, despite the higher organic matter enrichment observed in Adélie Cove Bay compared to the other bays, the abundance and biomass of meiofauna were lower than expected. This allows us to hypothesize an inhibitory effect due to penguin guano.

However, other environmental factors operating locally at smaller spatial scales (ranging from meters to a few kilometers) may also influence meiofaunal abundance and biomass. In this regard, our study revealed that all coast-offshore transects were characterized by the lowest abundance and biomass at 25-m depth where we could expect the occurrence of the detrimental effect of the ice scouring on meiofaunal assemblages. This disturbance preferentially occurs at shallow depths where signs of seafloor erosion are documented along the coast of Antarctica (Lee et al. 2001; Brown et al. 2004; Barnes and Souster 2011; Pasotti et al. 2015). Based on this literature information, we hypothesized that the severe effects of the ice scouring could be extended up to 70 m depth in Rod Bay where we reported lower meiofaunal abundance and biomass than in the sediments of other bays (at the same depth). The predominance of the gravel fraction only in the grain size composition of this station alone might represent a sign of the disruptive effect of this phenomenon (Condron and Hill 2021).

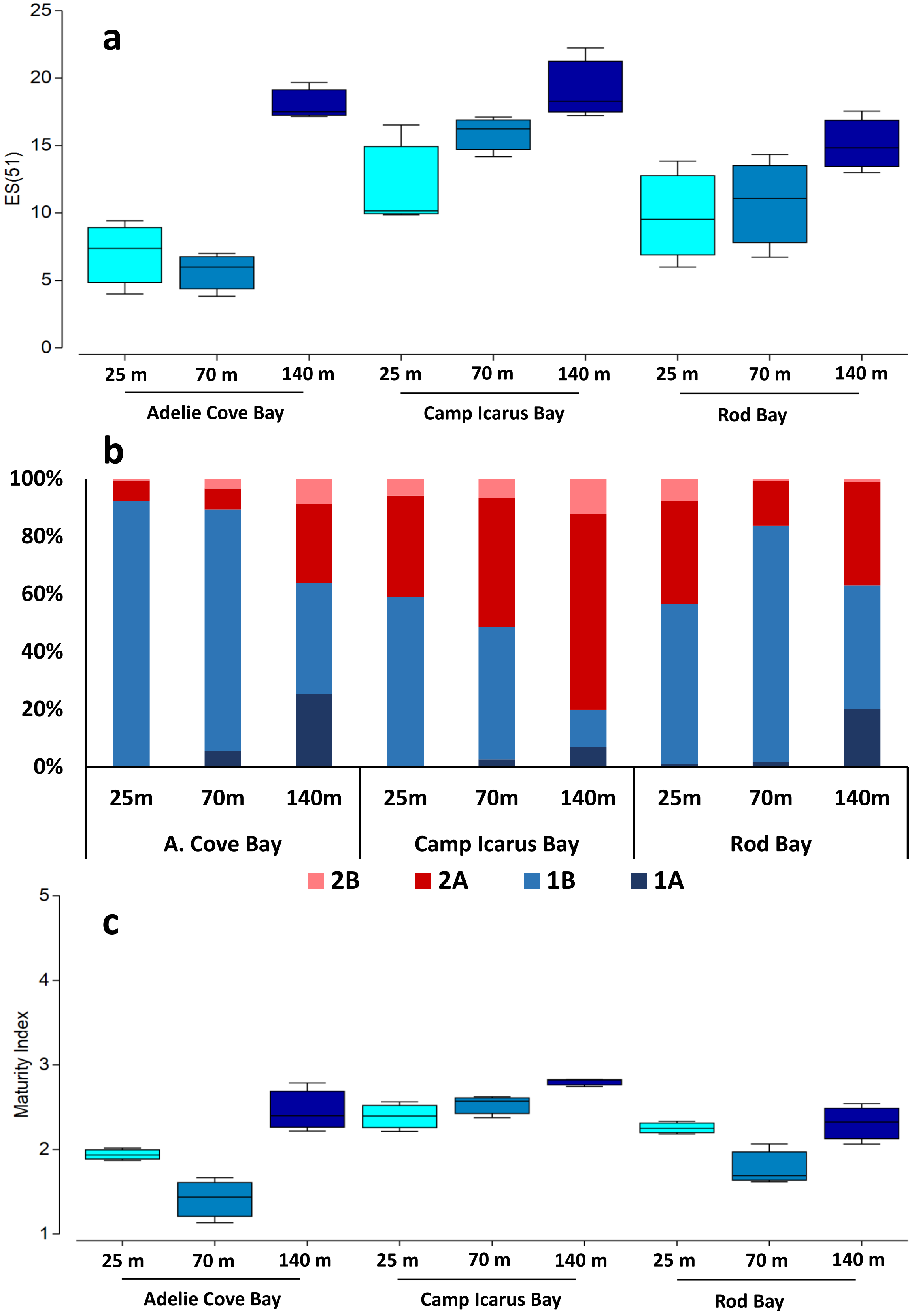

Fig. 4 Spatial distribution of nematode diversity in the three investigated bays of the Ross Sea. Reported are **a** nematode diversity as ES(51), **b** trophic composition and **c** Maturity Index at 25 m, 70 m and 140 m in Adélie Cove Bay, Camp Icarus Bay and Rod Bay

Table 2 Relative importance of the main nematode species in the three investigated bays of the Ross Sea at different sampling depths

	25 m	70 m	140 m
Adélie Cove Bay	*Odontophora sp1*, 45%	*Thalassomonhystera sp11*, 78%	*Marylynnia sp1* and *Paramonohystera sp5*, both 13%
Camp Icarus Bay	*Prochromadorella sp3*, 22%	*Odontophora sp1*, 28%	*Sigmophoronema sp2*, 36%
Rod Bay	*Odontophora sp1*, 36%	*Paramonohystera sp5*, 33%	*Halomonhystera sp 1*, 25%

Meiofaunal diversity (as richness of the higher taxa) was lower in the Adélie Cove sediments enriched with organic matter from the penguin colony than in the sediments of the other bays. Only four taxa (mainly nematodes and copepods, and few specimens of acarians and isopods) were able to live in the hypertrophic conditions observed at 70 m depth. The highest richness of meiofaunal taxa occurred at 140 m depth in all coast-offshore transects as a combined response to the large food availability and a minor destructive effect of the ice-scouring. Nematodes and copepods were the only two higher taxa commonly found in all stations and bays, and they represented 99–100% of the meiofaunal assemblages. The dominance of nematodes, followed by copepods, in all investigated stations, is a common feature of all marine sediments, including the Southern Ocean (Herman and Dahms 1992; Vanhove et al. 2004; Gutzmann et al. 2004; Semprucci et al. 2021; Huang et al. 2022). All other fifteen taxa were rare and exclusive contributing to the high overall diversity encountered in this region. The highest values of the richness of higher taxa and many exclusive taxa, including sipunculids (exclusive of Camp Icarus Bay), priapulids (Camp Icarus and Rod Bay), oligochaetes (Adélie Cove and Rod Bay), and loriciferans (Camp Icarus and Rod Bay) were all observed in the deepest stations (140 m depth). The highest richness of exclusive taxa, including also tanaidaceans and gastrotrichs, was probably associated with a coarser grain size of the sediments and less food availability observed at 25 m and 70 m depth in Rod Bay. The high variability in the number of higher taxa observed in each bay determined a high (turnover) dissimilarity in the taxa composition (up to 100% for rare taxa) and contributed to the high regional diversity in Antarctica.

Table 3 Summary of the conditional tests of the DISTLM analyses performed when meiofaunal and nematode variables showed significant differences among bays and depths

	Variable	F	P	Var%	Cum%
Abundance	Depth	11.4	***	31	31
Biomass	Depth	12.5	***	33	33
	Biopolymeric C	6.0	*	13	46
Richness of taxa	Depth	12.7	***	34	38
	Biopolymeric C	4.2	*	1	39
All taxa composition	Depth	5.2	***	17	17
Rare taxa composition	Depth	2.3	*	8	8
	Total Phytopigments	2.3	*	8	16
ES(51)	Depth	19.4	***	44	44
	Biopolymeric C	10.6	***	17	61
Evenness	Total phytopigments	13.9	***	36	36
	Depth	7.9	*	16	52
Trophic composition	Depth	11.2	***	31	
Species composition	Depth	6.8	***	21	21
	Silt–clay	4.4	***	12	33
	Biopolymeric C	2.6	***	7	40
	Total Phytopigments	2.6	***	6	46
Maturity index	Biopolymeric C	13.6	***	31	31

Explanatory variables are depth, grain size (silt–clay%), total phytopigments, Biopolymeric C, and the P/C ratio. F_F statistic; P = probability level; Var. (%) = percentage of the variance explained by that explanatory variable; Cumul. (%) = cumulative percentage of variance explained by the explanatory variables. Reported are those variables that display a P level: $*p < 0.05$; $***p < 0.001$

Drivers of meiofaunal assemblages

The results of the DistLM analysis (Table 3) indicate that depth plays a key role in driving the spatial distribution of meiofaunal abundance, biomass, and richness of higher taxa. Meiofaunal variables, indeed, showed generally increasing values with increasing depth and distance from the shore. This pattern is a common feature of benthic assemblages in Antarctica (e.g., Huang et al. 2022) and can be related to the impact of ice scouring that determines a major disturbance at shallow depths, whereas typically does not or rarely reach the deepest bottom sediments (Smale et al. 2008; Barnes and Souster 2011). The second main ecological driver of the observed pattern is the amount of organic matter accumulated in the sediments (expressed either as biopolymeric C or total phytopigment concentrations). Overall, the combination of these two factors explained ca. half of the variance of the patterns of meiofaunal abundance, biomass, and assemblage composition (expressed in terms of higher taxa). We can hypothesize that these variables, including other factors related to the habitat features (heterogeneity/topography, water currents) and the biological interactions with other benthic components, can contribute to explain the meiofaunal distribution and shape its biodiversity.

Impact of the penguin colony on nematode diversity and life strategies

Nematode species diversity was generally low at shallow depths (either in the sediments impacted or not by the penguin deposition), consistent with the hypothesized impact of ice-scouring processes on shallow-depth meiofaunal assemblages. At the same time, nematode assemblages were characterized by a high fraction of exclusive species in each sampling area that determined a high turnover in species composition within different bays of the Ross Sea. A high turnover of nematode diversity has been reported also in other coastal Antarctic sediments, reflecting the variability of physical conditions (Hauquier et al. 2011; Semprucci et al. 2021; Kang et al. 2022).

Changes in species composition were reflected by changes in the trophic groups (i.e., feeding traits) and life strategy of the nematode assemblages. The extraordinary dominance of non-selective deposit feeders, able to exploit a wide range of food sources and the organic matter accumulated in the sediments, was a common feature in the investigated bays and elsewhere in Antarctica (Pasotti et al. 2012; Raes et al. 2010) but reached a peak in the sediments of Adélie Cove Bay. These results suggest that the extraordinary deposition of organic matter due to the penguin guano had an impact on the trophic structure of the meiofaunal assemblages.

The analysis of the nematode life strategies revealed the dominance of opportunistic colonizers (r-strategists), especially in the shallowest sediments affected by major environmental and trophic changes. Among them, the opportunistic genera Odontophora and Halomonystera dominated at shallow depths of all sampling bays, probably favored by the frequent and intense seafloor physical disturbance (e.g., ice scouring) and consequent defaunation in the stations closer to the shore (Derycke et al. 2007; Van Gaever et al. 2009; Raes et al. 2010; Alves et al. 2015; Shimada et al. 2021). The hyper-eutrophic sediments at 70 m depth facing the penguin colony were dominated by the opportunistic/pioneer genus *Thalassomonhyster*a, a non-selective deposit feeder able to exploit the large organic deposits (Sebastian et al. 2007; Vanreusel et al. 2010). This genus, belonging to Monhysteridae family, is an opportunistic and efficient colonizer, whose presence, can have a relevant effect on the assemblage's development inhibiting the settlement of other species as documented in the Weddell Sea (Sebastian et al. 2007). The lower levels of physical disturbance in the deepest stations (i.e., 140 m depth) were confirmed by the large presence of K-strategy species, including a relevant fraction of predators (family Enoplidae, genera *Halichoanolaimus*, *Syringolaimus*, and *Subsphaerolaimus*) that suggests the potential of predation in shaping assemblage structure and biodiversity at deeper sediments. This is apparently a common feature of the nematode trophic structure response to physical disturbances in coastal sediments (Gambi et al. 2022).

Conclusion

Overall, our investigation suggests that the three coastal areas of the Ross Sea showed important differences in terms of meiofaunal abundance, biomass, assemblage structure, and biodiversity. The physical disturbance in shallower-depth stations and the large spatial variability of the availability of organic matter contribute to create a mosaic of meiofaunal assemblages that increases the turnover diversity either in terms of higher taxa or of nematode species/genera. Finally, the presence of a high number of rare meiofaunal taxa and exclusive nematode species/genera contributes to increase the overall biodiversity of the Antarctic coastal sediments.

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Author contributions C.C. conceived the study. E.R. conducted the sampling activities. C.G., M.L.M., A.C. performed laboratory analyses. C.G. conducted statistical analyses. C.G., R.D. and C.C. contributed to data elaboration and interpretation. C.G., R.D. and C.C. drafted the first version of the manuscript. All authors contributed to the preparation of final version of the manuscript.

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Data availability All data supporting the findings of this study can be obtained from the corresponding authors on reasonable request (if appropriate).

Declarations

Competing interests The authors declare no competing interests.

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