



A pioneer morphological and genetic study of the intertidal fauna of the Gerlache Strait (Antarctic Peninsula)

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Abstract The underexplored intertidal ecosystems of Antarctica are facing rapid changes in important environmental factors. Associated with temperature increase, reduction in coastal ice will soon expose new ice-free areas that will be colonized by local or distant biota. To enable detection of future changes in faunal composition, a biodiversity baseline is urgently required. Here, we evaluated intertidal faunal diversity at 13 locations around the Gerlache Strait

(western Antarctic Peninsula), using a combination of a quadrat approach, morphological identification and genetic characterization. Our data highlight a community structure comprising four generally distributed and highly abundant species (the flatworm *Obrimoposthia wandeli*, the bivalve *Kidderia subquadrata*, and the gastropods *Laevilitorina umbilicata* and *Laevilitorina caliginosa*) as well as 79 rarer and less widely encountered species. The most abundant species thrive in the intertidal zone due to their ability to either survive overwinter *in situ* or to rapidly colonize this zone when conditions allow. In addition, we confirmed the presence of multiple

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trophic levels at nearly all locations, suggesting that complex inter-specific interactions occur within these communities. Diversity indices contrasted between sampling locations (from 3 to 32 species) and multivariate approaches identified three main groups. This confirms the importance of environmental heterogeneity in shaping diversity patterns within the investigated area. Finally, we provide the first genetic and photographic baseline of the Antarctic intertidal fauna (106 sequences, 137 macrophotographs), as well as preliminary insights on the biogeography of several species. Taken together, these results provide a timely catalyst to assess the diversity and to inform studies of the potential resilience of these intertidal communities.

Keywords Benthic ecology · Community structure · DNA barcoding · Seashore · Southern Ocean

Introduction

The intertidal zone (i.e., seashore or foreshore) in Antarctica is a unique environment at the interface between marine and terrestrial habitats (Waller, 2008). This zone provides a broad range of ecosystem functions and is often considered a harbinger for the effects of climate change and invasive species (Griffiths & Waller, 2016, Thyrring & Peck, 2021). Whereas Antarctic intertidal ecosystems normally experience significant seasonal and shorter-term variation in ice conditions, salinity, and temperature (Peck et al., 2006,

Kuklinski & Balazy, 2014, Clarke & Beaumont, 2020), they are currently facing challenges from drastic changes in multiple environmental factors including sea surface temperature, pH, salinity, and sedimentation rates (Convey & Peck, 2019, Brasier et al., 2021, Figuerola et al., 2021). Associated with increasing temperature, reduction in coastal ice extent and duration will expose extensive new ice-free intertidal areas in the near future, especially in the region of the Antarctic Peninsula (Griffiths & Waller, 2016, Convey & Peck, 2019, Siegert et al., 2019, Hillebrand et al., 2021). These newly available areas have the potential to be colonized by faunal assemblages of local or distant origin (Griffiths et al., 2017, Lagger et al., 2017, Fraser et al., 2018, Galera et al., 2018, López-Farrán et al., 2021). To evaluate and document future changes in faunal composition, a current intertidal biodiversity baseline is urgently needed (Irvine & Shelly, 2013, Griffiths & Waller, 2016).

Relative to most of the world's coastlines, the Antarctic intertidal zone remains underexplored (Schiaparelli et al., 2013, Lee et al., 2017, Convey & Peck, 2019). Antarctic intertidal studies commenced more than a hundred years ago, with the first records of Antarctic intertidal diversity obtained during the Belgica expedition (1897–1899; De Deckker, 2018). Intertidal locations in Antarctica have subsequently been investigated at varying levels of detail, from opportunistic sampling to the generation of detailed inventories (Griffiths & Waller, 2016 and references therein, Aghmich et al., 2016, Chelchowski et al., 2022). Historical studies generally assessed the zone as being depauperate (e.g., Hedgpeth, 1969), but

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this initial view has progressively changed and it is now accepted that some Antarctic continental locations have a level of intertidal diversity comparable to that of the sub-Antarctic (Griffiths & Waller, 2016). In an extensive review of the biodiversity and biogeographical patterns of intertidal organisms in the Southern Ocean, Griffiths & Waller (2016) referenced 3902 occurrences of 1416 intertidal species (<https://doi.org/10.15468/doy-fzk>). However, this inventory remains incomplete compared to those from both adjacent deeper waters and terrestrial habitats (Convey, 2010, Terauds et al., 2012, De Broyer et al., 2014). This review also highlighted an important bias in the geographic areas studied as well as a general lack of standardized and quantitative sampling approaches applied (e.g., Bick & Arlt, 2013, Waller, 2013, Aghmich et al., 2016).

The production of biodiversity inventories and baselines is dependent on accurate biological identification (Tautz et al., 2003, Christiansen et al., 2018). Support from appropriate taxonomic expertise is therefore required to ensure that identification is carried out reliably at the appropriate taxonomic level (Costello et al., 2013, Saucède et al., 2021). Morphological data usually derive primarily from direct observation of living or preserved organisms, but can be complemented with other methods such as macrophotography or scanning electron microscopy (SEM) (Dayrat, 2005). Photographs allow additional observations (e.g., informative characters that could be lost during preservation), without the need to re-examine or handle the specimen. They can also be shared in multiple scientific and outreach initiatives and thus be accessed by the community at large (e.g., World Register of Marine Species (WoRMS) - marinespecies.org, Barcode of Life Data Systems (BOLD) - boldsystems.org, Biodiversity.aq). In addition, molecular markers can be crucial for identification, especially of underexplored taxa or groups (e.g., Nemertea, Platyhelminthes) that are difficult to identify morphologically (e.g., Pante et al., 2015, Christiansen et al., 2018, Peck et al., 2018; Jossart et al., 2021). Molecular characterization can also facilitate the discovery of cryptic species, resolution of synonymies, and highlight intraspecific genetic structure (Hajibabaei et al. 2007, Krishnamurthy & Francis, 2012, Christiansen et al., 2018, Moreau et al., 2021). It is, therefore, unsurprising that achieving a comprehensive genetic data archive is considered a top priority for Antarctic research (Kennicutt et al., 2014, Convey & Peck, 2019).

In the present study, we evaluated intertidal faunal diversity at 13 sampling locations around the Gerlache Strait, western Antarctic Peninsula (Fig. 1). Based on examination of more than 8,000 individual specimens, we combined an *in situ* quadrat approach with morphological and genetic data to characterize the faunal assemblages at each location. Considering the environmental heterogeneity in the area of investigation, we expected the faunal composition to be highly variable between the different locations. Morphological identification was achieved with the support of taxonomic experts while genetic characterization was based on the barcode region of the cytochrome c oxidase I gene (COI). The dataset generated was also used to produce the first genetic and photographic baseline of the Antarctic intertidal fauna, containing 106 sequences and 137 photographs from both living and preserved specimens, while also providing a significant update to existing occurrence databases (672 records, dataset of the associated expedition Belgica121).

Methods

Field studies

Fieldwork was performed during the Belgica121 expedition in February-March 2019 (Danis et al., 2019, 2021, 2022). This expedition, supported by the motor vessel R/V *Australis*, aimed to complete a biodiversity census of shallow coastal (up to 40 m depth) benthic communities around the Gerlache Strait, western Antarctic Peninsula. The Gerlache Strait water masses are characterized by both Bellingshausen Sea (upper layer) and Weddell Sea influences (underlying bottom-reaching layer; Garcia et al., 2002). The tidal regime in the area is mainly semidiurnal, with a maximal tidal range of 2 meters (Dewart, 1972, Dragani et al., 2004). Intertidal communities were investigated at 13 study locations from eight distinct sites (Fig. 1): Melchior Islands (MI), Føyn Harbor (FH), Green Reef (GR), Useful Island (UI), Neko Harbor (NH), Skontorp Cove (SK) and Hovgaard Islands (HI_M1 & HI_M2). Details of each site are presented in Danis et al. (2021). First, each site was explored with a tender to locate suitable intertidal areas for landing and sampling. At low tide, a faunal inventory was made at the mid-shore level at all sites (locations noted as

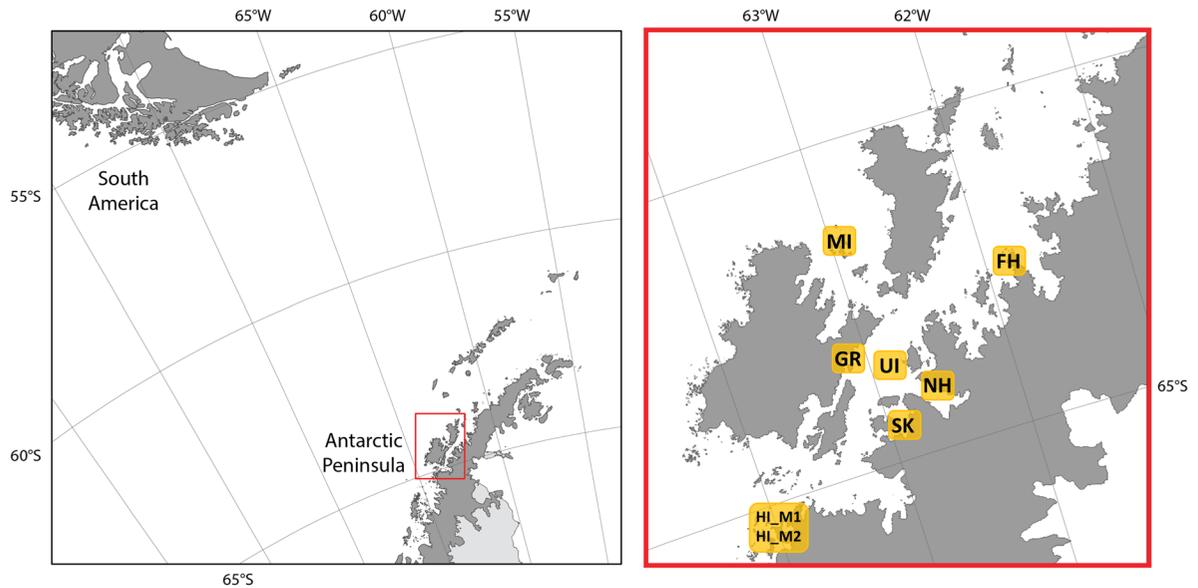


Fig. 1 Intertidal sites in and around the Gerlache Strait (western Antarctic Peninsula) investigated in the current study. MI: Melchior Islands, FH: Føyn Harbor, GR: Green Reef, UI: Use-

ful Island, NH: Neko Harbor, SK: Skontorp Cove, HI_M1: Hovgaard Islands 1, HI_M2: Hovgaard Islands 2

“M” hereafter, corresponding to tidal heights of ~0.55–0.75 m according to the best tide chart available). At some sites, we were able to complement the inventory with high-shore level sampling (MI, SK, noted as “H” hereafter, corresponding to tidal heights of ~1.2 m) or sampling of intertidal pools (MI, NH, UI, noted as “P” hereafter). Two sampling procedures were used to characterize faunal biodiversity and abundance at sampling locations: (1) Ten quadrats (25 cm x 25 cm, Supplementary material 1) were randomly distributed (at one height along the accessible shore) and the species (morphotypes) present in each quadrat were collected; (2) a detailed examination (1 hour) in the immediate vicinity (ca 10 m radius) of the quadrats was carried out to search for any species not recorded within the quadrats and thus obtain a better overview of the total biodiversity. When necessary, the substrate was sieved with 5 mm and 1 mm mesh sieves. Specimens were preserved in 96% ethanol (stored at -20°C) for subsequent identification and analyses. Prior to preservation, several morphotypes were photographed using an Olympus OMD-EM1 body with a 60 mm macro lens, two flashes and accessories to diffuse or reflect the light (e.g., flash diffuser, white paper). These photographs were used as further information aiding the identification process and to document the samples.

Integrative identification

Morphological identification and photography

Each specimen was first examined under a stereomicroscope (Leica MZ7.5) and a preliminary identification was obtained using available taxonomic resources such as legacy literature, recent scientific papers and field guides (e.g., O’Loughlin & VandenSpiegel, 2010, Taboada et al., 2013, Schories & Kohlberg, 2016). Each morphotype was also photographed (as described above) in order to compile a comprehensive photographic library (which was combined with the pictures of living specimens). Twenty taxonomic experts were subsequently contacted to confirm and/or refine these preliminary identifications. Macro-photographs were sent to each taxonomist together with voucher specimens, when deemed necessary.

DNA barcoding

The barcode region of the cytochrome c oxidase subunit I (COI; 658 base pairs) was sequenced for each morphotype (one to five specimens individually sequenced per morphotype). DNA extractions followed the salting-out protocol of Sunnucks & Hales (1996). PCR conditions consisted of 35–45 cycles for each of

the three temperature steps [30 s at 94 °C (denaturation), 30–45 s at 45–55 °C (annealing) and 30 s at 72 °C (elongation)]. These cycles were preceded by 3 min at 94 °C and followed by 2–10 min at 72 °C. Depending on target taxon, we used either universal or taxon-specific primers, which are listed along with taxon-specific PCR conditions in Supplementary Material 2 (Folmer et al., 1994, Meyer, 2003; Erpenbeck et al., 2004, Teske et al., 2006, Handy et al., 2011, Laforest et al., 2013, Layton et al., 2016). An EXOSAP purification (incubation at 37 °C for 15 min followed by further incubation at 80 °C for 15 min) was carried out before sending PCR products to MACROGEN Europe BV for sequencing (Amsterdam, The Netherlands). Sequences were edited and checked for stop codons using Geneious 11.1.5 (Kearse et al., 2012). Barcodes were then compared to both GenBank and BOLD records (Ratnasingham & Hebert, 2007) to confirm or refine identifications. Combining morphological and genetic data, a final identification was established at the most accurate taxonomic level possible.

Community structure

Building matrices

Abundances were characterized through a semi-quantitative approach based on the following scoring categories: 0 - species absent; 1 - species absent from quadrats but present in their vicinity; 2 - species present in <25% of quadrats; 3 - species present in 25–49% of quadrats, 4 - species present in 50–74% of quadrats, 5 - species present in 75–100% of quadrats. Considering the difficulty in estimating amphipod abundances *in situ* (especially when sampling in intertidal pools where they were able to swim away from the quadrats), this group was taken into account in the overall diversity baseline but excluded from abundance comparisons.

We also investigated the distribution and abundance of functional groups (according to trophic role). Based on literature review and personal communications from experts, each identified species/taxon was assigned to one of the following groups: deposit-feeders (detritivores), grazers (including scrapers), predators (including scavengers) and suspension-feeders. In total, 58 species/taxa were included in this analysis (Supplementary Material 3).

Diversity indices and multivariate statistics

Based on the number of presence records in quadrats (species data), the following alpha diversity indices were calculated using SpadeR v1.0 (Chao et al., 2015): species richness in quadrats (S_q), coefficient of variation (CV) and the Chao2 estimator.

Principal Component Analyses (PCA) were performed on covariance matrices and visualized with the ‘ade4’ v1.7–16, ‘factoextra’ v1.0.7, ‘cluster’ v2.1.3 and ‘vegan’ v2.5–7 packages in R v4.0.3 (Oksanen et al., 2020, R Core Team, 2020, Dray et al., 2021, Maechler et al., 2021). PCAs were performed on both species and functional groups. For the latter, the abundance of each functional group corresponded to the mean of the species abundance within that group. The Broken Stick method was used to determine the number of principal components to be retained (Legendre & Legendre, 1983). Ward Clustering was subsequently applied on the retained principal components. Fusion Level Values, silhouette widths, branch length and bootstrap values were used to determine the optimal division of each dendrogram (number of groups, Borcard et al., 2018).

Contribution to DNA barcoding and occurrence initiatives

A public Barcode of Life (BOLD) project (INTGS: Intertidal fauna from the Gerlache Strait) was created on the dedicated website “boldsystems.org”. High-quality macro-photographs (both living and preserved individuals) were uploaded for each specimen as well as COI barcodes, when successfully obtained. In addition, the occurrence dataset of the associated expedition (Belgica121) was amended on the Global Biodiversity Information Facility (GBIF; B121 dataset: <https://doi.org/10.15468/56bv6z>).

Results

Overall diversity of taxonomic and functional groups

More than 8,000 specimens representing 83 putative species were collected in the overall study area (Table 1). These species represented 11 phyla: Arthropoda (24 species), Mollusca (12), Annelida (10), Porifera

(10), Echinodermata (6), Nemertea (6), Bryozoa (5), Cnidaria (5) Chordata (2), Platyhelminthes (2) and Nematoda (1) (Supplementary Material 4). While five phyla were frequent (present at >85% of sampling locations; Annelida, Arthropoda, Mollusca, Nemertea and Platyhelminthes), others were scarce (<30% of the sampling locations; Chordata, Nematoda and Porifera).

Four species were particularly abundant (number of quadrats occupied) and widespread (number of sampling locations occupied). These were the flatworm *Obrimoposthia wandeli* (Hallez, 1906) (present in 79% of quadrats and 11 locations), the bivalve *Kidderia subquadrata* (Pelseneer, 1903) (present in 69% of quadrats and 11 locations), and the gastropods *Laevilitorina umbilicata* Pfeffer, 1886 (present in 68% of quadrats and 11 locations) and *Laevilitorina caliginosa* (Gould, 1849) (present in 75% of quadrats and 12 locations). All remaining species were far less abundant or widespread (Fig. 2). The fifth most abundant species (10% of quadrats) was the springtail *Archisotoma brucei* (Carpenter, 1907) and the fifth most widespread species (8 locations) was the nemertean *Antarctonemertes valida* (Bürger, 1893) (Table 1). Approximately two-thirds of species (65%) were very scarce (52% of species were detected at a single location) or occurred at very low abundance (49% of species were absent from the quadrat surveys, Table 1, Fig. 2). The striking variation in species abundance was confirmed by the high value of the overall coefficient of variation (CV = 1.88, Table 2).

In terms of trophic functional groups, suspension-feeders had the greatest species-level diversity (36% of species), followed by predators/scavengers (34%), deposit-feeders (16%) and grazers (14%) (Supplementary Material 5). All these functional groups were present together at 77% of the locations. Suspension feeders were mainly represented by bryozoans (e.g., *Inversiula nutrix* Jullien, 1888), bivalves (e.g., *K. subquadrata*) and sponges (e.g., *Homaxinella balfourensis* (Ridley & Dendy, 1886)). Predators/scavengers included polychaetes (e.g., *Pterocirrus giribeti* Leiva & Taboada, 2018), fish (*Harpagifer antarcticus* Nybelin, 1947), sea stars (e.g., *Odonotaster validus* Koehler, 1906), ribbon worms (e.g., *Antarctonemertes valida*), flatworms (*O. wandeli*) and cnidarians (e.g., *Candelabrum austrogeorgiae* (Jäderholm, 1904)). Deposit feeders included polychaetes (e.g., Terebellidae), oligochaetes (e.g., *Lumbricillus*) and isopods (*Cymodocella*). Grazers

included springtails (*Archisotoma brucei*) and gastropods (e.g., *Nacella concinna* (Strebel, 1908)).

Diversity across sampling locations

Mean species richness (S) across all sampling locations was 17.38 (SE \pm 2.86), with the greatest values found at Green Reef (32 species, mid-shore level), Føyn Harbor (31 species, mid-shore level) and Useful Island (31 species, intertidal pools) (Table 2). The lowest species richness was found in Neko Harbor (3 species, mid-shore level; 7 species, intertidal pools) and Melchior Islands (7 species, high-shore level). The coefficient of variation ranged from 0.50 (Neko Harbor, intertidal pools) to 1.01 (Useful Island, mid-shore), indicating a moderate to high degree of heterogeneity (mean value: 0.74, SE \pm 0.05) (Table 2). The mean number of phyla (P) was 6.31 (SE \pm 0.60), with the greatest value (9 phyla) found in Skontorp Cove (mid-shore level), Føyn Harbor (mid-shore level) and Useful Island (intertidal pools) (Table 2). The lowest number of phyla was found in Neko Harbor (P = 3, mid-shore level; P = 4, intertidal pools), Hovgaard Island 1 (P = 4, mid-shore level) and Melchior Islands (P = 4, high-shore level).

Community structures and spatial distribution: species composition

The PCA combined with Ward clustering highlighted three main groups of sampling locations (Fig. 3A), with the first two PC axes accounting for 51.1% of the variation in species composition. Group 1 comprised the two locations in Neko Harbor (mid-shore level: NH_M and intertidal pools: NH_P), which were characterized by limited diversity, high abundance of Nematoda spp. (NEMAT_A; mid-shore level), and relatively high abundances of the polychaete Eusyllinae sp. (POL_C) and the nemertean *Antarctonemertes riesgoae* (NEM_H). Groups 2 and 3 were both characterized by high abundances of *Kidderia subquadrata* (KID_A), *Obrimoposthia wandeli* (PLA_A), *Laevilitorina caliginosa* (LAE_A), and *L. umbilicata* (GAS_B). Group 2 included the three locations with the most diverse fauna (Green Reef-mid-shore level: GR_M, Useful Island-intertidal pools: UL_P, Føyn Harbor-mid-shore level: FH_M), while Group 3 included all the remaining locations. Group 3 differed from Group 2 on the second PC axis, mostly representing differences in relative

Table 1 - Taxa found in the study area. N locations: number of locations (maximum = 13) where the species was found either within or in the vicinity of quadrats. % quadrats: percentage of quadrats where the species was found (out of the 130 quadrats investigated in total). BOLD: Public accession number of one specimen from each taxon (INTGS project). * indicates that a COI barcode is available for that specimen

Taxa (ordered by Phylum and Class)	Code	N locations	% quadrats	BOLD
Annelida - Clitellata				
<i>Lumbricillus</i> sp1 Ørsted (1844)	OLI_B	4	5%	INTGS100-22*
<i>Lumbricillus</i> sp2 Ørsted (1844)	OLI_F	2	5%	INTGS103-22*
<i>Lumbricillus</i> sp3 Ørsted (1844)	OLI_G	3	3%	INTGS105-22*
Naididae sp. Ehrenberg (1831)	OLI_A	1	1%	INTGS099-22*
Annelida - Polychaeta				
Capitellidae sp. Grube (1862)	POL_W	3	2%	INTGS122-22
Eusyllinae sp. Malaquin (1893)	POL_C	5	9%	INTGS115-22*
Orbiniidae sp. Hartman (1942)	POL_F	4	9%	INTGS119-22
Phyllodocidae sp. Ørsted (1843)	POL_U	1	1%	INTGS121-22
Pterocirrus giribeti Leiva et al. (2018)	POL_N	1	1%	INTGS120-22*
Terebellidae sp. Johnston (1846)	POL_B	5	3%	INTGS111-22*
Arthropoda - Collembola				
<i>Archisotoma brucei</i> (Carpenter, 1907)	COL_A	2	10%	INTGS054-22*
Arthropoda - Amphipoda				
<i>Bovallia gigantea</i> Pfeffer (1888)	AMP_F	2	-	INTGS012-22*
<i>Cheirimedon femoratus</i> (Pfeffer, 1888)	AMP_ZI	1	-	INTGS033-22*
Corophiida sp. Leach (1814)	AMP_P	1	-	INTGS027-22*
<i>Djerboa furcipes</i> Chevreux (1906)	AMP_ZO	1	-	INTGS034-22*
<i>Eurymera monticulosa</i> Pfeffer (1888)	AMP_K	4	-	INTGS021-22*
Eusiroidea sp1 Stebbing (1888)	AMP_G	4	-	INTGS014-22*
Eusiroidea sp2 Stebbing (1888)	AMP_M	1	-	INTGS024-22*
Eusiroidea sp3 Stebbing (1888)	AMP_W	3	-	INTGS029-22*
<i>Gondogeneia antarctica</i> (Chevreux, 1906)	AMP_C	7	-	INTGS004-22*
Lysianassoidea sp. Dana (1849)	AMP_ZB	1	-	INTGS032-22
<i>Oradarea cf. tridentata</i> Barnard (1932)	AMP_S	1	-	INTGS028-22*
<i>Oradarea</i> sp. Walker (1903)	AMP_E	4	-	INTGS008-22*
<i>Paraceradocus miersi</i> (Pfeffer, 1888)	AMP_O	1	-	INTGS026-22
<i>Prostebbingia brevicornis</i> (Chevreux, 1906)	AMP_D	1	-	INTGS007-22
<i>Schraderia cf. gracilis</i> Pfeffer (1888)	AMP_A	2	-	INTGS003-22
<i>Tryphosella</i> sp. Bonnier (1893)	AMP_N	1	-	INTGS025-22
Arthropoda - Euphausiacea				
<i>Euphausia superba</i> Dana (1850)	KRI_A	1	0%	INTGS079-22*
Arthropoda - Isopoda				
<i>Cymodocella</i> sp1 Pfeffer (1887)	ISO_B	1	0%	INTGS074-22*
<i>Cymodocella</i> sp2 Pfeffer (1887)	ISO_F	1	0%	INTGS076-22
<i>Iathrippa sarsi</i> (Pfeffer, 1887)	ISO_A	4	2%	INTGS073-22
<i>Munna</i> sp. Krøyer (1839)	ISO_D	1	0%	INTGS075-22*
Serolidae sp. Dana (1852)	SER_A	1	0%	INTGS134-22*
Arthropoda - Pycnogonida				
<i>Achelia</i> sp. Hodge (1864)	PYC_A	1	0%	INTGS133-22
Bryozoa - Gymnolaemata				
<i>Antarctothoa</i> sp. Moyano (1987)	BRY_D	1	0%	INTGS047-22*

Table 1 (continued)

Taxa (ordered by Phylum and Class)	Code	N locations	% quadrats	BOLD
<i>Chaperiopsis cf. quadrispinosa</i> (Kluge, 1914)	BRY_G	1	0%	INTGS049-22
<i>Gymnolaemata</i> sp1 Allman (1856)	BRY_C	1	0%	INTGS046-22
<i>Hippadenella inerma</i> (Calvet, 1909)	BRY_F	1	0%	INTGS048-22
<i>Inversiula nutrix</i> Jullien (1888)	BRY_A	5	1%	INTGS041-22*
Chordata - Actinopterygii				
<i>Harpagifer antarcticus</i> Nybelin (1947)	HAR_A	2	0%	INTGS067-22*
Chordata - Ascidiacea				
<i>Cnemidocarpa verrucosa</i> (Lesson, 1830)	ASC_A	1	0%	INTGS037-22*
Cnidaria - Anthozoa				
<i>Edwardsia</i> sp. Quatrefages (1842)	ANE_A	2	3%	INTGS035-22
<i>Glyphoperidium bursa</i> Roule (1909)	ANE_B	2	0%	INTGS036-22*
Cnidaria - Hydrozoa				
<i>Candelabrum austrogeorgiae</i> (Jäderholm, 1904)	CAN_A	2	0%	INTGS050-22*
<i>Staurocladia charcoti</i> (Bedot, 1908)	STA_A	2	1%	INTGS136-22*
Cnidaria - Staurozoa				
<i>Lucernaria cf. australis</i> Vanhöffen (1908)	STA_B	1	0%	INTGS137-22*
Echinodermata - Asteroidea				
<i>Adelasterias papillosa</i> (Koehler, 1906)	ADE_A	2	0%	INTGS001-22*
<i>Granaster nutrix</i> (Studer, 1885)	GRA_A	5	1%	INTGS065-22*
<i>Lysasterias</i> sp. Fisher (1908)	LYS_A	2	0%	INTGS083-22*
<i>Odontaster validus</i> Koehler (1906)	ODO_A	2	0%	INTGS097-22*
Echinodermata - Holothuroidea				
<i>Psolus granulatus</i> Vaney (1906)	HOL_A	2	0%	INTGS071-22*
<i>Sigmodota contorta</i> (Ludwig, 1875)	HOL_B	1	0%	INTGS072-22*
Mollusca - Bivalvia				
<i>Altenaeum</i> sp. Spaink (1972)	BIV_A	5	6%	INTGS038-22
<i>Kidderia subquadrata</i> (Pelseneer, 1903)	KID_A	11	69%	INTGS077-22*
<i>Lissarca miliaris</i> (Philippi, 1845)	BIV_B	2	2%	INTGS040-22*
Mollusca - Gastropoda				
<i>Laevilacunaria antarctica</i> (von Martens, 1885)	GAS_H	1	1%	INTGS064-22*
<i>Laevilacunaria bennetti</i> (Preston, 1916)	GAS_A	5	5%	INTGS055-22*
<i>Laevilitorina caliginosa</i> (Gould, 1849)	LAE_A	12	75%	INTGS080-22*
<i>Laevilitorina umbilicata</i> Pfeffer (1886)	GAS_B	11	68%	INTGS059-22*
<i>Margarella antarctica</i> (Lamy, 1906)	MAR_A	5	2%	INTGS085-22
<i>Nacella concinna</i> (Strebel, 1908)	NAC_A	7	8%	INTGS087-22*
<i>Onoba</i> sp. Adams and Adams (1852)	GAS_F	1	5%	INTGS063-22
Mollusca - Polyplacophora				
<i>Hemiarthrum setulosum</i> Carpenter [in Dall] (1876)	CHI_B	2	0%	INTGS053-22*
<i>Tonicina zschau</i> (Pfeffer, 1886)	CHI_A	4	0%	INTGS052-22*
Nematoda				
Nematoda spp. Diesing (1861)	NEMAT_A	1	8%	INTGS096-22
Nemertea - Hoplonemertea				
<i>Eumonostilifera</i> sp1 Chernyshev (2003)	NEM_C	1	1%	INTGS090-22*
<i>Eumonostilifera</i> sp2 Chernyshev (2003)	NEM_E	1	0%	INTGS094-22
<i>Antarctonemertes riesgoae</i> Taboada et al. (2013)	NEM_H	6	2%	INTGS095-22*
<i>Antarctonemertes valida</i> (Bürger, 1893)	NEM_A	8	8%	INTGS088-22*

Table 1 (continued)

Taxa (ordered by Phylum and Class)	Code	N locations	% quadrats	BOLD
<i>Nipponnemertes</i> sp. Friedrich (1968)	NEM_B	2	0%	INTGS089-22*
Nemertea - Piliophora				
<i>Parborlasia corrugatus</i> (McIntosh, 1876)	NEM_D	2	0%	INTGS093-22*
Platyhelminthes				
<i>Obrimoposthia wandeli</i> (Hallez, 1906)	PLA_A	11	79%	INTGS108-22*
Platyhelminthes sp. Minot (1876)	PLA_B	1	0%	INTGS110-22
Porifera - Demospongiae				
Halichondrida sp. Gray (1867)	POR_D	1	0%	INTGS125-22
<i>Haliclona</i> sp. Grant (1841)	POR_F	1	0%	INTGS127-22
<i>Homaxinella</i> cf. <i>balfourensis</i> (Ridley & Dendy, 1886)	POR_E	1	0%	INTGS126-22*
<i>Homaxinella</i> sp. Topsent (1916)	POR_B	1	0%	INTGS123-22
<i>Hymeniacion</i> cf. <i>torquata</i> Topsent (1916)	POR_C	1	0%	INTGS124-22
<i>Tedania</i> (<i>Tedaniopsis</i>) <i>charcoti</i> Topsent (1907)	POR_G	1	0%	INTGS128-22
Porifera - Calcarea				
Calcarea sp1 Bowerbank (1862)	POR_H	1	0%	INTGS129-22
Calcarea sp2 Bowerbank (1862)	POR_I	1	0%	INTGS130-22
<i>Leucosolenia</i> sp1 Bowerbank (1864)	POR_J	1	1%	INTGS131-22
<i>Leucosolenia</i> sp2 Bowerbank (1864)	POR_K	1	0%	INTGS132-22

abundance of *Orbiniidae* sp. (POL_F), *Antarctone-
mertes valida* (NEM_A), and *A. riesgoae* (NEM_H),
which were overall high in Group 2 and low in Group 3.
Within Group 3, the two high-shore sampling locations

(SK_H and MI_H) also showed very high abundances
of the springtail *Archisotoma brucei* (COL_A). Inter-
tidal pool sites harboured 7 of the 10 species of sponges
that were found in the area of investigation.

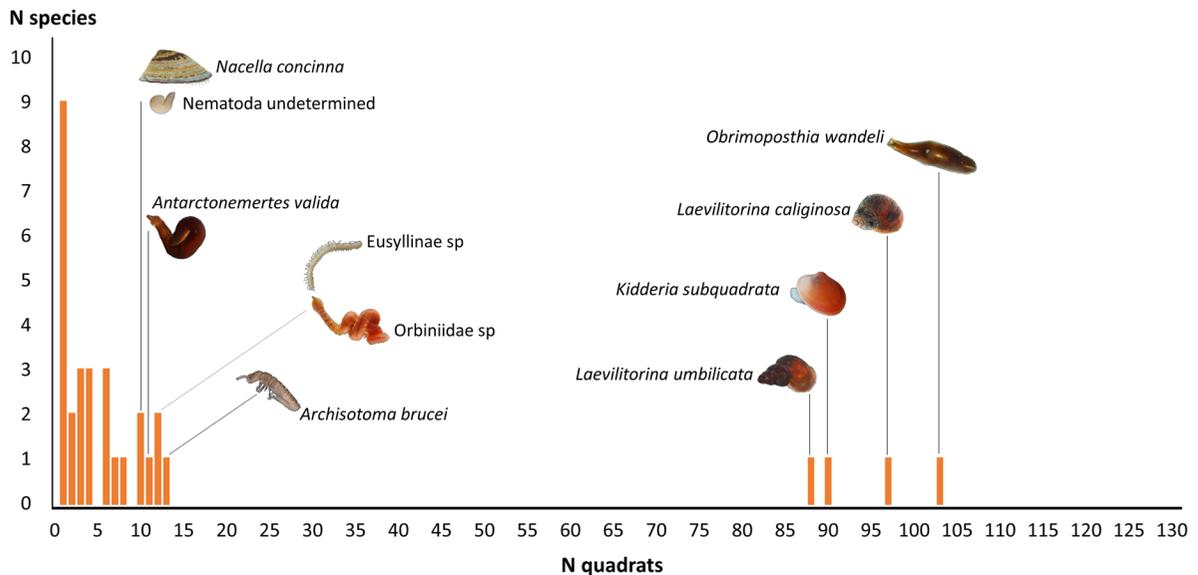


Fig. 2 Species distributions in the study area. Number of species versus number of quadrats, with the species illustrated being the ten most abundant in the entire area. Each species illustrated

refers to the exact number of quadrats in which the species was found (e.g. *Obrimoposthia wandeli* was reported in 103 quadrats while *Archisotoma brucei* was reported in 13 quadrats)

Table 2 Diversity indices (S_q , CV, Chao2, S, P) for each sampling location, both within quadrats and within quadrats combined with vicinity explorations

Sampling Location	Within Quadrats			Quadrats + Vicinity	
	Species richness (S_q)	Coefficient of Variation (CV)	Chao2 estimator ($\pm SE$)	N species total (S)	N phyla total (P)
MI_H (Melchior Isl. high-shore)	7	0.60	7.45 (± 1.21)	7	4
MI_M (Melchior Isl. mid-shore)	7	0.79	9.70 (± 4.02)	11	6
MI_P (Melchior Isl. intertidal pools)	8	0.62	8.23 (± 0.67)	24	8
NH_M (Neko Harbor mid-shore)	2	0.91	2.00 (± 0.47)	3	3
NH_P (Neko Harbor intertidal pools)	4	0.50	5.80 (± 3.39)	7	4
UI_M (Useful Isl. mid-shore)	10	1.01	21.25 (± 15.46)	19	6
UI_P (Useful Isl. intertidal)	12	0.77	13.35 (± 2.10)	31	9
SK_H (Skontorp Cove high-shore)	7	0.66	7.90 (± 2.03)	12	5
SK_M (Skontorp Cove mid-shore)	9	0.99	18.00 (± 9.54)	26	9
HI_M1 (Hovgaard Isl. 1 mid-shore)	6	0.61	6.00 (± 0.54)	9	4
HI_M2 (Hovgaard Isl. 2 mid-shore)	6	0.45	6.00 (± 0.47)	14	7
GR_M (Green Reef mid-shore)	14	0.96	36.05 (± 28.04)	32	8
FH_M (Føyn Harbor mid-shore)	14	0.85	21.20 (± 10.53)	31	9
<i>All locations</i>	32	1.88	52.09 (± 20.04)	88	11

Community structure and spatial distribution: functional groups

PCA on functional groups combined with Ward clustering highlighted five groups of sampling locations (Fig. 3B), with the first two PC axes explaining 90.8% of variability: Group 1 included only Neko Harbor (NH_M and NH_P), where only a few predators/scavengers and one grazer were found; Group 2 included Green Reef (mid-shore level, GR_M) and Føyn Harbor (mid-shore level, FH_M), where high abundances of all functional groups were found, especially grazers; Group 3 included Useful Island-intertidal pools (UI_P), which had the highest abundances of deposit and suspension-feeders of any location, and high abundances of predators/scavengers; Group 4 included Useful Island and Hovgaard Island 1 (mid-shore level, UI_M and HI_M1), which also had high abundance of deposit-feeders but low abundances of predators/scavengers, suspension-feeders and grazers; Group 5, which included all remaining locations, was characterized by high abundance of grazers, low abundance of deposit-feeders and

intermediate abundances of predators/scavengers and suspension-feeders.

Contribution to DNA barcoding and occurrence initiatives

The INTGS (BOLD) project referenced 137 voucher specimens representing 83 different species recorded in the current study. Macro-photographs were uploaded for all the specimens alongside 106 COI barcodes representing 55 different taxa (Table 1). Among these taxa, 53% were barcoded for the first time. In addition, a new version of the B121 occurrence dataset was published in GBIF, which includes finer taxonomic resolution for the identifications. This represents a major improvement (672 records) in the knowledge of the biogeography of a number of species, either as geographic extension of their known distribution or in total number of occurrence records in GBIF (e.g., from 96 to 200 occurrences for the flatworm *Obrimoposthia wandeli*; from 43 to 84 occurrences for the gastropod *Laevilitorina umbilicata*; from 3 to 14 occurrences for the springtail *Archisotoma brucei*).

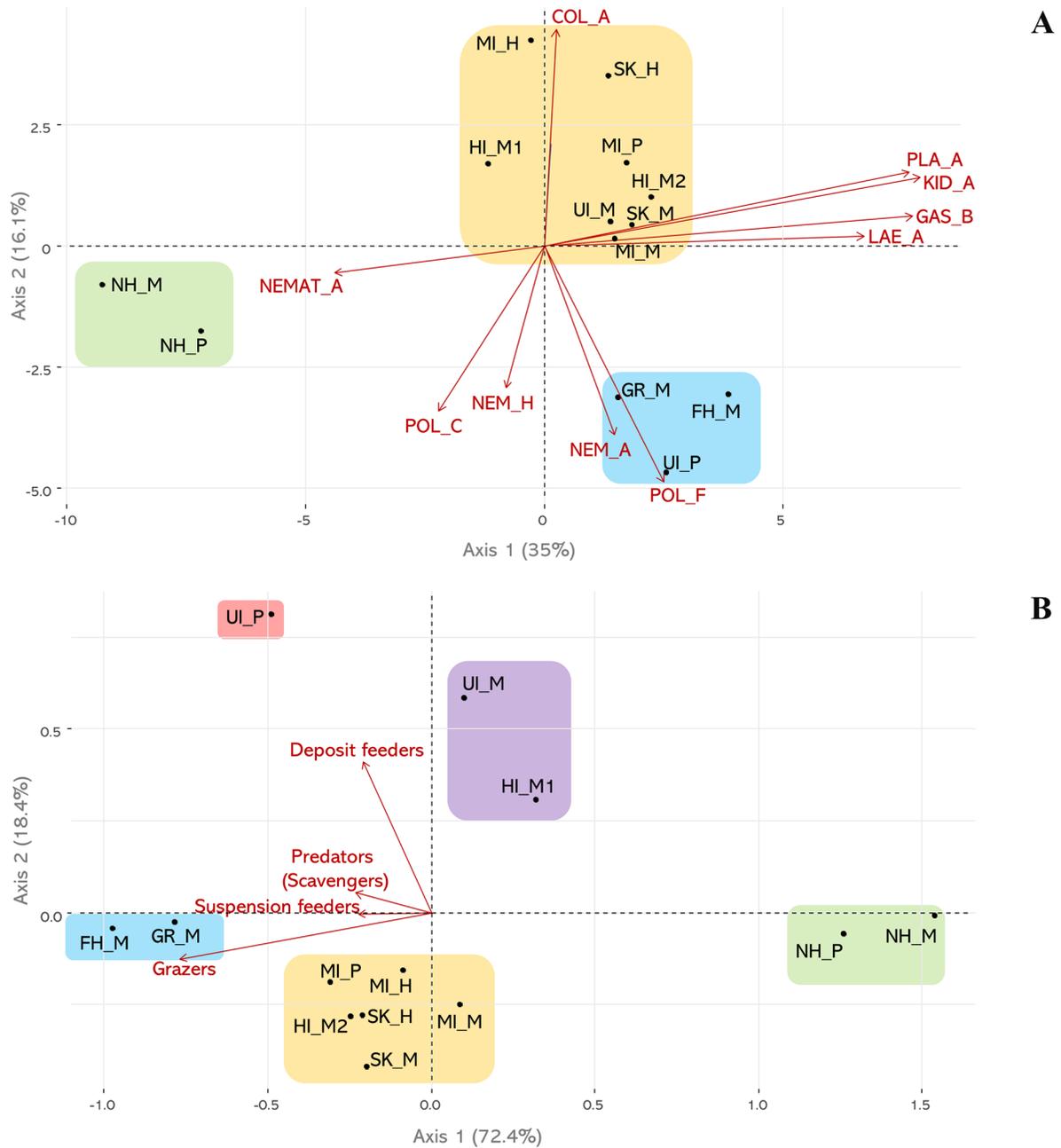


Fig. 3 Principal Component Analysis (PCA) based on species data (A) and functional group data (B). Sampling locations are represented by black dots and species/functional groups by red arrows (see full names in Tables 1 & 2). Colored squares represent the groups defined by Ward clustering. For clearer visu-

alization, the five main contributors (species) to each axis are shown in (A). MI: Melchior Islands; FH: Føyen Harbor; GR: Green Reef; UI: Useful Island; NH: Neko Harbor; SK: Skontorp Cove; HI: Hovgaard Islands. Mid-shore level sampling: M; High-shore level sampling: H; Intertidal pools: P

Discussion

Overall diversity of taxonomic and functional groups

The current integrative diversity study within and around the Gerlache Strait (Antarctic Peninsula) confirmed the presence of a total of 83 different species. Among these species, the most represented phyla were arthropods (24 species), followed by molluscs (12) and annelids (10). While not in the same proportions, these three phyla were also the most diverse in two comparable studies from the South Shetland Islands (Aghmich et al., 2016, Chelchowski et al., 2022). There was great variation in abundance and distribution across these 83 species, with four species being highly abundant and widespread while all other species were much scarcer and more restricted in terms of distribution. This is a typical diversity pattern found in disturbed environments (in this region mainly due to frequent ice encasement or scouring), which has also been highlighted in the Antarctic shallow subtidal zone (Verberk, 2011, Robinson et al., 2020). The four particularly abundant and widespread species were the flatworm *Obrimoposthia wandeli*, the bivalve *Kidderia subquadrata*, and the gastropods *Laevilitorina umbilicata* and *L. caliginosa*. These species were also reported in high abundances by Aghmich et al. (2016) and Chelchowski et al. (2022). The latter study also reported high abundances of other molluscs (*Onoba* sp. and *Altenaeum charcoti*) that were much less common in our study. Dominant species are able to thrive under the extreme environmental conditions that typify the Antarctic coastline, such as intense ice scouring, high freshwater input, high UV radiation levels and significant temperature and salinity variation (Peck et al., 2006, Clarke & Beaumont, 2020). The small size of these species (only a few millimetres) allows them to occupy interstitial habitats within the shore matrix where the extreme environmental conditions are buffered (Waller et al., 2006a, Waller, 2008). While our data cannot confirm this, other studies have proposed that some intertidal species can survive in the intertidal zone throughout the year, despite ice-encasement in winter (Waller et al., 2006a, Bick & Arlt, 2013, Chelchowski et al., 2022). Chelchowski et al. (2022) notably reported 13 species in this zone in the middle of winter (August). These, all present in low abundance compared to their summer population densities, included the four most dominant species in our study. Such winter survival could be linked to ecophysiological strategies related

to cold tolerance, which require further investigation (Waller et al., 2006b). This is notably the case for the nemertean *Antarctonemertes valida* (fifth most frequent species in the current study), that is characterized by the presence of antifreeze proteins in its haemolymph (Waller et al., 2006b). Another non-exclusive hypothesis is that these species have the ability to rapidly reproduce (r-selection strategy), which could allow them to rapidly recolonise and thrive in the intertidal zone even if restricted to the subtidal zone during the winter months (Parry, 1981). Contrasting with these species, the intertidal zone in the Gerlache Strait also hosts more elusive species, with low abundance and limited distribution. This group includes most of the 83 species present in our inventory. Given the rapid environmental changes observed and predicted in the Antarctic Peninsula, it is possible that some of these species (as well as others not recorded in our inventory) will be able to increase their occurrence in the intertidal zone under different environmental conditions (e.g., less ice impact, higher temperatures; Griffiths et al., 2017, Convey & Peck, 2019). This might be the case for species shared with more northern latitudes (e.g. the sub-Antarctic) or others that are not yet present in Antarctica. Recent occurrence records of species from northern latitudes have been highlighted in recent years (via larval dispersal, kelp rafting or hull fouling/transport) and are expected to increase in the future, although are yet to result in confirmed colonization and establishment (Fraser et al., 2018, McCarthy et al., 2019, López-Farrán et al., 2021). Other future candidates could include species from the adjacent Antarctic subtidal zone. Examples of subtidal species that might have (recently) colonized the intertidal zone include the bivalve *Laternula elliptica* (King, 1832) in the mid-shore (Waller et al., 2017) and the fish *Trematomus borchgrevinki* Boulenger, 1902 (formerly *Pagothenia borchgrevinki*) in intertidal pools (Griffiths & Waller, 2016). However, it is also important to highlight that other cold-adapted species (both dominant or rare in our inventory) may be negatively affected by future (warmer) conditions. Numerous studies of various taxa have demonstrated the particular sensitivity of some cold-adapted Antarctic species to rising temperatures (Convey & Peck, 2019; Molina et al., 2023; and references therein).

The presence of multiple trophic levels at virtually all sampling locations also confirms that the Gerlache Strait intertidal zone harbors diverse communities where complex inter-specific interactions occur

(e.g., predation, grazing). We observed patterns in functional group diversity even though all the groups (suspension feeders, predators/scavengers, deposit feeders and grazers) were present at most locations (especially if excluding the distinct and low diversity Neko Harbor). Among suspension feeders, the bryozoan *Inversiula nutrix* and the bivalve *Kidderia subquadrata* were common across the study area, as previously reported in other studies of intertidal and/or subtidal benthic communities (e.g., Barnes & Arnold, 2003; Griffiths & Waller, 2016; Krzeminska & Kuklinski, 2018; Figuerola et al., 2019; Zenteno et al., 2019). *Inversiula nutrix* is more tolerant to sediment deposition than other bryozoan species and may also be more resilient to acidification due to the lower magnesium content of its skeleton, both of which could benefit this species in intertidal habitats (Clark et al., 2017; Figuerola et al., 2019, 2023). We also recorded several predators/scavengers known to be widely distributed throughout the intertidal and shallow subtidal waters of the Antarctic Peninsula region, such as the polychaete species *Pterocirrus giribeti*, the fish *Harpagifer antarcticus*, the sea star *Odontaster validus*, the nemertean *Antarctonemertes valida* and the platyhelminth *Obrimoposthia wandeli* (e.g., Sluys & De Vries, 1988; Eastman, 1993; Taboada et al., 2013; Leiva et al., 2018). The overall high abundance of predators matches the Southern Hemisphere pattern recently highlighted in a meta-analysis, in which the proportion of predators increases towards higher latitudes (Thyrring & Peck, 2021). Grazers notably included *Laevilitorina* microgastropods (Valdivia et al., 2014) and the limpet *Nacella concinna*, which have long been known to be present from intertidal rocky shores down to over 100 m depth (Powell, 1951). In contrast, no deposit feeder was particularly abundant, the most frequently recorded being the polychaete *Orbiniidae* sp. (Fig. 2). The trophic relationships between these species, and in particular the four dominant species, remain to be investigated.

Biogeographic and phylogeographic implications

When considering the regional scale of the western Antarctic Peninsula, high abundances of small bivalves (representatives of the genera *Kidderia*, *Lasaea* and *Mysella*), flatworms (*Obrimoposthia* and *Procerodes*) and microgastropods (various genera) have been reported

in several studies (e.g., Anvers Island: Stockton, 1973; Adelaide Island: Waller et al., 2006a; South Shetland Islands: Aghmich et al., 2016, Chelchowski et al., 2022). Our genetic data for the bivalve *K. subquadrata* and the flatworm *O. wandeli* indicated very high genetic similarity (99.6 to 100%, uncorrected p-distance) with specimens obtained in other studies from Anvers Island and the South Shetlands Islands (Yang et al., 2019, Levicoy et al., 2021a). It is, therefore, likely that the four most dominant species found in our study are the same as those reported in the aforementioned studies (even if under various names), and that they may dominate intertidal assemblages along the northern part of the western Antarctic Peninsula. In terms of wider species distribution patterns, it has recently been demonstrated that two species of the bivalve genus *Kidderia* exist, one in Antarctica (*K. subquadrata*) and one in the sub-Antarctic (*K. minuta*) (Levicoy et al., 2021b). A similar pattern might exist in the flatworm genus *Obrimoposthia* (*O. wandeli* in Antarctica and *O. ohlini* (Bergendal, 1899) in the sub-Antarctic) but this is yet to be verified using an integrative approach (Kenny & Haysom, 1962, Griffiths & Waller, 2016). The situation is less clear in the microgastropod genus *Laevilitorina* due to taxonomic uncertainties and little genetic data being available. Nevertheless, *L. caliginosa* is thought to be a single species throughout the Southern Ocean (Williams et al., 2003, Rosenfeld et al., 2022). Our three barcoded specimens of *L. caliginosa* showed 99.69 to 99.82% genetic similarity with two individuals collected in the Ross Sea, East Antarctica (Ratnasingham & Hebert, 2007). Genetic similarity across such large distances supports the hypothesis of circumpolar distribution and long-range dispersal such as via rafting on kelp (or other drift material) in this brooding species (Adami & Gordillo, 1999; Fraser et al., 2018).

Other species recorded in our study show important variations of their reported geographic and bathymetric distributions. In all species, our records are consistent with currently known geographic distributions. Nevertheless, we report the presence of three species previously only recognized in the subtidal zone: the anemone *Glyphoperidium bursa* Roule, 1909, the hydrozoan *Staurocladia charcoti* (Bedot, 1908), and the sea cucumber *Sigmodota contorta* (Ludwig, 1875). Our genetic data showed high similarity (98–100%) of the specimens examined here with those from other intertidal and subtidal studies around the Antarctic Peninsula (e.g., the sea star *Granaster nutrix*: Moreau

et al., 2021; the nemertean *Antarctonemertes valida*: Taboada et al., 2013; the chiton *Hemiarthrum setulosum* Carpenter [in Dall], 1876: Irisarri et al., 2020; the fish *Harpagifer antarcticus*: Mbragaña et al., 2016; and the polychaete *Pterocirrus giribeti*: Leiva et al. 2018). Characterization of the biogeographic patterns of taxa presumably found in other regions of the Southern Ocean remains to be explored (e.g., the isopod *Iathrippa sarsi* (Pfeffer, 1887), the chiton *Hemiarthrum setulosum*, and the gastropod *Margarella antarctica* (Lamy, 1906)). Many nominal species in the Southern Ocean, previously considered to be widely distributed have now been shown to be complexes of unrecognized “cryptic” species, and it is likely that cryptic species are also common in the intertidal fauna (Brasier et al., 2016; González-Wevar et al., 2019; Jossart et al., 2019; Moreau et al., 2021). Cryptic/undescribed species may be particularly common in taxa with brooding developmental mode that generally display lower connectivity than broadcasting species (Arnaud, 1974, Kelly & Palumbi, 2010, Moreau et al., 2017). Another important perspective is the evaluation of the relationship between the intertidal zone and the higher part of the subtidal zone. Our data, alongside other studies (e.g., Barnes et al., 2009; Griffiths & Waller, 2016), suggest that intertidal species in Antarctica are also distributed in the higher part of the subtidal zone, but that the most abundant species differ between the two zones. The connectivity within species should be also characterized, as extreme and specific environmental conditions in the intertidal zone represent strong selective pressure that could promote divergence over small spatial scales (Muths et al., 2006, Hoffman et al., 2010).

Diversity and community structure among and within sampling locations

An important diversity contrast was observed between the 13 locations examined. Neko Harbor appeared depauperate, with intertidal communities of low diversity and low abundance of nearly all functional groups or taxa (except for nematodes, some ribbon worm and polychaete species). In contrast, all other sampling locations were notably richer, showing high abundances of the four most abundant species (*O. wandeli*, *K. subquadrata*, *L. umbilicata* and *L. caliginosa*) while having more heterogeneity in rarer species. At the mid-shore level, the three richest locations were Green

Reef (32 species in total, 14 in quadrats), Føyn Harbor (31 species in total, 14 in quadrats), and Useful Island (19 species in total, 10 in quadrats). Based on species composition data, the community structure analyses identified three groups. The depauperate Neko Harbor sampling locations formed one group, Useful Island (intertidal pools), Green Reef and Føyn Harbor (mid-shore level) another group, with all other locations forming the third group. Functional group data indicated five clusters, representing a subdivision of the grouping from the species data. While PCA and Ward clustering did not support either the segregation of intertidal pools (MI_P, UI_P) or the high-shore level (MI_H, SK_H), these habitats still exclusively shared some species, such as the springtail *Archisotoma brucei* (high abundances at the high-shore level) or 70% of the sponges that were reported from intertidal pools. While being preliminary at this stage, some initial hypotheses can be proposed to link environmental parameters with the above groupings. The segregation and low diversity at Neko Harbor could be related to an important direct glacial influence combined with a high proportion of sands (Valdivia et al., 2020, Secretariat of the Antarctic Treaty, 2022). A more diverse granulometry (mix of boulders, cobbles, gravels, and sands) was observed at all other locations. The grouping of Useful Island (intertidal pools), Green Reef and Føyn Harbor (mid-shore level), sharing high abundances of the nemertean *A. valida* and the polychaete *Orbiniidae* sp., remains unexplained. However, one potential constraint on the distribution of *A. valida* might be the presence of its prey, as it is known to have a very narrow prey preference (McDermott & Roe, 1985, Norenburg pers. obs).

Conclusions

This study provides a timely catalyst to initiate unravelling the diversity and community structure of the intertidal fauna in other parts of the Southern Ocean beyond the Gerlache Strait. Following the suggestions of Griffiths and Waller (2016), we have completed an occurrence dataset and created an openly available genetic and photographic baseline that can easily be enhanced with further sampling and analyses. At every sampling location, our data highlight a community structure comprising four highly abundant and widespread species and many much rarer species.

Consistent with previous studies, our results indicate that some intertidal species can thrive in summer, which may indicate either an ability to survive *in situ* overwinter or to rapidly colonize and reproduce when conditions become favourable. The high number of rare species may suggest that some of these species (e.g. the ones shared with northern latitudes) could establish larger populations under the changed environmental conditions predicted in the near future (e.g., higher temperature, shorter or no encasement by ice). However, other (cold-adapted) species may be negatively affected by these future warmer conditions. Further studies are required to better understand the biodiversity of intertidal communities at polar land-sea interfaces. Biogeographic and phylogeographic patterns need to be determined in both sub-Antarctic and Antarctic areas. Investigating the biotic and abiotic factors shaping the structure of these communities across spatial scales is a further research priority highlighted by the Antarctic research community (Gutt et al., 2019; Brasier et al., 2021). Together, such investigations will provide the necessary baseline to better assess the resilience of intertidal communities to rapid environmental change.

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Author contributions Conceived and designed the study: Quentin Jossart, Camille VE Moreau, Thomas Saucède, Bruno Danis; Performed fieldwork: Quentin Jossart, Camille VE Moreau, Thomas Saucède, Henrik Christiansen, Bruno Danis; Performed taxonomic work: Quentin Jossart, Camille VE Moreau, Thomas Saucède, Madeleine J Brasier, Peter Convey, Rachel Downey, Blanca Figuerola, Patrick Martin, Jon Norenburg, Sebastian Rosenfeld, Marie Verheye; Performed genetic laboratory work: Quentin Jossart, Henrik Christiansen; Analysed the data: Quentin Jossart, David Bauman, Bruno Danis; Wrote the paper: Quentin Jossart, David Bauman, Camille VE Moreau, Thomas Saucède, Henrik Christiansen, Madeleine J Brasier, Peter Convey, Rachel Downey, Blanca Figuerola, Patrick Martin, Jon Norenburg, Sebastian Rosenfeld, Marie Verheye, Bruno Danis.

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Data availability All genetic data, as well as photographs of voucher specimens, can be publicly accessed and downloaded on boldsystems.org, under the “INTGS” project (Intertidal fauna from the Gerlache Strait). Occurrence data can be found on the Global Biodiversity Information Facility (GBIF, B121 dataset) using the following link: <https://doi.org/10.15468/56bv6z>. Additional data, tables and figures are also provided as Supplementary materials. The specimens used in this study are hosted at the Université Libre de Bruxelles (ULB, Brussels, Belgium) – Laboratoire de Biologie Marine.

Declarations

Ethical approval All authors have read, understood, and have complied as applicable with the statement on "Ethical responsibilities of Authors" as found in the Instructions for Authors and are aware that with minor exceptions, no changes can be made to authorship once the paper is submitted.

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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