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# 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 *Laevitorina umbilicata* and *Laevitorina 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 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

# 1 INTRODUCTION

2 The intertidal zone (i.e., seashore or foreshore) in Antarctica is a unique environment at  
3 the interface between marine and terrestrial habitats (Waller 2008). This zone provides  
4 a broad range of ecosystem functions and is often considered a harbinger for the effects  
5 of climate change and invasive species (Griffiths & Waller 2016, Thyrring & Peck 2021).  
6 Whereas Antarctic intertidal ecosystems normally experience significant seasonal and  
7 shorter-term variation in ice conditions, salinity, and temperature (Peck et al. 2006,  
8 Kuklinski & Balazya 2014, Clarke & Beaumont 2020), they are currently facing challenges  
9 from drastic changes in multiple environmental factors including sea surface  
10 temperature, pH, salinity, and sedimentation rates (Convey & Peck 2019, Brasier et al.  
11 2021, Figuerola et al. 2021). Associated with increasing temperature, reduction in coastal  
12 ice extent and duration will expose extensive new ice-free intertidal areas in the near  
13 future, especially in the region of the Antarctic Peninsula (Griffiths & Waller 2016, Convey  
14 & Peck 2019, Siegert et al. 2019, Hillebrand et al. 2021). These newly available areas have  
15 the potential to be colonized by faunal assemblages of local or distant origin (Griffiths et  
16 al. 2017, Lager et al. 2017, Fraser et al. 2018, Galera et al. 2018, López-Farrán et al. 2021).  
17 To evaluate and document future changes in faunal composition, a current intertidal  
18 biodiversity baseline is urgently needed (Irvine & Shelly 2013, Griffiths & Waller 2016).  
19 Relative to most of the world's coastlines, the Antarctic intertidal zone remains  
20 underexplored (Schiaparelli et al. 2013, Lee et al. 2017, Convey & Peck 2019). Antarctic  
21 intertidal studies commenced more than a hundred years ago, with the first records of  
22 Antarctic intertidal diversity obtained during the Belgica expedition (1897-1899; De  
23 Deckker 2018). Intertidal locations in Antarctica have subsequently been investigated at  
24 varying levels of detail, from opportunistic sampling to the generation of detailed  
25 inventories (Griffiths & Waller 2016 and references therein, Aghmich et al. 2016,

26 Chelchowski et al. 2022). Historical studies generally assessed the zone as being  
27 depauperate (e.g., Hedgpeth 1969), but this initial view has progressively changed and it  
28 is now accepted that some Antarctic continental locations have a level of intertidal  
29 diversity comparable to that of the sub-Antarctic (Griffiths & Waller 2016). In an extensive  
30 review of the biodiversity and biogeographical patterns of intertidal organisms in the  
31 Southern Ocean, Griffiths & Waller (2016) referenced 3902 occurrences of 1416 intertidal  
32 species (<https://doi.org/10.15468/doyfzk>). However, this inventory remains incomplete  
33 compared to those from both adjacent deeper waters and terrestrial habitats (Convey  
34 2010, Terauds et al. 2012, De Broyer et al. 2014). This review also highlighted an  
35 important bias in the geographic areas studied as well as a general lack of standardized  
36 and quantitative sampling approaches applied (e.g., Bick & Arlt 2013, Waller 2013,  
37 Aghmich et al. 2016).

38 The production of biodiversity inventories and baselines is dependent on accurate  
39 biological identification (Tautz et al. 2003, Christiansen et al. 2018). Support from  
40 appropriate taxonomic expertise is therefore required to ensure that identification is  
41 carried out reliably at the appropriate taxonomic level (Costello et al. 2013, Saucède et al.  
42 2021). Morphological data usually derive primarily from direct observation of living or  
43 preserved organisms, but can be complemented with other methods such as  
44 macrophotography or scanning electron microscopy (SEM) (Dayrat 2005). Photographs  
45 allow additional observations (e.g., informative characters that could be lost during  
46 preservation), without the need to re-examine or handle the specimen. They can also be  
47 shared in multiple scientific and outreach initiatives and thus be accessed by the  
48 community at large (e.g., World Register of Marine Species (WoRMS) - [marinespecies.org](http://marinespecies.org),  
49 Barcode of Life Data Systems (BOLD) - [boldsystems.org](http://boldsystems.org), Biodiversity.aq). In addition,  
50 molecular markers can be crucial for identification, especially of underexplored taxa or

51 groups (e.g., Nemertea, Platyhelminthes) that are difficult to identify morphologically  
52 (e.g., Pante et al. 2015, Christiansen et al. 2018, Peck et al. 2018; Jossart et al. 2021).  
53 Molecular characterization can also facilitate the discovery of cryptic species, resolution  
54 of synonymies, and highlight intraspecific genetic structure (Hajibabaei et al. 2007,  
55 Krishnamurthy & Francis 2012, Christiansen et al. 2018, Moreau et al. 2021). It is,  
56 therefore, unsurprising that achieving a comprehensive genetic data archive is considered  
57 a top priority for Antarctic research (Kennicutt et al. 2014, Convey & Peck 2019). In the  
58 present study, we evaluated intertidal faunal diversity at 13 sampling locations around  
59 the Gerlache Strait, western Antarctic Peninsula (Figure 1). Based on examination of more  
60 than 8,000 individual specimens, we combined an *in situ* quadrat approach with  
61 morphological and genetic data to characterize the faunal assemblages at each location.  
62 Considering the environmental heterogeneity in the area of investigation, we expected  
63 the faunal composition to be highly variable between the different locations.  
64 Morphological identification was achieved with the support of taxonomic experts while  
65 genetic characterization was based on the barcode region of the cytochrome c oxidase I  
66 gene (COI). The dataset generated was also used to produce the first genetic and  
67 photographic baseline of the Antarctic intertidal fauna, containing 106 sequences and 137  
68 photographs from both living and preserved specimens, while also providing a significant  
69 update to existing occurrence databases (672 records, dataset of the associated  
70 expedition Belgica121).

## 71 **METHODS**

### 72 **Field studies**

73 Fieldwork was performed during the Belgica121 expedition in February-March 2019  
74 (Danis et al. 2019, 2021, 2022). This expedition, supported by the motor vessel R/V  
75 *Australis*, aimed to complete a biodiversity census of shallow coastal (up to 40 m depth)  
76 benthic communities around the Gerlache Strait, western Antarctic Peninsula. The  
77 Gerlache Strait water masses are characterized by both Bellingshausen Sea (upper layer)  
78 and Weddell Sea influences (underlying bottom-reaching layer; Garcia et al. 2002). The  
79 tidal regime in the area is mainly semidiurnal, with a maximal tidal range of 2 meters  
80 (Dewart 1972, Dragani et al. 2004). Intertidal communities were investigated at 13 study  
81 locations from eight distinct sites (Figure 1): Melchior Islands (MI), Føyn Harbor (FH),  
82 Green Reef (GR), Useful Island (UI), Neko Harbor (NH), Skontorp Cove (SK) and Hovgaard  
83 Islands (HI\_M1 & HI\_M2). Details of each site are presented in Danis et al. (2021). First,  
84 each site was explored with a tender to locate suitable intertidal areas for landing and  
85 sampling. At low tide, a faunal inventory was made at the mid-shore level at all sites  
86 (locations noted as “M” hereafter, corresponding to tidal heights of ~0.55-0.75 m  
87 according to the best tide chart available). At some sites, we were able to complement the  
88 inventory with high-shore level sampling (MI, SK, noted as “H” hereafter, corresponding  
89 to tidal heights of ~1.2 m) or sampling of intertidal pools (MI, NH, UI, noted as “P”  
90 hereafter). Two sampling procedures were used to characterize faunal biodiversity and  
91 abundance at sampling locations: (1) Ten quadrats (25 cm x 25 cm, Supplementary  
92 material 1) were randomly distributed (at one height along the accessible shore) and the  
93 species (morphotypes) present in each quadrat were collected; (2) a detailed examination  
94 (1 hour) in the immediate vicinity (ca 10 m radius) of the quadrats was carried out to  
95 search for any species not recorded within the quadrats and thus obtain a better overview

96 of the total biodiversity. When necessary, the substrate was sieved with 5 mm and 1 mm  
97 mesh sieves. Specimens were preserved in 96% ethanol (stored at -20°C) for subsequent  
98 identification and analyses. Prior to preservation, several morphotypes were  
99 photographed using an Olympus OMD-EM1 body with a 60 mm macro lens, two flashes  
100 and accessories to diffuse or reflect the light (e.g., flash diffuser, white paper). These  
101 photographs were used as further information aiding the identification process and to  
102 document the samples.

### 103 **Integrative Identification**

#### 104 Morphological identification and photography

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

#### 114 DNA barcoding

115 The barcode region of the cytochrome c oxidase subunit I (COI; 658 base pairs) was  
116 sequenced for each morphotype (one to five specimens individually sequenced per  
117 morphotype). DNA extractions followed the salting-out protocol of Sunnucks & Hales  
118 (1996). PCR conditions consisted of 35-45 cycles for each of the three temperature steps  
119 [30 s at 94 °C (denaturation), 30-45 s at 45-55 °C (annealing) and 30 s at 72 °C  
120 (elongation)]. These cycles were preceded by 3 min at 94 °C and followed by 2-10 min at



121 72 °C. Depending on target taxon, we used either universal or taxon-specific primers,  
122 which are listed along with taxon-specific PCR conditions in Supplementary Material 2  
123 (Folmer et al. 1994, Meyer et al. 2003, Erpenbeck et al. 2004, Teske et al. 2006, Handy et  
124 al. 2011, Laforest et al. 2013, Layton et al. 2016). An EXOSAP purification (incubation at  
125 37 °C for 15 min followed by further incubation at 80 °C for 15 min) was carried out before  
126 sending PCR products to MACROGEN Europe BV for sequencing (Amsterdam, The  
127 Netherlands). Sequences were edited and checked for stop codons using Geneious 11.1.5  
128 (Kearse et al. 2012). Barcodes were then compared to both GenBank and BOLD records  
129 (Ratnasingham & Hebert 2007) to confirm or refine identifications. Combining  
130 morphological and genetic data, a final identification was established at the most accurate  
131 taxonomic level possible.

## 132 **Community structure**

### 133 Building matrices

134 Abundances were characterized through a semi-quantitative approach based on the  
135 following scoring categories: 0 - species absent; 1 - species absent from quadrats but  
136 present in their vicinity; 2 - species present in <25% of quadrats; 3 - species present in  
137 25-49% of quadrats, 4 - species present in 50-74% of quadrats, 5 - species present in 75-  
138 100% of quadrats. Considering the difficulty in estimating amphipod abundances *in situ*  
139 (especially when sampling in intertidal pools where they were able to swim away from  
140 the quadrats), this group was taken into account in the overall diversity baseline but  
141 excluded from abundance comparisons.

142 We also investigated the distribution and abundance of functional groups (according to  
143 trophic role). Based on literature review and personal communications from experts, each  
144 identified species/taxon was assigned to one of the following groups: deposit-feeders  
145 (detritivores), grazers (including scrapers), predators (including scavengers) and

146 suspension-feeders. In total, 58 species/taxa were included in this analysis  
147 (Supplementary Material 3).

#### 148 Diversity indices and multivariate statistics

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

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

#### 162 **Contribution to DNA barcoding and occurrence initiatives**

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

169 **RESULTS**

170 Overall diversity of taxonomic and functional groups

171 More than 8,000 specimens representing 83 putative species were collected in the overall  
172 study area (Table 1). These species represented 11 phyla: Arthropoda (24 species),  
173 Mollusca (12), Annelida (10), Porifera (10), Echinodermata (6), Nemertea (6), Bryozoa  
174 (5), Cnidaria (5) Chordata (2), Platyhelminthes (2) and Nematoda (1) (Supplementary  
175 Material 4). While five phyla were frequent (present at >85% of sampling locations;  
176 Annelida, Arthropoda, Mollusca, Nemertea and Platyhelminthes), others were scarce  
177 (<30% of the sampling locations; Chordata, Nematoda and Porifera).

178 Four species were particularly abundant (number of quadrats occupied) and widespread  
179 (number of sampling locations occupied). These were the flatworm *Obrimoposthia*  
180 *wandeli* (Hallez, 1906) (present in 79% of quadrats and 11 locations), the bivalve *Kidderia*  
181 *subquadrata* (Pelseneer, 1903) (present in 69% of quadrats and 11 locations), and the  
182 gastropods *Laevilitorina umbilicata* Pfeffer, 1886 (present in 68% of quadrats and 11  
183 locations) and *Laevilitorina caliginosa* (Gould, 1849) (present in 75% of quadrats and 12  
184 locations). All remaining species were far less abundant or widespread (Figure 2). The  
185 fifth most abundant species (10% of quadrats) was the springtail *Archisotoma brucei*  
186 (Carpenter, 1907) and the fifth most widespread species (8 locations) was the nemertean  
187 *Antarctonemertes valida* (Bürger, 1893) (Table 1). Approximately two-thirds of species  
188 (65%) were very scarce (52% of species were detected at a single location) or occurred  
189 at very low abundance (49% of species were absent from the quadrat surveys, Table 1,  
190 Figure 2). The striking variation in species abundance was confirmed by the high value of  
191 the overall coefficient of variation (CV = 1.88, Table 2).

192 In terms of trophic functional groups, suspension-feeders had the greatest species-level  
193 diversity (36% of species), followed by predators/scavengers (34%), deposit-feeders

194 (16%) and grazers (14%) (Supplementary Material 5). All these functional groups were  
195 present together at 77% of the locations. Suspension feeders were mainly represented by  
196 bryozoans (e.g., *Inversiula nutrix* Jullien, 1888), bivalves (e.g., *K. subquadrata*) and sponges  
197 (e.g., *Homaxinella balfourensis* (Ridley & Dendy, 1886)). Predators/scavengers included  
198 polychaetes (e.g., *Pterocirrus giribeti* Leiva & Taboada, 2018), fish (*Harpagifer antarcticus*  
199 Nybelin, 1947), sea stars (e.g., *Odontaster validus* Koehler, 1906), ribbon worms (e.g.,  
200 *Antarctonemertes valida*), flatworms (*O. wandeli*) and cnidarians (e.g., *Candelabrum*  
201 *austrogeorgiae* (Jäderholm, 1904)). Deposit feeders included polychaetes (e.g.,  
202 Terebellidae), oligochaetes (e.g., *Lumbricillus*) and isopods (*Cymodocella*). Grazers  
203 included springtails (*Archisotoma brucei*) and gastropods (e.g., *Nacella concinna* (Strebel,  
204 1908)).

#### 205 Diversity across sampling locations

206 Mean species richness (S) across all sampling locations was 17.38 (SE  $\pm$  2.86), with the  
207 greatest values found at Green Reef (32 species, mid-shore level), Føyn Harbor (31  
208 species, mid-shore level) and Useful Island (31 species, intertidal pools) (Table 2). The  
209 lowest species richness was found in Neko Harbor (3 species, mid-shore level; 7 species,  
210 intertidal pools) and Melchior Islands (7 species, high-shore level). The coefficient of  
211 variation ranged from 0.50 (Neko Harbor, intertidal pools) to 1.01 (Useful Island, mid-  
212 shore), indicating a moderate to high degree of heterogeneity (mean value: 0.74, SE  $\pm$   
213 0.05) (Table 2). The mean number of phyla (P) was 6.31 (SE  $\pm$  0.60), with the greatest  
214 value (9 phyla) found in Skontorp Cove (mid-shore level), Føyn Harbor (mid-shore level)  
215 and Useful Island (intertidal pools) (Table 2). The lowest number of phyla was found in  
216 Neko Harbor (P = 3, mid-shore level; P = 4, intertidal pools), Hovgaard Island 1 (P = 4,  
217 mid-shore level) and Melchior Islands (P = 4, high-shore level).

218 Community structures and spatial distribution: species composition

219 The PCA combined with Ward clustering highlighted three main groups of sampling  
220 locations (Figure 3A), with the first two PC axes accounting for 51.1% of the variation in  
221 species composition. Group 1 comprised the two locations in Neko Harbor (mid-shore  
222 level: NH\_M and intertidal pools: NH\_P), which were characterized by limited diversity,  
223 high abundance of Nematoda spp. (NEMAT\_A; mid-shore level), and relatively high  
224 abundances of the polychaete *Eusyllinae* sp. (POL\_C) and the nemertean  
225 *Antarctonemertes riesgoae* (NEM\_H). Groups 2 and 3 were both characterized by high  
226 abundances of *Kidderia subquadrata* (KID\_A), *Obrimoposthia wandeli* (PLA\_A),  
227 *Laevilitorina caliginosa* (LAE\_A), and *L. umbilicata* (GAS\_B). Group 2 included the three  
228 locations with the most diverse fauna (Green Reef-mid-shore level: GR\_M, Useful Island-  
229 intertidal pools: UI\_P, Føyn Harbor-mid-shore level: FH\_M), while Group 3 included all the  
230 remaining locations. Group 3 differed from Group 2 on the second PC axis, mostly  
231 representing differences in relative abundance of *Orbiniidae* sp. (POL\_F),  
232 *Antarctonemertes valida* (NEM\_A), and *A. riesgoae* (NEM\_H), which were overall high in  
233 Group 2 and low in Group 3. Within Group 3, the two high-shore sampling locations (SK\_H  
234 and MI\_H) also showed very high abundances of the springtail *Archisotoma brucei*  
235 (COL\_A). Intertidal pool sites harboured 7 of the 10 species of sponges that were found in  
236 the area of investigation.

237 Community structure and spatial distribution: functional groups

238 PCA on functional groups combined with Ward clustering highlighted five groups of  
239 sampling locations (Figure 3B), with the first two PC axes explaining 90.8% of variability:  
240 Group 1 included only Neko Harbor (NH\_M and NH\_P), where only a few  
241 predators/scavengers and one grazer were found; Group 2 included Green Reef (mid-  
242 shore level, GR\_M) and Føyn Harbor (mid-shore level, FH\_M), where high abundances of

243 all functional groups were found, especially grazers; Group 3 included Useful Island-  
244 intertidal pools (UI\_P), which had the highest abundances of deposit and suspension-  
245 feeders of any location, and high abundances of predators/scavengers; Group 4 included  
246 Useful Island and Hovgaard Island 1 (mid-shore level, UI\_M and HI\_M1), which also had  
247 high abundance of deposit-feeders but low abundances of predators/scavengers,  
248 suspension-feeders and grazers; Group 5, which included all remaining locations, was  
249 characterized by high abundance of grazers, low abundance of deposit-feeders and  
250 intermediate abundances of predators/scavengers and suspension-feeders.

#### 251 Contribution to DNA barcoding and occurrence initiatives

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

263

## 264 **DISCUSSION**

### 265 Overall diversity of taxonomic and functional groups

266 The current integrative diversity study within and around the Gerlache Strait (Antarctic  
267 Peninsula) confirmed the presence of a total of 83 different species. Among these species,  
268 the most represented phyla were arthropods (24 species), followed by molluscs (12) and  
269 annelids (10). While not in the same proportions, these three phyla were also the most  
270 diverse in two comparable studies from the South Shetland Islands (Aghmich et al. 2016,  
271 Chelchowski et al. 2022). There was great variation in abundance and distribution across  
272 these 83 species, with four species being highly abundant and widespread while all other  
273 species were much scarcer and more restricted in terms of distribution. This is a typical  
274 diversity pattern found in disturbed environments (in this region mainly due to frequent  
275 ice encasement or scouring), which has also been highlighted in the Antarctic shallow  
276 subtidal zone (Verberk 2011, Robinson et al. 2020). The four particularly abundant and  
277 widespread species were the flatworm *Obrimoposthia wandeli*, the bivalve *Kidderia*  
278 *subquadrata*, and the gastropods *Laevitorina umbilicata* and *L. caliginosa*. These species  
279 were also reported in high abundances by Aghmich et al. 2016 and Chelchowski et al.  
280 2022. The latter study also reported high abundances of other molluscs (*Onoba* sp. and  
281 *Altenaeum charcoti*) that were much less common in our study. Dominant species are able  
282 to thrive under the extreme environmental conditions that typify the Antarctic coastline,  
283 such as intense ice scouring, high freshwater input, high UV radiation levels and  
284 significant temperature and salinity variation (Peck et al. 2006, Clarke & Beaumont 2020).  
285 The small size of these species (only a few millimetres) allows them to occupy interstitial  
286 habitats within the shore matrix where the extreme environmental conditions are  
287 buffered (Waller et al. 2006a, Waller 2008). While our data cannot confirm this, other  
288 studies have proposed that some intertidal species can survive in the intertidal zone

289 throughout the year, despite ice-encasement in winter (Waller et al. 2006a, Bick & Arlt  
290 2013, Chelchowski et al. 2022). Chelchowski et al. (2022) notably reported 13 species in  
291 this zone in the middle of winter (August). These, all present in low abundance compared  
292 to their summer population densities, included the four most dominant species in our  
293 study. Such winter survival could be linked to ecophysiological strategies related to cold  
294 tolerance, which require further investigation (Waller et al. 2006b). This is notably the  
295 case for the nemertean *Antarctonemertes valida* (fifth most frequent species in the current  
296 study), that is characterized by the presence of antifreeze proteins in its haemolymph  
297 (Waller et al. 2006b). Another non-exclusive hypothesis is that these species have the  
298 ability to rapidly reproduce (r-selection strategy), which could allow them to rapidly  
299 recolonise and thrive in the intertidal zone even if restricted to the subtidal zone during  
300 the winter months (Parry 1981). Contrasting with these species, the intertidal zone in the  
301 Gerlache Strait also hosts more elusive species, with low abundance and limited  
302 distribution. This group includes most of the 83 species present in our inventory. Given  
303 the rapid environmental changes observed and predicted in the Antarctic Peninsula, it is  
304 possible that some of these species (as well as others not recorded in our inventory) will  
305 be able to increase their occurrence in the intertidal zone under different environmental  
306 conditions (e.g., less ice impact, higher temperatures; Griffiths et al. 2017, Convey & Peck  
307 2019). This might be the case for species shared with more northern latitudes (e.g. the  
308 sub-Antarctic) or others that are not yet present in Antarctica. Recent occurrence records  
309 of species from northern latitudes have been highlighted in recent years (via larval  
310 dispersal, kelp rafting or hull fouling/transport) and are expected to increase in the  
311 future, although are yet to result in confirmed colonization and establishment (Fraser et  
312 al. 2018, McCarthy et al. 2019, López-Farrán et al. 2021). Other future candidates could  
313 include species from the adjacent Antarctic subtidal zone. Examples of subtidal species



314 that might have (recently) colonized the intertidal zone include the bivalve *Laternula*  
315 *elliptica* (P.P.King, 1832) in the mid-shore (Waller et al. 2017) and the fish *Trematomus*  
316 *borchgrevinki* Boulenger, 1902 (formerly *Pagothenia borchgrevinki*) in intertidal pools  
317 (Griffiths & Waller 2016). However, it is also important to highlight that other cold-  
318 adapted species (both dominant or rare in our inventory) may be negatively affected by  
319 future (warmer) conditions. Numerous studies of various taxa have demonstrated the  
320 particular sensitivity of some cold-adapted Antarctic species to rising temperatures  
321 (Convey & Peck 2019, Molina et al. 2022 and references therein).

322 The presence of multiple trophic levels at virtually all sampling locations also confirms  
323 that the Gerlache Strait intertidal zone harbors diverse communities where complex  
324 inter-specific interactions occur (e.g., predation, grazing). We observed patterns in  
325 functional group diversity even though all the groups (suspension feeders,  
326 predators/scavengers, deposit feeders and grazers) were present at most locations  
327 (especially if excluding the distinct and low diversity Neko Harbor). Among suspension  
328 feeders, the bryozoan *Inversiula nutrix* and the bivalve *Kidderia subquadrata* were  
329 common across the study area, as previously reported in other studies of intertidal and/or  
330 subtidal benthic communities (e.g., Barnes & Arnold 2003, Griffiths & Waller 2016,  
331 Krzeminska & Kuklinski 2018, Figuerola et al. 2019, Zenteno et al. 2019). *Inversiula nutrix*  
332 is more tolerant to sediment deposition than other bryozoan species and may also be  
333 more resilient to acidification due to the lower magnesium content of its skeleton, both of  
334 which could benefit this species in intertidal habitats (Clark et al. 2017, Figuerola et al.  
335 2019, 2023). We also recorded several predators/scavengers known to be widely  
336 distributed throughout the intertidal and shallow subtidal waters of the Antarctic  
337 Peninsula region, such as the polychaete species *Pterocirrus giribeti*, the fish *Harpagifer*  
338 *antarcticus*, the sea star *Odontaster validus*, the nemertean *Antarctonemertes valida* and

339 the platyhelminth *Obrimoposthia wandeli* (e.g., Sluys & De Vries 1988, Eastman 1993,  
340 Taboada et al. 2013, Leiva et al. 2018). The overall high abundance of predators matches  
341 the Southern Hemisphere pattern recently highlighted in a meta-analysis, in which the  
342 proportion of predators increases towards higher latitudes (Thyrring & Peck 2021).  
343 Grazers notably included *Laevitorina* microgastropods (Valdivia et al. 2014) and the  
344 limpet *Nacella concinna*, which have long been known to be present from intertidal rocky  
345 shores down to over 100 m depth (Powell 1951). In contrast, no deposit feeder was  
346 particularly abundant, the most frequently recorded being the polychaete *Orbiniidae* sp.  
347 (Figure 2). The trophic relationships between these species, and in particular the four  
348 dominant species, remain to be investigated.

#### 349 Biogeographic and phylogeographic implications

350 When considering the regional scale of the western Antarctic Peninsula, high abundances  
351 of small bivalves (representatives of the genera *Kidderia*, *Lasaea* and *Mysella*), flatworms  
352 (*Obrimoposthia* and *Procerodes*) and microgastropods (various genera) have been  
353 reported in several studies (e.g., Anvers Island: Stockton 1973; Adelaide Island: Waller et  
354 al. 2006a; South Shetland Islands: Aghmich et al. 2016, Chelchowski et al. 2022). Our  
355 genetic data for the bivalve *K. subquadrata* and the flatworm *O. wandeli* indicated very  
356 high genetic similarity (99.6 to 100%, uncorrected p-distance) with specimens obtained  
357 in other studies from Anvers Island and the South Shetlands Islands (Yang et al. 2019,  
358 Levicoy et al. 2021a). It is, therefore, likely that the four most dominant species found in  
359 our study are the same as those reported in the aforementioned studies (even if under  
360 various names), and that they may dominate intertidal assemblages along the northern  
361 part of the western Antarctic Peninsula. In terms of wider species distribution patterns,  
362 it has recently been demonstrated that two species of the bivalve genus *Kidderia* exist,  
363 one in Antarctica (*K. subquadrata*) and one in the sub-Antarctic (*K. minuta*) (Levicoy et al.

364 2021b). A similar pattern might exist in the flatworm genus *Obrimoposthia* (*O. wandeli* in  
365 Antarctica and *O. ohlini* (Bergendal, 1899) in the sub-Antarctic) but this is yet to be  
366 verified using an integrative approach (Kenny & Haysom 1962, Griffiths & Waller 2016).  
367 The situation is less clear in the microgastropod genus *Laevilitorina* due to taxonomic  
368 uncertainties and little genetic data being available. Nevertheless, *L. caliginosa* is thought  
369 to be a single species throughout the Southern Ocean (Williams et al. 2003, Rosenfeld et  
370 al. 2022). Our three barcoded specimens of *L. caliginosa* showed 99.69 to 99.82% genetic  
371 similarity with two individuals collected in the Ross Sea, East Antarctica (Ratnasingham  
372 & Hebert 2007). Genetic similarity across such large distances supports the hypothesis of  
373 circumpolar distribution and long-range dispersal such as via rafting on kelp (or other  
374 drift material) in this brooding species (Adami & Gordillo 1999; Fraser et al. 2018).  
375 Other species recorded in our study show important variations of their reported  
376 geographic and bathymetric distributions. In all species, our records are consistent with  
377 currently known geographic distributions. Nevertheless, we report the presence of three  
378 species previously only recognized in the subtidal zone: the anemone *Glyphoperidium*  
379 *bursa* Roule, 1909, the hydrozoan *Staurocladia charcoti* (Bedot, 1908), and the sea  
380 cucumber *Sigmodota contorta* (Ludwig, 1875). Our genetic data showed high similarity  
381 (98-100%) of the specimens examined here with those from other intertidal and subtidal  
382 studies around the Antarctic Peninsula (e.g., the sea star *Granaster nutrix*: Moreau et al.  
383 2021; the nemertean *Antarctonemertes valida*: Taboada et al. 2013; the chiton  
384 *Hemiarthrum setulosum* Carpenter [in Dall], 1876: Irisarri et al. 2020; the fish *Harpagifer*  
385 *antarcticus*: Mabragaña et al. 2016; and the polychaete *Pterocirrus giribeti*: Leiva et al.  
386 2018). Characterization of the biogeographic patterns of taxa presumably found in other  
387 regions of the Southern Ocean remains to be explored (e.g., the isopod *Iathrippa sarsi*  
388 (Pfeffer, 1887), the chiton *Hemiarthrum setulosum*, and the gastropod *Margarella*

389 *antarctica* (Lamy, 1906)). Many nominal species in the Southern Ocean, previously  
390 considered to be widely distributed have now been shown to be complexes of  
391 unrecognized “cryptic” species, and it is likely that cryptic species are also common in the  
392 intertidal fauna (Brasier et al. 2016; González-Wevar et al. 2019; Jossart et al. 2019;  
393 Moreau et al. 2021). Cryptic/undescribed species may be particularly common in taxa  
394 with brooding developmental mode that generally display lower connectivity than  
395 broadcasting species (Arnaud 1974, Kelly & Palumbi 2010, Moreau et al. 2017). Another  
396 important perspective is the evaluation of the relationship between the intertidal zone  
397 and the higher part of the subtidal zone. Our data, alongside other studies (e.g., Barnes et  
398 al. 2009, Griffith & Waller 2016), suggest that intertidal species in Antarctica are also  
399 distributed in the higher part of the subtidal zone, but that the most abundant species  
400 differ between the two zones. The connectivity within species should be also  
401 characterized, as extreme and specific environmental conditions in the intertidal zone  
402 represent strong selective pressure that could promote divergence over small spatial  
403 scales (Muths et al. 2006, Hoffman et al. 2010).

#### 404 Diversity and community structure among and within sampling locations

405 An important diversity contrast was observed between the 13 locations examined. Neko  
406 Harbor appeared depauperate, with intertidal communities of low diversity and low  
407 abundance of nearly all functional groups or taxa (except for nematodes, some ribbon  
408 worm and polychaete species). In contrast, all other sampling locations were notably  
409 richer, showing high abundances of the four most abundant species (*O. wandeli*, *K.*  
410 *subquadrata*, *L. umbilicata* and *L. caliginosa*) while having more heterogeneity in rarer  
411 species. At the mid-shore level, the three richest locations were Green Reef (32 species in  
412 total, 14 in quadrats), Føyn Harbor (31 species in total, 14 in quadrats), and Useful Island  
413 (19 species in total, 10 in quadrats). Based on species composition data, the community

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

#### 432 Conclusions

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

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

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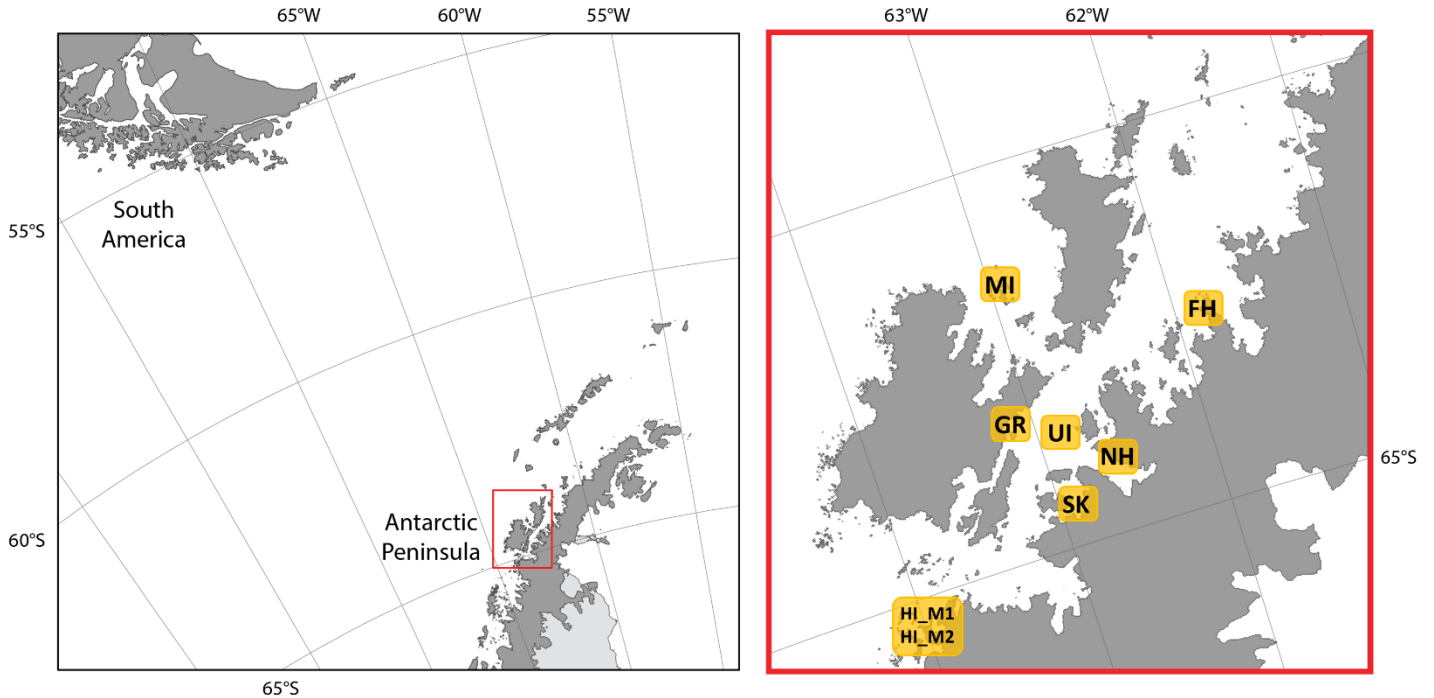
**Author Contributions:** Conceived and designed the study: Quentin Jossart, Camille VE Moreau, Thomas Saucède, Bruno Danis; Performed fieldwork: Quentin Jossart, Camille VE Moreau, Thomas Saucède, Henrik Christiansen, Bruno Danis; Performed taxonomic work: Quentin Jossart, Camille VE Moreau, Thomas 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.

**Availability of data and materials:** All genetic data, as well as photographs of voucher specimens, can be publicly accessed and downloaded on [boldsystems.org](https://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

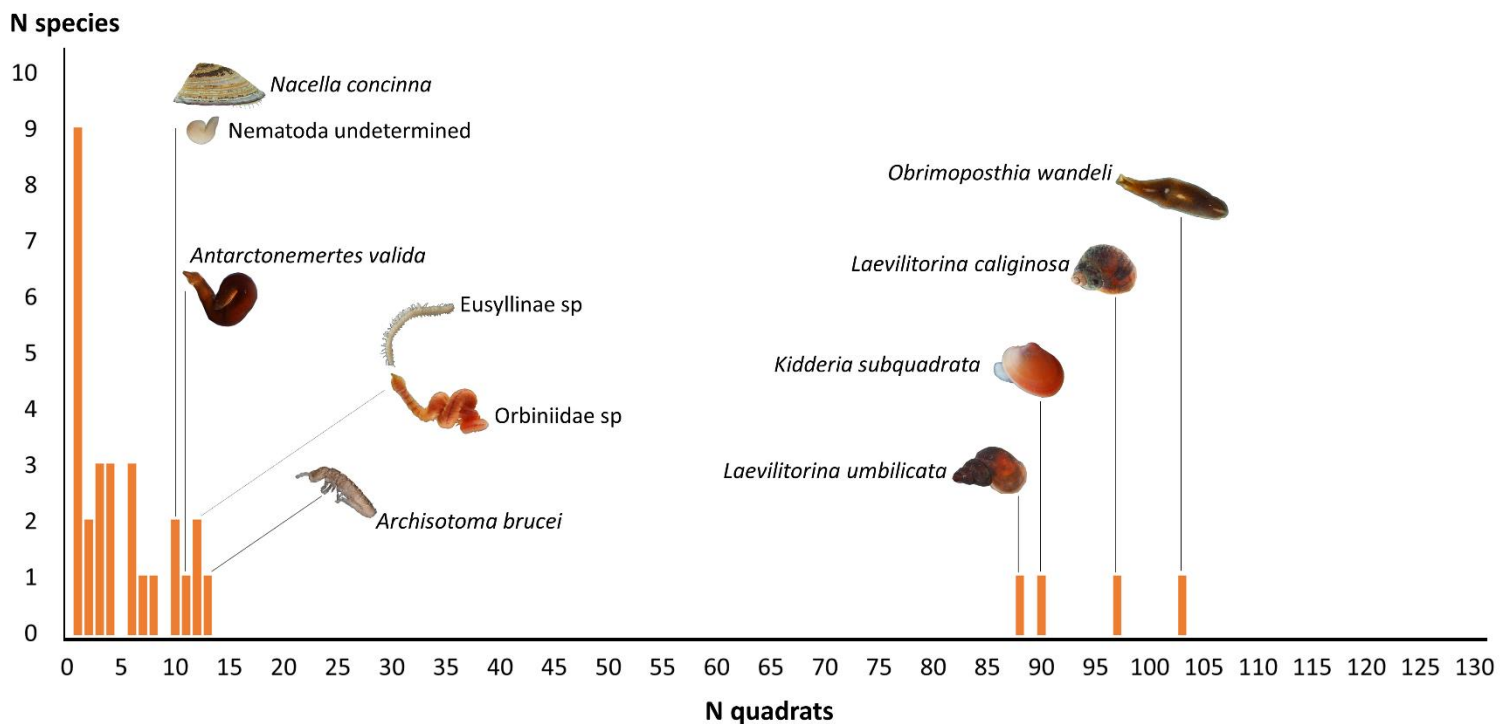
provided as Supplementary materials. The specimens used in this study are hosted at the Université Libre de Bruxelles (ULB, Brussels, Belgium) – Laboratoire de Biologie Marine.

## FIGURES & TABLES

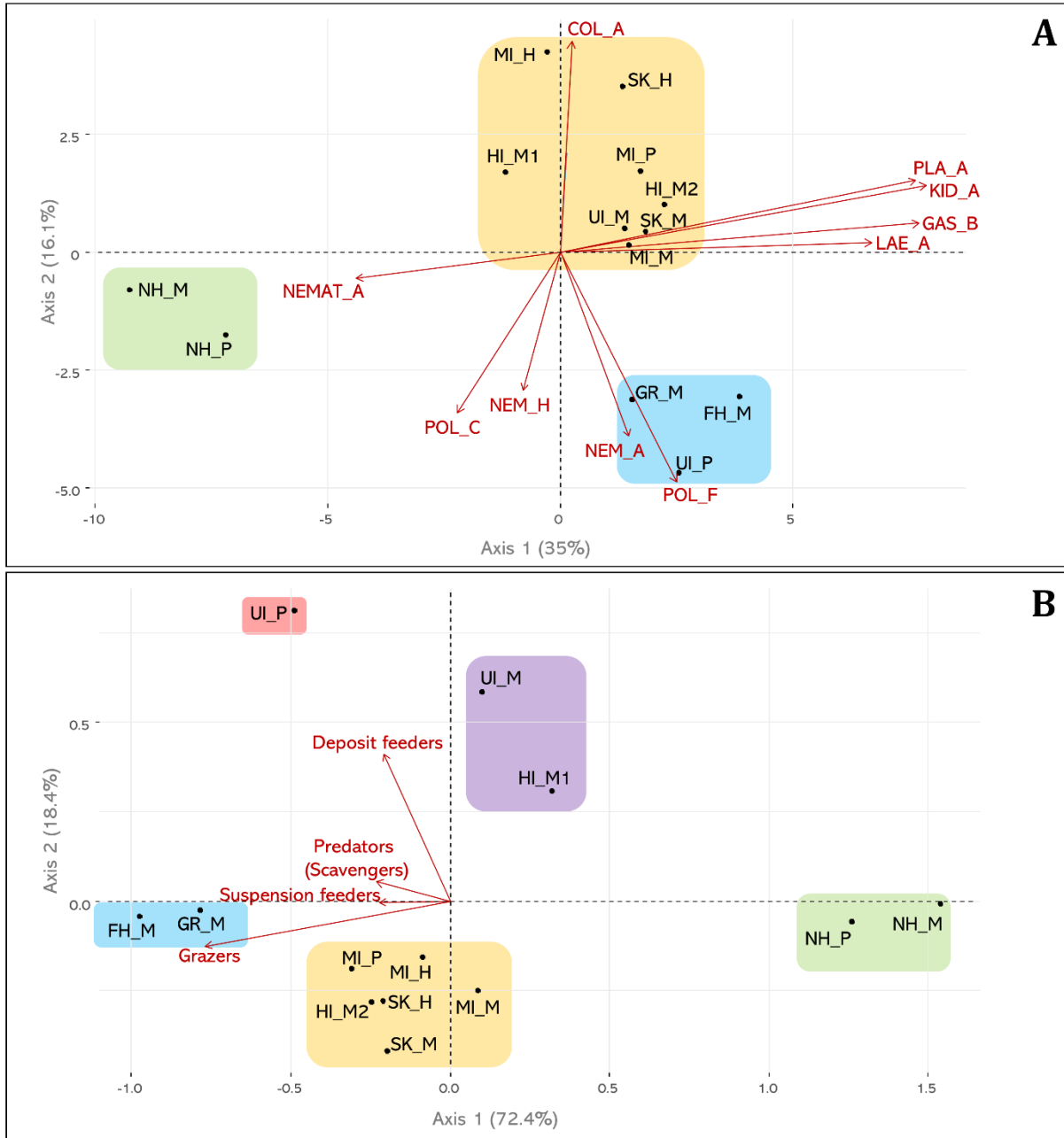
**Fig. 1 – Intertidal sites in and around the Gerlache Strait (western Antarctic Peninsula) investigated in the current study.** MI: Melchior Islands, FH: Føyen Harbor, GR: Green Reef, UI: Useful Island, NH: Neko Harbor, SK: Skontorp Cove, HI\_M1: Hovgaard Islands 1, HI\_M2: Hovgaard Islands 2.



**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).



**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 visualization, the five main contributors (species) to each axis are shown in (A). MI: Melchior Islands; FH: Føyn 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.



**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.

<b>Taxa (ordered by Phylum and Class)</b>	<b>Code</b>	<b>N locations</b>	<b>% quadrats</b>	<b>BOLD</b>
<b>Annelida - Clitellata</b>				
<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*
<b>Annelida - Polychaeta</b>				
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
<i>Pterocirrus giribeti</i> Leiva et al., 2018	POL_N	1	1%	INTGS120-22*
Terebellidae sp. Johnston, 1846	POL_B	5	3%	INTGS111-22*
<b>Arthropoda - Collembola</b>				
<i>Archisotoma brucei</i> (Carpenter, 1907)	COL_A	2	10%	INTGS054-22*
<b>Arthropoda - Amphipoda</b>				
<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> K.H. 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
<b>Arthropoda - Euphausiacea</b>				
<i>Euphausia superba</i> Dana, 1850	KRI_A	1	0%	INTGS079-22*
<b>Arthropoda - Isopoda</b>				
<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*
<b>Arthropoda - Pycnogonida</b>				
<i>Achelia</i> sp. Hodge, 1864	PYC_A	1	0%	INTGS133-22
<b>Bryozoa - Gymnolaemata</b>				
<i>Antarctothoa</i> sp. Moyano, 1987	BRY_D	1	0%	INTGS047-22*
<i>Chaperiopsis cf. quadrispinosa</i> (Kluge, 1914)	BRY_G	1	0%	INTGS049-22
Gymnolaemata 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*
<b>Chordata - Actinopterygii</b>				
<i>Harpagifer antarcticus</i> Nybelin, 1947	HAR_A	2	0%	INTGS067-22*
<b>Chordata - Ascidiacea</b>				
<i>Cnemidocarpa verrucosa</i> (Lesson, 1830)	ASC_A	1	0%	INTGS037-22*

<b>Cnidaria - Anthozoa</b>				
<i>Edwardsia</i> sp. Quatrefages, 1842	ANE_A	2	3%	INTGS035-22
<i>Glyphoperidium bursa</i> Roule, 1909	ANE_B	2	0%	INTGS036-22*
<b>Cnidaria - Hydrozoa</b>				
<i>Candelabrum austrogeorgiae</i> (Jäderholm, 1904)	CAN_A	2	0%	INTGS050-22*
<i>Staurocladia charcoti</i> (Bedot, 1908)	STA_A	2	1%	INTGS136-22*
<b>Cnidaria - Staurozoa</b>				
<i>Lucernaria cf. australis</i> Vanhöffen, 1908	STA_B	1	0%	INTGS137-22*
<b>Echinodermata - Asteroidea</b>				
<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*
<b>Echinodermata - Holothuroidea</b>				
<i>Psolus granulosus</i> Vaney, 1906	HOL_A	2	0%	INTGS071-22*
<i>Sigmoidota contorta</i> (Ludwig, 1875)	HOL_B	1	0%	INTGS072-22*
<b>Mollusca - Bivalvia</b>				
<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*
<b>Mollusca - Gastropoda</b>				
<i>Laevilacunaria antarctica</i> (E. von Martens, 1885)	GAS_H	1	1%	INTGS064-22*
<i>Laevilacunaria bennetti</i> (Preston, 1916)	GAS_A	5	5%	INTGS055-22*
<i>Laevitorina caliginosa</i> (Gould, 1849)	LAE_A	12	75%	INTGS080-22*
<i>Laevitorina 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. H. Adams & A. Adams, 1852	GAS_F	1	5%	INTGS063-22
<b>Mollusca - Polyplacophora</b>				
<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*
<b>Nematoda</b>				
Nematoda spp. Diesing, 1861	NEMAT_A	1	8%	INTGS096-22
<b>Nemertea - Hoplonemertea</b>				
<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*
<i>Nipponnemertes</i> sp. Friedrich, 1968	NEM_B	2	0%	INTGS089-22*
<b>Nemertea - Pilidiophora</b>				
<i>Parborlasia corrugatus</i> (McIntosh, 1876)	NEM_D	2	0%	INTGS093-22*
<b>Platyhelminthes</b>				
<i>Obrimoposthia wandeli</i> (Hallez, 1906)	PLA_A	11	79%	INTGS108-22*
<i>Platyhelminthes</i> sp. Minot, 1876	PLA_B	1	0%	INTGS110-22
<b>Porifera - Demospongiae</b>				
<i>Halichondrida</i> sp. Gray, 1867	POR_D	1	0%	INTGS125-22
<i>Haliclona</i> sp. Grant, 1841	POR_F	1	0%	INTGS127-22
<i>Homaxinella cf. balfourensis</i> (Ridley & Dendy, 1886)	POR_E	1	0%	INTGS126-22*
<i>Homaxinella</i> sp. Topsent, 1916	POR_B	1	0%	INTGS123-22
<i>Hymeniacidon cf. torquata</i> Topsent, 1916	POR_C	1	0%	INTGS124-22
<i>Tedania (Tedaniopsis) charcoti</i> Topsent, 1907	POR_G	1	0%	INTGS128-22
<b>Porifera - Calcarea</b>				
<i>Calcarea</i> sp1 Bowerbank, 1862	POR_H	1	0%	INTGS129-22
<i>Calcarea</i> 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

**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)
<b>MI_H</b> (Melchior Isl. high-shore)	7	0.60	7.45 ( $\pm 1.21$ )	7	4
<b>MI_M</b> (Melchior Isl. mid-shore)	7	0.79	9.70 ( $\pm 4.02$ )	11	6
<b>MI_P</b> (Melchior Isl. intertidal pools)	8	0.62	8.23 ( $\pm 0.67$ )	24	8
<b>NH_M</b> (Neko Harbor mid-shore)	2	0.91	2.00 ( $\pm 0.47$ )	3	3
<b>NH_P</b> (Neko Harbor intertidal pools)	4	0.50	5.80 ( $\pm 3.39$ )	7	4
<b>UI_M</b> (Useful Isl. mid-shore)	10	1.01	21.25 ( $\pm 15.46$ )	19	6
<b>UI_P</b> (Useful Isl. intertidal)	12	0.77	13.35 ( $\pm 2.10$ )	31	9
<b>SK_H</b> (Skontorp Cove high-shore)	7	0.66	7.90 ( $\pm 2.03$ )	12	5
<b>SK_M</b> (Skontorp Cove mid-shore)	9	0.99	18.00 ( $\pm 9.54$ )	26	9
<b>HI_M1</b> (Hovgaard Isl. 1 mid-shore)	6	0.61	6.00 ( $\pm 0.54$ )	9	4
<b>HI_M2</b> (Hovgaard Isl. 2 mid-shore)	6	0.45	6.00 ( $\pm 0.47$ )	14	7
<b>GR_M</b> (Green Reef mid-shore)	14	0.96	36.05 ( $\pm 28.04$ )	32	8
<b>FH_M</b> (Føyn Harbor mid-shore)	14	0.85	21.20 ( $\pm 10.53$ )	31	9
<b>All locations</b>	32	1.88	52.09 ( $\pm 20.04$ )	88	11