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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,
49 Barcode of Life Data Systems (BOLD) - 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.

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*: Mabragaña 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*

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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Availability of data and materials: 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.

FIGURES & TABLES

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

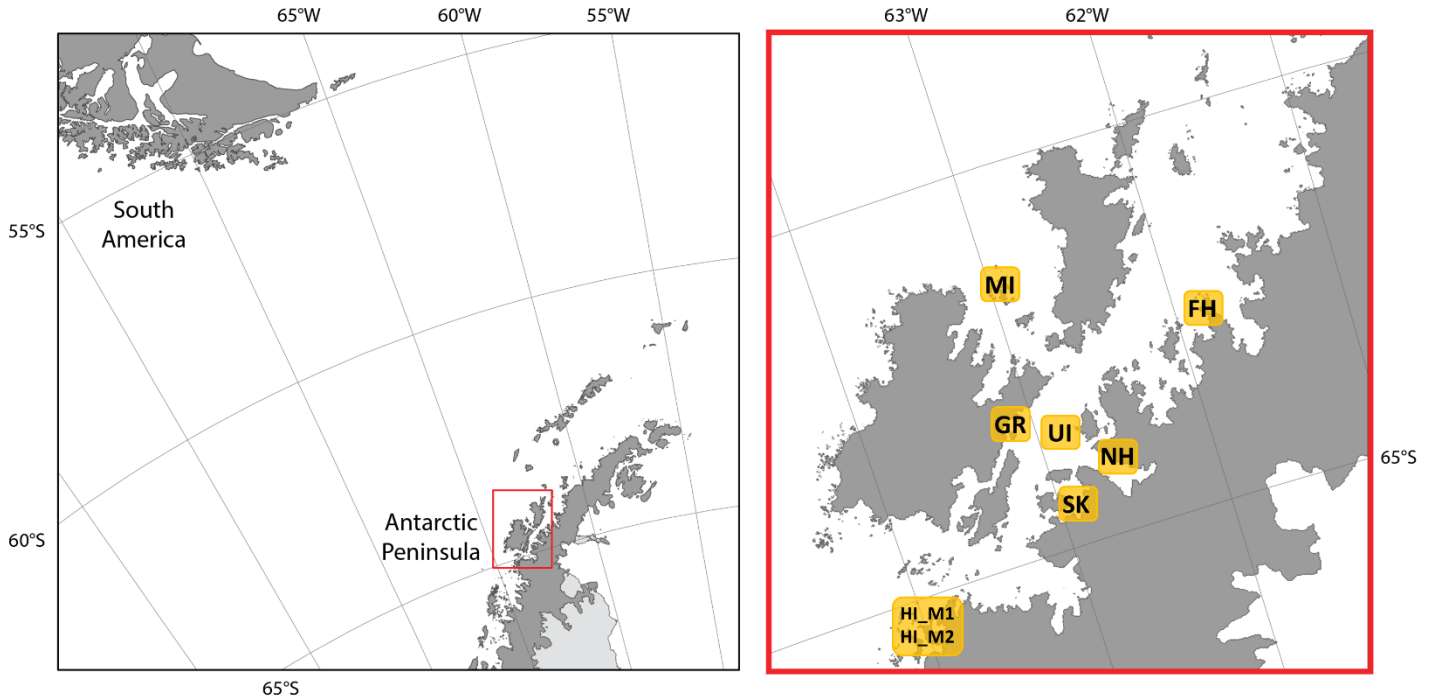


Fig. 2 – Species distributions in the study area. Number of species versus number of quadrats, with the species illustrated being the ten most abundant in the entire area. Each species illustrated refers to the exact number of quadrats in which the species was found (e.g. *Obrimoposthia wandeli* was reported in 103 quadrats while *Archisotoma brucei* was reported in 13 quadrats).

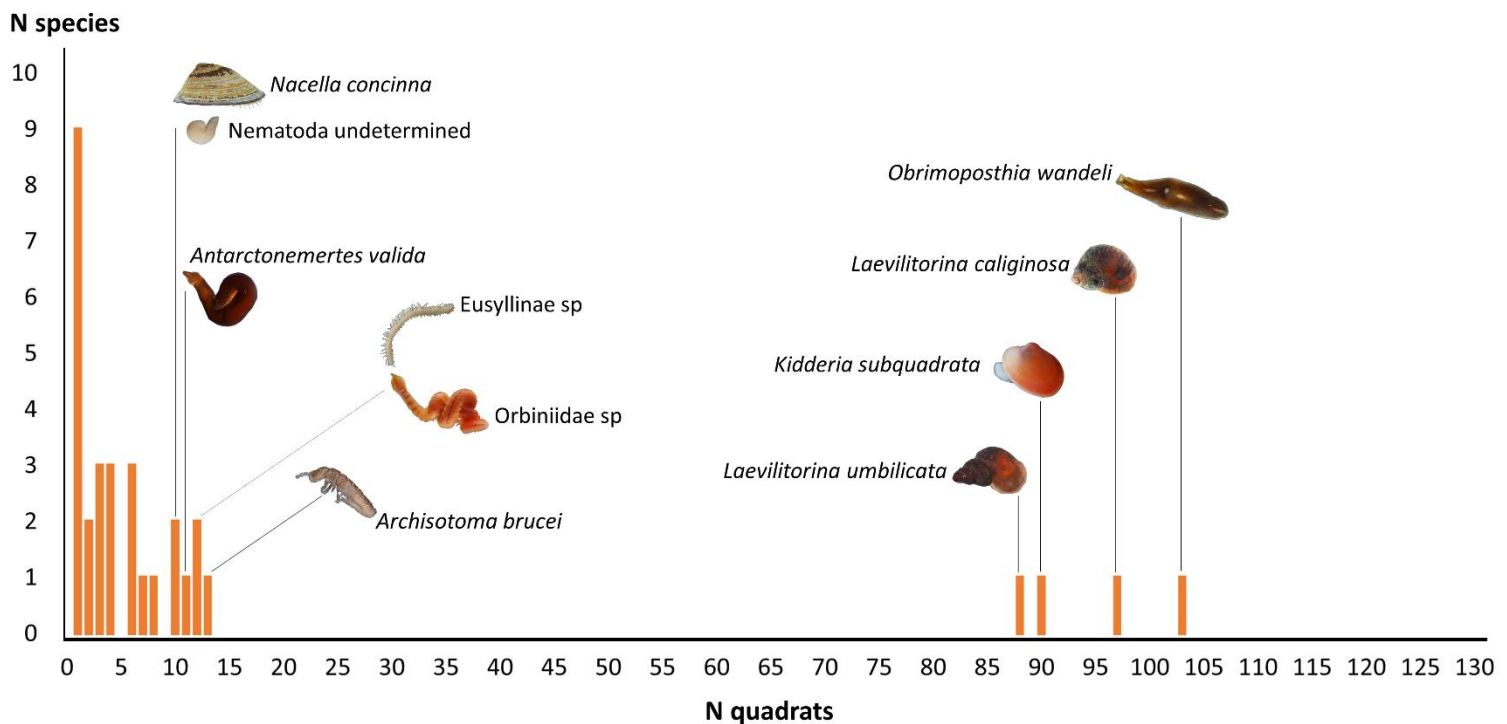


Fig. 3 – Principal Component Analysis (PCA) based on species data (A) and functional group data (B). Sampling locations are represented by black dots and species/functional groups by red arrows (see full names in Tables 1 & 2). Colored squares represent the groups defined by Ward clustering. For clearer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

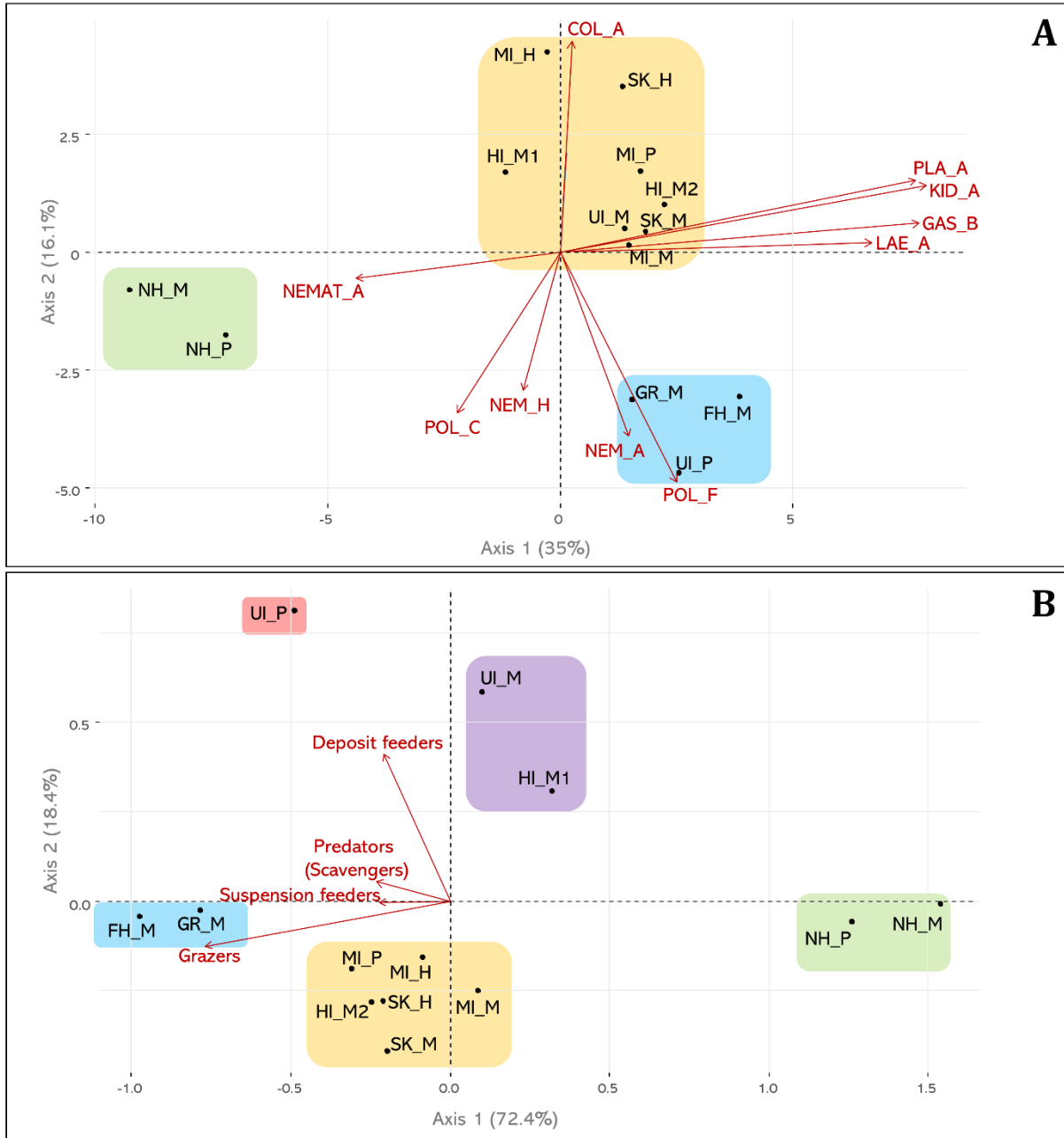


Table 1 - Taxa found in the study area. N locations: number of locations (maximum = 13) where the species was found either within or in the vicinity of quadrats. % quadrats: percentage of quadrats where the species was found (out of the 130 quadrats investigated in total). BOLD: Public accession number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

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
<i>Pterocirrus giribeti</i> 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> 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
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*
<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*
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 granulosus</i> Vaney, 1906	HOL_A	2	0%	INTGS071-22*
<i>Sigmoidota 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> (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
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*
<i>Nipponnemertes</i> sp. Friedrich, 1968	NEM_B	2	0%	INTGS089-22*
Nemertea - Pilidiophora				
<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*
<i>Platyhelminthes</i> sp. Minot, 1876	PLA_B	1	0%	INTGS110-22
Porifera - Demospongiae				
<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
Porifera - Calcarea				
<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)
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
All locations	32	1.88	52.09 (± 20.04)	88	11