1   **TITLE: Diversity and spatial variability of shallow benthic macrofaunal assemblages in**

2   **a high-Arctic fjord (Young Sound, North-East Greenland)**

3

4   Guillaume Bridier[1,2], Frédéric Olivier[3], Lucas Pinsivy[1], Jérôme Jourde[4], Laurent

5   Chauvaud[1], Mikael K. Sejr[5], Thomas Burel[1], Michel Le Duff[6], Jacques Grall[1,6]

6

7   Research article submitted to *Polar Biology*.

8

9

10 [1]Laboratoire   des   Sciences   de   l'Environnement   Marin   (LEMAR)   UMR   6539

11 UBO/CNRS/IRD/Ifremer, rue Dumont D'Urville, 29280 Plouzané, France

12 [2]Present Address: Institut des Sciences de la mer de Rimouski, Université du Québec à

13 Rimouski, 310 allée des Ursulines, QC G5L 2Z9 Rimouski, Canada

14 [3]Biologie   des   Organismes   et   Ecosystèmes   Aquatiques   (BOREA)   UMR   7208

15 MNHN/SU/UA/CNRS/IRD, 61 Rue Buffon CP53, 75005 Paris, France

16 [4]OBIONE (Observatoire de la Biodiversité Faune Flore des Pertuis Charentais) UMR 7266

17 LIENSs CNRS/Université de La Rochelle, 2 rue Olympe de Gouges, 17000 La Rochelle,

18 France

19 [5]Department of EcoScience & Arctic Research Centre, Aarhus University, C.F. Møller Alle 3,

20 bld. 1131, 8000 Aarhus, Denmark

21 [6]Observatoire Marin, UMS 3113, Institut Universitaire Européen de la Mer, rue Dumont

22 D'Urville, 29280 Plouzané, France

23

24

25 Corresponding author: Guillaume Bridier (guillaume.bridier@live.ie)

26

27   **Abstract**

28   Although knowledge of Arctic benthic biodiversity has increased considerably in recent
29   decades, some regions, such as Northeast Greenland, remain poorly studied. The aim of this
30   study was to complement a previous macrofaunal inventory carried out in Young Sound, a
31   High-Arctic fjord in this region (74°N). We sampled shallow benthic assemblages along a small
32   inner/outer fjord gradient, including one station previously prospected two decades ago and
33   three new stations. This sampling strategy revealed highly diversified benthic assemblages (166
34   species identified on a total sampling area of 1.32 m²), which considerably increases the number
35   of species recorded for the fjord (i.e. 225 species vs 100 previously recorded). The outermost
36   station was dominated in abundance by various assemblages of bivalves, while the middle
37   stations showed greater species evenness, including numerous species of polychaetes, bivalves
38   and crustaceans. The innermost station was dominated by ostracods, gammarid amphipods and
39   tube-dwelling polychaetes. Overall, benthic assemblages varied little between the four stations
40   and the transect as a whole exhibited characteristics typical of outer fjord habitats, reflecting
41   the rather moderate impact of meltwater inputs in this part of the fjord. Finally, trophic plasticity
42   and omnivory were observed in most of the recorded macrobenthic species, highlighting the
43   adaptability of these species to low trophic availability in the ecosystem. Future biodiversity
44   studies will need to explore the innermost and deepest areas to provide a more comprehensive
45   inventory and understanding of the influence of environmental conditions on the structure and
46   functioning of Young Sound benthic habitats.

47   **Key words**

48   **Benthic ecosystems • Macrofauna • Community structure • Spatial variability • Meltwater**
49   **inputs • Arctic fjord**

Introduction

To date, Arctic benthic biodiversity remains poorly studied although species colonizing the seafloor represent around 90 % of the total estimated species richness of Arctic invertebrates (Sirenko 2001; Gradinger et al. 2010). While Arctic benthic ecosystems have long been considered as areas of low species diversity (e.g. Knox and Lowry 1977), there is increasing evidence that this assumption has likely been biased by the scarcity of surveys conducted at high latitudes (Piepenburg 2005; Piepenburg et al. 2011). Recent inventories estimate the diversity of Arctic benthic species to be over 4600 species, a much higher number than previously estimated, while several thousand species are likely to remain to be discovered (Bluhm et al. 2011; Josefson et al. 2013). Although considerable progress has been made in Arctic biodiversity in recent decades, some geographic areas remain understudied such as East Greenland (Piepenburg et al. 2011).

Under climate change, Arctic benthic ecosystems are expected to undergo major modifications driven by changes in sea ice cover, salinity and temperature, acidification, or sedimentation (AMAP 2017). It is very likely that these changes will impact benthic biodiversity, especially in coastal areas, which are expected to be the most exposed to future environmental changes (Węsławski et al. 2011). The expansion of boreal species into high latitudes is also expected to affect benthic biodiversity by bringing new species into Arctic areas (Węsławski et al. 2011; Kotwicki et al. 2021; Cottier-Cook et al. 2023), with likely consequences for species interactions and ecosystem functioning. Indeed, the recent expansion of several engineer species with boreal affinities into the Arctic (e.g. mussel species from the *Mytilus* spp. complex or the kelp *Laminaria hyperborea*) has had implications for the structure of shallow benthic ecosystems by increasing habitat heterogeneity and complexity, facilitating the arrival of species new to these ecosystems (Berge et al. 2005; Krause-Jensen and Duarte 2014; Mathiesen et al. 2017; Filbee-Dexter et al. 2019; Kotwicki et al. 2021). Many questions remain unresolved regarding how endemic benthic species will cope with new abiotic conditions (increases in temperature or sedimentation, decreases in seawater salinity) and associated changes on biotic interactions (e.g. the arrival of new predators or competitors, Renaud et al. 2015). Assessing the vulnerability of Arctic benthic communities experiencing such environmental and ecological changes thus remains challenging and highlights the strong need for initial references states in benthic biodiversity in all Arctic ecoregions.

81   In this context, any increase in knowledge of the benthic biodiversity of poorly characterized
82   Arctic ecoregions is crucial, especially in shallow coastal ecosystems. For example, the only
83   studies conducted on the North-Eastern coasts of Greenland have focused on epifauna and/or
84   megafauna shelf communities (e.g. Piepenburg and Schmid 1996; Brandt and Schnack 1999;
85   Starmans et al. 1999; Fredriksen et al. 2020). To our knowledge, for such real *Terra Incognita*
86   of Arctic ecoregions (Piepenburg et al. 2011), only Sejr et al. (2000) provided quantitative
87   datasets on shallow macrozoobenthos assemblages in a high-Arctic fjord (Young Sound, NE
88   Greenland). Few studies have also investigated trophic linkages in macrobenthic ecosystems
89   from the Northeast Water Polynya providing only limited details on their biodiversity (Hobson
90   et al. 1995; Ambrose and Renaud 1997; Piepenburg et al. 1997). Finally, although many older
91   studies from the mid-20th century have been conducted on the shallow habitats (e.g. Ockelmann
92   1958), they have mostly focused on the occurrence of individual taxa than providing insights
93   into the structure and diversity of macrobenthic communities.

94   The aim of the present study is to complement the inventory of benthic macrofaunal species
95   carried out by Sejr et al. (2000) in Northeast Greenland (Young Sound, 74°N) with additional
96   sampling sites. While Sejr et al. (2000) examined the macrobenthic communities in vertical
97   zonation (from 20 to 85 m), this study prospects shallow benthic macrofaunal assemblages (≈
98   20 m) distributed along a small inner/outer gradient located in the most marine part of the fjord.
99   We resampled the shallowest Daneborg station from Sejr et al. (2000) and investigated three
100   new stations, one towards the outer fjord (Kap Breusing) and two towards the inner fjord (Basalt
101   Island, Pass Hytten). The description of the assemblages, coupled with those of Sejr et al.
102   (2000), aims to provide a baseline for future studies investigating the temporal variability of
103   Arctic shallow coastal soft-bottom communities and their response to ongoing climate change.

Materials and Methods

104

Study sites

105

106   Young Sound is a high Arctic fjord located in North-East Greenland (Fig. 1) of about 90 km
107   long and 2-7 km wide (Rysgaard et al. 2003). A sill is located at its outer section (≈ 45 m depth,
108   see Fig. 1) limiting seawater exchanges between the inner parts of the fjord and the shelf
109   (Bendtsen et al. 2007) where average and maximum depths reach 100 and 360 m, respectively
110   (Rysgaard et al. 2003). This fjord is characterized by extreme seasonal variations, thick sea ice
111   (> 150 cm) and snow cover (20 – 100 cm) covering the fjord for 9 to 10 months per year (Glud

112   et al. 2007) and strongly limiting the annual primary production, estimated to be about 10 g C

113   m^{-2} yr^{-1} (Rysgaard et al. 1999). During the summer, glacier and snow melt generate strong river

114   flows ranging annually from 0.9 to 1.4 km^3 (Bendtsen et al. 2014). Such freshwater inputs

115   induce strong spatial salinity and temperature gradients in summer surface waters, with

116   temperature decreasing from 9 to 2°C and salinity increasing from 8 to 30, from the inner to the

117   outer part of the fjord, respectively (Bendtsen et al. 2007). In contrast, deeper waters (> 20 m)

118   generally remain stable throughout the year (i.e. > 2° C) along the entire fjord length (Holding

119   et al. 2019). Vertical variations in salinity induce a strong permanent haline stratification at 5

120   to 10 m depth, which limits pelagic primary production by reducing nutrient exchange between

121   surface and subsurface waters (Holding et al. 2019; Sejr et al. 2022). On a decadal scale, the

122   sea ice conditions in the fjord have changed with a gradual increase in the duration of the ice-

123   free season from about 80 days per year (1950-2000) to more than 90 days per year but

124   combined with a significant increase in the year-to-year variability since 2000. At the same

125   time, freshwater runoff (mostly glacial meltwater) is estimated to have increased 6-7 fold since

126   the 1960s (Sejr et al. 2022). Annual monitoring of main Young Sound environmental

127   parameters (physico-chemical, pelagic productivity and community structure) has been made

128   for three decades by the Greenland Ecosystem Monitoring – Marine Basis program, making

129   Young Sound ideal for studying the effects and feedback of climate change in the high Arctic.

130   However, the macrozoobenthic benthic communities are not part of the monitoring program

131   since the study by Sejr et al. (2000), highlighting the crucial need to reacquire biodiversity data.

132   **Sampling and laboratory analyses**

133   Sampling was conducted in August 2016 at four stations distributed along an inner/outer marine

134   fjord gradient: Pass Hytten, Basalt Island, Daneborg and Kap Breusing (Fig. 1, Table 1).

135   Macrofauna samples were collected by scuba divers for each replicate using a modified Hiscock

136   and Hoare suction dredge (Eleftheriou and McIntyre 2005), fitted with a suction pipe directly

137   connected to a nylon mesh sample bag (square mesh = 1 mm). Each replicate was collected

138   over an area of 0.09 m² (except for one replicate at Kap Breusing, which was collected over

139   0.0625 m²) and then fixed directly in 10% buffered formalin. Sediment samples were also

140   collected at both Pass Hytten and Kap Breusing using small sediment cores for grain size

141   analysis. Due to logistical problems, we were unable to collect sediment samples at either

142   Daneborg or Basalt Island. Once in the laboratory, the animals were sorted, transferred to 70%

143   ethanol and then identified to the lowest taxonomic level. Sediment samples were analyzed by

144   the private company "*Eurofins – Analyses pour l'environnement*" (Saverne, France) using laser

145   methods: samples were sieved through a 2 mm square mesh and then analyzed using a Malvern

146   Mastersizer 2000 laser particle size analyzer to provide different size fractions ranging from 2

147   to 2000 µm.

148   **Statistical analyses**

149   Spatial differences in benthic assemblage structure were visualized using Principal Component

150   Analysis (PCA) performed on Hellinger-transformed fauna abundances. This transformation

151   was selected to reduce the weight of rare species in the analysis (Legendre and Gallagher 2001).

152   The first twenty species explaining the most spatial variation in the ordination (i.e. accounting

153   for more than 60% of SIMPER dissimilarities) were plotted in a second graph to visualize which

154   species contributed to the benthic structure of each station. Spatial differences in community

155   structure were tested using one-way permutational multivariate analysis of variance

156   (PERMANOVA) performed on Bray-Curtis transformed fauna abundances. Homoscedasticity

157   was checked using a permutational analysis of multivariate dispersions (PERMDISP) test to

158   ensure that data dispersion did not influence the PERMANOVA result (Anderson et al. 2008;

159   Anderson and Walsh 2013). Species rarefaction curves were calculated for each replicate to

160   compare trends in species richness between stations. Species richness was compared among

161   replicates based on rarefaction curves by standardizing all data to the same abundance

162   (corresponding to the number of individuals in the replicate with the lowest abundance) to

163   remove any abundance bias on taxa richness (Gotelli and Colwell 2001). An additional

164   rarefaction curve was plotted to estimate the specific richness for the entire Young Sound

165   system and Hulbert's diversity index was calculated to estimate the expected number of species

166   within a random sample of 35 individuals (based on the lowest number of individuals observed

167   in a replicate). Jacknife1 Chao2 estimates were calculated and plotted as accumulation curves

168   to estimate the total species richness in case species rarefaction curves did not reach their

169   asymptotes (Colwell et al. 2004; Chao and Chiu 2016). Finally, we calculated the Pielou's

170   evenness index to take into account the diversity observed at each station along with the

171   associated species richness using the "vegan" R package (Oksanen et al. 2019). All other

172   diversity indices were calculated using EstimateS v9.1 software.

Results

Structure of benthic community

Significant differences in benthic community structure were observed between sampling stations (degrees of freedom for treatment and error [df] = 3 and 11, pseudo-F = 8.2529, p-perm = 0.001). Pairwise analyses revealed that such differences were observed between all stations (the smallest significant difference was observed between Basalt Island and Kap Breusing, df = 1 and 4, pseudo-F = 7.4856, p-perm = 0.049). PCA analysis showed that more than half of the spatial variability was explained by the first three principal components (PC1, PC2 and PC3 explained 24.36, 17.92 and 17.27 % of the variance, respectively). Low dispersion was observed among the replicates of each station (Fig. 2a, c). Significant differences in Pielou's evenness index were observed between stations (df = 3 and 14, pseudo-F = 36.4600, p-perm = 0.001). These differences were observed between all stations by pairwise PERMANOVA analyses (the smallest significant difference was observed between Daneborg and Kap Breusing, df = 1 and 4, pseudo-F = 16.2496, p-perm == 0.048), except between Pass Hytten and Kap Breusing (df = 1 and 4, pseudo-F = 0.0386, p-perm = 1).

Benthic assemblages at Pass Hytten were strongly dominated by crustaceans (relative abundance = 52.9 - 78.0%, Fig. 3a, b), mainly due to high densities of ostracods and the amphipod *Metopa glacialis* (Fig. 2b). The community structure at Daneborg and Basalt Island was more evenly balanced between taxa (Fig. 3a, b), although polychaetes were the most dominant group (relative abundance = 32.6 - 58.3% at Daneborg and 44.9 - 55.9% at Basalt Island). *Euchone analis*, *E. incolor* and *Laphania boecki* were the most abundant polychaete species at Daneborg, while *Abyssoninoe* sp., *Laphania boecki* and *Nereimyra aphroditoides* dominated the polychaete assemblage at Basalt Island (Fig. 2b, d). Finally, bivalves were the dominant taxonomic group at Kap Breusing (relative abundance = 67.5 - 68.5%, Fig. 3a, b), largely represented by high densities of the filter-feeding bivalves *Hiatella arctica* and *Musculus discors* (> 50%, Fig. 2b, d).

Total abundance showed large variation among stations and replicates (Fig. 3b). The highest abundances were observed in the second replicate from Kap Breusing (reaching 6044 ind. m^{-2}, Fig. 2b). In contrast, the first replicate from Kap Breusing showed a much lower total abundance (1824 ind. m^{-2}), which was in the same order of magnitude as the abundances observed at Daneborg (from 933 to 1733 ind. m^{-2}) and Pass Hytten (from 1467 to 2667 ind. m^{-2}, Fig. 2b).

204   Finally, the lowest total abundances were observed at Basalt Island (from 389 to 1611 ind. m^{-2},
205   Fig. 2b).

Abiotic and biotic description of benthic habitats

207   *Pass Hytten*

208   The sediment texture is dominated by fine silt particles (55% of the total size fraction for
209   particles < 63 µm) mixed with fine sands (25%) and gravels (20%, Fig. 1 in Online Resource
210   1). Significant bioturbation activity probably occurs due to high abundances of epifauna (e.g.
211   *Ophiocten sericeum*, Fig. 4a, Table 2) and burrowing shrimps (e.g. *Sclerocrangon boreas*, L.
212   Chauvaud pers. obs.). The associated macrozoobenthic assemblage shows a low species
213   evenness with ten taxa representing 83.5% of the total abundance (Table 2), including
214   crustaceans such as ostracods, the amphipod *Metopa glacialis* and the cumacean *Diastylis*
215   *scorpioides* (59 % of the total abundance). The strictly benthic species (epifauna and endofauna)
216   were dominated by both tube-dwelling (*Euchone incolor* [see high abundances in Fig. 3a],
217   *Lyssipe labiata*, *Maldane sarsi* and *Owenia borealis*) and errant polychaetes (*Abyssoninoe* sp.
218   and *Leitoscoloplos mammosus*). Bivalves *Astarte moerchi*, *Hiatella arctica*, *Mya truncata* and
219   *Musculus discors*) also occur but in much lower proportions (< 15 % of the total abundance).

220   *Basalt Island*

221   Here, the sediment is a mixture of stone, sand and small gravel (2-5 mm) associated with detrital
222   organic matter (mainly macroalgae and shell debris) accumulated on the seafloor (Fig. 4b).
223   However, we were unable to sample the sediment at this station due to the dominance of stones.
224   The steep slope of the seafloor (slope gradient ≈ 80 – 100 %, see Fig. 4b) probably makes the
225   bottom unstable due to the downward export of mineral material towards the deep fjord basins.
226   The species assemblage at Basalt Island shows greater species evenness than Pass Hytten and
227   Kap Breusing, with the ten most dominant species accounting for only 51.3% of total abundance
228   (Table 2). Polychaetes dominate the species assemblage with *Abyssoninoe* sp., *Clymenura* sp.,
229   *Laphania boecki*, *Nereimyra aphroditoides* and *Pholoe* sp. representing 26.4 % of the total
230   abundance. Several bivalves such as *A. moerchi*, *H. arctica* or *M. truncata* were also found at
231   the site but in low abundances, as well as the brittle star *Ophiocten sericeum* (Table 2, Table S1
232   in Online Resource 1). Among crustaceans, ostracods show a high abundance (5.9 %, Table 2).

233   *Daneborg*

234   Based on underwater pictures and previous data on particle size distribution (Sejr et al. 2000),
235   the seabed was characterized by a mixture of fine and very fine sand (particles [63 - 125 µm] =

236   24.6 % and particles > 125 µm = 44.2 %). The species evenness of the species assemblage was

237   close to that observed at Basalt Island (Table 2). Daneborg is mainly dominated by two taxa,

238   bivalves and in particular the species *Astarte moerchi* (18.6 %) and crustaceans (ostracods and

239   *D. scorpioides* representing 11.8 % and 3.1 % of the total abundance, respectively). Polychaetes

240   complete the assemblage, including *Euchone incolor*, *Laphania boecki*, *Euchone analis*, *Chone*

241   sp. and *Clymenura* sp., which all account for 23.6% of the total abundance.

242   *Kap Breusing*

243   The grain size distribution of Kap Breusing was variable between replicates, but overall it was

244   a poorly sorted sandy sediment (the 63-2000 µm grain size range varied from 53 to 80 %, Fig.

245   S1 in Online Resource 1). Heterogeneous medium/coarse sand (38 to 55 % of the particles

246   between 250 and 2000 µm) was found in two of the three replicates, the other was largely

247   composed of fine sand (61 % of particles between 63 and 250 µm).

248   The species assemblage here was associated with a rock wall close to the location where the

249   sediment samples were collected and included Sertulariidae hydrozoans and *Musculus discors*

250   bivalves (L. Chauvaud, pers. obs., see background of Fig. 4d). Both species form a complex

251   three-dimensional structure hosting a highly diversified assemblage including the gastropod

252   *Alvania scrobiculata* and the bivalves *A. moerchi*, *H. arctica*, *M. discors* and *M. truncata*,

253   representing more than 68% of the total abundance (Table 2). Four vagile polychaete species

254   were also found as *Harmothoe* sp., *Nereimyra aphroditoides*, *Nereis zonata* and *Syllis* sp. (11.3

255   % of total abundance) and the sedentary terebellid *Polycirrus medusa* (2.8 %; Table 2).

256   **Biodiversity estimates of benthic habitats**

257   Based on a total area of 1.32 m^2 sampled by 15 suction dredge replicates, we collected a total

258   of 2322 individuals belonging to 166 species (Table S1 in Online Resource 1). The polychaete

259   phylum was by far the most diverse (67 species), followed by mollusks (33 species) and

260   crustaceans (31 species). Echinoderms, nemerteans, sipunculans, pycnogonids, tunicates,

261   nematodes, brachiopods and platyhelminths were also found but always displayed with much

262   lower species richness. Macroalgae randomly collected in our samples were also identified, and

263   the species list is included in the supplementary material as complementary observations (Table

264   S2 in Online Resource 1).

265   Species accumulation curves did not reach their asymptotes for all stations (Fig 5). The initial

266   slope of the species accumulation curves was highly variable between stations, but more

267   consistent between intra-site replicates. Based on the lowest number of individuals (i.e. 35 in

268   the 5th Basalt Island replicate), Hulbert's expected species richness within a random sample of

269   35 individuals (ES$_{35}$) displayed the lowest levels in Pass Hytten and Kap Breusing (i.e. range

270   ES$_{35}$ = 9 − 13 and 12 − 13 for Pass Hytten and Kap Breusing, respectively). Expected species

271   richness showed intermediate values in Daneborg (range ES$_{35}$ = 15 − 21) and the highest levels

272   in Basalt Island (range ES$_{35}$ = 19 − 22). Based on the total number of species per replicate (S$_{tot}$),

273   species richness was also lower at Pass Hytten (range S$_{tot}$ = 17 − 31) than at Basalt Island (range

274   S$_{tot}$ = 19 − 43) and Daneborg (range S$_{tot}$ = 32 − 47), while Kap Breusing had the highest intra-

275   station variability (range S$_{tot}$ = 27 − 59). A rarefaction curve based on the total set of fauna

276   samples (i.e. all replicates from the four sampled stations combined) also does not reach an

277   asymptote either, despite the much higher number of individuals (i.e. > 2000).

278   The rarefaction curves of Chao2 and Jackkniffe1 estimates slightly differ from the species

279   accumulation curves (Fig. 6a, b). Based on the lowest number of replicates (i.e. 2 sampled

280   stations at Kap Breusing), biodiversity estimates were lowest at Pass Hytten (Chao2 = 48,

281   Jackknife1 = 51), intermediate at Basalt Island (Chao2 = 62, Jackknife1 = 64) and Daneborg

282   (Chao2 = 77, Jackknife1 = 78), and highest at Kap Breusing (Chao2 = 95, Jackknife1 = 91).

283   Based on the entire dataset, Chao2 and Jackknife1 estimates predicted a total species richness

284   of 204 and 221 species, respectively.

Discussion

Benthic species richness of the study area: historical and recent data comparison

287   The present study complements the previous work of Sejr et al. (2000) conducted twenty years

288   ago in Young Sound, which described gradual, spatially limited changes in species assemblages

289   along a depth gradient (from 20 to 85 m) in the vicinity of Daneborg station (Fig. 1). Our study

290   conducted along a small inner/outer fjord gradient in the most marine part of Young Sound

291   shows little spatial variation in shallow (above 20 m depth) benthic community structure. This

292   pattern suggests that our four sampling stations cover a relatively continuous and uniform

293   habitat. The sampled habitat is mostly dominated by large tubicolous polychaetes (e.g.

294   Maldanidae, *Euchone*) and some specific motile polychaetes (*Leitoscoloplos*, *Lumbreneris*),

295   and has a high abundance of suspension-feeding bivalves (e.g. *Astarte*, *Bathyarca*, *Hiatella*).

296   Turbidity and meltwater inputs are generally factors that control community structure in Arctic

297   fjords, decreasing the presence of filter feeders towards the inner areas of fjords exposed to

298   glacial melt (Włodarska-Kowalczuk and Pearson 2004; Sejr et al. 2010; Włodarska-Kowalczuk

299   et al. 2012; Udalov et al. 2021). However, we doubt that turbidity and meltwater inputs account

300   for the spatial variations observed between our four stations, as weak environmental forcing is

301   observed along the small inner/outer fjord gradient studied in our survey. In fact, although

302 turbidity reaches more than 50 NTU in the innermost parts of Young Sound, it only varies from

303 2-3 to less than 1 NTU between Pass Hytten and Kap Breusing (Meire et al. 2017). It is therefore

304 more likely that the observed spatial variability in community structure reflects small-scale

305 habitat variation (bottom varying abundance in bare rock, fine sand, mixed sand and gravel or

306 mud) rather than large-scale environmental variation (i.e. differences in exposure to meltwater

307 inputs).

308 The present study provides a complementary census of 166 benthic species, including

309 numerically dominant polychaetes (67 species), crustaceans (46 species) and mollusks (33

310 species). It complements the previous work by Sejr et al. (2000) which listed a total of 100

311 species despite a higher sampling effort (total sampled surface = 2.24 m^2 vs 1.3225 m^2 here).

312 With only 41 species in common between both studies, the total number of benthic invertebrate

313 species recorded from the Young Sound now reaches a total of 225. The relatively low number

314 of taxa shared between the two inventories mainly reflects the different sampling strategies as

315 Sejr et al. (2000) targeted species assemblages from increasing depths while our sampling

316 focused on a limited spatial fjord gradient that covers contrasting shallow habitats (i.e. silt,

317 sand/gravel, rocky wall) and their associated species assemblages.

318 It should also be noted that identification bias cannot be excluded as a single species may be

319 recorded under two different names over time, as different identification experts were involved

320 and taxonomical descriptions have been produced since 2000. As an example, *Scoloplos*

321 *armiger* (only in Sejr et al. 2000) and *Leitoscolopos mammosus* (only here) have been reported

322 to taxonomic confusion (Mackie 1987; Renaud et al. 2007). Further census efforts will include

323 harmonization of the species list with the involvement of benthic taxonomy experts. It could be

324 assumed that the relatively low number of species common to this inventory and the study by

325 Sejr et al. (2000) is due to long-term variability in benthic community structure. However, this

326 seems unlikely as previous studies conducted in Arctic silled-fjord show a high stability of

327 benthic community structure over several decades (Renaud et al. 2007), in contrast to open

328 fjords (Beuchel et al. 2006; Kortsch et al. 2012).

329 As indicated by the slopes of the species accumulation curves, the inventory of benthic

330 biodiversity in this fjord is far from being complete, with many rare species likely yet to be

331 recorded at all study sites. The expected number of species per 35 individuals (ES_{35}) varies

332 between 9 and 22 species, underlining the high biodiversity but also the heterogeneity across

333 stations and replicates. Based on biodiversity estimates, total species richness of the outer fjord

334   shallow sites should reach around 204-221 species, much higher than previous estimates based
335   on Sejr et al. (2000) and this should be much higher as only a very limited part of the shallow
336   Young Sound has been visited and a wide variety of habitats remains unexplored. Inventory
337   studies on shallow and deep areas of both outer and inner fjord usually find much higher species
338   diversity than in the present work. For example, Kędra et al. (2010) recorded more than 300
339   taxa after extensive multi-year sampling of all soft-bottom habitats in Hornsund (SW Svalbard,
340   from 30 m to 250 m), and Voronkov et al. (2013) found 403 benthic taxa in shallow hard-bottom
341   communities from Kongsfjorden (NW Svalbard). We thus think that the actual benthic species
342   inventory of the Young Sound is far from complete, as it is limited to the only most marine
343   section.

344   **Ecological characteristics and insights about the functioning of the benthic fauna**
345   *Ecological characteristics of benthic assemblages*
346   The current inventory identifies four major benthic assemblages, all belonging to the Young
347   Sound outer fjord benthic community: 1) the rocky outer fjord assemblage (Kap Breusing), 2)
348   the sandy outer fjord assemblage (Daneborg), 3) the sand-gravelly outer fjord assemblage
349   (Basalt Island) and 4) the silty outer fjord assemblage (Pass Hytten).

350   The macrobenthic assemblage collected at Kap Breusing was composed of a unique and poorly
351   described species assemblage dominated by two engineer species, the bivalve *Musculus discors*
352   and the sertulariid colonial hydroids. Several studies have highlighted the ability of some
353   bivalve species to secrete byssus threads to construct nests that host a high diversity of other
354   benthic invertebrate species (e.g. *Arcuatula senhousia*, *Limaria hians*; Morton 1974; Hall-
355   Spencer and Moore 2000). Byssus threads produced by these species transform the physical
356   habitat into a complex three-dimensional structure that is then colonized by hydroids (Merrill
357   and Turner 1963). To our knowledge, only one study has reported this ability for *M*. *discors*
358   (Merrill and Turner 1963). The high biodiversity observed at Kap Breusing (where the highest
359   number of species was observed within a single replicate) reflects the structuring effect of the
360   *M*. *discors* / Sertulariidae assemblage on the community structure. The high abundance and
361   diversity of motile polychaetes in this assemblage, especially for Nereididae, Polynoidae or
362   Syllidae, is similar to assemblages observed in complex three-dimensional habitats such as
363   maerl beds, kelp forests or artificial structures (Grall et al. 2006; Yakovis et al. 2007; Pabis and
364   Sicinski 2010). The *M*. *discors* / Sertulariidae assemblage was also dominated by large
365   suspension-feeding bivalves (*Hiatella arctica*, *Musculus discors* and *Mya truncata*), which is

366 more in line with common species assemblages observed on seafloors protected from sediment
367 disturbance caused either by freshwater inputs or by burrowing species (Włodarska-Kowalczuk
368 2007).

369 The outer fjord sandy assemblage of Daneborg was dominated by the bivalve *Astarte moerchi*,
370 ostracods and polychaetes of the genus *Euchone*. The dominance of *A. moerchi* among the
371 bivalves collected at Daneborg is similar to that observed by Sejr et al. (2000) at the same
372 station but community structure differs with our data: several abundant polychaete species
373 found in 2016 (e.g. *Clymenura* sp., *Euchone* spp., *Laphania boecki*) were not observed by Sejr
374 et al. (2000) while other species abundant in 1995 (e.g. *Dipolydora quadrilobate* and
375 *Lumbriclymene minor*) were not collected in 2016. Such long-term differences could be
376 explained either by long-term changes in the benthic assemblages but also to our weak sampling
377 effort that is submitted to small scale habitat heterogeneity.

378 The Basalt Island sand-gravel outer fjord assemblage is dominated by an association of motile
379 polychaetes (*Abyssoninoe* sp., *Clymenura* sp., *L. boecki*, *Nereimyra aphroditoides*, *Pholoe* sp.),
380 ostracods and the bivalve *A. moerchi*. Although the associated community structure differs with
381 that of Daneborg, both display several common dominant species (e.g. *A. morchi*, *Clymenura*
382 sp., *L. boecki*) indicating common ecological characteristics potentially related to their vicinity
383 in the fjord and similar environmental constraints.

384 Finally, the silty outer fjord assemblage collected at Pass Hytten is dominated by ostracods, the
385 *Metopa glacialis* amphipod as well as tube-dwelling polychaete species (e.g. *Maldane sarsi*,
386 *Owenia borealis*, *Euchone* sp.) and crustaceans. Surprisingly, several species described in the
387 literature as typical of either outer or inner fjord assemblages are found in association in Pass
388 Hytten. For instance, the sub-surface deposit feeder *M. sarsi* is the most dominant polychaete
389 although it is reported to be typical of outer fjord assemblages (Gulliksen et al. 1985; Renaud
390 et al. 2007; Kędra et al. 2013), whereas it is absent from inner fjord areas (Włodarska-
391 Kowalczuk et al. 2012). Surface deposit-feeding thyasirids and nuculanids are also present,
392 albeit in moderate abundance, at Pass Hytten, although they are generally representative of
393 benthic assemblages from inner fjord areas (Włodarska-Kowalczuk and Pearson 2004). The
394 presence of *Euchone* sp. or *Leitoscoloplos mammosus* polychaetes in Pass Hytten is also
395 consistent with previous observations made in shallow and deep areas exposed to high
396 sedimentation rates (Sejr et al. 2010; Kędra et al. 2013; McGovern et al. 2020). Therefore, the
397 coexistence of several species typical of both outer and middle/inner fjord assemblages at Pass

398   Hytten suggests that although this site is more similar to outer fjord habitats, the presence of a

399   handful of species adapted to high sediment loads would indicate that this station is approaching

400   the transition zone between the outer and inner parts of the fjord. This could be explained by

401   the more interior location of Pass Hytten compared to the other three stations sampled, as well

402   as its location closer to the Zackenberg River delta. We hypothesize that future sampling, either

403   in the innermost part of the fjord or closer to the Zackenberg delta, will identify new species

404   assemblages typical of benthic habitats from areas exposed to glacial and freshwater inputs.

405   *New insights about the functioning of the shallow benthic outer fjord community*

406   The new data from our study provide a better understanding of the importance of trophic

407   adaptations for benthic community functioning in outer fjord habitats. A complete analysis of

408   the trophic structure of benthic assemblages has already been conducted at Pass Hytten and Kap

409   Breusing by Bridier et al. (2021). It appears that several dominant species in our study are

410   known to have high trophic plasticity (i.e. feeding on several carbon sources, De Cesare et al.

411   2017; Bridier et al. 2021). The bivalves *Astarte moerchi*, *Astarte elliptica*, *Hiatella arctica*, and

412   *Musculus discors* in Young Sound appear to feed on a range of carbon sources such as

413   phytoplankton, benthic organic matter (i.e. macroalgae and/or microphytobenthos) or

414   sedimentary organic matter (detritus, Bridier et al. 2021). For some species (e.g. the astartidae

415   *A. moerchi* and *A. elliptica*), the proportion of alternative organic matter resources can even

416   reach almost 50% of their diet (Bridier et al. 2021). In addition, other species abundant in Young

417   Sound are known to be omnivores (i.e. feeding on several trophic levels, McMeans et al. 2015;

418   Bridier et al. 2021). This is particularly true for the brittle star *Ophiocten sericeum*, the

419   amphipod *Metopa glacialis* and the polychaete *Nereis zonata*, which were observed in high

420   abundance at all stations. Although the brittle star *O. sericeum* is generally considered a surface

421   feeder, it falls between the primary and the secondary consumer levels in Young Sound (Bridier

422   et al. 2021). Conversely, the polychaete *N. zonata* and the amphipod *M. glacialis* exhibit trophic

423   levels below those of the strict predators with which they are generally associated (Bridier et

424   al. 2021). These variations in trophic position show that these species are capable of feeding at

425   multiple trophic levels, feeding on sources of primary organic matter when these are available

426   in the ecosystem, or feeding at higher trophic levels when the availability of primary production

427   is low (McMeans et al. 2015; Bridier et al. 2021). All these trophic adaptations likely reflect

428   the low pelagic productivity of Young Sound, which ranks among the least productive coastal

429   ecosystems in the world, with pelagic primary production estimated at 10 g C m^{-2} yr^{-1} (Rysgaard

430   et al. 1999; Cloern et al. 2014). Trophic plasticity might therefore allow species to adapt to this

431 low pelagic primary production by optimizing carbon flows through food webs through the
432 exploitation of all carbon sources available in the ecosystem (e.g. microphytobenthos,
433 macroalgae, detritus, Mincks et al. 2008; Renaud et al. 2015). Omnivory may also help benthic
434 species to adapt to low pelagic primary production by reusing carbon that has already passed
435 through the food web a second time, thus participating in the recycling of carbon circulating in
436 the community.

437 The present study complements previous work by Bridier et al. (2021) on the functioning of
438 benthic communities in the shallow habitats of Young Sound. Although Bridier et al. (2021)
439 highlighted the existence of trophic adaptations for several benthic species in Young Sound,
440 the paucity of information on benthic community structure prevents drawing conclusions on
441 the functioning of benthic communities in outer fjord habitats. The new data presented here
442 show that the observations on community trophic adaptations involve species that are
443 numerically dominant in the inventoried benthic habitats (i.e. the rocky, sandy and silty outer
444 fjord assemblages). For example, the species *H. arctica*, *M. discors* (characterized by high
445 trophic plasticity) and *N. zonata* (characterized by high levels of omnivory) alone account for
446 66.5% of the total abundance at Kap Breusing. It could be argued that biomass data would have
447 been more appropriate than abundance data to discuss the role of these latter species in
448 community carbon fluxes. However, considering that all species mentioned as omnivorous or
449 trophically plastic are larger than the rest of the species identified in this study, the biomass
450 dominance of these individuals is likely greater than their numerical dominance, suggesting
451 then an even greater role for community carbon fluxes. Trophic adaptations thus play a
452 predominant role in the functioning of the outer fjord benthic communities, which feed only
453 partially on fresh organic matter from pelagic primary production. These results also highlight
454 the crucial role of benthic primary producers in the functioning of shallow Arctic coastal
455 ecosystems, whose importance is often underestimated, although they represent a significant
456 carbon source (Attard et al. 2016; Gaillard et al. 2017; Ørberg et al. 2022). With climate change,
457 increased meltwater inputs will have multiple consequences for Young Sound's pelagic
458 environments, including impacts on pelagic primary production, organic matter quality and
459 organic matter transfers to zooplankton (Meire et al. 2017; Middelbo et al. 2018; Bridier et al.
460 2019). The existence of trophic adaptations in several species that dominate the benthic
461 communities of the outer fjord (and therefore potentially represent major carbon transfer
462 pathways) could thus be a crucial advantage for their resilience in the face of upcoming
463 environmental changes. In the future, it would be important to investigate the community and

464 trophic structures of the inner fjord to observe how the dominance of these trophic adaptations

465 evolves in habitats exposed to stronger meltwater inputs and higher trophic constraints. In

466 addition, it would also be interesting to describe the structure of benthic communities and food

467 webs in the deeper basins of the fjord (up to 350 m), which do not benefit from local benthic

468 primary production.

469   **Conclusion and further directions of research**

470 The species list obtained in this study is a substantial addition to the inventory carried out two

471 decades ago, adding 66 new species to the 100 already listed by Sejr et al. (2000). The sampling

472 of three new stations (Pass Hytten, Basalt Island, Kap Breusing) in addition to the station

473 previously described by Sejr et al. (2000) (i.e. Daneborg) also provides new insights into the

474 spatial variability of benthic communities in this fjord. Although the community structure

475 differs significantly between the four stations, these differences remain small overall,

476 suggesting that these stations all belong to the same habitat type. Comparison of the community

477 structure with that of the literature suggests that the four stations are characteristic of outer fjord

478 assemblages.

479 Young Sound is a unique location in the Arctic where annual monitoring has been conducted

480 for over 20 years by the Greenland Ecosystem Monitoring - MarineBasis Program. This fjord

481 is therefore an ideal candidate for future biodiversity inventories in northeast Greenland which

482 is one of the Arctic regions with the least studied benthic communities (Piepenburg et al. 2011).

483 Additional sampling will undoubtedly be needed to improve our knowledge of the structure,

484 dynamics and functioning of the Young Sound benthic habitats and associated biodiversity.

485 This sampling should be prioritized in the deeper silty basins (up to 350 m), but also in the inner

486 (i.e. Tyrolerfjord) and intermediate sections of the fjord, which are more exposed to strong

487 freshwater inputs, turbidity and sedimentation. On the opposite, the fjord mouth should also be

488 explored to sample various habitats made up of coarse sands, gravels or potentially biogenic

489 habitats. According to the literature, the innermost parts of the fjord should be dominated by

490 opportunistic species (e.g. the cirratulid polychaete *Chaetozone* spp.) and mollusks feeding on

491 surface deposits such as small thyasirid and nuculanid bivalves (e.g. Włodarska-Kowalczuk

492 and Pearson 2004; Sejr et al. 2010; Włodarska-Kowalczuk et al. 2012), which seem to be

493 underrepresented in the samples analyzed in this study. Finally, the more oceanic part of the

494 fjord should contain a wide variety of benthic habitats characterized by a high and original

495 biodiversity, including biogenic habitats (e.g. maerl/rhodolith or horse mussel beds could be
496 typical in such an environment).

497 These data will be crucial for future predictions on the evolution of benthic communities in
498 response to future global changes, and in particular increased freshwater inputs to coastal areas
499 in response to the accelerated melting of the Greenland Ice Sheet (Mouginot et al. 2019; Höning
500 et al. 2023). Although the structure of benthic communities from sill fjords is generally
501 considered to be stable on multi-decadal scales (Renaud et al. 2007), the long-term dynamics
502 of benthic communities in Artic fjords are still poorly understood. To date, few long-term
503 monitoring studies have been carried out in the Arctic, and to our knowledge none in East
504 Greenland. It would therefore be important to carry out such monitoring to ensure community
505 stability over longer time scales, especially when warmer water masses of Atlantic origin are
506 increasing along the Northeast Greenland Shelf (Gjelstrup et al. 2022) and could drive an
507 expansion of boreal species into the region. Complementary sampling methods, including
508 scientific SCUBA diving, have been used in other Arctic regions (e.g., Svalbard) to study
509 shallow benthic communities (i.e., < 30 m, e.g., Jørgensen and Gulliksen 2001). For example,
510 image analysis based on photographs taken by SCUBA divers has been used to study small-
511 scale spatial variability in benthic communities (Jørgensen and Gulliksen 2001) or long-term
512 successional dynamics following episodes of disturbance or climate change (Beuchel et al.
513 2006; Beuchel and Gulliksen 2008; Al-Habahbeh et al. 2020). Applying these methods to future
514 studies in Young Sound could be an interesting way to obtain complementary data on benthic
515 communities and would also allow comparative studies with Svalbard fjords, which have been
516 studied for several decades.

517

Author contributions

FO, LC, MKS conducted the field sampling campaign. GB, LP, JJ, TB, MLD and JG conducted species identifications. GB carried out the statistical analyses, interpreted the results and wrote the original draft of the manuscript. FO, LP, JJ, LC, MKS, TB, MLD, and JG helped to interpret the results and write the manuscript. FO, LC, MKS, and JG obtained the necessary funding for the study. FO, LC, and JG developed the sampling design. All authors read and approved the manuscript.

Acknowledgements

Statements and Declarations

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

Data availability: All data supporting the results and analyses in this article are available in the tables included in Online Resource 1.

References

Al-Habahbeh AK, Kortsch S, Bluhm BA, Beuchel F, Gulliksen B, Ballantine C, Cristini D, Primicerio R (2020) Arctic coastal benthos long-term responses to perturbations under climate warming. Phil Trans R Soc A 378: 20190355. http://dx.doi.org/10.1098/rsta.2019.0355

547   AMAP (Arctic Monitoring and Assessment Programme) (2017) Snow, water, ice and
548   permafrost in the Arctic (SWIPA). Arctic Monitoring and Assessment Programme
549   (AMAP), Oslo. http://hdl.handle.net/11374/1931

550   Ambrose WG, Renaud PE (1997) Does a pulsed food supply to the benthos affect polychaete
551   recruitment patterns in the Northeast Water Polynya? J Mar Syst 10:483-495.
552   https://doi.org/10.1016/S0924-7963(96)00053-X

553   Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: Guide to Software
554   and Statistical Methods. Primer-E, Plymouth

555   Anderson MJ, Walsh, DC (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of
556   heterogeneous dispersions: what null hypothesis are you testing? Ecol Monogr 83:557-
557   574. https://doi.org/10.1890/12-2010.1

558   Attard KM, Hancke K, Sejr MK, Glud RN (2016) Benthic primary production and
559   mineralization in a High Arctic fjord: in situ assessments by aquatic eddy covariance.
560   Mar Ecol Prog Ser 554:35-50. https://doi.org/10.3354/meps11780

561   Bendtsen J, Gustafsson KE, Rysgaard S, Vang T (2007) Physical conditions, dynamics and
562   model simulations during the ice-free period of the Young Sound/Tyrolerfjord system,
563   p. 46-59. In: Rysgaard S, Glud RN (eds.) Carbon cycling in Arctic marine ecosystems:
564   Case study Young Sound, v. 58. Meddr. Grønland. Bioscience.

565   Bendtsen J, Mortensen J, Rysgaard S (2014) Seasonal surface layer dynamics and sensitivity to
566   runoff in a high Arctic fjord (Young Sound/Tyrolerfjord, 74°N). J Geophys Res Oceans
567   119:6461-6478. https://doi.org/10.1002/2014JC010077

568   Berge J, Johnsen G, Nilsen F, Gulliksen B, Slagstad D (2005) Ocean temperature oscillations
569   enable reappearance of blue mussels *Mytilus edulis* in Svalbard after a 1000 year
570   absence. Mar Ecol Prog Ser 303:167-175. https://doi.org/10.3354/meps303167

571   Beuchel F, Gulliksen B (2008) Temporal patterns of benthic community development in an
572   Arctic fjord (Kongsfjorden, Svalbard): results of a 24-year manipulation study. Polar
573   Biol 31:913-924. https://doi.org/10.1007/s00300-008-0429-9

574   Beuchel F, Gulliksen B, Carroll ML (2006) Long-term patterns of rocky bottom macrobenthic
575   community structure in an Arctic fjord (Kongsfjorden, Svalbard) in relation to climate
576   variability (1980–2003). J Mar Syst 63:35-48.
577   https://doi.org/10.1016/j.jmarsys.2006.05.002

578   Bluhm BA, Gebruk AV, Gradinger R, Hopcroft RR, Huettmann F, Kosobokova KN, Sirenko
579   BI, Węsławski JM (2011) Arctic marine biodiversity: An update of species richness and
580   examples of biodiversity change. Oceanography 24:232-248.
581   https://doi.org/10.5670/oceanog.2011.75

582   Brandt A, Schnack K (1999) Macrofaunal abundance at 79°N off East Greenland: opposing
583   data from epibenthic-sledge and box-corer samples. Polar Biol 22:75-81.
584   https://doi.org/10.1007/s003000050392

585   Bridier G, Meziane T, Grall J, Chauvaud L, Sejr MK, Menneteau S, Olivier F (2019) Coastal
586   waters freshening and extreme seasonality affect organic matter sources, quality, and
587   transfers in a High Arctic fjord (Young Sound, Greenland). Mar Ecol Prog Ser 610:15-
588   31. https://doi.org/10.3354/meps12857

589   Bridier G, Olivier F, Chauvaud L, Sejr MK, Grall J (2021) Food source diversity, trophic
590   plasticity, and omnivory enhance the stability of a shallow benthic food web from a
591   high-Arctic fjord exposed to freshwater inputs. Limnol Oceanogr 66:S259-S272.
592   https://doi.org/10.1002/lno.11688

593   Chao A, Chiu CH (2016) Species richness: estimation and comparison. Wiley StatsRef:
594   Statistics Reference Online 1-26.
595   https://doi.org/10.1002/9781118445112.stat03432.pub2

596   Cloern JE, Foster SQ, Kleckner AE (2014) Phytoplankton primary production in the world's
597   estuarine-coastal ecosystems. Biogeosciences 11:2477-2501.
598   https://doi.org/10.5194/bg-11-2477-2014

599   Colwell RK, Mao CX, Chang J (2004) Interpolating, extrapolating, and comparing incidence-
600   based species accumulation curves. Ecology 85:2717-2727. https://doi.org/10.1890/03-
601   0557

602   Cottier-Cook EJ, Bentley-Abbot J, Cottier FR, Minchin D, Olenin S, Renaud PE (2023)
603   Horizon scanning of potential threats to high-Arctic biodiversity, human health and the
604   economy from marine invasive alien species: A Svalbard case study. Glob Change Biol
605   30:e17009. https://doi.org/10.1111/gcb.17009

606   De Cesare S, Meziane T, Chauvaud L, Richard J, Sejr MK, Thébault J, Winkler G, Olivier F
607   (2017) Dietary plasticity in the bivalve *Astarte moerchi* revealed by a multimarker study
608   in two Arctic fjords. Mar Ecol Prog Ser 567:157-172.
609   https://doi.org/10.3354/meps12035

610   Filbee-Dexter K, Wernberg T, Fredriksen S, Norderhaug KM, Pedersen MF (2019) Arctic kelp
611   forests: diversity, resilience and future. Global Planet Change 172:1-14.
612   https://doi.org/10.1016/j.gloplacha.2018.09.005

613   Fredriksen R, Christiansen JS, Bonsdorff E, Larsen LH, Nordström MC, Zhulay I, Bluhm BA
614   (2020) Epibenthic megafauna communities in Northeast Greenland vary across coastal,
615   continental shelf and slope habitats. Polar Biol 43:1623-1642.
616   https://doi.org/10.1007/s00300-020-02733-z

617   Gaillard B, Meziane T, Tremblay R, Archambault P, Blicher ME, Chauvaud L, Rysgaard S,
618   Olivier F (2017) Food resources of the bivalve *Astarte elliptica* in a sub-Arctic fjord: a
619   multi-biomarker approach. Mar Ecol Prog Ser 567:139-156.
620   https://doi.org/10.3354/meps12036

621   Gjelstrup CVB, Sejr MK, de Steur L, Christiansen JS, Granskog MA, Koch BP, Møller EF,
622   Winding MHS, Stedmon CA (2022). Vertical redistribution of principle water masses
623   on the Northeast Greenland Shelf. Nat Commun 13:7660.
624   https://doi.org/10.1038/s41467-022-35413-z

625   Glud RN, Rysgaard S, Kühl M, Hansen JW (2007) The sea ice in Young Sound: Implications
626   for carbon cycling, p. 62-85. In: Rysgaard S, Glud RN (eds.) Carbon cycling in Arctic
627   marine ecosystems: Case study Young Sound, v. 58. Meddr. Grønland. Bioscience.

628   Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the
629   measurement and comparison of species richness. Ecol Lett 4:379-391.
630   https://doi.org/10.1046/j.1461-0248.2001.00230.x

631 Gradinger R, Bluhm BA, Hopcroft RR, Gebruk AV, Kosobokova KN, Sirenko BI, Węsławski
632   JM (2010) Chapter 10. Marine life in the Arctic, p. 183-202. In: McIntyre AD (ed) Life
633   in the World's Ocean: Diversity, Distribution, and Abundance. Wiley-Blackwell,
634   Oxford.

635 Grall J, Le Loc'h F, Guyonnet B, Riera P (2006) Community structure and food web based on
636   stable isotopes (δ^{15}N and δ^{13}C) analysis of a North Eastern Atlantic maerl bed. J Exp
637   Mar Biol Ecol 338:1-15. https://doi.org/10.1016/j.jembe.2006.06.013

638 Gulliksen B, Holte B, Jakola K-J (1985) The soft bottom fauna in Van Mijenfjord and
639   Raudfjorden, Svalbard, p. 199-215. In: Gray JS, Christiansen ME (eds). Marine Biology
640   of Polar Regions and Effects on Marine Organisms. Wiley, Oslo.

641 Hobson KA, Ambrose WG, Renaud PE (1995) Sources of primary production, benthic-pelagic
642   coupling, and trophic relationships within the Northeast Water Polynya: insights from
643   δ^{13}C and δ^{15}N. Mar Ecol Prog Ser 128:1-10. https://doi.org/10.3354/meps128001

644 Holding JM, Markager S, Juul-Pedersen T, Paulsen ML, Møller EF, Meire L, Sejr MK (2019)
645   Seasonal and spatial patterns of primary production in a high-latitude fjord affected by
646   Greenland Ice Sheet run-off. Biogeosciences 16:3777-3792. https://doi.org/10.5194/bg-
647   16-3777-2019

648 Höning D, Willeit M, Calov R, Klemann V, Bagge M, Ganopolski A (2023) Multistability and
649   Transient Response of the Greenland Ice Sheet to Anthropogenic CO_2 Emissions.
650   Geophys Res Lett 50:e2022GL101827. https://doi.org/10.1029/2022GL101827

651 Jørgensen LL, Gulliksen B (2001) Rocky bottom fauna in arctic Kongsfjord (Svalbard) studied
652   by means of suction sampling and photography. Polar Biol 24:113-121.
653   https://doi.org/10.1007/s003000000182

654 Josefson AB, Mokievsky V, Bergmann M, Blicher ME, Bluhm B, Cochrane S, Denisenko NV,
655   Hasemann C, Jørgensen LL, Klages M, Schewe I, Sejr MK, Soltwedel T, Węsławski
656   JM, Włodarska-Kowalczuk M (2013) Marine Invertebrates, p. 225-257. In: Meltofte H
657   (ed.) Arctic Biodiversity Assessment. Status and trends in Arctic biodiversity.
658   Conservation of Arctic Flora and Fauna, Akureyri.

659   Kędra M, Gromisz S, Jaskła R, Legeżyńska J, Maciejewska B, Malec E, Opanowski A,
660   Ostrowska K, Włodarska-Kowalczuk M, Węsławski JM (2010) Soft bottom macrofauna
661   of an All Taxa Biodiversity Site: Hornsund (77°N, Svalbard). Polar Res 31:309-326.
662   https://doi.org/10.2478/v10183-010-0008-y

663   Kędra M, Pabis K, Gromisz S, Węsławski JM (2013) Distribution patterns of polychaete fauna
664   in an Arctic fjord (Hornsund, Spitsbergen). Polar Biol 36:1463-1472.
665   https://doi.org/10.1007/s00300-013-1366-9

666   Knox GA, Lowry JK (1977) A comparison between the benthos of the Southern Ocean and the
667   North Polar Ocean, with special reference to the Amphipoda and the Polychaeta. In:
668   Dunbar MJ (ed) Polar Oceans. Arctic Institute of North America, Calgary, p 423–462

669   Kortsch S, Primicerio R, Beuchel F, Renaud PE, Rodrigues J, Lønne OJ, Gulliksen B (2012)
670   Climate-driven regime shifts in Arctic marine benthos. Proc Natl Acad Sci USA
671   109:14052-14057. https://doi.org/10.1073/pnas.1207509109

672   Kotwicki L, Węsławski JM, Włodarska-Kowalczuk M, Mazurkiewicz M, Wenne R, Zbawicka
673   M, Minchin D, Olenin S (2021) The re-appearance of the *Mytilus* spp. complex in
674   Svalbard, Arctic, during the Holocene: The case for an arrival by anthropogenic flotsam.
675   Glob Planet Change 202:103502. https://doi.org/10.1016/j.gloplacha.2021.103502

676   Krause-Jensen D, Duarte CM (2014) Expansion of vegetated coastal ecosystems in the future
677   Arctic. Front Mar Sci 1:77. https://doi.org/10.3389/fmars.2014.00077

678   Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of
679   species data. Oecologia. 129:271-280. https://doi.org/10.1007/s004420100716

680   Mackie SY (1987) A review of species currently assigned to the genus *Leitoscoloplos* Day,
681   1977 (Polychaeta: Orbiniidae), with description of species newly referred to *Scoloplos*
682   Blainville, 1982. Sarsia 72:1-28. https://doi.org/10.1080/00364827.1987.10419701

683   Mathiesen SS, Thyrring J, Hemmer-Hansen J, Berge J, Sukhotin A, Leopold P, Bekaert M, Sejr
684   MK, Nielsen EE (2017) Genetic diversity and connectivity within *Mytilus* spp. in the
685   subarctic and Arctic. Evol Appl 10:39-55. https://doi.org/10.1111/eva.12415

686   McGovern M, Poste AE, Oug E, Renaud PE, Trannum HC (2020) Riverine impacts on benthic
687   biodiversity and functional traits: A comparison of two sub-Arctic fjords. Estuar Coast
688   Shelf Sci 240:106774. https://doi.org/10.1016/j.ecss.2020.106774

689   McMeans BC, McCann KS, Humphries M, Rooney N, Fisk AT (2015) Food web structure in
690   temporally-forced ecosystems. Trends Ecol Evol 30:662-672.
691   https://doi.org/10.1016/j.tree.2015.09.001

692   Meire L, Mortensen J, Meire P, Juul‑Pedersen T, Sejr MK, Rysgaard S, Nygaard R,
693   Huybrechts P, Meysman FJR (2017) Marine‑terminating glaciers sustain high
694   productivity in Greenland fjords. Glob Change Biol 23:5344-5357.
695   https://doi.org/10.1111/gcb.13801

696   Merrill AS, Turner RD (1963) Nest building in the bivalve genera *Musculus* and *Lima*. Veliger
697   6:55-59.

698   Middelbo AB, Sejr MK, Arendt KE, Møller EF (2018) Impact of glacial meltwater on
699   spatiotemporal distribution of copepods and their grazing impact in Young Sound NE,
700   Greenland. Limnol Oceanogr 63:322-336. https://doi.org/10.1002/lno.10633

701   Mincks SL, Smith CR, Jeffreys RM, Sumida PYG (2008) Trophic structure on the West
702   Antarctic Peninsula shelf: Detritivory and benthic inertia revealed by δ^{13}C and δ^{15}N
703   analysis. Deep Sea Res II 55:2502-2514. https://doi.org/10.1016/j.dsr2.2008.06.009

704   Mouginot J, Rignot E, Bjørk AA, van den Broeke M, Millan R, Morlighem M, Noël B,
705   Scheuchl B, Wood M (2019) Forty-six years of Greenland Ice Sheet mass balance from
706   1972 to 2018. Proc Natl Acad Sci USA, 116:9239-9244.
707   https://doi.org/10.1073/pnas.1904242116

708   Ockelmann WK (1958) The zoology of East Greenland: marine Lamellibranchiata. Medd
709   Groenl 122:1-256.

710   Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara
711   RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2019) Vegan:
712   community ecology package. R package version 2.5-6. Available at https://CRAN.R-
713   project.org/package=vegan

714   Ørberg SB, Duarte CM, Geraldi NR, Sejr MK, Wegeberg S, Hansen JLS, Krause-Jensen D
715   (2022) Prevalent fingerprint of marine macroalgae in arctic surface sediments. Sci Total
716   Environ 898:165507. https://doi.org/10.1016/j.scitotenv.2023.165507

717   Pabis K, Sicinski J (2010) Polychaete fauna associated with holdfasts of the large brown alga
718   *Himantothallus grandifolius* in Admiralty Bay, King George Island, Antarctic. Polar
719   Biol 33:1277-1288. https://doi.org/10.1007/s00300-010-0816-x

720   Piepenburg D, Schmid MK (1996) Distribution, abundance, biomass, and mineralization
721   potential of the epibenthic megafauna of the Northeast Greenland shelf. Mar Biol
722   125:321-332. https://doi.org/10.1007/BF00346313

723   Piepenburg D, Ambrose WG, Brandt A, Renaud PE, Ahrens MJ, Jensen P (1997) Benthic
724   community patterns reflect water column processes in the Northeast Water polynya
725   (Greenland). J Mar Syst 10:467-482. https://doi.org/10.1016/S0924-7963(96)00050-4

726   Piepenburg D (2005) Recent research on Arctic benthos: common notions need to be revised.
727   Polar Biol 28:733-755. https://doi.org/10.1007/s00300-005-0013-5

728   Piepenburg D, Archambault P, Ambrose WG, Blanchard AL, Bluhm BA, Carroll ML, Conlan
729   KE, Cusson M, Feder HM, Grebmeier JM, Jewett SC, Lévesque M, Petryashev VV,
730   Sejr MK, Sirenko BI, Włodarska-Kowalczuk M (2011) Towards a pan-Arctic inventory
731   of the species diversity of the macro-and megabenthic fauna of the Arctic shelf seas.
732   Mar Biodiv 41:51-70. https://doi.org/10.1007/s12526-010-0059-7

733   Renaud PE, Włodarska-Kowalczuk M, Trannum H, Holte B, Węsławski JM, Cochrane S, Dahle
734   S, Gulliksen B (2007) Multidecadal stability of benthic community structure in a high-
735   Arctic glacial fjord (van Mijenfjord, Spitsbergen). Polar Biol 30:295-305.
736   https://doi.org/10.1007/s00300-006-0183-9

737   Renaud PE, Sejr MK, Bluhm BA, Sirenko B, Ellingsen IH (2015) The future of Arctic benthos:
738   Expansion, invasion, and biodiversity. Prog Oceanogr 139:244-257.
739   https://doi.org/10.1016/j.pocean.2015.07.007

740   Rysgaard S, Nielsen TG, Hansen BW (1999) Seasonal variations in nutrients, pelagic primary
741   production and grazing in a high-Arctic coastal marine ecosystem, Young Sound,

742   Northeast Greenland. Mar Ecol Prog Ser 179:13-25.
743   https://doi.org/10.3354/meps179013

744 Rysgaard S, Vang T, Stjernholm M, Rasmussen B, Windelin A, Kiilsholm S (2003) Physical
745   conditions, carbon transport, and climate change impacts in a northeast Greenland fjord.
746   Arct Antarct Alp Res 35:301-312. https://doi.org/10.1657/1523-
747   0430(2003)035[0301:PCCTAC]2.0.CO;2

748 Sejr MK, Jensen KT, Rysgaard S (2000) Macrozoobenthic structure in a high-Arctic East
749   Greenland fjord. Polar Biol 23:792−801. https://doi.org/10.1007/s003000000154

750 Sejr MK, Włodarska-Kowalczuk M, Legeżyńska J, Blicher ME (2010) Macrobenthic species
751   composition and diversity in the Godthaabsfjord system, SW Greenland. Polar Biol
752   33:421-431. https://doi.org/10.1007/s00300-009-0717-z

753 Sejr MK, Bruhn A, Dalsgaard T, Juul-Pedersen T, Stedmon CA, Blicher M, Meire L, Mankoff
754   KD, Thyrring J (2022) Glacial meltwater determines the balance between autotrophic
755   and heterotrophic processes in a Greenland fjord. Proc Natl Acad Sci USA
756   119:e2207024119. https://doi.org/10.1073/pnas.2207024119

757 Sirenko BI (2001) List of species of free-living invertebrates of Eurasian Arctic seas and
758   adjacent deep waters. Explorations of the Fauna of the Seas 51:1-129

759 Starmans A, Gutt J, Arntz WE (1999) Mega-epibenthic communities in Arctic and Antarctic
760   shelf areas. Mar Biol 135:269-280. https://doi.org/10.1007/s002270050624

761 Udalov A, Chikina M, Chava A, Vedenin A, Shchuka S, Mokievsky V (2021) Patterns of
762   Benthic Communities in Arctic Fjords (Novaya Zemlya Archipelago, Kara Sea):
763   Resilience vs. Fragility. Front Ecol Evol 9:777006.
764   https://doi.org/10.3389/fevo.2021.777006

765 Voronkov A, Hop H, Gulliksen B (2013) Diversity of hard-bottom fauna relative to
766   environmental gradients in Kongsfjorden, Svalbard. Pol Res 32:11208.
767   https://doi.org/10.3402/polar.v32i0.11208

768 Węsławski JM, Kendall MA, Włodarska-Kowalczuk M, Iken K, Kędra M, Legezynska J, Sejr
769   MK (2011) Climate change effects on Arctic fjord and coastal macrobenthic diversity—

770   observations and predictions. Marine Biodiversity 41:71-85.
771   https://doi.org/10.1007/s12526-010-0073-9

772 Włodarska-Kowalczuk M, Pearson TH (2004) Soft-bottom macrobenthic faunal associations
773   and factors affecting species distributions in an Arctic glacial fjord (Kongsfjord,
774   Spitsbergen). Polar Biol 27:155-167. https://doi.org/10.1007/s00300-003-0568-y

775 Włodarska-Kowalczuk M (2007) Molluscs in Kongsfjorden (Spitsbergen, Svalbard): a species
776   list and patterns of distribution and diversity. Polar Res 26:48-63.
777   https://doi.org/10.1111/j.1751-8369.2007.00003.x

778 Włodarska-Kowalczuk M, Renaud PE, Węsławski JM, Cochrane SKJ, Denisenko SG (2012)
779   Species diversity, functional complexity and rarity in Arctic fjordic versus open shelf
780   benthic systems. Mar Ecol Prog Ser 463:73-87. https://doi.org/10.3354/meps09858

781 Yakovis EL, Artemieva AV, Fokin MV, Varfolomeeva MA, Shunatova NN (2007) Effect of
782   habitat architecture on mobile benthic macrofauna associated with patches of barnacles
783   and ascidians. Mar Ecol Prog Ser 348:117-124. https://doi.org/10.3354/meps07060
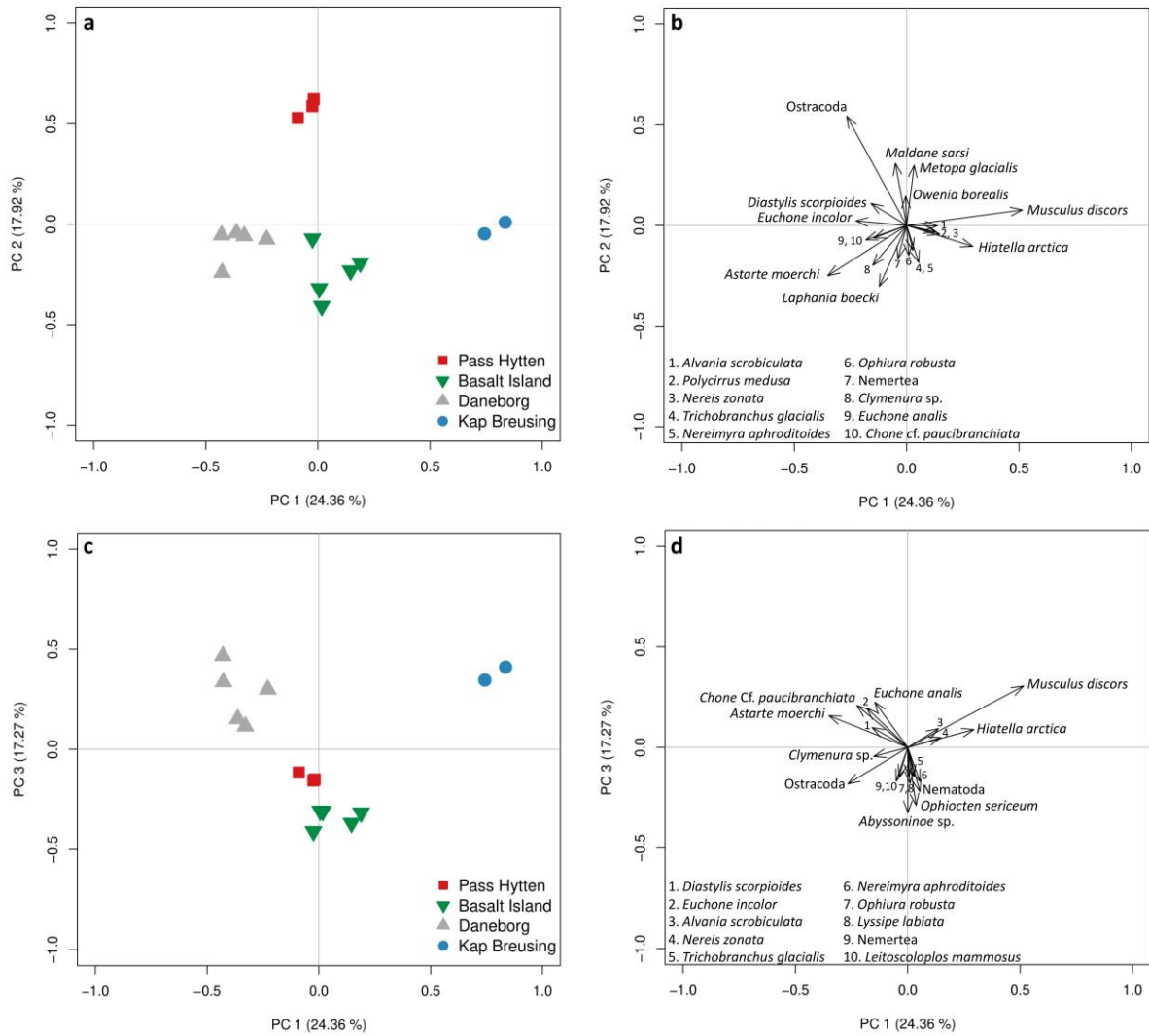
784

785 **Figures**

786 **Figure 1**
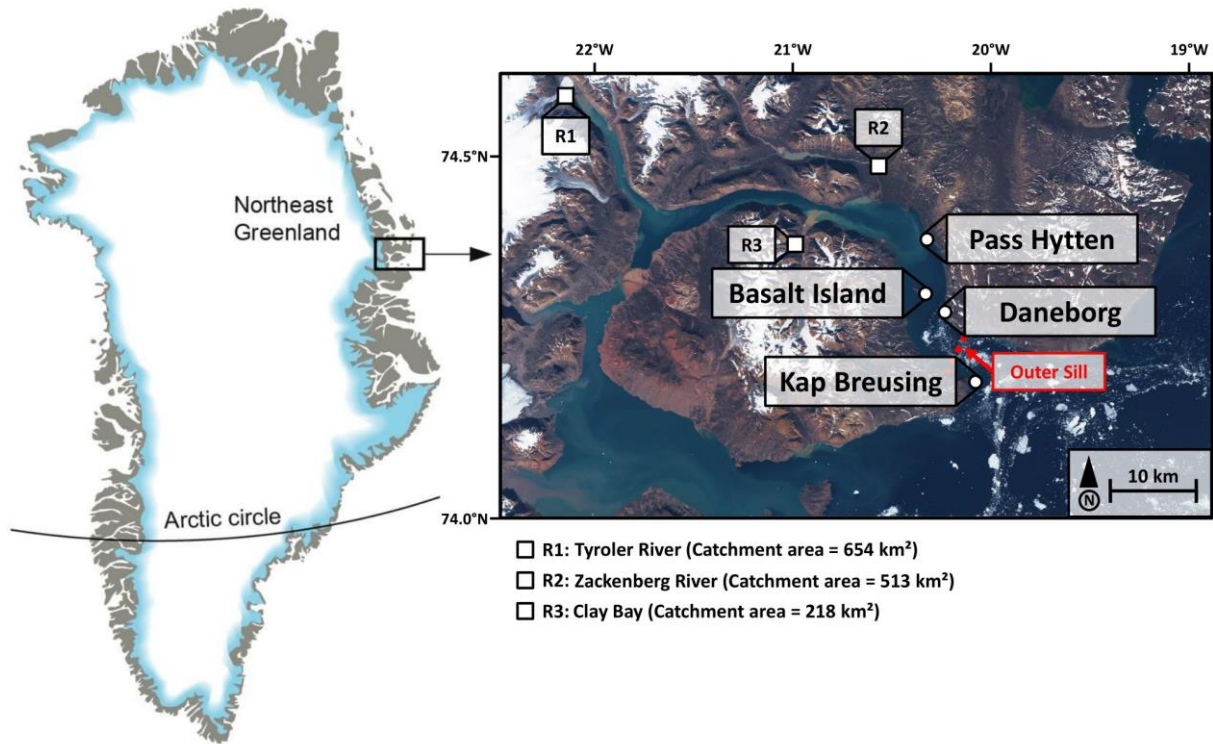
787

788 **Figure 1** Map showing the four sampling stations (white dots) and the three main rivers (white

789 squares) in Young Sound. River catchment areas are from Bendtsen et al. (2014)

790   **Figure 2**

791

792   **Figure 2** Principal component analyses based on Hellinger-transformed fauna abundances.
793   Upper plots (a, b) show the first two principal components while lower plots show the first and
794   third principal components. Left plots (a, c) represent the position of each replicate while right
795   plots (b, d) represent the position of the first twenty species that explain at least 60 % of the
796   spatial variation

797
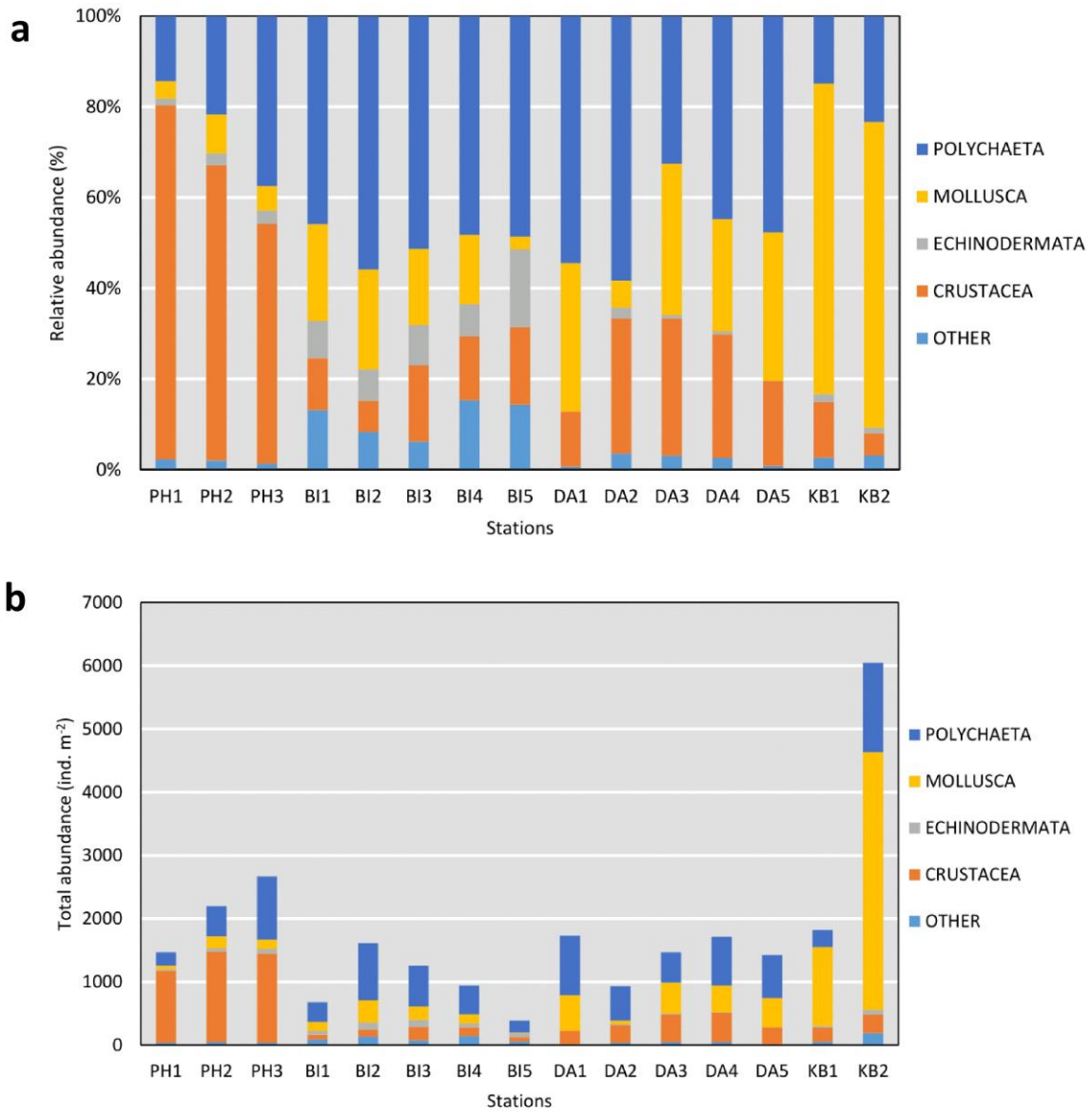
Figure 3

799

800 **Figure 3** Relative abundance (%, a) and total abundance (ind. m⁻², b) of major taxonomic groups
801 from Pass Hytten (from PH 1 to PH 3), Basalt Island (from BI 1 to BI 5), Daneborg (from DA
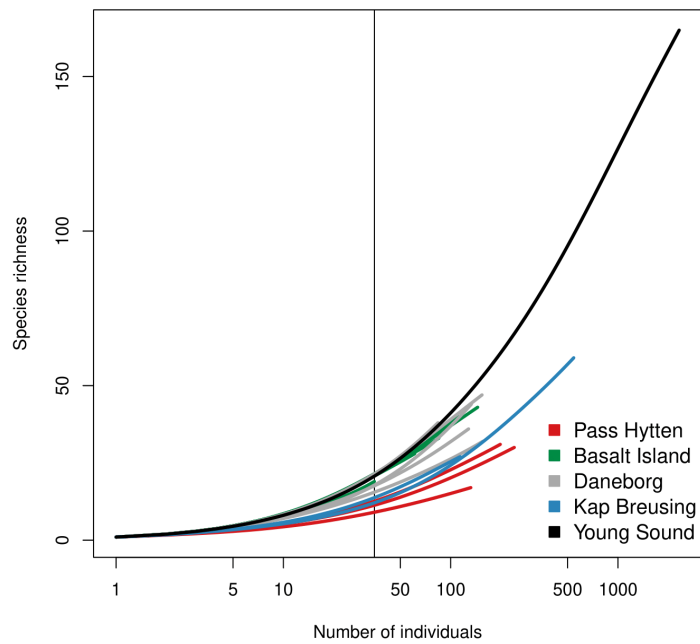802 1 to DA 2) and Kap Breusing (KB 1 & KB 2) stations

803

804 **Figure 4**

805

806 **Figure 4** Submarine landscapes of Pass Hytten (a, depth = 18 m), Basalt Island (b, depth = 21.5
807 m), Daneborg (c, depth = 20 m) and Kap Breusing stations (d, depth = 20 m). Photo credits:
808 Erwan Amice
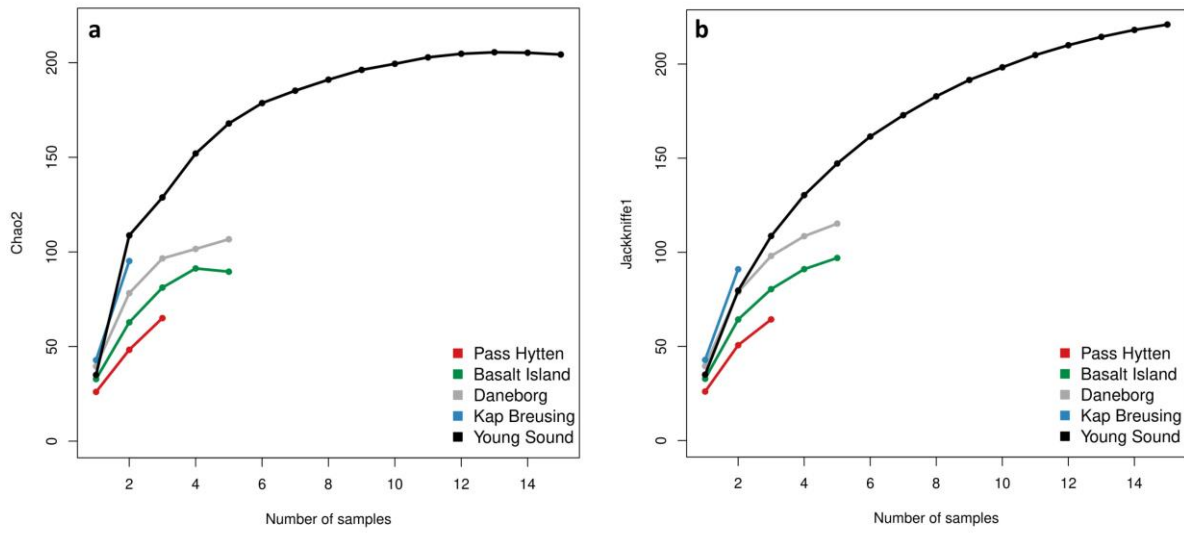
809

810   **Figure 5**

811

812   **Figure 5** Accumulation curves for each replicate from Pass Hytten, Basalt Island, Daneborg
813   and Kap Breusing stations and the entire Young Sound site (combining 15 replicates). The
814   vertical line represents the number of individuals selected for comparisons between replicates
815   (35 individuals)

816

817 **Figure 6**

818

819 **Figure 6** Chao2 (a) and Jackknife1 (b) accumulation curves calculated for Pass Hytten, Basalt

820 Island, Daneborg, Kap Breusing and the four stations combined.

821

822 **Tables**

823 **Table 1** Geographic coordinates, depth, total area sampled, and material collected (with number

824 of replicates in brackets) for each station

Station	Latitude	Longitude	Depth (m)	Total sampled area (m^2)	Collected material
Pass Hytten	N 74.41'	W 20.33'	18.0	0.2700	Macrofauna ($n = 3$) and sediment ($n = 1$)
Basalt Island	N 74.33'	W 20.36'	21.5	0.4500	Macrofauna ($n = 5$)
Daneborg	N 74.31'	W 20.24'	20.0	0.4500	Macrofauna ($n = 5$)
Kap Breusing	N 74.21'	W 20.11'	20.0	0.1525	Macrofauna ($n = 2$) and sediment ($n = 3$)

825

826 **Table 2** List of the ten most abundant taxa for each station, with their relative abundance (%),
827 their cumulative relative abundance (% Cum.), their abundance (Abund., number of individuals
828 per square meter [ind. m⁻²]) and the Pielou index (mean ± standard error of the mean) of the
829 corresponding station (calculated at the scale of the whole community)

Species	Phylum	Abund.	%	Cum. %
Pass Hytten		[Pielou index = 0.622 ± 0.027]		
Ostracoda Latreille, 1802	Arthropoda	996.3	47.2	47.2
Metopa glacialis (Krøyer, 1842)	Arthropoda	185.2	8.8	56.0
Maldane sarsi Malmgren, 1865	Polychaeta	166.7	7.9	63.9
Owenia borealis Koh, Bhaud & Jirkov, 2003	Polychaeta	114.8	5.4	69.3
Leitoscoloplos mammosus Mackie, 1987	Polychaeta	63.0	3.0	72.3
Diastylis scorpioides (Lepechin, 1780)	Arthropoda	63.0	3.0	75.3
Abyssoninoe sp. Orensanz, 1990	Polychaeta	48.1	2.3	77.5
Lysippe labiata Malmgren, 1866	Polychaeta	44.4	2.1	79.6
Euchone incolor Hartman, 1965	Polychaeta	40.7	1.9	81.6
Ophiocten sericeum (Forbes, 1852)	Polychaeta	37.0	1.8	83.3
Basalt Island		[Pielou index = 0.916 ± 0.004]		
Laphania boecki Malmgren, 1866	Polychaeta	64.4	6.6	6.6
Ostracoda Latreille, 1802	Arthropoda	57.8	5.9	12.5
Abyssoninoe sp. Orensanz, 1990	Polychaeta	55.6	5.7	18.2
Nereimyra aphroditoides (O. Fabricius, 1780)	Polychaeta	55.6	5.7	23.9
Nematoda	Nematoda	55.6	5.7	29.6
Ophiocten sericeum (Forbes, 1852)	Echinodermata	51.1	5.2	34.9
Astarte moerchi Hopner Petersen, 2001	Mollusca	46.7	4.8	39.6
Clymenura sp. Verrill, 1900	Polychaeta	42.2	4.3	44.0
Harmothoe cf. *imbricata* (Linnaeus, 1767)	Polychaeta	42.2	4.3	48.3
Pholoe assimilis Örsted, 1845	Polychaeta	40.0	4.1	52.4
Daneborg		[Pielou index = 0.834 ± 0.022]		
Astarte moerchi Hopner Petersen, 2001	Mollusca	271.1	18.6	18.6
Ostracoda Latreille, 1802	Arthropoda	171.1	11.8	30.4
Euchone incolor Hartman, 1965	Polychaeta	91.1	6.3	36.6
Laphania boecki Malmgren, 1866	Polychaeta	75.6	5.2	41.8
Euchone analis (Kröyer, 1856)	Polychaeta	62.2	4.3	46.1
Chone cf. *paucibranchiata* (Kröyer, 1856)	Polychaeta	57.8	4.0	50.1
Clymenura sp. Verrill, 1900	Polychaeta	57.8	4.0	54.0
Diastylis scorpioides (Lepechin, 1780)	Arthropoda	51.1	3.5	57.6
Chaetozone sp. 1 Malmgren, 1867	Polychaeta	31.1	2.1	59.7
Harmothoe cf. *imbricata* (Linnaeus, 1767)	Polychaeta	24.4	1.7	61.4
Kap Breusing		[Pielou index = 0.634 ± 0.062]		
Musculus discors (Linnaeus, 1767)	Mollusca	1875.4	43.7	43.7
Hiatella arctica (Linnaeus, 1767)	Mollusca	800.0	18.7	62.4
Harmothoe cf. *imbricata* (Linnaeus, 1767)	Polychaeta	242.6	5.7	68.0
Nereis zonata Malmgren, 1867	Polychaeta	177.0	4.1	72.2
Polycirrus medusa Grube, 1850	Polychaeta	85.2	2.0	74.2
Alvania scrobiculata (Møller, 1842)	Mollusca	78.7	1.8	76.0
Mya truncata Linnaeus, 1758	Polychaeta	65.6	1.5	77.5
Polycirrus latidens Eliason, 1962	Polychaeta	52.5	1.2	78.7
Nereimyra aphroditoides (O. Fabricius, 1780)	Polychaeta	45.9	1.1	79.8
Apherusa sarsi Shoemaker, 1930	Arthropoda	45.9	1.1	80.9

830