

Towards a pan-Arctic inventory of the species diversity of the macro- and megabenthic fauna of the Arctic shelf seas

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Abstract

Although knowledge of Arctic seas has increased tremendously in the past decade, benthic diversity was investigated at regional scales only, and no attempt had been made to examine it across the entire Arctic. We present a first pan-Arctic account of the species diversity of the macro- and megabenthic fauna of the Arctic marginal shelf seas. It is based on an analysis of 25 published and unpublished species-level data sets, together encompassing 14 of the 19 marine Arctic shelf ecoregions and comprising a total of 2636 species, including 847 Arthropoda, 668 Annelida, 392 Mollusca, 228 Echinodermata, and 501 species of other phyla. For the four major phyla, we also analyze the differences in faunal composition and diversity among the ecoregions. Furthermore, we compute gross estimates of the expected species numbers of these phyla on a regional scale. Extrapolated to the entire fauna and study area, we arrive at the conservative estimate that 3900 to 4700 macro- and megabenthic species can be expected to occur on the Arctic shelves. These numbers are smaller than analogous estimates for the Antarctic shelf but the difference is on the order of about two and thus less pronounced than previously assumed. On a global scale, the Arctic shelves are characterized by intermediate macro- and megabenthic species numbers. Our preliminary pan-Arctic inventory provides an urgently needed assessment of current diversity patterns that can be used by future investigations for evaluating the effects of climate change and anthropogenic activities in the Arctic.

Keywords: Arctic, macrobenthos, megabenthos, shelf, pan-Arctic inventory, diversity

43 **Introduction**

44 *Background*

45 The circum-Arctic shelf seas are generally characterized by pronounced seasonality in solar
46 radiation and nutrient availability, as well as long-lasting ice cover and water temperatures
47 close to the freezing point (Carmack and Wassmann 2006). Furthermore, the northernmost
48 regions are limited in their connections with adjacent boreal regions (Curtis 1975).

49 Consequently, Arctic seas have long been considered to be among the most hostile habitats on
50 Earth and, hence, the poorest regions, in terms of biodiversity, of the world's oceans (Hempel
51 1985).

52 The low species diversity of the Arctic benthic biota is often contrasted to highly diverse
53 Antarctic benthos. The differences between the two polar regions are attributed to several
54 factors, including the 'harshness' and relative homogeneity of Arctic benthic habitats, the
55 younger geological age and less pronounced biogeographic isolation of the Arctic marine
56 environments or the predominance of hard-bottom habitats, inhabited by rich epifaunal
57 assemblages, on the Antarctic shelves (Dayton 1990; Clarke and Crame 1992; Sirenko 2009).

58 *Motivation*

59 The paradigm of low Arctic diversity, as opposed to highly diverse Antarctic fauna, has
60 recently been questioned (Piepenburg 2005; Włodarska-Kowalczyk et al. 2007). Moreover,
61 regional studies in the European sector have failed to document decreasing biodiversity with
62 higher latitudes (e.g., Kendall and Aschan 1993; Renaud et al. 2009). The notion of a
63 comparatively poor Arctic was actually supported by limited data, as the knowledge of the
64 composition of Arctic sea life was still inadequate due to the logistical constraints resulting
65 from the remoteness, inhospitable climate, and heavy ice cover characterizing the region
66 (Carmack et al. 2006). Hence, comprehensive species inventories and comparisons of
67 biodiversity among Arctic regions were relatively scarce (Zenkevitch 1963; Curtis 1975).

68 Our knowledge on Arctic seas has increased tremendously in the past two decades as a
69 result of novel sampling efforts made possible for several reasons, such as the availability of
70 new research ice breakers and the political opening of the vast Russian Arctic regions to
71 international research efforts after a decade-long period of isolation. Although it is commonly
72 acknowledged that there is an urgent need to address biodiversity patterns at larger scales
73 (i.e., the entire Arctic; Piepenburg 2005), most biodiversity research on the Arctic benthos has

74 mainly focused at local to regional scales (e.g., MacGinitie 1955; Feder et al. 1994, 2005,
75 2007; Denisenko 2003; Sirenko 2004; Bluhm et al. 2005; Conlan and Kvitek 2005; Cusson et
76 al. 2007). Nevertheless, Zenkevitch (1963), Sirenko and Piepenburg (1994) and Sirenko
77 (2001) provided large-scale inventories of the macrozoobenthic diversity of the entire eastern
78 (Eurasian) Arctic. A truly circum-Arctic biodiversity census, however, is currently not
79 available.

80 ***Objectives***

81 We present the first pan-Arctic inventory of the species diversity (more precisely: the species
82 numbers) of the benthic fauna of the marginal shelf seas of the eastern (Eurasian) and western
83 (North American) Arctic. Our study is confined to 'large' seabed animals, the macro- and
84 megafaunal benthos. According to a well-established operational definition proposed by Gage
85 and Tyler (1991), this ecological group encompasses those seafloor organisms that are large
86 enough to be retained on sieves with a mesh size of 0.5 mm (macro-benthos, mostly infaunal)
87 or to be visible in seabed images and/or to be caught by towed sampling gear (megabenthos,
88 mostly epifaunal). Moreover, our census covers only invertebrate taxa, fishes were not
89 considered.

90 Instead of only reviewing published biodiversity reports we performed a synoptic numerical
91 analysis of published and unpublished data compiled in the Arctic Ocean Diversity database
92 (www.arcodiv.org) and contributed by the authors of this paper. Our primary goals were to
93 produce up-to-date and comprehensive information on the current knowledge of what lives on
94 the seabed of Arctic shelves and to analyze large-scale spatial patterns across the Arctic shelf
95 regions for the most widely distributed diverse and abundant phyla (Annelida, Mollusca, ,
96 Arthropoda, and Echinodermata).

97 More specifically, the issues addressed in this paper are:

- 98 (1) Summarizing on a pan-Arctic scale the current state of knowledge of the diversity of the
99 macro- and megafaunal seabed fauna of shelf seas
- 100 (2) Assessing the total number of macro- and megabenthic species known from the Arctic
101 shelves
- 102 (3) Estimating the total number of macro- and megabenthic species expected to occur on
103 Arctic shelves

104 (4) Describing spatial distribution patterns of benthic diversity and comparing the faunal
105 composition among Arctic shelf regions (for dominant phyla)

106 These objectives required the compilation and validation of species lists from a broad range
107 of regions for all major macro- and megabenthic taxa. The resulting database was then
108 analyzed for spatial trends in species diversity and distribution among major regional units.

109 Our census provides an urgently needed assessment of current diversity patterns that can be
110 used by future biodiversity investigations evaluating and predicting the effects of rapid
111 climate change or increasing anthropogenic activities (e.g., exploration and exploitation of
112 natural resources, coastal development, shipping, tourism) in the Arctic.

113 **Material and methods**

114 *Definition of the study area*

115 We use a definition of 'Arctic seas' that is largely based on a widely accepted scheme
116 proposed by the Arctic Monitoring and Assessment Programme (AMAP) (1998). The AMAP
117 boundary of the Arctic, however, extends down to southern Norway's west coast, through the
118 Norwegian and into the North Seas, which we do not regard as being 'Arctic'. Consequently,
119 as an exception of the AMAP approach, we define the Arctic Circle (66°33.5' N) as the
120 southern boundary of our study area in the northeastern Atlantic, thus excluding the waters off
121 southern Iceland and off mid- and south Norway (while South Greenland is still included).
122 The southeastern Bering Sea is also included, as the Arctic shelf extends from the Chukchi
123 Sea through the Bering Sea to the Aleutian Islands.

124 Our analysis is confined to Arctic shelf regions and complements similar investigations on
125 the benthos of Arctic coastal waters and fjords (Weslawski et al. this volume) and the Arctic
126 deep sea (Bluhm et al. this volume). As the boundary between shelf and deep sea we chose
127 the shelf break, represented by a rapid increase in depth with distance off shore, which occurs
128 at different water depths in the various seas but was always < 500 m (Jakobsson 2002). The
129 distinction between Arctic shelf and coastal areas was more difficult to define. Here, we
130 excluded stations that are both closer than 10 km to shore and shallower than 30 m. This
131 approach is based on the assumption that these are 'coastal' sites, which are under the
132 strongest influence of wave action, ice scourer, land discharge of freshwater and sediments
133 and where the seabed is within the euphotic zone. We acknowledge that this boundary is to

134 some extent arbitrary and that some overlap of the shelf and coastal inventory is inevitable,
135 especially in the Canadian Archipelago.

136 As a result, our study area largely comprises the Arctic shelf regions, the geographic
137 boundaries of which are defined according to the "IHO Arctic Ocean Provinces"
138 (International Hydrographic Organization 2001) and minor modifications suggested by
139 Jakobsson (2002). From an ecological point of view, the shelf seas represent marine
140 ecoregions, which are defined as "distinct areas of relatively homogeneous species
141 composition, which is likely to be determined by the predominance of a small number of
142 ecosystems and/or a distinct suite of oceanographic or topographic features" (Spalding et al.
143 2007). According to Spalding et al. (2007) "the dominant biogeographic forcing agents
144 defining the ecoregions vary from location to location but may include isolation, upwelling,
145 nutrient inputs, freshwater influx, temperature regimes, ice regimes, exposure, sediments,
146 currents, and bathymetric and coastal complexity" (as well as biological factors such as
147 interspecific interactions and dispersal). Following this approach, nineteen shelf ecoregions,
148 ranging widely in areal extent from 79,000 km² (North and East Iceland) to 1,536,000 km²
149 (North and East Barents Sea), are distinguished in the Arctic realm (Table 1, Fig. 1).

150 Together, the Arctic shelf ecoregions comprise more than half of the Arctic Ocean, as
151 defined by the International Hydrographic Organization (2001). Although they are
152 characterized by a number of general similarities in the environmental setting (Hempel 1985),
153 there are also some ecologically important contrasts between them, due to differences in
154 geographical position, topography, bathymetry, climate, hydrography, sea ice dynamics, and
155 terrestrial impact, as described in detail in a number of review articles, e.g., Curtis (1975),
156 Dayton (1990), Grebmeier and Barry (1991), Carmack et al. (2006), and Witman et al. (2008).

157 ***Data compilation***

158 We compiled an Arctic biodiversity database, representing species collected across the
159 various regions of the entire study area, from a total of 25 sources (the ArcOD database,
160 published literature as well as yet unpublished scientific cruise data provided by the authors:
161 Anonymous (1978); Archambault et al. (subm); Atkinson and Wacasey (1989a,b); Bluhm et
162 al. (1998, 2009); Brandt et al. (1996); Carey (1981); Carroll et al. (2008); Cochrane et al.
163 (2009); Conlan et al. (2008); Cusson et al. (2007); Feder et al. (1980, 2005, 2007); Hopky et
164 al. (1994); Lalande (2003); MacLaren MAREX (1978); Piepenburg (1988); Piepenburg et al.
165 (1996); Schnack (1998); Sejr et al. (2000, 2010); Starmans et al. (1993); Steffens et al.

166 (2006); Wacasey et al. (1976, 1977, 1979, 1980); Wenzel (2007); Włodarska-Kowalczyk et
167 al. (2004); see Table A in the Electronic Supplementary Material of this paper). Each ‘record’
168 is a taxon (i.e., a species or a higher taxonomic group in case species identification was not
169 possible), which was reported from a georeferenced sample, such as a trawl, epibenthic
170 sledge, grab, core, seabed photograph, or ROV video footage, and which was identified based
171 on morphological characteristics. The final database contained 65,138 records of 4900 taxa
172 from 4452 stations (i.e., locations), distributed across 18 of the 19 Arctic ecoregions (Table
173 1). The unpublished data sets considered in this study will be transferred to the Arctic Ocean
174 Diversity (ArcOD) database and will thus be available for public interactive searches through
175 both the Ocean Biogeographic Information System (OBIS) and the Global Biodiversity
176 Information System (GBIF) web portals.

177 ***Data validation***

178 The use of both accepted species names and unaccepted synonyms confounds cross-dataset
179 comparability, especially between Russian and ‘western’ investigations. Therefore, we
180 consistently used the valid species names according to the *World Register of Marine Species*
181 (WoRMS; <http://www.marinespecies.org/>). All species names in the data sets provided by the
182 contributors were submitted to WoRMS’ Taxon Match online tool. Spelling errors were
183 corrected and information not part of the Latin binomial were excluded (i.e., ‘cf.’, ‘non-
184 determ’, ‘indeterm’, ‘type 1’, ‘var.’). All records were excluded that represent higher taxa
185 (genera, families, orders) and clearly encompassed several species (as other species of this
186 higher taxon were also in the station data). Therefore, in the validated data set each record
187 represents, to our best knowledge, a single species, even in case it was not possible to assign a
188 definite species name to it. For taxa identified by WoRMS as ambiguous, an arbitrary choice
189 was often made, usually based on the first name presented. The taxon match tool was also
190 used to extract the taxonomic hierarchy (phylum to subspecies), which is needed for the
191 computation of taxonomic distinctness values. Several names not listed in WoRMS were
192 listed on the uBio web portal, usually leading to their synonym entries in the ITIS database.
193 Taxa with no available synonym in WoRMS were left unchanged (retaining the original
194 name), because WoRMS is not complete yet.

195 After this matching procedure, the unique species list amounted to approximately half of
196 the total list of taxon names in the original combined data sets (2636 species compared to
197 about 4900 taxa). The reduction of record numbers after performing the quality control
198 procedures was similar in magnitude to those documented in other large-scale dataset

199 compilations, e.g., in a pan-European compilation of the Marbef LargeNet project dataset
200 (Vandepitte et al. 2010).

201 ***Data aggregation***

202 Initial data analyses showed that a 'station' does not have the same meaning across the entire
203 database: it can represent quite a comprehensive inventory of the whole macro- and
204 megabenthic community present at a location, encompassing dozens of species from a broad
205 variety of phyla, or be a unique sample of a single or a few species. Therefore, comparative
206 analyses at 'station' level would be severely biased and are thus not meaningful. This also
207 means that the number of stations per unit area, e.g., per ecoregion, is not a consistent
208 measure of sampling effort.

209 Nonetheless, it is evident that the number of stations varied considerably among the
210 ecoregions (Table 1). Five ecoregions were particularly poorly represented in our data, i.e.,
211 present with only 0-17 stations or less than 100 records (North and East Iceland, Northern
212 Grand Banks - Southern Labrador, Lancaster Sound, Baffin Bay, and the High Arctic
213 Archipelago) and hence they were not considered in the comparative analyses. It should be
214 noted, however, that the number of stations primarily quantifies data availability to this study,
215 which does not necessarily reflect real sampling intensity. While some poorly represented
216 regions are truly little studied, such as the High Arctic Archipelago, others are actually well
217 covered in a number of studies, such as the Northern Grand Banks - Southern Labrador
218 (Archambault et al. submitted), the southeastern Bering Sea (Feder et al. 1980, 1982;
219 Haflinger 1981), but are not sufficiently represented in our database, partly because these
220 regions were not considered as being 'Arctic' before we started the compilation. The total
221 number of stations from the remaining 14 regions amounted to 4419, and the number of
222 stations from individual ecoregions ranged between 19 from North Greenland to 1799 from
223 the North and East Barents Sea (Table 1).

224 To minimize the bias introduced by uneven sampling effort and by different sampling
225 methods, we confined our synoptic analyses to presence-absence data and aggregated the
226 records by larger spatial units, i.e., the ecoregions outlined above.

227 ***Data analyses***

228 Two metrics were used to quantify biodiversity. First, the number of species (S) was
229 determined, at the scales of both the entire study area and ecoregions. Since S is very sensitive

230 to sampling effort, we also calculated the average taxonomic distinctness (Δ^+) using the
231 PRIMER software (Version 6; Clarke and Gorley 2006). This presence/absence-based
232 measure quantifies a further trait of biodiversity, which Clarke and Warwick (2001) termed as
233 the "taxonomic breadth" (i.e., the average evolutionary distance between species) of a sample
234 or area. Δ^+ describes the average 'path length' between two species following Linnean
235 taxonomy of all species within a studied sample or area. Seven taxonomic levels were used in
236 calculations: species, genus, family, order, class, phylum, and kingdom, and equal step levels
237 between successive taxonomic levels were assumed. Being largely independent of both
238 species number and sample number, taxonomic distinctness measures are particularly suited
239 for comparisons of historic data sets, for which sampling effort is uncontrolled, unknown or
240 unequal (Clarke and Warwick 2001a), as is the case for the between-ecoregion analyses.

241 Even at a spatial level as coarse as that of ecoregions, both the sampling effort and the
242 overall taxonomic comprehensiveness of the faunal inventories varied greatly. From both the
243 White and Kara Seas, for instance, only reports of species from a rather narrow taxonomic
244 range, encompassing three major phyla (Mollusca, Arthropoda, and Echinodermata), are
245 included in our database, whereas there are no data on all other taxa. In contrast, the records
246 from other regions include a greater taxonomic breadth. Due to this pronounced unevenness
247 in the taxonomic census range, comparative analyses of diversity and faunal composition
248 across all taxa in our data would inevitably provide misleading results. Therefore, we
249 performed two separate between-ecoregion analyses limited to taxa that were most
250 comprehensively represented in our dataset: (1) one that was confined to the three dominant
251 phyla Mollusca, Arthropoda, and Echinodermata (*MAE*; encompassing a total of 1467 species
252 from 4417 stations), which were present in each of the 14 ecoregions considered here, and (2)
253 another one for only Annelida (*A*; encompassing 668 species from 3662 stations), for which
254 data were available from 12 ecoregions.

255 Values of average taxonomic distinctness of the mollusk, arthropod and echinoderm faunas
256 and the annelid faunas observed in the studied ecoregions were compared to the expected
257 mean Δ^+ values and 0.95 probability limits, which were computed for 1000 randomized
258 frequency-based simulations of sub-samples of varying size (10 to 600 species and 10 to 400
259 species, respectively) drawn from a 'pan-Arctic' species pool consisting of the total of 1467
260 *MAE* species and 668 *A* species contained in our dataset by means of the PRIMER software
261 (Clarke and Gorley 2006).

262 Station-based rarefaction curves, which are equivalent of 'randomized' or 'smoothed' species
263 accumulation curves (Gotelli and Colwell 2001), were used as a further tool to compare
264 species numbers among ecoregions differing widely in sampling effort (Clarke and Warwick
265 2001b). They were generated by means of the PRIMER software as averages of 400 species
266 accumulation curves based on randomly permuted order of samples (Clarke and Gorley
267 2006). Furthermore, we computed from the station-based rarefaction curves the rarefied
268 numbers of species that are expected to be recorded in an ecoregion after taking samples at
269 only 19 stations (RS_{19} , with 19 being the minimum number of stations from an ecoregion in
270 our dataset).

271 We computed non-parametric Chao2 estimators by means of the PRIMER software (Clarke
272 and Gorley 2006) to predict the expected number of species, which would be observed for an
273 infinite number of samples, for both MAE and A for each ecoregion. This parameter is based
274 on the number of 'rare' species in the ecoregion data sets ($Chao2 = S_{obs} + Q_1^2/2Q_2$, where S_{obs}
275 is the total number of observed species, Q_1 the number of species that occur at just one station
276 (uniques) and Q_2 the number of species that occur at exactly two stations (duplicates); Chao
277 1987).

278 The regional patterns in multivariate faunal resemblance, quantified by the Sorensen (or
279 Dice) coefficient, were visualized by means of Multidimensional Scaling (MDS; Clarke and
280 Warwick 2001b) for MAE as well as A . In addition to the species-based analyses, the
281 distribution patterns for data aggregated to higher taxonomic levels (genus, family) were also
282 examined. This approach is assumed to be more appropriate for our data set because it can be
283 expected to be less biased than species-based analyses, particularly when looking at finer
284 spatial levels such as that of ecoregions. The lowering of taxonomic resolution of data can be
285 advantageous for the analyses of large databases containing several datasets that can be
286 inconsistent in the accuracy of species-level identifications. Several studies have
287 demonstrated taxonomic sufficiency of genera and families for detecting major discontinuities
288 in benthic distributions (e.g., Cusson et al. 2007; Włodarska-Kowalczyk and Kedra 2007).

289 In a second-stage approach, the relationships among the between-ecoregion similarities
290 (computed based on the distribution of mollusks, arthropods, echinoderms, treated both
291 separately and combined (MAE), as well as annelids (A) analyzed at species, genera and
292 families level each) were examined using the Spearman's rank correlation coefficient (ρ)
293 computed between corresponding elements of the first-stage similarity matrices. The
294 resemblances among the first-stage between-ecoregion similarities were compared using the

295 method of Somerfield and Clarke (1995), resulting in a second-stage MDS ordination
296 showing the degree of concordance in the spatial distribution patterns of Mollusca, Annelida,
297 Arthropoda, and Echinodermata assessed at various taxonomic levels, and the statistical
298 significance of the resemblance concordances was tested by means of the RELATE routine.
299 All computations were performed with the PRIMER software (Clarke and Gorley 2006).

300 **Results**

301 ***Overall inventory***

302 Our joint database, covering 14 of 19 marine shelf ecoregions of the Arctic, comprises a total
303 of 2636 benthic species, including 847 Arthropoda (32%), 668 Annelida (25%), 392 Mollusca
304 (15%), 228 Echinodermata (9%), 205 Bryozoa (8%), and 296 (11%) species of other phyla
305 (Fig. 2; see also Table B in the Electronic Supplementary Material of this paper).

306 Within the Arthropoda, Malacostraca are the most diverse class with 805 species (including
307 494 Amphipoda, 112 Isopoda, 26 Tanaidacea, 88 Cumacea, and 61 Decapoda), followed by
308 Pycnogonida (29) and Maxillopoda (11) (Fig. 2). The composition of the mollusk fauna is
309 strongly dominated by Gastropoda (205) and Bivalvia (156) (Fig. 2). Most annelid species
310 belong to the Polychaeta (659) (Fig. 2). The major echinoderm classes are Ophiuroidea (98
311 species), followed by Asteroidea (61), Holothuroidea (53), Echinoidea (11), and Crinoidea (5)
312 (Fig. 2).

313 ***Most common species***

314 The most widely distributed species (i.e., those occurring in at least 13 of the 14 ecoregions
315 considered in our analysis) are the brittle stars *Ophiocten sericeum*, *Ophiura robusta*, and
316 *Ophiacantha bidentata*, the amphipods *Ampelisca eschrichti*, *Anonyx nugax*, *Arrhis*
317 *phyllonyx*, *Byblis gaimardi*, and *Haploops tubicola*, and the cumaceans *Diastylis* spp. and
318 *Leucon nasica*.

319 The most common mollusks, occurring in at least 12 of 14 ecoregions, are the bivalves
320 *Astarte montagui*, *Macoma calcarea*, *Musculus niger*, *Serripes groenlandicus*, and *Yoldiella*
321 *lenticula*.

322 Among the polychaetes, the species *Nothria conchylega*, *Aglaophamus malmgreni*, *Eteone*
323 *longa*, *Lumbrineris fragilis*, *Nicomache lumbricalis*, *Pholoe minuta*, and *Scalibregma*

324 *inflatum* are most widely distributed (i.e., reported from at least 10 of the 12 ecoregions, for
325 which polychaete distribution data are available).

326 ***Diversity comparisons between ecoregions***

327 In our data, the number of Mollusca, Arthropoda, and Echinodermata (hereafter called *MAE*)
328 species recorded in individual ecoregions ranged from 40 for the East Greenland shelf to 595
329 for the NE Barents Sea (Table 2a, Fig. 3a). Average *MAE* taxonomic distinctness values (Δ^+)
330 computed for the ecoregions were in the range from 67.5 in the Kara Sea to 72.5 in the
331 Eastern Bering Sea (Table 2a). The numbers of annelid species (hereafter called *A*) in the
332 ecoregions varied between 24 in the eastern Bering Sea and 322 in North and East Barents
333 Sea (Table 2b, Fig. 3b). The annelid Δ^+ values ranged from 54.0 in the Laptev Sea to 55.3 in
334 the Eastern Bering Sea (Table 2b).

335 Both diversity parameters, total numbers of species (*S*) recorded in the ecoregions and
336 average taxonomic distinctness (Δ^+), tend to increase with sampling effort, approximated by
337 the total number of stations from each ecoregion. These relationships are, however, rather
338 weak, for Δ^+ even weaker than for *S*, and not significant for any of the taxonomic subsets
339 examined (Fig. 4a-d).

340 For both *MAE* and *A*, Δ^+ values are also not significantly related to observed species
341 numbers (Fig. 5a; Spearman's rank correlation $\rho = 0.216$, $P = 0.459$, and Fig. 5b: $\rho = 0.053$, P
342 $= 0.871$, respectively). For *MAE*, it is evident that the taxonomic breadth of a number of
343 ecoregions (White and Kara Seas, Hudson Complex, North and West Greenland, as well as
344 North Labrador) is, regardless of observed species numbers, not only lower than that of the
345 other ecoregions but also significantly smaller than the 95 % probability limit of expected
346 values of the overall taxonomic distinctness of the pan-Arctic *MAE* fauna (Fig. 5a). This is
347 not the case with regard to Annelida, for which all Δ^+ values cluster around the overall mean
348 value and fall within the 95% probability limits (Fig. 5b).

349 ***Station-based rarefaction curves***

350 From station-based rarefaction analyses (Fig. 6a, for *MAE*; Fig. 6b, for *A*) it is evident,
351 regardless of the number of stations available: (i) almost all ecoregion curves show no sign of
352 approaching an asymptote and (ii) for a given number of stations pronounced differences in
353 species number appear to exist between ecoregions. According to the rarefaction curves, the
354 shelves off West and North Greenland and North Labrador are characterized by highest

355 diversities, the White Sea and the seas off Siberia are least diverse, and the regions north of
356 Canada and the Chukchi Sea have an intermediate position in this diversity gradient.

357 The rarefied numbers of species RS_{19} range from 27 ± 3 s.d. in the White Sea to 299 ± 25
358 s.d. in North Labrador for *MAE* (Table 2a, Fig. 3a). For Annelida, the RS_{19} estimates run from
359 3 ± 9 s.d. in the East Siberian Sea to 211 ± 23 s.d. in West Greenland (Table 2b, Fig. 3b).
360 Observed and rarefied species numbers are significantly positively correlated for *MAE*
361 (Spearman's rank correlation $\rho = 0.676$, $P = 0.008$) and Annelida ($\rho = 0.650$, $P = 0.022$).

362 *Estimation of expected numbers of species*

363 The Chao2 values used to estimate 'expected total species numbers' of *MAE* for each
364 ecoregion range from 55 ± 9 s.d. off East Greenland to 745 ± 47 s.d. in the Beaufort Sea
365 (Table 2a, Fig. 3a). These estimates exceed the observed species numbers by $11\% \pm 4\%$
366 (Chukchi Sea) to $64\% \pm 14\%$ (Hudson Complex). On weighted average (weighted by the
367 ratio of the number of stations per 1000 km² ecoregion area), our results suggest that further
368 sampling would increase the number of *MAE* species known to occur in the entire study area
369 by 26 to 52% ($39 \pm 13\%$), indicating that between about a fifth and a third ($28 \pm 12\%$) of the
370 expected *MAE* species pool is still unknown.

371 In the case of Annelida, the Chao2 values range from 24 ± 0 s.d. in the Eastern Bering Sea
372 to 390 ± 27 s.d. off West Greenland (Table 2b, Fig. 3b). For ecoregions, which are obviously
373 underrepresented in our data, such as the Eastern Bering and East Siberian Seas, Chao2 values
374 are not higher than the observed species numbers; for the other ecoregions they are greater
375 than the observed species numbers by $10 \pm 3\%$ (Northeastern Barents Sea) to $51 \pm 20\%$ (North
376 Greenland). On weighted average (excluding the severely under-represented ecoregions
377 mentioned above), Chao2 values are 12 to 32% ($22 \pm 10\%$) greater than the observed species
378 numbers, suggesting that between about a tenth and a quarter ($18 \pm 7\%$) of the annelid species
379 actually occurring on Arctic shelves have not been reported yet.

380 For both *MAE* and *A*, the rank order of Arctic shelf ecoregions remains largely the same,
381 when considering expected instead of observed number of species. Both parameters are
382 highly correlated (Spearman's rank correlation $\rho = 0.939$, $P < 0.0001$ for *MAE*, and $\rho = 0.972$,
383 $P < 0.0001$, for *A*).

384 ***Faunal resemblance patterns between ecoregions***

385 The ecoregions also differ in terms of the taxonomic composition of their *MAE* fauna (Fig.
386 7a). Two major faunal gradients are discernible: one along the x axis of the MDS plot
387 between East Greenland and the Bering and Chukchi Seas and another one along the y axis
388 ranging from the White Sea over a series of Eurasian-Arctic seas to West Greenland. This
389 overall pattern was largely consistent when the faunal resemblances between the ecoregions
390 are examined on the level of genera (Fig. 7b) and families (Fig. 7c), as indicated by highly
391 significant rank correlations between the between-ecoregion similarity values computed at
392 different taxonomic levels (RELATE Rho coefficients range between 0.915 and 0.984, all
393 with $P = 0.001$).

394 The resemblance patterns of the annelid fauna among ecoregions were analyzed for only
395 nine ecoregions. The Laptev, East Siberian and Eastern Bering Seas were excluded, as the
396 species numbers are too small, and thus the faunal ranges in our data are too narrow, for a
397 meaningful comparison with the other regions that are better represented in our data. At the
398 species level, the annelid fauna of North and East Greenland are clearly distinct from those in
399 the remaining ecoregions, particularly as compared to the Chukchi Sea region (Fig. 7d). As in
400 the case of the *MAE* fauna, the annelid-based between-ecoregion resemblance patterns at
401 different taxonomic levels (Fig. 7d,e,f) are very similar to each other (RELATE Rho
402 coefficients fall in the range between 0.623, $P = 0.004$, and 0.880, $P = 0.001$).

403 A second-stage analysis compared the between-ecoregion patterns of different taxonomic
404 groups (Mollusca, Arthropoda, Echinodermata, *MAE*, Annelida) at different taxonomic levels
405 (species, genus, and family) for the nine ecoregions considered in the annelid resemblance
406 analysis (Fig. 7g). It is evident that pattern similarities are highest among taxonomic levels
407 within phyla. This is least so for Annelida, but even for this phylum the RELATE Rho
408 coefficients indicate significant between-pattern correlations ($P < 0.05$). Furthermore, the
409 MDS plot shows that the annelid between-ecoregion resemblances are most different from
410 those of Echinodermata and Arthropoda (all RELATE Rho correlations are not significant
411 with $P > 0.05$) and more similar to those of Mollusca and *MAE* (all RELATE Rho
412 correlations are significant with $P < 0.05$).

413 **Discussion**

414 *Arctic-wide species inventory*

415 We present the first pan-Arctic inventory of the macrobenthic and megabenthic shelf species.
416 Nevertheless, there are other large-scale studies with which some of our results can be
417 compared. Sirenko and Piepenburg (1994) reported a total of more than 4000 zoobenthic
418 species for the entire Eurasian Arctic, and seven years later Sirenko (2001) listed about 20%
419 more species, primarily because of the analysis of additional samples taken in the course of
420 intensified research efforts such as the 10-year Russian-German Laptev Sea study (Kassens et
421 al. 1999). Although our pan-Arctic census covers a larger area, namely both the eastern and
422 the western Arctic, the total number of species in our data (2636) is smaller than the figure
423 reported by Sirenko (2001), whose inventory of the "free-living invertebrates of Eurasian
424 Arctic seas and adjacent deep waters" comprises a total of 4814 species, 4357 of which can be
425 regarded as being benthic.

426 In general, it is acknowledged that all diversity inventories are potentially biased to some
427 degree by a host of methodological factors, e.g., differences in sampling intensity, taxonomic
428 scope and spatial scales covered, and therefore any large-scale comparisons of species
429 diversity are rather problematic (Hurlbert 1971). In this case, the taxonomic coverage of our
430 inventory must be taken into account when comparing the results to other studies of Arctic
431 diversity. Sirenko (2001), for instance, considered 56 invertebrate higher taxa at different
432 levels (including 24 phyla) in his census. Our analyses, however, were confined to
433 macrobenthic and megabenthic species of shelf regions and, therefore, a range of higher taxa
434 included in his lists (Foraminifera, Radiolaria, Ciliophora, Scyphozoa, Ctenophora,
435 Nematoda, Rotifera, Tardigrada, Acari, Cladocera, Calanoida, Harpacticoida, Euphausiacea,
436 Chaetognatha, and Appendicularia) are not considered in our analyses. If restricted to the 38
437 higher taxa from 16 phyla, usually regarded to encompass primarily macro- or megabenthic
438 species, Sirenko's (2001) list contains a total of 3054 species, including 485 Mollusca, 890
439 Arthropoda, 150 Echinodermata (1525 species combined), and 522 Annelida. These figures
440 are quite close to our numbers of observed species, 16% higher for the total number of species
441 and between 24 % higher and 34% lower for the number of species of the four major phyla.
442 Overall, this comparison suggests that our inventory provides comparable accounts of the
443 major phyla Mollusca, Arthropoda, Annelida and Echinodermata, whereas the minor phyla
444 appear to be less well represented in our data, as indicated by the particularly small species
445 numbers of some taxa such as, e.g., sponges. The poor representation of these taxa is likely

446 related to several reasons, e.g., the poor taxonomic emphasis and training for those groups in
447 most western ecologists and bias in the sampling data sets such that their preferred hard-
448 bottom habitats were poorly sampled relative to soft-bottom sites.

449 In an approach similar to ours, Bluhm et al. (this volume) assessed the biodiversity of the
450 Arctic deep sea, i.e., the Arctic regions beyond the shelf break (> 500 m depth). Their pan-
451 Arctic deep-sea database comprises 725 macro- and megabenthic species, a large part of
452 which (444 species, equivalent to 61% of their total species number) have been reported from
453 the Arctic shelves covered in our study. This finding suggests that many known Arctic deep-
454 sea species are actually eurybathic animals occurring over a wide water depth range. It should
455 be noted, however, that for the deep sea the difference between the number of known species
456 and those actually occurring there is very likely much larger than for the shelf regions (Gray
457 et al. 1997) and, hence, this conclusion is only preliminary and could be disproven by further
458 investigations.

459 Our estimates of the expected numbers of species are confined to the ecoregion scale and to
460 the major, reasonably well represented phyla Mollusca, Arthropoda, Echinodermata and
461 Annelida. Based on certain assumptions, however, we can also provide a gross estimate of
462 expected species for the entire study area and the whole macro- and megabenthic fauna. Our
463 analyses of species diversity in the ecoregions suggest that on average the expected numbers
464 of species exceed the observed numbers of mollusk, arthropod and echinoderm species by
465 $39 \pm 13\%$ based on the Chao2 estimate. Extrapolated to the entire study area, from which a
466 total of 1467 species are included in our database, this would mean that the expected number
467 of *MAE* is about 2040 ± 190 . In the case of annelids, an analogue approximation approach,
468 based on an across-ecoregion mean ratio of expected to observed species of 1.22 ± 0.1 and a
469 total number of 668 observed species, yields a total of 816 ± 71 expected annelid species.
470 Together, the expected species numbers of the four major phyla total between 2596 and 3116
471 (2856 ± 260) species. In the comprehensive inventory of Sirenko (2001), Mollusca, Annelida,
472 Arthropoda and Echinodermata account together for about two-thirds of the entire macro- and
473 megabenthic fauna. We regard Sirenko's inventory to be more realistic than our data in terms
474 of the overall species shares of the entire range of phyla because compiled by taxonomic
475 experts only. Applying the two-thirds ratio to our pan-Arctic estimates, we conclude that
476 about 3894 to 4674 (4284 ± 390) macro- and megabenthic species can be expected to inhabit
477 the Arctic shelf regions.

478 Due to several biases (see methodological considerations below), our figures of observed
479 and expected numbers of species are without doubt only gross and conservative
480 approximations of the numbers of species occurring in Arctic shelf seas. Archambault et al.
481 (submitted) provided evidence of unusually high numbers of known species in Arctic regions
482 compared to Atlantic waters in a review of the marine biodiversity of the three oceans around
483 Canada, despite pronouncedly lower sampling effort levels. This conclusion casts doubts on
484 the general validity of the commonly assumed latitudinal diversity decline in species diversity
485 (Gray et al. 1997). Furthermore, published species numbers are very likely underestimating
486 the real diversity, since numerous currently-known species, that are identified based on
487 morphological traits, are actually representing a set of genetically distinct cryptic species. For
488 instance, DNA barcoding efforts showed recently that this is the case for at least one quarter
489 of the polychaete species (morphospecies) known from Canadian waters (Radulovici et al.
490 2010; C. Carr, pers. comm.).

491 Gutt et al. (2004) presented gross estimates of how many macrobenthic species might
492 inhabit the shelf of the Weddell Sea (2100 to 10,500, excluding the so-called "shallow fauna"
493 species, in an area of 7000 km²) as well as the entire Antarctic shelf (9000 to 14,000 species
494 in an area of 2,200,000 km²). The latter area is only about a quarter of the total extent of the
495 Arctic shelves considered in our inventory (see Table 1)). Their estimates are not entirely
496 comparable to ours, since they were not based on the evaluation of a great number of faunal
497 lists from a wide variety of regions. Instead, their estimate only consisted of the analysis of 16
498 trawl catches in the Weddell Sea (yielding 820 species in total), a suite of non-parametric
499 rarefaction-based approaches (including computation of Chao2 values), and assumptions
500 about the species shares of taxa not considered in the survey and scaling their limited survey
501 up to the entire Antarctic shelf. Considering the smaller area of the Antarctic shelves, a
502 comparison of Gutt et al. (2004) and our estimates suggests that the number of benthic shelf
503 species in the Antarctic appears to be slightly higher than in the Arctic. The difference
504 between the two faunas is, however, not as pronounced as assumed two or three decades ago
505 (Knox and Lowry 1977; Dayton 1990); it appears to be at a factor of only about two rather
506 than an order of magnitude. Our results provide further evidence for the notion that, on a
507 global scale and compared to other large marine ecosystems, such as the entire deep sea
508 (500,000 species, May 1992; 10,000,000 species; Grassle and Maciolek 1992) and all tropical
509 coral reefs (up to 670,000 species; Reaka-Kudla 1997), both Arctic and Antarctic shelves are
510 characterized by intermediate macro- and megabenthic species numbers (Gutt et al. 2004;
511 Piepenburg 2005).

512 ***Regional patterns***

513 Sirenko (2001) also demonstrated that known benthic diversity varies broadly (by a factor of
514 three) among Eurasian Arctic seas from the Barents Sea to the East Siberian Sea, suggesting a
515 clear eastward decline in species numbers. Our macro- and megabenthic inventory largely
516 corroborates Sirenko's (2001) findings, which confirmed those values reported by Zenkevitch
517 (1963). Our analysis also explicitly shows that the trend of decreasing species numbers from
518 the Barents to the East Siberian Sea in the Eurasian Arctic may not only reflect a
519 zoogeographic pattern, caused by differences in climate, geographic position and immigration
520 rates of Atlantic and Pacific immigrants (Zenkevitch 1963, Carmack and Wassmann 2006),
521 but also the pronounced differences in sampling effort among regions. For instance, the
522 Barents Sea is still much more thoroughly studied than the Laptev or East Siberian Seas,
523 despite recently intensified sampling efforts in the latter regions. We found a quite high,
524 statistically significant correlation between observed species numbers, which are known to be
525 very dependent on sampling effort, and rarefied species numbers, which are much less
526 dependent on sampling effort. This indicates that, on a large scale, the between-ecoregion
527 differences in observed and rarefied species numbers reflect a very similar pattern of diversity
528 disparities among ecoregions. There are, however, also notable exceptions. Such is the case
529 for the particularly well-studied Barents Sea (~1800 samples), which not surprisingly ranks
530 first in terms of observed species numbers (595 mollusk, arthropod and echinoderm species,
531 322 annelid species) but only ninth in case of both *MAE* and *A* in terms of rarefied species
532 numbers (62 ± 26 s.d. and 29 ± 36 s.d., respectively). Moreover, rarefied species numbers are
533 not significantly higher in the Barents Sea than in the seas off Siberia. These findings
534 highlight the necessity of accounting for differences in sampling effort when comparing
535 species diversity parameters. Based on our data we cannot confirm that the Barents Sea is
536 truly richer in benthic species than the more eastern shelf regions off Siberia. However, if a
537 difference exists, it may, in fact, result from a higher riverine freshwater inflow and thus
538 higher seasonal salinity fluctuations influencing the Siberian shelf systems (Carmack et al.
539 2006).

540 Overall, the distribution of species numbers and species distinctness across ecoregions is
541 quite similar in our data for *MAE* and *A*, indicating that diversity differences between
542 ecoregions are consistent across these two faunal subsets. Furthermore, the various diversity
543 measures we used, observed and rarefied species numbers, as well as station-based rarefaction
544 curves, provided largely comparable pictures of the potential diversity differences among the

545 Arctic shelf regions (while inconsistencies can be explained by the high variability of the
546 parameter estimates and the curves' trajectories). The shelves off Greenland (excluding East
547 Greenland, which is severely under-represented in our data) and North Labrador are
548 characterized by highest diversities, whereas the seas off Siberia are poorest (or most under-
549 represented in our data), and the species numbers of the regions north of Canada and the
550 Chukchi Sea are intermediate.

551 With regard to the between-ecoregion resemblance pattern in terms of the composition of
552 the mollusk, arthropod and echinoderm fauna combined and annelids only (Fig. 7a-f), there
553 are apparently two major faunal gradients. The first one along the horizontal axis of the MDS
554 plots, between East Greenland on the one side and the Chukchi and Bering Seas on the other
555 side, largely reflects a gross eastern Arctic–western Arctic grade with regard to biogeographic
556 affiliation. It is most pronounced at the species level and less discernible at higher taxonomic
557 levels, although the patterns at the different levels are largely comparable, as the high
558 RELATE correlation coefficients indicate. The second gradient along the vertical axis of the
559 MDS plots, ranging for *MAE* from the White Sea over a series of Eurasian-Arctic seas to
560 West Greenland, is more difficult to interpret. It most likely reflects a mixture of different
561 influences (geographic location, ice conditions, estuarine impact), which are known to shape
562 the environmental conditions of the ecoregions (Carmack et al. 2006) and can thus be
563 assumed to drive the diversity and composition of their faunas (Carmack and Wassmann
564 2006).

565 *Methodological considerations*

566 Our study is the first comprehensive circumpolar effort to assess the 'state-of-the-art'
567 knowledge on the diversity patterns of the Arctic shelf benthos. It should be noted, however,
568 that the numbers of species reported here represent conservative estimates because our
569 inventory is incomplete with regard to (i) the species already known from the Arctic but not
570 included in our data, and (ii) all species expected to occur in Arctic shelf regions but not
571 sampled yet.

572 The first deficiency is evident even at the coarsest spatial level of our study (the entirety of
573 all 19 Arctic shelf ecoregions). Only a subset of the entire taxonomic range is included in our
574 inventory. The census comprehensiveness strongly varies among taxonomic groups, and some
575 higher taxa are especially poorly covered, such as for instance Porifera. The number of
576 sponge species known from the shelves and slopes off Greenland totals 210 and for the entire

577 Arctic it is expected to be 250 to 300 species (Tendal, personal communication). The small
578 number of species in our data (35) clearly demonstrates that Porifera are particularly under-
579 represented (by ~80%) in our inventory. Other taxa are better represented than sponges but
580 even in these cases the overall number of species in our data does not represent the actual
581 number of known species from Arctic shelf regions. In the case of Bryozoa, for instance, the
582 total number of species in our data set adds up to 205, whereas more than 350 species are
583 actually known to inhabit Arctic shelves (Kuklinski, personal communication) and thus our
584 census underestimates the actual known species number of Bryozoa by 40%. Moreover, it
585 should be noted that some higher taxa, primarily those encompassing mostly small, less
586 prominent and difficult-to-identify animals, such as Hydrozoa or Nemertina, are not as
587 comprehensively investigated as Polychaeta, Bivalvia, Crustacea, and Echinodermata.

588 The caveats resulting from incomplete and unevenly distributed data are even more
589 pronounced at the level of single ecoregions. From one ecoregion (#10 - High Arctic
590 Archipelago), we do not have any record at all in our data set; from four others (#2 - North
591 Iceland, #5 - Northern Grand Banks - Southern Labrador, #7 - Baffin Bay, and #9 - Lancaster
592 Sound) our data are so scarce that they could not be included in the comparative between-
593 ecoregion analyses (Table 1), and the remaining 14 ecoregions considered in the comparative
594 analyses differ widely in the number of stations in our data, with most to be regarded as being
595 either truly under-sampled (e.g., East Greenland) or actually well-sampled but severely under-
596 represented in our database (e.g., Eastern Bering Sea).

597 In our data, there is only a weak positive trend between the number of stations (used as an
598 approximation of sampling effort) and the number of species recorded in the ecoregions (Fig.
599 4a,c). Nevertheless, these non-significant relationships were clearly stronger than those
600 between number of stations and taxonomic distinctness (Δ^+), indicating that (i) the species
601 inventory is incomplete for most ecoregions and due caution is advised when comparing
602 species diversity among regions, and (ii) taxonomic distinctness is independent from
603 sampling effort and thus better suited for viable between-ecoregion comparisons than
604 observed species numbers. Furthermore, the lack of a relation between species numbers (S)
605 and species distinctness (Δ^+) supports the notion that the latter quantifies an additional
606 biodiversity trait that is not connected with pure number of species (Clarke and Warwick
607 2001a).

608 The taxonomic distinctness of the *MAE* fauna in a number of ecoregions (White and Kara
609 Seas, Hudson Complex, North and West Greenland, North Labrador) is not only lower than

610 that in other ecoregions but also significantly lower than the overall taxonomic distinctness of
611 the pan-Arctic *MAE* fauna (Fig. 5a). There are two possible explanations for this pattern. It
612 may either indicate a truly reduced biodiversity (in terms of taxonomic breadth) in the
613 respective ecoregions or it is to a great extent caused by the rather narrow taxonomic range in
614 the faunal investigations of the respective ecoregions. The latter methodological constraint is
615 independent of the number of samples taken (and, hence, overall number of species recorded)
616 and noticeable even in presumably well-studied taxa, such as mollusks, arthropods and
617 echinoderms. The lack of such a pattern for Annelida (Fig. 5b) suggests, in terms of the
618 taxonomic breadth of the annelid fauna, that there is no significant difference between the
619 ecoregions considered in our analysis and/or that these ecoregions were studied with
620 comparable intensity.

621 Station-based rarefaction showed more clearly the influence of sampling effort variation on
622 the assessment of species diversity than the direct relationship between sampling effort and
623 observed species number. Therefore, we used species rarefaction curves for each ecoregion to
624 compare species numbers among ecoregions. The curves also clearly indicate that the
625 numbers of observed species in the data severely under-estimate potential total numbers of
626 species occurring in the region, even in case of relatively well sampled regions, such as the
627 Barents Sea, and well studied taxa, such as mollusks, arthropods, and echinoderms (Fig. 6a),
628 or annelids (Fig. 6b).

629 The difference between known and expected species numbers represents the second and
630 more obvious type of census incompleteness. The number of species known from an area is
631 largely dependent on the number of samples taken, and it is always lower than the total
632 expected number of species occurring in the area unless a very large number of samples are
633 analyzed. It is only then that rare species are included in the inventory. There are a number of
634 approaches that can be used to estimate the expected species numbers occurring in an area
635 (Colwell and Coddington 1994). Here, we computed Chao2 estimates for each ecoregion
636 (Table 2, Fig. 3). These estimates are based on the number of 'rare' species, i.e., those
637 occurring only at one or two stations in an ecoregion. Therefore, it should be noted again that
638 the concept of a 'station' varies among ecoregions: in some cases (e.g., North Labrador) it
639 includes many species from various phyla and represents quite a comprehensive inventory of
640 the whole macro- and megabenthic community at a location; in others (e.g., most stations
641 from the Barents Sea) it is a record of just a single or a few species. This variation in the type
642 of 'station' influences the computation of Chao2 values. Therefore, our values have to be

643 regarded as gross and rather conservative estimates. In our comparisons between ecoregions
644 the analyses do not necessarily reflect true diversity contrasts and differences in faunal
645 composition. To a certain degree, the observed patterns are also caused by methodological
646 differences in the taxonomic range/breadth of a typical 'station' in the ecoregion data.

647 The distinct position of the comparatively station-poor ecoregion East Greenland in the
648 MDS plots, used to illustrate the large-scale spatial faunal patterns (Fig. 7a-f), indicates that
649 differential sampling intensity (and, hence, method-based differences in species number) is a
650 confounding factor affecting the between-region resemblance computations and the observed
651 differences in faunal composition.

652 Finally, the potential influence of temporal dynamics in species composition has to be
653 considered. The samples included in our database were collected over a long period of time
654 (1955–2009). Temporal gaps in our data and uneven distribution in time may have
655 confounded our spatial analyses. The potential bias due to uncontrolled temporal variability is
656 minimized, however, by (i) analyzing presence/absence data only (as these data are not as
657 sensitive to change as species abundance or biomass), (ii) applying a rather coarse spatial data
658 aggregation approach, e.g., by grouping the data in ecoregions that represent 'natural
659 geographical units', and (iii) using a hierarchical taxonomic aggregation approach for
660 comparative between-ecoregion analyses. Furthermore, Cusson et al. (2007) showed that the
661 temporal variability (in benthic abundances) is of the same order as spatial variability at rather
662 small scales (few km) only and suggested that larger, Arctic-wide or ecoregion-wide patterns
663 may be less affected by changes in time.

664 *Perspectives for future work*

665 There are several possible avenues for future studies extending and refining our inventory,
666 which only represents a preliminary account of Arctic shelf diversity. First and foremost, the
667 issue of the incompleteness of our database has to be resolved. On the one hand, additional
668 field sampling is needed, particularly in hitherto poorly investigated regions such as the High
669 Arctic Archipelago. In general, novel field collections should be designed in such a way that
670 they cover environmental and geographic gradients and will thus help determining large-scale
671 cross-ecoregion patterns. Furthermore, our study also has clearly shown that a pan-Arctic
672 effort to regularly apply a suite of standardized sampling approaches and methods in future
673 field studies, in order to adequately sample the full range of taxa and habitats and to achieve
674 consistent and highly comparable species distribution data, should be a high priority.

675 On the other hand, and maybe even more pressing, further data mining work is required.
676 Without doubt, there are numerous historic data sets available (in zoological museums,
677 technical reports, etc.), which are not yet included in our pan-Arctic database but could help
678 in not only extending the geographic range of our current study but also enhancing its
679 taxonomic breadth, particularly for regions that are currently poorly represented in our data.
680 This data scarcity does not only apply to the number of stations, and thus to species number,
681 but also to the taxonomic range covered, which for some regions, such as the Kara Sea, was
682 very narrow in our data. Further examples are actually well-sampled but in our data under-
683 represented regions, such as the Eastern Bering Sea (from where comprehensive macrofaunal
684 data are not included in our inventory, e.g., from the southeastern Bering Sea, comprising 389
685 species (Feder et al. 1980; Haflinger 1981), and the northeastern Bering Sea, comprising 487
686 taxa (Feder et al. 1982)), or the Lancaster Sound, Eclipse Sound and northern and central
687 Baffin Bay (which were investigated by Thomson (1982) with 204 grab and diver-operated
688 airlift samples). Efforts to discover, retrieve, compile, validate and share such historic data
689 sets should have high priority in future projects. In addition, we strongly endorse ongoing and
690 future taxonomic studies based on molecular markers (Mincks Hardy et al. this issue;
691 Gradinger et al. 2010), which will surely lead to increased species numbers in most taxa and
692 have thus significant impacts on species diversity assessments. The Arctic Ocean Diversity
693 (ArcOD) initiative would provide an appropriate common framework for addressing these
694 issues.

695 Given that the issues of gathering additional data and expanded taxonomic work are
696 properly addressed, more advanced analyses will be feasible, as for example by applying a
697 nested approach of geographical data aggregation (e.g., by consecutively larger quadrates of
698 100 km², 1000 km² and 10,000 km²). By avoiding the caveats resulting from the inconsistent
699 meaning of the term ‘station’ in our study, this would allow for a meaningful study of
700 distribution patterns at smaller (‘local’ and ‘sub-regional’) spatial scales than that of ecoregions
701 (100,000-1,000,000 km²) applied in this paper. Furthermore, it would render explicit analyses
702 for identifying potential drivers and processes determining the observed species distribution
703 and diversity patterns possible.

704 **Conclusions**

705 We provide a first pan-Arctic assessment of the macro- and megabenthic biodiversity of Arctic
706 shelves. Based on an unprecedentedly thorough compilation of species distribution data from
707 almost all Arctic marine ecoregions, we were able to present a comparative view of the

708 current knowledge on benthic diversity patterns on a regional and Arctic-wide scale and give
709 conservative estimates of expected total number of benthic species for each ecoregion as well
710 as for the entire Arctic shelf. Our results provide further evidence that Arctic shelves are not
711 particularly impoverished, confuting a common paradigm on low Arctic diversity, but are
712 similar in overall species numbers to the Antarctic shelf, with both polar biomes
713 characterized, on a global scale, by intermediate values.

714 Our study also documents that despite recent sampling efforts in previously poorly studied
715 Arctic areas the quality and quantity of available information still broadly varies among both
716 regions and taxa. This imbalance in knowledge has the potential of severely confounding both
717 comparative analyses and predictive estimates of overall biodiversity. Due to the difficulties
718 generally encountered in biogeographic and species/taxa synopses of a study area as large as
719 the Arctic, the data presented here are still incomplete and our census is thus only
720 preliminary. Efforts to recover further historic data sets will be invaluable to future
721 inventories of benthic fauna in the Arctic.

722 We are confident that our inventory will lead the way for future investigations extending
723 and refining our findings which are essential to understand and evaluate possible changes in
724 the biodiversity of the still relatively pristine but increasingly threatened marine ecosystems
725 of the Arctic.

726

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746

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971 **Tables**

972 **Table 1** The Arctic shelf ecoregions according to the “Marine Ecoregions of the World”
 973 (MEOW) scheme proposed by Spalding et al. (2007). MEOW number, name and
 974 spatial extent of ecoregions (in 1000 km²), number of stations and records (before
 975 validation) in our data.

MEOW #	Ecoregion	Area (1000 km²)	Stations	Records
1	North Greenland	282	87	4385
2	North and East Iceland	79	17	22
3	East Greenland Shelf	365	19	545
4	West Greenland Shelf	281	45	4495
5	Northern Grand Banks - Southern Labrador	577	8	8
6	Northern Labrador	239	50	4825
7	Baffin Bay - Davis Strait	116	5	204
8	Hudson Complex	1172	89	1380
9	Lancaster Sound	230	3	86
10	High Arctic Archipelago	360	-	-
11	Beaufort-Amundsen-Viscount-Melville	464	131	4095
12	Beaufort Sea Shelf	145	518	11030
13	Chukchi Sea	605	337	8697
14	Eastern Bering Sea	910	177	3823
15	East Siberian Sea	906	155	946
16	Laptev Sea	533	255	1737
17	Kara Sea	900	567	3314
18	North and East Barents Sea	1536	1799	14494
19	White Sea	87	190	1052
Totals		9787	4452	65138

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978 **Table 2** Macro- and megabenthic species diversity of Arctic shelf ecoregions. Number of
 979 stations, observed number of species (S_{obs}), rarefied number of species to be
 980 expected in 19 samples (RS_{19}) \pm standard deviation, average taxonomic
 981 distinctness values (Δ^+), and Chao2 estimates of expected total species numbers (\pm
 982 standard deviation). a) Mollusca, Arthropoda and Echinodermata combined. b)
 983 Annelida only.

984 a)

MEOW #	Ecoregion	# of Stations	S_{obs}	RS_{19}	\pm SD	Δ^+	Chao2	\pm SD
1	N Greenland	87	355	201	27	70.5	478	30
3	E Greenland	19	40	40	0	72.8	55	9
4	W Greenland	45	332	239	22	69.9	432	24
6	N Labrador	50	406	299	25	70.9	591	38
8	Hudson	89	290	118	43	70.7	483	43
11	Amundsen	131	364	181	16	74.4	482	22
12	Beaufort	518	455	97	24	73.4	745	47
13	Chukchi	337	401	146	23	74.0	443	13
14	E Bering	176	146	66	9	75.2	204	23
15	E Siberian	155	113	43	6	71.9	161	21
16	Laptev	255	216	61	21	72.8	311	29
17	Kara	567	164	43	8	67.5	219	22
18	NE Barents	1798	586	62	26	72.3	712	24
19	White	190	73	27	3	69.1	117	23

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986 b)

MEOW #	Ecoregion	# of Stations	S_{obs}	RS_{19}	\pm SD	Δ^+	Chao2	\pm SD
1	N Greenland	87	104	47	16	54.2	157	21
3	E Greenland	19	88	88	0	54.5	123	17
4	W Greenland	45	292	211	23	54.2	390	27
6	N Labrador	50	218	165	15	54.7	274	19
8	Hudson	89	131	57	17	54.4	193	22
11	Amundsen	131	185	93	12	55.1	250	25
12	Beaufort	518	305	108	21	54.7	349	17
13	Chukchi	337	188	61	19	54.1	243	21
14	E Bering	176	24	21	1	55.3	24	0
15	E Siberian	155	28	3	9	54.4	28	0
16	Laptev	255	31	5	6	54.0	40	7
18	NE Barents	1798	322	29	36	54.5	355	12

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990 **Figures**

- 991 **Fig. 1** The Arctic region, with the location of shelf ecoregions defined in the "Marine
992 Ecoregions of the World" (MEOW) scheme proposed by Spalding et al. (2007).
993 MEOW numbers are explained in Table 1.
- 994 **Fig. 2** Taxonomic composition of the entire macro- and megabenthic fauna of the Arctic
995 shelf regions at phylum level (a), Annelida (b), Mollusca (c) and Echinodermata
996 (d) at class level, and Arthropoda (e) at order level.
- 997 **Fig. 3** Bar graphs showing the observed number of macro- and megabenthic species
998 (S_{obs}) in Arctic shelf ecoregions, as well as the rarefied number of species
999 expected to be recorded in each ecoregion if only 19 samples had been taken
1000 (RS_{19}) and Chao2 estimates of expected number of species. a) Mollusca,
1001 Arthropoda and Echinodermata combined, b) Annelida only (ND: no data for
1002 Kara and White Seas). RS_{19} and Chao2 values \pm standard deviation in 400 random
1003 permutations.
- 1004 **Fig. 4** Relationships between overall benthic species number (S), average taxonomic
1005 distinctness (Δ^+) and sampling intensity, estimated by number of stations (N) from
1006 Arctic shelf ecoregions. a-b: Mollusca, Arthropoda, and Echinodermata combined
1007 (a: S versus N (logarithmic scale), Spearman's rank correlation $\rho = 0.288$, $P =$
1008 0.318 ; b: Δ^+ versus N (logarithmic scale), $\rho = 0.027$, $P = 0.674$). c-d: Annelida
1009 only (c: S versus N (logarithmic scale), $\rho = 0.210$, $P = 0.513$; d: Δ^+ versus N
1010 (logarithmic scale), $\rho = 0.011$, $P = 0.974$).
- 1011 **Fig. 5** Relationship between average taxonomic distinctness values (Δ^+ ; in the figure:
1012 Delta +) and observed macro- and megabenthic species numbers in Arctic shelf
1013 ecoregions for a) Mollusca, Arthropoda and Echinodermata combined and b)
1014 Annelida only. The plots show the mean Δ^+ value and 95% probability limits,
1015 computed for 1000 frequency-based simulations of sub-samples of varying size
1016 (a: 10 to 600 species; 10 to 400 species) drawn from a presumed 'pan-Arctic'
1017 species pool consisting of the total of a) 1562 mollusk, arthropod and echinoderm
1018 species and b) 668 annelid species contained in our dataset.
- 1019 **Fig. 6** Station-based rarefaction curves (average curves from 400 permutations; double-
1020 logarithmic scale) for Arctic shelf ecoregions. (a) Mollusca, Arthropoda, and

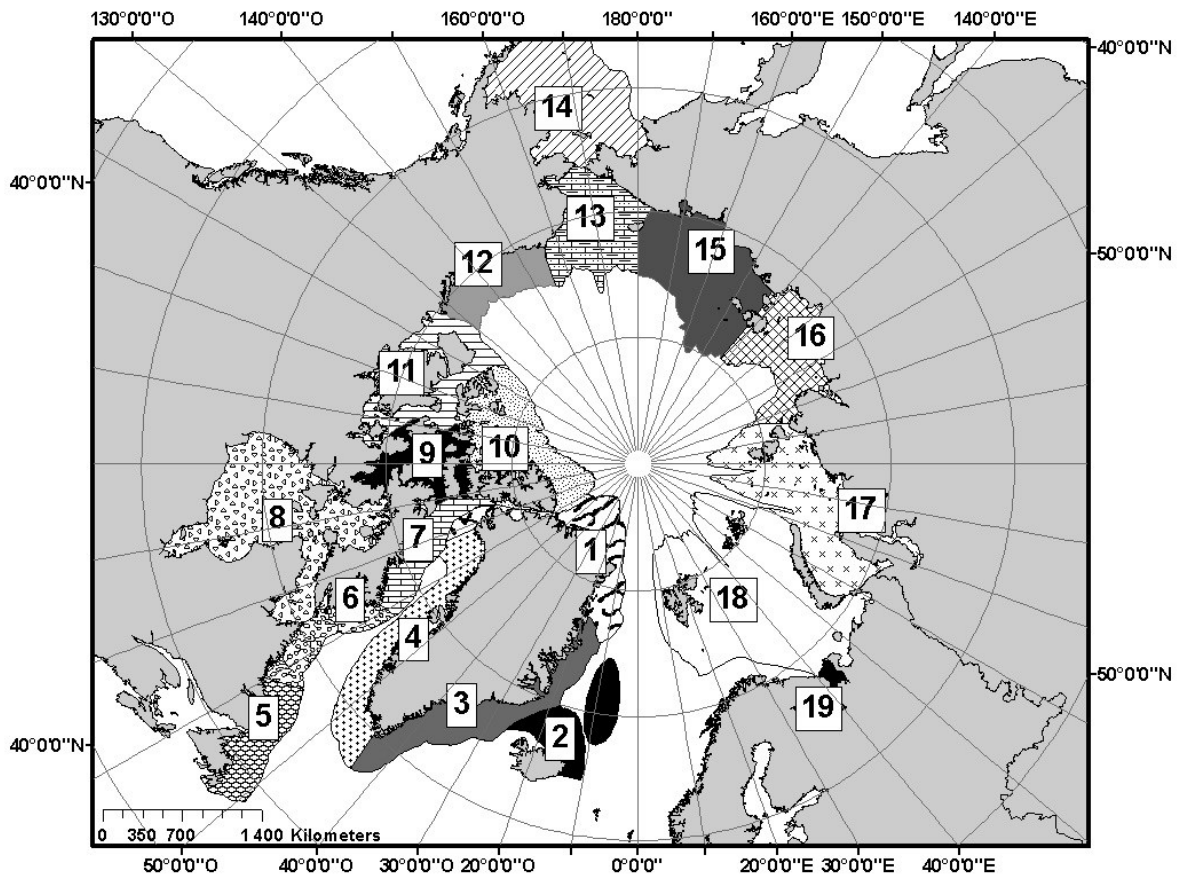
1021 Echinodermata combined; (b) Annelida only.

1022 **Fig. 7** Multidimensional scaling plots. a-f: Faunal resemblance patterns among Arctic
1023 shelf ecoregions, analyzed at the level of species (a), genera (b), and families (c)
1024 of Mollusca, Arthropoda, and Echinodermata combined (14 ecoregions), and
1025 species (d), genera (e), and families (f) of Annelida only. g: Second-stage analysis
1026 of between-ecoregion resemblance patterns of different taxonomic groups
1027 (Mollusca, Arthropoda, Echinodermata; Mollusca, Arthropoda and
1028 Echinodermata combined; Annelida) at different taxonomic levels (species,
1029 genus, and family) for the nine ecoregions considered in the annelid resemblance
1030 analysis.

1031

1032 **Fig.1**

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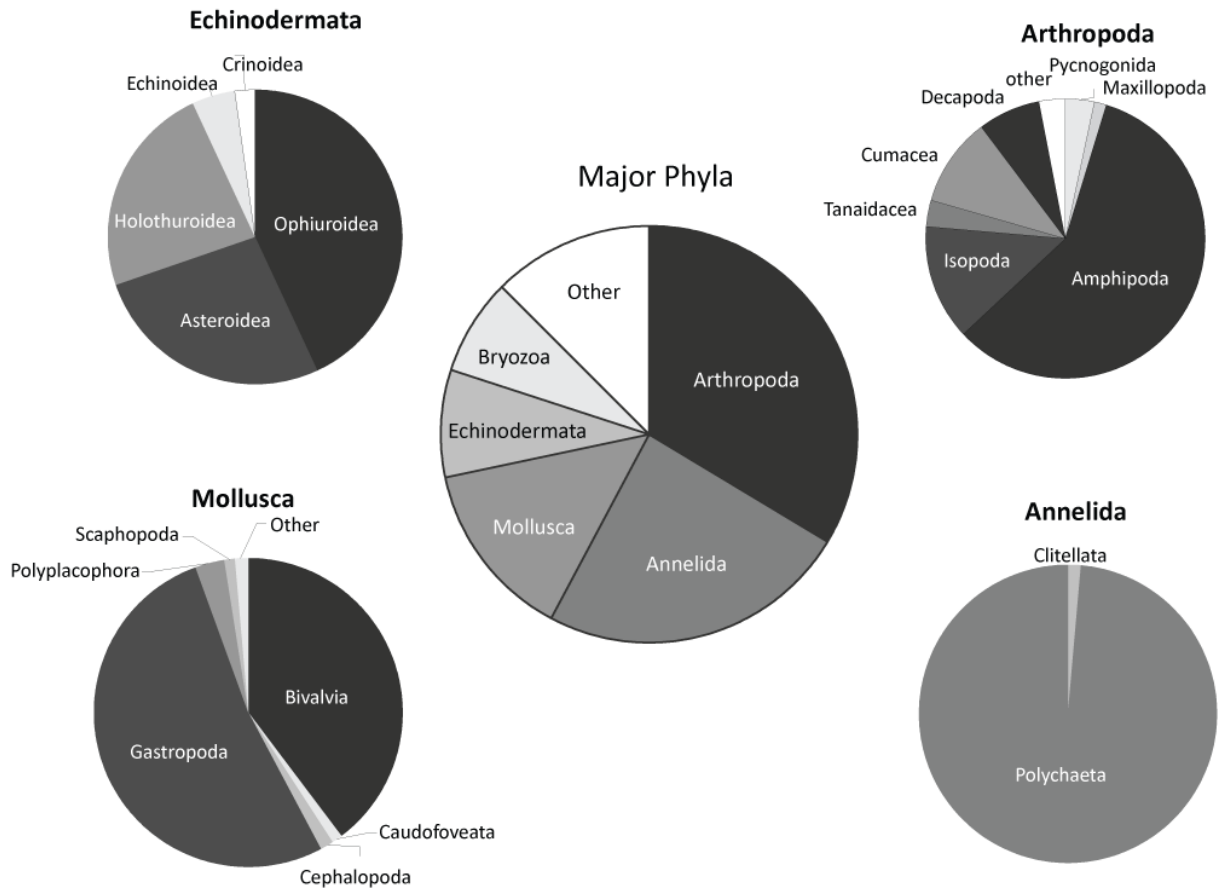
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1037 **Fig. 2**

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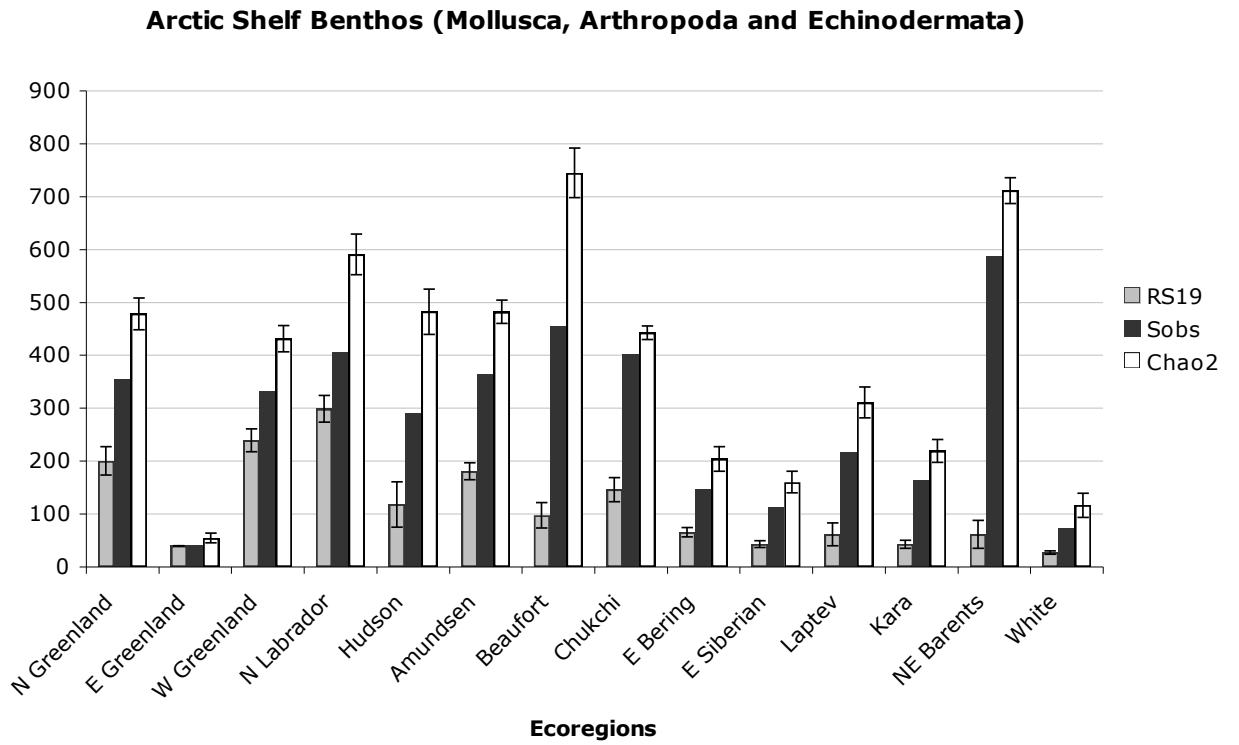
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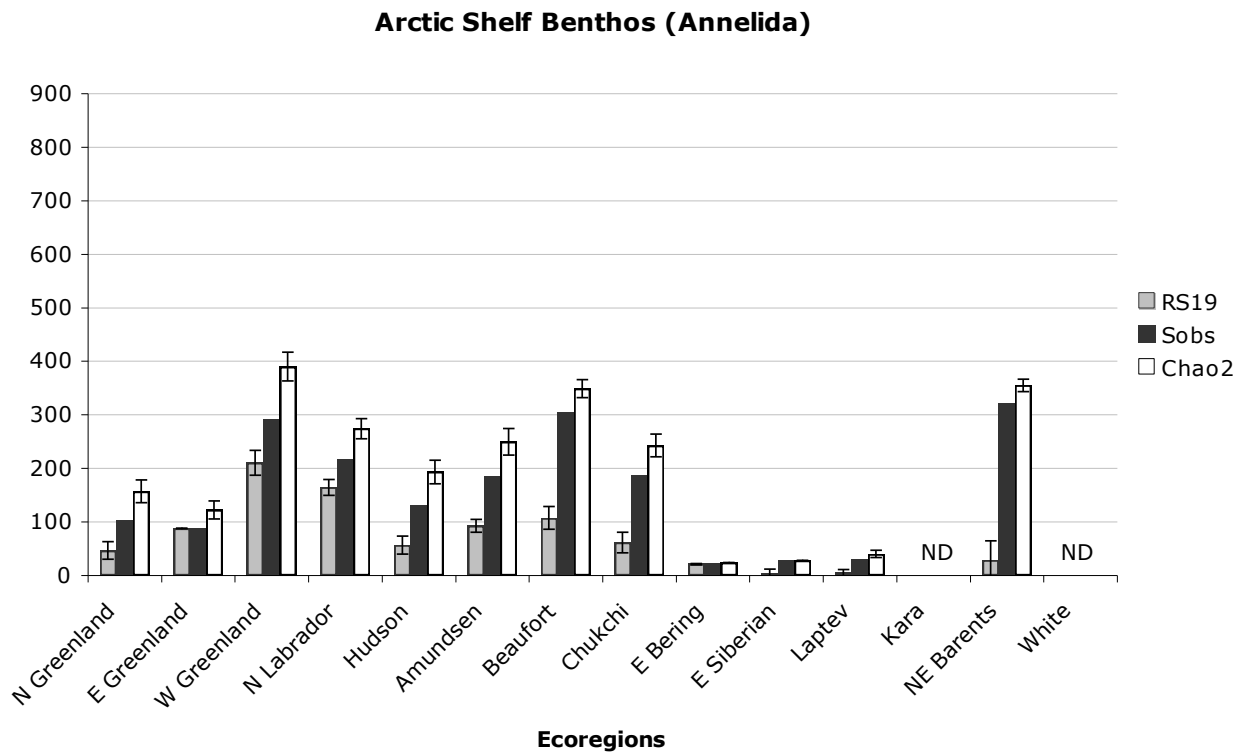
1043 **Fig. 3a**



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1046 **Fig. 3b**

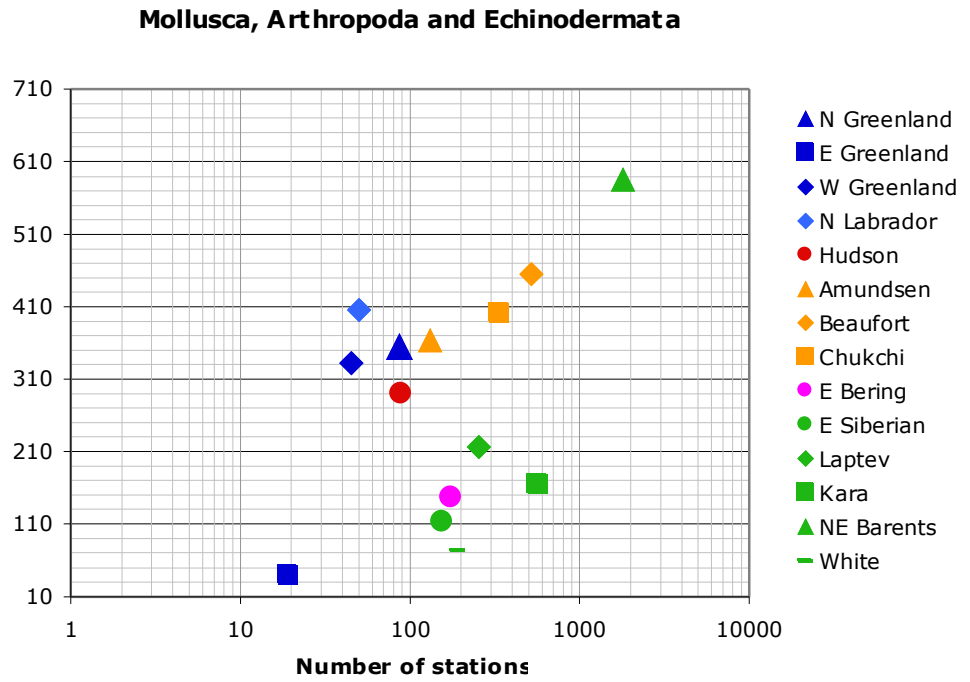


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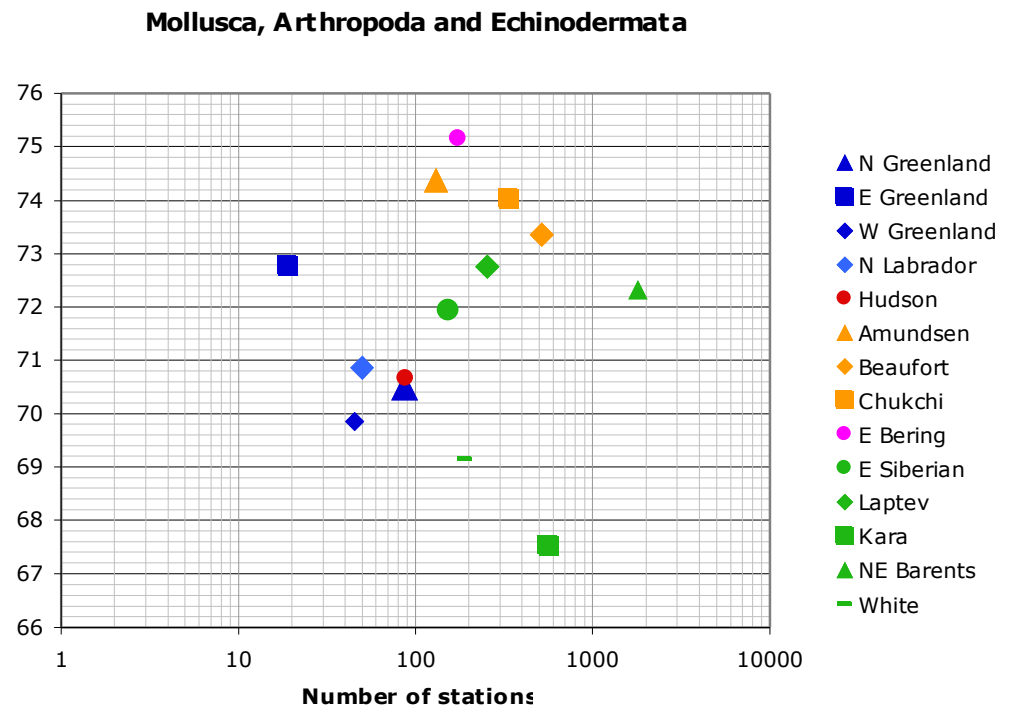
1050 **Fig. 4a**



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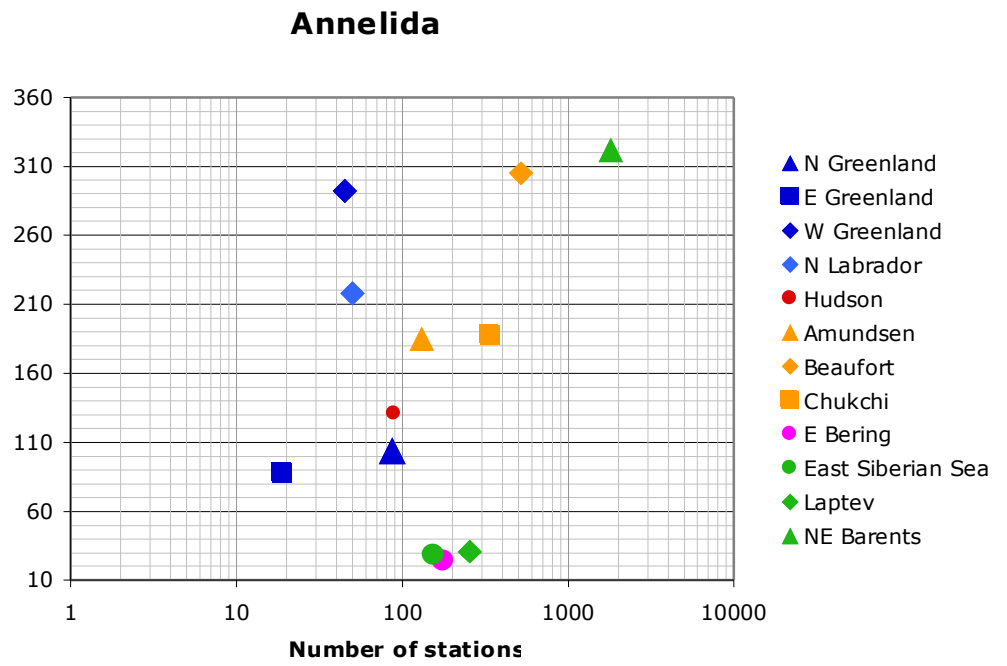
1053 **Fig. 4b**



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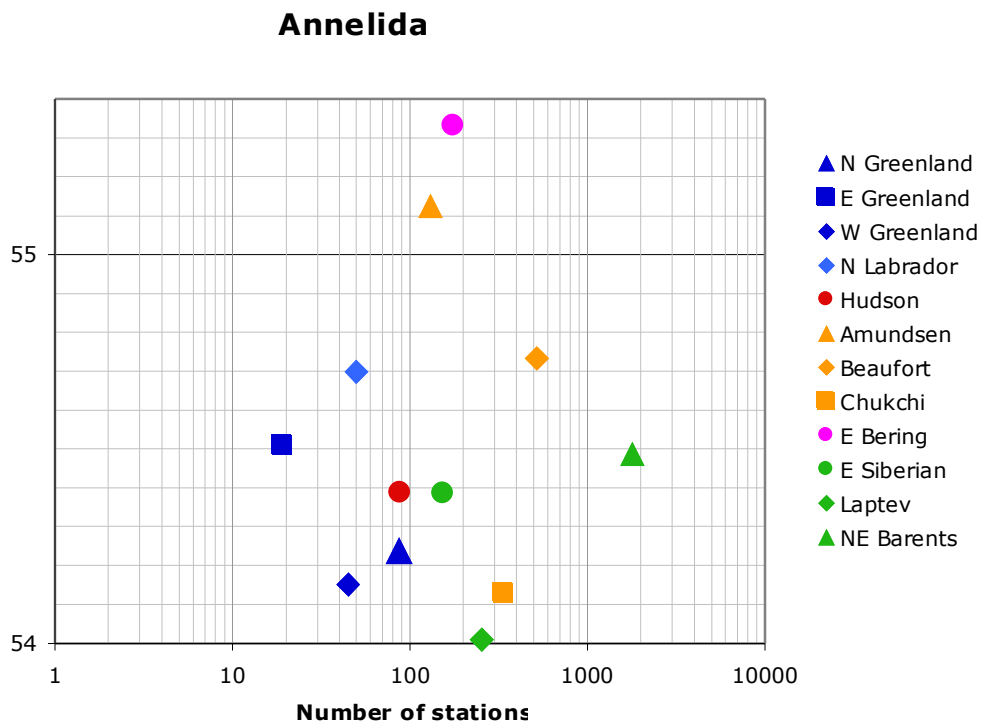
1056 **Fig. 4c**



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1059 **Fig. 4d**



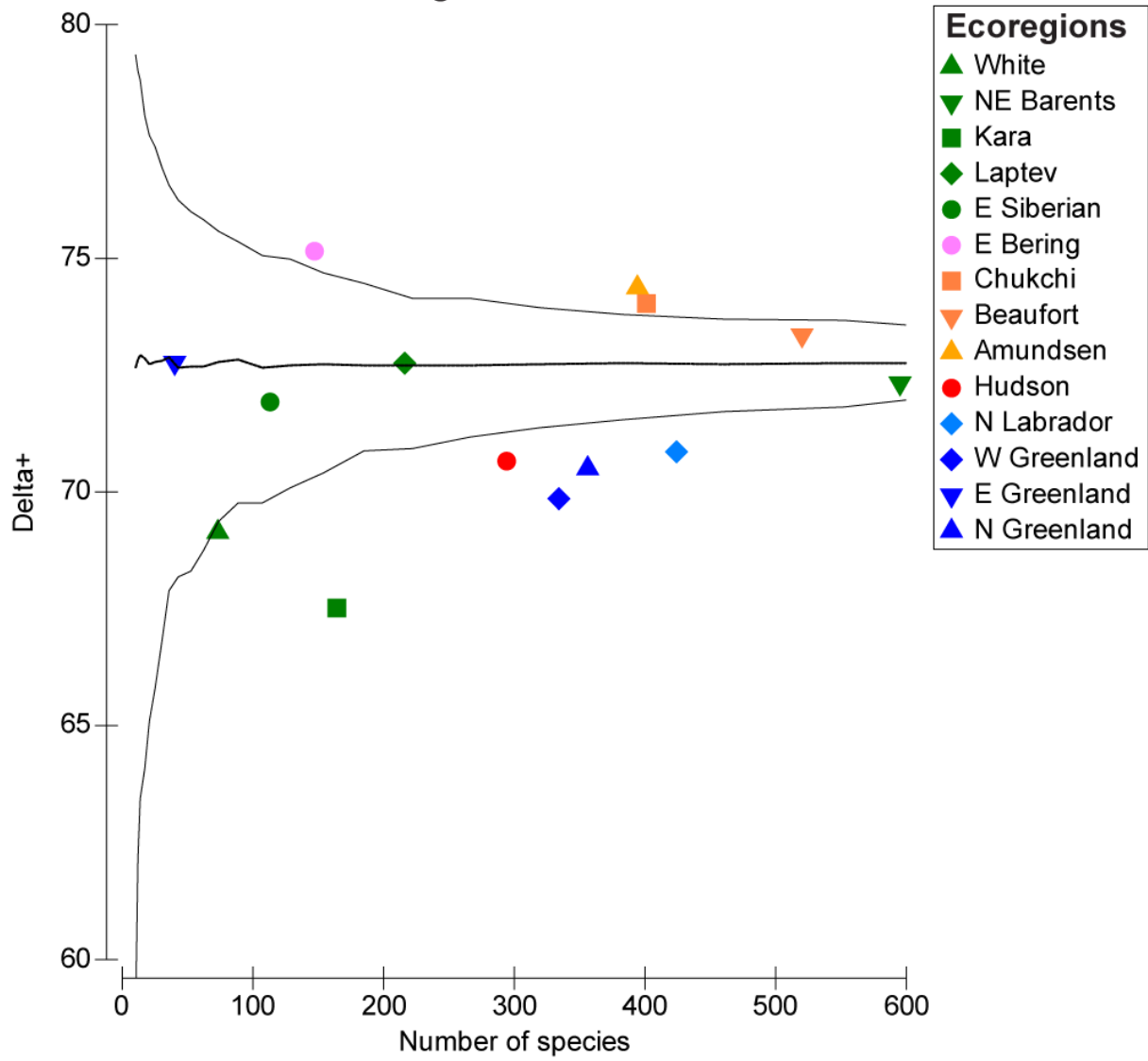
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1063 **Fig. 5a**

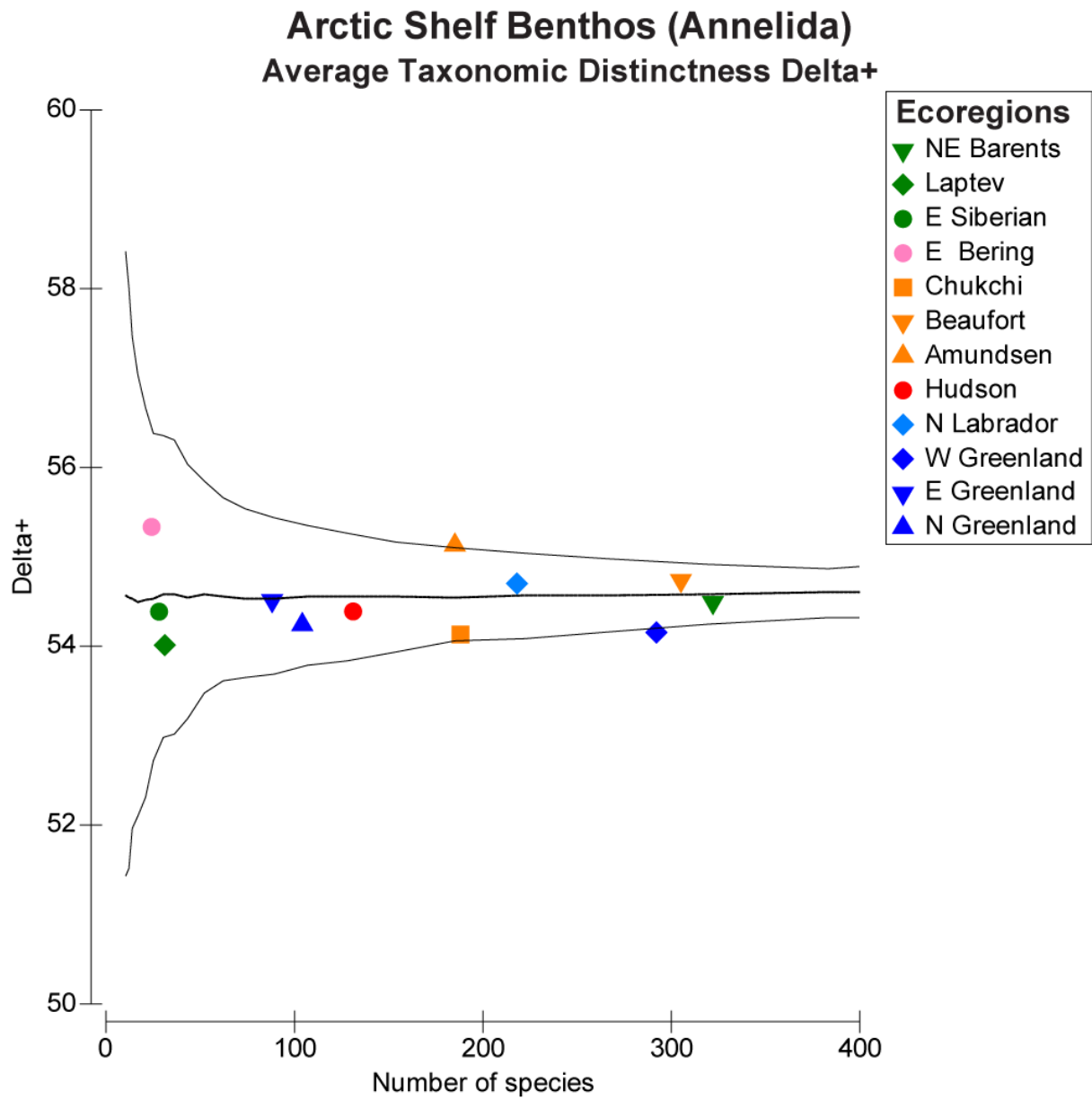
**Arctic Shelf Benthos (Mollusca, Arthropoda, and Echinodermata)
Average Taxonomic Distinctness**



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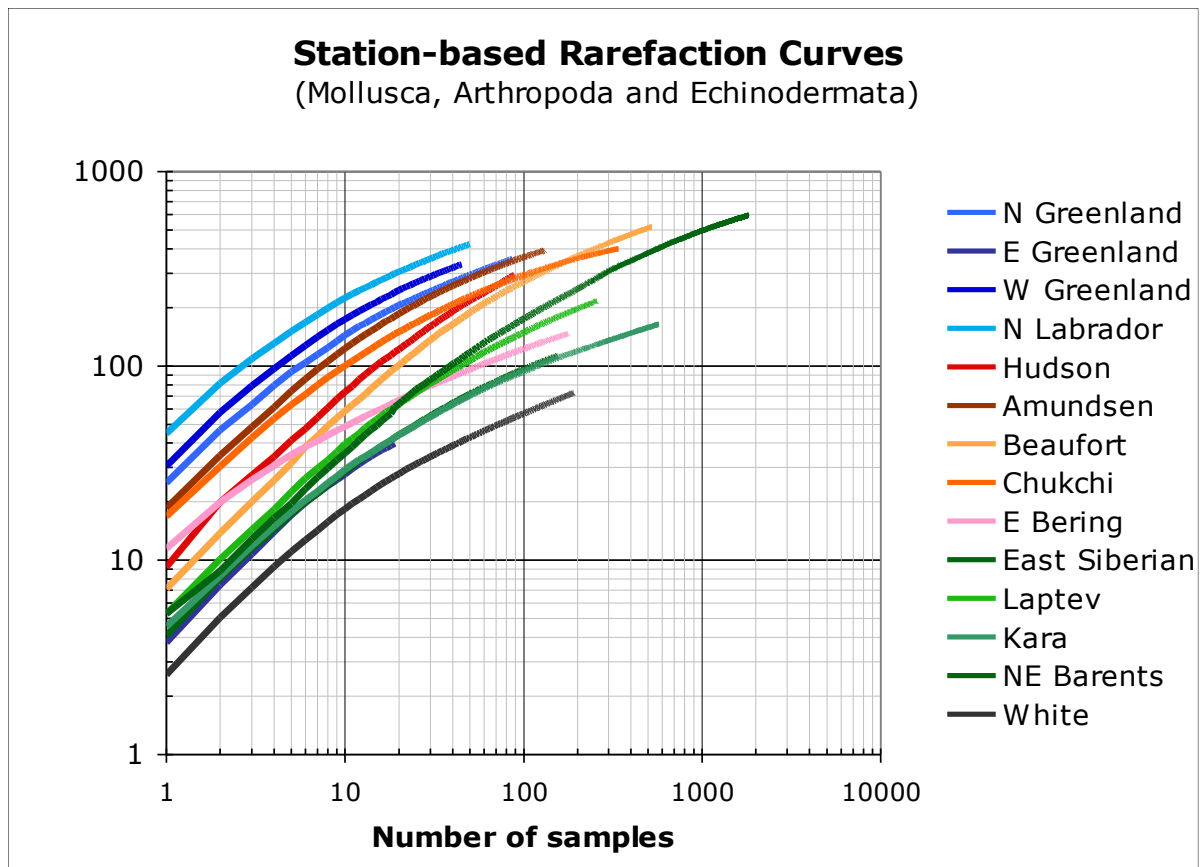
1066 **Fig. 5b**



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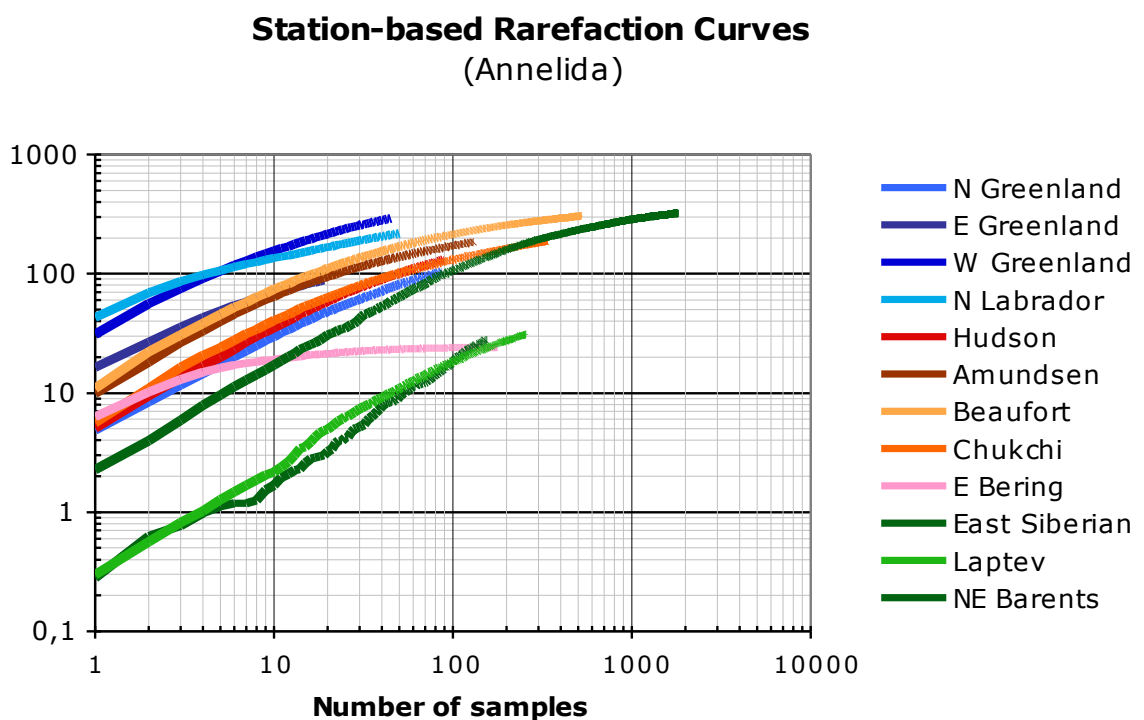
1069 **Fig. 6a**



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1072 **Fig. 6b**

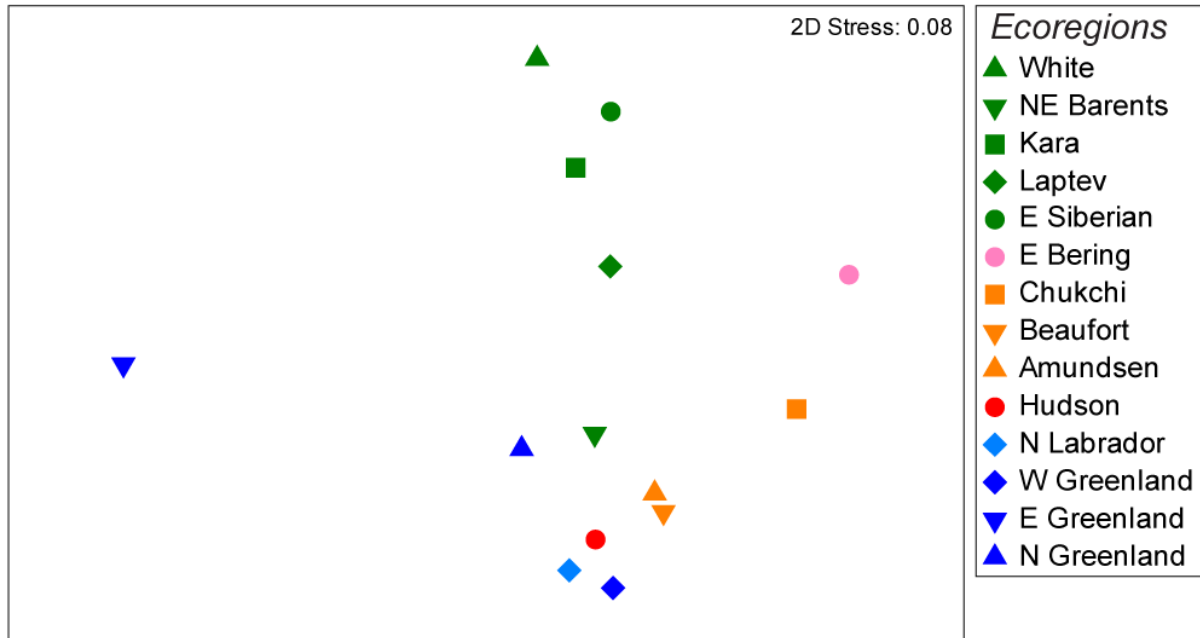


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1075 **Fig. 7a**

**Arctic Shelf Benthos (Mollusca, Arthropoda, Echinodermata)
Resemblances at species level**

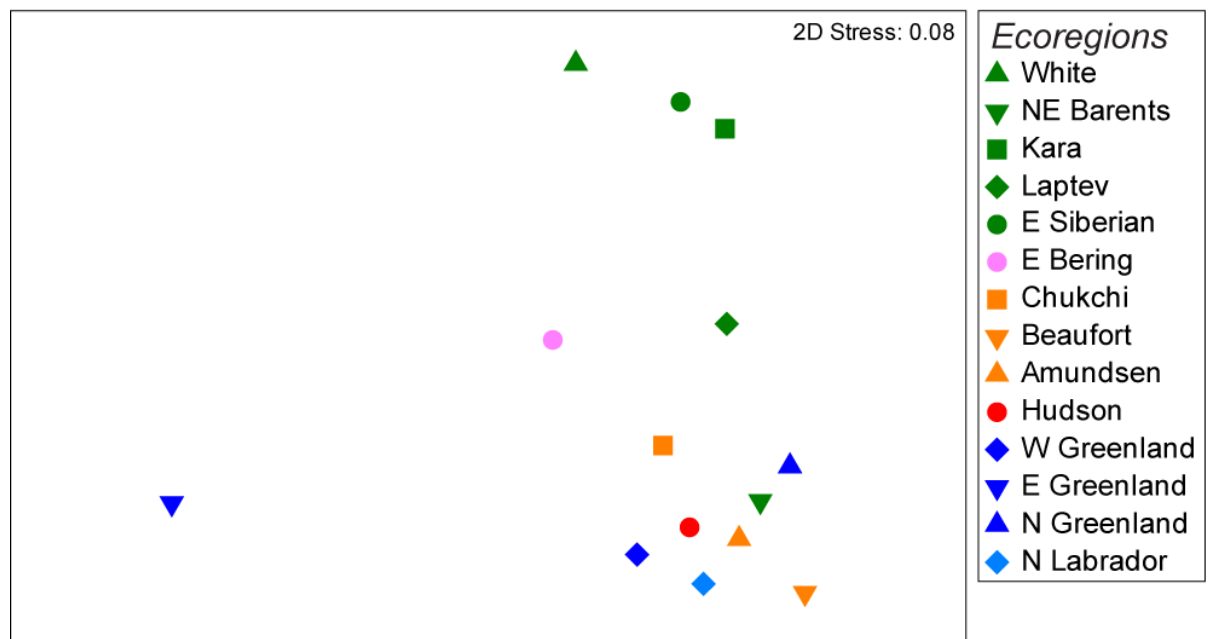


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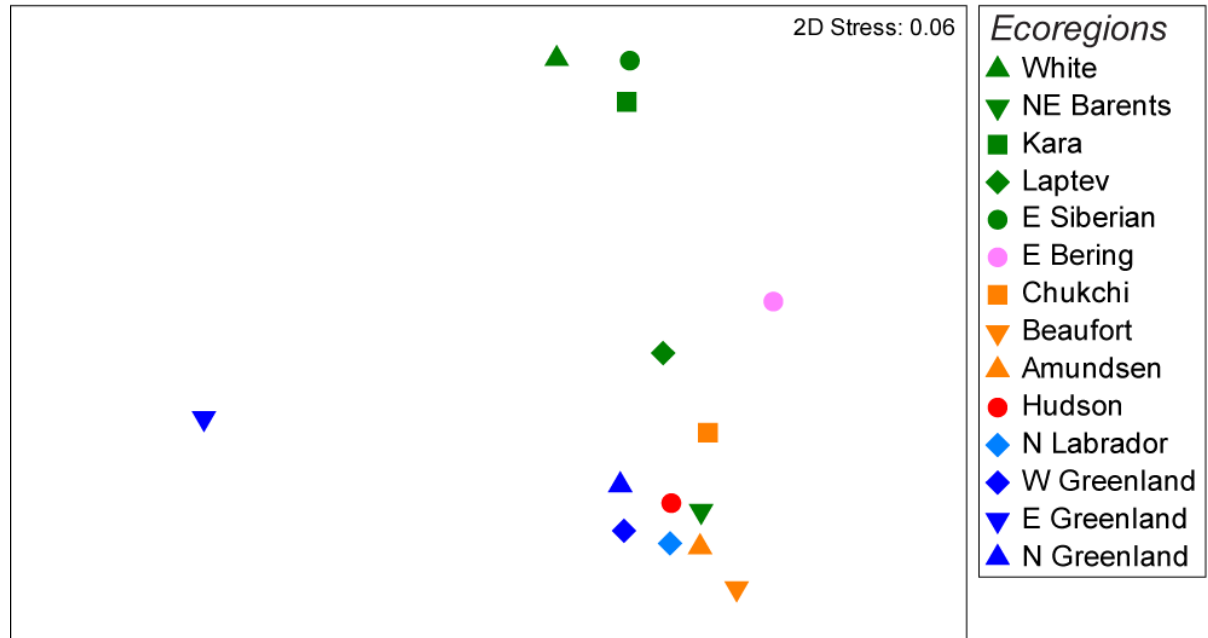
1078 **Fig. 7b**

**Arctic Shelf Benthos (Mollusca, Arthropoda, Echinodermata)
Resemblances at genus level**



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1081 **Fig. 7c****Arctic Shelf Benthos (Mollusca, Arthropoda, Echinodermata)
Resemblances at family level**

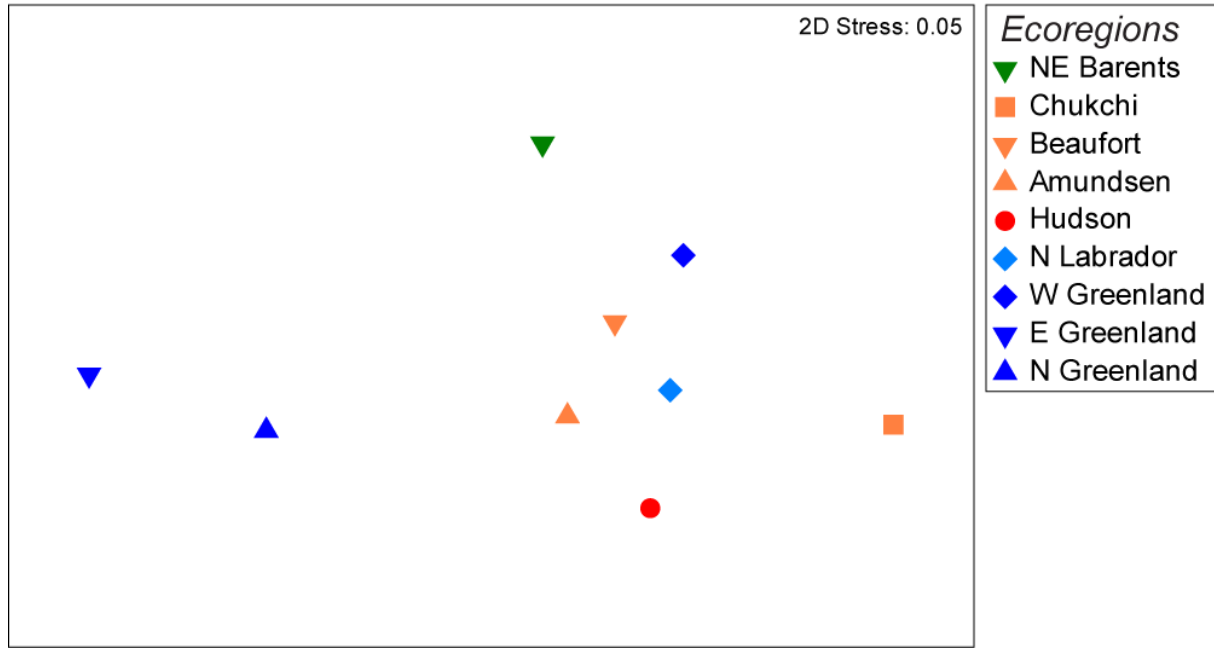
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1085 **Fig. 7d**

**Arctic Shelf Benthos (Annelida)
Resemblances at species level**

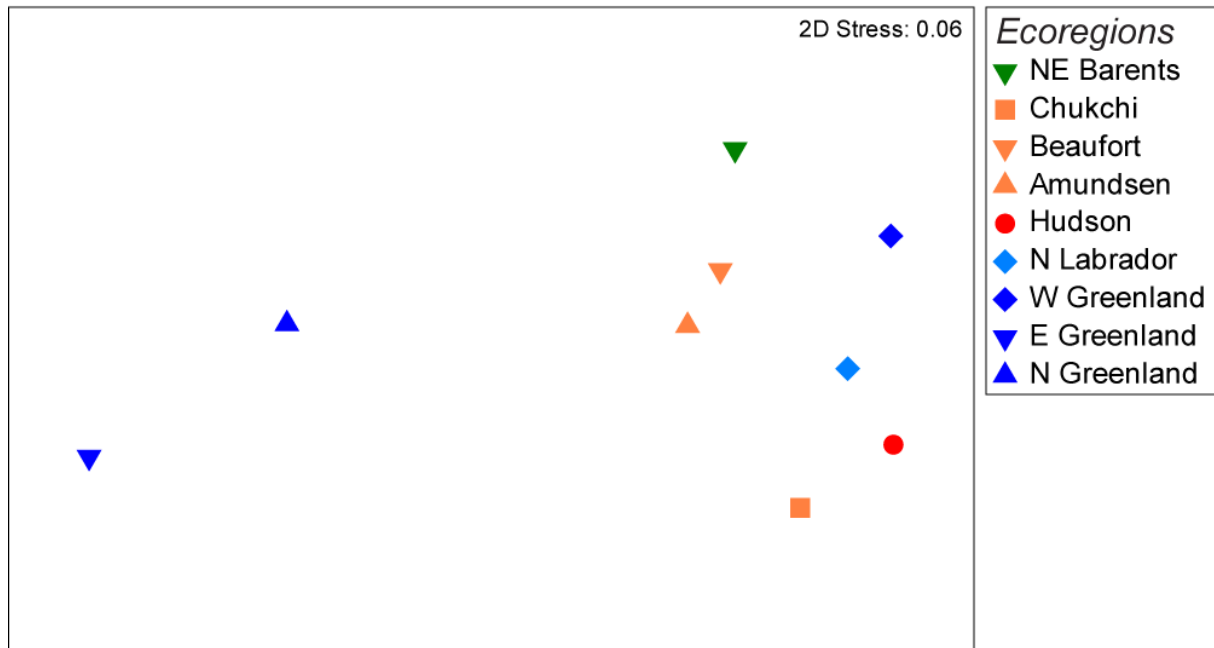


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1088 **Fig. 7e**

**Arctic Shelf Benthos (Annelida)
Resemblances at genus level**

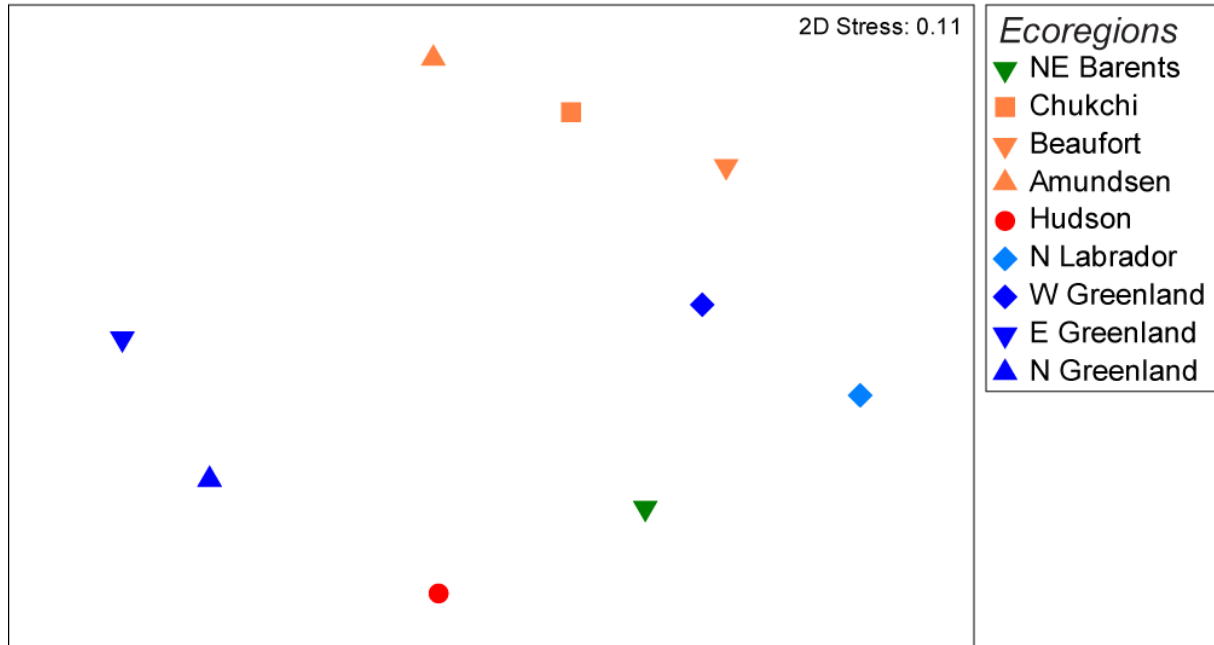


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1091 **Fig. 7f**

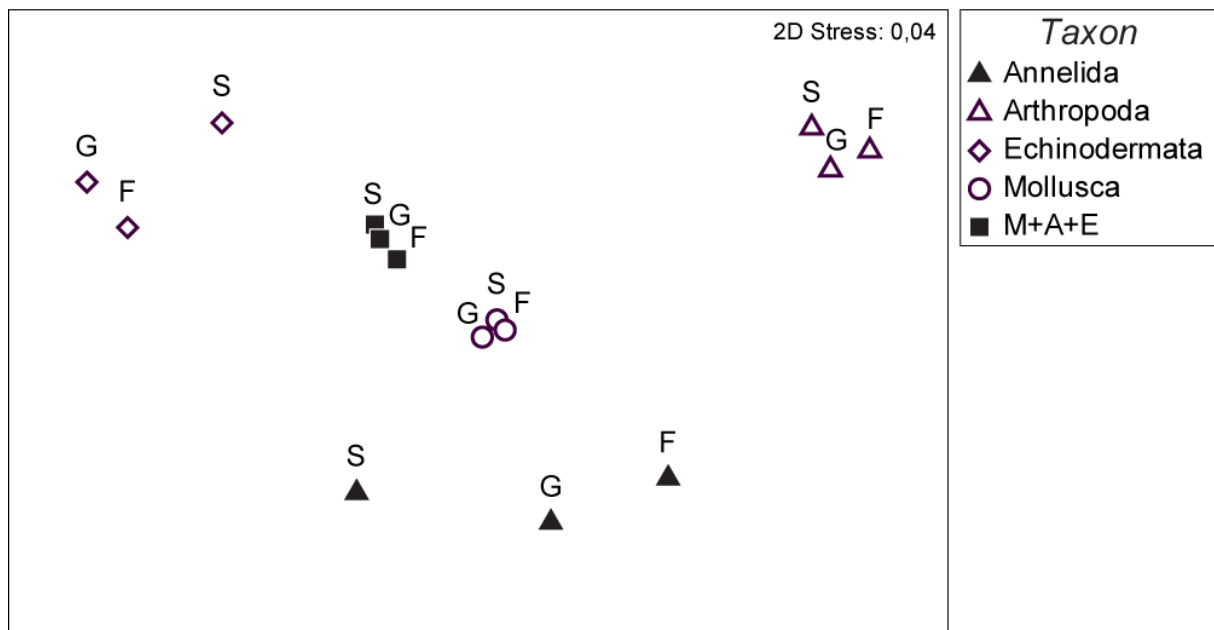
**Arctic Shelf Benthos (Annelida)
Resemblances at family level**



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1093 **Fig. 7g**

**Arctic Shelf Benthos
(Mollusca, Arthropoda, Annelida, Echinodermata)
Second-stage Analysis of Between-Ecoregion Resemblances**



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