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4 **Demersal fish assemblages in the boreo-Arctic shelf waters around Svalbard during the warm period**
5 **2007-2014**

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9 Odd Aksel Bergstad¹; Edda Johannesen¹; Åge Høines¹; Kari E. Ellingsen², Vidar S. Lien¹; Ingvar Byrkjedal³,
10 Nigel G. Yoccoz^{4,2}; Torkild Tveraa²; Rupert Wienerroither¹; Gunnar Langhelle³; Thomas de Lange Wenneck¹

11

12 ¹Institute of Marine Research, P. O. Box 1879 Nordnes, 5817 Nordnes, Norway.

13 ²Norwegian Institute for Nature Research, P.O. Box 6606 Langnes, 9296 Tromsø, Norway.

14 ³University Museum Bergen, Postboks 7800, 5020 Bergen, Norway.

15 ⁴Department of Arctic and Marine Biology, UiT The Arctic University of Norway, 9037 Tromsø, Norway.

16

17 **Acknowledgements**

18 The authors are grateful to the many technicians and scientists and research vessel crew who participated on
19 surveys and otherwise contributed to the study, and to Andrey Dolgov for comments and provision of Russian
20 literature. This work was partly financed by the Research Council of Norway (Project no. 234359/E40) and the
21 Fram Centre.

22

23 **Abstract**

24

25 The temporal and spatial resilience of abundance patterns of assemblages of organisms inhabiting transition
26 zones between Arctic and boreal regions is an issue of concern in relation to climate change. The recognition that
27 baseline information spanning such transition zones is required to facilitate future monitoring and assessments of
28 temporal dynamics provided the motivation for the present study. One such transition area is The Svalbard
29 archipelago of the North-East Atlantic, located between the Arctic and the boreal Atlantic, where significant
30 climate changes occur. The study aimed to utilize an existing data series from Svalbard to analyse and describe
31 demersal fish assemblage structure and distributions. Norwegian bottom trawl surveys sampled the area annually
32 in August-September 2007-2014, and the dataset is the first from this area which is sufficiently comprehensive to
33 carry out assemblage analyses. The survey years analysed represent the recent unprecedented warm period in the
34 Barents Sea-Svalbard region which started around 2004. The new baseline information improves the basis for
35 future studies of resilience under changing environmental conditions. A key finding was that the major transition
36 in species composition is that between deep Greenland Sea and Arctic Ocean assemblages (upper slope
37 assemblages) and the shelf assemblages. In shallower shelf areas (< 500m depth) structuring is weaker with
38 assemblages having many species in common. The expected association of fish assemblages with regional
39 bathymetric and hydrographic features was confirmed. The observed patterns probably reflect a comparatively
40 extensive Atlantic influence during the warm period.

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Keywords

Baseline, fishes, distributions, Arctic, Atlantic, Svalbard

Bergstad, Odd Aksel; Johannesen, Edda; Høines, Åge Sigurd; Ellingsen, Kari Elsa; Lien, Vidar Surén; Byrkjedal, Ingvar; Yoccoz, Nigel Gilles; Tveraa, Torkild; Wienerroither, Rupert; Langhelle, Gunnar; Wenneck, Thomas de Lange.
Demersal fish assemblages in the boreo-Arctic shelf waters around Svalbard during the warm period 2007–2014. Polar Biology 2017
10.1007/s00300-017-2176-2

47 **Introduction**

48 Quantification and characterization of potential future variation and change in marine communities and
49 ecosystems require knowledge of previous states. Well documented information on variability in distribution and
50 abundance patterns of species and assemblages constitute baselines for assessments and monitoring of impacts of
51 known or anticipated sources of variability. At high latitudes, the significance of updated baseline knowledge on
52 fish communities is especially pronounced as the natural variability is high and comprehensive information on
53 fish diversity is limited (Christensen and Reist 2013). Increasing human uses and the recent pronounced
54 warming trend with associated ice-cover changes may lead to wide-ranging ecosystem impacts potentially
55 altering species composition and abundance patterns. Accordingly, there is an increasing demand for pertinent
56 management advice, and baseline studies contribute significantly to the collective science effort required to
57 respond to this societal need. In this study information is presented on demersal fish assemblages inhabiting an
58 extensive continental shelf area of the Arctic Ocean-Atlantic transition zone, the Svalbard archipelago, based on
59 data collected during the recent warm period.

60
61 The fish fauna in the pan-Arctic region, including the Atlantic sector, was reviewed recently by Mecklenburg et
62 al. (2011). Regional analyses using extensive bottom trawl survey data, by Byrkjedal and Høines (2007), Dolgov
63 et al. (2011), Johannesen et al. (2012) and Fossheim et al. (2015), supplemented earlier smaller scaled
64 investigations by Burgos (1989) and Fossheim et al. (2006) of distribution of demersal fish in the Barents Sea.
65 An atlas of fishes of the Barents Sea has also resulted from joint trawl surveys by Russia and Norway
66 (Wienerroither et al. 2011, 2013). These efforts resulted in extensive baseline knowledge for areas with existing
67 or potential uses.

68
69 However, for the Svalbard archipelago (Fig. 1) significant data series are available but these were not fully
70 analysed in the previous studies. Reports on the fish fauna in that area were based on the Russian autumn-winter
71 surveys (Dolgov 2004; Smirnov et al. 2000), but comprehensive analyses were not conducted. Using a multi-
72 year survey dataset, the current account therefore extends the Barents Sea assemblage analyses (Johannesen et al.
73 2012) to comprise the shelves around Svalbard, including the Arctic Ocean shelf to the north of 80° N.

74
75 The Svalbard is the largest archipelago of the arcto-boreal Barents Sea (Ozhigin et al. 2011), characterised by
76 complex bathymetry and numerous islands, as well as steep and strong environmental gradients between the
77 warm areas of the Norwegian Sea under the influence of Atlantic Water and the Arctic Water to the north and
78 northeast (Loeng 1991; Ozhigin et al. 2011). Circulation features around the archipelago reflect the shallow
79 outflow of relatively low-salinity Arctic Water and the deeper saline and warm Atlantic Water flowing
80 northwards along the shelf-break on the western side of the western island Spitsbergen (Ozhigin et al. 2011).

81
82 The main objectives of this study were to identify and characterize demersal fish species assemblages and their
83 geographical patterns. Archived research bottom trawl survey data were used as the source of species-specific
84 abundance information. Our dataset comprised quality-controlled catch data from annual joint Norwegian-
85 Russian ecosystem surveys conducted in August-September 2007-2014. In that period, the Barents Sea was
86 exceptionally warm, i.e. with temperatures in the core of the Atlantic Water entering the Barents Sea, as recorded

87 in the Kola section, on the order of 1 °C above average in all years (Fig. 2c). A comparable increase in
88 temperature has been recorded along the western Spitsbergen shelf during the same period (Walczowski et al.
89 2012). The last decade (after 2000) was the warmest since the onset of regular measurements in 1900 in the Kola
90 section (Bochkov 1982; Tereschenko 1997; Skagseth et al. 2008; Polyakov et al. 2013), and paleo-records based
91 on foraminifera suggest that the Atlantic Water flowing into the Barents Sea area was at its warmest for the last
92 2000 years (Spielhagen et al. 2011).

93
94 In the earlier analyses of similar trawl survey datasets from Barents Sea (Burgos 1989; Fossheim et al. 2006;
95 Byrkjedal and Høines 2007; Johannesen et al. 2012; Aschan et al. 2013; Fossheim et al. 2015; Johannesen et al.
96 2016) spatial patterns at relatively large spatial scales were observed in the demersal fish community. The
97 patterns of distribution were associated with regional hydrography, particularly the geographical position and
98 character of the Polar Front between Atlantic and Arctic water masses (Loeng 1991; Byrkjedal and Høines 2007;
99 Johannesen et al. 2012). In the Svalbard shelf, similar associations were expected with regional hydrography but
100 probably sharper and more localized boundaries between assemblages associated with steep environmental
101 gradients. Diversity was expected to change both with latitude and depth, as well as position around the islands.
102 Generally, it was anticipated that the diversity and abundance in the high-Arctic subarea of the archipelago was
103 low compared with that observed in the warmer southwestern shelf areas facing the Norwegian and Greenland
104 Seas being under the influence of Atlantic Water.

105
106 The new results from the Svalbard archipelago are discussed in the context of climate change, fisheries, and
107 other potential anthropogenic activities in the area.

108

109 **Study area characteristics**

110

111 The Svalbard archipelago is located in the north-western part of the Barents Sea (Fig. 1). Towards the west and
112 north the archipelago faces the >3000 m deep basins of the Greenland Sea and Arctic Ocean, respectively,
113 whereas to the east and south there is no deepwater area delineating Svalbard from the shallow and partially ice-
114 covered Barents Sea. During winter, the polar ice cap is extending from the Polar Basin and covers the shallow
115 subareas of our study area (e.g. Onarheim et al. 2014, 2015). During summer, the polar ice cap retreats and most
116 of the study area is ice-free in an average year. However, the sea-ice extent varies considerably between years. In
117 recent years, with the exception of 2014, the coastal and shelf areas north of Svalbard were ice free during
118 summer.

119

120 The bathymetry in the area is complex. Habitats range from rather deep glacial fjords, to coastal shelves
121 extending from the sublittoral to 400 m with wide shallow banks, and to the outer shelf and upper continental
122 slope of 400-1300 m depth.

123

124 The hydrographic conditions around Svalbard are dominated by the Polar Front between relatively warm
125 Atlantic Water advected from the south and regionally generated cold Arctic water masses. The frontal zone
126 generally follows the bathymetric features of the Svalbard archipelago and the Svalbard Bank.

127

128 The continental shelf break to the west and north of Svalbard is dominated by the northward flow of Atlantic
129 Water in the West Spitsbergen Current (Beszczynzka-Möller et al. 2012), which continues eastward in the Arctic
130 Ocean on the northern side of Svalbard (e.g. Pnyushkov et al. 2013). To a varying degree, some of this sub-
131 surface Atlantic Water enters the Barents Sea from the north through canyons and troughs (Lind and Ingvaldsen
132 2012). In addition to the along-path temperature variability, there is considerable cross-slope temperature
133 variability reflecting cross-slope movements of the frontal zone due to temporal changes in the regional
134 atmospheric circulation (Cottier et al. 2007).

135

136 The Polar Front is topographically steered and located between the 150 m and 200 m isobaths separating colder
137 and relatively low-salinity Arctic-influenced water masses on the shallow Svalbard Bank from warmer and more
138 saline Atlantic-influenced water masses further out on the slope surrounding the bank (Parsons et al. 1996).
139 Although the Polar Front is tightly connected to the topography, the position of the front can vary depending on
140 the strength and position of the Atlantic Water inflow to the Barents Sea (Ingvaldsen 2005; Lien et al. 2013a).
141 The Svalbard Bank is seasonally ice covered, and thus, the temperature is at the freezing point throughout the
142 water column during winter. During summer, the temperature increases due to insolation. The Svalbard Bank is a
143 source of dense, brine-enriched water formed during freezing of sea ice (Sarynina 1969; Årthun et al. 2011).
144 These cold and dense water masses flow at the bottom along the slopes of the bank (Shapiro and Hill 2003; Lien
145 and Ådlandsvik 2014) and slowly descend into the Bear Island Channel and eventually the Norwegian Sea
146 (Blindheim 1989).

147

148

149

150 **Material and Methods**

151

152 **Geomorphology, hydrography and circulation in the study area**

153 Based on bathymetric and hydrographic conditions, the study area was divided into six sub-areas (Fig. 1 and 2)
154 used to provide an initial overview of sampling effort and fish occurrence patterns. The same subareas were
155 subsequently used to interpret results of ordination analyses to which the entire dataset was input. The six
156 subareas were:

157

158 *Atlantic continental shelf break*

159 The Atlantic continental shelf was split into a south-western (SW) and a north-eastern (NE) subarea at the 1000
160 m isobath along the western slope of the Yermack plateau, thereby delineating the two subareas facing the
161 Greenland Sea and Arctic Ocean, respectively.

162

163 *Hopen Deep*

164 The Hopen Deep forms the northeast extension of the Bear Island Trough and is dominated by Atlantic Water
165 circulating counter-clockwise within the Deep (Skagseth 2008). Intermittently, Atlantic Water flows
166 northeastward also in the western part along the slope of the Svalbard Bank (Lien et al. 2013a). Despite the
167 Atlantic influence throughout the Hopen Deep, the benthic megafauna here is mainly Arctic, i.e., located north of
168 the “benthic Polar Front”, probably due to intermittent flow of cold bottom water associated with sea-ice
169 freezing on surrounding banks (Jørgensen et al. 2015).

170

171 *Svalbard Bank*

172 The Svalbard Bank is the shallowest of the larger banks within the Barents Sea, with summit depth of 30-50 m.
173 A stationary front governed by the strong tidal currents is surrounding the bank. The front runs approximately
174 along the 50 m isobath, and in areas shallower than 50 m the water column is well-mixed and homogeneous
175 from surface to bottom (Fer and Drinkwater 2014).

176

177 *Svalbard East*

178 The area to the east of Svalbard exhibits a complex topography comprising several relatively small and shallow
179 bank structures divided by canyons and small basins with depths exceeding 300 m. The banks are dominated by
180 cold Arctic water masses throughout the water column (e.g. Pfirman et al. 1994), whereas the canyons are
181 influenced by inflow of Atlantic Water, typically at depths below 150-200 m (Lind and Ingvaldsen 2012).

182

183 *Svalbard coastal area*

184 The fjords of Svalbard are dominated by cold Arctic waters, including cold and dense brine-enriched bottom
185 water following sea-ice formation in winter. Along the western side of Svalbard, there is a variable influence
186 from Atlantic Water extending into the fjords, depending on the regional wind pattern (Cottier et al. 2007) and
187 the variable sea-ice production and subsequent interannual variability in density inside the fjords (Nilsen et al.
188 2008).

189

190 **Demersal fish survey design and sampling**

191 Species-specific occurrence and abundance data on fishes were available from bottom trawl catches from the
192 Barents Sea-Svalbard area in August-September 2007-2014. The effort in the Svalbard area formed part of the
193 Joint annual Norwegian/Russian Ecosystem Survey in the Barents Sea (Anon 2007; Anon 2009a, b; Anon 2010;
194 Anon 2011; Eriksen 2012; Prokhorova 2013; Eriksen 2014). The survey series started in 2004, however, since
195 the quality of species identifications for many taxa were judged unreliable before 2007, it was decided not to
196 include the first three years in the present study of species assemblages and diversity. Although scattered older
197 data exist from the Svalbard area, the selected series was deemed the most suitable for conducting assemblage
198 pattern analyses. The entire area of interest was sampled, and methods were standardized throughout the period
199 selected.

200

201 While the full annual survey was and is conducted jointly by the Institute of Marine Research (IMR), Norway,
202 and Polar Research Institute of Marine Fisheries and Oceanography (PINRO), Russia, only Norwegian vessels
203 sampled the Svalbard area and provided data to this study. Data were collected by five vessels and comprised
204 967 geo-referenced bottom trawl samples (Fig. 1, Table 1). For each sample bottom depth of the trawl tow was
205 recorded. A full list of samples is provided as Electronic Supplementary Information (Online Resource 1).

206

207 Fish were sampled with a Campelen 1800 bottom trawl towed on double warps. The mesh size was 80 mm
208 (stretched) in the front and 16–22 mm in the cod-end, allowing the capture and retention of small-sized fish. The
209 trawl configuration and bottom contact was monitored remotely by Scanmar trawl sensors. The horizontal
210 opening was 17 m, and the vertical opening 4-5 m. A rockhopper ground gear was used throughout. The standard
211 procedure was to tow for 15 minutes after the trawl had achieved contact with the bottom. Towing speed was 3
212 knots, equivalent to a towing distance of 0.75 nautical miles (ca. 1400 m) in a 15 min tow. Due to unfavourable
213 bottom conditions or other circumstances, a few (4 out of 967 tows) were interrupted after only 5 min but these
214 were still included as valid. Tows in deep areas (>500m) usually produced small samples and were extended
215 beyond 15 min, to a maximum of 65 min. This created challenges in the analyses, but only affected the deep
216 areas that were not the primary interest of the study.

217

218 Although sampling effort varied somewhat between years due to unforeseen circumstances, such as unfavorable
219 weather, the bottom trawl sampling comprised the entire shelf and coastal area of the Svalbard archipelago.
220 When samples from all years were pooled, the spatial distribution of the 967 samples (Fig. 1, Table 1, Online
221 Resource 1) was found adequate and sufficient to characterize demersal fish assemblages in the habitats trawled,
222 i.e. the predominant habitats of the mainly soft-substrate shelf and coastal waters beyond the shallowest coastal
223 zone (i.e. beyond the 50 m isobath) to the upper continental shelf depths. Once the design was set and trawl sites
224 selected, the same sites were, if practically possible, visited every year through the time series. A potential
225 shortcoming for the present analysis is that the survey was not originally designed to optimize assemblage
226 analyses. The sites were selected according to a systematic design spanning all habitats rather than to a stratified
227 random design that might have been more appropriate.

228

229 Hydrographically the area has strong spatial patterns and pronounced seasonality (Fig. 2 a and b), particularly in
230 the shallow subareas where winter cooling and summer warming combined with strong vertical mixing cause
231 bottom temperatures to vary much more than in the adjacent deep shelf waters. The trawl sampling was
232 distributed in all the relevant hydrographic conditions observed or derived from model outputs (Fig. 2 a and b).
233 Unfortunately, a limitation in the present study was that environmental data such as near-bottom salinity and
234 temperature and substrate data were not recorded for each trawl tow.

235

236 **Species identification and data processing**

237 Fish catches were sorted immediately on board by trained technicians to lowest possible taxonomic level.
238 Unidentifiable specimens were frozen on board and subsequently identified by experienced taxonomists. If
239 deemed necessary, voucher specimens were curated by the University Museum Bergen (Online Resource 1). A
240 full account of all species is beyond the scope of this study but further details on the fish records are provided in
241 the Barents Sea Fish Atlas generated from the same and other surveys (Wienerroither et al. 2011).

242

243 Only demersal fishes were retained in the dataset (55 species and four genera, Table 2). Predominantly pelagic
244 species: polar cod (*Boreogadus saida*), Arctic cod (*Arctogadus glacialis*), capelin (*Mallotus villosus*), Atlantic
245 herring (*Clupea harengus*), lesser sand-eel (*Ammodytes marinus*), Greenland shark (*Somniosus microcephalus*)
246 as well as mesopelagic species (myctophids, sternoptychids a.o.) were removed. Bottom trawl catches of pelagic
247 species, many which form aggregations or schools in midwater and only occasionally occur near the seabed,
248 were relatively common. However, they were unlikely to reflect the abundance and occurrence of such taxa.
249 Inclusion of such species in e.g. multivariate analyses would rather distort than add valid information to the
250 account of distribution and diversity of truly seabed-associated demersals, i.e. benthic or benthopelagic species.
251 Greenland shark was excluded because it is predominantly pelagic, but also because it is rare in the bottom trawl
252 catches. The species occurs in the area and catches are reported (Wienerroither et al. 2011, 2013), but it is
253 unlikely that the bottom trawl survey catches reflect abundance or distribution. Also pollock (*Pollachius*
254 *pollachius*) was removed because it was represented by a single possibly misidentified specimen not retained for
255 subsequent confirmation of identity. Furthermore, specimens identified to the genus level were removed
256 (representing <0.51% of the individuals recorded), except for specimens belonging to *Sebastes*, *Icelus*,
257 *Gymnelus*, and *Careproctus*. For the three *Sebastes* species Golden redfish (*Sebastes norvegicus*), beaked redfish
258 (*S. mentella*), and Norway redfish (*S. viviparus*) identification uncertainty based on morphology alone persists
259 (especially for juveniles). Up until 2014 the procedure was to only identify specimens >10 cm to the species
260 level. Therefore, not all specimens were identified to species and the decision was made to pool all *Sebastes*
261 records and use the genus as a valid category in the analyses. (However, most of the unidentified specimens were
262 probably *S. mentella* as this species is by far the most common in the Barents Sea. Amongst the *Sebastes*
263 individuals in our data set identified by skilled personnel, 93% were assigned to *S. mentella*. Only two percent
264 was *S. norvegicus*. The rest were recorded as *S. viviparus* but suspected to be misidentifications as *S. viviparus* is
265 a warmer-water coastal species found along the coast in the southwestern Barents Sea of which no records have
266 been confirmed from the Svalbard area).

267

268 The two *Icelus* species occurring in the area, *Icelus bicornis* and *I. spatula*, are very difficult to differentiate. The
269 *Gymnelus* and *Careproctus* genera probably have several species in the area but the taxonomy is unresolved.

270

271 **Data analysis**

272 Prior to exploring the data, the catches were standardized to number of individuals per 15 min tow. All analyses
273 were done using the software R (R Core Team 2017). Species accumulation curves were produced using the
274 function `Specaccum` in the package `Vegan` (Oksanen et al. 2016). Accumulation curves are built using random
275 permutations of sites (Gotelli and Colwell 2001), and 100 permutations were used to calculate standard errors of
276 estimated species richness. Approximate 95% confidence intervals are calculated using 2 standard errors. To
277 study changes in species composition and variation among sites, Correspondence Analysis (Jongman et al. 1995)
278 were run using the package `Ade4` (Dray et al. 2016). Correspondence analysis is a multivariate ordination
279 method derived from Principal Component Analysis but adapted to count data (Greenacre 2013). It results in a
280 joint ordination of species and sites, using the relative frequencies (i.e. species and site compositions). The joint
281 ordination is expressed through species and site scores, and the eigenvalues represent the abundance weighted
282 correlation between these scores. Input to the ordinations were the observed frequencies standardized to a tow
283 duration of 15 mins.

284

285 **Results**

286

287 **Species list, zoogeographical affinity and overall abundance patterns**

288 Table 2 lists the 59 species and higher taxa used in the multivariate analyses, and their zoogeographical
289 affinities. In a first effort to explore the dataset, Figure 3 presents mean abundances of the 59 taxa for each of the
290 survey years 2007-2014 split by subareas of the Svalbard shelf and slope shown in Figure 1. For the Atlantic
291 continental shelf break, the records were categorized into south-western and north-eastern subareas shallower
292 than 500 m, and an additional group of stations deeper than 500 m.

293

294 Albeit to varying degree, the species accumulation curves for most subareas approach asymptotes, suggesting
295 that the sampling was probably adequate to observe patterns for the major taxa occurring in the different
296 subareas (Fig. 4). In general, the Atlantic sector subareas (SW and NE) had 40-45 taxa and around 10 more taxa
297 than the Arctic subarea denoted Svalbard East. For the deepest stations (i.e. the upper continental slope deeper
298 than 500 m) the species accumulation curve was not asymptotic. At this depth, catches were generally small and
299 sampling probably also too limited to provide the full taxon list. Similarly, the Svalbard Bank subarea curve did
300 not reach an asymptote. This subarea is a shallow bank with strong seasonal variability in temperature (Fig. 2 a
301 and b). These conditions apparently produced rich samples with more variable species composition than adjacent
302 subareas where seasonal temperature variation is less.

303

304 The five first taxa listed in Figure 3 were essentially ubiquitous and common in all years of the series, i.e.
305 Atlantic cod (*Gadus morhua*), long rough dab (*Hippoglossoides platessoides*), redfish (*Sebastes* spp.),
306 *Artediellus atlanticus*, and Greenland halibut (*Reinhardtius hippoglossoides*). There was substantial similarity in
307 species composition between the six subareas.

308

309 However, single species/genera create dissimilarity by either being prominent or almost absent in individual
310 subareas. The group of stations from the deep Atlantic, essentially the shelf break and upper slope deeper than
311 500 m, was clearly different from the six subareas. This deep group had low abundances of the more typical
312 shelf species, and in contrast, a range of e.g. Arctic eelpouts that were absent from or uncommon in shallower
313 waters, were prominent. This was also the only area in which the sub-Arctic macrourid roughhead grenadier
314 (*Macrourus berglax*) and the Arctic skate (*Amblyraja hyperborea*) were consistently present.

315

316 **Distribution and abundance patterns**

317

318 *Patterns across entire sampling area*

319 The patterns shown in Figure 3 pre-supposes patterns associated with the selected subareas. Therefore, using
320 correspondence analyses, we explored patterns of variation inherent to the dataset, disregarding the subareas
321 selected. In a preliminary correspondence analyses (CA) of the entire dataset (i.e. samples from all years and all
322 depths pooled, result not shown) it was observed that the samples from depths >500 m tended to dominate the
323 analysis and hide patterns in shallower shelf waters. This confirmed the patterns observed in the overview plot of
324 the distribution and abundance of all species (Fig. 3) that the deep stations had a species composition distinctly
325 different from all shallower subareas. This contrasting shelf vs. upper slope pattern was an obvious main result
326 of the study.

327

328 To gain further insight, two further correspondence analyses were carried out. In the first, the >500 m depth
329 samples were omitted in order to explore patterns in the Svalbard shelf area. In the second, only the shelf break
330 areas (Atlantic SW and Atlantic NE) were considered, including also the stations from depths >500 m. Thus
331 three separate CAs were carried out, the one mentioned above on the entire dataset, and two on subsets of the
332 data.

333

334 *Patterns on the shelf (<500 m)*

335 Scores on Axis 1 and 2 resulting from the CA run with all stations shallower than 500 m depth are shown in
336 Figure 5. In the six plots shown in Figure 5, scores for all stations are provided but those for stations within
337 individual subareas (Fig. 1) are highlighted (black dots and lines). The eigenvalue distribution suggested that
338 main patterns of variation would be explained by Axis 1 and 2, each explaining roughly equal proportions of the
339 total variation (Eigenvalue Axis 1: 0.67, explained variation 10.6%; Axis 2: 0.64; 10.2%). Most samples (and
340 species) are concentrated in the centre of the plot confirming the above suggestion of a degree of homogeneity
341 amongst samples across the entire Svalbard shelf. There is, however, also a dispersion of samples along three
342 gradients suggesting a spatial pattern (Fig. 5).

343

344 The major pattern (i.e. separation along Axis 1) is that of Hopen Deep and Atlantic SW tending to have negative
345 scores and Svalbard Bank and Svalbard Coast tending to have positive scores. Taking also Axis 2 into account,
346 the Atlantic SW samples are placed in the upper left quadrant opposite Svalbard East samples in the lower left

347 quadrant, hence it is suggested that Axis 2 represents a gradient from cold Arctic shelf areas to warm Atlantic
348 waters.

349
350 As examples of species providing comparatively clear patterns, we selected 16 abundant species with contrasting
351 score patterns on Axes 1 and 2 (positive, negative and close to 0). For these species, CA site scores on Axis 1 vs.
352 2 were plotted with symbol sizes reflecting abundances in individual trawl samples (Fig. 6). Amongst these 16
353 selected species were examples of ubiquitous species showing no pattern, and in contrast, species showing clear
354 associations with the three gradients revealed by the CA. Since the input data were not log-transformed, it is
355 likely that abundant species tend to have a comparatively strong influence on the results. Haddock, Atlantic
356 wolfish (*Anarhichas lupus*), and to a lesser extent *Triglops murrayi* and Norway pout (*Trisopterus esmarkii*) are
357 species associated with the ‘Svalbard Bank-gradient’, whereas blue whiting (*Micromesistius poutassou*), *Lycodes*
358 *esmarki* and *Lycodes gracilis* are associated with the ‘Atlantic SW-gradient’. *Lycodes pallidus*, *Liparis fabricii*,
359 *Triglops nybelinii*, *Icelus* spp. and to some extent *L. eudipleurostictus* are abundant along the ‘Svalbard East-
360 gradient’. Other species, such as, Atlantic cod, redfish, long rough dab and *Artediellus atlanticus* are distributed
361 across the entire Svalbard shelf.

362
363 *Atlantic shelf break and upper slope*

364 A further CA was run for samples from the Atlantic subareas supposedly most influenced by Atlantic
365 watermasses, i.e. from subareas referred to as Atlantic SW and Atlantic NE in Figure 1, the latter representing
366 the subarea facing the Arctic Ocean. The deepest stations in the dataset derived from upper slope waters were
367 also included in that analysis.

368
369 The results suggested that Axis 1 (Eigenvalue=0.71; explained variation=9.5%) essentially represented a depth
370 gradient. The species scores formed a continuum from the deep-living species associated with the upper
371 continental slope with high positive scores to a range of shelf species clustering near the origo. On Axis 2
372 (Eigenvalue=0.62; explained variation=8.3%), blue whiting, a benthopelagic species known to be associated
373 with Atlantic water, was prominent with a low score compared with other species. In Figure 7a the two graphs
374 for Atlantic SW and NE, respectively, show CA site scores on Axis 1 vs. 2 represented by symbols of depth. In
375 both subareas, Axis 1 is clearly a depth gradient. In the SW, there is considerable variation on Axis 2,
376 independent of depth. This is not the case in the NE, where blue whiting was virtually absent.

377
378 In these two subareas, also the Axis 3 (Eigenvalue=0.53; explained variation=7.1%) and 4 (Eigenvalue=0.48,
379 explained variation=6.4%) of the CA appeared informative (Fig. 7b), particularly in the Atlantic NE subarea. In
380 Atlantic NE, a group of 7 relatively deep stations form a loose cluster in the lower part of the graph, suggesting a
381 relatively pronounced difference in species composition compared with other stations. The species composition
382 for those 7 species and the remainder of the stations (Fig. 8) showed that the seven stations have exclusively
383 Arctic species (*Amblyraja hyperborea*, *Lycodes* spp., and *Rhodichtys regina*). The remaining stations have
384 greater richness, and include also many boreal species.

385

386 These observations suggest that compared with the Atlantic SW there is greater structuring in the Atlantic NE
387 into a truly deep Arctic assemblage and a shelf assemblage (including also some deep stations) with more boreal
388 species composition. The Atlantic NE is hydrographically complex being a transition area between the
389 Greenland Sea and the Arctic Ocean with a significant inflow of Atlantic water at shelf depths.

390

391 **Discussion**

392

393 **Appropriateness of input data**

394 Although the surveys were not originally designed for assemblage studies, rather for monitoring abundance of
395 key species of commercial interest, the dataset generated was sufficiently comprehensive to carry out such
396 analyses. The sampling was apparently too limited at depth exceeding 500 m to obtain a full species list, and the
397 results may be weaker for that subarea than for the remainder of the Svalbard area. The identification of species
398 was consistent, and it was a benefit to future validation that voucher specimens were submitted to the University
399 Museum Bergen collection. The number of samples by year was not sufficient to study interannual variation, and
400 a significant shortcoming limiting the scope of the analyses was the lack of temperature, salinity and substrate
401 data for individual samples and trawl tows.

402

403 The species accumulation curves were approaching asymptotes for several subareas, suggesting that the
404 sampling was adequate to observe the majority of taxa occurring in each subarea. However, it is premature to
405 make firm subarea-comparisons of richness based on these results. The apparent lower species numbers in the
406 Svalbard East subarea are likely affected by identification problems (for the genus *Icelus*) and the unresolved
407 taxonomy of certain genera (e.g. *Gymnelus*, *Careproctus*). The latter is an issue of concern that requires more
408 taxonomic research. The species accumulation curve for the deepest slope areas >500 m was not asymptotic and
409 this may be attributed to the lower sampling levels at these depths but could also reflect greater heterogeneity of
410 habitats across the wider depth range in those areas compared with the shelf. On the shelf break and upper slope
411 >500 m the tow duration was increased to obtain larger samples, but the number of tows was comparatively low.

412

413 **Species occurrence and assemblages**

414 The descriptive data by individual subareas and the results of the exploratory multivariate analyses fill a major
415 gap in the understanding of fish assemblage patterns in the northeast Arctic, complementing earlier studies in the
416 Barents Sea (Burgos 1989; Fossheim et al. 2006; Byrkjedal and Høines 2007; Johannesen et al. 2012). The
417 Svalbard region is a transition zone between the Atlantic water masses from the boreal Norwegian Sea and
418 Southwestern Barents shelf Sea and the Arctic waters to the north. Northern parts of the archipelago have
419 extensive seasonally varying ice cover, even in the recent warm period. There are no apparent topographical or
420 other obstacles to preventing distributional overlap between the Barents Sea and Svalbard, hence it is not
421 unexpected that the Svalbard archipelago and the remainder of the Barents Sea shelf have species lists with most
422 species in common (Wienerroither et al. 2011). A full comparison between species compositions in the two
423 neighbouring areas is beyond the scope of this study, but some features are noteworthy. Species occurring at
424 Svalbard associated with deeper colder water (*Paraliparis bathybius*, *Rhodichthys regina*, *Lycenchelys muraena*,
425 *Lycodes adolfi*, *Lycodes frigidus*, *Lycodes luetkenii* and *Lycodes paamiuti*) are not found in the main shelf area

426 of the Barents Sea but have been observed in deeper trenches between Franz Josef's Land and Novaya Zemlya
427 (Johannesen et al. 2017). One difference from the entire Barents Sea shelf is that the Svalbard archipelago is
428 partly surrounded by cold deep oceans and thus has marginal deep fish assemblages. The Svalbard area lacks
429 some species associated with shallow soft bottom brackish waters found in the southeastern Barents Sea such as
430 flatfishes *Limanda limanda*, *Liopsetta glacialis* and European plaice (*Pleuronecta platessa*), a few cold-water
431 coastal species (*Lumpenus fabricii* and *Asidophoroides olrikii*), found in the eastern Barents Sea only, and a few
432 coastal boreal species reaching their northern distribution limit in the south-western Barents Sea (e.g. Atlantic
433 halibut *Hippoglossus hippoglossus*, Wienerroither et al. 2011).

434
435 The major transition in species composition was that between deep Greenland Sea and Arctic Ocean
436 assemblages (shelf break and upper slope assemblage) and the shelf assemblages. Different shelf assemblages
437 could be distinguished, but they had many species in common and were not very different. On the shelf, there
438 appeared to be a clear difference between the Atlantic SW and Svalbard Bank and Svalbard East. The expected
439 association of fish assemblages with regional bathymetric and hydrographic features was thus confirmed. An
440 interesting finding was indication of high richness on the Svalbard Bank, in the subarea experiencing the more
441 pronounced seasonal variation in hydrographic conditions. The varying conditions may facilitate occurrence of
442 comparatively many species with different zoogeographical affinities in this shallow subarea.

443
444 **Assemblage patterns and environmental conditions**
445 Prevailing hydrographic conditions may underlie the relatively small differences in the species composition of
446 fishes across the Svalbard shelf areas. Notwithstanding seasonality, during the recent and present warm period it
447 is likely that a greater hydrographic homogeneity across the archipelago occurred as Arctic water masses retract
448 from shallow areas of the shelf, and Atlantic water inflows are more prominent. The change from the Atlantic
449 SW to an Arctic assemblage on the Svalbard Bank and in the Svalbard East subarea contrasts somewhat with the
450 corresponding sharper transition observed in the Barents Sea where an association with the Polar Front was
451 observed in earlier studies (Burgos 1989; Fossheim et al. 2006; Byrkjedal and Høines 2007; Johannesen et al.
452 2012; Fossheim et al. 2015; Johannesen et al. 2016).

453
454 The Atlantic subareas to the southwest and northeast are characterized by the strongest influence of the Atlantic
455 Water influx from the south but also by the prominent deep front against the Norwegian Sea Deepwater with
456 sub-zero temperature. In these subareas, the analyses suggest strong depth-related patterns which probably also
457 reflect the depth-related hydrographical structure. This has been observed also in shelf-break studies further
458 south in the Norwegian Sea (Bergstad et al. 1999). There are also some differences between fish assemblage
459 pattern in the subareas facing the Norwegian/Greenland Sea (SW) and the Arctic Ocean (NE). Supposedly, the
460 Atlantic influence is weaker in the latter area, especially in deep shelf waters.

461
462 The Barents Sea and Svalbard region has in recent years experienced an unprecedented warming trend, and a
463 further warming may cause an abrupt northward shift of the Polar Front (Wassmann et al. 2015). Under
464 continued warming, our hypothesis is therefore that the entire Svalbard shelf and coastal waters will be inhabited
465 by an Atlantic species assemblage, leading to a "borealization" of the Svalbard shelf (Fossheim et al. 2015).

466 Since Arctic and Atlantic food webs have different properties (e.g. connectivity) (Korscht et al. 2015), the
467 dynamic properties of the ecosystem in the region is likely to change. Arctic species will likely retract to
468 northern and eastern waters of the high Arctic. Deep assemblages on the upper continental slope, however, will
469 likely be maintained because deep oceanic waters will remain of Arctic origin (Fossheim et al. 2015).

470

471 In contrast, if a cooling trend should occur, or even cooling events during the general warming trend, the Polar
472 Front would probably be stable. This was observed in earlier decades prior to the recent warming. A productivity
473 decline in pelagic system due to cooling and increasing ice cover may be expected. Some boreal species may
474 retract (e.g., Atlantic cod). However, the hypothesis is that the main distribution and species assemblage patterns
475 will be maintained as suggested in this study.

476

477 **Utility of results and future work**

478 The results generated in this study represent an improved baseline that will contribute to facilitating future
479 evaluations of states and trends in fish distributions and spatial abundance patterns. As such it is a contribution to
480 regional biodiversity analyses and assessments underlying management advisory processes. It will also benefit
481 the generation of testable hypothesis on structuring processes for this prominent and complex hydrographical
482 frontal zone.

483

484 Shortcomings in terms of sampling levels and design that prevented more thorough analyses of assemblage
485 patterns for the entire area as well as those specific to subareas should be taken into account in future efforts. In
486 order to facilitate temporal studies, the sampling design and level (the number of stations and their position)
487 should not change from year to year. If a systematic strategy is retained, a regular grid on the shelf should be
488 continued, but along the shelf break transects following the depth gradient with a shorter inter-station distance
489 should be applied. This will allow for finer resolution of the study of species-depth composition relationship and
490 how this relationship varies with time. Also, continued effort is recommended to reduce uncertainty by
491 improving species identification. The use of temperature sensors attached to the sampling gear (the trawl) is
492 suggested for future surveys.

493

494 Apart from assessing impacts of climate variation and change, future studies using the new baseline may
495 facilitate investigations of the influence of fisheries as well as increasing petroleum and mineral extraction
496 activity. The Svalbard archipelago has been the subject of commercial fisheries for at least 85-90 years (Boitsov
497 et al. 2004; Townshill et al. 2015). The present species composition in a major part of the Svalbard archipelago
498 is probably already affected by past exploitation and therefore not in a virgin state. There is a continued need for
499 monitoring and assessing fishing activities and to follow up new developments and potential northward shifts in
500 fishing effort during the recent warming trend (Haug et al. 2017). Based on the current regulation practices,
501 however, the expectation is that there will be limited effects of fisheries on the demersal fish community in the
502 Svalbard archipelago. All fisheries are regulated (Total Allowable Catches, technical regulations, Marine
503 Protected Areas) to maintain productivity and habitats, hence major changes may not be very likely. Bycatch
504 rates are assumed small under current move-on-rules and technical regulations. The trend in the recent 15 years
505 is rather declining than increasing shrimp trawling activity around Svalbard (ICES 2014). The possible

506 expansion in fisheries for Atlantic cod and pot fisheries that may happen will probably be possible without
507 significant additional impact on non-target species. If shrimp trawling and pot fishing for crabs become
508 substantial and venture into northern unexploited subareas, it is however relevant to consider what areas and
509 assemblages will be affected by an increased target and bycatch mortality. Impacts of oil and gas activity as well
510 as mining will naturally depend on scale, geographical distribution and technological approach of such activity.
511 Currently, the only permissions granted are exploratory licenses in the Hopen Deep. It is difficult to develop
512 scenarios, but a growing extractive industry is an issue of concern and enhances the need for monitoring and
513 assessments.

514
515 Future work should include continued and improved monitoring and assessments of fish assemblages and their
516 environment, and targeted monitoring of human activity and impacts. For most fish species that are not targeted
517 by current fisheries, i.e. ca. 90% of the species list, essential habitats, spawning and nursery areas are largely
518 unknown, hence there is limited data to make risk evaluations. To facilitate further monitoring and advisory
519 activity, there is thus a need for studies of essential habitats of different life stages of fishes, especially non-target
520 species.

521

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673

674

675 **Figure captions**

676

677 **Fig. 1** The Svalbard archipelago and the spatial distribution of trawl sites (black dots) sampled in the 2007-2014
678 annual bottom trawl surveys used in the analyses of demersal fish assemblages. The multishaded/colored study
679 area is the Svalbard Fishery Protection zone managed by Norway. For some of the analyses, the data set was
680 split into six subareas (shown by different shading/colours), based on bathymetry and information on regional
681 hydrography. The bathymetry used was that provided by the Norwegian Mapping Authority.

682

683 **Fig. 2** Modelled average temperature on the Svalbard archipelago across the time-series 2007-2014 in a) August-
684 September and b) March-April, as well as c) temperature anomalies from time-series in the Kola section 1950-
685 2014. For details on model set-up and performance, see Lien et al. (2013b; 2014).

686

687 **Fig. 3** Demersal fish abundance in Norwegian bottom trawl surveys on the Svalbard archipelago 2007-2014.
688 Overview of distribution and abundance (number of individuals sampled by a 15 min trawl tow) for all species
689 for each sampling year for six subareas of the Svalbard archipelago shown in Figure 1, and for the group of
690 stations deeper than 500 m. The taxa are listed in ascending order according to overall abundance in the pooled
691 dataset, and symbol sizes reflect mean abundance levels given in legend beneath the graph. Horizontal lines
692 connect symbols in the cases where a species occurs in two or more subsequent years. Numbers of trawl hauls by
693 subarea and year are shown as numbers above the horizontal axis.

694

695 **Fig. 4** Demersal fish data from Norwegian bottom trawl surveys on the Svalbard archipelago 2007-2014. Species
696 accumulation curves for all trawl samples from individual subareas of the Svalbard archipelago shown in Figure
697 1. Accumulation curves and associated 95% confidence intervals derived by 100 random permutations.

698

699 **Fig. 5** Correspondence analysis (CA) of demersal fish data from all the trawl sites shallower than 500 m depth of
700 the 2007-2014 Norwegian bottom trawl survey on the Svalbard archipelago. Sampling site scores on Axis 1 vs. 2
701 are given for all stations (grey dots). All plots show the entire output, but individual panels highlight the score
702 patterns of the sites in the six subareas as black lines and dots.

702

703 **Fig. 6** Correspondence analysis (CA) scores on Axis 1 vs. 2 and abundance (standardized to 15 min trawling
704 time) of 16 selected fish species observed during the 2007-2014 Norwegian bottom trawl survey on the Svalbard
705 archipelago. Sizes of squares indicate abundance at individual sites, and small dots represent absences (zero
706 observations).

706

707 **Fig. 7** Correspondence analysis (CA) of demersal fish data from the 2007-2014 Norwegian bottom trawl survey
708 on the Svalbard archipelago, using only the sub-set of data from the Atlantic SW and NE subareas (Fig 1). From
709 those subareas, all stations from the entire depth range are included. a) Site scores on Axis 1 and 2 , and b) Site
710 scores on Axis 3 and 4. Grey scale of symbols indicate site depth.

710

711 **Fig. 8** Correspondence analysis (CA) of demersal fish data from the 2007-2014 Norwegian bottom trawl survey
712 on the Svalbard archipelago, using only the sub-set of data from the Atlantic NE subarea (Fig 1). Comparison of
713 species compositions in tows (sites) from the Atlantic NE subarea with CA site scores on Axis 3 >-5, and sites
714 scores on Axis 3<-5 (7 sites occurred in this range).

714

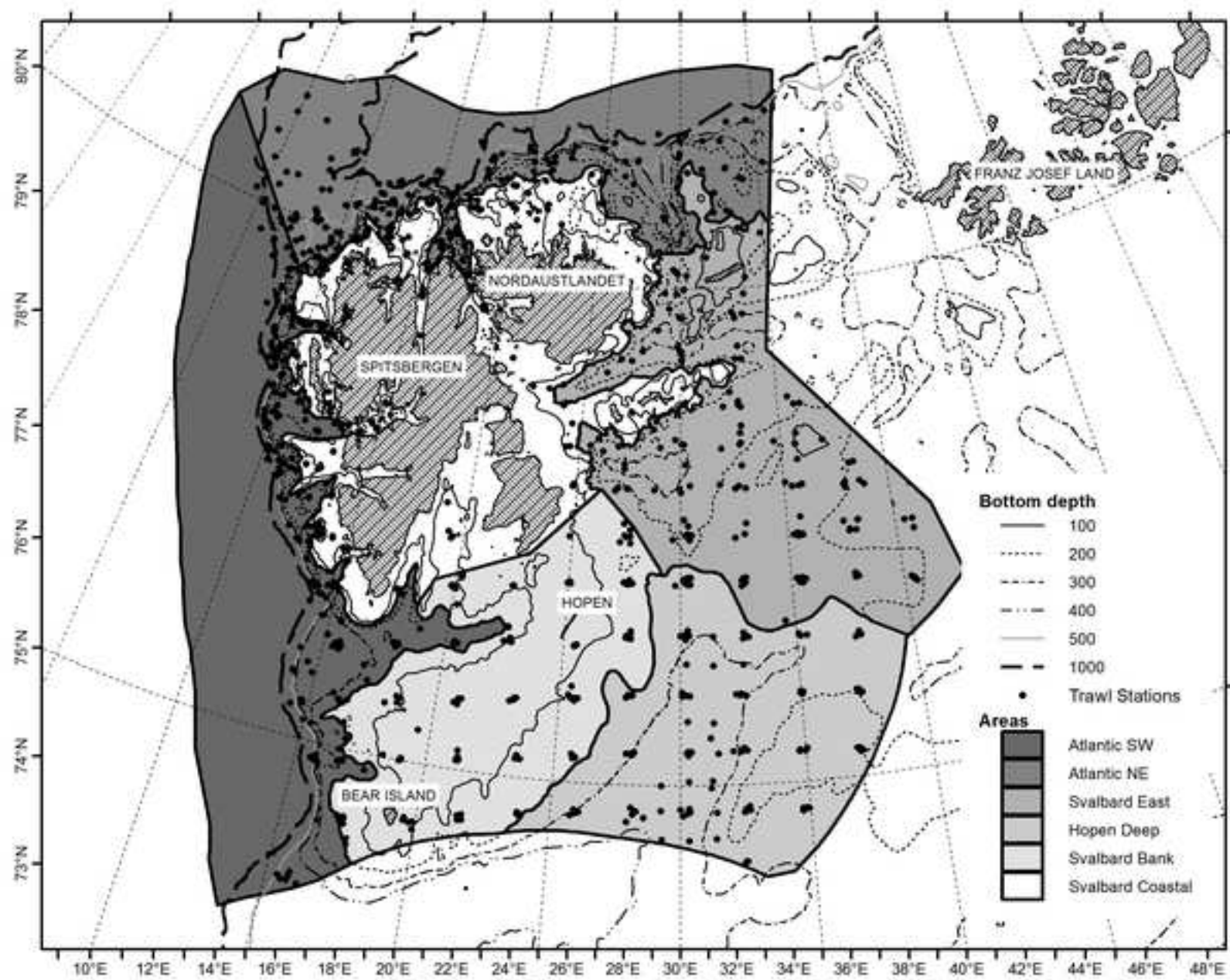
715

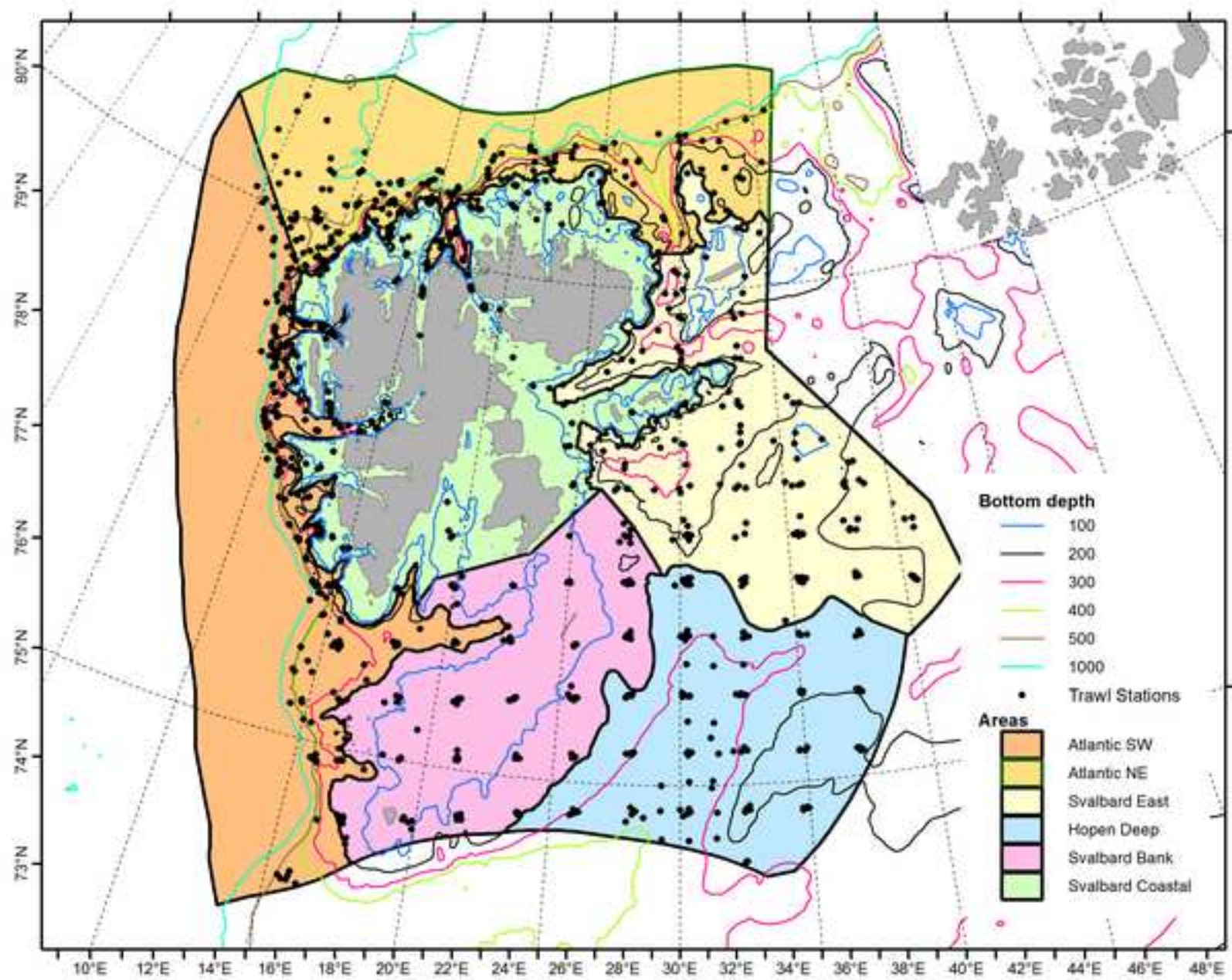
716 **Captions to online resources**

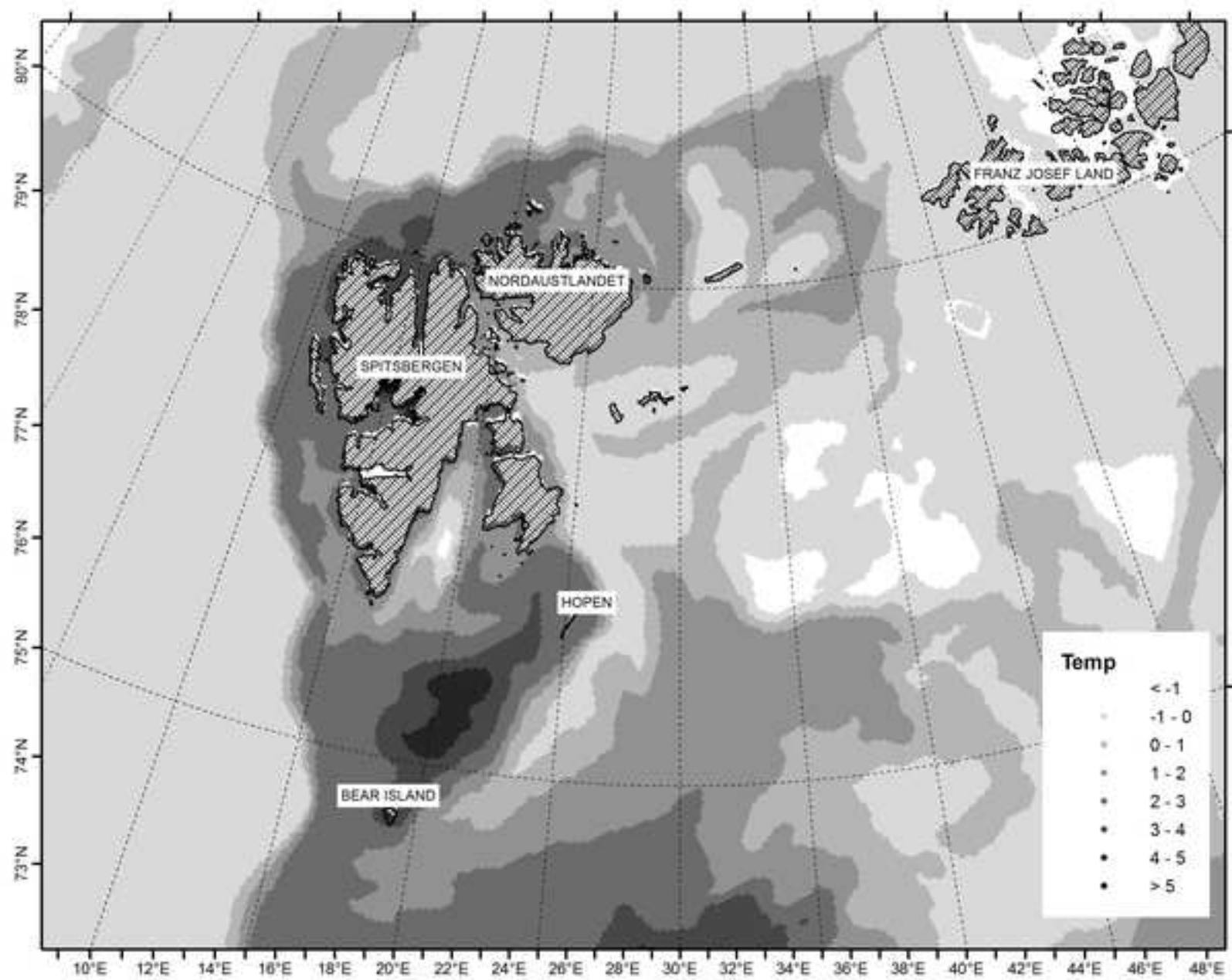
717 **Online resource 1** Data set used in the analysis

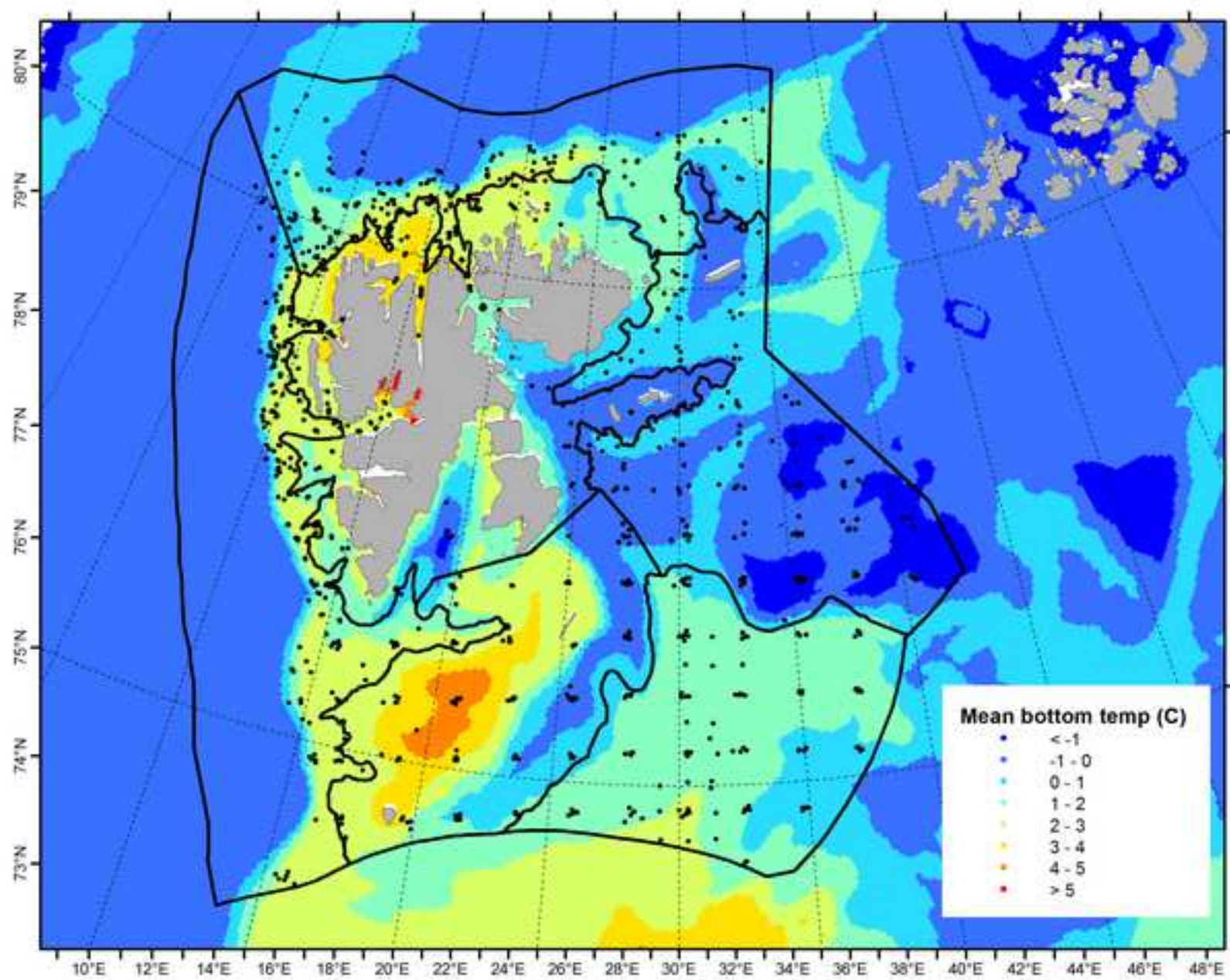
718

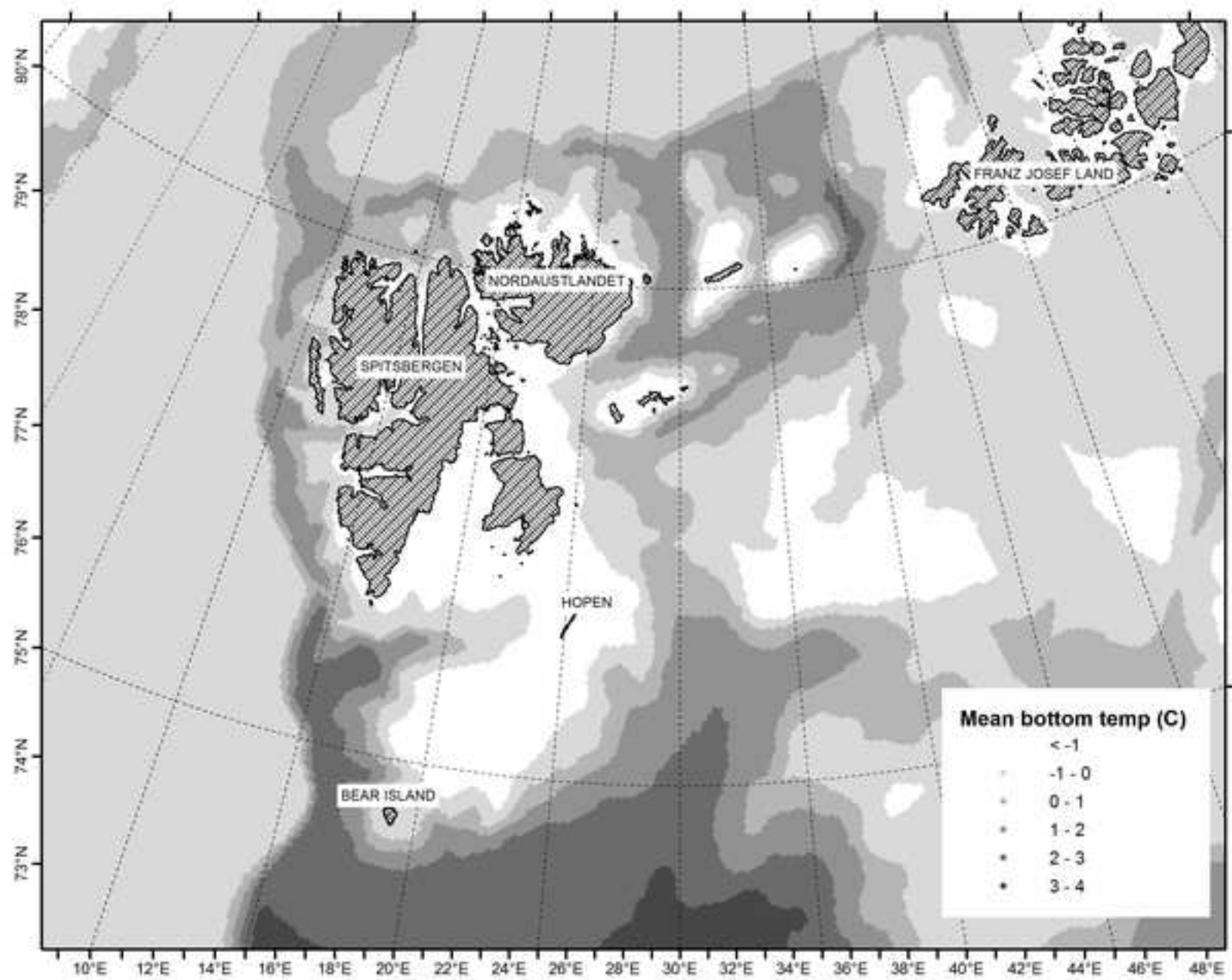
719

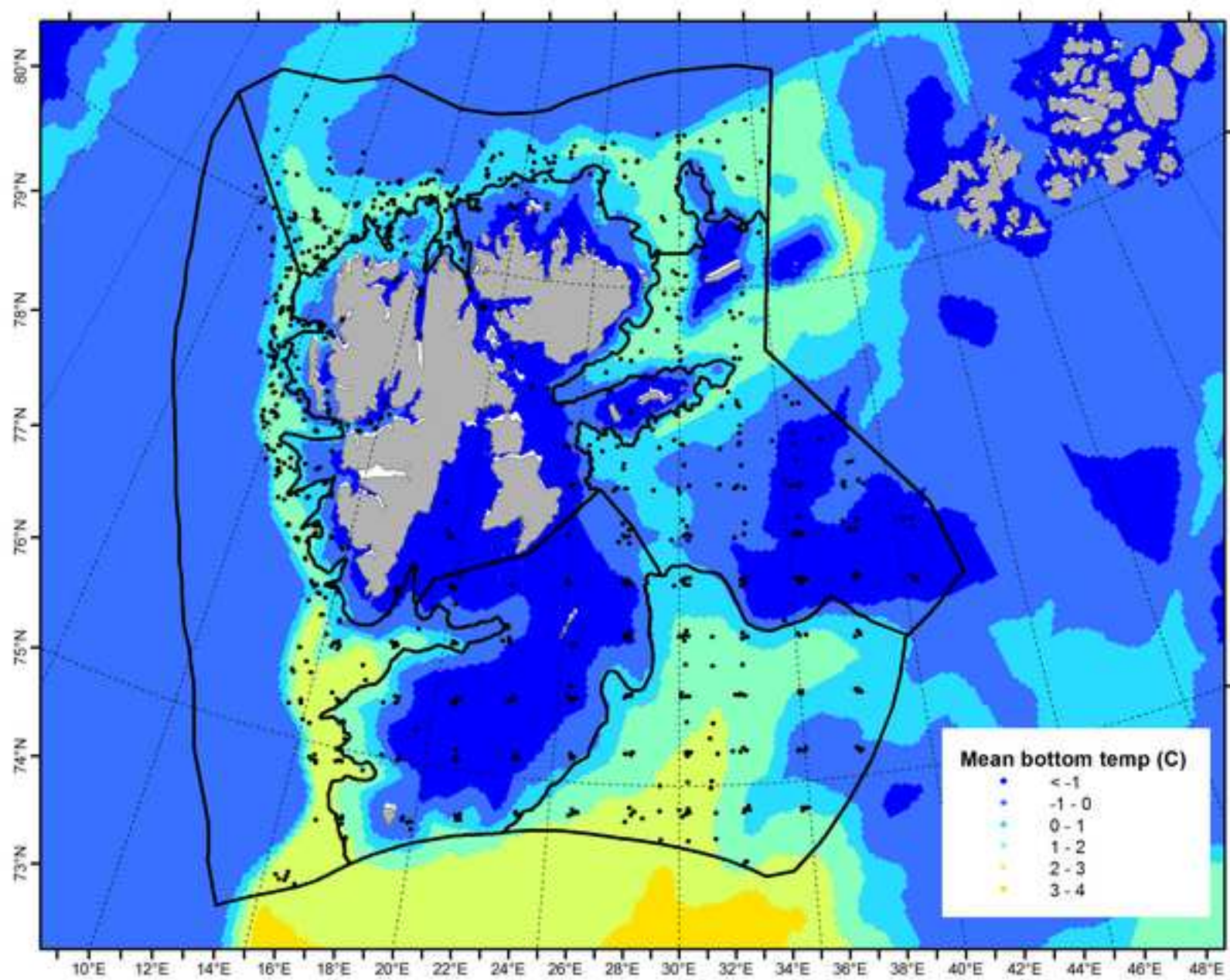


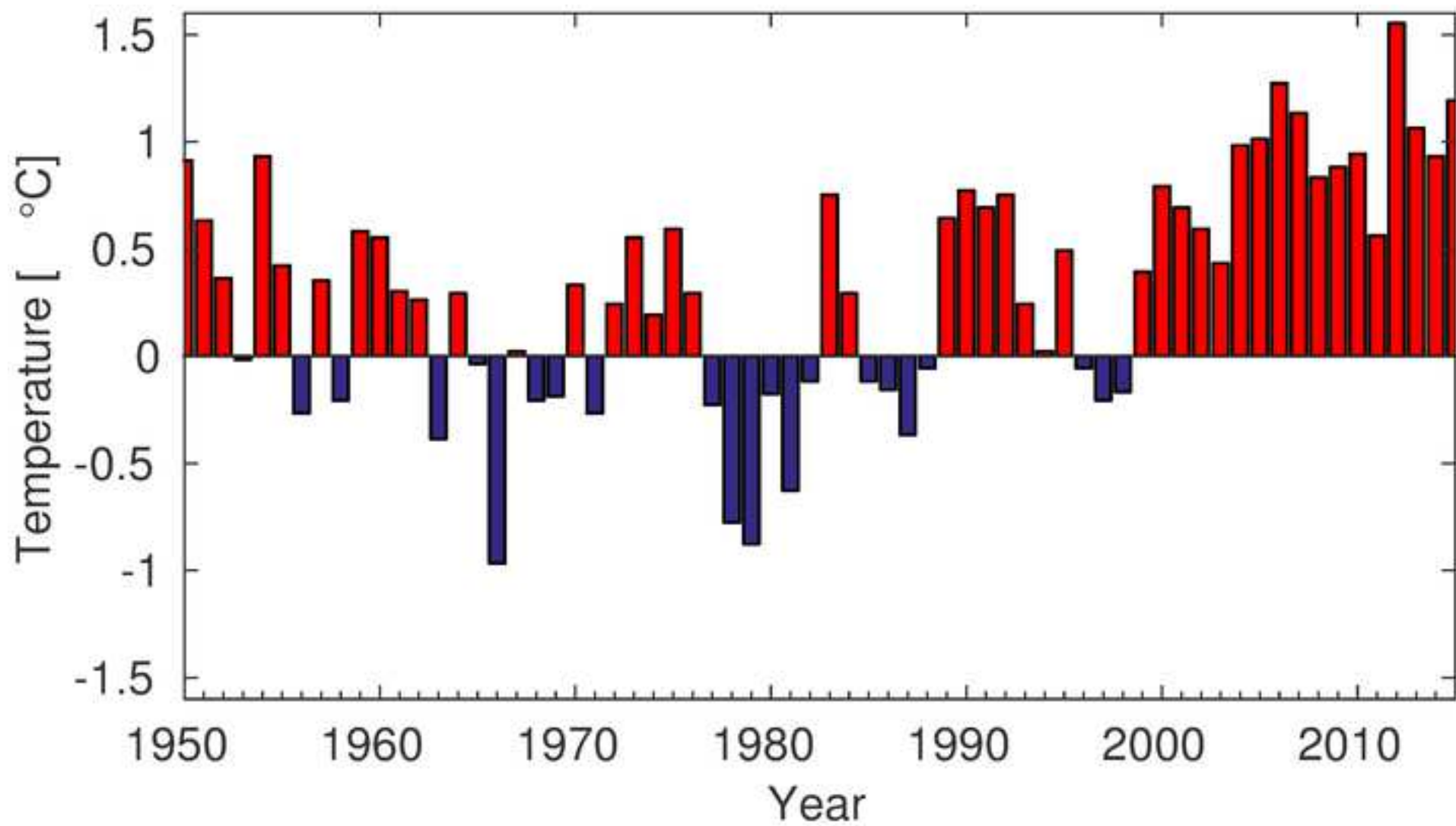


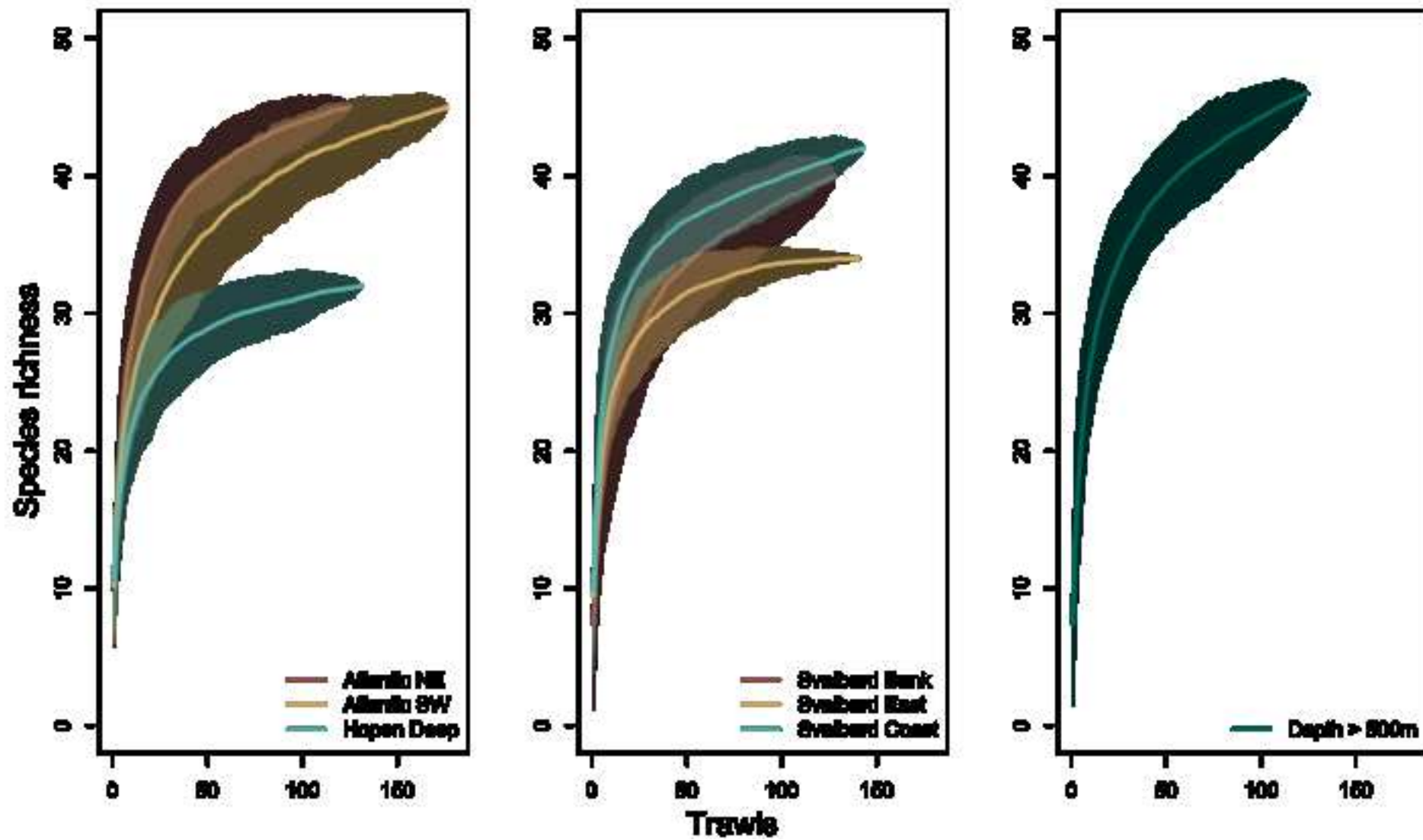


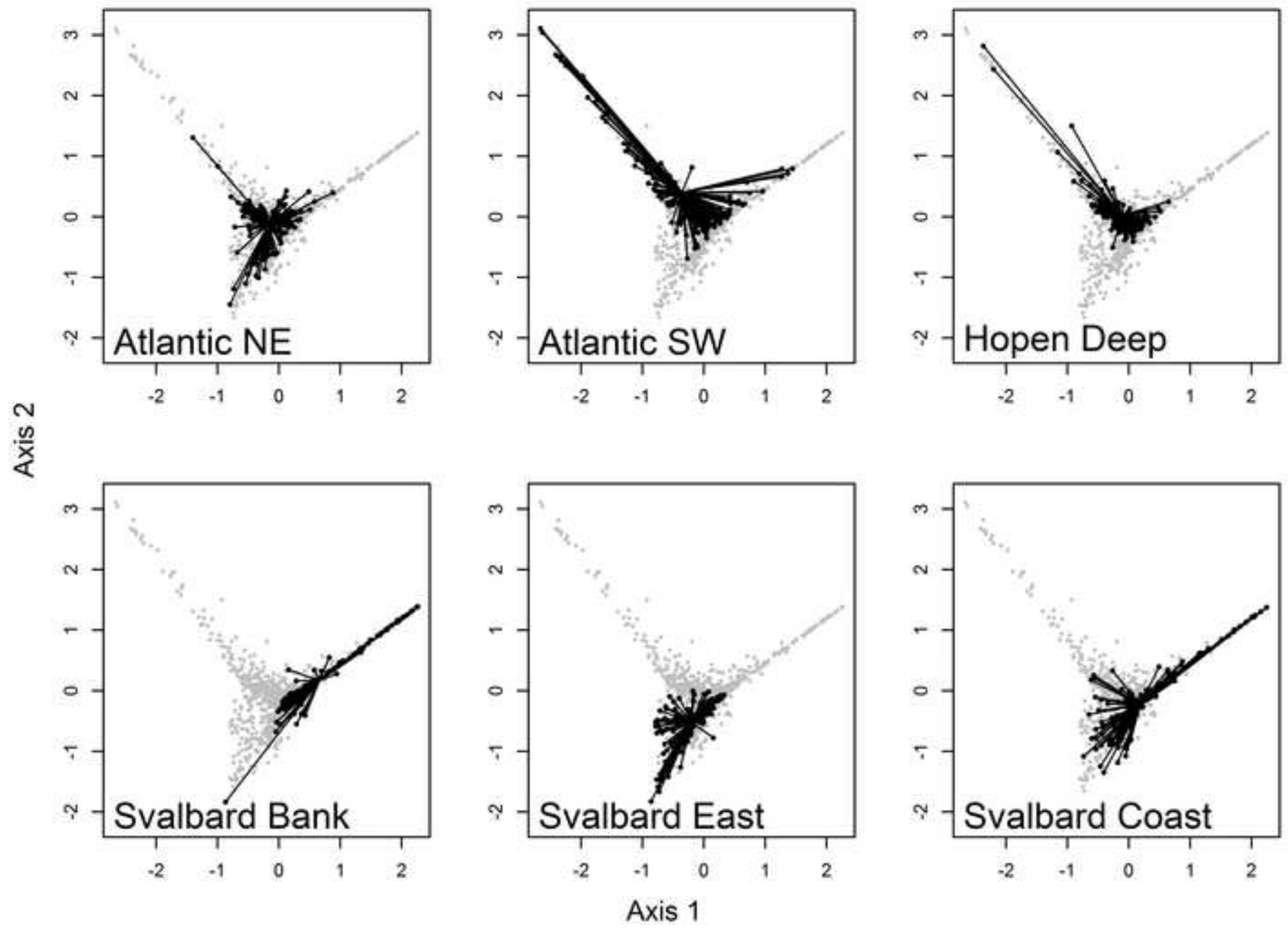


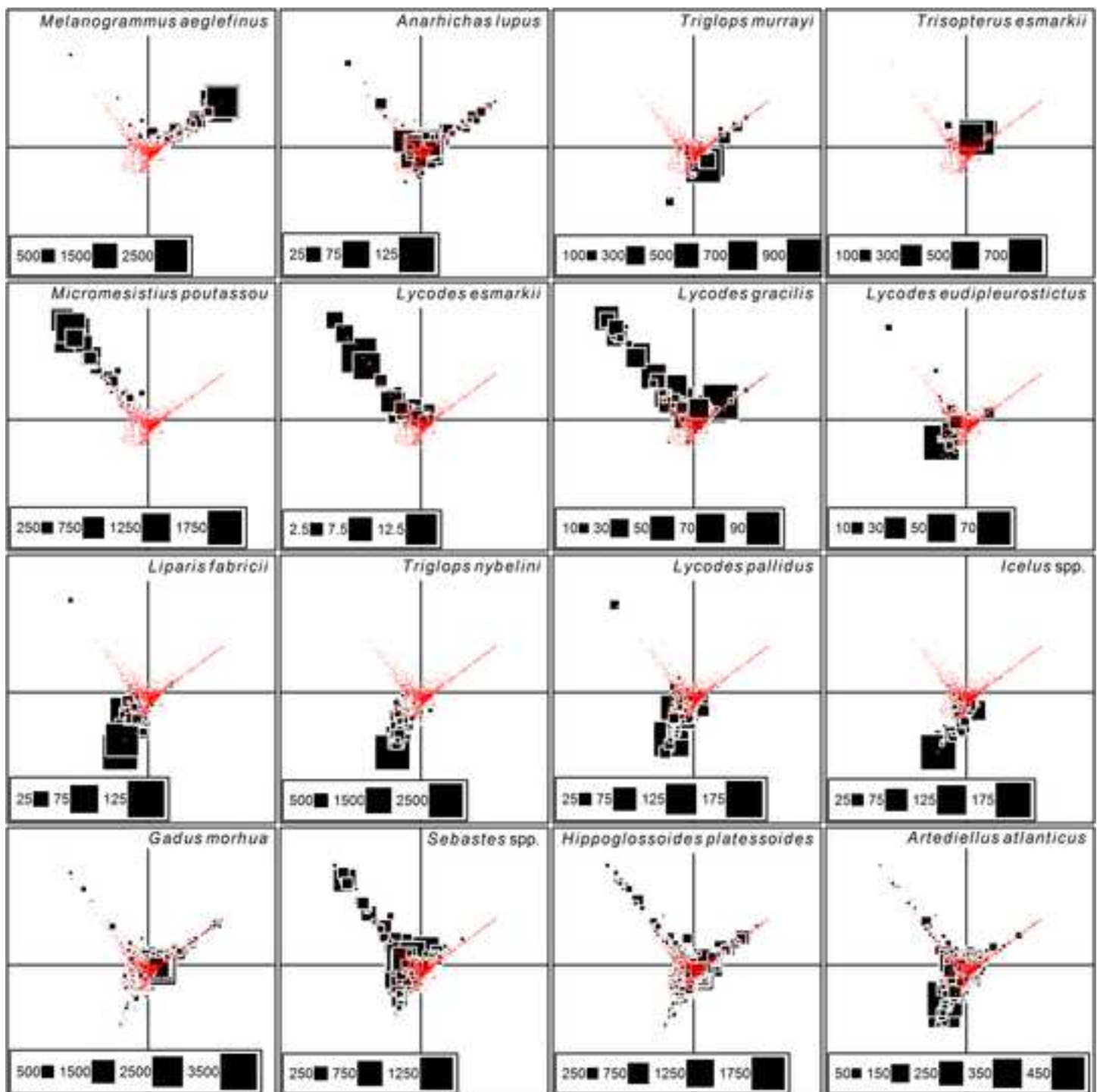


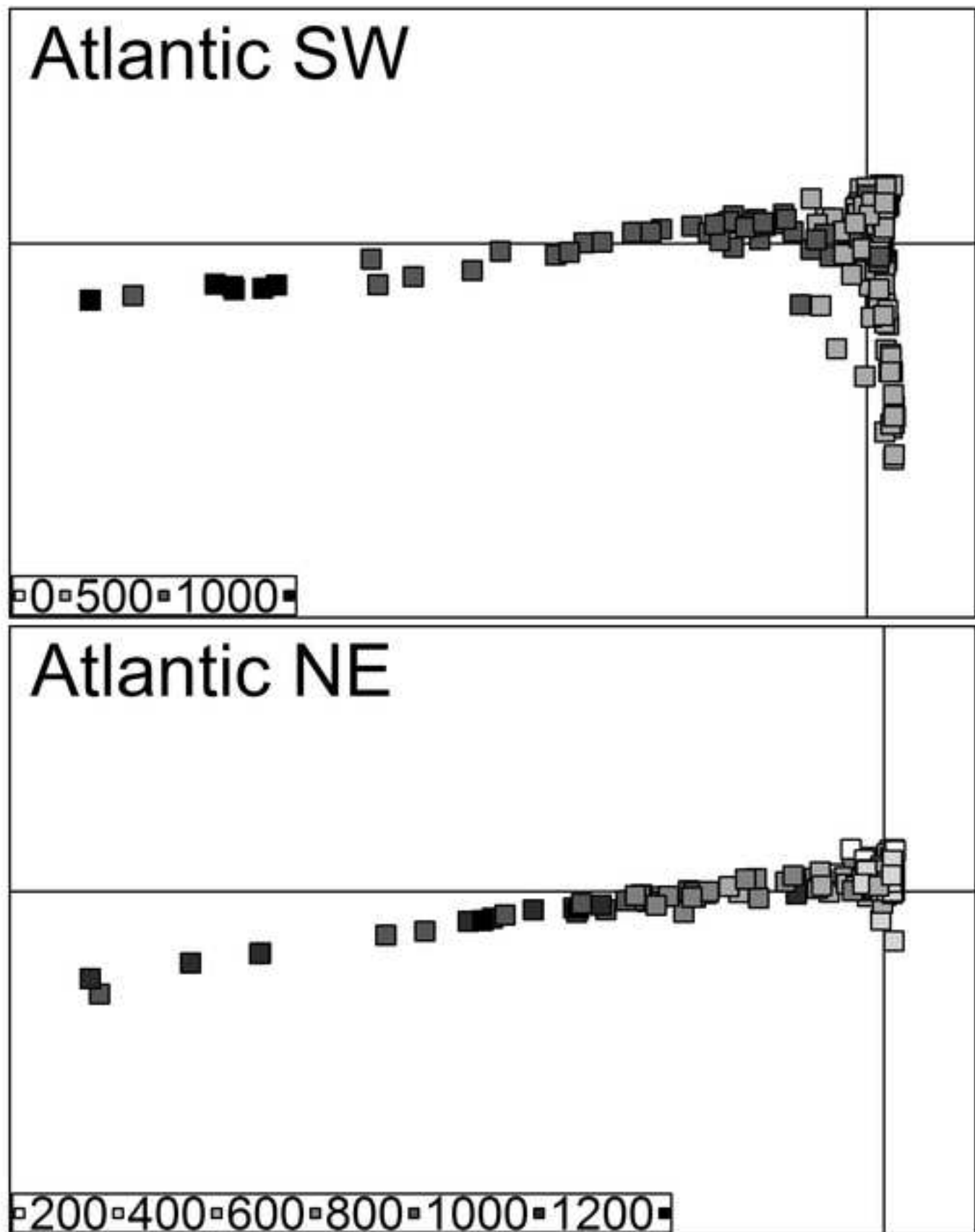


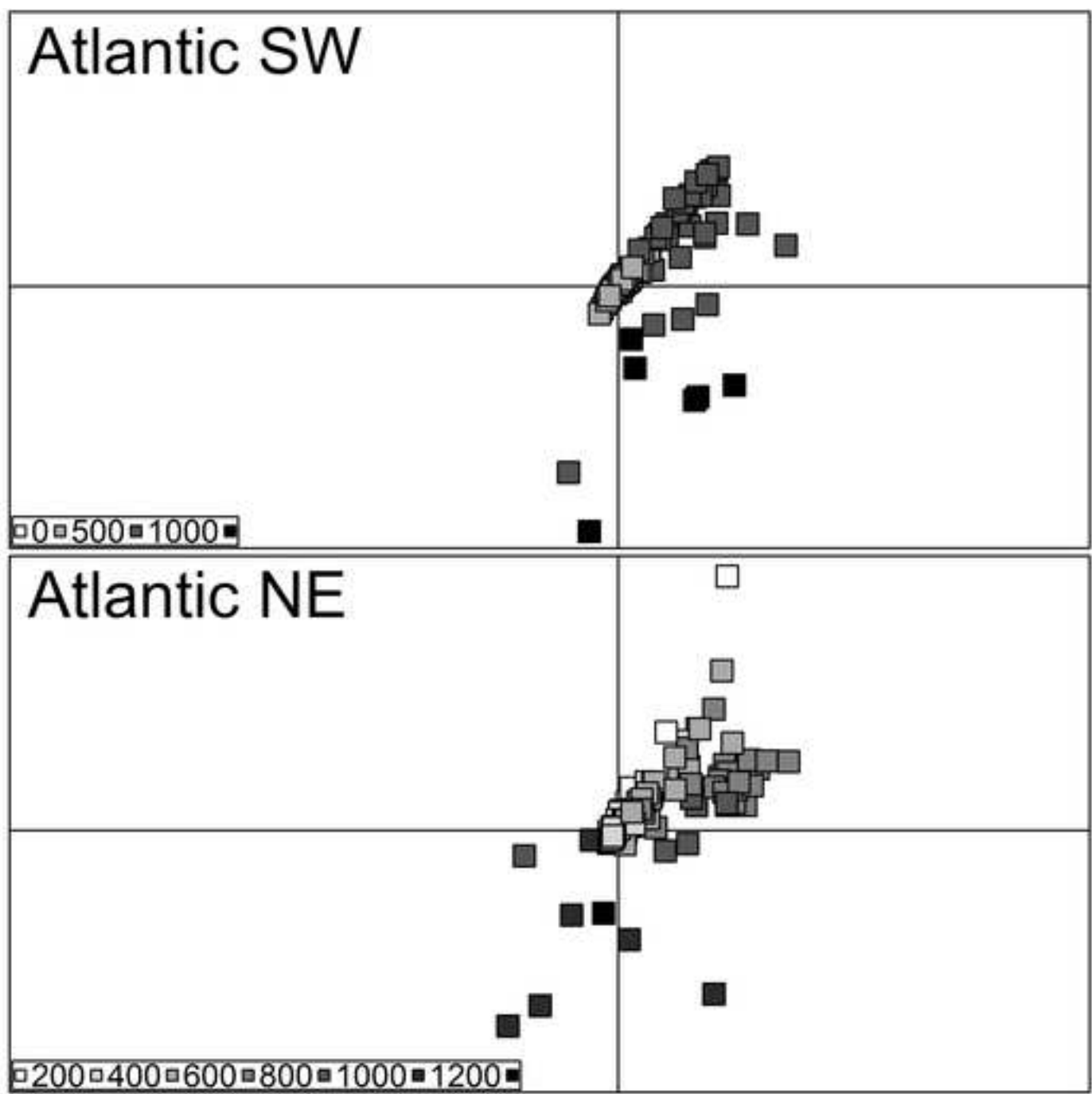




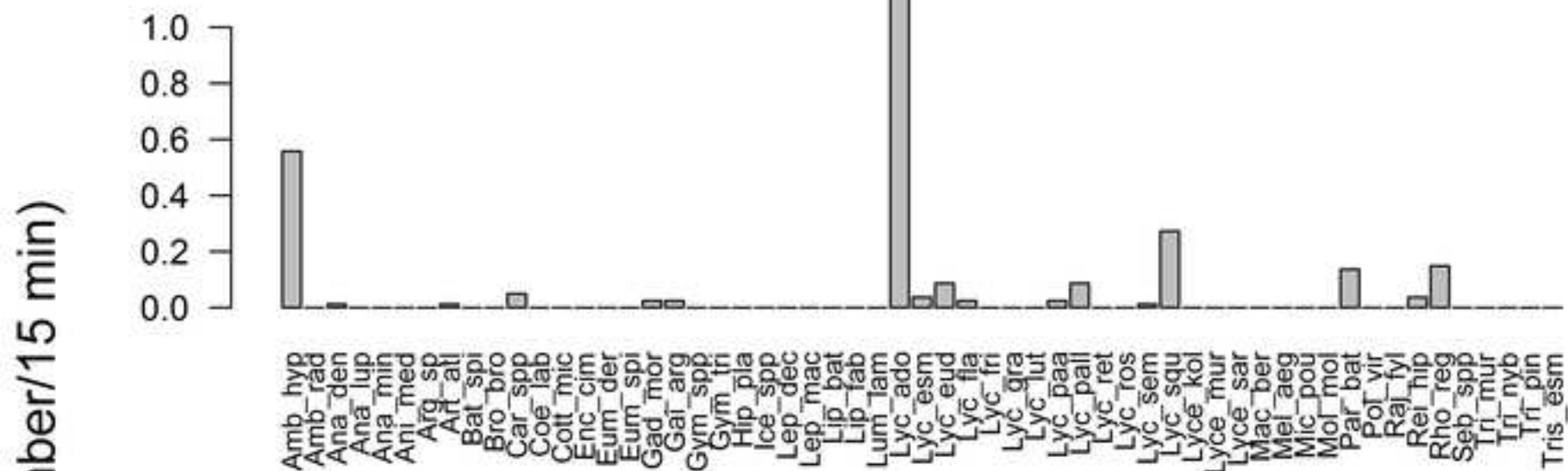








Scores Axis 3 < -5



Scores Axis 3 > -5

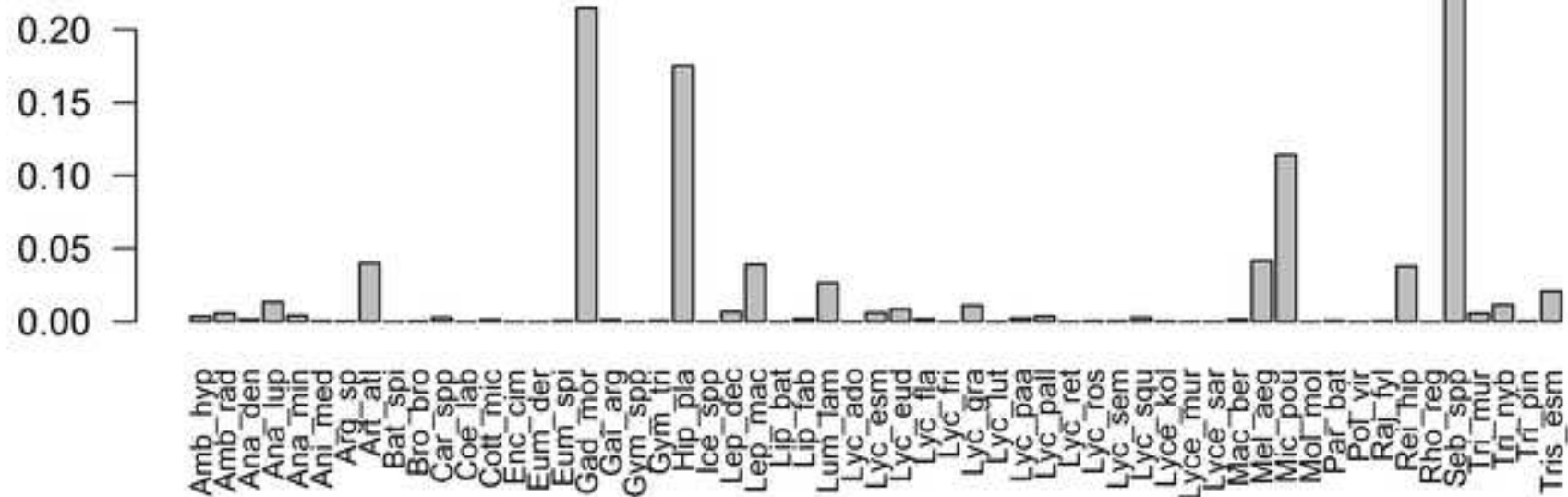
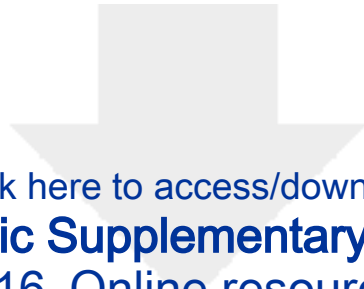


Table 1. - Norwegian bottom trawl surveys on the Svalbard archipelago 2007-2014. The number of trawl stations by subarea and year. Stations deeper than 500 m are given in parenthesis.

Year	Atlantic NE	Atlantic SW	Hopen Deep	Svalbard Coast	Svalbard Bank	Svalbard East
2007	22 (18)	44 (12)	32	24	21	18
2008	16 (13)	32 (13)	8	20	10	12
2009	12 (8)	9 (6)	12	15	8	15
2010	2 (0)	10 (3)	16	8	18	14
2011	16 (6)	21 (3)	7	8	18	25
2012	20 (18)	20 (6)	16	32	15	25
2013	26 (6)	26 (3)	20	33	21	24
2014	11 (1)	14 (8)	20	3	17	7

Table 2. Demersal fish data from Norwegian bottom trawl surveys on the Svalbard archipelago 2007-2014. Species list, with abbreviations used in the figures and zoogeographical groups according to Andriashev and Chernova (1995) and Mecklenburg et al. (2011). Where the zoogeographical classification differs among the two, the group according to Mecklenburg et al. (2011) is given in parenthesis. A: Arctic, MA: Mainly Arctic, AB: Arcto-Boreal, MB: Mainly Boreal and B: Boreal

Family	Species	Abbreviation	Zoogeographical affinity	
Arhynchobatidae	<i>Bathyraja spinicauda</i>	Bat.spi	MB	
Rajidae	<i>Amblyraja hyperborea</i>	Amb.hyp	A	
	<i>Amblyraja radiata</i>	Amb.rad	MB	
	<i>Rajella fyllae</i>	Raj.fyl	MB (B)	
Argentinidae	<i>Argentina silus</i>	Arg.sp	B	
Macrouridae	<i>Coelorinchus labiatus</i>	Coe.lab	-	
	<i>Macrourus berglax</i>	Mac.ber	B (MB)	
Gadidae	<i>Gadus morhua</i>	Gad.mor	MB	
	<i>Melanogrammus aeglefinus</i>	Mel.aeg	MB	
	<i>Micromesistius poutassou</i>	Mic.pou	MB	
	<i>Pollachius virens</i>	Pol.vir	MB (B)	
	<i>Trisopterus esmarkii</i>	Tris.esm	B	
Lotidae	<i>Brosme brosme</i>	Bro.bro	MB (B)	
	<i>Enchelyopus cimbrius</i>	Enc.cim	B	
	<i>Gaidropsarus argentatus</i>	Gai.arg	A (AB)	
	<i>Molva molva</i>	Mol.mol	B	
Sebastidae	<i>Sebastes</i> spp.	Seb.spp	MB	
Cottidae	<i>Artediellus atlanticus</i>	Art.atl	MB (AB)	
	<i>Gymnocanthus tricuspis</i>	Gym.tri	MA (A)	
	<i>Icelus</i> spp.	Ice.spp	AB and MA	
	<i>Myoxocephalus scorpius</i>	Myo.sco	MB (AB)	
	<i>Triglops murrayi</i>	Tri.mur	B (MB)	
	<i>Triglops nybelini</i>	Tri.nyb	A	
	<i>Triglops pingelii</i>	Tri.pin	AB	
Psychrolutidae	<i>Cottunculus microps</i>	Cott.mic	MA (AB)	
Agonidae	<i>Leptagonus decagonus</i>	Lep.dec	AB	
Cyclopteridae	<i>Eumicrotremus derjugini</i>	Eum.der	A	
	<i>Eumicrotremus spinosus</i>	Eum.spi	MA	
Liparidae	<i>Careproctus</i> spp.	Car.spp	MA, A and AB	
	<i>Liparis bathyarticus</i>	Lip.bat	MA	
	<i>Liparis fabricii</i>	Lip.fab	A	
	<i>Liparis tunicatus</i>	Lip.tun	A	
	<i>Paraliparis bathybius</i>	Par.bat	A	
	<i>Rhodichthys regina</i>	Rho.reg	A	
Zoarcidae	<i>Gymnelus</i> spp.	Gym.spp	A and AB	
	<i>Lycenchelys kolthoffi</i>	Lyc.ado	A	
	<i>Lycenchelys muraena</i>	Lyc.esm	A	
	<i>Lycenchelys sarsii</i>	Lyc.eud	B	
	<i>Lycodes adolffi</i>	Lyc.fla	A	
	<i>Lycodes esmarkii</i>	Lyc.fri	MB	
	<i>Lycodes eudipleurostictus</i>	Lyc.gra	A	
	<i>Lycodes frigidus</i>	Lyc.lut	A	
	<i>Lycodes gracilis</i>	Lyc.paa	MB	
	<i>Lycodes luetkenii</i>	Lyc.pall	A	
	<i>Lycodes paamiuti</i>	Lyc.ret	(A)	
	<i>Lycodes pallidus</i>	Lyc.ros	A (AB)	
	<i>Lycodes reticulatus</i>	Lyc.sem	A	
	<i>Lycodes rossi</i>	Lyc.squ	A	
	<i>Lycodes seminudus</i>	Lyce.kol	A	
	<i>Lycodes squamiventer</i>	Lyce.mur	A	
	<i>Lycodonus flagellicauda</i>	Lyce.sar	A	
	Stichaeidae	<i>Anisarchus medius</i>	Ani.med	B (AB)
		<i>Leptoclinus maculatus</i>	Lep.mac	MB (AB)
	Anarhichadidae	<i>Lumpenus lampretaeformis</i>	Lum.lam	MB
<i>Anarhichas denticulatus</i>		Ana.den	MB (AB)	
<i>Anarhichas lupus</i>		Ana.lup	MB	
Pleuronectidae	<i>Anarhichas minor</i>	Ana.min	MB	
	<i>Hippoglossoides platessoides</i>	Hip.pla	MB	
	<i>Reinhardtius hippoglossoides</i>	Rei.hip	MA (AB)	



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Electronic Supplementary Material
08122016_Online resource 1.xlsx

