

1 **Starfish (Asteroidea, Echinodermata) from Iceland; spatial distribution and** 2 **abundance**

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11

12 **Abstract**

13 The Benthic Invertebrates of Icelandic Waters programme (BIOICE) was conducted between
14 1991 and 2004, for the purpose of gathering specimens within the Icelandic Exclusive
15 Economic Zone (59° 58'N – 69° 35'N and 30° 52'W – 5° 34'W). In total 12961 asteroid
16 specimens were collected from 654 sampling stations, which comprises 63 % of all sampling
17 stations. Sampling depths were between 20 and 2700 m. Total recorded asteroids for Iceland
18 now include 64 species from 20 families and 44 genera, including 23 new species added from
19 this study. The most abundant asteroids collected by BIOICE were *Pontaster tenuispinus*,
20 *Bathybiaster vexillifer* and *Henricia pertusa* group. Maximum species richness was found at
21 depths 100-200 m and 400-500 m, located above the cold Norwegian Sea Deep Water (-1°C).
22 24 of the species were recorded at an abundance-weighted mean depth below 1300 m. The
23 area south of the Greenland-Scotland Ridge (GS-Ridge) was more species rich than north of
24 the ridge. Specimens within the rare Myxasteridae family were recorded.

25 A nonmetric multidimensional scaling (NMDS) converged fast from multiple starting
26 points with stress = 0.18. All five abiotic factors (depth, temperature, salinity, latitude and
27 longitude) were strongly related to two of the NMDS ordination axis. The first ordination axis
28 scores had strongest correlation with depth ($r = 0.84$), whereas the second ordination axis
29 scores had strongest correlation with latitude ($r = 0.71$).

30

31

32 **Keywords**

33 Asteroidea, Echinodermata, Iceland, BIOICE, abundance, distribution, Myxasteridae, NMDS

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35

36 **Introduction**

37 The Echinodermata phylum contains five classes which represent a large part of the marine
38 benthic ecosystem biomass, and are important in determining habitat structure for other
39 species (Brown and Cheng, 1946; Gebruk et al., 2010; Stone and Titgen, 2003; Watts and
40 Wasson, 2013). Asteroids are keystone species capable of adapting to different environments
41 and responsible for maintaining high species diversity due to their role as major predators on a
42 diverse range of species (Lawrence, 2013; Menge and Sanford, 2013; Paine, 1971, 1966). A
43 high species diversity may over time enhance discovery of e.g. bioactive compounds (Jha and
44 Zi-rong, 2004).

45

46 The first asteroid species found in Icelandic literature, *Asterias rubens* Linnaeus, 1758
47 and *Solaster endeca* (Linnaeus, 1771), were recorded in 1600s by Bishop Gisli Oddson and
48 Jon Guðmundsson (Guðmundsson, 1640; Oddson, 1638). A more comprehensive study on
49 asteroid distribution from Iceland was published three centuries later, by Einarsson (1948).
50 Other asteroid studies from nearby areas emphasized different biological aspects:
51 biogeography and distribution at the Reykjanes Ridge (Copley et al., 1997; Dilman, 2013a,
52 2013b, 2006; Gebruk et al., 2010; Mironov and Gebruk, 2006); a systematic account of
53 species from the Mid-Atlantic Ridge (Dilman, 2008); distribution and bathymetric zonation in
54 the Rockall Trough (Gage, 1986; Gage et al., 1985, 1983; Harvey et al., 1988); molecular
55 studies on *Henricia* (Knott et al., 2018), and depth-related distribution in the Porcupine
56 Seabight area and Faroe Island as well as quantitative studies on benthic communities and
57 distribution in deep sea basins of the Norwegian Sea and Atlantic, respectively (Dahl et al.,
58 1976; Howell et al., 2002; Ringvold, 1999; Ringvold and Andersen, 2016; Sibuet, 1984).
59 Studies on e.g., asteroid diversity and abundance, megafaunal communities and community
60 patterns from NE Greenland and Faroe Islands have also been conducted (Fredriksen et al.,

61 2020; Jones et al., 2006; Mayer and Piepenburg, 1996; Piepenburg et al., 2001, 1997;
62 Piepenburg and Schmid, 1996).

63

64 The Benthic Invertebrates of Icelandic Waters programme (BIOICE) was initiated in 1991,
65 with the main objective to explore biological diversity of larger benthic invertebrates (>0.5
66 mm) in Icelandic waters, of which the asteroids are a major component. BIOICE was
67 conducted after the Marine benthic fauna of the Faroe Islands programme (BIOFAR), a
68 somewhat similar programme from nearby Faroe Islands, and from where an account of
69 asteroids has already been published (Ringvold and Andersen, 2016). Previously, one study
70 on development within asteroids (Velatida order), using material from BIOICE, has been
71 conducted (Janies, 1995). In this BIOICE study we provide an account of all asteroid species
72 collected during the BIOICE programme, and identify possible patterns in the species
73 distribution in relation to environmental variables. In addition to the BIOICE collection, a
74 previously unreported collection by the late Jon Bogason, donated to IINH in Iceland, is also
75 included in our study.

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77

78 **Material and methods**

79

80 *The BIOICE programme and sampling*

81 BIOICE was conducted within the 200-mile Exclusive Economic Zone (EEZ) of Iceland (59°
82 58' N – 69° 35' N and 30° 52' W – 5° 34' W (www.marineregions.org)), an area
83 encompassing 750 000 km² (Guðmundsson et al., 2014; Steingrímsson et al., 2020) (**Fig. 1**).
84 The sampling phase of the programme started in 1991 and was completed in 2004. At each
85 BIOICE cruise station, several deployments were made. Each deployment was given a
86 sample number in consecutive order. Therefore, each cruise station typically had several
87 separately numbered samples. Each individual numbered sample is called a “sampling
88 station” and several sampling stations are within each cruise station. A total of 1031 sampling
89 stations were comprised from 579 cruise stations using the research vessels RV Bjarni
90 Sæmundsson (Iceland), RV Magnus Heinson (Faroe Island) and RV Haakon Mosby
91 (Norway). Cruise stations were selected on the basis of a stratified random sampling scheme

92 for 62% of the stations, while 38% of the stations were selected *ad hoc* during the cruises
93 based on topographical features, etc. (Guðmundsson et al., 2014).

94

95 At each cruise station, several devices were used to collect different components of the
96 benthos, depending on the variety of sea floor types, ranging from soft mud flats to steep
97 cliffs. A modified RP-sledge (Brattegard and Fosså, 1991; Rothlisberg and Percy, 1976) was
98 used to collect epifauna on relatively smooth bottom surfaces; a detritus Sneli-sledge (Sneli,
99 1998), collected infauna of soft and mixed substrates; an Agassiz trawl collected megafauna
100 on soft and even bottom while a triangular dredge was applied on rough rocky bottom.
101 Samples for sediment analysis were taken with a Shipek grab, and near bottom water
102 temperature and salinity were measured with a CTD (Conductivity-Temperature-Depth)
103 probe. The BIOICE stations span near bottom water temperatures ranging from -0.9°C to
104 9.64°C; water depths of 23 - 3006 m; and salinity range of 34.17 – 35.20 ‰. (Full information
105 on all BIOICE stations is available at [http://utgafa.ni.is/greinar/BIOICE_station_list_91-](http://utgafa.ni.is/greinar/BIOICE_station_list_91-04_Paper_A2.pdf)
106 [04_Paper_A2.pdf](http://utgafa.ni.is/greinar/BIOICE_station_list_91-04_Paper_A2.pdf) and in Steingrímsson et al. (2020).) Average depth for each species was
107 calculated as the abundance-weighted mean (also referred to as weighted depth), which takes
108 into account the numbers of specimens recorded at each depths, so that data from depths where
109 several specimens are recorded, contributes more to the mean.

110

111 All BIOICE zoology samples were handled by following a standardized procedure.
112 After collection, samples were washed in sea water through series of sieves, with mesh sizes
113 ranging from 16 to 0.5mm. The washed residue was fixed in 4% borax-buffered formalin.
114 Samples were brought to the Sandgerdi Marine Center (SMC) in Iceland, where they were
115 washed, and transferred to 80% ethanol within the first weeks after the cruises. Trained staff
116 at SMC picked asteroid specimens from the samples. These were deposited at the IINH
117 collection till further analysis.

118

119 Asteroid specimens sorted from the BIOICE samples made up the majority of the
120 material used in this study. Some additional specimens in the IINH collection were used as
121 well, especially those of the late Mr. Jon Bogason (1934-2009), a former research assistant at
122 the Marine Research Institute (MRI), who zealously collected all major invertebrate phyla that
123 came as by-catch in trawl hauls during some of the MRI annual ground fish surveys in

124 Icelandic waters. Jon Bogasons collection consists of about 3300 dried specimens from 293
125 locations.

126

127

128 *Taxonomic identification*

129 Identification of asteroids was based on “Starfishes of the Atlantic” and “Echinoderms of the
130 British Isles” (Clark and Downey, 1992; Mortensen, 1927). Scientific names were checked
131 with Worms (www.marinespecies.org). In echinoderms, small specimens often lack adult
132 character traits and may be difficult to identify with certainty (Laakmann et al., 2017; Stöhr,
133 2005), and were therefore omitted in our study. Specimens within genus *Henricia* Gray, 1840
134 were identified into two main groups, based on Madsen (1987), Ringvold and Stien (2001)
135 and Knott et al. (2018). Specimens within genus *Crossaster* Müller & Troschel, 1840 were
136 identified after Ringvold & Moum (Ringvold and Moum, 2020).

137

138 *Site description*

139 The Iceland plateau is a part of the Mid-Atlantic Ridge. Another ridge, the Greenland-
140 Scotland Ridge (GS-Ridge), is a submarine mountain chain, which extends east-westward,
141 from Greenland to Scotland, where Iceland and the Faroe Islands are but the highest peaks.
142 The GS-Ridge marks the boundary between the relatively cold waters of the deep-seas in the
143 Norwegian-Greenland Sea and the somewhat warmer and more saline waters of the North
144 Atlantic (Hansen, 1985; Jochumsen et al., 2016; Mackensen, 1987; Malmberg, 1985;
145 Malmberg and Kristmannson, 1992; Stefansson, 1962; Stefansson and Jonsdottir, 1974;
146 Westerberg, 1990).

147 Bottom water temperature north of GS-Ridge is constant, at around -1°C (Norwegian
148 Sea Deep Water, NSDW), at greater depths than 600 to 1200 m which is characteristic of the
149 Arctic Ocean and the Norwegian Sea. However, in the deep-waters south of the GS-Ridge,
150 below the 1000 m to 1500 m depth contours, the near bottom water temperature remains
151 around 2° to 3°C, which is characteristic of the North-Atlantic (Bainbridge, 1981; Burkov,
152 1993; Jochumsen et al., 2016; Maillard, 1986; Stefansson and Jonsdottir, 1974). The
153 transition zone at the northern parts of the GS-Ridge is more or less at the same depth as in
154 the Norwegian Sea (~600-900 m (Ringvold et al., 2014)), except that the pattern is somewhat
155 interrupted where the overflow takes place, especially in the Denmark strait and in the Faroe-

156 Shetland Through. Around the top and the upper slopes of the GS-Ridge the near bottom
157 water temperature is much more variable: it may reach over 8°C at the southern and western
158 sides of the GS-Ridge, but remains cooler on the northern slopes, around 2° or 3°C
159 (Jochumsen et al., 2016; Stefansson and Jonsdottir, 1974).

160
161 A persistent southward current of cold bottom waters flows through the deepest sills of
162 the GS-Ridge (Hansen and Østerhus, 2000). The deepest saddle depths are between the Faroe
163 Islands and Scotland (840 m), between Iceland and the Faeroes Islands (480 m), and in the
164 Denmark Strait, between Greenland and Iceland (620 m). The two latter overflow sites are
165 within the study area. The overflow currents at these three main sites, join a larger and
166 relatively cold bottom water current which runs from east to west, along the southern slope of
167 the GS-Ridge, below 600 m depth (Dickson et al., 1990; Dorn and Werner, 1993; Westerberg,
168 1990).

169 These variations in oceanographic properties north and south of the GS-Ridge, mark the well-
170 known boundaries of the benthic faunas of the Boreal and Arctic regions (Briggs, 1974, 1970;
171 Brix and Svavarsson, 2010; Einarsson, 1948; Ekman, 1953; Gudmundsson, 1998; Nesis,
172 1958).

173

174

175 *Ordination analysis*

176 To examine spatial patterns of asteroid assemblages, we carried out a nonmetric
177 multidimensional scaling (NMDS) ordination based on Jaccard dissimilarity
178 (presence/absence). Many of our samples contained only one species, which is problematic
179 because many species assemblages algorithms interpret shared absences as representing
180 similarity across sites (i.e., the “double-zero problem”, (Legendre and Legendre, 2012)).
181 However, the low occurrence and diversity of asteroids in our samples is not necessarily
182 representative of sites sampled and may be due to the low catchability of asteroids with the
183 methods used. To avoid stability and convergence problems, as with the single-species
184 samples in BIOFAR, in Ringvold & Andersen (2016), sampling stations were aggregated by
185 latitude, longitude, and depth with so-called K-means clustering, creating a grouping of
186 sampling stations that were as similar as possible with respect to location and depth, while
187 presenting a more representative community composition for each cluster. Of the original 654
188 sampling stations, we excluded 15 because they were collected with gear other than the

189 majority (Agassiz trawl, Detritus sledge, RP sledge, or Triangle dredge). We grouped the
190 remaining sampling stations into 135 spatial clusters, which we found empirically to be the
191 largest number of K-means clusters that would consistently contain no single species groups.
192 The number of stations per cluster ranged from 1 to 11 with a median of 4.7, and with 50% of
193 the clusters having between 3 and 6 stations. In visualizations, station clusters were delineated
194 by the convex hulls of the station positions (computed by the `chull` function in the R statistical
195 computing environment (R Core Team, 2019)). In the plane, a convex hull is the smallest
196 polygon that encloses a set of points. We calculated within-cluster distances with the `spDists`
197 function from the `sp` package (Bivand et al., 2013). Presence/ absence in the aggregated
198 species lists for each cluster was used in ordination analysis NMDS, using the `metaMDS`
199 function from the `vegan` package (Oksanen et al., 2013). Relationships between ordination
200 axes and environmental variables were investigated with the `envfit` function from the same
201 package. We also did a Detrended Correspondence Analysis (DCA) using `vegan`'s `decorana`
202 function and assessed the association between DCA and NMDS axis scores by their Kendall's
203 tau correlation.

204

205 The aggregated species lists for each cluster was used as the basis for the analysis. The
206 NMDS analyses were done using the `vegan` package (Oksanen et al., 2013) for the R
207 statistical computing environment (R Core Team, 2019). The polygons were delineated by
208 the convex hulls of station positions, using the base R `chull()` function. In the plane, a convex
209 hull is the smallest polygon that encloses a set of points. We also did a Detrended
210 Correspondence Analysis (DCA) using `vegan::decorana`, and assessed the association
211 between DCA and NMDS axis scores by their Kendall's tau correlation".

212

213 Appendix A and B were conducted in order to include station raw-data, and distribution maps
214 for species included in the ordination analysis, respectively. Additional comments on some
215 genera and species relevant to future studies has been included in Appendix C.

216

217 **Results**

218 A total of 12961 asteroid specimens were recorded during BIOICE, including juveniles. They
219 were collected from 654 sampling stations, comprising 63% of the total BIOICE sampling

220 stations (654 of 1031). After omitting juveniles, 8118 specimens were included in our study
221 **(Appendix A, Table 1)**. 64 asteroid species have been recorded from within Icelandic EEZ
222 (both original and literature data), including 20 families and 44 genera, of which 23 have been
223 added by our study **(Table 2)**.

224 The most abundant asteroids recorded from BIOICE were *Pontaster tenuispinus*,
225 *Bathybiaster vexillifer*, *Henricia pertusa* group, *Ctenodiscus crispatus* and *Hymenaster*
226 *pellucidus* (1693, 1298, 972, 779 and 671 specimens, respectively). This is also somewhat
227 coinciding with asteroid species as the number of K-means clusters where each species occurs
228 **(Fig. 2)**, showing e.g. *H. pertusa* group was widespread, and recorded in over 80 % of the
229 clusters. Seven asteroid orders were present in our study, with specimens within Paxillosida
230 and Notomyotida representing the most numerous, accounting for 55% total, or 31% and
231 24%, respectively. Within Notomyotida order, some specimens of *Pontaster tenuispinus* and
232 possibly *Cheiraster* sp. were difficult to separate, and this group was therefore named *P.*
233 *tenuispinus*/ *Cheiraster* sp. Specimens within Spinulosida order consists of only one genus,
234 *Henricia*, and accounts for 13% **(Fig. 3)**.

235

236

237 Asteroids were recorded at all depth intervals, while maximum species richness occurred at
238 two depth intervals, 100-200 m and 400-500 m (23-24 species each). However, all depth
239 intervals between 100 to 1000 m depth had relatively high species richness (~18 species),
240 before decreasing towards deeper waters **(Fig. 4)**. The three most frequently used gear types
241 were RP-sledge, detritus sledge and Agassiz trawl, and number of deployments decreased
242 from ~300 m down to 2700-2800 m depth **(Fig. 5)**.

243

244 Abundance-weighted mean depth for all species spans from ~100 to ~2300 m depth, with a
245 gap around ~900-1300 m depth **(Fig. 6)**. Four species with the shallowest abundance-
246 weighted mean depths, above 200 m, within genera *Asterias*, *Astropecten*, *Hippasteria* and
247 *Luidia*, are located mainly on the shelf, with abundance-weighted mean temperatures above 5
248 °C. Species with abundance-weighted mean depth below approximately 1300 m depth, and
249 with abundance-weighted mean temperatures above 2°C, are located to the south/ south west
250 of Iceland, and include *Benthopecten spinosissimus*, *Freyella elegans*, *F. microspina*,

251 *Hymenaster rex*, *Mediaster bairdi*, *Myxasteridae*, *Paragonaster subtilis*, *Pectinaster filholi*,
252 *Persephonaster patagiatus*, *Porcellanaster ceruleus*, *Pteraster* sp. *hystrix* and *Solaster*
253 *benedicti*. In total, 24 of the species in our study were recorded at an abundance-weighted
254 mean depth below 1300 m. *Hymenaster pellucidus* and *Porcellanaster ceruleus* were the
255 deepest recorded asteroids in Icelandic waters (2609 m and 2707 m depth, respectively).

256

257 The Venn diagram shows Iceland and neighboring Faroe Islands and Norway sharing 36
258 asteroid species (**Fig. 7**).

259

260 More comments on taxonomy for some species and genera, as well as distribution maps for
261 species included in the ordination analysis, can be found in **Appendix B and C**.

262

263 *Ordination analysis*

264 Cluster polygons of sampling stations are evenly distributed around Iceland (**Fig. 8**), with up
265 to 11 sampling stations per cluster. The clusters are also reasonably close together (**Fig. 9**),
266 and relative depth variation within clusters ranged between 0% and 65% with a mean of 17%.
267 The maximal horizontal distance within clusters varied between 0.3 and 155 km with mean of
268 44 km. The NMDS ordination (**Fig. 10**) converged from multiple starting points with an
269 acceptable stress (0.18), and typically converged fast (after 50-70 iterations).

270 An independent ordination with detrended correspondence analysis (DCA) was highly
271 consistent with the NMDS ordination (Kendall's τ correlation coefficient equal to -0.65 and -
272 0.61 for the first and second axis scores, respectively). The envfit analysis showed that five
273 continuous environmental variables (latitude, longitude, depth, temperature, and salinity) were
274 all strongly related to two first NMDS axis scores (all p-values = 0.001 with 999
275 permutations), and also illustrated by the environmental vectors in **Fig. 10**. The first
276 ordination axis scores had strongest correlation with depth ($r = 0.84$), whereas the second
277 ordination axis scores had strongest correlation with latitude ($r = 0.71$). NMDS1 captures
278 more of the depth and temperature gradient while NMDS2 seems to capture a NE - SW
279 spatial gradient as well as the salinity gradient. Deep water species *Benthopecten simplex* and
280 *Bathybiaster vexillifer* are placed to the far right, and shallow water species *Asterias rubens*
281 and *Crossaster papposus* to the left (**Fig. 11**). E.g. *Korethraster hispidus* is situated high up

282 along the NMDS2 axis, supporting other studies considering it «primarily N boreal» and
283 «Arctic» species (**Fig. 12**) (Anisimova and Cochrane, 2003; Clark and Downey, 1992).

284

285 **Discussion**

286 *Species richness*

287 We report on 64 asteroid species within Icelandic EEZ, of which include 23 species new to
288 the area (**Table 2**). From nearby Faroe Islands (BIOFAR programme) 50 asteroid species
289 have been recorded (Ringvold and Andersen, 2016), and from Norway 50 asteroid species
290 have been recorded (Brattegard, 2001; Ringvold et al., 2017), supporting the claim by
291 Einarsson (1948) that the Icelandic echinoderm fauna is relatively rich compared to
292 neighboring areas. In our study, *H. cylindrella*, originally counted as a species from the
293 Faroes, by Ringvold & Andersen (2016), has been placed within the *H. pertusa* group,
294 changing the Faroe asteroid species to 50, down from 51. The Venn diagram (**Fig. 7**) shows
295 the Icelandic- Norwegian- and Faroe asteroid fauna have many species in common (36).
296 Icelandic fauna has more species in common with both Norway and the Faroes (42 and 44,
297 respectively), than between Norway and the Faroes separately (39). 13 species were only
298 recorded from Iceland, including 12 located to the S/ SW of the GS-Ridge below ~1300 m
299 abundance-weighted mean depth (listed in the result section), as well as *Pteraster hastatus*
300 (also S of the GS-Ridge (Einarsson, 1948)). Even though about 50% of the species with
301 weighted depths below ~ 1300 m were recorded from Iceland only, many of the shelf species
302 (above ~2-300 m) were in common for Iceland and the Faroe Island (BIOICE and BIOFAR,
303 respectively).

304

305 Seven asteroid orders were recorded by both BIOICE and BIOFAR programmes, as also
306 shown in Fig. 3. In general, Paxillosida order is known to occupy an infaunal habitat, whereas
307 all others an epifaunal habitat (Blake, 1990). Paxillosida and Notomyotida orders contributed
308 the largest number of specimens within the BIOICE collection, respectively (31% and 24 %),
309 whereas Forcipulatida and Brisingida contributed the least number (6% and 1%). Somewhat
310 the same pattern was found in the BIOFAR data (Ringvold and Andersen, 2016). Why
311 specimens within the infaunal Paxillosida order dominates over the epifaunal groups from
312 these areas is uncertain, but may be due to factors such as favorable substrate or food

313 conditions. Valvatida was the most species-rich order in our data set (20 species), using
314 classification from www.marinespecies.org, followed by Velatida, Paxillosida and
315 Forcipulatida orders, with about 50% less species each (11-12 species). This is in contrast to a
316 global pattern, showing Paxillosida as the second most species-rich order (Mah and Blake,
317 2012). The reason for this is unknown, but could be due to e.g., sampling methods. One of the
318 most common species from both BIOICE and BIOFAR programmes was *Pontaster*
319 *tenuispinus*, within Notomyotida order. It is characterized as a subsurface deposit feeder
320 (Anisimova et al., 2010) and known to occur in muddy sediments where it consumes minute
321 organisms and detritus (Clark and Downey, 1992; Mortensen, 1927). *P. tenuispinus* and
322 *Ctenodiscus crispatus* also dominated the shelf and slope megafauna at Svalbard (Piepenburg
323 et al., 1996).

324

325 Einarsson (1948) claimed the Icelandic echinoderm fauna is closer to the European than the
326 American fauna. Dilman's recent study (2006), from the Reykjanes Ridge, to the S/ SW of
327 Iceland (but mainly outside Icelandic EEZ), supports this by showing that the number of
328 species in common with the eastern regions of the Atlantic is higher than those in common
329 with the western regions. Reykjanes Ridge is poorly separated (in terms of geomorphology)
330 from the southern Icelandic shelf, and 86% of the species recorded from Dilman's study (op.
331 cit.) were in common with our recorded species from within Icelandic EEZ.

332

333

334 *Ordination analysis*

335 Echinoderms are known for patchy distributions and aggregations (Howell et al., 2002). Such
336 distribution patterns can be reflected as patchiness and high between-sample variability at
337 certain scales, as was the case for our original data with low specimens and species counts at
338 some sampling stations. Using K-means clustering improved the convergence of the NMDS
339 ordination by avoiding the possibility of sampling stations with a single species not shared by
340 any others. Accordingly, information from almost all BIOICE sampling stations could be
341 used.

342 The first NMDS axis reflected measured environmental gradients more strongly than the
343 second axis. As such we can identify NMDS1 as reflecting the vertical gradient in depth and

344 temperature, while NMDS2 is reflecting the NE-SW spatial gradient as well as salinity.
345 Latitude can affect benthic biodiversity (Rex et al., 1993) in more or less the same way as for
346 other habitats and organism groups. In the BIOFAR data, latitudinal range was too short to
347 reflect climatic gradients (Ringvold and Andersen, 2016), whereas for our BIOICE data,
348 collected from a larger area, latitude showed the strongest correlation with NMDS2 axis ($r =$
349 0.71). Variable gear type reflected a significant gradient in the BIOFAR data ($p = 0.004$)
350 (Ringvold and Andersen, 2016). Unfortunately, in our data, this could not be investigated due
351 to sampling station clustering procedure used in this analysis, since there is no meaningful
352 way to average a categorical variable like gear type across clusters.

353 As in Ringvold & Andersen (2016) and Howell et al. (2002), our ordination biplot (**Fig. 10**)
354 also separates the predators at shallower depths (e.g., *Crossaster papposus*, *Asterias rubens*)
355 from deposit- or mollusc eaters deeper down (*Pontaster tenuispinus*, *Bathybiaster vexillifer*,
356 *Psilaster andromeda*).

357

358

359 *Environmental factors and distribution*

360 Temperature is an important abiotic factor regarding distribution of nekton (Astthorsson et al.,
361 2012) and benthos (Einarsson, 1948; Franz et al., 1981; Gage, 1986). Several studies also
362 relate water mass (defined by temperature and salinity) to distribution of macro-benthos
363 (Copley et al., 1996; Stewart et al., 1985). A characteristic feature north and south of the GS-
364 Ridge is the change of water mass temperature, and echinoderm fauna off the south and
365 southwest coasts of Iceland have been reported to be more varied than off the north and east
366 coasts (Einarsson, 1948). Our results show the most species rich region is S/ SW of the GS-
367 Ridge where 50 species have been recorded, of which 31 species were only recorded from
368 here. This contrasts with 31 species north of the GS-Ridge, of which 12 species were only
369 recorded from here. 19 species showed a distribution around all of Iceland (**Table 2**).

370

371 Although more asteroid species, and specimens, were recorded from the BIOICE programme
372 (Iceland) compared with the BIOFAR programme (Faroe Islands), the most species rich 100
373 m depth intervals were recorded from BIOFAR, with 33-34 species from 500-700 m depth,
374 coinciding with the upper continental slope and the water mass transition zone (Ringvold and

375 Andersen, 2016). In BIOICE, the two most species rich depth intervals, 100-200 and 400-500
376 m depth, contained 23 and 24 species. However, all depth intervals between about 100 to
377 1000 m depth had relatively high species richness (~18 species), before decreasing towards
378 deeper waters. A small increase of species also from 1600 to 1800 m. Fewer species below
379 1000 m found in the BIOICE study coincides somewhat with the shift in bottom water
380 temperature (north of the GS-Ridge constant around -1°C below about 600 m), but may also
381 reflect the bathymetric conditions, as the steep continental slope to the south rapidly descends
382 from ~2-500 m down to ~1300 m depth, making dredging impossible. The decrease in
383 species, found in both BIOFAR and BIOICE, are found below ~700 and 1000 m depth,
384 respectively. These depths are somewhat coinciding with asteroid faunal changes in distinct
385 zones reported from nearby Porcupine Seabight; ~700, 1100 and 1700 m (Howell et al.,
386 2002). However, the same study also reports the greatest diversities at 4700 m, which are
387 much deeper than for BIOFAR and BIOICE findings. Important faunal boundaries (found
388 globally) are also believed to occur around the shelf/ break slope 200-500 m and 1000-4700
389 m depth (Howell et al., 2002). Previous studies from the N Atlantic have shown that the water
390 mass transition zone (from 800-1000 m) represents the maximum species diversity, and a
391 major shift in benthic species composition (Howell et al., 2002). The species rich depth
392 interval at 400-500 m (BIOICE data) coincides somewhat with the water mass transition zone
393 and upper continental slope. In a study from Reykjanes Ridge, a multivariate analysis of
394 between-sample species similarity revealed a two-zone bathymetric faunal distribution with
395 the transition at 800 - 1 000 m, a faunal zonation probably influenced by the water mass
396 structure (Copley et al., 1996).

397

398 Effect of gear types, and numbers used, may also have influenced differences in
399 species numbers from Iceland and the Faroe Islands. During BIOICE, areas above 300 m
400 depth were covered with approximately 160 dredgings, mainly using detritus sledge and RP-
401 sledge, whereas during BIOFAR (with approximately half the number of dredgings (85)
402 above 300 m), heavy triangular sledge and detritus sledge were the main sampling gears used.
403 Fewer sledge runs below 300 m depth may account for fewer species caught at great depths.

404 Abiotic factors such as sediment and current may also be important regarding species
405 distribution. In a study from nearby Greenland, the general depth zonation of macrobenthos
406 provided evidence for the importance of a water column process (a pelago-benthic coupling).
407 However, for e.g. megafaunal echinoderms, community patterns on a 10-km scale, and

408 dispersion of organisms on a 100-m scale, were best explained by seafloor properties,
409 suggesting that processes related to pelago-benthic coupling are of less importance for this
410 community fraction and at these spatial scales (Piepenburg et al., 2001). Unfortunately, our
411 sediment data was unfortunately too incomplete to be included in the analysis.

412

413 Our results indicate that the Icelandic EEZ is relatively rich in asteroid species compared with
414 neighbouring areas. The BIOICE programme revealed several new species for the area,
415 extending their known distribution. Especially depth and latitude contributed in explaining
416 species distribution, but also longitude, salinity, variable gear type, and temperature.

417 One aim of the BIOICE programme was to procure knowledge of species composition of
418 benthic communities at a given time since of crucial interest to evaluate possible effects of
419 e.g. environmental changes. Other anthropogenic impact, as a possible oil and gas industry at
420 Iceland, may significantly reduce megafaunal abundance, as shown from the Faroe Islands
421 (Jones et al., 2006), and should thus be monitored.

422

423

424 **Acknowledgements**

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426 Christopher Mah is thanked for participating in identifying specimens within the *Brisingidae*
427 family, Ellý Renée Guðjohnsen for sorting the *Henricia* genus, Anna Dilman for fruitful
428 discussions, and Marcia Kyle for carefully proofreading the manuscript.

429

430 Jon Bogason (1923-2009) was a self-educated naturalist, working most of his career as a
431 research assistant at IMR, Iceland. His by-catch samplings were anecdotal, and not conducted
432 consistently over the years. Bogasons asteroid collection was donated to IINH, and is highly
433 appreciated for this study.

434

435

436 **Appendix A. Supplementary material. Table 1**

437 **Appendix B. Supplementary material.** Distribution maps

438 **Appendix C. Supplementary material.** Comments on taxonomy and distribution

439

440

441 **Credit author statement**

442 **Halldis Ringvold:** Conceptualization, administration, visualization, writing (original draft,
443 reviewing and editing), morphological identification, interpreting ordination analysis, diving
444 and photographing. **Gudmundur Gudmundsson:** Conceptualization, administration,
445 visualization, writing (original draft, reviewing and editing). **Tom Andersen:** Conducting and
446 interpreting ordination analysis, visualization and writing (original draft, reviewing and
447 editing).

448

449

(Anisimova and Cochrane, 2003; Mah, 2021; Mortensen, 1913)

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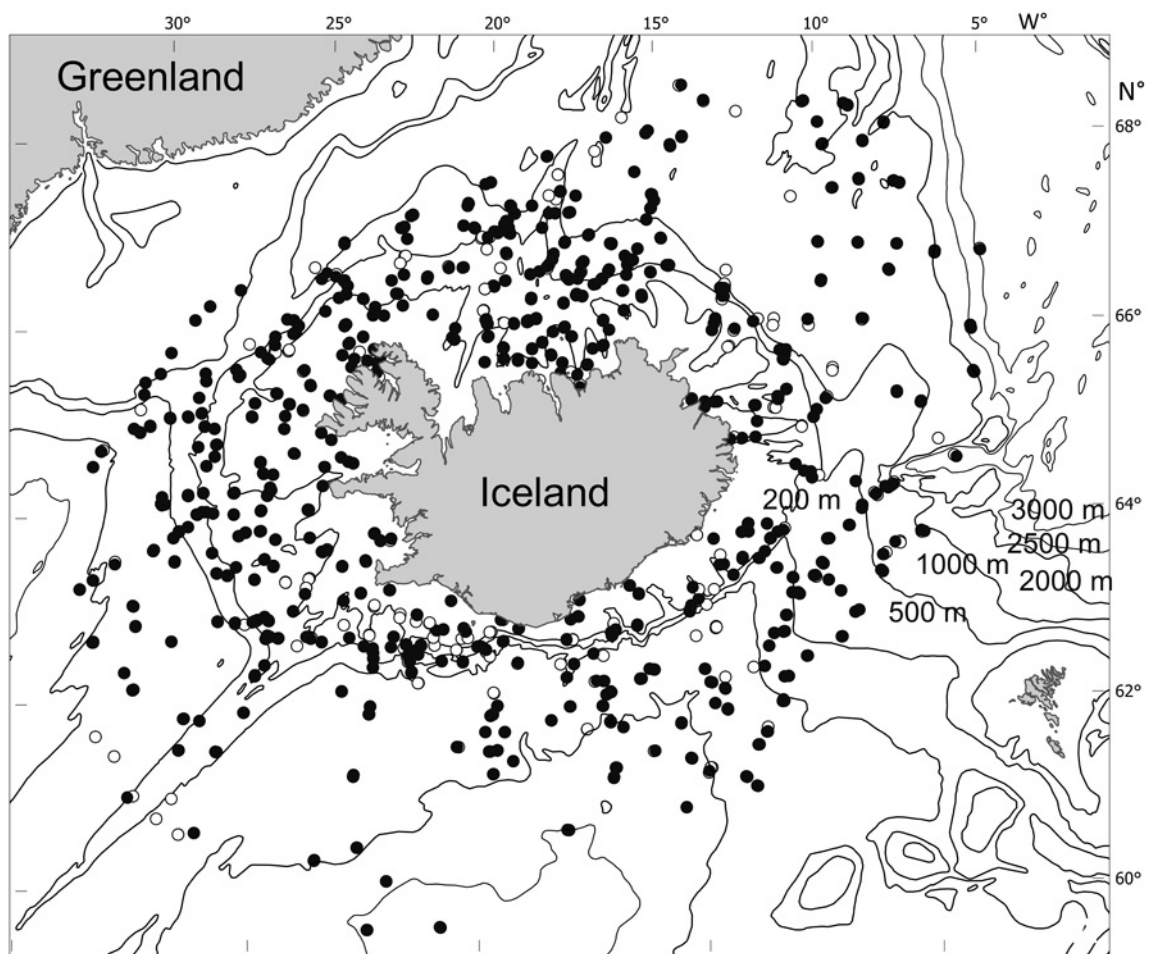
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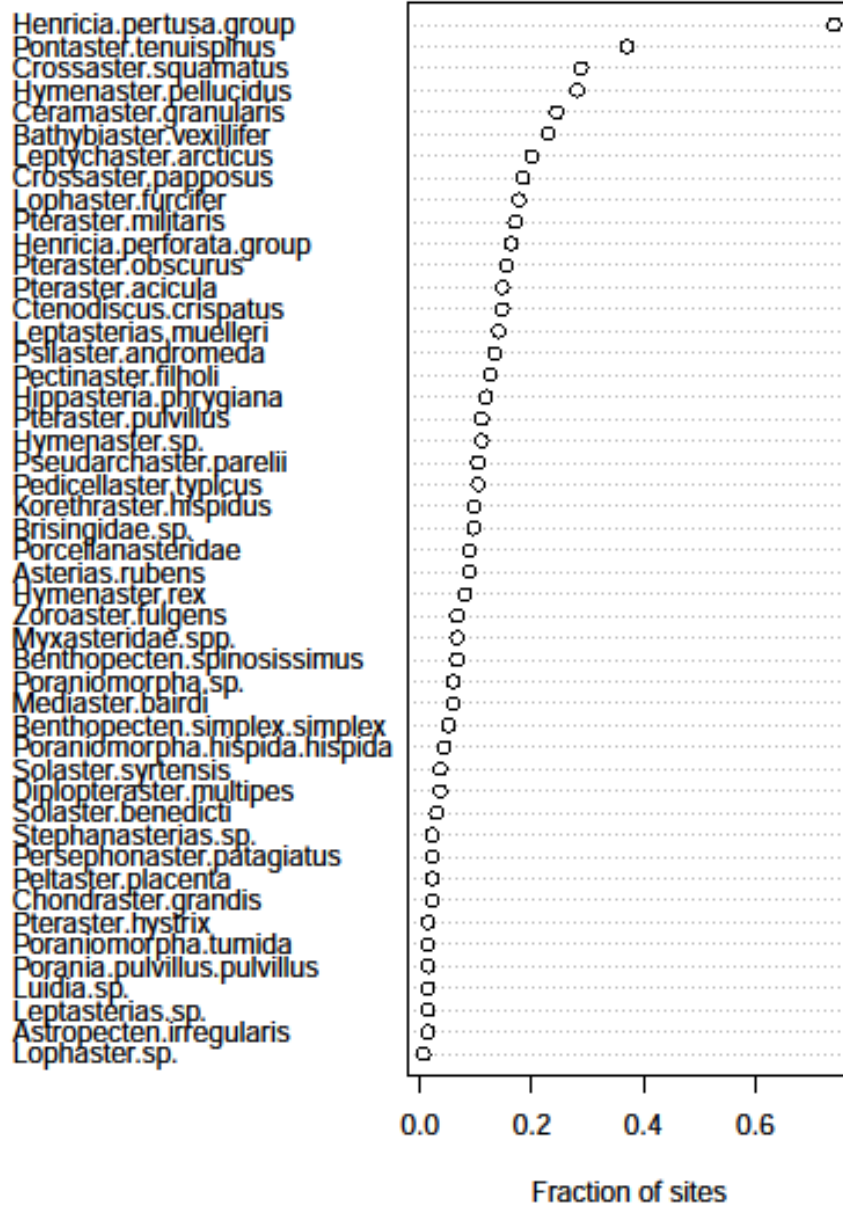
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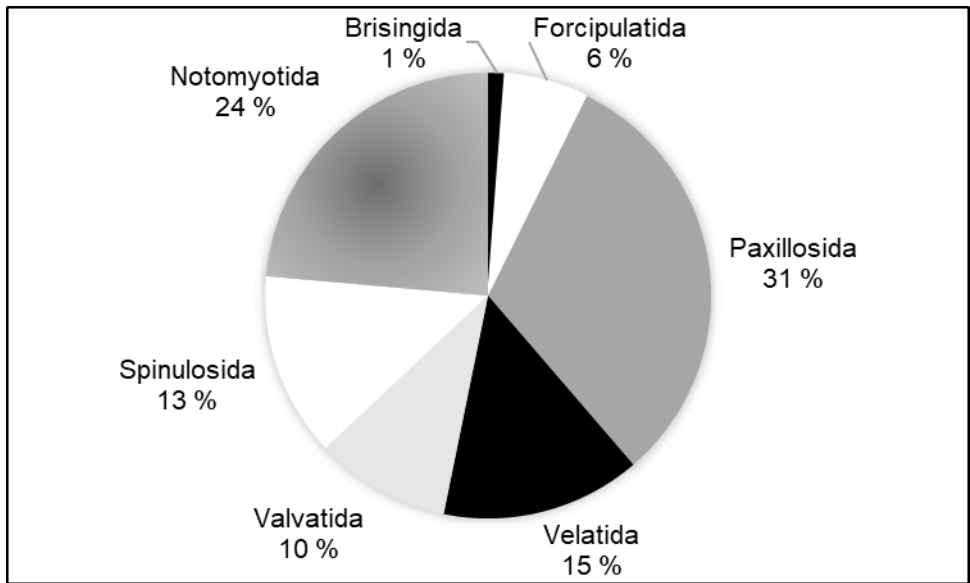


670 Fig. 1. Sampling stations of the BIOICE programme (Benthic Invertebrates of Icelandic
671 Waters). Filled circles indicate Asteroidea presence, and open circles, absence.



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677 Fig. 2. Frequency of occurrence of Asteroidea species identified in the BIOICE programme,
 678 as percentage of K-means clusters where each species occurs. All species, except the *Henricia*
 679 *pertusa* group, occur in less than 40% of the K-means clusters.



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682 Fig. 3. The percentage of Asteroidea orders found in the BIOICE material. The Paxillosida
 683 and Notomyotida orders contribute 55% of all specimens recorded (31% and 24%,
 684 respectively).

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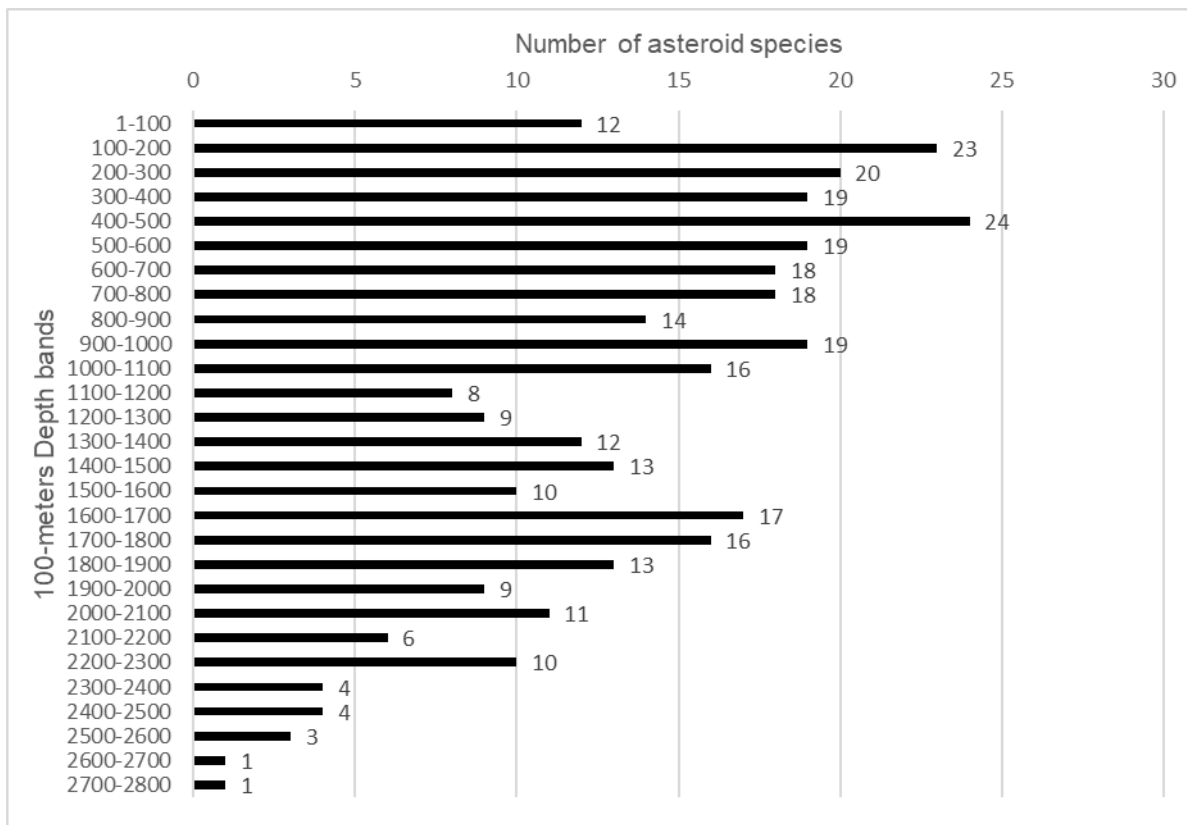
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705 Fig. 4. Asteroidea species from the BIOICE programme, recorded in 100-m depth intervals.

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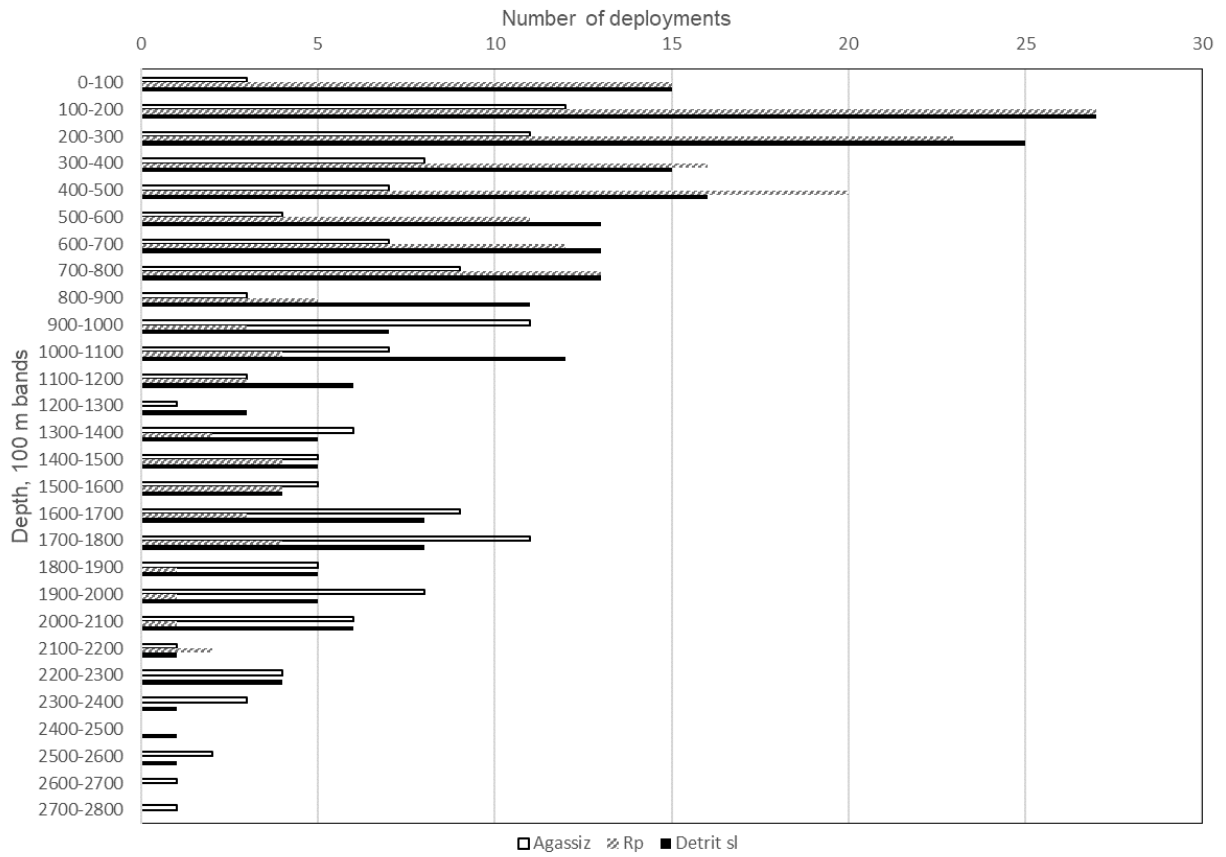
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722 Fig. 5. Number of deployments of the three most frequently used gear types (Detritus sledge
 723 (Ds), RP-sledge (Rp), and Agassiz trawl (Agassiz)) in the BIOICE programme, in 100-m
 724 depth intervals.

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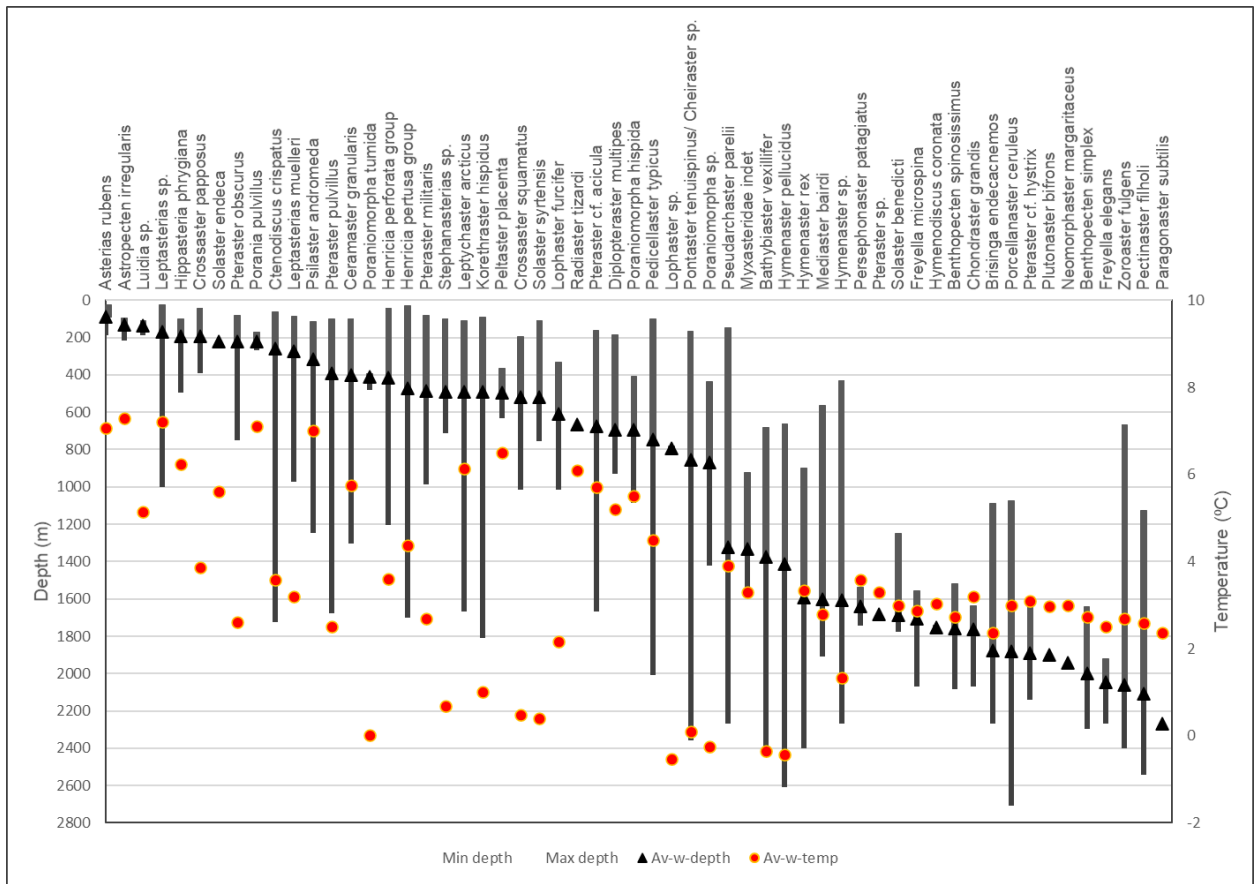
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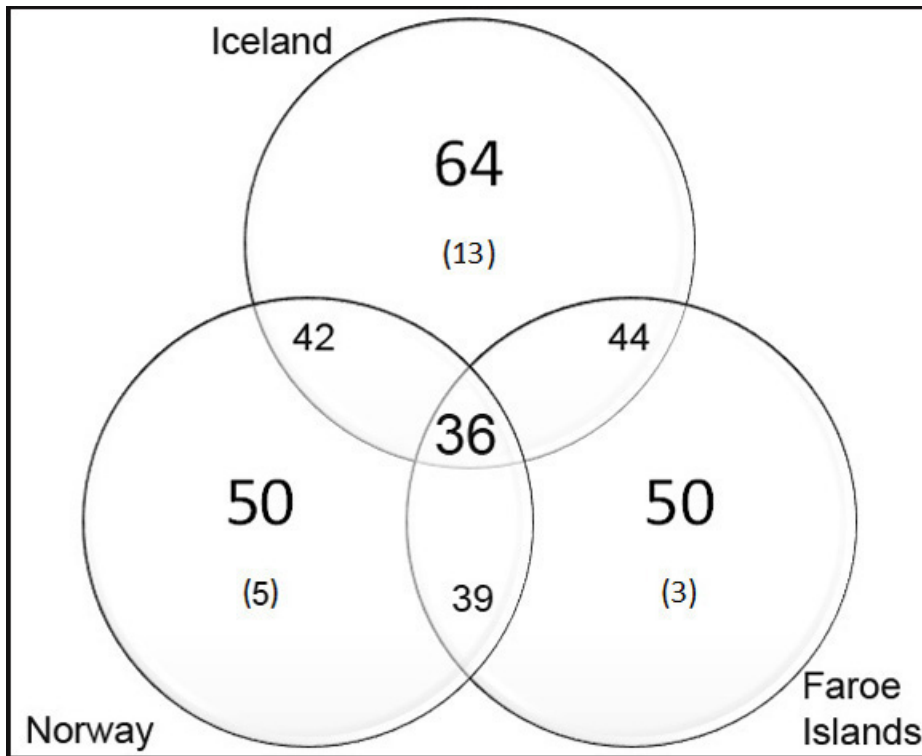
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Fig. 6. Distribution of Asteroidea species from Iceland in relation to depth and sea floor temperature recorded during the BIOICE programme. The vertical bars indicate the minimum and maximum depths. The black triangles indicate abundance-weighted mean depth, and the orange circles abundance-weighted mean sea floor temperatures. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



758

759 Fig. 7. Venn diagram comparing Asteroidea species recorded from Iceland, Norway and the
 760 Faroe Islands (from Table 2). A total of 64 species have been recorded from Iceland, and all
 761 three neighboring countries share 36 species. Iceland and the Faroe Islands have 44 species in
 762 common, whereas Iceland and Norway have 42 species in common. 13 species were only
 763 recorded from Iceland (compared with the two other countries).

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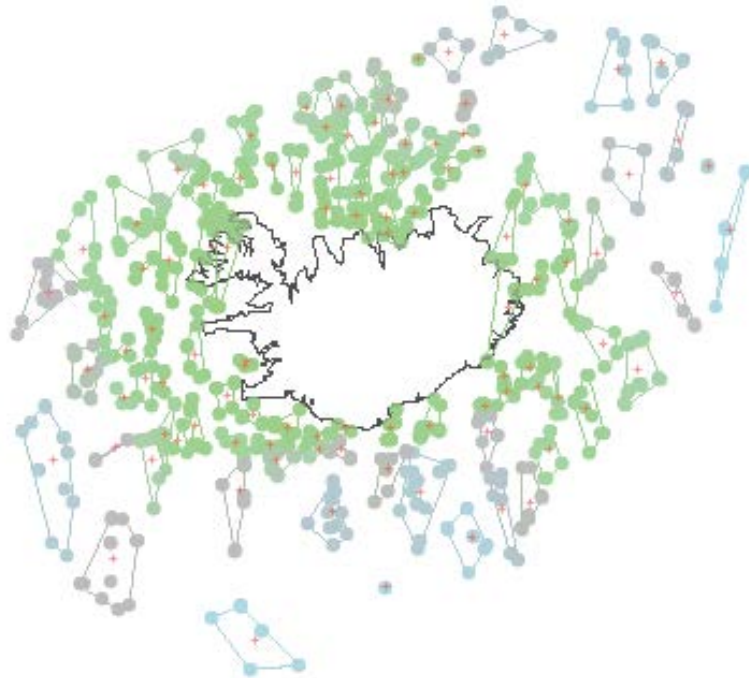
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776 Fig. 8. Polygons represent the convex hulls of K-means clusters of BIOICE sampling
777 stations aggregated by latitude, longitude, and depth. Points are individual sampling stations
778 color coded by depth from shallow (green) to deep (blue). Points are individual sampling
779 stations color coded by a continuous logarithmic depth scale from shallow (< 50 m; green) to
780 deep (>2000 m; blue).

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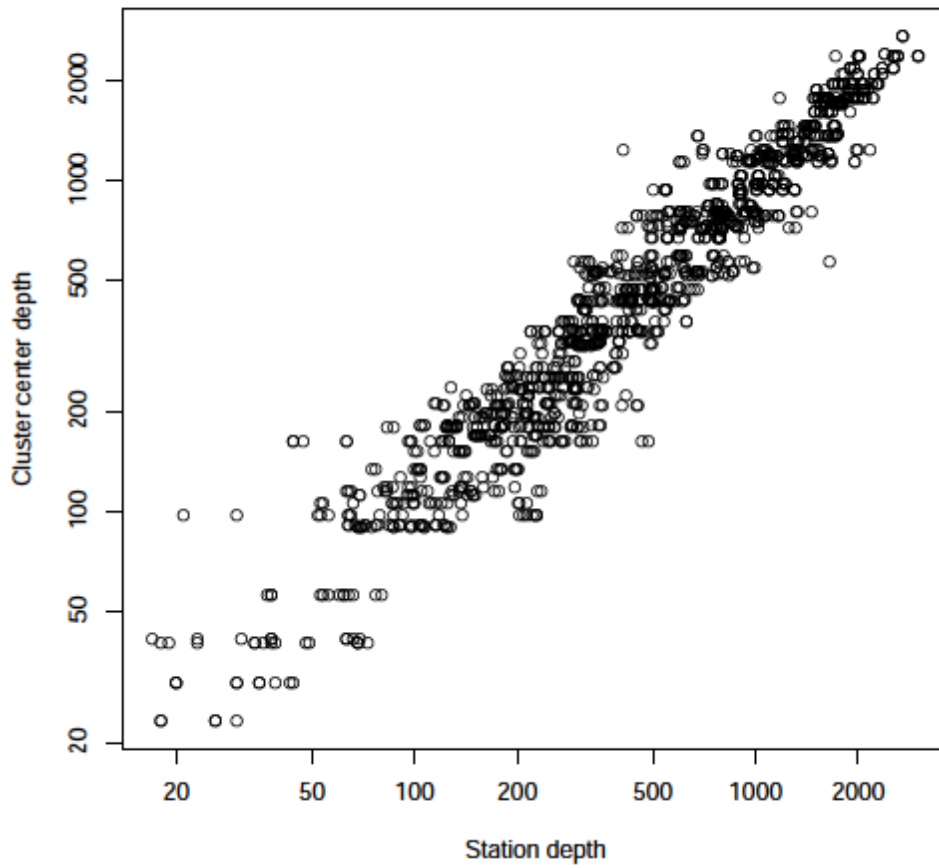
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789 Fig. 9. Sampling station depths versus cluster center depths, from the BIOICE material.
790 Clusters are reasonably close together. Sampling station depths appear to be closer to cluster
791 centers in deep waters due to the logarithmic scaling of the axes.

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809 Fig. 11. Depth distributions of species fitted by kernel density smoothing with bandwidth =
 810 400 m, and sorted by scores on the first NMDS axis. Dots represent the depths of individual
 811 clusters. Distributions are visualized as violin plots such that the probability of occurrence at a
 812 given depth proportional to the width of the violin polygon. E.g., *Asterias*
 813 *rubens* and *Astropecten irregularis* are shelf species, *Ctenodiscus crispatus* and *Zoroaster*

814 *fulgens* are species with a wide depth range, whereas species within the *Benthopecten* genera
 815 are deep-water species.

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819 Fig. 12. Latitudinal distributions of species fitted by kernel density smoothing with bandwidth
820 = 0.8 degrees latitude and sorted by scores on the second NMDS axis. Dots represent the
821 latitudes of individual clusters. Distributions are visualized as violin plots such that
822 the probability of occurrence at a given latitude is proportional to the width of the violin
823 polygon.

824

825 -----

826 Table 2. Asteroidea recorded from Iceland (x). Family and authority is given as well as
827 recordings prior to Einarsson (1948), in Einarsson (1948), unpublished notes from Jon
828 Bogason and BIOICE material. Species new for Iceland (from this study), in bold. Indications
829 on distribution preferences (1), north and south of the GS-Ridge, is also given: N=north,
830 S=south, A=all round Iceland (*=see column Comments). Recordings from nearby Faroe
831 Islands (Ringvold & Andersen, 2016) and Norway (Ringvold et al. 2017), are also given.

832

Family	Authority	Prior to Einarsson 1948 (in Einarsson 1948)	Einarsson (1948)	Others, see comments	Jon Boggason (private collection, now at EINI)	BORCE	N	S	A	Faroe Islands	Norway	Comments
Asteriidae												
<i>Asterias rubens</i>	Linnæus, 1758	x	x		x	x				x	x	
<i>Asterias panopla</i>	(Stenborg, 1879)	x		x*	x			1				*Iceland (Antonova & Cochran 2003)
<i>Lepasterias arctica</i>	(Madsch, 1885)			x*							x**	**Iceland (Mah 2020), ** <i>Lepasterias islandica</i> in Southam (2001)
<i>Lepasterias denticata</i>	(Lévesque, 1887)										x	
<i>Lepasterias smelleri</i>	(M. Sars, 1846)		x		x	x				1	x	
<i>Lepasterias grosslandica</i>	(Steenstrup, 1875)	x	x					1			x	
<i>Lepasterias leporiborea</i>	(Danielsen & Koren, 1882)				x*			1			x	*ID by Jon Boggason
<i>Lepasterias</i> sp.						x						
<i>Mesasterias glacialis</i>	(Linnæus, 1758)	x*									x	*Abiöns recording
<i>Stephanasterias albulus</i>	(Simpson, 1853)	x	x		x			1			x	
<i>Stephanasterias</i> sp.						x						
<i>Uvanasterias lincki</i>	(Müller & Troschel, 1842)										x	
Asteriidae												
<i>Tremaster mirabilis</i>	Verrill, 1880			x*	x				1		x	*SE Iceland (Clark & Downey 1992)
Astropectinidae												
<i>Astropecten irregularis</i>	(Pennant, 1777)	x*	x		x	x			1		x	* <i>Asterias arcticus</i> , in Raber (1829)
<i>Bathaster scylliter</i>	(W. Thomson, 1873)	x	x		x	x				1	x	
<i>Lepidaster arcticus</i>	(M. Sars, 1850)	x	x		x	x			1		x	
<i>Plataster bifrons</i>	(W. Thomson, 1873)				x	x					x	
<i>Perophomaster patungatus</i>	(Sladen, 1889)			x*		x			1			*South of Iceland (Clark & Downey 1992)
<i>Pilaster andromeda</i>	(Müller & Troschel, 1842)	x	x		x	x				1	x	
Benthoplectinidae												
<i>Benthopecten simplex</i>	(Perrier, 1881)					x			1		x	
<i>Benthopecten apiculatus</i>	(Sladen, 1889)					x			1		x	
<i>Panaster tenuispinus</i>	(Dibben & Koren, 1846)	x	x		x	x				1	x	
<i>Chiraster</i> sp.												
<i>Pectinaster filholii</i>	Perrier, 1885			x*		x			1			*South of Iceland (Clark & Downey 1992)
Beringiidae												
<i>Beringia endocentron</i>	(Johnson, 1856)				x	x			1		x	
<i>Freyella elegans</i>	(Verrill, 1884)					x					x	
<i>Freyella microspina</i>	Verrill, 1894					x			1		x	
<i>Hymenodiscus coronatus</i>	(Sars G.O., 1872)			x*		x					x	*Reykjanes Ridge (Dilman 2006)
<i>Novodinia pandina</i>	(Sladen, 1889)	x	x		x				1		x	
Ctenodiscidae												
<i>Ctenodiscus crispatus</i>	(Retzius, 1805)	x	x		x	x			1		x	
Echinasteridae												
<i>Henricia perforata</i> group					x	x					1	x
<i>Henricia pertusa</i> group		x	x		x	x					1	x
Goniasteridae												
<i>Goniaster granulatus</i>	(O. F. Müller, 1776)	x	x		x	x				1	x	
<i>Hippasteria phryganea</i>	(Parellus, 1768)		x		x	x				1	x	
<i>Medaster bairdi</i>	(Verrill, 1882)				x	x				1	x	
<i>Paragonaster subulii</i>	(Perrier, 1881)				x	x				1	x	
<i>Pleuaster placens</i>	(Müller & Troschel, 1842)			x*	x	x				1	x	*Iceland (Clark & Downey 1992)
<i>Pleuaster dentatus</i>	(Perrier, 1884)										x	
Korellasteridae												
<i>Korellaster hispidus</i>	W. Thomson, 1873		x		x	x			1		x	
Laeliidae												
<i>Laelia</i> sp.						x						
<i>Laelia elliana</i>	(Phillips, 1837)				x						x	
<i>Laelia sarri</i>	(Dibben & Koren, 1844)										x	
Myasteridae												
cf. <i>Myaster sol</i>	Perrier, 1885				x	x				1		
Nesomphasteridae												
<i>Nesomphaster margaritaceus</i>	(Perrier, 1882)					x					x	
Odontasteridae												
<i>Odontaster</i> sp.	Verrill, 1880										x	
Pediculariidae												
<i>Pedicularis rufus</i>	M. Sars, 1861	x	x			x				1	x	
Poramidae												
<i>Chondaster grandis</i>	(Verrill, 1878)					x			1		x	
<i>Caloptilia borealis</i>	(Stöckh & Breckner, 1911)				x*					1	x	*ID by Jon Boggason
<i>Porania pulvillus</i>	(O. F. Müller, 1776)	x	x		x	x				1	x	
<i>Porania nitens</i>	Dom, 1936										x	
<i>Poraniomphala badeni</i>	(Mortensen, 1932)				x				1		x	
<i>Poraniomphala hispidus</i>	(M. Sars, 1872)		x		x	x				1	x	
<i>Poraniomphala zamuda</i>	(Stenborg, 1878)		x		x	x				1	x	
<i>Pylaster willii</i>	(Danielsen & Koren, 1881)			x*	x			1			x	*deep sea, Iceland (Mortensen 1927)
Porcellasteridae												
<i>Porcellaster veridicus</i>	W. Thomson, 1877					x				1		
Pseudochasteridae												
<i>Pseudochaster gracilis</i>	(Sladen, 1889)										x	
<i>Pseudochaster patrellii</i>	(Dibben & Koren, 1846)	x	x		x	x				1	x	
Pterasteridae												
<i>Diplopteraster multipes</i>	(M. Sars, 1866)				x	x				1	x	
<i>Hymenaster pallidus</i>	W. Thomson, 1873	x	x		x	x				1	x	
<i>Hymenaster rex</i>	Perrier, 1885					x				1		
<i>Pteraster cf. aculeatus</i>	(Downey, 1970)					x					x	
<i>Pteraster hians</i>	Mortensen, 1913	x		x*						1		*belongs within warm area of N Atlantic (Mortensen 1913)
<i>Pteraster cf. laticornis</i>	Harvey, 1989					x				1		
<i>Pteraster milligani</i>	(O. F. Müller, 1776)	x	x		x	x				1	x	
<i>Pteraster cf. obtusus</i>	(H.L. Clark, 1908)	x*		x*								*Abiöns recording, <i>P. obtusus</i> is described from Japan (Clark 1908)
<i>Pteraster obtusatus</i>	(Perrier, 1891)B	x	x		x	x			1		x	
<i>Pteraster pulvillus</i>	M. Sars, 1861	x	x		x	x				1	x	
Radiasteridae												
<i>Radiaster bairdi</i>	(Sladen, 1882)				x	x				1	x	
Solasteridae												
<i>Crossaster papposus</i>	(Linnæus, 1766)	x	x		x	x				1	x	
<i>Crossaster agannurus</i>	(Döderlein, 1900)		x		x	x			1		x	
<i>Lophaster furcifer</i>	(Dibben & Koren, 1846)		x		x	x				1	x	
<i>Solaster obliquicostus</i>	Verrill, 1885	x	x		x					1	x	
<i>Solaster benedicti</i>	Verrill, 1894					x				1		
<i>Solaster endeus</i>	(Linnæus, 1771)	x	x		x	x				1	x	
<i>Solaster glacialis</i>	(Danielsen & Koren, 1881)										x	
<i>Solaster noronhai</i>	Verrill, 1894		x		x	x				1	x	
Sichasteridae												
<i>Sichasterella rosea</i>	Perrier, 1885										x	
Zonasteridae												
<i>Zonasteris</i> sp.											x*	*Close to Svalbard
<i>Zonasteris fulgens</i>	W. Thomson, 1873			x*	x	x					x	*Iceland (Mortensen 1927)
SUM								12	31	19		