

1 Recruitment of benthic invertebrates in high Arctic fjords:
2 relation to temperature, depth, and season

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19 Running head: Recruitment in Arctic fjords

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23 **Abstract**

24 In the high Arctic, recruitment of hard-bottom benthic organisms has been studied at single
25 locations, but little is known about how it varies spatially or temporally, or how it is influenced
26 by abiotic factors. In this study, settlement plates were simultaneously deployed at five locations
27 in three Svalbard (Norway) fjords at depths ranging from 7 – 215 m. Recruitment was
28 significantly different among fjords and among locations within a fjord. Recruits at each site co-
29 occurred randomly even though interspecific overgrowth was observed. This finding provides
30 further evidence that there is not necessarily a relationship between non-random co-occurrence
31 and interspecific competition, such as is traditionally assumed for other isolated, island-like
32 habitats. We found significantly lower recruitment in an Arctic-influenced fjord than in more
33 Atlantic-influenced fjords. The abundance and richness of recruits was significantly lower in
34 fall-winter than in spring-summer, but the spirorbid *Circeis armoricana* recruited in high
35 abundance in fall-winter. Both the abundance and taxonomic richness of recruits declined
36 exponentially with depth, with the hydroid *Stegopoma plicatile* dominating at 215 m in an
37 Atlantic-influenced fjord. The most abundant recruiting taxa (*C. armoricana*, *Semibalanus*
38 *balanoides*, *Harmeria scutulata*, *Celleporella hyalina*) can be described as pioneer (early-
39 succession) species. Crustose coralline algae, a slow-growing superior competitor, also recruited
40 at one location. Recruitment in Svalbard is highly variable, both spatially and temporally, and
41 our results show the influence of local factors such as adult species composition.

42

43 **Keywords:** Hard-bottom, fouling fauna, assembly rules, settlement, competition, Svalbard

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46 **Introduction**

47 Community assembly in marine hard-bottom habitats integrates larval dispersal,
48 recruitment, competition, facilitation, predation, and succession (Meyer 2016). Recruitment is
49 important in this process, because the species that recruit first to a substratum can facilitate or
50 inhibit the establishment of other species (Sutherland 1974; Osman and Whitlatch 1995; Walters
51 et al. 1997).

52 Hard-bottom habitats in the marine environment are often isolated “islands in a sea of
53 mud,” (Young 2009) including natural (Oschmann 1990; Schulz et al. 2010), anthropogenic
54 (Taylor et al. 2014), and biogenic structures (Gutt and Schickan 1998; Beaulieu 2001; Hétérier et
55 al. 2008). Many marine island-like habitats have the same faunal distribution patterns as
56 observed for terrestrial islands, though the mechanisms are not necessarily the same (Abele and
57 Patton 1976; Schoener and Schoener 1981; Huntington and Lirman 2012; Meyer et al. 2016).
58 Whereas community composition on terrestrial islands is related to island size, distance to a
59 mainland, (MacArthur and Wilson 1967) and biotic interactions (Diamond 1975), these
60 processes have rarely been addressed for habitat islands in the marine environment (but see
61 Benedetti-Cecchi et al., 2003).

62 Pairs of species often co-occur non-randomly on islands and island-like hard substrata
63 (Diamond 1975). Non-random co-occurrence refers to pairs of species being found together less
64 (negative non-random co-occurrence) or more (positive non-random co-occurrence) often than
65 expected by chance (Gotelli and McCabe 2002; Meyer 2016). Negative non-random co-
66 occurrence patterns have been attributed to interspecific competition (Diamond 1975), though
67 this interpretation has been criticized for its lack of supporting evidence (Connor and Simberloff
68 1979). Positive non-random co-occurrence can be the result of epibiotic relationships (Meyer et

69 al. 2016). Encrusting marine fauna may have negative non-random co-occurrence but in the
70 absence of interspecific overgrowth competition (Meyer et al. 2016), indicating that there is not
71 necessarily a relationship between these two concepts for marine island-like habitats. Non-
72 random co-occurrence has been studied in mature communities, but not among first recruits to a
73 substratum, where there may be more available space and less interspecific competition.

74 The Arctic provides a good opportunity to study non-random co-occurrence where there
75 is likely to be available free space and low interspecific competition among recruits, because
76 recruitment there is very slow. At an isolated hard-bottom habitat in the Beaufort Sea (Konar and
77 Iken 2005; Wilce and Dunton 2014), 10% of available space on experimentally-cleared boulders
78 had been colonized after 7 years (Konar 2007, 2013). More than 10 years were required for
79 community composition on cleared patches to resemble control sites on Svalbard (Norway) reefs
80 (Beuchel and Gulliksen 2008). The possible reasons for this include low dispersal of
81 propagules/larvae, barriers to settlement, slow growth, and physical disturbance.

82 Recruitment has been studied at single locations in Svalbard, and shown much lower
83 recruitment but comparable species richness of recruits compared to temperate latitudes (Barnes
84 and Kukliński 2005; Schmiing 2005; Kukliński et al. 2013). The first colonists on isolated hard
85 substrata (at temperate latitudes) are typically fast-growing poor competitors, such as acorn
86 barnacles and spirorbid polychaetes (Dean and Hurd 1980; Chalmer 1982). Later in succession,
87 slow-growing superior competitors dominate (Perkol-Finkel et al. 2005, 2006; Edwards and
88 Stachowicz 2010). We hypothesize that the recruits to our experimental substrata will be
89 primarily fast-growing, poor competitors.

90 In this study, we seek to understand how recruitment on isolated hard substrata in
91 Svalbard fjords is influenced by depth, season, and biotic interactions, and how it differs between

92 Atlantic- and Arctic-influenced fjords. We present simultaneous data from multiple locations in
93 three fjords (Fig. 1): the Atlantic-influenced fjords (Svendsen et al. 2002) Isfjorden and
94 Kongsfjorden, where warm, saline water has facilitated colonization of Atlantic fauna, including
95 boreal fish and mussels in recent years (Berge et al. 2005, 2015b; Renaud et al. 2012), and a
96 “true” Arctic fjord (Wallace et al. 2010; Berge et al. 2014), Rijpfjorden. In addition to abiotic
97 factors, we consider the life-history strategies of each recruiting species. We also test for non-
98 random co-occurrence among recruiting species, to understand if and how these artificial hard
99 substrata resemble other island-like habitats.

100

101 **Methods**

102 *Deployment of settlement plates*

103 Settlement plates were deployed in September-October 2014 from R/V *Helmer Hanssen*.
104 Four frames of settlement plates were deployed at each of five locations: three shallow locations
105 (Longyearbyen, Ny-Ålesund, Kvadehuken) reached by SCUBA divers, and at 2 depths on
106 oceanographic moorings in Kongsfjorden and Rijpfjorden (Fig. 1). At Longyearbyen (7 m, in
107 Isfjorden) and Ny-Ålesund (7 m, in Kongsfjorden), plates were affixed to underwater structures
108 associated with piers. At Kvadehuken (15 m, in Kongsfjorden), a hard-bottom site used for
109 diving and long-term benthic studies (Beuchel and Gulliksen 2008; Kortsch et al. 2012), frames
110 were bolted directly to the bedrock. Frames were affixed to the moorings in Kongsfjorden and
111 Rijpfjorden in pairs, two close to the seafloor (~10 m above the seafloor, corresponding to ~200
112 m depth) and two at 30 m depth. Moorings were recovered approximately one year after
113 deployment. Settlement plates (15 x 15 cm) were clear acrylic (0.32 cm thick) roughened with
114 sandpaper. Plates were mounted in groups of four on PVC frames (75 x 15 cm) and attached with

115 zip ties (Fig. 2). Settlement plates at all locations were oriented vertically in order to prevent
116 recruits from being smothered by sedimentation.

117 Two frames (8 settlement plates) were recovered (showing fall-winter recruitment) from
118 each shallow location in January 2015, and new frames (two at each site) were deployed to
119 capture spring-summer recruitment. The other two frames at each shallow location were left
120 undisturbed. The January 2015 dive at Kvadehuken had to be aborted because of logistical
121 difficulty, so no fall-winter plates could be recovered nor spring-summer plates deployed at this
122 location. One frame of plates was also lost. Therefore, three frames (12 settlement plates) were
123 recovered from Kvadehuken after a year-long deployment (Supplementary Material). All
124 remaining settlement plates from moorings and shallow locations were recovered in September
125 2015 during a cruise aboard R/V *Helmer Hanssen*.

126

127 *Water temperature*

128 TidbiT v2 temperature loggers (Onset, USA) were attached to one frame of settlement
129 plates at each shallow location. Water temperature was recorded every 15 minutes during the
130 year-long deployment. The temperature logger was lost along with its frame at Kvadehuken (15
131 m), so data from a logger (SBE 56, Sea-Bird Electronics, USA) at 13 m on the Kongsfjorden
132 mooring were used to approximate water temperature at this site. Water temperature at the
133 mooring locations was recorded every 12 minutes during the year-long deployment using
134 temperature loggers (SBE 56) deployed near the settlement plates: at 33 m and 207 m in
135 Kongsfjorden, and at 32 m and 215 m in Rijpfjorden.

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139 *Analysis of settlement plates*

140 Immediately following recovery, all plates were held in cold (~4°C) seawater aboard R/V
141 *Helmer Hanssen*. Settlement plates were removed from their frames and examined under a
142 dissecting microscope within 5 days of recovery. Only the side of the plate most exposed to the
143 water column was examined. Sessile fauna on each plate were counted and identified by
144 referencing pertinent literature (Kluge 1975; Klekowski 1995) and consulting experts (see
145 Acknowledgments). Eight of 48 observed taxa could not be identified and were labelled as
146 morphotypes. For especially abundant taxa (i.e. *Semibalanus balanoides*, *Circeis armoricana*),
147 settlement plates were sub-divided into 36 equal units, six of which were randomly sub-sampled
148 for counting. The number of individuals was then extrapolated to the full size of the plate. Deep
149 (215 m) settlement plates on the Kongsfjorden mooring were covered by the hydroid *Stegopoma*
150 *plicatile*, including numerous stolons and upright, branched forms. It was impossible to
151 determine the number of recruiting individuals of this species, so the number of upright forms
152 was used as an indirect proxy for recruitment.

153

154 *Statistical analysis of data*

155 A test for significant differences between plates on different frames showed no blocking
156 effect (analysis of similarity, $p > 0.05$ for each season and location), so plates were treated as true
157 replicates for statistical analysis. Univariate t-tests were used to test for significant differences in
158 the abundance and richness of recruits between locations and seasons and were conducted in
159 SPSS (International Business Machines, USA), using a Levene's test to establish
160 homoscedasticity. Mann-Whitney U-tests (M-W) were used for non-parametric cases.

161 Multivariate statistics including analysis of similarity (ANOSIM) and multi-dimensional scaling
162 (MDS) were used to test for significant differences in community composition of recruits among
163 locations and depths and were conducted in Primer v6 (Clarke and Gorley 2006) following a
164 $\log(x+1)$ transformation. We tested for non-random co-occurrence among plates at each location
165 in EcoSim (Entsminger 2014) using a fixed-fixed null model and the C-score index (Gotelli
166 2000).

167

168 **Results**

169 *Water temperature*

170 Water temperatures at each location are depicted in Fig. 3. Temperatures at the shallow (7
171 – 15 m) locations varied between -2 and 9°C over the year-long deployment. Temperatures were
172 largely similar between Longyearbyen and Ny-Ålesund, but slightly colder at Kvadehuken
173 between May and July 2015 (Fig. 3A). Water temperature at the Kongsfjorden mooring was
174 coldest (-0.8°C) in February 2015 and warmed to a maximum of 6°C at 33 m and 3°C at 207 m
175 in August 2015 (Fig. 3B). In Rijpfjorden, water was much colder, being 0°C at 32 m and -1.5°C
176 at 215 m in October 2014 (Fig. 3C). Temperatures at both depths remained between -2 and -1°C
177 from February to June 2015 (Fig. 3C).

178

179 *Species distribution patterns*

180 A total of 48 species and morphotypes recruited to the settlement plates in this study,
181 almost half of which were bryozoans (22 of 48). The most abundant species were the alga
182 *Dermatocelis laminariae*, the spirorbid polychaete *Circeis armoricana*, and the acorn barnacle

183 *Semibalanus balanoides*. Raw recruitment data and plate deployment metadata are reported in
184 the supplementary material.

185 Species distribution patterns on settlement plates were not significantly different from the
186 distribution generated by a fixed-fixed null model ($C > e$ and $C < e$, $p > 0.05$). Species on
187 settlement plates co-occurred randomly. Nevertheless, overgrowth competition was observed on
188 some spring-summer and year-long settlement plates, with the barnacle *Semibalanus balanoides*
189 and the spirorbid *Circeis armoricana* being overgrown by bryozoans (Fig. 4).

190

191 *Seasonal patterns in recruitment*

192 During fall-winter, there was significantly higher recruitment per plate at Ny-Ålesund
193 than at Longyearbyen (t-test, $t = 4.33$, $p = 0.001$), but the richness of recruits at each location was
194 not significantly different (t-test, $t = 0.75$, $p = 0.46$) (Fig. 5). *Circeis armoricana* recruited in
195 high density at each location, with up to 862 individuals plate⁻¹. The bryozoans *Celleporella*
196 *hyalina* and *Callopora craticula* were also common on the fall-winter plates. Differences in the
197 abundance and richness of recruits at Longyearbyen and Ny-Ålesund were not significantly
198 different for spring-summer or year-long plates (Fig. 5).

199 Significantly higher recruitment densities were observed at both Longyearbyen and Ny-
200 Ålesund for spring-summer than fall-winter (Longyearbyen, M-W, $U = 0.00$, $p = 0.001$; Ny-
201 Ålesund, M-W, $U = 0.00$, $p = 0.001$) (Fig. 5). The number of taxa per plate was also significantly
202 greater in the spring-summer than fall-winter at both locations (Longyearbyen, t-test, $t = 13.32$, p
203 < 0.001 ; Ny-Ålesund, t-test, $t = 12.28$, $p < 0.001$) (Fig. 5).

204 At Ny-Ålesund, there was a significantly lower number of recruits on plates deployed all
205 year than on plates deployed in the spring-summer (t-test, $t = 2.90$, $p = 0.01$), but there was a

206 significantly higher number of taxa (t-test, $t = 3.60$, $p = 0.003$) (Fig. 5). Differences between
207 numbers of recruits and taxa in spring-summer and all-year deployments were not significant at
208 Longyearbyen (t-test, N, $t = 0.98$, $p = 0.34$; S, $t = 1.47$, $p = 0.16$) (Fig. 5). For both locations, *C.*
209 *armoricana* and *S. balanoides* recruited in high numbers. Dense macroalgae, including
210 *Desmarestia aculeata* (spring-summer, 285 ± 44.9 ; year, 659 ± 74.7 plate⁻¹, mean \pm standard
211 error), *Dermatocelis laminariae* (spring-summer, 2759 ± 343 ; year, 1366 ± 203 plate⁻¹), and
212 *Chorda* sp. (spring-summer, 134 ± 20.4 ; year, 85.5 ± 17.9 plate⁻¹), recruited to spring-summer
213 and year-long settlement plates at Ny-Ålesund. No algae recruited at Longyearbyen. Only year-
214 long plates could be retrieved from Kvadehuken, but the abundance and richness of recruits at
215 this site were significantly lower than at Longyearbyen (S, t-test, $t = 4.67$, $p < 0.001$; N, t-test, $t =$
216 8.72 , $p < 0.001$) and Ny-Ålesund (S, t-test, $t = 6.15$, $p < 0.001$; N, t-test, $t = 8.56$, $p < 0.001$).

217 There were significant multivariate differences among the assemblages of recruits in
218 different seasons (fall-winter, spring-summer, and year) and locations (Longyearbyen and Ny-
219 Ålesund) (two-way crossed ANOSIM; deployment period, $R = 0.837$, $p = 0.001$; location, $R =$
220 0.905 , $p = 0.001$; Fig. 6). Pairwise differences between the deployment periods were significant
221 for fall-winter and spring-summer ($R = 1$, $p = 0.001$), fall-winter and year ($R = 1$, $p = 0.001$);
222 pairwise differences between spring-summer and year-long recruitment were significant but not
223 as extreme, as indicated by the lower R value ($R = 0.521$, $p = 0.001$) and their relative locations
224 in the MDS plot (Fig. 6).

225 Only four species recruited to settlement plates in both fall-winter and spring-summer:
226 the spirorbid *C. armoricana*, the bivalve *Hiatella arctica*, and bryozoans *C. hyalina* and *Crisiella*
227 *producta*. The bryozoan *C. craticula* was abundant on fall-winter plates (Longyearbyen, $5.00 \pm$

228 1.15 plate⁻¹; Ny-Ålesund, 47.8 ± 13.3 plate⁻¹) but not observed on spring-summer or year-long
229 settlement plates. No algal taxa recruited in the fall-winter.

230

231 *Differences among shallow locations*

232 For settlement plates deployed at shallow sites for the entire year (Longyearbyen, Ny-
233 Ålesund, Kvadehuken), there was a significant difference among the assemblages at different
234 locations (ANOSIM, $R = 1$, $p = 0.001$; Fig. 7). Spring-summer and year-long plates from Ny-
235 Ålesund had long, dense strands of *Desmarestia aculeata* (spring-summer, 285 ± 44.9; year, 659
236 ± 74.7 plate⁻¹), while plates from Longyearbyen had high numbers of encrusting bryozoans.
237 Year-long plates from Kvadehuken were covered by small algae, *Dermatocelis laminariae* (789
238 ± 86.9 plate⁻¹), *Chorda* sp. (32 ± 12.1 plate⁻¹), and a crustose coralline alga (61.7 ± 15.8 plate⁻¹).
239 There were significant pairwise differences between all locations ($R = 1$, $p = 0.001$ for each pair).
240 Points representing settlement plates deployed for the full year formed distinct clusters for each
241 shallow location in the MDS plot (Fig. 7).

242

243 *Recruitment across depth*

244 Significantly different assemblages of organisms recruited to year-long settlement plates
245 on the moorings (30 and 195 – 215 m) and at shallow locations (ANOSIM, $R = 0.989$, $p =$
246 0.001), and all pairwise differences were significant ($R = 0.931 – 1$, $p = 0.001 – 0.02$). An MDS
247 plot shows these differences graphically, with plates from the deep sites (195 and 215 m)
248 clustering closest to one another, far away from the shallower sites (7 – 30 m) (Fig. 7).

249 Settlement plates at 30 m on the Kongsfjorden mooring had dense *Saccharina latissima*
250 (237 ± 59.9 plate⁻¹), *Dermatocelis laminariae* (242 ± 51.1 plate⁻¹), and *Chorda* sp. (110 ± 23.8

251 plate⁻¹), while deep (215 m) settlement plates were covered by the hydroid *Stegopoma plicatile*.
252 Single individuals of *Saccharina latissima*, *Dermatocelis laminariae*, and the crustose coralline
253 alga also occurred on 215 m plates in Kongsfjorden. Settlement plates at 30 m on the Rjippfjorden
254 mooring had dense *Saccharina latissima* (498 ± 167 plate⁻¹) and conspicuous (~2.5 cm across)
255 colonies of *Alcyonidium gelatinosum*, while the deep plates (195 m) were almost uninhabited.
256 Only one individual each of *C. armoricana* and *H. arctica* occurred on the 8 settlement plates
257 from this location.

258 There was a negative exponential relationship between the number of recruiting
259 individuals and depth across full-year deployments ($R^2 = 0.9916$, Fig. 8A). There was also a
260 negative logarithmic relationship between the number of recruiting taxa and depth ($R^2 = 0.7648$,
261 Fig. 8B).

262

263 **Discussion**

264 *Species distribution patterns*

265 Meyer et al. (2016) found non-random co-occurrence of encrusting fauna on dropstones
266 in the Fram Strait, west of Svalbard, but never observed overgrowth competition among
267 dropstone morphotypes. In this study, by contrast, we found only random co-occurrence of taxa,
268 but overgrowth competition was observed on the settlement plates (Fig. 4). Overgrowth
269 competition is the dominant form of competition for sessile suspension feeders (Lohse 2002).
270 Our results, from a very young community (≤ 1 year), combined with those of Meyer et al.
271 (2016) for a more mature community, demonstrate there is not necessarily a link between
272 interspecific competition and non-random co-occurrence for hard-bottom marine fauna at high
273 latitudes, as has been traditionally assumed for other island-like habitats (Diamond 1975). Non-

274 random co-occurrence may be the result of other factors, such as epibiotic relationships and even
275 stochastic processes (Ulrich 2004; Meyer et al. 2016).

276

277 *Seasonality of recruits*

278 Many more taxa recruited in spring-summer than in fall-winter. This was expected as
279 many studies (Kukliński et al. 2013; Silberberger et al. 2016; Stübner et al. 2016) suggest larval
280 release, at least for planktotrophic larvae, should coincide with the presence of ample food in the
281 water column (phytoplankton). We found significant differences between assemblages of recruits
282 on spring-summer and year-long plates. Recruitment is often patchy, and small-scale variations
283 in recruitment over the course of the year could lead to these differences. Also, the higher
284 taxonomic richness but lower abundance on year-long plates at Ny-Ålesund compared to spring-
285 summer plates could indicate that some recruits were overgrown or consumed throughout the
286 deployment period. Predation and competition could decrease the number of individuals but
287 could also clear space for the recruitment of new taxa.

288 Perhaps even more interesting than spring-summer recruitment is the number of taxa (13)
289 and individuals that recruited in fall-winter. Kukliński et al. (2013) hypothesized that some
290 species recruited in winter to avoid competition with spring recruits. Winter-recruiting polar
291 species are efficient suspension feeders at low food concentrations and gain nutrition from
292 nanoplankton (Barnes and Clarke 1995; Bowden 2005). This would allow fall-winter recruits to
293 grow when the availability of most food is low, and perhaps increase their ability to compete
294 with later-arriving taxa. However, our results suggest that this advantage may be minimal or vary
295 by species. For example, the bryozoan *Callopora craticula* recruited exclusively in fall-winter

296 with up to 124 individuals plate⁻¹ but was never found on settlement plates deployed all year,
297 implying that it was consumed or overgrown by spring-summer recruits.

298 There is mounting evidence that the polar night is not a time of cessation for ecological
299 processes (Berge et al. 2015a). The results of this and previous studies (Kukliński et al. 2013;
300 Berge et al. 2015a) suggest that recruiting in fall-winter may be adaptive, though more research
301 is required to understand the exact advantage.

302

303 *Differences in recruitment among sites*

304 The communities of recruits at the two shallowest locations, Longyearbyen and Ny-
305 Ålesund, were significantly different for every deployment period (fall-winter, spring-summer,
306 and year), despite apparent similarities between the two locations. Both are in Atlantic-
307 influenced fjords and adjacent to populated areas. Both deployment locations were on
308 underwater structures associated with docks. Water temperatures were also almost identical over
309 the course of the year, but nevertheless, recruiting communities were significantly different. The
310 Ny-Ålesund deployment location is surrounded by populations of macroalgae, and multiple algal
311 species, including *Desmarestia aculeata*, *Dermatocelis laminariae*, and *Chorda* sp., recruited in
312 high densities at this location. By contrast, the dock in Longyearbyen is not surrounded by
313 macroalgae, and no algal species recruited at Longyearbyen. Thus, local species composition and
314 larval/spore availability likely influenced recruitment at these locations. Local control of
315 recruitment has also been shown for temperate latitudes and can lead to the dominance of a few
316 taxa at a location over many years (Osman and Whitlach 1998). Local species composition also
317 likely influenced recruitment at Kvadehuken, where recruitment could have been expected to be
318 similar to Ny-Ålesund (both sites are at similar depth in the same fjord). However, Kvadehuken

319 had a significantly lower number of recruits than Ny-Ålesund and had abundant crustose
320 coralline algae. This morphotype covers much of the rocky seafloor at Kvadehuken (Beuchel and
321 Gulliksen 2008), and it recruited only at Kvadehuken and at 30 m on the nearby Kongsfjorden
322 mooring, demonstrating the influence of local species composition on recruitment.

323 In Svalbard, there is a much stronger influence of local species composition on
324 recruitment than substratum type (natural or artificial) (Bałazy and Kukliński 2017). Recruitment
325 can vary strongly between natural and artificial substrata in some cases, but this difference
326 depends more on predator access to settlement surfaces than on the nature of the surface (Dayton
327 et al. 2016). Settlement plates at shallow locations in this study (Longyearbyen, Ny-Ålesund,
328 Kvadehuken) were accessible to benthic predators and thus show “realized recruitment”
329 according to the terminology of Dayton et al. (2016). The extent of predation on our plates is not
330 known, but our results from shallow locations can be a proxy for recruitment on new natural
331 substrata at their respective locations, showing the influence of local species composition.

332 One of the most striking differences between sets of settlement plates was for the 30 m
333 mooring stations in Kongsfjorden and Rijpfjorden. Settlement plates on moorings were not
334 accessible to benthic predators and show “potential recruitment” according to the terminology of
335 Dayton et al. (2016). The Rijpfjorden plates were dominated by *Saccharina latissima* and
336 *Alcyonidium gelatinosum*, whereas the Kongsfjorden 30 m plates had these species but also a
337 diverse community of macroalgae and invertebrates, with 15 morphotypes recorded. The *S.*
338 *latissima* blades in the two fjords were also of vastly different size: several cm long in
339 Kongsfjorden, and only visible under a dissecting microscope in Rijpfjorden (K. Meyer, pers.
340 obs.). The lower water temperature, later warming and ice break-up observed in Rijpfjorden
341 could mean that *S. latissima* individuals settled later in the year or grew more slowly in this

342 fjord. The low recruitment in Rjipfjorden contrasts starkly with the high diversity of the benthic
343 adults. Underwater photography revealed a diverse benthic hard-bottom community at the mouth
344 of Rjipfjorden, including boulders inhabited by sponges and bryozoans (Meyer et al. 2015).
345 Hard-bottom species are clearly able to recruit near the location of the mooring, but only two
346 individuals recruited to a total of eight settlement plates deployed at 195 m in Rjipfjorden. The
347 plates themselves were also quite clean, without even a noticeable biofilm (K. Meyer, pers. obs.).
348 Low recruitment may mean that Rjipfjorden benthic communities take a long time to develop.

349 Community assembly on marine hard substrata is often influenced by stochastic factors,
350 including patchy recruitment and variable outcomes of competition (Sutherland 1974; Walters
351 and Wethey 1986). Our results point to the influence of local factors, especially local adult
352 species composition. Spring-summer recruits dominate despite a competitive advantage for fall-
353 winter recruits, and interspecific competition (which is more strongly hierarchical at higher
354 latitude (Barnes and Kukliński 2003)) begins almost as soon as organisms recruit. Each of these
355 factors could constrain the community composition on a substratum to a narrow range of
356 possibilities.

357

358 *Recruitment across depth*

359 Our data revealed a strong decline in both the number and richness of recruits with
360 increasing depth (Fig. 8). Low recruitment could be related to the colder water temperature at
361 greater depth in the summer months in Kongsfjorden and Rjipfjorden. There may also be
362 reduced circulation or slower bottom currents at greater depth (Svendsen et al. 2002), causing
363 lower larval supply to settlement plates at these depths. Lower recruitment at greater depth may
364 mean these communities develop more slowly.

365 A deep (150 – 200 m) hard-bottom habitat in Kongsfjorden is dominated by the serpulid
366 polychaete *Protula tubularia*, anemones (*Hormathia* spp.), and sponges (Laudien and Orchard
367 2012). However, none of these species recruited to deep (215 m) settlement plates in
368 Kongsfjorden in this study. *P. tubularia* has a demersal, lecithotrophic larva (Tampi 1960),
369 which may not have dispersed to the location of the mooring. Plates were instead dominated by
370 *Stegopoma plicatile*, a common deep-water hydrozoan (Vervoort 1966; Edwards 1973) that
371 occurs on the west Svalbard continental shelf and slope down to 1300 m (Bergmann et al. 2011;
372 Meyer et al. 2013). Hydrozoans are commonly the first recruits to substrata in deep water. They
373 are poor competitors and are easily overgrown (Ronowicz et al. 2008). The dominance of *S.*
374 *plicatile* on the 215 m Kongsfjorden settlement plates implies that communities on these plates
375 were at an early stage of succession.

376

377 *Life-history traits of recruits and their roles in succession*

378 Recruitment is the first step in succession. While succession on hard substrata is poorly
379 understood for the high Arctic, the tolerance model (Connell and Slatyer 1977) is often applied
380 in temperate latitudes (Edwards and Stachowicz 2010). According to this model, fast-growing,
381 poor-competitive pioneer species (typically acorn barnacles and spirorbid polychaetes (Osman
382 1977; Dean and Hurd 1980)) colonize first but are overgrown by slower-growing superior
383 competitors as succession proceeds. We thus hypothesized that the recruits to settlement plates in
384 Svalbard waters would be fast-growing, poor competitors.

385 The spirorbid polychaete *Circeis armoricana* was a dominant recruiting species at
386 shallow stations in all seasons. *Semibalanus balanoides*, an acorn barnacle, and the bryozoans
387 *Harmeria scutulata* and *Celleporella hyalina* also recruited in high density at all shallow stations

388 during spring-summer and year-long deployments. *S. balanoides* and *C. armoricana* were
389 overgrown by bryozoans on the settlement plates (Fig. 4). *Harmeria scutulata* is an
390 opportunistic, annual species, and is one of the fastest-growing Arctic bryozoans (Kukliński and
391 Taylor 2006). It loses >70% of interspecific competitive interactions with other bryozoans
392 (Barnes and Kukliński 2003). *Celleporella hyalina* is also a poor competitor, losing >85% of
393 interspecific interactions (Barnes and Kukliński 2003). Therefore, most common taxa observed
394 on shallow settlement plates in this study (*C. armoricana*, *S. balanoides*, *H. scutulata*, *C.*
395 *hyalina*) can be characterized as early-succession species.

396 One well-known superior competitor, a crustose coralline alga, also recruited in high
397 abundance to settlement plates at Kvadehuken, where the rocky seafloor is virtually covered by
398 this morphotype (Beuchel and Gulliksen 2008). However, recruits were very small and often
399 barely visible on the settlement plates, even with magnification (K. Meyer, pers. obs.). Crustose
400 coralline algae grow very slowly and win all interspecific competitive interactions (Kukliński
401 2009). This morphotype has the life history characteristics of a late-successional species
402 according to the tolerance model (Connell and Slatyer 1977; Edwards and Stachowicz 2010),
403 though it recruits to settlement plates in high numbers at both poles (Bowden et al. 2006).
404 Coralline algae increased in percent cover over time and were much more prominent on
405 settlement plates exposed for three years at Kvadehuken than on plates exposed for one or two
406 years (Schmiing 2005).

407 Taxa conspicuously absent from our shallow settlement plates included ascidians and
408 sponges. Epifaunal and encrusting species of both taxa, notably *Didemnum albinum* and
409 *Halichondria* sp., are present at Kvadehuken (Jørgensen and Gulliksen 2001; Beuchel and
410 Gulliksen 2008; Laudien and Orchard 2012), but none recruited to the settlement plates there or

411 at any other station. *D. albinum* and species of *Halichondria* brood their larvae (Marks 1996;
412 Maldonado 2006), potentially leading to restricted dispersal. Ascidians and sponges are superior
413 competitors in Svalbard waters (Barnes and Kukliński 2004) and are characteristic late-
414 succession species at temperate latitude (Osman and Whitlatch 1995; Edwards and Stachowicz
415 2010). *Urticina eques* and *Hormathia nodosa* are abundant anemones at Kvadehuken, but only a
416 single individual of *U. eques* recruited to a settlement plate there. *U. eques* lives over 40 years
417 (Beuchel and Gulliksen 2008) and is well-defended against predators in the field (Lippert et al.
418 2004), so it is likely a late-succession or climax-community species.

419

420 **Conclusions**

421 Recruitment in high Arctic fjords shows wide variation in recruitment among sites, strong
422 seasonality, and interspecific interactions on a short time-scale. Some species may recruit in fall-
423 winter to reduce interspecific competition. Recruits co-occurred randomly, indicating that there
424 is not necessarily a relationship between non-random co-occurrence and interspecific
425 competition for isolated marine hard substrata. Much lower recruitment was observed in an
426 Arctic-influenced fjord compared to Atlantic-influenced fjords, and there was an exponential
427 decline in recruitment with depth. Hard-bottom communities at deeper locations may develop
428 more slowly. The most abundant recruits were fast-growing poor competitors, with late-
429 succession species being conspicuously absent, except for crustose coralline algae.

430

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447 **References**

448 Abele, L. G., and W. K. Patton. 1976. The size of coral heads and the community biology of
449 associated decapod crustaceans. *J. Biogeogr.* 3: 35–47.

450 Bałazy, P., and P. Kukliński. 2017. Arctic field experiment shows differences in epifaunal
451 assemblages between natural and artificial substrates of different heterogeneity and origin. *J.*
452 *Exp. Mar. Bio. Ecol.* 486: 178–187. doi: 10.1016/j.jembe.2016.10.012

453 Barnes, D. K. A., and A. Clarke. 1995. Seasonality of feeding activity in Antarctic suspension
454 feeders. *Polar Biol.* 15: 335–340.

455 Barnes, D. K. A., and P. Kukliński. 2003. High polar spatial competition: extreme hierarchies at
456 extreme latitude. *Mar. Ecol. Prog. Ser.* 259: 17–28. doi:10.3354/meps259017

457 Barnes, D. K. A., and P. Kukliński. 2004. Scale-dependent variation in competitive ability
458 among encrusting Arctic species. *Mar. Ecol. Prog. Ser.* 275: 21–32.
459 doi:10.3354/meps275021

460 Barnes, D. K. A., and P. Kukliński. 2005. Low colonisation on artificial substrata in arctic
461 Spitsbergen. *Polar Biol.* 29: 65–69. doi:10.1007/s00300-005-0044-y

462 Beaulieu, S. E. 2001. Colonization of habitat islands in the deep sea: recruitment to glass sponge
463 stalks. *Deep-Sea Res. I* 48: 1121–1137. doi:10.1016/S0967-0637(00)00055-8

- 464 Benedetti-Cecchi, L., E. Maggi, I. Bertocci, and others. 2003. Variation in rocky shore
465 assemblages in the northwestern Mediterranean: contrasts between islands and the
466 mainland. *J. Exp. Mar. Biol. Ecol.* 293: 193–215. doi: 10.1016/S0022-0981(03)00220-X
- 467 Berge, J., F. Cottier, Ø. Varpe, and others. 2014. Arctic complexity: a case study on diel vertical
468 migration of zooplankton. *J. Plankton Res.* 36: 1279–1297. doi:10.1093/plankt/fbu059
- 469 Berge, J., M. Daase, P. E. Renaud, and others. 2015a. Unexpected levels of biological activity
470 during the polar night offer new perspectives on a warming Arctic. *Curr. Biol.* 25: 2555–
471 2561. doi:10.1016/j.cub.2015.08.024
- 472 Berge, J., K. Heggland, O. J. Lønne, F. Cottier, H. Hop, G. W. Gabrielsen, L. Nøttestad, and O.
473 A. Misund. 2015b. First records of Atlantic mackerel (*Scomber scombrus*) from the
474 Svalbard Archipelago, Norway, with possible explanations for the extension of its
475 distribution. *Arctic* 68: 54–61. doi:10.14430/arctic4455
- 476 Berge, J., G. Johnsen, F. Nilsen, B. Gulliksen, and D. Slagstad. 2005. Ocean temperature
477 oscillations enable reappearance of blue mussels *Mytilus edulis* in Svalbard after a 1000
478 year absence. *Mar. Ecol. Prog. Ser.* 303: 167–175. doi:10.3354/meps303167
- 479 Bergmann, M., N. Langwald, J. Ontrup, T. Soltwedel, I. Schewe, M. Klages, and T. W.
480 Nattkemper. 2011. Megafaunal assemblages from two shelf stations west of Svalbard. *Mar.*
481 *Biol. Res.* 7: 525–539. doi:10.1080/17451000.2010.535834
- 482 Beuchel, F., and B. Gulliksen. 2008. Temporal patterns of benthic community development in an
483 Arctic fjord (Kongsfjorden, Svalbard): results of a 24-year manipulation study. *Polar Biol.*
484 31: 913–924. doi:10.1007/s00300-008-0429-9
- 485 Bowden, D. A. 2005. Seasonality of recruitment in Antarctic sessile marine benthos. *Mar. Ecol.*
486 *Prog. Ser.* 297: 101–118. doi:10.3354/meps297101
- 487 Bowden, D. A., A. Clarke, L. S. Peck, and D. K. A. Barnes. 2006. Antarctic sessile marine
488 benthos: colonisation and growth on artificial substrata over three years. *Mar. Ecol. Prog.*
489 *Ser.* 316: 1–16. doi:10.3354/meps316001
- 490 Chalmer, P. N. 1982. Settlement patterns of species in a marine fouling community and some
491 mechanisms of succession. *J. Exp. Mar. Bio. Ecol.* 58: 73–85. doi:10.1016/0022-
492 0981(82)90098-3
- 493 Clarke, K., and R. Gorley. 2006. Primer v6: user manual/tutorial, Primer-E.
- 494 Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and
495 their role in community stability and organization. *Am. Nat.* 111: 1119–1144.
496 doi:10.2307/2678832
- 497 Connor, E., and D. Simberloff. 1979. The assembly of species communities: chance or
498 competition? *Ecology* 60: 1132–1140.
- 499 Dayton, P., S. Jarrell, S. Kim, S. Thrush, K. Hammerstrom, M. Slattery, and E. Parnell. 2016.
500 Surprising episodic recruitment and growth of Antarctic sponges: implications for
501 ecological resilience. *J. Exp. Mar. Bio. Ecol.* 482: 38–55. doi: 10.1016/j.jembe.2016.05.001

- 502 Dean, T. A., and L. E. Hurd. 1980. Development in an estuarine fouling community: the
503 influence of early colonists on later arrivals. *Oecologia* 46: 295–301. doi:10.1007/S00442-
504 004-V
- 505 Diamond, J. M. 1975. Assembly of island communities, p. 342–444. *In* M.L. Cody and J.M.
506 Diamond [eds.], *Ecology and Evolution of Communities*. Belknap Press of Harvard
507 University Press.
- 508 Edwards, C. 1973. The medusa *Modeeria rotunda* and its hydroid *Stegopoma fastigiatum*, with a
509 review of *Stegopoma* and *Stegolaria*. *J. Mar. Biol. Assoc. U.K.* 53: 573–600.
- 510 Edwards, K. F., and J. J. Stachowicz. 2010. Multivariate trade-offs, succession, and phenological
511 differentiation in a guild of colonial invertebrates. *Ecology* 91: 3146–3152. doi:10.1890/10-
512 0440.1
- 513 Entsminger, G. 2014. EcoSim Professional: null modeling software for ecologists, version 1,
514 Acquired Intelligence Inc., Kesey-Bear and Pinyon Publishing.
- 515 Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81: 2606–
516 2621.
- 517 Gotelli, N. J., and D. J. McCabe. 2002. Species co-occurrence: a meta-analysis of J. M.
518 Diamond’s assembly rules model. *Ecology* 83: 2091–2096. doi:10.1890/0012-
519 9658(2002)083[2091:SCOAMA]2.0.CO;2
- 520 Gutt, J., and T. Schickan. 1998. Epibiotic relationships in the Antarctic benthos. *Antarct. Sci.* 10:
521 398–405. doi:10.1017/S0954102098000480
- 522 Hétériér, V., B. David, C. De Ridder, and T. Rigaud. 2008. Ectosymbiosis is a critical factor in
523 the local benthic biodiversity of the Antarctic deep sea. *Mar. Ecol. Prog. Ser.* 364: 67–76.
524 doi:10.3354/meps07487
- 525 Huntington, B. E., and D. Lirman. 2012. Species-area relationships in coral communities:
526 evaluating mechanisms for a commonly observed pattern. *Coral Reefs* 31: 929–938.
527 doi:10.1007/s00338-012-0917-9
- 528 Jørgensen, L. L., and B. Gulliksen. 2001. Rocky bottom fauna in arctic Kongsfjord (Svalbard)
529 studied by means of suction sampling and photography. *Polar Biol.* 24: 113–121.
530 doi:10.1007/s003000000182
- 531 Klekowski, R. Z. 1995. Atlas of the marine flora of southern Spitsbergen, Institute of
532 Oceanology, Polish Academy of Sciences.
- 533 Kluge, G. A. 1975. Bryozoa of the northern seas of the USSR, Amerind Publishing Co.
- 534 Konar, B. 2007. Recolonization of a high latitude hard-bottom nearshore community. *Polar Biol.*
535 30: 663–667. doi:10.1007/s00300-007-0261-7
- 536 Konar, B. 2013. Lack of recovery from disturbance in high-arctic boulder communities. *Polar*
537 *Biol.* 36: 1205–1214. doi:10.1007/s00300-013-1340-6
- 538 Konar, B., and K. Iken. 2005. Competitive dominance among sessile marine organisms in a high

- 539 Arctic boulder community. *Polar Biol.* 29: 61–64. doi:10.1007/s00300-005-0055-8
- 540 Kortsch, S., R. Primicerio, F. Beuchel, P. E. Renaud, J. Rodrigues, O. J. Lønne, and B.
541 Gulliksen. 2012. Climate-driven regime shifts in Arctic marine benthos. *Proc. Natl. Acad.*
542 *Sci.* 109: 14052–14057. doi:10.1073/pnas.1207509109
- 543 Kukliński, P. 2009. Ecology of stone-encrusting organisms in the Greenland Sea - a review.
544 *Polar Res.* 28: 222–237.
- 545 Kukliński, P., J. Berge, L. McFadden, K. Dmoch, M. Zajaczkowski, H. Nygård, K. Piwosz, and
546 A. Tatarek. 2013. Seasonality of occurrence and recruitment of Arctic marine benthic
547 invertebrate larvae in relation to environmental variables. *Polar Biol.* 36: 549–560.
548 doi:10.1007/s00300-012-1283-3
- 549 Kukliński, P., and P. D. Taylor. 2006. Unique life history strategy in a successful Arctic
550 bryozoan, *Harmeria scutulata*. *J. Mar. Biol. Assoc. UK* 86: 1305–1314.
551 doi:10.1017/S0025315406014330
- 552 Laudien, J., and J. B. Orchard. 2012. The significance of depth and substratum incline for the
553 structure of a hard bottom sublittoral community in glacial Kongsfjorden (Svalbard, Arctic)-
554 an underwater imagery approach. *Polar Biol.* 35: 1057–1072. doi:10.1007/s00300-011-
555 1153-4
- 556 Lippert, H., K. Iken, C. Volk, M. Köck, and E. Rachor. 2004. Chemical defence against
557 predators in a sub-Arctic fjord. *J. Exp. Mar. Bio. Ecol.* 310: 131–146.
558 doi:10.1016/j.jembe.2004.03.023
- 559 Lohse, D. P. 2002. Relative strengths of competition for space and food in a sessile filter feeder.
560 *Biol. Bull.* 203: 173–180.
- 561 MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*, Princeton
562 University Press.
- 563 Maldonado, M. 2006. The ecology of the sponge larva. *Can. J. Zool.* 84: 175–194.
- 564 Marks, J. A. 1996. Three sibling species of didemnid ascidians from northern Norway:
565 *Didemnum albidum* (Verrill, 1871), *Didemnum polare* (Hartmeyer, 1903), and *Didemnum*
566 *romssae* sp nov. *Can. J. Zool.* 74: 357–379. doi:10.1139/z96-043
- 567 Meyer, K. S. 2016. Islands in a sea of mud: insights for community assembly on isolated marine
568 hard substrata from terrestrial island theory. *Adv. Mar. Biol.* 76: 1–40.
569 doi:10.1016/bs.amb.2016.09.002
- 570 Meyer, K. S., M. Bergmann, and T. Soltwedel. 2013. Interannual variation in the epibenthic
571 megafauna at the shallowest station of the HAUSGARTEN observatory (79 N, 6 E).
572 *Biogeosciences* 10: 3479–3492. doi:10.5194/bg-10-3479-2013
- 573 Meyer, K. S., S. D. Brooke, A. K. Sweetman, M. Wolf, and C. M. Young. Invertebrate
574 communities on historical shipwrecks in the western Atlantic: relation to islands. *Mar. Ecol.*
575 *Prog. Ser.* 566: 17–29. doi:10.3354/meps12058
- 576 Meyer, K. S., A. K. Sweetman, C. M. Young, and P. E. Renaud. 2015. Environmental factors

- 577 structuring Arctic megabenthos - a case study from a shelf and two fjords. *Front. Mar. Sci.*
578 2: 1–14. doi:10.3389/fmars.2015.00022
- 579 Meyer, K. S., C. M. Young, A. K. Sweetman, J. Taylor, T. Soltwedel, and M. Bergmann. 2016.
580 Rocky islands in a sea of mud: biotic and abiotic factors structuring deep-sea dropstone
581 communities. *Mar. Ecol. Prog. Ser.* 556: 45–57. doi:10.3354/meps11822
- 582 Oschmann, W. 1990. Dropstones - rocky mini-islands in high-latitude pelagic soft-substrate
583 environments. *Senckenbergiana maritima* 21: 55–75.
- 584 Osman, R. W. 1977. The establishment and development of a marine epifaunal community.
585 *Ecol. Monogr.* 47: 37–63.
- 586 Osman, R. W., and R. B. Whitlatch. 1995. The influence of resident adults on recruitment: a
587 comparison to settlement. *J. Exp. Mar. Bio. Ecol.* 190: 169–198. doi:10.1016/0022-
588 0981(95)00035-P
- 589 Perkol-Finkel, S., N. Shashar, O. Barneah, and others. 2005. Fouling reefal communities on
590 artificial reefs: does age matter? *Biofouling* 21: 127–140. doi:10.1080/08927010500133451
- 591 Perkol-Finkel, S., N. Shashar, and Y. Benayahu. 2006. Can artificial reefs mimic natural reef
592 communities? The roles of structural features and age. *Mar. Environ. Res.* 61: 121–135.
593 doi:10.1016/j.marenvres.2005.08.001
- 594 Renaud, P. E., J. Berge, O. Varpe, O. J. Lønne, J. Nahrgang, C. Ottesen, and I. Hallanger. 2012.
595 Is the poleward expansion by Atlantic cod and haddock threatening native polar cod,
596 *Boreogadus saida*? *Polar Biol.* 35: 401–412. doi:10.1007/s00300-011-1085-z
- 597 Ronowicz, M., M. Włodarska-Kowalczyk, and P. Kukliński. 2008. Factors influencing hydroids
598 (Cnidaria: Hydrozoa) biodiversity and distribution in Arctic kelp forest. *J. Mar. Biol. Assoc.*
599 U.K. 88: 1567–1575. doi:10.1017/S0025315408001495
- 600 Schmiing, M. 2005. Sukzession in benthischen Makrofauna-Gemeinschaften der Arktis - ein
601 Jahresvergleich. Universität Bremen.
- 602 Schoener, A., and T. W. Schoener. 1981. The dynamics of the species-area relation in marine
603 fouling systems 1. Biological correlates of changes in the species-area slope. *Am. Nat.* 118:
604 339–360.
- 605 Schulz, M., M. Bergmann, K. von Juterzenka, and T. Soltwedel. 2010. Colonisation of hard
606 substrata along a channel system in the deep Greenland Sea. *Polar Biol.* 33: 1359–1369.
607 doi:10.1007/s00300-010-0825-9
- 608 Silberberger, M. J., P. E. Renaud, B. Espinasse, and H. Reiss. 2016. Spatial and temporal
609 structure of the meroplankton community in a sub-Arctic shelf system. 555: 79–93.
610 doi:10.3354/meps11818
- 611 Stübner, E. I., J. E. Søreide, M. Reigstad, M. Marquardt, and K. Blachowiak-Samolyk. 2016.
612 Year-round meroplankton dynamics in high-Arctic Svalbard. *J. Plankton Res.* 0: fbv124.
613 doi:10.1093/plankt/fbv124
- 614 Sutherland, J. P. 1974. Multiple stable points in natural communities. *Am. Nat.* 108: 859–873.

- 615 Svendsen, H., A. Beszczynska-Møller, J. O. Hagen, and others. 2002. The physical environment
616 of Kongsfjorden – Krossfjorden, an Arctic fjord system in Svalbard. *Polar Res.* 21: 133–
617 166. doi:10.1111/j.1751-8369.2002.tb00072.x
- 618 Tampi, P. R. S. 1960. On the early development of *Protula tubularia* (Montagu). *J. Mar. Biol.*
619 *Assoc. India* 2: 53–56.
- 620 Taylor, J. R., A. P. DeVogelaere, E. J. Burton, and others. 2014. Deep-sea faunal communities
621 associated with a lost intermodal shipping container in the Monterey Bay National Marine
622 Sanctuary, CA. *Mar. Pollut. Bull.* 83: 92–106. doi:10.1016/j.marpolbul.2014.04.014
- 623 Ulrich, W. 2004. Species co-occurrences and neutral models: reassessing J. M. Diamond’s
624 assembly rules. *Oikos* 107: 603–609.
- 625 Vervoort, W. 1966. Bathyal and abyssal hydroids, Danish Science Press.
- 626 Wallace, M. I., F. R. Cottier, J. Berge, G. A. Tarling, C. Griffiths, and A. S. Brierley. 2010.
627 Comparison of zooplankton vertical migration in an ice-free and a seasonally ice-covered
628 Arctic fjord: An insight into the influence of sea ice cover on zooplankton behavior.
629 *Limnol. Oceanogr.* 55: 831–845. doi:10.4319/lo.2009.55.2.0831
- 630 Walters, L., M. Hadfield, and K. del Carmen. 1997. The importance of larval choice and
631 hydrodynamics in creating aggregations of *Hydroides elegans* (Polychaeta: Serpulidae).
632 *Invertebr. Biol.* 116: 102–114. doi:10.2307/3226974
- 633 Walters, L. J., and D. S. Wethey. 1986. Surface topography influences competitive hierarchies
634 on marine hard substrata: a field experiment. *Biol. Bull.* 170: 441–449.
- 635 Wilce, R. T., and K. H. Dunton. 2014. The boulder Patch (North Alaska, Beaufort Sea) and its
636 benthic algal flora. *Arctic* 67: 43–56. doi:10.14430/arctic4360
- 637 Young, C. M. 2009. Communities on deep-sea hard bottoms, p. 39–60. *In* M. Wahl [ed.], *Marine*
638 *hard bottom communities*. Springer-Verlag.
- 639
- 640 **Fig. 1.** Map of deployment locations. Circles indicate shallow locations (7 – 15 m) reached by
641 SCUBA divers; squares indicate moorings (30 and 195 – 215 m). Depth contours shown every
642 100 m.
- 643 **Fig. 2.** Settlement plate design. Individual plates are 15 x 15 cm.
- 644 **Fig. 3.** Water temperature at settlement-plate deployment sites. A, shallow dock sites; B,
645 Kongsfjorden mooring; C, Rijpfjorden mooring.

646 **Fig. 4.** Examples of *Semibalanus balanoides* and *Circeis armoricana* being overgrown
647 (examples shown by white arrows) by different bryozoan species on settlement plates. A, *Tegella*
648 *arctica*; B, *Cribrilina annulata*; C, *Harmeria scutulata*; D, *Umbonula arctica*.

649 **Fig. 5.** Seasonal recruitment at shallow locations, Longyearbyen and Ny-Ålesund, 7 m;
650 Kvadehuken, 15 m. A, number of recruits per 225 cm²; B, number of taxa per 225 cm². Error
651 bars show 95% confidence intervals.

652 **Fig. 6.** Non-metric multidimensional scaling (MDS) plot showing differences in communities of
653 recruits in different seasons and at different locations. Only shallow locations shown.

654 **Fig. 7.** MDS plot showing differences in communities recruiting to various piers and moorings in
655 Svalbard fjords over a year. “Kongsfjorden” and “Rijpfjorden” locations are moorings, where
656 plates were deployed at two depths.

657 **Fig. 8.** A, number of individuals; B, number of taxa recruiting to settlement plates over a year-
658 long deployment at various depths in Svalbard fjords. White point indicates settlement plates
659 deployed at 215 m on the Kongsfjorden mooring, which were not included in the exponential
660 trendline, because on these plates, upright forms of the hydroid *Stegopoma plicatile* were
661 counted as a relative proxy for recruitment of this species. Error bars show 95% confidence
662 intervals.

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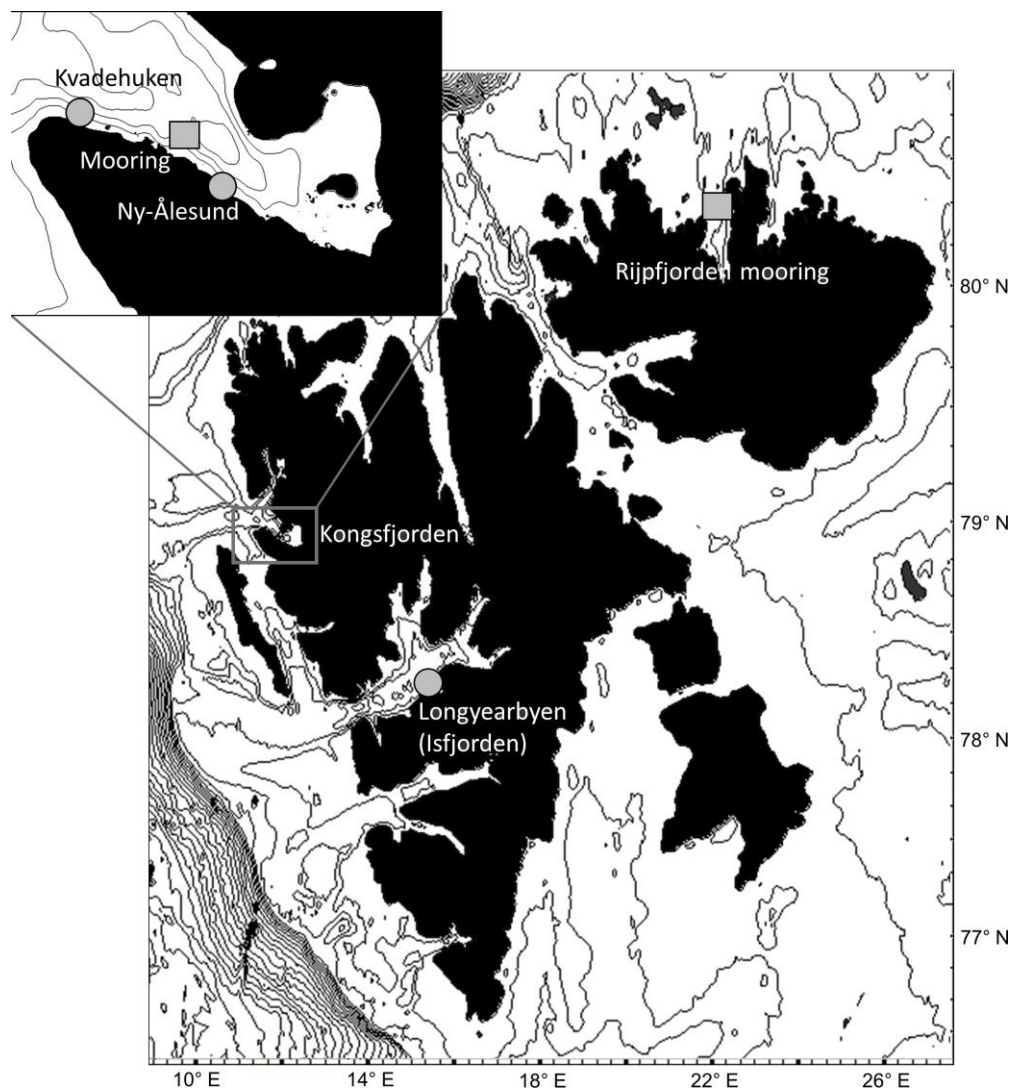
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669 Fig. 1



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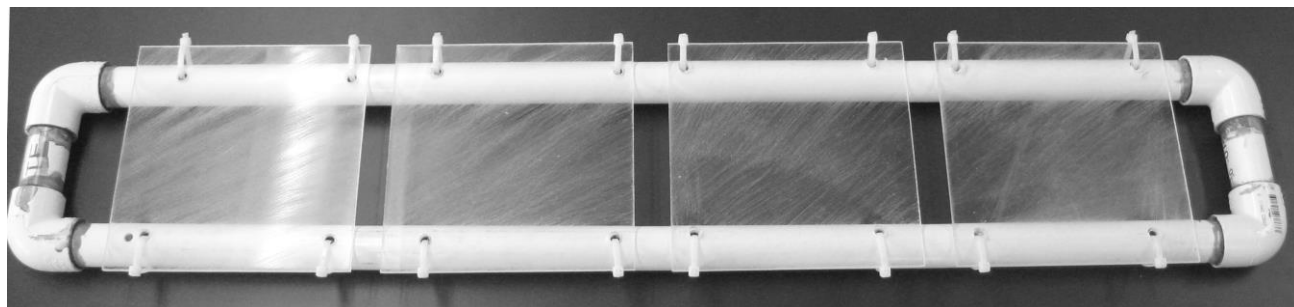
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678 Fig. 2



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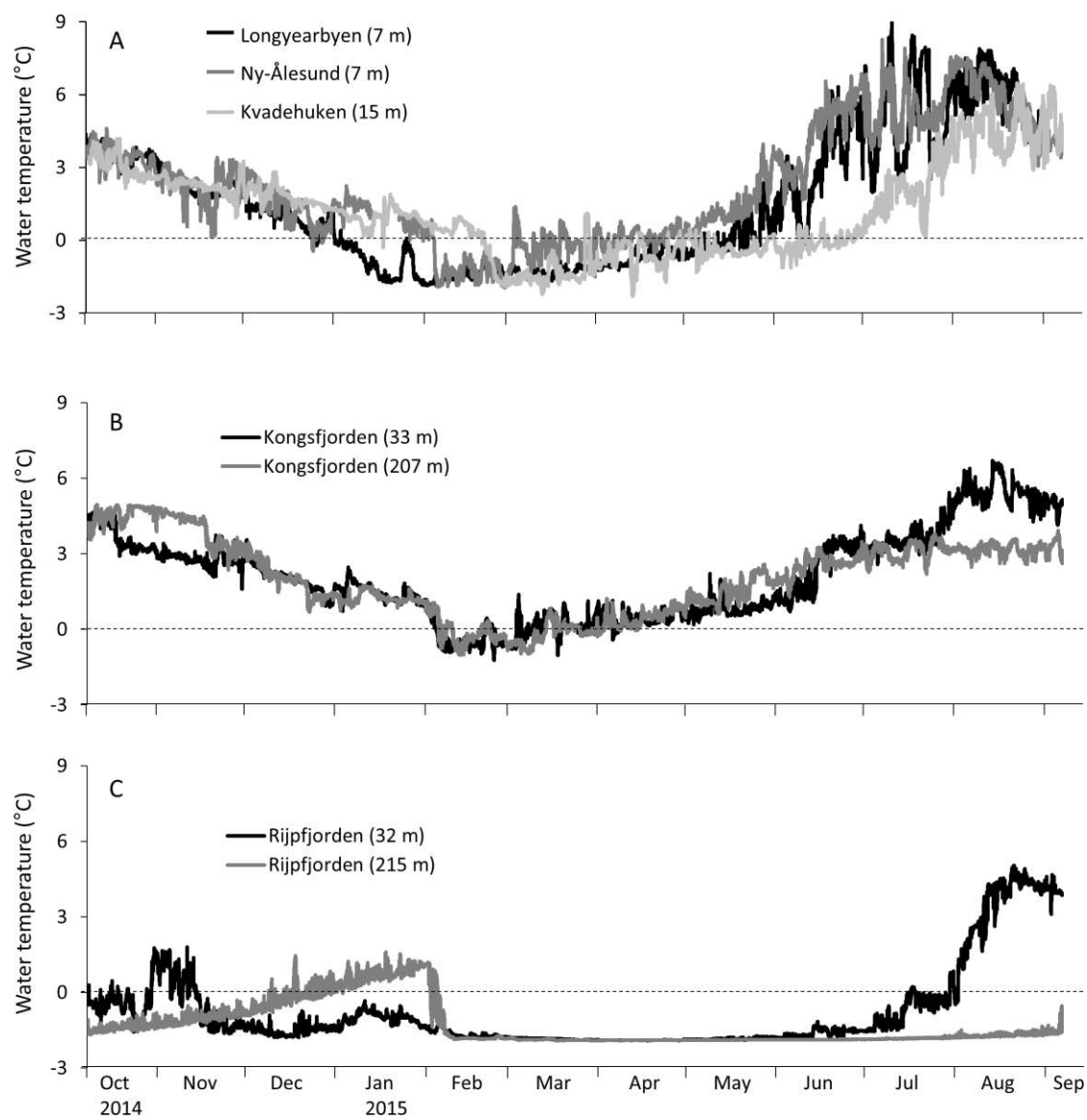
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698 Fig. 3



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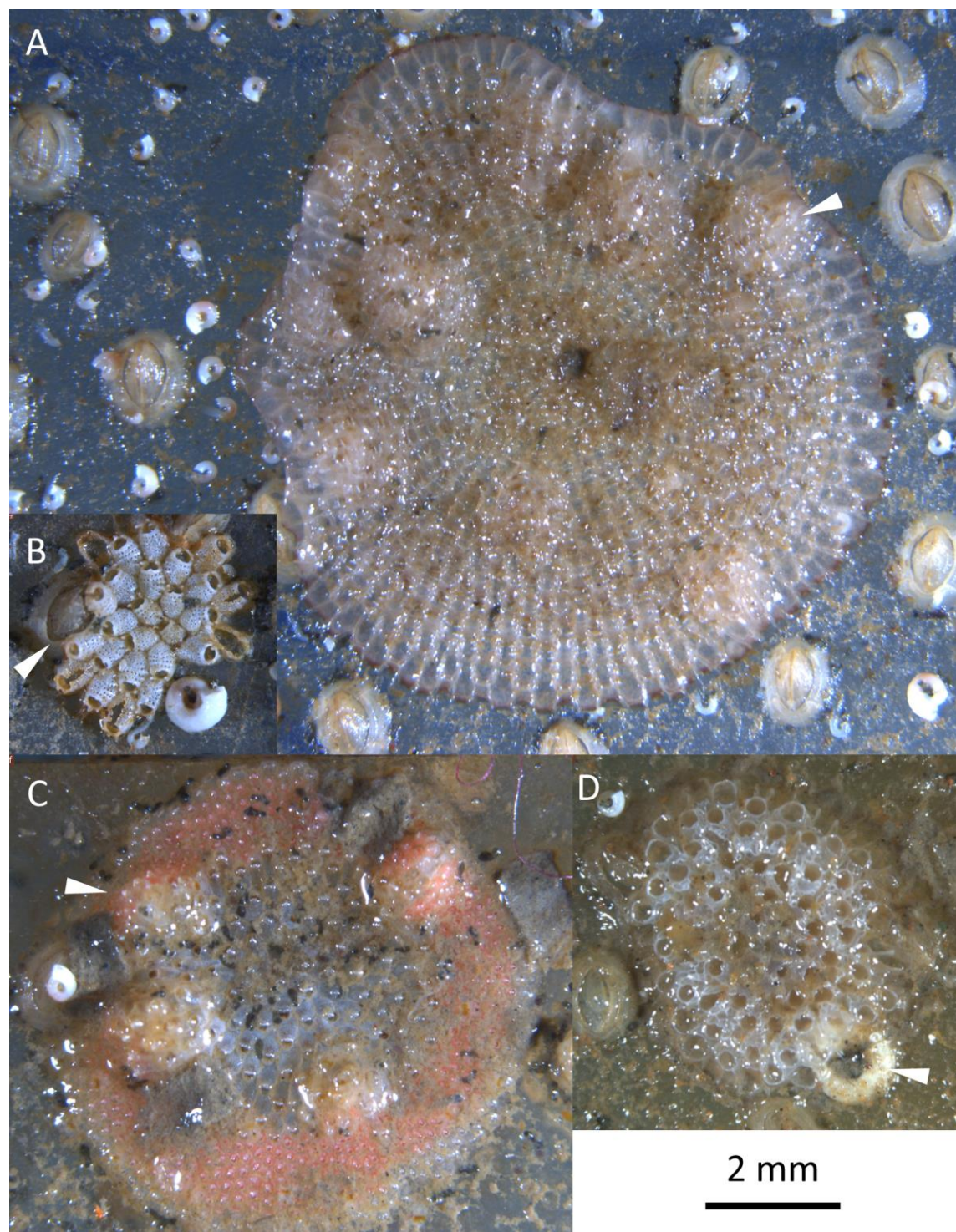
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706 Fig. 4

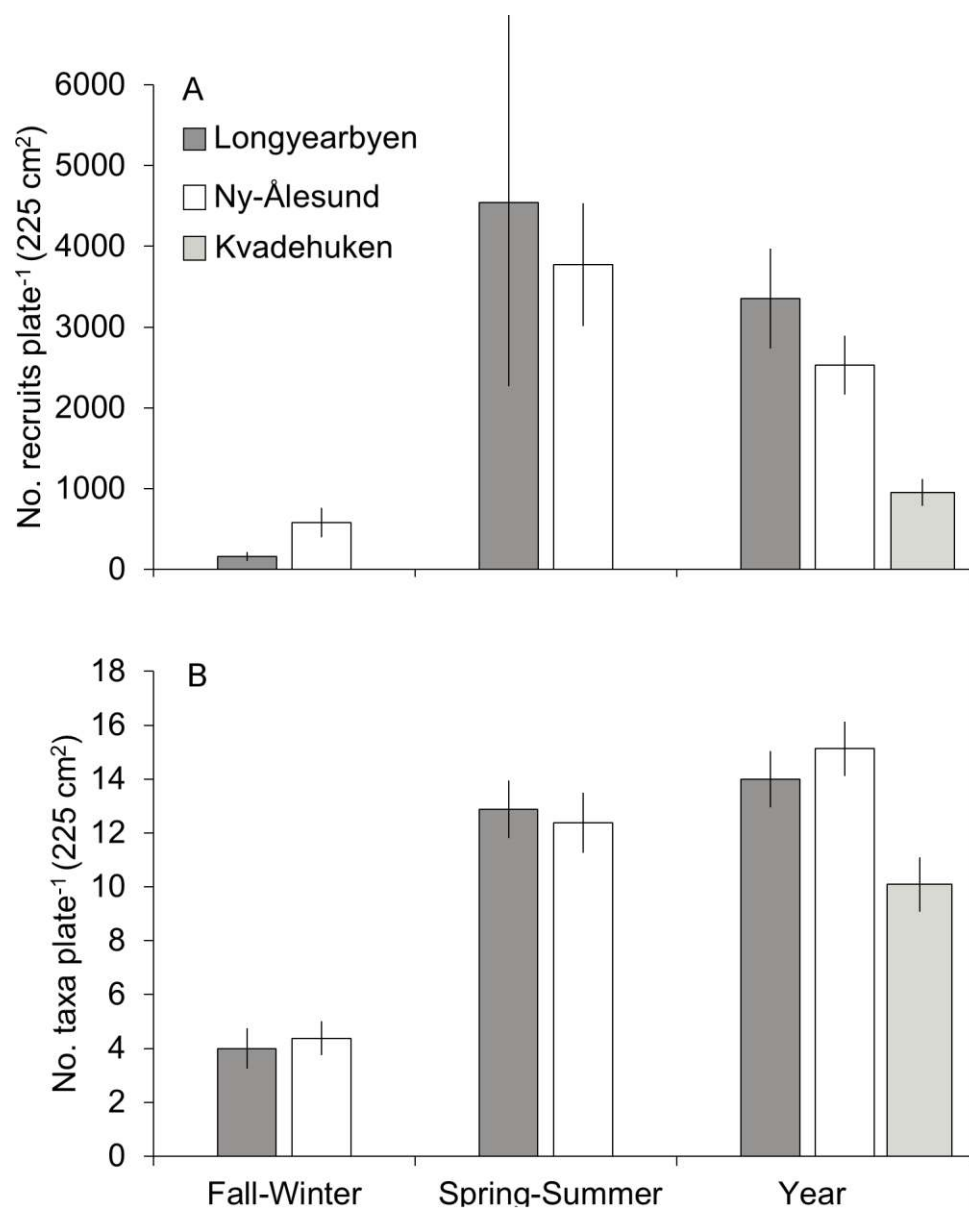


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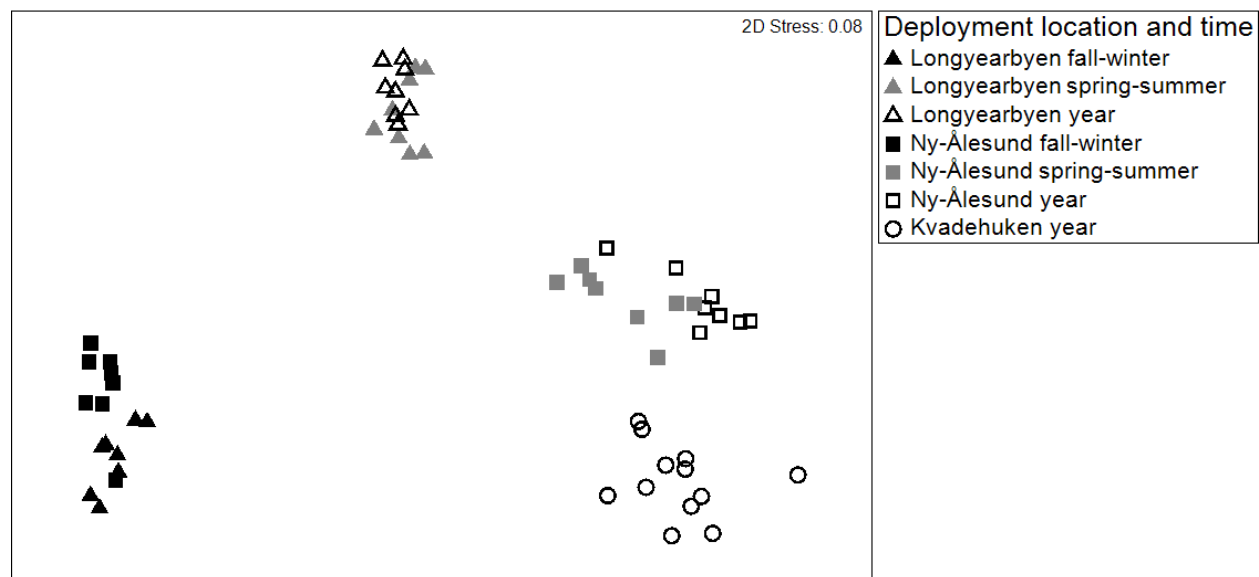
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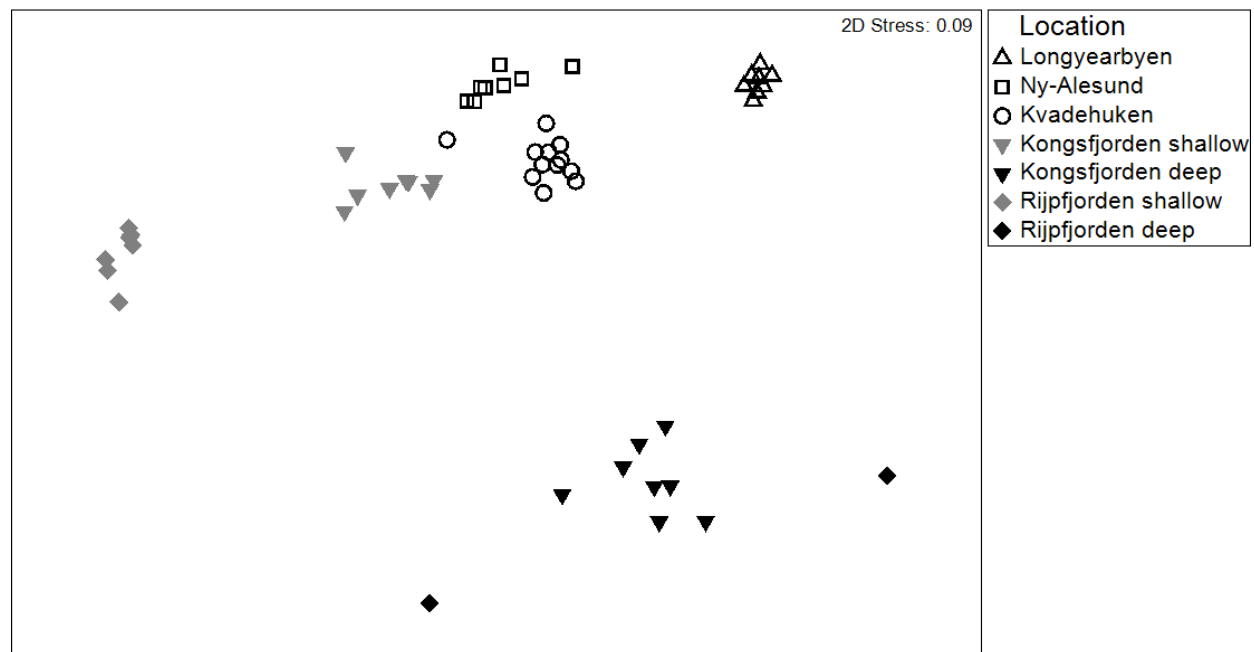
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733 Fig. 7



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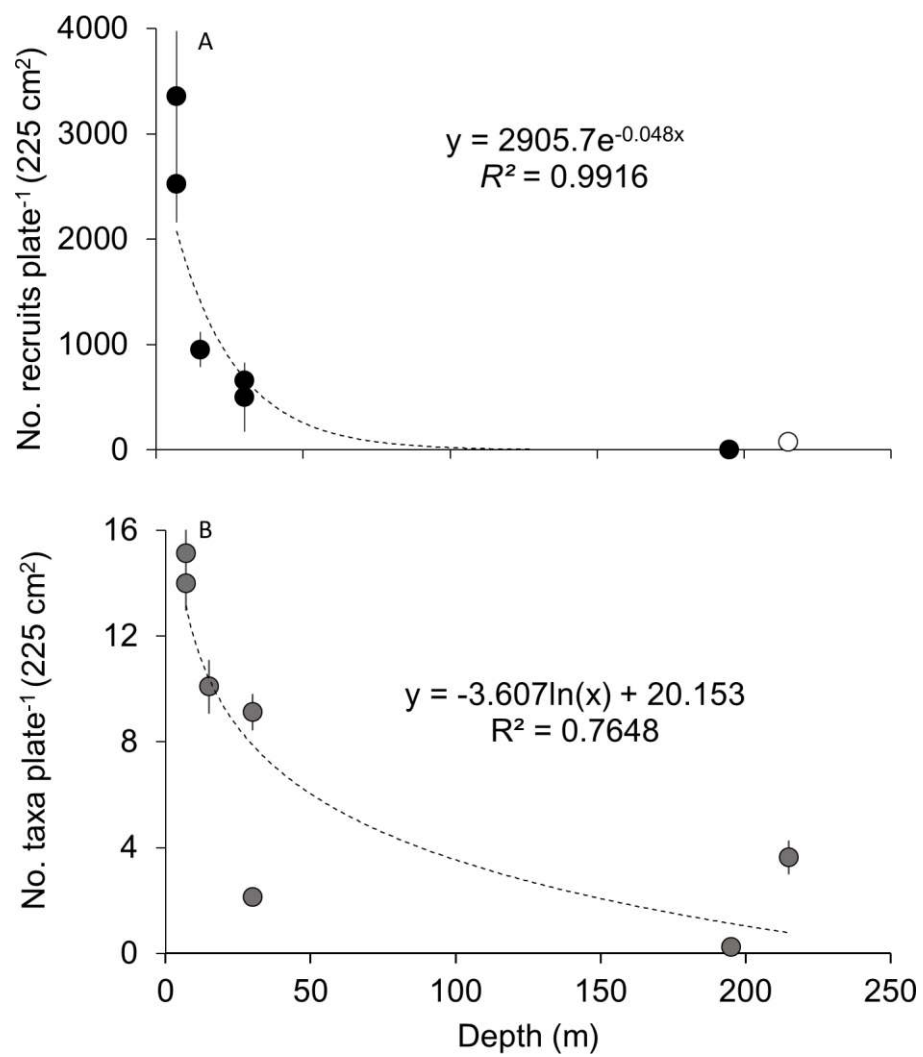
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748 Fig. 8



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