

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<sup>-1</sup>. 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,  $285 \pm 44.9$ ; year,  $659 \pm 74.7$  plate<sup>-1</sup>, mean  $\pm$  standard  
211 error), *Dermatocelis laminariae* (spring-summer,  $2759 \pm 343$ ; year,  $1366 \pm 203$  plate<sup>-1</sup>), and  
212 *Chorda* sp. (spring-summer,  $134 \pm 20.4$ ; year,  $85.5 \pm 17.9$  plate<sup>-1</sup>), 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<sup>-1</sup>; Ny-Ålesund,  $47.8 \pm 13.3$  plate<sup>-1</sup>) 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,  $285 \pm 44.9$ ; year,  $659$   
236  $\pm 74.7$  plate<sup>-1</sup>), 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  $\pm 86.9$  plate<sup>-1</sup>), *Chorda* sp. ( $32 \pm 12.1$  plate<sup>-1</sup>), and a crustose coralline alga ( $61.7 \pm 15.8$  plate<sup>-1</sup>).  
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 ( $237 \pm 59.9$  plate<sup>-1</sup>), *Dermatocelis laminariae* ( $242 \pm 51.1$  plate<sup>-1</sup>), and *Chorda* sp. ( $110 \pm 23.8$

251 plate<sup>-1</sup>), 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* ( $498 \pm 167$  plate<sup>-1</sup>) 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 ( $\leq 1$  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<sup>-1</sup> 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

## 431 **Acknowledgements**

432 We thank the officers and crew of R/V *Helmer Hanssen* for their assistance at sea. J.  
433 Johnson, M. Allman, M. Johnson, M. Bouch, and K. Robbins (OIMB) assisted with the

434 construction and shipment of settlement plates and frames. M. Ronowicz (IOPAS, hydroids), A.  
435 Pop (UNIS, algae), and N. Shunatova (St. Petersburg State Univ., various invertebrates) assisted  
436 with the identification of morphotypes from voucher specimens. This material is based upon  
437 work supported by the National Science Foundation Graduate Research Fellowship Program  
438 under Grant No. DGE-0829517. Additional support for this project was provided by the  
439 Research Council of Norway (Marine Night Project #226417 to J. Berge), Akvaplan-niva, and  
440 the University Centre in Svalbard. Comments from 2 anonymous reviewers improved a previous  
441 version of this manuscript.

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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 cm<sup>2</sup>; B, number of taxa per 225 cm<sup>2</sup>. 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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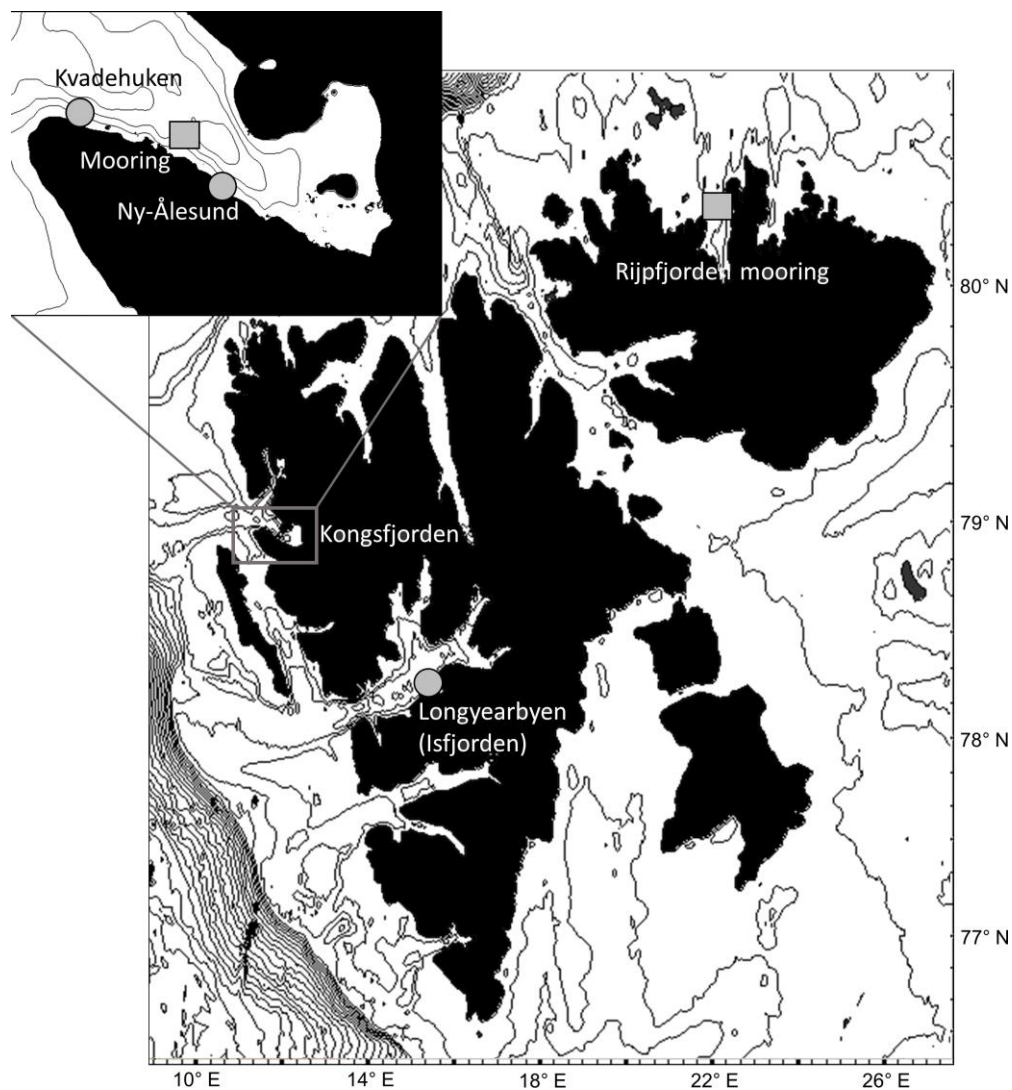
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669 Fig. 1



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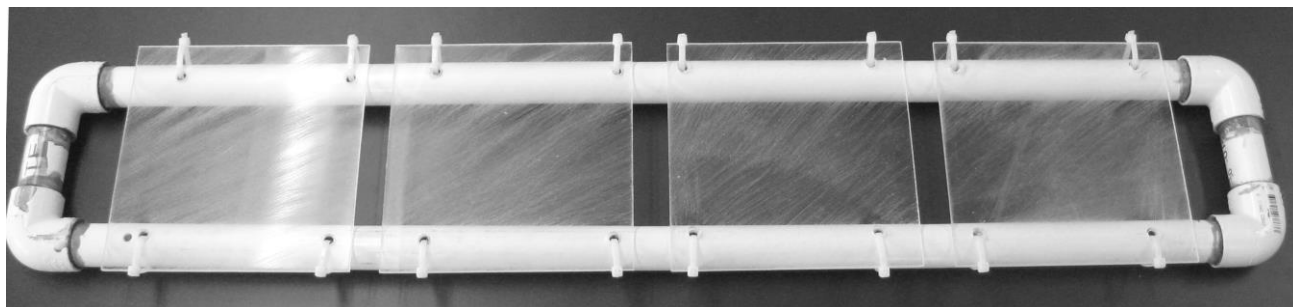
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678 Fig. 2



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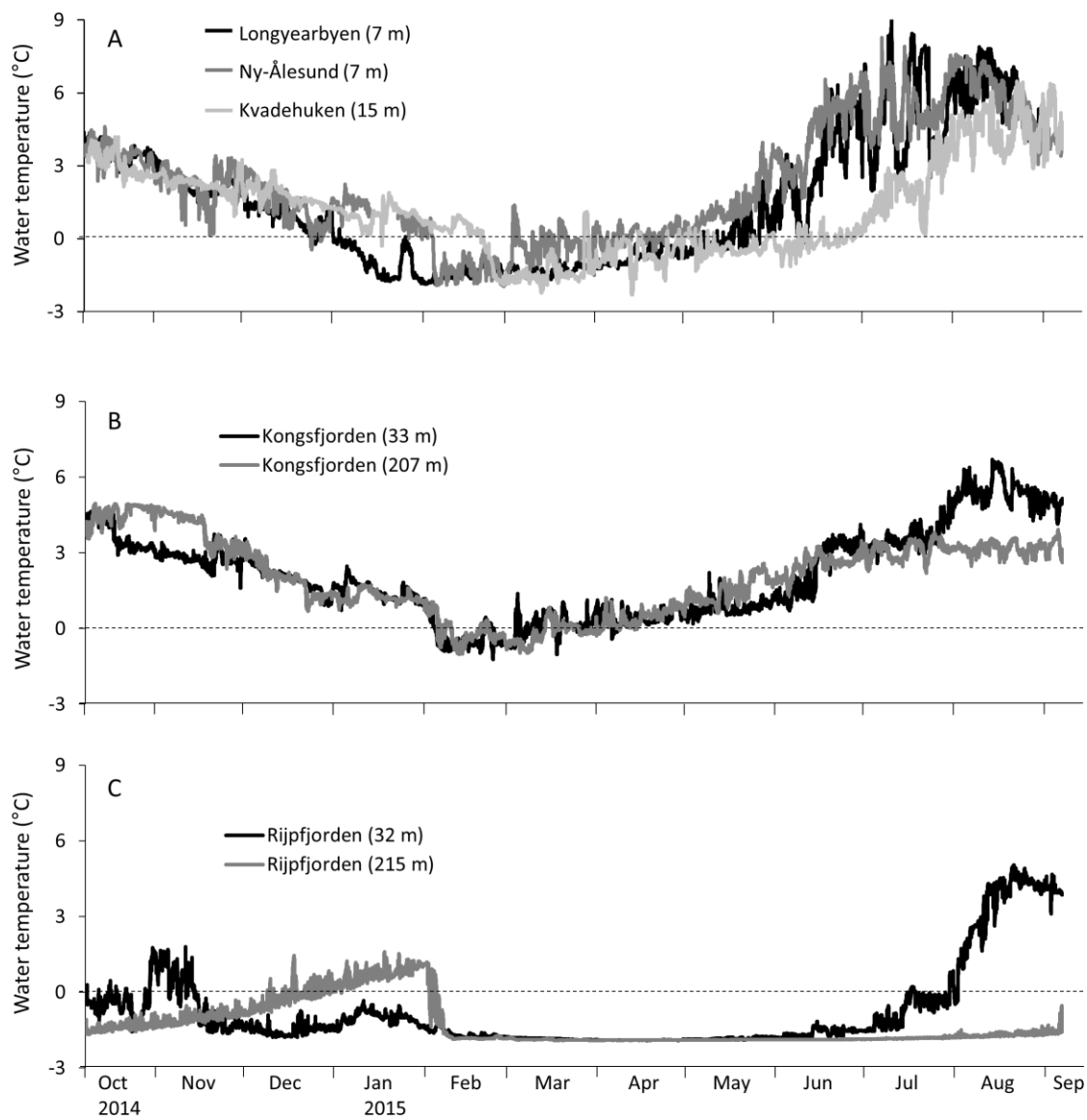
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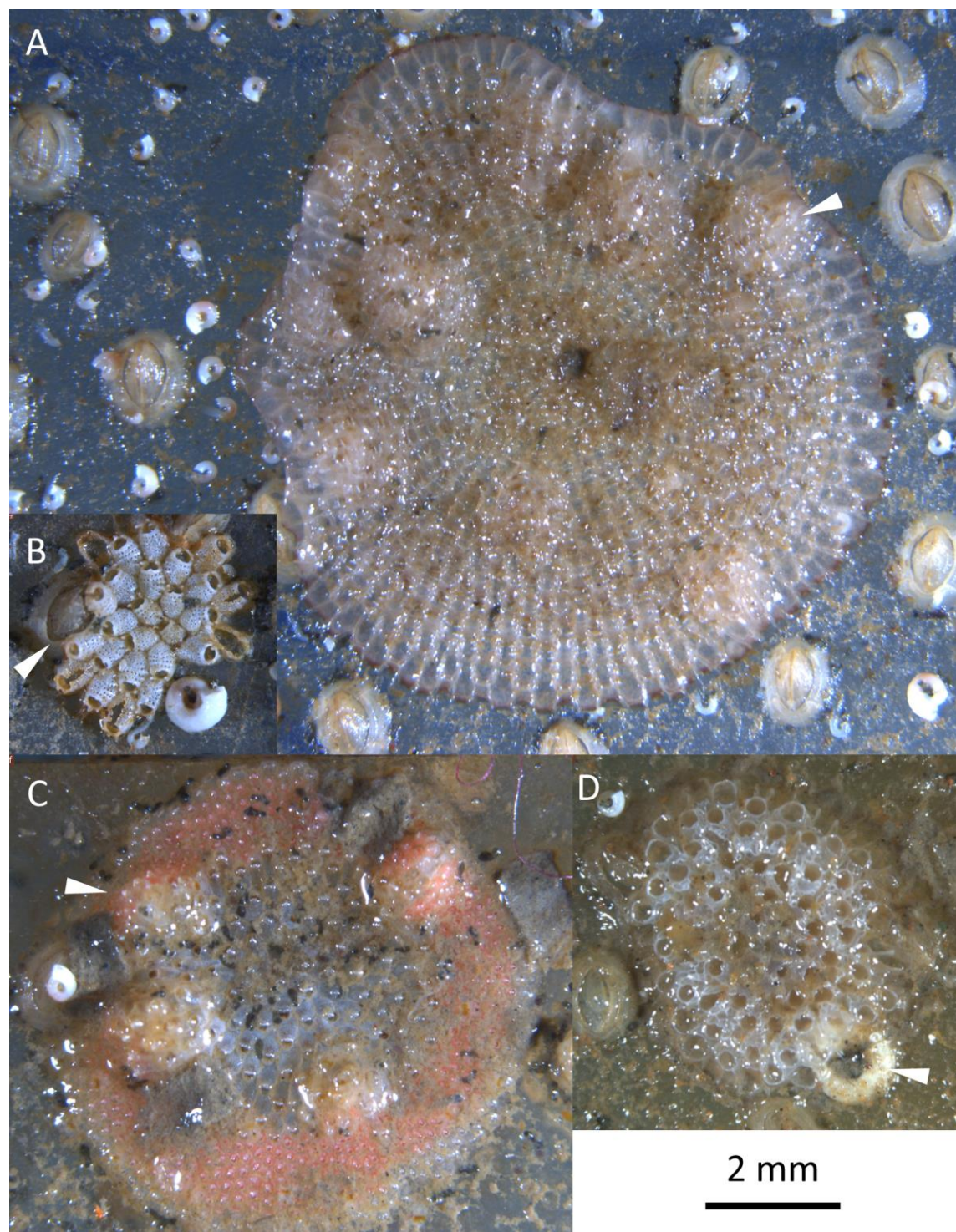
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706 Fig. 4

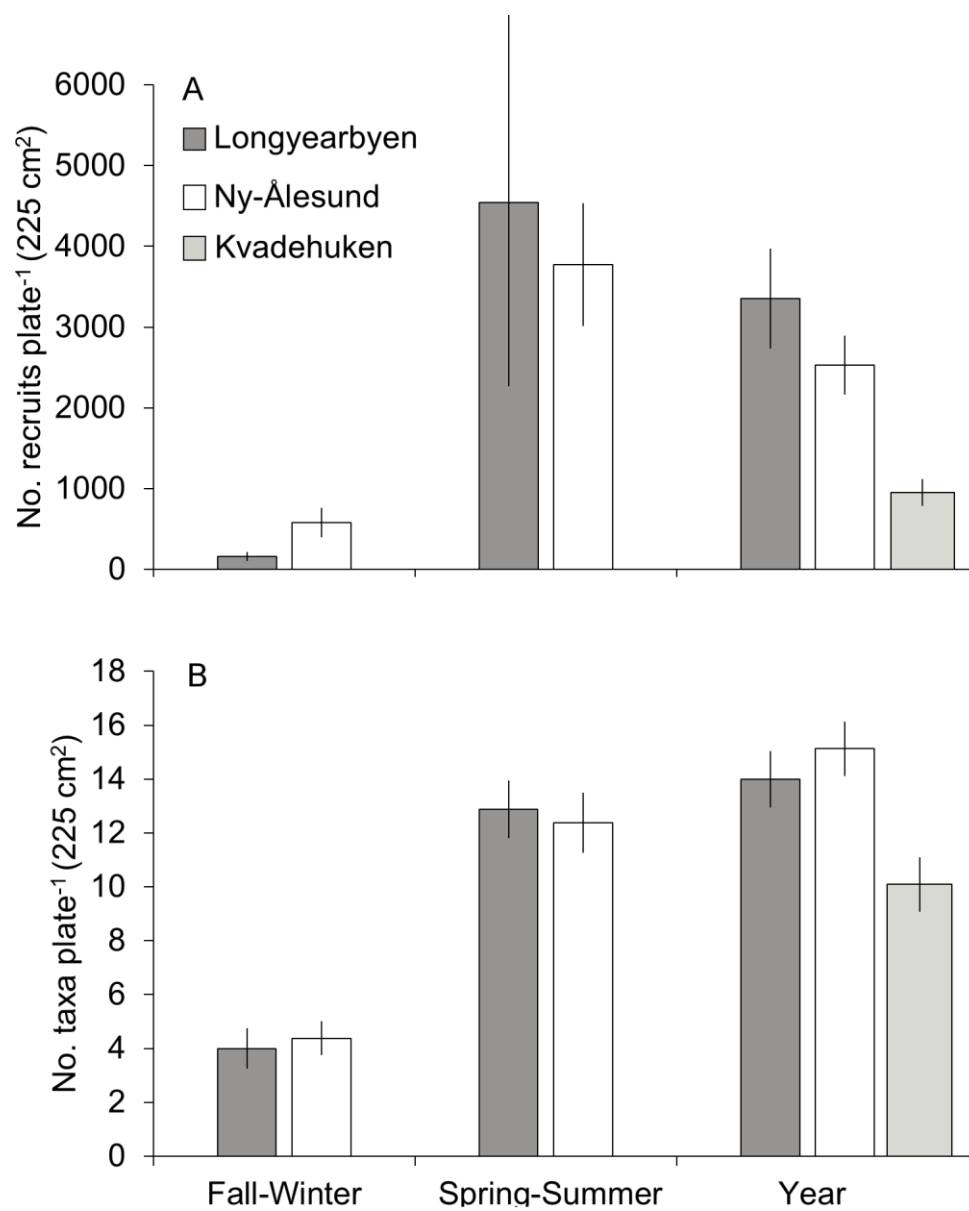


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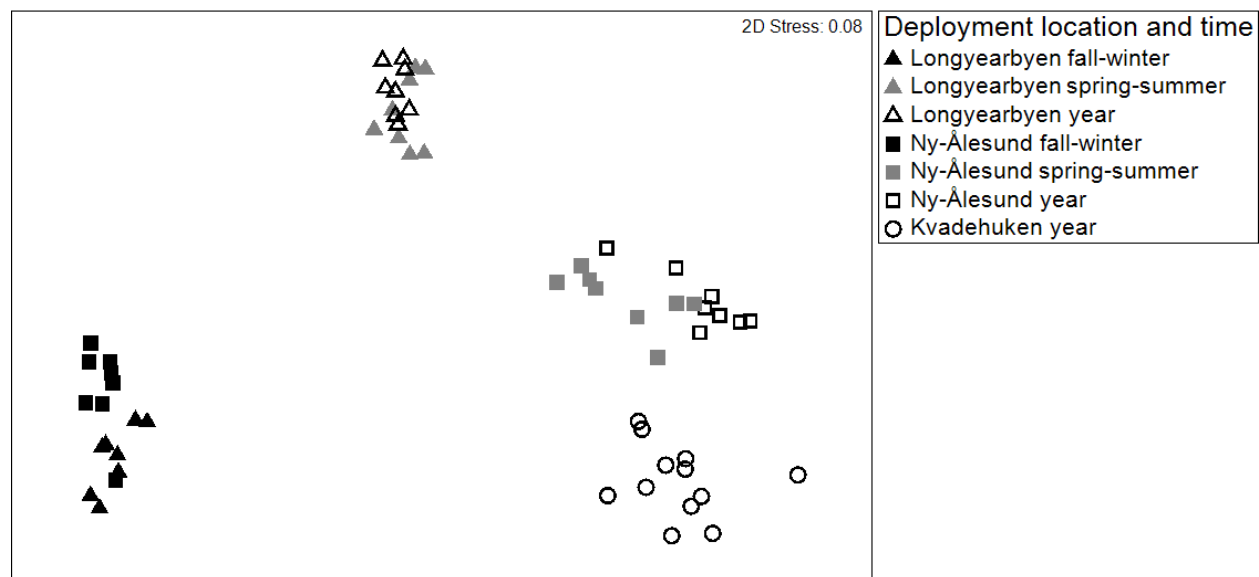
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717 Fig. 6



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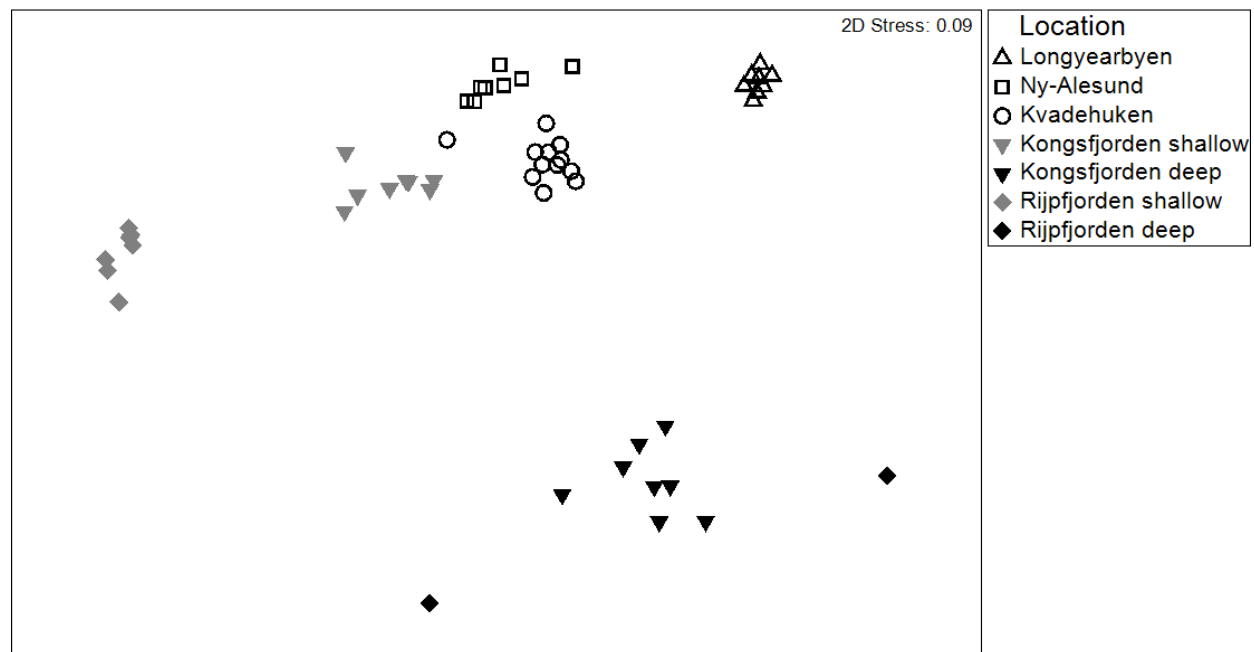
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733 Fig. 7



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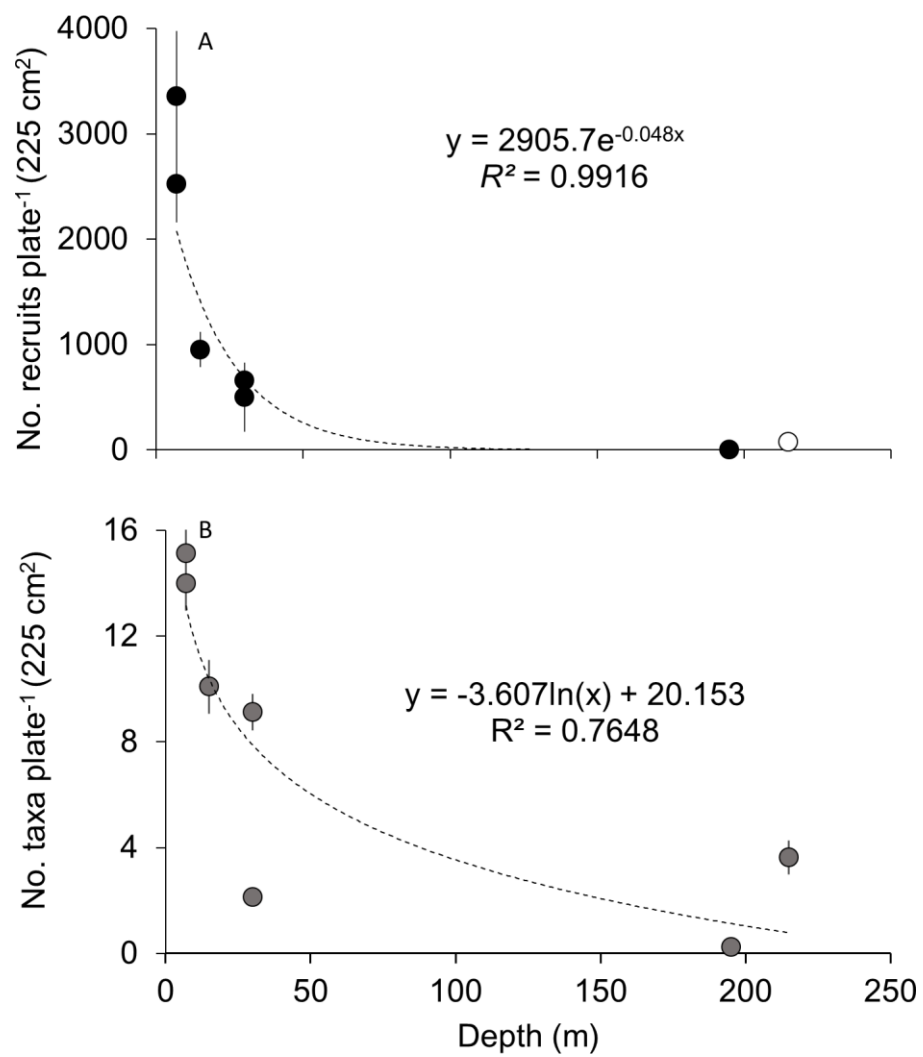
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748 Fig. 8



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