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

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Abstract

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

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

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

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

Pairs of species often co-occur non-randomly on islands and island-like hard substrata (Diamond 1975). Non-random co-occurrence refers to pairs of species being found together less (negative non-random co-occurrence) or more (positive non-random co-occurrence) often than expected by chance (Gotelli and McCabe 2002; Meyer 2016). Negative non-random co-occurrence patterns have been attributed to interspecific competition (Diamond 1975), though this interpretation has been criticized for its lack of supporting evidence (Connor and Simberloff 1979). Positive non-random co-occurrence can be the result of epibiotic relationships (Meyer et
Encrusting marine fauna may have negative non-random co-occurrence but in the absence of interspecific overgrowth competition (Meyer et al. 2016), indicating that there is not necessarily a relationship between these two concepts for marine island-like habitats. Non-random co-occurrence has been studied in mature communities, but not among first recruits to a substratum, where there may be more available space and less interspecific competition.

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

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

In this study, we seek to understand how recruitment on isolated hard substrata in Svalbard fjords is influenced by depth, season, and biotic interactions, and how it differs between
Atlantic- and Arctic-influenced fjords. We present simultaneous data from multiple locations in three fjords (Fig. 1): the Atlantic-influenced fjords (Svendsen et al. 2002) Isfjorden and Kongsfjorden, where warm, saline water has facilitated colonization of Atlantic fauna, including boreal fish and mussels in recent years (Berge et al. 2005, 2015b; Renaud et al. 2012), and a “true” Arctic fjord (Wallace et al. 2010; Berge et al. 2014), Rijpfjorden. In addition to abiotic factors, we consider the life-history strategies of each recruiting species. We also test for non-random co-occurrence among recruiting species, to understand if and how these artificial hard substrata resemble other island-like habitats.

Methods

Deployment of settlement plates

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

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

Water temperature

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

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

Statistical analysis of data

A test for significant differences between plates on different frames showed no blocking effect (analysis of similarity, p > 0.05 for each season and location), so plates were treated as true replicates for statistical analysis. Univariate t-tests were used to test for significant differences in the abundance and richness of recruits between locations and seasons and were conducted in SPSS (International Business Machines, USA), using a Levene’s test to establish homoscedasticity. Mann-Whitney U-tests (M-W) were used for non-parametric cases.
Multivariate statistics including analysis of similarity (ANOSIM) and multi-dimensional scaling (MDS) were used to test for significant differences in community composition of recruits among locations and depths and were conducted in Primer v6 (Clarke and Gorley 2006) following a log(x+1) transformation. We tested for non-random co-occurrence among plates at each location in EcoSim (Entsminger 2014) using a fixed-fixed null model and the C-score index (Gotelli 2000).

Results

Water temperature

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

Species distribution patterns

A total of 48 species and morphotypes recruited to the settlement plates in this study, almost half of which were bryozoans (22 of 48). The most abundant species were the alga *Dermatocelis laminariae*, the spirorbid polychaete *Circeis armoricana*, and the acorn barnacle
*Semibalanus balanoides*. Raw recruitment data and plate deployment metadata are reported in the supplementary material.

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

**Seasonal patterns in recruitment**

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

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

At Ny-Ålesund, there was a significantly lower number of recruits on plates deployed all year than on plates deployed in the spring-summer \((t\text{-test, } t = 2.90, p = 0.01)\), but there was a
significantly higher number of taxa (t-test, $t = 3.60$, $p = 0.003$) (Fig. 5). Differences between numbers of recruits and taxa in spring-summer and all-year deployments were not significant at Longyearbyen (t-test, $N, t = 0.98$, $p = 0.34$; $S, t = 1.47$, $p = 0.16$) (Fig. 5). For both locations, *C. armoricana* and *S. balanoides* recruited in high numbers. Dense macroalgae, including *Desmarestia aculeata* (spring-summer, $285 \pm 44.9$; year, $659 \pm 74.7$ plate$^{-1}$, mean $\pm$ standard error), *Dermatocelis laminariae* (spring-summer, $2759 \pm 343$; year, $1366 \pm 203$ plate$^{-1}$), and *Chorda* sp. (spring-summer, $134 \pm 20.4$; year, $85.5 \pm 17.9$ plate$^{-1}$), recruited to spring-summer and year-long settlement plates at Ny-Ålesund. No algae recruited at Longyearbyen. Only year-long plates could be retrieved from Kvadehuken, but the abundance and richness of recruits at this site were significantly lower than at Longyearbyen ($S$, t-test, $t = 4.67$, $p < 0.001$; $N$, t-test, $t = 8.72$, $p < 0.001$) and Ny-Ålesund ($S$, t-test, $t = 6.15$, $p < 0.001$; $N$, t-test, $t = 8.56$, $p < 0.001$).

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

Only four species recruited to settlement plates in both fall-winter and spring-summer: the spirorbid *C. armoricana*, the bivalve *Hiatella arctica*, and bryozoans *C. hyalina* and *Crisiella producta*. The bryozoan *C. craticula* was abundant on fall-winter plates (Longyearbyen, $5.00 \pm$
1.15 plate$^{-1}$; Ny-Ålesund, $47.8 \pm 13.3$ plate$^{-1}$) but not observed on spring-summer or year-long settlement plates. No algal taxa recruited in the fall-winter.

**Differences among shallow locations**

For settlement plates deployed at shallow sites for the entire year (Longyearbyen, Ny-Ålesund, Kvadehuken), there was a significant difference among the assemblages at different locations (ANOSIM, $R = 1$, $p = 0.001$; Fig. 7). Spring-summer and year-long plates from Ny-Ålesund had long, dense strands of *Desmarestia aculeata* (spring-summer, $285 \pm 44.9$; year, $659 \pm 74.7$ plate$^{-1}$), while plates from Longyearbyen had high numbers of encrusting bryozoans.

Year-long plates from Kvadehuken were covered by small algae, *Dermatocelis laminariae* ($789 \pm 86.9$ plate$^{-1}$), *Chorda* sp. ($32 \pm 12.1$ plate$^{-1}$), and a crustose coralline alga ($61.7 \pm 15.8$ plate$^{-1}$).

There were significant pairwise differences between all locations ($R = 1$, $p = 0.001$ for each pair). Points representing settlement plates deployed for the full year formed distinct clusters for each shallow location in the MDS plot (Fig. 7).

**Recruitment across depth**

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

Settlement plates at 30 m on the Kongsfjorden mooring had dense *Saccharina latissima* ($237 \pm 59.9$ plate$^{-1}$), *Dermatocelis laminariae* ($242 \pm 51.1$ plate$^{-1}$), and *Chorda* sp. ($110 \pm 23.8$ plate$^{-1}$).
plate$^{-1}$), while deep (215 m) settlement plates were covered by the hydroid *Stegopoma plicatile*. Single individuals of *Saccharina latissima*, *Dermatocelis laminariae*, and the crustose coralline alga also occurred on 215 m plates in Kongsfjorden. Settlement plates at 30 m on the Rijpfjorden mooring had dense *Saccharina latissima* (498 ± 167 plate$^{-1}$) and conspicuous (~2.5 cm across) colonies of *Alcyonidium gelatinosum*, while the deep plates (195 m) were almost uninhabited. Only one individual each of *C. armoricana* and *H. arctica* occurred on the 8 settlement plates from this location.

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

**Discussion**

*Species distribution patterns*

Meyer et al. (2016) found non-random co-occurrence of encrusting fauna on dropstones in the Fram Strait, west of Svalbard, but never observed overgrowth competition among dropstone morphotypes. In this study, by contrast, we found only random co-occurrence of taxa, but overgrowth competition was observed on the settlement plates (Fig. 4). Overgrowth competition is the dominant form of competition for sessile suspension feeders (Lohse 2002). Our results, from a very young community ($\leq 1$ year), combined with those of Meyer et al. (2016) for a more mature community, demonstrate there is not necessarily a link between interspecific competition and non-random co-occurrence for hard-bottom marine fauna at high latitudes, as has been traditionally assumed for other island-like habitats (Diamond 1975). Non-
random co-occurrence may be the result of other factors, such as epibiotic relationships and even stochastic processes (Ulrich 2004; Meyer et al. 2016).

Seasonality of recruits

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

Perhaps even more interesting than spring-summer recruitment is the number of taxa (13) and individuals that recruited in fall-winter. Kukliński et al. (2013) hypothesized that some species recruited in winter to avoid competition with spring recruits. Winter-recruiting polar species are efficient suspension feeders at low food concentrations and gain nutrition from nanoplankton (Barnes and Clarke 1995; Bowden 2005). This would allow fall-winter recruits to grow when the availability of most food is low, and perhaps increase their ability to compete with later-arriving taxa. However, our results suggest that this advantage may be minimal or vary by species. For example, the bryozoan *Callopora craticula* recruited exclusively in fall-winter.
with up to 124 individuals plate\(^{-1}\) but was never found on settlement plates deployed all year, implying that it was consumed or overgrown by spring-summer recruits.

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

Differences in recruitment among sites

The communities of recruits at the two shallowest locations, Longyearbyen and Ny-Ålesund, were significantly different for every deployment period (fall-winter, spring-summer, and year), despite apparent similarities between the two locations. Both are in Atlantic-influenced fjords and adjacent to populated areas. Both deployment locations were on underwater structures associated with docks. Water temperatures were also almost identical over the course of the year, but nevertheless, recruiting communities were significantly different. The Ny-Ålesund deployment location is surrounded by populations of macroalgae, and multiple algal species, including *Desmarestia aculeata*, *Dermatocelis laminariae*, and *Chorda* sp., recruited in high densities at this location. By contrast, the dock in Longyearbyen is not surrounded by macroalgae, and no algal species recruited at Longyearbyen. Thus, local species composition and larval/spore availability likely influenced recruitment at these locations. Local control of recruitment has also been shown for temperate latitudes and can lead to the dominance of a few taxa at a location over many years (Osman and Whitlach 1998). Local species composition also likely influenced recruitment at Kvadehuken, where recruitment could have been expected to be similar to Ny-Ålesund (both sites are at similar depth in the same fjord). However, Kvadehuken
had a significantly lower number of recruits than Ny-Ålesund and had abundant crustose coralline algae. This morphotype covers much of the rocky seafloor at Kvadehuken (Beuchel and Gulliksen 2008), and it recruited only at Kvadehuken and at 30 m on the nearby Kongsfjorden mooring, demonstrating the influence of local species composition on recruitment.

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

One of the most striking differences between sets of settlement plates was for the 30 m mooring stations in Kongsfjorden and Rijpfjorden. Settlement plates on moorings were not accessible to benthic predators and show “potential recruitment” according to the terminology of Dayton et al. (2016). The Rijpfjorden plates were dominated by Saccharina latissima and Alcyonidium gelatinosum, whereas the Kongsfjorden 30 m plates had these species but also a diverse community of macroalgae and invertebrates, with 15 morphotypes recorded. The S. latissima blades in the two fjords were also of vastly different size: several cm long in Kongsfjorden, and only visible under a dissecting microscope in Rijpfjorden (K. Meyer, pers. obs.). The lower water temperature, later warming and ice break-up observed in Rijpfjorden could mean that S. latissima individuals settled later in the year or grew more slowly in this
fjord. The low recruitment in Rijpfjorden contrasts starkly with the high diversity of the benthic
adults. Underwater photography revealed a diverse benthic hard-bottom community at the mouth
of Rijpfjorden, including boulders inhabited by sponges and bryozoans (Meyer et al. 2015).
Hard-bottom species are clearly able to recruit near the location of the mooring, but only two
individuals recruited to a total of eight settlement plates deployed at 195 m in Rijpfjorden. The
plates themselves were also quite clean, without even a noticeable biofilm (K. Meyer, pers. obs.).
Low recruitment may mean that Rijpfjorden benthic communities take a long time to develop.

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

Recruitment across depth

Our data revealed a strong decline in both the number and richness of recruits with
increasing depth (Fig. 8). Low recruitment could be related to the colder water temperature at
greater depth in the summer months in Kongsfjorden and Rijpfjorden. There may also be
reduced circulation or slower bottom currents at greater depth (Svendsen et al. 2002), causing
lower larval supply to settlement plates at these depths. Lower recruitment at greater depth may
mean these communities develop more slowly.
A deep (150 – 200 m) hard-bottom habitat in Kongsfjorden is dominated by the serpulid polychaete *Protula tubularia*, anemones (*Hormathia* spp.), and sponges (Laudien and Orchard 2012). However, none of these species recruited to deep (215 m) settlement plates in Kongsfjorden in this study. *P. turbularia* has a demersal, lecithotrophic larva (Tampi 1960), which may not have dispersed to the location of the mooring. Plates were instead dominated by *Stegopoma plicatile*, a common deep-water hydrozoan (Vervoort 1966; Edwards 1973) that occurs on the west Svalbard continental shelf and slope down to 1300 m (Bergmann et al. 2011; Meyer et al. 2013). Hydrozoans are commonly the first recruits to substrata in deep water. They are poor competitors and are easily overgrown (Ronowicz et al. 2008). The dominance of *S. plicatile* on the 215 m Kongsfjorden settlement plates implies that communities on these plates were at an early stage of succession.

Life-history traits of recruits and their roles in succession

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

The spirorbid polychaete *Circeis armoricana* was a dominant recruiting species at shallow stations in all seasons. *Semibalanus balanoides*, an acorn barnacle, and the bryozoans *Harmeria scutulata* and *Celleporella hyalina* also recruited in high density at all shallow stations.
during spring-summer and year-long deployments. *S. balanoides* and *C. armoricana* were overgrown by bryozoans on the settlement plates (Fig. 4). *Harmeria scutulata* is an opportunistic, annual species, and is one of the fastest-growing Arctic bryozoans (Kukliński and Taylor 2006). It loses >70% of interspecific competitive interactions with other bryozoans (Barnes and Kukliński 2003). *Celleporella hyalina* is also a poor competitor, losing >85% of interspecific interactions (Barnes and Kukliński 2003). Therefore, most common taxa observed on shallow settlement plates in this study (*C. armoricana, S. balanoides, H. scutulata, C. hyalina*) can be characterized as early-succession species.

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

Taxa conspicuously absent from our shallow settlement plates included ascidians and sponges. Epifaunal and encrusting species of both taxa, notably *Didemnum albinum* and *Halichondria* sp., are present at Kvadehuken (Jørgensen and Gulliksen 2001; Beuchel and Gulliksen 2008; Laudien and Orchard 2012), but none recruited to the settlement plates there or
at any other station. *D. albinum* and species of *Halichondria* brood their larvae (Marks 1996; Maldonado 2006), potentially leading to restricted dispersal. Ascidians and sponges are superior competitors in Svalbard waters (Barnes and Kukliński 2004) and are characteristic late-succession species at temperate latitude (Osman and Whitlatch 1995; Edwards and Stachowicz 2010). *Urticina eques* and *Hormathia nodosa* are abundant anemones at Kvadehuken, but only a single individual of *U. eques* recruited to a settlement plate there. *U. eques* lives over 40 years (Beuchel and Gulliksen 2008) and is well-defended against predators in the field (Lippert et al. 2004), so it is likely a late-succession or climax-community species.

**Conclusions**

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

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References


Fig. 1. Map of deployment locations. Circles indicate shallow locations (7 – 15 m) reached by SCUBA divers; squares indicate moorings (30 and 195 – 215 m). Depth contours shown every 100 m.

Fig. 2. Settlement plate design. Individual plates are 15 x 15 cm.

Fig. 3. Water temperature at settlement-plate deployment sites. A, shallow dock sites; B, Kongsfjorden mooring; C, Rijpfjorden mooring.
Fig. 4. Examples of *Semibalanus balanoides* and *Circeis armoricana* being overgrown (examples shown by white arrows) by different bryozoan species on settlement plates. A, *Tegella arctica*; B, *Cribrilina annulata*; C, *Harmeria scutulata*; D, *Umbonula arctica*.

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

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

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

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