



Recruitment dynamics of *Hiatella arctica* within a high Arctic site (Young Sound Fjord, NE Greenland)

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Abstract

Recruitment dynamics including what determines the success or failure of Arctic benthic invertebrates are poorly known despite their important role for population dynamics. The main objective of this study was to assess the potential influence of extreme physical constraints related to freshwater discharge on the recruitment of a dominant bivalve *Hiatella arctica* within a High Arctic fjord (Young Sound, NE Greenland). We collected young recruits over several sampling periods from 2016 to 2018 at two contrasting sites (inner vs. middle fjord) for 5-weeks to 12-months and measured their abundance, size at metamorphosis and lipid class composition. Young stages of *H. arctica* settled from June to the end of October, when trophic conditions are optimal. We hypothesize that growth stops during winter due to poor trophic conditions. Data suggest that abundance of recruits, their total lipid concentration and composition of lipid classes are similar at both sites. However, size classes were different with six separate cohorts detected at one station and one at the inner station, which may be attributed to discrete spawning events and possible secondary migration. Based on an assessment of their potential age, we hypothesize that spat batches recruiting earlier in the summer exhibit better growth performance probably related to better food quality and quantity.

Keywords Arctic · Bivalve recruitment · Prodissoconch II · Lipids classes

Introduction

The structure of communities and dynamics of populations are strongly influenced by the supply of recruits and their settlement and post-settlement success (Butman 1987; Ólafsson et al. 1994), but these processes are poorly known in polar regions. In the Arctic, bivalves often spawn directly after the phytoplankton bloom (Kuklinski et al. 2013), but data on recruitment are limited to a few species (Stanwell-Smith and Barnes 1997).

Global warming induces major modifications in the Arctic marine environment, e.g., a decrease in sea-ice cover (extent and thickness) and an increase in freshwater discharge (Kwok and Rothrock 2009; McPhee et al. 2009) leading to the intensification of the stratification (Bridier et al. 2021). In Greenland, warming drives increasing melt of the Greenland ice sheet and results in increased discharge of ice and meltwater (Howat et al. 2007; Kjeldsen et al. 2015). Released icebergs increase the risk of ice scouring (Sejr et al. 2021) while meltwater is likely to impact fjord circulation, surface-water temperature, salinity, and turbidity (Mortensen et al. 2013); low salinity also increases

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the susceptibility of marine organisms to other stressors (Nielsen et al. 2021). These physical parameters are often suggested to be important drivers of benthic recruitment in coastal areas (Yakovis et al. 2013), which can influence benthic productivity (Bashevkin et al. 2020; Leal et al. 2022). Increased temperature and turbidity or decreased salinity could lower survival rates of larvae as already documented in the White Sea (Ushakova and Saranchova 2003) or in the Kongsfjorden fjord (Svalbard Archipelago, Zajaczkowski and Legezyska 2001).

Because of its high abundance, colonizing various hard-bottom and soft-sediment habitats, *Hiatella arctica* (up to 57 ind m⁻², Sejr et al. 2002) is a promising marine bivalve model to study recruitment. This species has a variable duration of larval occurrence depending on the latitude (8 months at higher latitude and 1–2 months at lower latitude) (Brandner et al. 2017). It is a widespread and common circumpolar bivalve exhibiting substantial morphological/physiological plasticity and inhabiting coastal at depths down to 175 m (Ockelmann 1958) in temperate to polar areas (Gordillo 2001). The main objective of this study was to compare the seasonal recruitment success of *H. arctica* at two sites within a high Arctic fjord, i.e., the number of new recruits. We compare a site in the inner fjord (near the Zackenberg River called Pass Hytten) more influenced by low salinity and high turbidity due to freshwater run-off compared to a site in the outer fjord (middle fjord, Basalt Island). Sejr et al. (2022) observed a distinct surface freshwater lens throughout the fjord system, strongest in the inner fjord. We expected that recruitment of *H. arctica* would be lower in the inner fjord compared to a more marine area. The specific objectives were therefore (1) to measure the spatial (2 sites) and temporal variability of recruitment (a sampling scheme spanning 12 months) of a dominant marine polar bivalve, (2) to identify the presence of cohorts of recruits and assess their age, (3) to estimate the size at metamorphosis of each cohort, and finally (4) to obtain initial results on the physiological condition of young recruits by their lipid class composition.

Materials and methods

Study site and sampling strategy

The study was conducted in a ~90 km long and 2–7 km wide sill fjord where the maximum depth is 330 m and the sill at the entrance of the fjord is at 45 m depth (Young Sound, 74°18'N, 20°18'W, NE Greenland, Fig. 1). The shallow sill reduces exchanges with the open sea (Bendtsen et al. 2007). The fjord system is influenced by freshwater inputs from snow and ice melting, especially during summer (Bendtsen et al. 2007), and is covered by sea ice from late October

through June. Whereas water temperature and salinity at 60 m depth remain relatively stable around -1.8 °C and 32 psu respectively, they are much more variable at shallower depths with variations around two units for each parameter (~30 m) (Fig. 1, but also see De Cesare et al. 2017; Sejr et al. 2017; Bridier et al. 2019 for details). This trend is, however, higher in lower depth as observed by Sejr et al. (2022) at 17 m with salinity decrease from 31.5 to 27. These data agree with the model developed by Bendtsen et al. (2007) using averaged temperature and salinity in Young Sound confirming the desalination on upper water layers. Our sampling strategy included several deployment periods of either 5 weeks (August–September 2016), 9 months (August 2016–May 2017) and 12 months (May 2017–May 2018) at two contrasting sites (Fig. 1). Basalt Island (BI) (depth=21.5 m, 74.33°N, 20.36°W) is located in the most marine part of the fjord whereas Pass Hytten (PH) (depth=16.5 m, 74.41°N, 20.33°W) is in a more upstream section at the outlet of a river on silted and more turbid bottoms (Bridier et al. 2019; Holding et al. 2019). Both sites are influenced by an inflow of nutrient-depleted freshwater, with CO₂-desaturated, lower salinity and higher turbidity measurements (Fig. 1). Settling larvae and subsequent juveniles were collected with 'Tuffy' traps, extensively used in recruitment studies of invertebrate species (Menge et al. 1994). At each site mooring lines with subsurface buoys located at 5 m from the bottom were deployed by divers (Fig. 1). At each site, 9 to 15 replicate traps were collected. The biological material found on the traps were directly frozen and preserved at -80 °C until laboratory analyses.

Sample analyses

For each trap, recruits were retrieved by sieving it gently on a 200-micron square mesh with filtered seawater. Each batch of recruits was examined and counted under a binocular microscope to assess abundance per trap and subsequent recruitment rate (see below). Morphometric analysis of ~30 randomly selected individuals per trap were performed using the methods described in Martel et al. (1995) under a binocular stereomicroscope. For the examination of Prodissoconch PII (PII), the longest distance was measured along the anteroposterior axis (Fig. 2). Following the settlement and metamorphosis, when the veliger resorbs the velum to develop gills and transforms into a juvenile, the mantle initiates the secretion of a new dissoconch (D) shell resulting in the formation of a distinct demarcation line, the PII (between the veliger and juvenile shell, Martel et al. 1995). All measurements were made using Keyence VHX-2000 Series digital microscope with VH-Z100UR objectives (Osaka, Japan, 1 μm and HDR resolution). Lipids were extracted in dichloromethane-methanol as described in Parrish et al. (1999) using a modified Folch et al. (1957) procedure. Extracts were

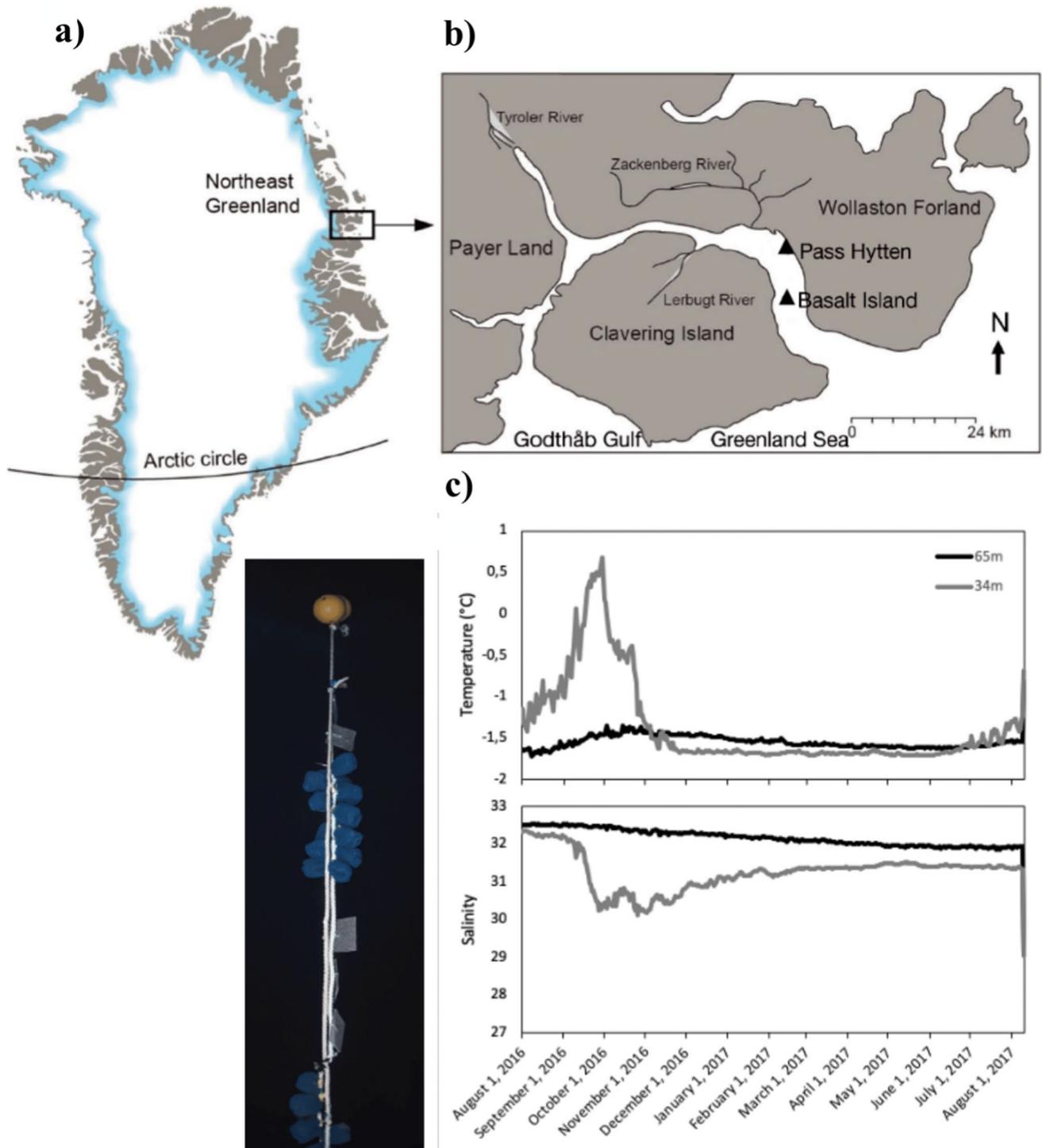


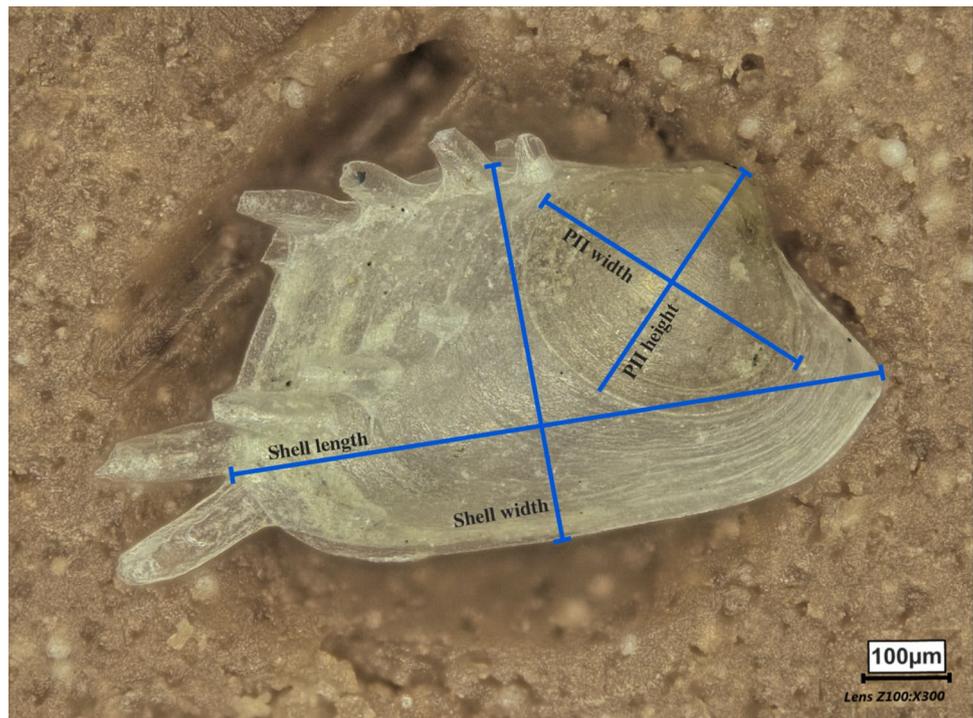
Fig. 1 **a** Location of studied sites, Pass Hytten and Basalt Island, in the fjord of Young Sound (YS), NE Greenland. **b** Picture of a long-period mooring deployed in each sampling station with 15 spat traps.

c Typical temperature and salinity (CTD) annual cycle (August 2016–August 2017) in YS close to the Basalt Island station

separated and analyzed by thin-layer chromatography using flame ionization detection with an Iatroscan MK-6 (Shell USA, Fredericksburg, VA, USA). This method separates aliphatic hydrocarbons (HCs), ketones (KETs), triglycerides

(TAGs), free fatty acids (FFAs), free fatty alcohol (ALCs), free sterols (STs), diglycerides (DGs), acetone mobile polar lipids (AMPLs), and phospholipids (PL). Lipid classes were identified and quantified with the use of standard calibration

Fig. 2 Picture of a recruit of *H. arctica* using a Keyence VHX-2000 Series digital microscope showing the various measurements acquired



curves obtained for each lipid class. Lipid classes were quantified in $\text{mg.individual}^{-1}$, summed up and expressed as a percentage of total lipids. Lipids were analyzed only on 9 months samples due to their higher biomass availability, as these analyses required at least $50 \mu\text{g}$ of tissues.

Data analyses

In *Hiatella arctica*, little is known about larval growth in the Arctic, and we estimated post-larval growth by firstly quantifying the difference between total shell length and PII size. Then, to assess days since metamorphosis, i.e. the distinct line where the prodissoconch II stage ends and a new shell begins known as the dissoconch (D), we used a growth estimate of $8 \mu\text{m.day}^{-1}$ from the study of Flyachinskaya (1999) focusing on the larval development of *Hiatella arctica* L. in one other Arctic area, the White Sea. Differences in the abundances of recruits were investigated by performing permutational univariate analyses of variance (PERMANOVA, 9999 permutations) and matrix of similarity based on the Euclidean Distance using PRIMER 7/PERMANOVA+. Two sources of variation were tested among treatments including ‘Sites’ (BI or PH) and ‘Period’ (2016: 5 weeks; 2017: 9 months and 2018: 12 months). The number of replicates was determined by the number of traps used and varied between 9 and 11. Owing to logistical limitations of divers’ availability in this Arctic environment, mooring line was limited per site and not fully replicated. Therefore, the unit of replication used in these analyses was the trap. In

theory, our approach could be perceived to violate the fundamental assumption of independence between replicates. However, the independence of data among samples is a biological issue (Underwood 1997, Sect. 7.14, p. 159) and we considered that each standardized trap was an appropriate replicate to measure the recruitment success. To investigate cohort composition and age structure, we performed a length frequency analysis and estimated the proportion of individuals in each cohort. We used a Gaussian mixture model to account for the length distribution and identify the number of cohorts in each sample. The number of components of the finite mixture model was assessed using an information criterion. More specifically, we used the Singular Bayesian Information Criterion (sBIC) (Drton and Plummer 2013). This information criterion is robust in situations where models are irregular, which can be the case for Gaussian mixture models. This criterion allows determining the model (i.e., the number of components) that best accounts for the data-generating process. The R (R Core Team 2013) package ‘sBIC’ (Weihs and Plummer 2016) uses the Expectation–Maximization (EM) algorithm to approximate maximum likelihood estimates of model parameters, estimate the posterior probabilities of cluster membership for each data point, and model posterior probabilities. We considered a maximum of 10 components and the sBIC allowed ranking models including a different number of components and selecting the model that best accounts for the process that generated the data. Once the number of components has been determined, the R package ‘mclust’ (Scrucca et al.

2016) was used to produce a density estimate for each data point and estimate the mean and standard deviation of each Gaussian component of the mixture model. The analysis associated to one year's data was performed on either 171 and 255 length measurements corresponding to PH or BI respectively. The 5-week period data included 14 (PH) and 80 (BI) length measurements. Lipid classes of young recruits were analyzed on the 9-month period data via 1-way PERMANOVAs (9999 permutations) with 2 fixed levels (BI and PH) and 10 replicates. One-way ANOVA was used to compare mean PII sizes between the 2 'Period' (2016: 5 weeks and 2018: 12 months). Shapiro test and Bartlett test were tested to validate normality and homoscedasticity assumptions. For all statistical tests, a level was set to 0.05 and statistical analyses were performed using R software (R Core Team 2013).

Results

Abundance pattern

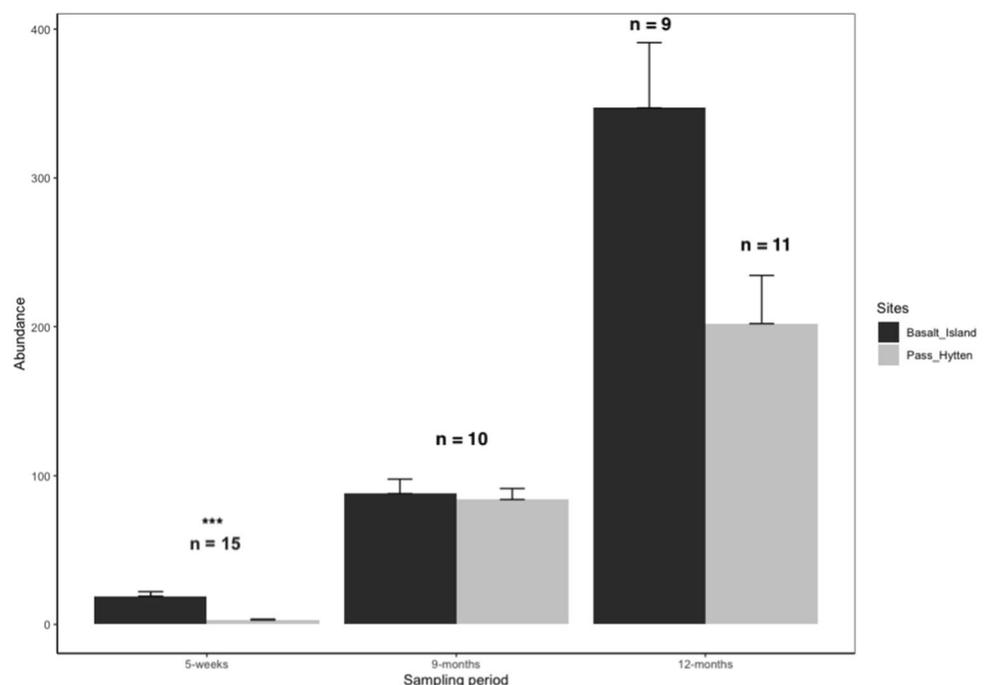
Hiatella arctica was the dominant species recruiting on traps, its relative abundance exceeding 92% for long sampling periods in both stations (Online Resource 1, Table A1). For the 9- and 12-month periods 937 and 909 recruits or 2909 and 3286 recruits were collected in PH and BI, respectively. By contrast, the proportion of *H. arctica* collected over 5 weeks during the fall season was quite low, with 9 and 25% of the total abundance of recruits at PH and BI,

respectively (581 and 1156 individuals). However, this is mostly due to the high proportion of unidentified post-larvae during this period (64% at BI, 70% at PH). Abundances of *H. arctica* were similar between both stations (P-perm = 0.1833, Pseudo-F = 1.8681, Df = 1 and Df residuals = 64), but differences appeared between sampling periods (P-perm = 0.0001, Pseudo-F = 142.7, Df = 2 and Df residuals = 64), without interaction between 'Site' and 'Period' (P-perm = 0.5875, Pseudo-F = 0.5288, Df = 2 and Df residuals = 64) (Fig. 3). The increase in the number of recruits as the duration of the sampling period increases reveals a cumulative recruitment starting with fewer than 19 ± 3.0 recruits (\pm SE) collected during 5-week periods in PH and 3 ± 1.0 recruits in BI, and mean abundance per trap increasing up to 84 ± 7 (PH) and 88 ± 10 (BI) during the 9-month period, and to 288 ± 32 individuals for 12-month periods in PH and 347 ± 42 in BI (Online Resource 1, Table A1).

Size-class distribution and growth

For the 12-month sampling period, shell length of *H. arctica* recruits collected in PH varied from 485.7 to 976.0 μm (mean value of 721.3 ± 8.1 μm ; \pm SE, $n = 171$) and from 495.6 to 971.7 μm (mean value of 687.2 ± 6.3 μm ; \pm SE, $n = 255$) in BI (Fig. 4) (Table 1). In BI, five independent cohorts were detected (Fig. 4) (posterior model probability = 0.79, $\log(\text{likelihood}) = -1514.62$, Df = 14, Online Resource 1, Fig. A1) whose mean shell length was equal to 523.1, 607.4, 678.6, 765.3 and 884.4 μm (Table 1), contrasting with one sole cohort in PH (posterior model probability = 0.61,

Fig. 3 Mean abundance per spat trap (\pm Standard Error) of recruits of *H. arctica* collected at both studied sites over either 5 weeks, 9, or 12 months. *** Indicates a significant difference at 0.0001



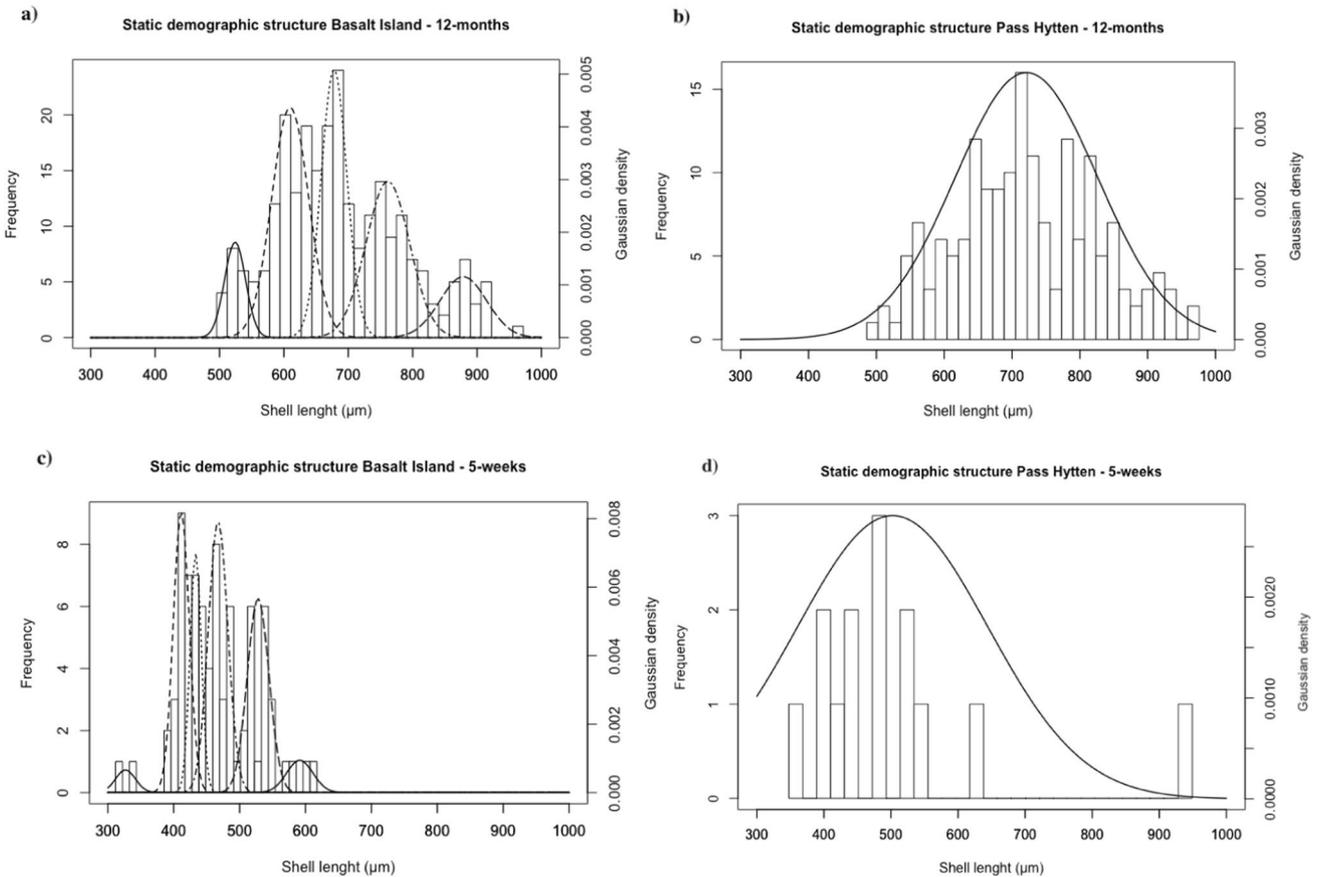


Fig. 4 Size-class of recruits of *H. arctica* collected in 12 months' spat traps (immersed from mid-May 2017 to mid-May 2018) at either **a** Basalt Island or **b** Pass Hytten and in 5-week samples (immersed from August 2016 to September 2016) at **c** Basalt Island and **d** Pass

Hytten. Lines represent the estimated Gaussian densities (probability density) corresponding to the different cohorts (Gaussian finite mixture model), one-line type by cohorts

Table 1 Size distributions for post-larvae of *H. arctica* observed in samples collected during different sampling periods on both sampling sites

Site	Size classes	<i>n</i>	Mean full length (µm)	SE	Mean PII size (µm)	SE	Δ (full length – PII size (µm))	Approximate age (days)
Basalt Island 12 months	1 [495; 555]	19	523.1	3.4	287.3	3.2	235.7	~ 29.5
	2 [555; 648]	78	607.4	2.8	291.2	1.4	316.2	~ 39.5
	3 [648; 712]	69	678.6	2.0	291.9	1.9	386.7	~ 48.3
	4 [712; 834]	64	765.3	3.8	291.8	2.9	473.5	~ 59.2
	5 [834; 972]	25	884.4	6.3	291.3	4.4	593.1	~ 74.1
Pass Hytten 12 months	1 [485; 980]	171	721.3	8.1	282.6	1.4	438.7	~ 54.8
Basalt Island 5 weeks	1 [310; 385]	2	326.7	15.1	326.4	10.3	0.3	~ 0
	2 [385; 423]	19	409.5	2.4	301.4	2.7	108.0	~ 13.5
	3 [423; 445]	13	433.6	1.6	311.4	3.3	122.1	~ 15.3
	4 [445; 500]	24	468.4	14.0	314.8	2.8	153.6	~ 19.2
	5 [500; 560]	18	528.6	3.4	313.8	2.7	214.8	~ 26.9
	6 [560; 618]	4	591.1	10.6	316.1	1.3	275.0	~ 34.4
Pass Hytten 5 weeks	1 [347; 950]	14	502.6	39.4	306.1	6.5	196.5	~ 24.6

$\log(\text{likelihood}) = -1038.79$, $Df = 2$, Online Resource 1, Figs. A1 and 4). Based on 5-week sampling period, size classes of recruits varied from 311.6 to 617.4 μm (mean value of $464.9 \pm 6.4 \mu\text{m}$; $\pm \text{SE}$, $n = 80$) in BI and from 347.8 to 949.2 μm (mean value of $502.6 \pm 39.4 \mu\text{m}$; $\pm \text{SE}$, $n = 14$) in PH (Table 1, Fig. 4). Whereas no cohorts could be detected in PH ($\log(\text{likelihood}) = -89.25$, $Df = 2$), six were observed in BI (Fig. 4) (posterior model probability = 0.33, $\log(\text{likelihood}) = -425.94$, $Df = 17$, Online Resource 1, Fig. A1) with corresponding mean lengths of 326.7, 409.5, 433.6, 468.4, 528.6 and 591.1 μm (Table 1). In fact, size-class distributions were similar for 5-week and 12-month data in BI, but with a larger size range in the 12-month sample (Fig. 4). Moreover, at BI the mean PII size of each cohort was very close to the same sampling duration, but not for different duration, with a mean value of 314.0 μm over 5 weeks and 290.7 μm over 12 months ($F\text{-value} = 39.23$, $P\text{-value} = 0.000147$, $Df = 1$, $Df \text{ residuals} = 9$, Anova) (Table 1). At PH, the mean PII size for the two periods were similar as in BI, with a mean value of 306.1 μm over 5 weeks and 282.6 μm over 12 months (Table 1). Assuming a means post-larval growth of 8 μm per day, approximated ages of *H. arctica* recruits in BI ranged from ~29 to 74 days in the 12-month period, and from ~0 to 34 days in the 5-week sampling period, respectively (Table 1).

Lipid classes

The total concentration of lipids in recruits collected over the 9-month sampling period was similar in both sites (Pseudo- $F = 0.0209$, $P\text{-perm} = 0.8755$, $Df = 1$, $Df \text{ residuals} = 18$), with a mean value of $0.61 \pm 0.15 \text{ mg} \cdot \text{individual}^{-1}$. Seven lipid classes were detected with the highest contributions of phospholipid (PL), representing near 90% of the total lipids, and low values of 1% for triglycerides (TAG) (Online Resource 1, Table A2).

Discussion

Spatial bivalve recruitment patterns in the Young Sound fjord

H. arctica was the dominant species recruiting on the spat traps throughout the surveys at both sampling sites (PH, BI). No difference was observed between sites for the abundance of *Hiatella* recruits with an increasing number of recruits found in samples collected over 5 weeks, 9 months and 12 months, respectively. No spatial differences were observed in 9-month samples for the total lipid concentration and the lipid class composition. Such results are quite surprising because PH and BI sites are submitted to contrasting freshwater inputs (Bridier et al. 2019, 2021) that

could have influenced the survival and growth of the young bivalve recruits (Bashevkin et al. 2020). In the White Sea, Saranchova et al. (2006) showed that pediveliger larvae of *H. arctica* display a higher resistance to low salinity than those of *Heteranomia ovata*. The larval stage of *H. arctica* can endure reduced salinity for 2 weeks, with survival rates of 25% at a salinity of 12‰ (Saranchova et al. 2006). Such data could explain the dominance of *H. arctica* in the assemblages of recruits observed in spat traps, especially if, during their pelagic dispersal with the currents, bivalve larvae enter the surface layers of the fjord that exhibit the most variable salinity, temperature, and turbidity during summer (Bendtsen et al. 2007).

The size-class distributions displayed both spatial and temporal differences. At the BI site, we detected 6 cohorts but only one at PH. The single cohort at PH could result from too much overlap of cohort-specific size distributions (i.e., failure to identify cohorts), although a similar 500–1000 μm size's range was observed at both sites and we did find evidence of cohorts in BI. In addition, we hypothesize that the shift between the size ranges of the two sampling periods from 300 to 650 μm over 5 weeks and from 500 to 1000 μm over 12 months reveals secondary settlement stimulated by trophic conditions, as observed by Forêt et al. (2018, 2020). In YS, we suggest that recruits drifting with the currents from the middle to the inner fjord could be bigger in PH due to the trophic conditions. As pointed out by Forêt et al. (2018, 2020) secondary dispersal temporal patterns depend on both the physiology of bivalve recruits and the pelagic trophic environment, a phenomenon called “trophic migration trigger”, analogous to “trophic settlement trigger” (Toupoint et al. 2012; Androuin et al. 2022).

Trophic constraints on larvae of filter-feeding bivalves

To survive within Arctic Fjords, planktotrophic larvae, feeding on phytoplankton, must be able to respond to short periods of high food availability and prolonged periods of low resources during the polar night (Weslawski et al. 1991). In the present study, we determined that the concentration of total lipids found in *H. arctica* recruits was about 0.6 $\text{mg} \cdot \text{individual}^{-1}$ and associated with a low energetic lipid (TAG) accumulation of 1% at the end of the winter 2017. Gallagher et al. (1986) studied the lipid class composition of healthy and starved larvae of *Crassostrea virginica* and *Mercenaria mercenaria* and showed that energetic (TAG) and structural (PL) lipids were roughly in equal proportion throughout the development of healthy larvae. TAG content is an indicator of larval quality and is directly affected by exogenous food intake and also influenced by environmental stress increasing metabolic activity and reducing food intake (Fraser 1989). In our study, no data on larvae are available, but the

very weak TAG accumulation in the recruits sampled seems to indicate starvation in May and potentially poor physiological condition at the end of winter. Another explanation could be the complete use of energy obtained from food to direct transfers to growth without energetic reserve accumulation. However, in optimal laboratory condition, bivalve post-larvae fed ad libitum without environmental stressful conditions showed important TAG accumulation concomitant with substantial shell growth (Gagné et al. 2010).

Temporal pattern of bivalve recruitment within the YS fjord

The mean PII sizes of *H. arctica* recruits in the YS fjord of 290 μm (12-month period) and 314 μm (5-week period) are significantly lower than previous values of 380–400 μm observed for the same species in the White Sea by Flyachinskaya and Lezin (2008). Such values of 290–314 μm can be compared to PII sizes of post-larvae and juveniles of other bivalves of subarctic areas, which can reach up to 422 μm for the blue mussel *Mytilus edulis* (Martel et al. 2014; South 2016). Food supply during the planktonic phase, as well as seawater temperature, are among the most important factors determining the size of veliger larvae at metamorphosis, that is, at the end of the planktonic life (Pechenik 1990; Emler and Sadro 2006). As hypothesized by Pechenik and Levine (2007) and Martel et al. (2014), a short larval phase associated to small PII size at the settlement could decrease larval mortality within the water column due to reduced exposure to predation or dispersal to unsuitable habitats. It is also suggested that a longer larval phase associated to large PII size at the settlement could decrease the probability of early mortality of juveniles because of a larger size and a larger pump for more filter-feeding activity (Pechenik et al. 1996). However, data obtained with oysters *Crassostrea gigas* in a Mediterranean lagoon were not consistent with this hypothesis: an inverse relationship between PII size and survival after metamorphosis was observed, showing that recruitment success was associated with smaller PII sizes (Lagarde et al. 2018). The relatively small and uniform size at metamorphosis (PII size < 310 μm) observed in this study is probably related to a trade-off between growth and the necessity for pediveliger larvae to undergo metamorphosis rapidly and access to the more rapid post-larval growth thanks to the development of gills (Gagné et al. 2010). Because of low seawater temperatures throughout the year, metabolism and growth of marine invertebrates are classically slowed down in the polar environment (Clarke 1992). However, Sejr et al. (2004), working on the resource limitations to growth and production of YS *H. arctica* populations, suggested that despite low rates of assimilation and growth at low temperature, *H. arctica* adults were able to grow much faster in laboratory experiments than observed in YS when provided

with food. Thus, low food availability seems to be the major factor of growth regulation.

In this study, data collection was constrained by difficulties accessing the marine station of the YS fjord. The sampling scheme covers various recruitment periods over several years from 2016 to 2018. While the 5-week period provides a state in late summer/early fall 2016, the 9-month period extends to the end of winter 2016–2017, and the 12-month period includes the summer of 2017 and lasts up to the end of winter 2017–2018. The size-class distributions of recruits collected during 1 year at both sampling sites reveal the occurrence of several successive cohorts with small PII size differences, which suggests several spawning events in *H. arctica*, and a similar size at metamorphosis. As emphasized by Martel et al. (2014), in *Mytilus edulis* recruits mean PII size can be highly variable, which reflects metamorphosis delays later in the recruitment season. Here, with relatively small and constant PII size (< 310 μm), we suggest that there is no metamorphosis delay, and that primary settlement is probably controlled by a similar triggering cue. Many studies have focused on such settlement cues, including trophic signals linked to phytoplankton blooms (*Trophic Settlement Trigger* TST, Toupoint et al. 2012; Lagarde et al. 2018; Leal et al. 2018), to water temperature (mussels: Bayne 1964, clams: Lutz and Jablonski 1978; Bayne and Newell 1983) or to chemical cues (Hadfield and Paul 2001). The synchronization between the larval cycle and primary production is related to the 'match/mismatch' theory (Cushing 1990). Thus, an earlier break up of sea ice in spring followed by an early phytoplankton bloom, could in turn lead to a temporal desynchronization between this peak of primary production and that of pelagic secondary consumers such as zooplankton, including meroplankton (Søreide et al. 2010; Leu et al. 2011).

Spawning and larval presence of *H. arctica* in Arctic waters

Based on previous larval growth studies on *H. arctica* (Flyachinskaya 1999) and on the size of the five different cohorts identified at BI (12-months), we estimated that the age of oldest recruits, around 884.4 μm (i.e., those that have settled at the earliest), could reach 74 days or more. Such an age would indicate the beginning of spawning in February 2018 which seems unlikely given the conditions, a period with ice cover, without light or primary production. Nevertheless, a study of the occurrence and abundance of pelagic bivalve larvae within a high Arctic fjord (Adventfjorden, Svalbard) identified a strong seasonality in the occurrence of bivalve larvae, largely coinciding with periods of primary productivity (Brandner et al. 2017). The seasonal occurrence of bivalve larvae shows variation in duration across the biogeographic range of *H. arctica*, with longer

duration at higher latitudes (8 months at 56°N and 78°N) and shorter duration at lower latitude populations (1–2 months at 42°–46°N) (Brandner et al. 2017). Such results contradict those of Ockelmann (1958) who observed only 2 months of *H. arctica* larval presence at a latitude of 78°N. According to Kulikova et al. (2013) larvae of *H. arctica* drift in the water column between May and December at all latitudes whereas the period of presence shifts to Autumn (September–October) at lower latitudes. The spawning season of *H. arctica* has been determined in the White Sea, lasting from June to November in a study conducted at a lower latitude (Flyachinskaya and Lezin 2006, 2008). For the data of 5-weeks at BI, we estimated that the age of oldest recruits (i.e., those that have settled at the earliest) could reach 34 days or more. Thus, we suggest that the spawning of *H. arctica* in YS starts potentially in June until the end of October in relation to the phytoplankton blooms related to the break up of ice cover around mid-July (Rysgaard et al. 1999) for a period of around 80 days. This hypothesis could agree with the age estimate integrating a slower growth during the unfavorable winter conditions.

Perspectives

Climate change with declining sea-ice cover and accelerated melting of glacial ice should increase freshwater input and turbidity in the water column (Sejr et al. 2022). Whereas the high phenotypic plasticity of *H. arctica* to freshwater input is well detailed (Saranchova et al. 2006), the primary production in Young Sound should be more structuring on such a species. Indeed, as sea-ice cover (extent and thickness) will decline under warming, this will have an impact on the production of sympagic algae which will also impact pelagic and benthic communities through loss of ice algal production (Søreide et al. 2013). However, the magnitude and direction of these effects on the various fjord ecosystems around Greenland are still largely unclear. The desynchronization between an earlier phytoplankton bloom during the season due to advanced ice retreat and peaks of zooplankton (Søreide et al. 2010; Leu et al. 2011; Gaillard et al. 2017) could be important for the recruitment success of *H. arctica* (growth, size at the settlement, physiological state of larvae and post-larvae). Starvation due to poor trophic conditions, depleting the nutritional reserves, could lead larvae of *H. arctica* to settle with low energetic contents, which would be consistent with the ‘*Desperate larvae Hypothesis*’ (Knight-Jones 1953; Toonen and Pawlik 2001; Elkin and Marshall 2007). Under climate change, modifications in the composition or dynamics of the phytoplankton community could lead to asynchronies between different trophic levels such as an increase in the proportion of dinoflagellates upon diatoms (Hernández-Fariñas et al. 2014). The trophic regimes and their dynamics that control the functioning of

benthic marine invertebrate communities, including their dominant component such as *H. arctica* in the Arctic, would be deeply modified. As an example, phytoplankton communities should be dominated by smaller cells such as picophytoplankton (Holding et al. 2019) that are known to synchronize the primary settlement of mussel larvae (Toupoint et al. 2012; Androuin et al. 2022), and thus potential risks of mismatches. Because *H. arctica* is one of the preferred preys of walrus and eider ducks, a reduction in population sizes as well as energy reserves of adults could impact the benthic-pelagic coupling in polar areas, with cascading effects on higher trophic levels (Kędra et al. 2015; Jézéquel et al. 2022).

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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