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

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## Research Article

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# Abstract

Recruitment dynamics including what determines 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 seasonal/physical constraints, in particular freshwater discharge, on the recruitment of a dominant bivalve *Hiatella arctica* within a High Arctic fjord. 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 in both sites. By contrast, analyses of size-class show differing temporal and spatial patterns with 6 cohorts detected in middle fjord and only one at the inner station, which can 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 because of higher food quality and availability.

## 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 spawn directly after the phytoplankton bloom (Kuklinski et al. 2013), but data on recruitment are limited to few species (Stanwell-Smith and Barnes 1997). According to Thorson (1950), high latitude marine invertebrates exhibit mostly lecithotrophic development (i.e., the larvae rely on energy reserves but not on food sources), due to low and unpredictably phytoplankton biomass. Nevertheless, in recent years, the discovery of more pelagic larvae in polar waters than expected questioned on the general validity of the Thorson model (Pearse 1994). It is becoming increasingly clear that mixed types of development coexist, even within a single species, and that the flexibility and plasticity of life strategies are substantial (Hadfield and Strathmann 1996).

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 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 Legezynska 2001).

Because of its high abundance, colonizing various hard-bottom and soft-sediment habitats, *Hiatella arctica* (up to 57 ind.m<sup>-2</sup>, Sejr et al. 2002) is a promising marine bivalve model to study recruitment. This species has a long pelagic larval stage (Gordillo 2001). It is a widespread common circumpolar bivalve exhibiting substantial morphological/physiological plasticity and inhabiting shores up to 175 m depth (Ockelmann 1958) in temperate to polar areas (Gordillo 2001). The main objective of this study was to evaluate the seasonal recruitment success of *H. arctica* at two sites in a high Arctic fjord. A site in the inner fjord more influenced by low salinity and high turbidity due to freshwater run-off compared to a site in the outer fjord (Sejr et al. 2022). We expected that recruitment of *H. arctica* would be lower at the site near the Zackenberg River (inner fjord, Pass Hytten) compared to a more marine area (middle fjord, Basalt Island). 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

### 1. Study site and sampling strategy

The study was conducted in the ~ 90 km long and 2–7 km wide deep-sill fjord of 330 m depth with an entrance of 45 m depth (Young Sound, 74°18'N, 20°18'W, NE Greenland, Fig. 1), reducing exchanges with the open sea (Bendtsen et al. 2007). This 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 September to June. Whereas bottom water temperature and salinity at 60 m depth remain relatively steady around -1.8°C and 32 psu respectively, they are much more variable during summer at shallower depths (~ 30 m) (Fig. 1, but also see De Cesare et al. 2017; Bridier et al. 2019; Sejr et al. 2022 for details). 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) in 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; Sejr et al. 2022). Both sites are influenced by an inflow of nutrient-depleted freshwater, with CO<sub>2</sub>-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). In each site mooring

lines with subsurface buoys located at 5 m from the bottom were deployed by divers at a depth of 20 m. At each site, 10 replicate traps were collected. The biological material found on traps were directly frozen and preserved at -80°C until laboratory analyses.

## 2. Sample analyses

For each trap/replicate, 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 settlement 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). All measurements were made using Keyence VHX-2000 Series digital microscope with VH-Z100UR objectives (Osaka, Japan, 1µm and HDR resolution). Lipids were extracted in dichloromethane-methanol as in Parrish (1999) by using a modified Folch procedure (1957). Extracts were 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 curves obtained for each lipid class. Lipid classes were evaluated in  $\text{mg.individual}^{-1}$ , summed 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 50µg of tissues.

## 3. Data analyses

In *Hiatella arctica*, little is known about larval growth in the Arctic, and we approximated value of post-larval growth by firstly quantifying the difference between total shell length and PII size. Then, to assess days since metamorphosis, we used a growth estimate of 7 µm/day from the study of Flyachinskaya and Lezin (2017) focusing on the larval development of *Mya arenaria* in the White Sea, an environment close to our study area. 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: 5weeks; 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. 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 2017). 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 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. Non-parametric Wilcoxon test was used to compare mean PII sizes and means of Gaussian components in the size-class distribution. For all statistical tests, a level was set to 0.05.

## Results

### 1. Abundance pattern

*Hiatella arctica* was the dominant species recruiting on traps, its relative abundance exceeding 92% for long sampling periods in both stations. For the 9- and 12-month periods 909 and 937 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 28% of the total abundance of recruits at PH and BI, respectively (339 and 863 individuals). However, this is mostly due to the high proportion of unidentified post-larvae during this period (60% at BI, 75% at PH). Abundances of *H. arctica* were similar between both stations (P-perm = 0.1983, Pseudo-F = 134.99, Df = 2 and Df residuals = 62), but differences appeared between sampling periods (P-perm = 0.0001, Pseudo-F = 1.7474, Df = 1 and Df residuals = 62), without interaction between 'Site' and 'Period' (P-perm = 0.6093, Pseudo-F = 0.5152, Df = 2 and Df residuals = 62). The increase in the number of recruits as the duration of the sampling period increases reveals a cumulative recruitment starting with fewer than  $19 \pm 3.0$  recruits ( $\pm$  SE) collected during 5-week periods in PH and BI, and mean abundance per trap increasing up to  $> 83 \pm 7.4$  during the 9-month period, and to  $> 302 \pm 32.5$  individuals for 12-month periods at both sites (Fig. 3).

### 2. 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  $\mu\text{m}$  (mean value of  $721.3 \pm 8.1$   $\mu\text{m}$ ;  $\pm$  SE, n = 171) and from 495.6 to 971.7  $\mu\text{m}$  (mean value of  $687.2 \pm 6.3$   $\mu\text{m}$ ;  $\pm$  SE, n = 255) in BI (Fig. 4) (Table 1). In BI, five independent cohorts were detected (posterior model probability = 0.79, log(likelihood) = -1514.62, Df = 14, Supplementary File 1) (Fig. 4)

whose mean shell length was equal to 523.1, 607.4, 678.6, 765.3 and 884.4  $\mu\text{m}$  (Table 1), contrasting with one sole cohort in PH (posterior model probability = 0.61,  $\log(\text{likelihood}) = -1038.79$ ,  $Df = 2$ , Supplementary File 1) (Fig. 4). Based on 5-week sampling period, size classes of recruits varied from 311.6 to 617.4  $\mu\text{m}$  (mean value of  $464.9 \pm 6.4 \mu\text{m}$ ;  $\pm SE$ ,  $n = 80$ ) in BI and from 347.8 to 949.2  $\mu\text{m}$  (mean value of  $502.6 \pm 39.4 \mu\text{m}$ ;  $\pm SE$ ,  $n = 14$ ) 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 (posterior model probability = 0.33,  $\log(\text{likelihood}) = -425.94$ ,  $Df = 17$ , Supplementary File 1) (Fig. 4) with corresponding mean lengths of 326.7, 409.5, 433.6, 468.4, 528.6 and 591.1  $\mu\text{m}$  (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 for the same sampling duration, but not for different durations, with a mean value of 314.0  $\mu\text{m}$  over 5 weeks and 290.7  $\mu\text{m}$  over 12 months ( $F\text{-value} = 39.23$ ,  $P\text{-value} = 0.000147$ ,  $Df = 1$ ,  $Df \text{ residuals} = 9$ , Anova) (Table 1). Assuming a mean post-larval growth of 7  $\mu\text{m}$  per day, approximated ages of *H. arctica* recruits in BI ranged from  $\sim 33$  to 85 days in the 12-month period, and from  $\sim 0$  to 40 days in the 5-week sampling period, respectively (Table 1).

Table 1

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

Site	Group	n	Mean Full length	SE	Mean PII Size	SE	$\Delta$ (Full length-PII size)	Approximate age (days)
Basalt Island 12 months	1	[495; 555]	19	523.1	3.4	287.3	3.2	235.7 ~ 33.7
	2	[555; 648]	78	607.4	2.8	291.2	1.4	316.2 ~ 45.2
	3	[648; 712]	69	678.6	2.0	291.9	1.9	386.7 ~ 55.2
	4	[712; 834]	64	765.3	3.8	291.8	2.9	473.5 ~ 67.6
	5	[834; 972]	25	884.4	6.3	291.3	4.4	593.1 ~ 84.7
Pass Hytten 12 months	1	[485; 980]	171	721.3	8.1	282.6	1.4	438.7 ~ 62.7
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 ~ 15.4
	3	[423; 445]	13	433.6	1.6	311.4	3.3	122.1 ~ 17.4
	4	[445; 500]	24	468.4	14.0	314.8	2.8	153.6 ~ 21.9
	5	[500; 560]	18	528.6	3.4	313.8	2.7	214.8 ~ 30.7
	6	[560; 618]	4	591.1	10.6	316.1	1.3	275.0 ~ 39.3
Pass Hytten 5 weeks	1	[347; 950]	14	502.6	39.4	306.1	6.5	196.5 ~ 28.1

### 3. 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-perm = 0.8755, Df = 1, Df residuals = 18), with a mean value of  $0.61 \pm 0.15$  mg/individual. Seven lipid classes were detected with highest contributions of Phospholipid (PL), representing near 90% of the total lipids, and low values of 1% for Triglycerides (TAG) (Supplementary File 1).

## 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 classes 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 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 larvae stage *H. arctica* can endure reduced salinity for 2 weeks, with survival rates of 25% at salinities at 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, 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 size range was observed at both sites 500 to 1000µm 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 650µm over 5 weeks and from 500 to 1000µm over 12 months reveals secondary settlement stimulated by trophic conditions, as observed by Forêt et al. (2018, 2020). In YS, recruits would drift from the middle to the inner fjord in response to better food conditions or to density dependence interactions allowing an allochthonous recruitment in PH. 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” (TMT), analogous to “trophic settlement trigger” (TST) (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 in YS collected in both sites seem to be low with values around  $0.6 \text{ mg.individual}^{-1}$  and 1% of TAG 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 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 young juveniles 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  $290\mu\text{m}$  (12-month period) and  $314\mu\text{m}$  (5-week period) are clearly larger than previous values of  $200\mu\text{m}$  observed for the same species in the White Sea by Lyachinskaya and Lezin (2008). Such values of  $290\text{--}314\mu\text{m}$  can be compared to PII sizes of post-larvae and juveniles of other bivalves of subarctic areas, which can reach up to  $422\mu\text{m}$  for the blue mussel *Mytilus edulis* (South 2016; Martel et al. 2014). 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 et al. 1990; Emllet 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 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 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 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  $< 310\mu\text{m}$ ) 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-larvae 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 2017 and lasts up to the end of winter 2017–2018. The size-class distributions of recruits collected during one 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 (< 310µm), 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 ice breakout earlier in the season could lead to an early phytoplankton bloom, which in turn could lead to a temporal desynchronization between this peak of primary production and that of pelagic secondary consumers such as zooplankton, including meroplankton (Sørense 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 and Lezin 2017) and on the size of the five different cohorts identified at BI (12-months), we estimated that the age of oldest recruits (i.e., those that have settled the earliest), could reach 85 days or more. Such an age would indicate the beginning of spawning in February 2018, a period with ice cover, without light or primary production. Moreover, 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 the earliest) could reach 39 days or more. So, it is possible that the spawning of *H. arctica* in YS starts in June and lasts up to the end of October because

timing of blooms is related to the break-up of ice cover around mid-July (Rysgaard et al. 1999) for a period of around 80 days.

## 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 *Hiatella 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, as will the production of sympagic algae, the dynamics of stratification and light conditions will occur (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 peak of zooplankton (Søreide et al. 2010; Leu et al. 2011; Gaillard 2017) could be important for the recruitment success of *H. arctica* (growth, size at 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' (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; Zéquel et al. 2022).

## Declarations

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### Author contributions

DV acquired shell length and fatty acid data, performed statistical analyses, and wrote the initial MS draft. RT supervised fatty acid and shell length analyses, contributed to results interpretation and manuscript review. MKS helped in field operations and collecting biological and environmental data, contributed to results interpretation and manuscript review. LC helped in field operations (scuba-diving) and collecting biological and environmental data, contributed to results interpretation and manuscript review. EC supervised modal decomposition analysis of shell length data, contributed to results interpretation and manuscript review. FO conceived and supervised the sampling survey, led the project administration and funding acquisition, contributed to results interpretation and manuscript review.

### Conflict of interest

The authors declare that they have no conflict of interest.

### Informed consent

All authors consent to the publication of this manuscript.

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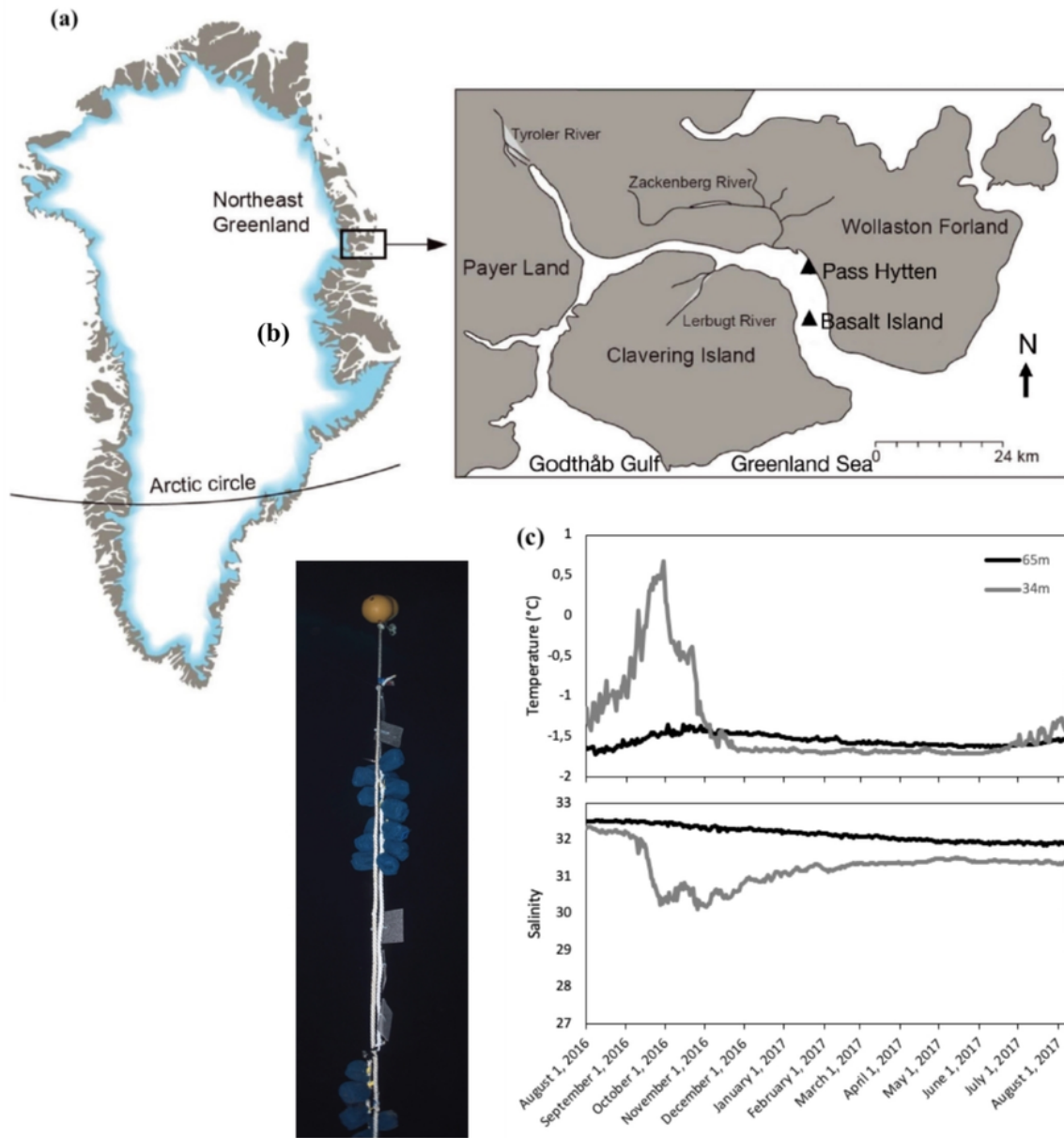


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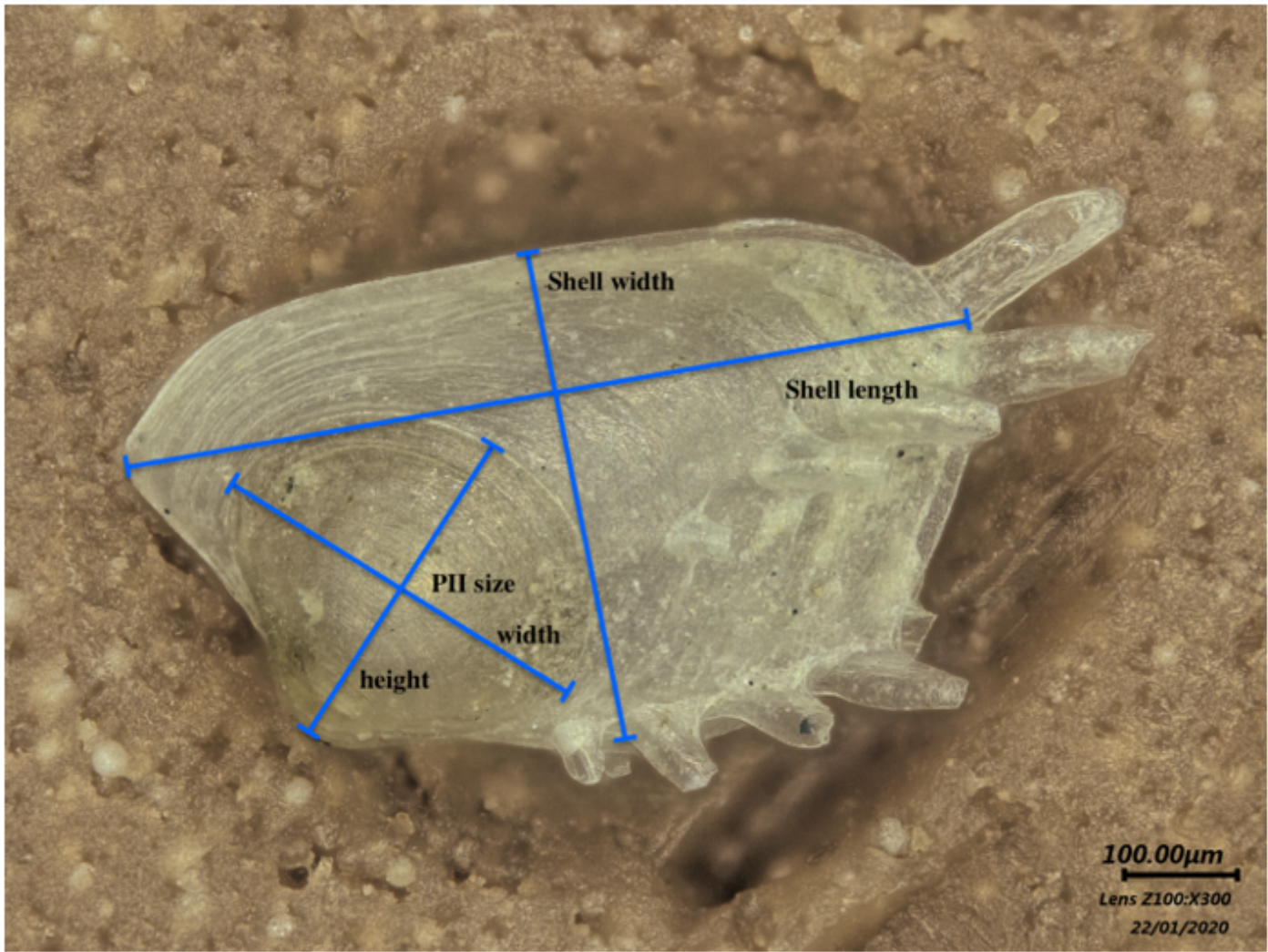
## Figures

**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 to August 2017) in YS close to the Basalt Island station.



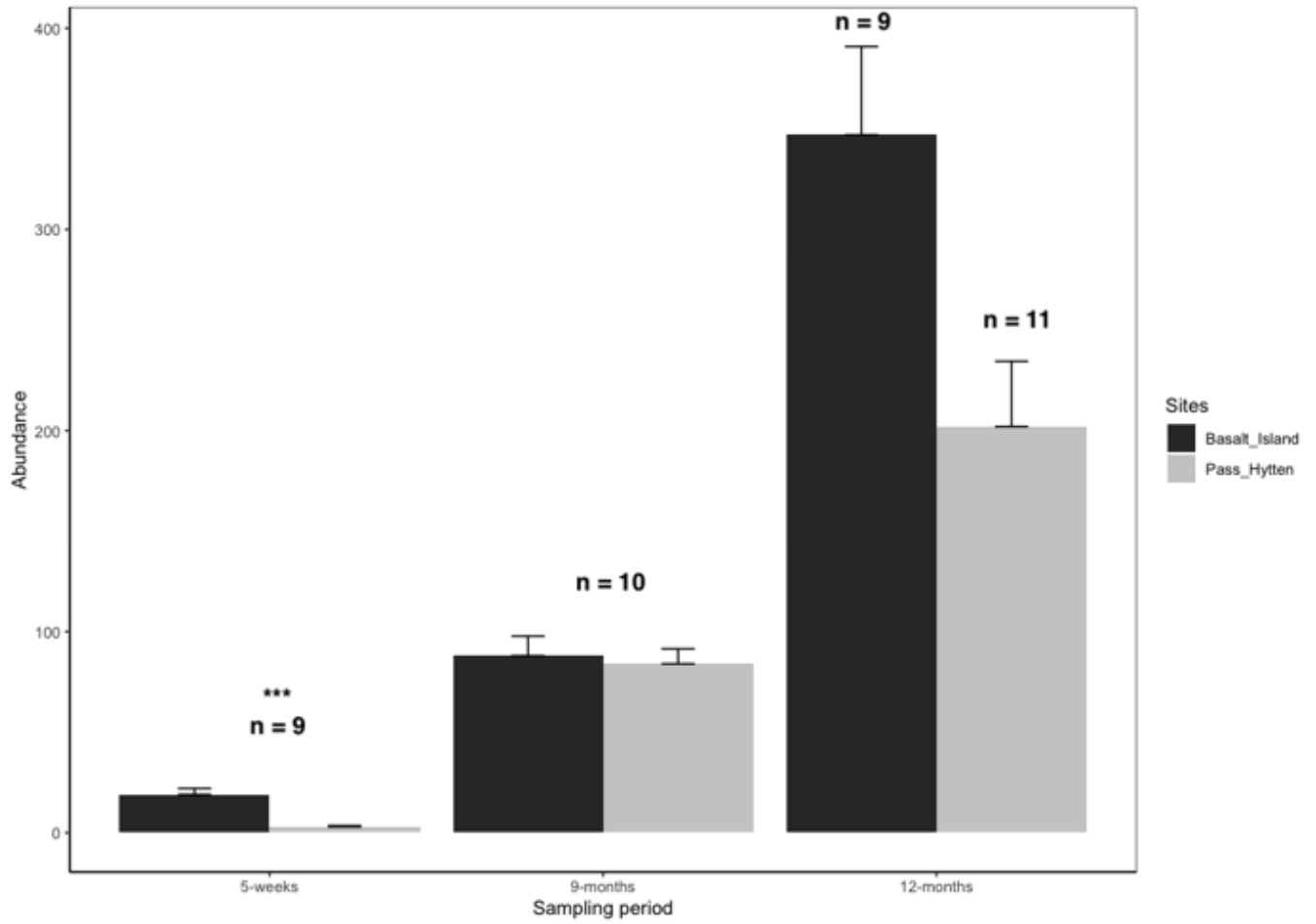
**Figure 1**

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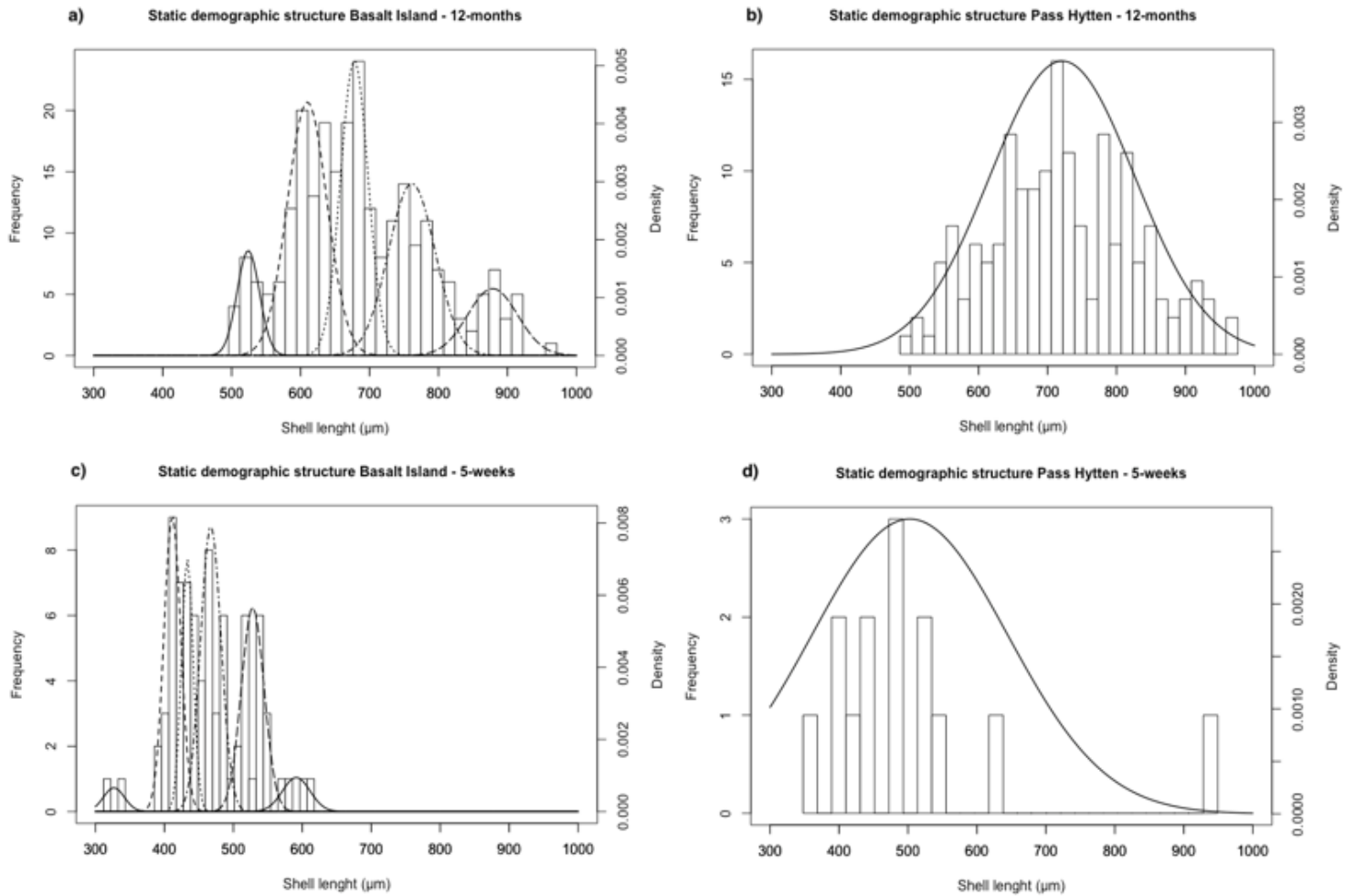
**Figure 2**

Picture of a recruit of *H. arctica* taken under a Keyence VHX-2000 Series digital microscope showing the various measurements acquired here (Prodissoconch size (PII): height and width; Shell length; Shell width).



**Figure 3**

Mean abundance per spat trap ( $\pm$  Standard Error) of recruits of *Hiatella arctica* collected at both studied sites over either 5 weeks, 9, or 12 months.



**Figure 4**

Size-class of recruits of *H. arctica* collected in 12 month 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 cohorts (Gaussian finite mixture model).

## Supplementary Files

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