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ORIGINAL PAPER

Year-round population dynamics of *Limacina* spp. early stages in a high-Arctic fjord (Adventfjorden, Svalbard)

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Abstract

The thecosome pteropods *Limacina helicina* and *L. retroversa* are important contributors to the zooplankton community in high-latitude environments but little is known about their distribution and life cycle under polar conditions. We collected the early life stages (< 1 mm) of the thecosome population in 2012 and 2013 at a bi-weekly to monthly resolution in fjord highly influenced by Arctic waters as well as Atlantic inflows (Adventfjorden, Svalbard, 78°N), together with environmental parameters. *L. retroversa* only occurred episodically, in association with the inflow of Atlantic water, with low numbers and random size distributions. This suggests that this boreal species does not fulfill its life cycle in Adventfjorden. In contrast, young specimens of *L. helicina* were present during the entire study. Veligers hatched in late summer/autumn and measured 0.14 mm on average. They grew with rates of 0.0006 mm day^{-1} over the 10–11 months of development. Only thereafter, growth accelerated by one order of magnitude and maximal rates were reached in autumn (0.0077 mm day^{-1}). Our results indicate that *L. helicina* reaches a size of 1 mm after approximately 1.5 years in Adventfjorden. We therefore suggest that *L. helicina* overwinters the first year as a small juvenile and that it needs at least 2 years to reach an adult size of 5 mm in Adventfjorden. This reveals an complex and delicate aspect of the life-cycle of *L. helicina* and further research is needed to determine if it makes the population especially vulnerable towards climate changes.

Keywords Thecosome pteropods · Veligers and juveniles · Distribution · Growth rate · Svalbard · Polar conditions

Introduction

Shelled pteropods (thecosomes) are significant components of polar marine ecosystems. They can dominate the zooplankton community at times (Blachowiak-Samolyk et al. 2008) and are considered key species in the pelagic food web. They graze on phytoplankton and other small particles (Perissinotto 1992; Noji et al 1997; Bernard and Froneman 2009) and are in turn preyed upon by large zooplankton, birds, fish and marine mammals (Hopkins and Torres 1989; Lalli and Gilmer 1989; Lancraft et al. 1991; Hunt and al 2008). Thecosomes also have a significant role in the production and export of organic matter and calcium carbonate (Berner and Honjo 1981; Bathmann et al. 1991; Hunt et al. 2008). During the productive season, they may contribute up to 72% of the organic carbon export in the Southern Ocean

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(Manno et al. 2010). Part of this flux is related to the excretion of feacal pellets that sink to deeper layers (Gilmer and Harbison 1991; Accornero et al. 2003) as well as pseudofaeces, which are the result of the degradation of mucus nets used for grazing (Harbison and Gilmer 1986). Due to the production of aragonite shells, thecosomes also substantially contribute to the calcium carbonate export in polar waters (Byrne et al. 1984; Tsurumi et al. 2005; Bauerfeind et al. 2014; Buitenhuis et al. 2019).

Rising CO_2 concentrations might not only shift the areas of distributions of the different thecosome pteropod species through climate change and alterations of ocean currents, but also impact their survival success on a more fundamental level their very thin aragonite shell makes thecosome pteropods highly sensitive to acidification (e.g., Comeau et al. 2012; Lischka and Riebesell 2012; Bednaršek et al. 2014). Both, climate change and ocean acidification are particularly rapid in polar regions (IPCC 2019), exposing thecosomes to dramatic alterations. The combination of pCO_2 increase and pH decrease is expected to lead to a reduced growth due to a limited calcification and could result in a decline of the population in the next decades with possible cascading impacts on the entire Arctic pelagic food chain and the carbon pump (Lischka et al. 2011; Lishcka and Riebesell 2012; Manno et al. 2012). Although the physiological response of thecosomes to climate change stressors is well documented, there is a major lack of knowledge regarding their life history, especially in Arctic fjords characterized by polar conditions. The population structure, the longevity of individuals, and the growth rates are decisive parameters for the resilience against environmental changes.

In Arctic ecosystems, two species of thecosome pteropods are present, *Limacina helicina* and *L. retroversa* (Kattner et al. 1998; Hop et al. 2006; Bauerfeind et al. 2014). Both species live in a narrow range of temperature and salinity, which make them useful biological indicators of water mass origins and environmental changes. *Limacina helicina* inhabits polar waters and is adapted to temperatures between − 1.6 and 4 °C (Conover and Lalli 1972; Hopkins 1985, 1987). *L. retroversa* is a boreal species, thriving at temperatures ranging from 2 to 7 °C (Chen and Bé 1964; van der Spoel 1967; Bé and Gilmer 1977). *L. helicina* is a prominent member of the Arctic zooplankton community while *L. retroversa* occurs episodically when introduced by Atlantic water masses (Hop et al. 2006; Walkusz et al. 2009). During the last decade, a shift from a dominance of *L. helicina* to *L. retroversa* has been observed in the Fram Strait as a consequence of increased inflow of warm Atlantic water (Bauerfeind et al. 2014).

Several studies have been conducted to assess the population dynamics of *L. helicina*, but their findings differ considerably and make it difficult to draw general conclusions. Data from high- and temperate latitudes in both hemispheres suggest between 1 and 2 generations per year, longevity from 1 to 3 years, a maximum size range from 3.7 to > 10 mm and continuous or discrete reproduction once or twice a year (summarized in Table 1 in Wang et al. 2017). These large variations can, at least in part, be attributed to differences in environmental conditions related to the geographical locations of the sampling sites. In the Svalbard Archipelago, data are only available from Kongsfjorden, Svalbard, which is however strongly influenced by Atlantic water (Svendsen et al. 2002), and thus mirrors boreal rather than polar conditions. In this fjord, *L. helicina* has a live span of one year and reproduces once per year, in late summer/autumn (Gannefors et al. 2005). The maximum size of the individuals found in Kongsfjorden is 13 mm, which is typical of sub-Arctic regions (Lalli and Wells 1978; Gilmer and Harbison 1991), but 2 to 3 times bigger than in the Arctic Ocean (Kobayashi 1974). In winter, growth apparently ceases and resumes in spring (Lischka et al. 2011; Lischka and Riebesell 2012; Gannefors et al. 2005; Comeau et al. 2010). In contrast to Kongsfjorden, the population dynamics of *L. helicina* in Adventfjorden, Svalbard has not yet been documented, except for yearly observations of swarms composed of large individuals (> 10 mm) between June and August (pers. obs.). This fjord is mainly influenced by Arctic water while Atlantic waters reach the fjord only occasionally (Nilsen et al. 2008; Cottier et al. 2010), allowing to study the life cycle of *L. helicina* under polar conditions.

The life cycle of *L. retroversa* (maximum size of 3 mm, Hsiao 1939) has been studied less than that of *L. helicina*. Some studies conducted in sub-polar environments suggested a 1-year life cycle, with one reproductive event in spring (Hsiao 1939) or in autumn (Meinecke and Wefer 1990). However, constant reproductive activity throughout the year has been considered the most likely, with an intense spawning event in spring and another one in autumn (Lebour 1932; Dadon and De Cidre 1992). The Arctic represents the northern limit of *L. retroversa*'s area

Table 1 Samples collected for the molecular identification of *Limacina helicina* and *L. retroversa*

Date	Number of individuals	Size range (mm)	Depth range (m)
6 September 2012	6	0.11–0.34	25–0
6 September 2012	6	0.15–0.24	65–25
19 September 2012	6	0.13–0.33	25–0
19 September 2012	6	0.23–0.34	65–25
18 October 2012	6	0.24–0.42	25–0
18 October 2012	6	0.20–0.50	65–25
12 December 2012	6	0.14–0.38	25–0
12 December 2012	10	0.15–0.38	65–25

of distribution; but it is still unknown, whether or not *L. retroversa* is an expatriate or is able to successfully complete its life cycle in these waters (Lischka and Riebesell 2012).

One limitation to better understanding the life cycles of *L. helicina* and *L. retroversa* is that previous works focused mainly on larger individuals (at the exception of Lischka and Hagen 2016 and Lischka and Riebesell 2012). The reason for this restriction to large individuals may be related to sampling limitations and to the fact the veligers and juveniles of *L. helicina* and *L. retroversa* are morphologically indiscernible (Lischka, pers. Comm.). However, they can be clearly identified when using molecular markers (Kohnert, unpublished data). In addition, previous studies focusing on Arctic regions were conducted either on short periods or with sparces temporal resolutions, which made it difficult to interpolate results to a more complete understanding of thecosomes life dynamics.

The goal of this study was to examine the life history of thecosomes in a fjord predominantly influenced by Arctic waters by monitoring their population structure for 2 years. Our research objectives were in particular to (1) apply barcoding methods for the identification of *Limacina* spp. Early veliger and juvenile stages, (2) relate the occurrence of *L. helicina* and *L. retroversa* to environmental parameters and (3) determine the annual growth of veligers and juveniles by measuring shell sizes in a high temporal resolution year-round.

Materials and methods

Study region and environmental conditions

The study was conducted during two consecutive years from January 2012 to December 2013 in Adventfjorden at the time-series Isfjorden-Adventfjorden sampling station (Stn. IsA: 78.261°N, 15.542°E, Fig. 1). Adventfjorden is small side-fjord of Isfjorden, on the west coast of Svalbard. The fjord is 8.3 km long, 3.4 km wide and 80 m deep. It is mainly exposed to the cold Arctic-derived East Spitsbergen Current. Occasionally, it can experience inflow of warm Atlantic Water from the West Spitsbergen Current, which penetrates into the fjord to an extent that shows great annual variations (Nilsen et al. 2008; Cottier et al. 2010). Two larger and several smaller rivers discharge freshwater and sediments in Adventfjorden during the main melting season in summer (Leikvin and Evenset 2009).

Salinity, temperature, and density as well as *in-situ* Chlorophyll *a* (Chl *a*) fluorescence were measured at each sampling event at Stn IsA, from bottom to surface using a hand-held CTD (CTD, SAIV A/S) with an attached fluorometer. Water masses were defined according to Svendsen et al. (2002). Air temperature, precipitation, wind direction and wind speed data were provided by the Norwegian Meteorological Institute. This data set includes measurements conducted every 6 h from January 2012 to December 2013 at the station Svalbard Lufthavn, (78.242°N, 15.502°E, Fig. 1). Data were analyzed using the free software R (R Core Team

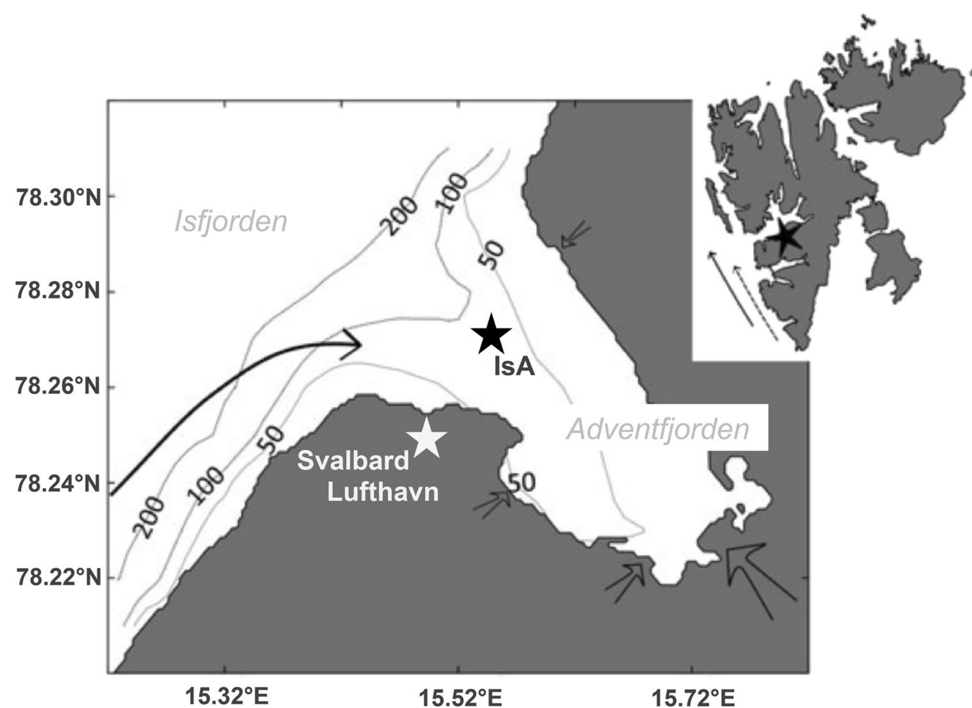

Fig. 1 Map of the sampling station Isfjorden-Adventfjorden (IsA; 78.261°N, 15.542°E), and the meteorological station Svalbard Lufthavn (78.242°N, 15.502°E). The dashed arrow represents the influence of the Arctic water masses and the plain arrow represents the general influences of Atlantic water masses. Open arrows indicate fresh water influences from rivers into Adventfjorden (modified from Stübner et al. 2016)

2019), interpolations were made with the package akima (Akima et al. 2020).

Sampling

The zooplankton community was sampled once a month and when the weather conditions allowed, twice a month. Sampling was conducted at Stn IsA (80 m deep), on board a small boat (PolarCirkel, Akva Group) in 2012 and 2013. Zooplankton were collected between 08:00 and 14:00 by vertical hauls from 65 to 25 m (deep layer) and 25 to 0 m (surface layer) using a WPII closing net (63 µm mesh size, 0.25 m^2 net opening, Hydro-Bios). These nets efficiently capture *Limacina* spp. Of small size, which are present in relatively high abundances. The densities of large *Limacina* specimen are generally low in this fjord and their occurrence is restricted to June–August (pers. obs.). It was, thus, not very likely to capture them by vertical tows with fine mashes, and accordingly, they were not found in our samples. The samples were immediately fixed in a seawater/formaldehyde (4%) solution for later determination of the species and size composition. Additional samples were fixed in ethanol (70%) and stored dark and cold 4 °C for subsequent molecular analyses. No flowmeter was used, and volume filtered was calculated from net opening and sampling depth, assuming 100% filtration efficiency.

Limacina spp. Specimens were measured to 0.01 mm precision (shell diameter) and counted under a Leica MZ12 Stereomicroscope. Identification to the species level was done in parallel to counting of specimens larger than 0.5 mm, considering that *L. retroversa* has a pointed spiral shell while *L. helicina* has a flat shell (van der Spoel and Dadon 1999). Morphological identification was not possible for specimens smaller than 0.5 mm since first life stages of both *L. retroversa* and *L. helicina* have a flat shell (Lischka, pers. Comm).

Molecular analyses

To determine the smallest individuals to species level, 52 veliger (0.11–0.41 mm) were randomly picked from the samples fixed in 70% ethanol (Table 1). Due to their small size, whole individuals were used to extract genomic DNA. We followed the CTAB extraction method (Knebelsberger and Stöger 2012) with a modified collection of dissolved DNA in a spin column from a NucleoSpin Tissue set (Macherey–Nagel GmbH & Co) to assure maximum DNA recovery (Kohnert unpublished data). Nuclear Histone 3 marker (H3) contains a diagnostic nucleotide to distinguish between *L. helicina* and *L. retroversa*, as base 307 is G in *L. helicina* and T in *L. retroversa* (Kohnert, unpublished data). H3 was amplified in 0.2 ml illustra™ PuReTaq™ Ready-To-Go™ PCR tubes (GE Healthcare) with 23 µl molecular water, 1 µl of template DNA and 0.5 µl of forward and reverse primer (10 pm/µl), respectively. We used the primers H3aF: 5′-ATG GCT CGT ACC AAG CAG ACV GC-3′ and H3aR: 5′-ATA TCC TTR GGC ATR ATR GTG AC-3′ (Colgan et al. 2000) with the following PCR settings: initial denaturation for 5 min. at 94 °C followed by 36 cycles of denaturation for 45 s at 94 °C, annealing for 50 s at 45 °C, elongation and extension at 72 °C for 200 s and a final elongation step at 72 °C for 10 min. Successful amplicons were purified using a DNA Clean & Concentrator Kit (ZYMO Research) according to the manufacturer's manual with a final elution volume of 15 µl. Molecular analyses were performed at the Bavarian State Collection of Zoology (ZSM Munich).

Sequencing was performed using Big Dye 3.1 with 5 µl diluted (2 pm/µl) amplification primers and 2 µl of purified PCR-product. Sequences were edited in Geneious R8 (8.1.7.) (www.geneious.com, Kearse et al. 2012) and aligned with the implemented Mafft plugin (Katoh et al. 2009). As a reference, *Limacina* spp. Sequences generated from clearly identifiable adult specimens of the respective species were included. These samples were collected in Svalbard (*L. helicina*) and Bergen (*L. retroversa*). Genetic vouchers are stored at the ZSM Munich. A 336 bp long sequence was successfully amplified for 39 specimens. 11 samples failed in PCR or resulted in sequences that could not be assembled/aligned, rendering a success rate of 78%.

Identification of cohorts and growth rates

To examine the size-distribution patterns of the thecosome populations, the shell diameters of each *L. helicina* and *L. retroversa* were displayed in size-frequency histograms for each sampling date (Fig. 2). Replicates from deep (65–25 m) and surface (25–0 m) layers were pooled, since no size difference was detectable (*L. helicina: t-test*, $t_{47.15} = 1.8595$, $p = 0.0692$; *L. retroversa: t-test, t-test*, $t_{47.612} = 0.781$, $p = 0.4387$). To further investigate the growth rates, the next step was to identify different cohorts that possibly co-occurred at all sampling dates. We used the package mixdist (Macdonald and Du 2018) in the free software R (R Core Team 2019) to fit mixture distribution models to the shell diameter distributions of *L. helicina* ($n = 3620$) and *L. retroversa* ($n = 220$) separately. Based on the best fit for the mixture distribution model, samples were separated into 20 size classes ranging from 0.1 to 1 mm (0.05 mm intervals). Initial values (frequency of each size class) were implemented, and parameters (mean values and standard deviations of sub-distributions) were estimated by the Kernel density estimation. This non-parametric method estimates the probability density function of a random discrete variable (Botev et al. 2010). From the Kernel density estimation, and the size-range of individuals captured by our nets, we identified three cohorts of *L. helicina* throughout the study

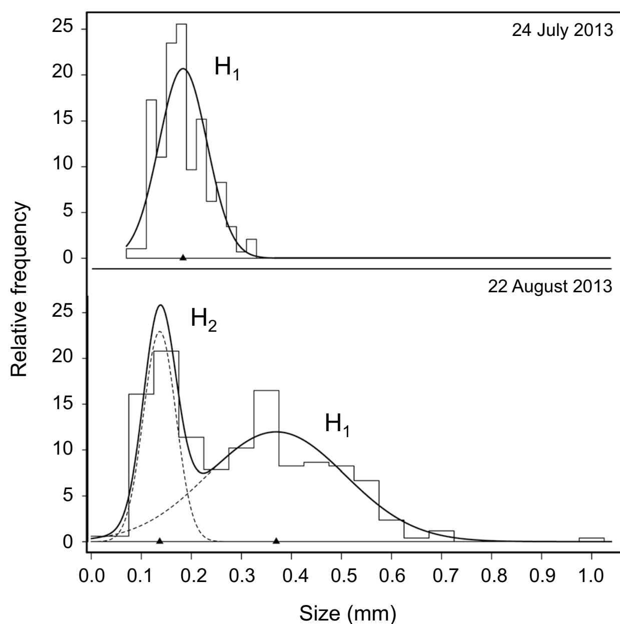

Fig. 2 Size-frequency histograms of *Limacina helicina* caught on 24 July 2013 and 22 August 2013 as an example of the population structure reflected by the samples. This configuration is the same in 2012 and 2013, with 1 cohort present in late winter to summer (represented by H_1 in 2013) and 2 cohorts in autumn/early winter (H_1 and H_2 in 2013). Overlaying solid lines are best fitting mixture models. Mean shell diameter values are represented by triangles. Dotted curved lines represent the different cohorts

period in total with one or two cohorts being present at the same time (Fig. 2). From 27 January to 19 September 2012, size frequency followed a normal distribution, representing one cohort referred to as H_0. Between 19 September and 15 November 2012, a bimodal distribution was observed, corresponding to the cohort H_0 and a new cohort, named H_1, which was characterized by smaller sizes. On 15 November 2012 H_0 disappeared from the samples, possibly due to the capacity of grown individuals to escape from the nets. H_1 was then the only cohort until 13 August 2013 when another cohort, H_2, appeared. Both cohorts co-occurred until the end of our study, as revealed by the bimodal distribution of sizes. In contrast to *L. helicina*, shell size distribution of *L. retroversa* was heterogeneous and inconsistent, thus no distinct cohorts could be identified in this species.

Growth rates of *L. helicina* were calculated based on the estimated cohorts and calculated as (1), according to Bednaršek et al. (2012):

$$(L)\, G_{H_{n,t1\rightarrow 2}} = \frac{L_{t_2} - L_{t_1}}{t_2 - t_1}$$

where H_n is the cohort of interest, L is the mean shell diameter in mm (estimated by the Kernel density estimation), and t is the time (in days). The statistical significance (p) of seasonal growth rates was tested with a Fisher test (ANOVA), using locally linear regressions. Significance level was set to $p < 0.05$.

Analyses of thecosome densities and growth rates

Statistical analyses were performed using the free software R (R Core Team 2019). To assess the environmental forcing on the thecosomes densities and growth rates in the entire water column, 2 principal component analyses (PCA) were performed using the R package FactoMineR (Lê et al. 2008). The environmental data (water properties and meteorology) as well as time (expressed as day of the year) were computed as active variables (used for the determination of principal components). Seawater densities were not included in the PCA because they were computed from temperature (T) and salinity (S), and the strong correlation among these variables could alter PCA results. Biological data were added as supplementary variables (projected on the results drawn from active variables). Thecosome densities were imputed as biological data as well as growth rates of the cohorts H_0 and H_1 of *L. helicina*. Growth rates of H_2 could not be included in the analysis because there was too little data. Missing values were estimated with the package missMDA (Husson and Josse 2010) using the relations between all variables from 2 dimensions of the PCA.

Results

Environmental conditions

Adventfjorden was influenced by Arctic water and Atlantic water in similar seasonal succession in 2012 and 2013 (Fig. 3). Arctic water (S < 34.7) mostly prevailed in the fjord. Between January and June, the water was characterized by cold temperatures (T < 1 °C), with the exception of a warm and saline Atlantic water inflow in March/April 2012 (T > 1 °C and S > 34.7). From June to September, river runoff led to stratification of the water column, with a warm and low saline freshwater layer in the upper 10 m (T > 8 °C and S < 33) while deep layer was still characterized by cold Arctic Water. From September on, the water column started to mix, leading to the formation of an intermediate layer that remained until the end of the year (34 < S < 34.7). In addition, Atlantic water (T > 1 °C and S > 34.7) penetrated in the fjord in September–November both in 2012 and 2013, in the deep layers.

Chl *a* concentrations as indicated by fluorescence measurements were low in both years from January to mid-April (Fig. 3). From then on, they increased to maximum values of 4 µg L^{-1} in mid-May 2012 and 7 µg L^{-1} in late April 2013, on average. Chl *a* concentrations remained high in the entire

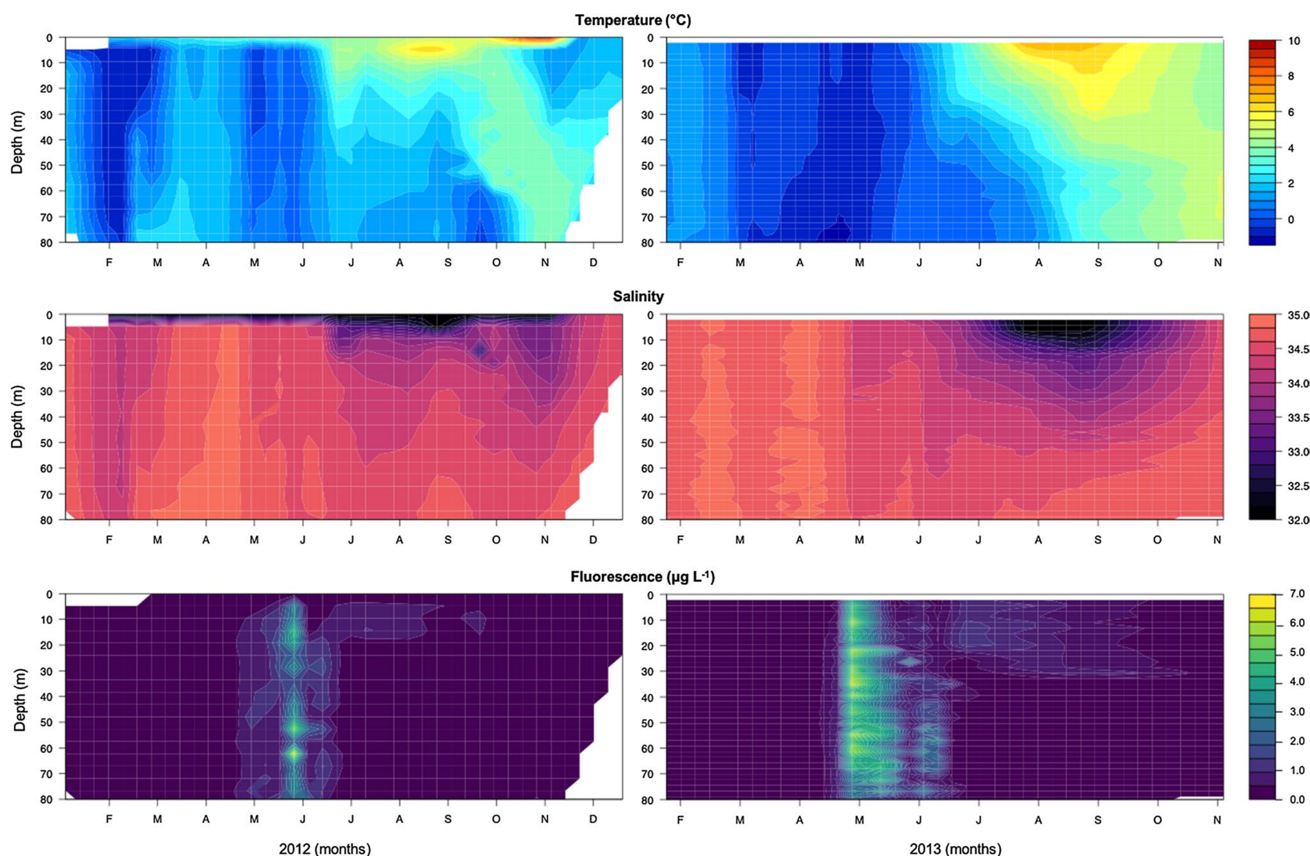

Fig. 3 Contour plots of environmental variables at the sampling station Isfjorden-Adventfjorden (IsA). Temperature (upper panel), salinity (middle panel) and fluorescence as a proxy for Chlorophyll *a* (lower panel) were linearly interpolated between measurements

water column until June. Between July and September, Chl *a* values decreased and showed a distinct near-surface maximum. From September/October on, Chl *a* concentrations were low again (< 0.1 µg L^{-1}).

Population structure

Species identification

Among 52 individuals allocated to molecular analyses, only 1 was identified as *L. retroversa* (6 September 2012, deep layer), indicating that 98% of the specimens < 0.5 mm were *L. helicina* (see Online Resource 1 for Genbank accession numbers). Therefore, for the following analyses, we decided to consider all individuals (also those < 0.5 mm) with flat shell as *L. helicina*.

Population densities

L. helicina was found on most sampling days between January 2012 and October 2013 (Fig. 4a). In 2012, an average of 108 individuals m^{-3} were found in January and February. In spring and summer, densities did not exceed 50 ind. m^{-3}, except for July when > 300 ind. m^{-3} were found. In September 2012, there was a sudden increase in density to > 1500 ind. m^{-3} whereas in October-December less than 250 ind. m^{-3} were counted. In 2013, the densities in winter and spring were much lower than in the previous year, varying between 0.4 and 4 ind. m^{-3} from January to June. In July, the numbers increased again, reaching the yearly maximum of 1700 ind. m^{-3} in September. In congruence with the previous year, the numbers decreased in October to 270 ind. m^{-3}. The abrupt increase in density of young stages around September 2012 and 2013 suggests that hatching occurred at this time of the year. In contrast, the dramatic decrease in density suggests high mortality rates between September and October in both years (50 ind. day^{-1} in 2012 and 46 ind. day^{-1} in 2013) whereas mortality was negligible during the rest of the sampling period. Throughout the sampling period, twice as many individuals were found in the surface layer (25-0 m) as compared to the deeper layer (65-25 m), and in September, individuals were even > 20 times more abundant in surface than deep waters.

L. retroversa was only observed from 19 September 2012 to 11 February 2013, with an average of 14 ind. M^{-3}. Individuals were 2 times more dense in deep waters as compared

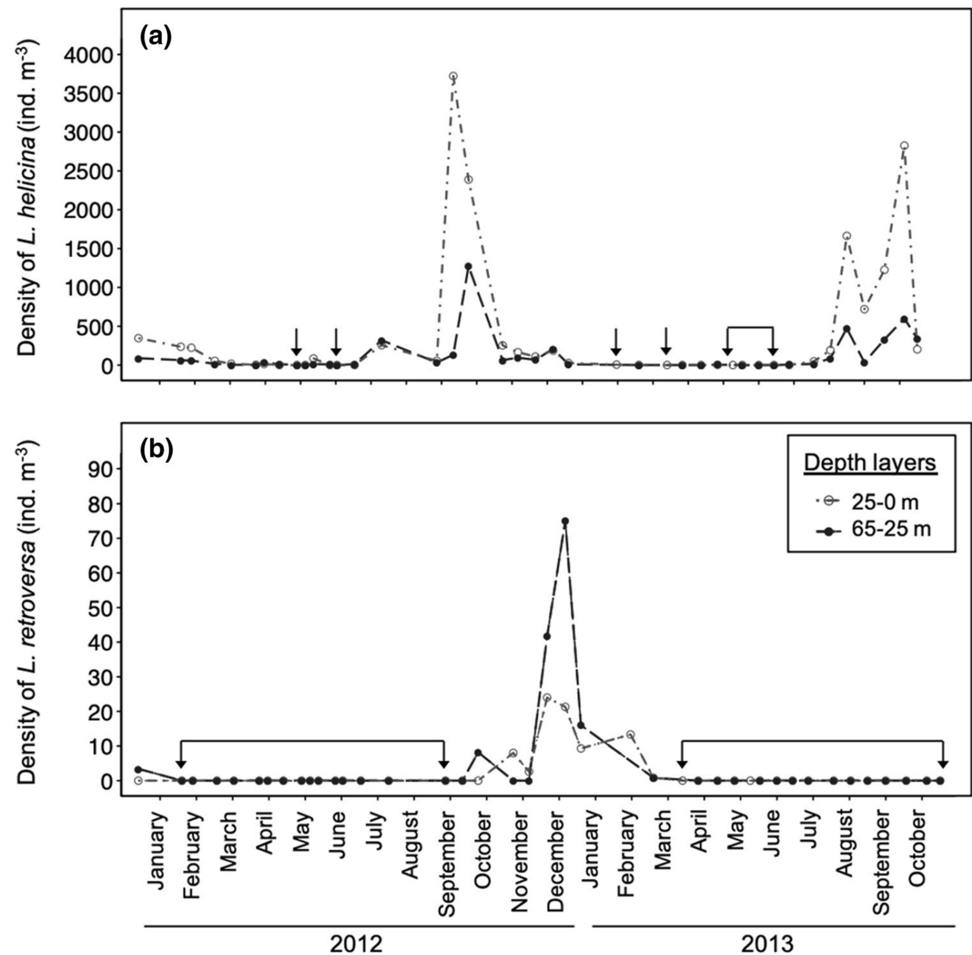

Fig. 4 Densities of (**a**) *Limacina helicina* and (**b**) *L. retroversa* in the surface (25–0 m) and deep (65–25 m) layers at Isfjorden-Adventfjorden sampling station (IsA), in 2012 and 2013. Densities were calculated for the entire population (all sizes combined). *L. retroversa* was only found between 19 September 2012 and 11 February 2013. Arrows represent the dates/periods when no *Limacina* was found in the samples

to surface. A peak of density was observed on 29 November 2012, with 75 ind. M^{-3} in the surface layer and 21 ind.m^{-3} in the deep layer (Fig. 4b).

The first and second principal components of the PCA performed on environmental variables explained 34% and 16% of the variance in the dataset, respectively (Fig. 5). Water temperature, wind speed and time were positively correlated, while being negatively correlated with salinity. *L. helicina* densities were positively correlated with water temperature and Julian day, while they were negatively correlated with salinity. *L. retroversa* had no strong correlation with any environmental variables.

Size distribution and growth

The mixed distribution model applied to the population data of young *L. helicina* showed that the population was composed of either 1 or 2 cohorts at a time (Fig. 6). The cohort H_0 (*n* = *905*) was observed from the start of our study, on 27 January 2012. The estimated mean size at this date was 0.14 ± 0.05 mm (*n* = *140*), with a minimum shell diameter of 0.11 mm (Fig. 7). In the winter months (27 January to 29 March 2012), the growth of these individuals was slow, at a rate of 0.0002 mm day^{-1} (*ANOVA*, $F_{227} = 3.425$, $p = 0.0355$) (Fig. 6). By the end of winter, the shell diameter had reached only 0.15 ± 0.05 mm (*n* = *89*). The growth was still slow in spring/early summer (29 March to 6 July, at a rate of 0.0004 mm day^{-1} (*ANOVA*, $F_{276} = 3.161$, $p = 0.0465$) resulting in a size of 0.19 ± 0.06 mm (*n* = *155*) in the beginning of July. In summer, (6 July to 19 September), individuals grew at a rate of 0.0011 mm day^{-1} (*ANOVA*, $F_{355} = 133.5$, $p < 0.0001$) reaching a shell diameter of 0.24 ± 0.09 mm (*n* = *202*). In autumn (19 September to 15 November), individuals showed a maximum growth rate of 0.0066 mm day^{-1} (*ANOVA*, $F_{454} = 980.8$, $p < 0.0001$). During this season, sizes more than doubled, reaching 0.81 ± 0.08 mm (*n* = *45*) in November. From January to November 2012, the shells thus increased sixfold in diameter.

The cohort H_1 (*n* = *1703*) appeared on 19 September 2012 and had an estimated mean size of 0.13 ± 0.06 mm (*n* = *319*), with minimum shell diameter of 0.05 mm (Fig. 8). In the following months (19 September to 15 November), H_1 grew at a rate of 0.0012 mm day^{-1} (*ANOVA*, $F_{626} = 1.778$, $p = 0.0478$) (Fig. 6). In the period

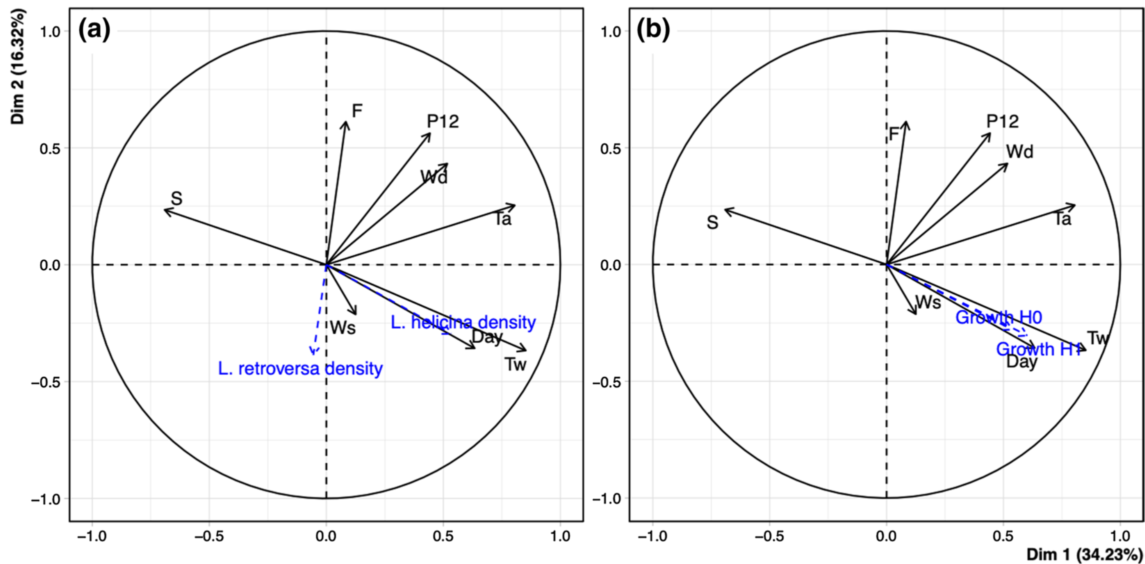

Fig. 5 Principal component analysis of environmental variables in Adventfjorden. Water properties are imputed as *Tw* water temperature, *S* salinity and *F* fluorescence. Meteorological data include *Ta* air temperature, *P12* precipitations in the last 12 h, *Wd* wind direction and *Ws* wind speed, *Day* Day of the year. Biological data are imputed as supplementary variables, they represent **a** densities of *Limacina helicina* and *L. retroversa* and **b** growth rates of H_0 and H_1 of *L. helicina*

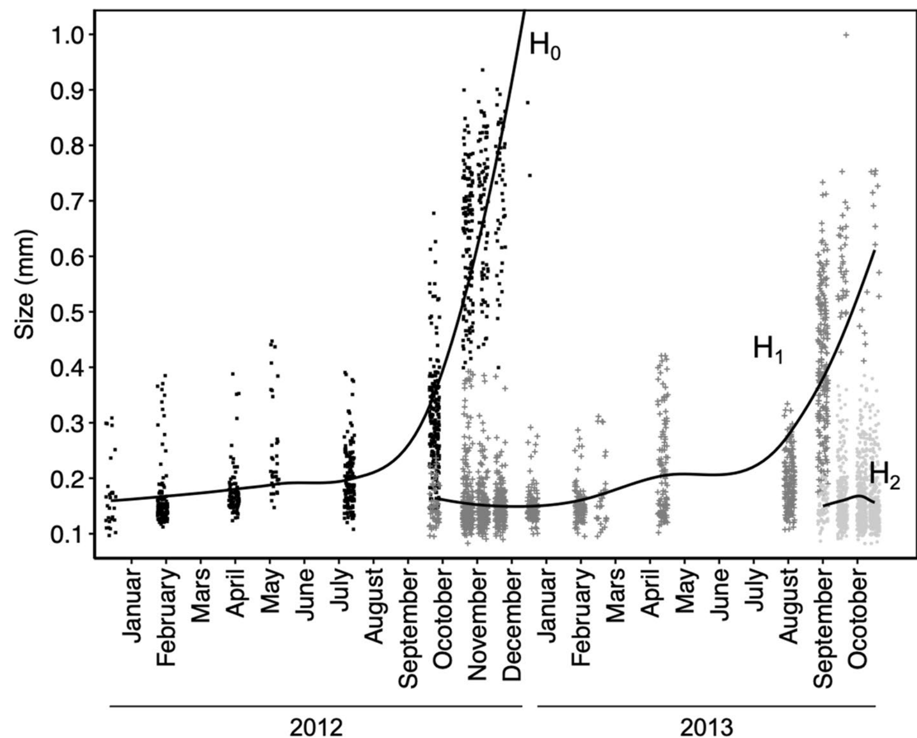

Fig. 6 Individual sizes of the three cohorts of *Limacina helicina* present during our study. Points represent measured data. For better visualization of data, overlap of points was avoided by adding a small amount of random variation to the location of each point. Cohort H_0 (individuals present from the beginning of the study) is represented in black squares H_1 (hatched in September 2012) in dark grey crosses and H_2 (hatched in August 2013) in light grey dots. Trend lines were added to better visualize the growth of each cohort. They represent local regressions of the size

from late autumn through winter (31 October 2012 to 5 April 2013) and spring (5 April to 24 July), the growth rate was 0.0003 mm day^{-1} (*ANOVA*, $F_{879} = 133.8$, $p = 0.0216$). In summer (24 July to 8 September), individuals had a growth rate of 0.0088 mm day^{-1} (*ANOVA*, $F_{483} = 364.7$, $p < 0.0001$) and reached a size of 0.60 ± 0.10 mm ($n = 212$). In autumn 2013, the growth rate decreased to 0.0044 mm day^{-1} (*ANOVA*, $F_{431} = 781.9$, $p < 0.0001$) but was still 4 times higher than during the previous autumn, when H_1 first appeared. In October, individuals measured 0.73 ± 0.07 mm ($n = 34$); thus, they were 6 times bigger than after hatching.

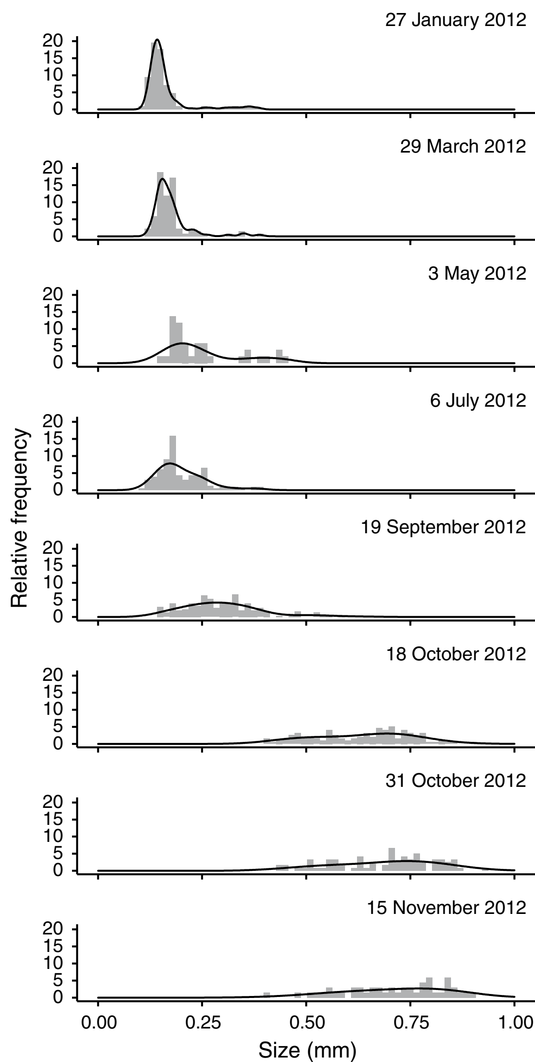

Fig. 7 Size-frequency distribution of the H_0 cohort of *Limacina helicina*, divided into different months between January and December 2012. The modal curve fitted to the sample plot represents the probability of density of each date

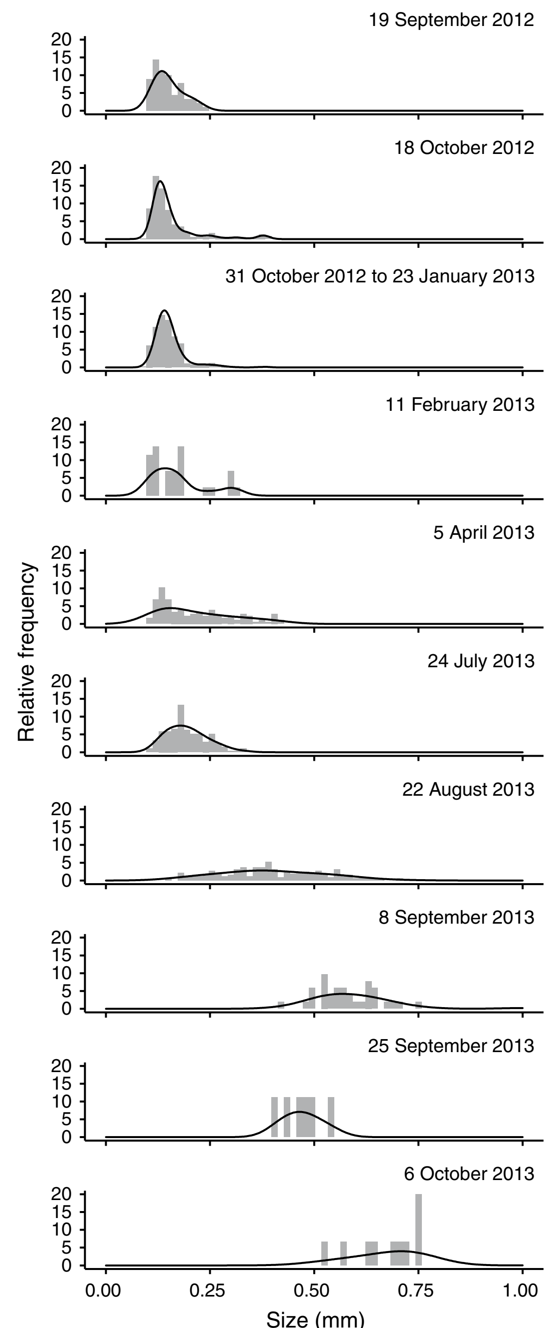

Fig. 8 Size-frequency distribution of the H_1 cohort of *Limacina helicina*, divided into different months between September 2012 and December 2013. The modal curve fitted to the sample plot represents the probability of density of each date

The cohort H_2 ($n = 1012$) appeared in August 2013 and had an estimated mean of 0.16 ± 0.03 mm ($n = 309$), with minimum shell diameter of 0.05 mm (Fig. 9). Growth rate was not statistically significant until the end of the sampling period (*ANOVA*, $F_{1010} = 0.4333$, $p = 0.5106$) (Fig. 6).

The PCA analysis revealed that growth rates of H_0 and H_1 were positively correlated with water temperature and Julian day, while they were negatively correlated with salinity (Fig. 5). Growth rates of *L. helicina* were placed on the PCA in a very similar way as density of individuals, and were also positively correlated with temperature.

L. retroversa showed a random distribution of size classes for all sampling dates, hence no unimodal distribution could be fitted for this species (Fig. 10). Samples ranged between 0.48 and 1.60 mm shell diameter.

Discussion

Identification of *L. helicina* and *L. retroversa*

Most of the larger individuals (85%) were clearly identified as *L. helicina* characterized by a spiral shell. In addition, out of 52 small specimens (< 0.5 mm) allocated to

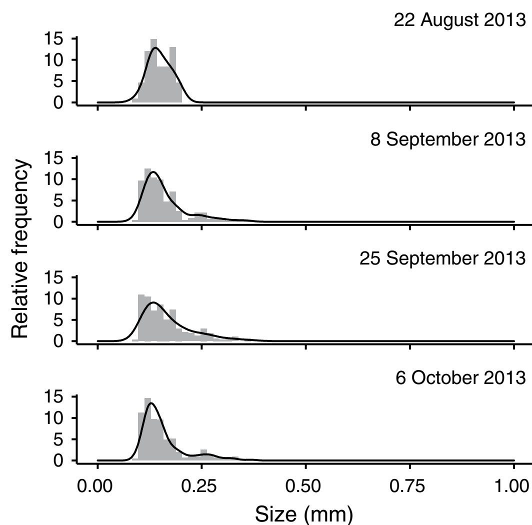

Fig. 9 Size-frequency distribution of the H_2 cohort of *Limacina helicina*, divided into different months between September 2012 and December 2013. The modal curve fitted to the sample plot represents the probability of density of each date

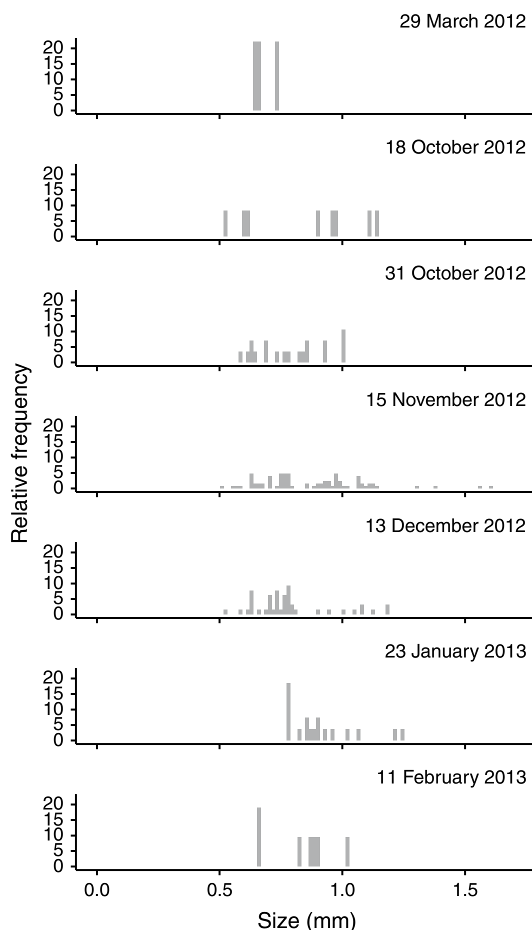

Fig. 10 Size-frequency distribution of *Limacina retroversa*, divided into different months between March 2012 and February 2013

molecular analysis, only one was identified as *L. retroversa*. Unfortunately, our samples for molecular analyses did not cover the entire sampling period but were restricted to September–December 2012. Thus, the species identification of small specimens, which did not exhibit the typical adult shell morphology is limited to these months. It is therefore possible that there were some *L. retroversa* among the small individuals during the remaining sampling period. However, Adventfjorden was mostly influenced by Arctic waters and even during the seasonal shifts in water masses, i.e., the inflow of Atlantic water, we did not observe considerable increases in large (> 0.5 mm) *L. retroversa* with a pointed shell. We therefore assume that the vast majority of small *Limacina* individuals were indeed *L. helicina* during the entire study period and have analyzed the population structure accordingly.

Life cycle of *L. helicina*

Young *Limacina helicina* were present in Adventfjorden throughout the entire study period from January 2012 through September 2013, indicating that this species was a permanent member of the Arctic zooplankton community, in line with some other studies (Kobayashi 1974; Gilmer and Harbison 1991; Gannefors et al. 2005). Most studies, however, concluded that *L. helicina* is distributed patchily in both, time and space (Kattner et al. 1998; Gannefors et al. 2005; Howes et al. 2015), because *L. helicina* adults tend to gather in large swarms to reproduce (Dadon 1990; Dadon and de Cidre 1992; Noji et al. 1997); but, those sampling efforts were limited to only a few weeks or months and focused on the adult population. Since our high-resolution data reveal a less patchy distribution of small individuals (< 0.5 mm) in time than previously thought, we recommend using small sized meshes in addition to larger nets, when sampling *Limacina* spp. populations.

Vertically, we found maximum densities of *L. helicina* in the sample integrating the upper 25 m of the water column. This layer, however, was stratified in late summer when the upper 10 m of the water column were characterized by warm freshwater in June–September in both years. Since salinity dilution apparently leads to an increase in negative buoyancy (Manno et al. 2012), it is possible that individuals were gathering in the colder Arctic waters below.

The densities of young *L. helicina* changed drastically over the year, likely as a consequence of spawning events. We observed that the maximum densities occurred in late summer/early autumn and coincided with the smallest shell diameters (0.05 mm). We interpret this as a result of summer/autumn reproduction and thus hatching of the new generation, which is similar to the conclusions drawn by Gannefors et al. (2005) for the *L. helicina* population in Kongsfjorden. However, they only found individuals ≥ 0.2 mm, most likely

because of the larger nets they used for sampling, which had a mesh size of 180 µm. It has been suggested that the timing of reproduction of *Limacina* spp. depends on the feeding conditions of adults in spring (Böer et al. 2006; Bernard and Froneman 2009) as the females need to accumulate sufficient amounts of lipids (Maas et al. 2011). In a situation of low primary production, they would need to feed longer to build up sufficient lipid reserves. The earlier onset of reproduction in 2013 (August vs. September in 2012) may therefore partly relate to a higher food availability (as Chl *a* concentrations were almost 2 times higher than in 2012) together with an earlier onset of the phytoplankton bloom, even though the PCA did not indicate a correlation between Chl *a* concentrations and population densities.

Our high-resolution data provide strong support for a non-linear growth of young *L. helicina*, with a growth rate of 0.0006 mm day^{-1} within the first 10–11 months, which accelerates thereafter to reach a maximal rate of 0.0077 mm day^{-1} in autumn. This is similar to the results from Kobayashi (1974) who estimated a growth rate of approx. 0.001 mm day^{-1} during the first year of development, and a higher growth rate of 0.010 mm day^{-1} during the second year, even though he combined several years of data from stations across the Central Arctic (with > 1336 km distance). When comparing our data to growth rates obtained in the neighboring Kongsfjorden (0.013 mm day^{-1}), our growth rates were lower by an order of magnitude. Differences in growth rates and life history traits may be driven by environmental conditions related to geography (Hunt et al., 2008), and can explain the rapid growth of 0.03 mm day^{-1} observed in temperate regions (Wang et al. 2017). However, Kongsfjorden and Adventfjorden are located in close proximity and are characterized by similar light and hydrographic regimes. Kongsfjorden is generally more influenced by Atlantic waters than Adventfjorden (S > 34.7, T > 1 °C, Svendsen et al. 2002) but differences in temperature are small. Lower temperatures may cause some reduction in growth (as suggested by the PCA) but certainly alone cannot explain the drastic differences found between the two fjords. The factor, which we believe is most likely the most important one, is the difference in the sampling efforts. Gannefors et al. (2005) have only sampled from May through September and they have used larger mesh sizes (180 and 1000 µm). Thus, they have mainly collected larger, fast-growing individuals than we have. We therefore suggest that the growth rates from Gannefors et al. (2005) mirror the second year of development while our growth rates are representative for the early development of *L. helicina* in Arctic waters.

In contrast to a short-term study conducted in Kongsfjorden in winter (Lischka and Riebesell, 2012), we observed growth throughout the entire year, with the highest rates between September and December during the second year of the life cycle. Autumn-growth may have been supported by opportunistic feeding on small particles, which *L. helicina* seems to prefer (Howes et al. 2014), while winter-growth may have been possible through the use of internal lipid reserves (Boissonnot et al. 2019). During both winter and autumn, *L. helicina* might also be favored by little competition for feeding (Vader et al. 2015) due to the diapause of other zooplankton (Hagen and Auel 2001).

Studies conducted in the Arctic assume that the *L. helicina* population is composed of only one cohort at a time (Kobayashi 1974; Gannefors et al. 2005) while more recent studies conducted in the Southern Ocean argue for an overlap of ≥ 2 cohorts (Hunt et al. 2008; Bednaršek et al. 2012). In our study, the size-frequency distributions of small individuals (< 1 mm) indicate an overlap of 2 cohorts, the overwintering juveniles and the new-hatched veligers. At which size *L. helicina* reaches sexual maturity is yet unclear. According to Kobayashi (1974), *L. helicina* is mature at 0.8 mm shell diameter, while Lalli and Gilmer (1978) argue that maturation does not happen before individuals are 4–5 mm. In our study, when a new cohort appeared as indicated by very small sizes, the individuals from the previous cohort measured 0.35 mm on average (≤ 0.7 mm), and thus very likely not ready to reproduce. We therefore conclude that mature females must have been present in order to produce the new veligers, and, hence, argue that 3 cohorts have been present in late summer/autumn. In support of this argument, large *L. helicina* have been regularly observed in Adventfjorden between June and August (pers. obs.). Overlapping cohorts could help to sustain a population in extremely variable ecosystems such as Arctic fjords and buffer substantial losses in offspring during 1 year (Bednaršek et al. 2012). This is particularly important for slowly developing species.

Given that in our study 1 year-old *L. helicina* measured about 0.8 mm and considering that adults can reach a size of 5 mm (Gannefors et al. 2005 in Kongsfjorden, pers. obs. in Adventfjorden), an average growth rate of 0.0077 mm day^{-1} within the second year of development suggests that individuals must live approximately 2.5 years in order to reach that size. This reveals again a strong contrast with the life cycle in Kongsfjorden, where *L. helicina* is suggested to have a 1-year life span (Gannefors et al. 2005). It is, however, in line with Bednaršek et al. (2012) who suggested that *L. helicina* in the Southern Ocean can also be up to 3 years old.

Presence of *L. retroversa*

In Svalbard waters, the sub-polar species *L. retroversa* has been reported to occur episodically and at low densities (Lalli and Gilmer 1989; Kattner et al. 1998). Whether or not *L. retroversa* reproduces in polar latitudes is still under debate (Lischka and Riebesell 2012). We did not find clear indication for successful reproduction, (e.g., no sudden increase in veliger densities). Both juveniles and adults

were present in Adventfjorden but exhibited a patchy size distribution.

Limacina retroversa is considered a marker species of Atlantic waters (Lebour 1932; Morton 1954). In agreement, we observed *L. retroversa* in autumn 2012, when Adventfjorden was influenced by Atlantic waters. The warm and saline Atlantic inflow was primarily transported into the deep layer, as also observed by Svendsen et al. (2002) and Marquardt et al. (2016). Accordingly, *L. retroversa* was present in higher densities in the 65–25 m layer. *Limacina retroversa* was not found in autumn 2013 although at that time the fjord was also influenced by Atlantic waters. The distribution of *L. retroversa*, however, is patchy in its area of origin (Meinecke and Wefer 1990), and it is thus possible that the Atlantic waters that had advected into the fjord in 2013 did not contain any specimen. It has been reported that pteropods that enter eddies are retained as juveniles or adults (Tsurumi et al. 2005). It is therefore likely that in our study, *L. retroversa* had been advected with Atlantic water masses, and was not able to fulfill its life cycle in these high latitudes.

In the early twentieth century, *L. retroversa* was regarded as a species that only occurred south of 65°N (Lebour 1932; Redfield 1939). However recently, *L. retroversa* expanded northwards and has been found in the Barents Sea and up to 79°N in Fram Strait during the last few decades (Bathmann et al. 1991; Bauerfeind et al. 2009). A long-term study based on sediment traps in the Fram Strait suggested that the thecosome community shifted from a dominance of *L. helicina* to a dominance of *L. retroversa* since 2005/2006 (Bauerfeind et al. 2014). This change would be associated with a warming of the water since 2000 (Schauer et al. 2008; Beszczynska-Möller et al. 2012; Bauerfeind et al. 2014). However, our study does not confirm this trend for the community in Adventfjorden. While we also observed a warm Atlantic inflow, when *L. retroversa* were present, they were on average 4 times less abundant than *L. helicina*. Further long-term investigations are needed to clarify this possible shift of the community composition.

Conclusion

The temporal distribution of *L. helicina* in Arctic waters has often been described as patchy. This seems to apply to adults, whereas veligers and juveniles are continuously present at all seasons. Our data suggest that *L. helicina* in Adventfjorden hatches in late summer/autumn and needs at least 2 years to reach adult size (5 mm). The population structure reflected the co-occurrence of two cohorts of young individuals (< 1 mm). These veligers and juveniles grew slowly during the first 10–11 months of development, and about 10 times as fast thereafter (up to 0.0077 mm day^{-1} in autumn). In contrast to *L. helicina*, *L. retroversa* was not able to fulfill its life cycle in Adventfjorden and was only sporadically present during times of intrusion of Atlantic water masses. More pronounced and frequent Atlantic inflows into Arctic fjords (Spielhagen et al. 2011) could thus lead to a shift from *L. helicina* to *L. retroversa,* similar to what has been reported from Fram Strait (Bauerfeind et al. 2014). On the other hand, *L. helicina* does sustain in the Kongsfjorden, indicating that this species can thrive at Atlantic conditions. Besides warming and Atlantification, Arctic waters are also expected to acidify in future (Orr et al. 2005). Ocean acidification could reduce growth of both species due to lower calcification rates (Comeau et al. 2009; Lischka et al. 2011; Manno et al, 2012). It is thus not clear yet how *Limacina* spp. populations will develop in Arctic fjords. Especially *L. helicina*, with such slow juvenile growth and a multiyear life cycle, may be severely affected by climate change and it may be not sufficient to conduct short-term studies to address its response to environmental conditions. We therefore recommend to conduct systematic high resolution long-term studies, including veliger, juveniles and large individuals.

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Author contributions LB, JES and BN conceived the study based on field observations performed by JES and ES on the entire mesozooplankton community. PK performed molecular analyses with the help of MS and wrote the corresponding section of material and methods. LB analyzed the pteropod distribution as well as the meteorological data, with help of BN, MG and JES. LB, BE and BN interpreted the data, wrote the manuscript and revised it. All authors read and approved the manuscript.

Declarations

Conflict of interest The authors declare that there is no conflict of interest related the findings presented in this manuscript.

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