



Oceanographic influence on the early life-history stages of benthic invertebrates during the polar night

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Abstract

Recent research has illuminated biological processes taking place during the polar night in the high Arctic, while simultaneously, the polar regions are undergoing rapid climate-driven change. There is a pressing need for research to establish baseline conditions and understand the influence of oceanographic factors on polar communities. We collected plankton samples in Kongsfjorden (Svalbard, Arctic) in January 2020, in order to study the early life-history stages of benthic invertebrates during the polar night. Specimens were identified using morphology and DNA barcoding. During our field campaign, a strong wind event occurred, which caused upwelling of Arctic water in the fjord. Therefore, we also investigated the influence of oceanographic factors on benthic invertebrate larvae, including temperature, salinity, and depth. Our samples included 19 different species or morphotypes belonging to ten invertebrate phyla, including three embryo morphotypes. The collection of embryos indicates that at least some taxa are reproducing in the polar night. Larval community structure at shallow stations was significantly different before and after the upwelling event. Our samples also reflected patchiness in the larval community and a significant influence of depth. The most common nutrition mode among the larval taxa we collected was lecithotrophy (energy derived from maternal yolk), but we also collected a few taxa that may be planktotrophic (feeding). Development via lecithotrophy could increase larval survival and settlement success in the low-food environment of the Arctic winter. This study provides essential data on the early life-history stages of benthic invertebrates in an understudied season.

Keywords Larva · Juvenile · Embryo · Meroplankton · Zooplankton · Kongsfjorden · CTD · Upwelling · Svalbard · Fjord

Introduction

The polar night—the period of the year when a polar region is dark 24 h per day—was long considered a period of low biological activity. While darkness inhibits photosynthesis, the assumption that it hinders other biological processes such as feeding and reproduction is biased by anthropocentric perspectives and the historical tendency for sampling to take place in summer (Berge et al. 2015a). Recent research

has revealed unexpectedly high levels of biological activity in marine environments during the polar night (Berge et al. 2015b), including diel vertical migration of zooplankton (Berge et al. 2014; Grenvald et al. 2016) and fish (Benoit et al. 2010), active feeding by zooplankton (Kraft et al. 2013) and seabirds (Gremillet et al. 2005; Ostaszewska et al. 2017), and recruitment of benthic invertebrates (Kukliński et al. 2013; Meyer et al. 2017).

One understudied component of the marine ecosystem during polar night is meroplanktonic larvae. These early life-history stages are critical for dispersal of benthic invertebrates, especially for sessile taxa, which are attached to a substratum during the juvenile and adult life-stages (Pechenik 1999). Meroplankton can be planktotrophic (i.e., feeding in the water column) or lecithotrophic (i.e., relying on nutrition from maternal yolk) (Young et al. 2001). The scarcity of food sources in the water column, particularly phytoplankton, during the polar night suggests that planktotrophic larvae would have low survival. Lecithotrophic larvae may be better able to survive during polar night conditions, but

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the high energetic investment required for maternal provisioning of these larvae may curtail reproduction during the winter. Still, species that utilize stored energy reserves for reproduction (i.e., capital breeders) or that have food sources that are available year-round (i.e., scavengers) could produce larvae during winter. Investigating the meroplankton community during the polar night will expand our understanding of these dynamics.

Even as baseline research is being conducted on polar night marine biology, environmental conditions in the Arctic Ocean are rapidly changing. In the European Arctic, warm Atlantic waters are transported northward in the West Spitsbergen Current (WSC). Water temperatures in this important conduit are rising at the surface (leading to reductions in sea ice cover) and in the deep sea (Beszczyńska-Möller et al. 2012; Soltwedel et al. 2015). Recession of the ice edge is particularly pronounced in winter, so that large swaths of the high Arctic now remain ice-free all year (Onarheim et al. 2014). There is a pressing need to conduct baseline research in polar regions, especially in understudied seasons such as the polar night, so that future changes can be tracked.

Fjords on the western side of Svalbard (European Arctic) are influenced by Atlantic water from the WSC in summer and cold, salty “winter water” formed locally during sea ice formation in winter (Cottier et al. 2005). Stratification can occur, with winter water at the bottom, Atlantic water (when present) in the middle of the water column, and a lens of cold, low-salinity water derived from glacier and sea-ice melt on the surface (Cottier et al. 2005). However, this stratification can break down in some seasons as one water mass fills the fjord and can also be altered by wind (Cottier et al. 2010). Strong down-fjord winds set up Ekman transport of surface waters to the right of the wind direction, which leads to tilted isopycnals with downwelling to the right and upwelling to the left of the wind direction (Cottier et al. 2010). Such events can set up strong cross-fjord gradients, dramatically affect the salinity at a given depth, and increase exchange with shelf waters (Cottier et al. 2010). Climate-driven changes have also led to the occasional penetration of Atlantic water into western Svalbard fjords in mid-winter, but the conditions leading to winter upwelling of Atlantic water are highly specific and occur rarely (Cottier et al. 2007).

In January 2020, we conducted an observational study in Kongsfjorden, a western Svalbard fjord, to examine the meroplankton community during the polar night. Kongsfjorden is an appropriate system for such a study given the wealth of background information available from prior oceanographic and biological investigations (Hop et al. 2002; Svendsen et al. 2002; Wiencke and Hop 2016). During our study, we observed an upwelling event driven by strong down-fjord winds, allowing us to examine aspects of oceanographic forcing on the local meroplankton community.

Our study provided an opportunity to document species of marine benthic invertebrates with early life-history stages present in the polar night and to contribute to our growing knowledge of winter ecology in the high Arctic. In particular, we addressed two key questions with our study:

(1) What species of benthic invertebrate larvae are in the water column during the polar night?

(2) How are the distributions and abundances of these larvae influenced by oceanographic factors?

Methods

Field sampling and environmental data

All samples were collected in Kongsfjorden, Svalbard in January 2020, using *M/S Teisten* (Kings Bay AS) or a *Polarcirkel* zodiac (Table 1). Sampling stations were located along the southern coast of the fjord near the research station Ny-Ålesund at 5–200 m depth (Fig. 1). Temperature and salinity of the water column were measured at 1 m intervals using an SD204 CTD (SAIV), which was lowered vertically through the water column using the winch on *Teisten* or by hand on the *Polarcirkel* boat. Data reported here were recorded on the up-cast of the CTD.

Wind speed and direction were measured at 1-min intervals at 10 m above ground at the AWIPEV meteorological station in Ny-Ålesund. Data for January 2020 were downloaded from the online archive Pangaea (Maturilli 2020).

Zooplankton were collected using a 150 µm mesh net with a 1 m diameter opening (Sea-Gear). The net was lowered vertically through the water column to < 3 m above the seafloor and then raised using the winch on *Teisten* or by hand on the *Polarcirkel* boat. Therefore, plankton samples were integrated through the whole water column. We elected for this sampling design because depth-stratified samples would have been very challenging given the environmental conditions (high wind, sea ice). Three replicate vertical tows were conducted at each station on each sampling date. For sample P5, the shallow depth at the station (5 m) made a vertical tow impractical, so the plankton net was deployed over the side of the *Polarcirkel* boat, which drifted down-current for 10 min. The volume filtered for each sample was recorded using a flow-meter (Sea-Gear). For some vertical deployments, the flow-meter was frozen; we estimated the volume filtered during these tows by multiplying the surface area of the net opening (0.78 m²) by the depth of the sample. Weights deployed on the bottom of the zooplankton net ensured tows were as vertical as possible. We also compared flowmeter-recorded values to estimated values for a sub-set of tows and found good support for the accuracy of our estimation method.

Table 1 Stations sampled as part of this study in Kongsfjorden (Svalbard) in January 2020

Date	Sample	Latitude (N)	Longitude (E)	Depth (m)	Sampler	Volume (m ³)
5 Jan	A1	78° 55.748'	11° 56.141'	13	CTD	
5 Jan	A2	78° 55.751'	11° 56.148'	14	Net	2.51
5 Jan	A3	78° 55.751'	11° 56.147'	14	Net	4.95
5 Jan	A4	78° 55.750'	11° 56.141'	14	Net	2.98
5 Jan	B1	78° 55.920'	11° 56.152'	38	CTD	
5 Jan	B3	78° 55.927'	11° 56.078'	35	Net	27.5
5 Jan	B4	78° 55.970'	11° 56.045'	36	Net	28.3
8 Jan	P5	78° 55.711'	11° 56.174'	5	Net	607
8 Jan	P7	78° 55.711'	11° 56.174'	5	CTD	
9 Jan	C1	78° 55.866'	11° 54.927'	12	CTD	
9 Jan	C2	78° 55.868'	11° 54.900'	12	Net	24.2
9 Jan	C3	78° 55.871'	11° 54.871'	12	Net	36.8
9 Jan	C4	78° 55.873'	11° 54.824'	12	Net	46.9
9 Jan	D1	78° 55.991'	11° 54.747'	14	CTD	
9 Jan	D2	78° 56.005'	11° 54.683'	15	Net	11.8
9 Jan	D3	78° 56.005'	11° 54.682'	14	Net	36.1
9 Jan	D4	78° 56.066'	11° 54.471'	15	Net	79.3
10 Jan	A9	78° 55.766'	11° 56.056'	15	CTD	
10 Jan	A10	78° 55.761'	11° 56.068'	20	Net	15.7
10 Jan	A11	78° 55.775'	11° 56.091'	20	Net	15.7
10 Jan	A12	78° 55.781'	11° 56.108'	21	Net	17.3
10 Jan	E1	78° 55.733'	11° 56.751'	10	CTD	
10 Jan	E2	78° 55.733'	11° 56.751'	10	Net	7.85
10 Jan	E3	78° 55.733'	11° 56.751'	10	Net	7.85
10 Jan	E4	78° 55.733'	11° 56.751'	10	Net	7.85
11 Jan	F2	78° 56.086'	11° 56.995'	130	Net	91.1
11 Jan	F3	78° 56.044'	11° 56.989'	108	Net	192
11 Jan	F4	78° 56.036'	11° 56.875'	98	Net	413
11 Jan	F5	78° 56.069'	11° 57.046'	127	CTD	
11 Jan	G1	78° 56.285'	11° 56.948'	221	CTD	
11 Jan	G2	78° 56.250'	11° 57.268'	231	Net	371
11 Jan	G3	78° 56.234'	11° 56.992'	193	Net	419
11 Jan	G4	78° 56.221'	11° 57.421'	224	Net	270

Zooplankton samples were stored in 500 mL jars on board the boat and kept cool until investigators returned to shore. Larvae were sorted live by hand from whole samples in the Kings Bay Marine Laboratory (Ny-Ålesund, Svalbard) using a dissecting microscope and individually preserved in 0.25–1 mL vials in 95% ethanol.

Laboratory analysis

Larval samples were analyzed further at Woods Hole Oceanographic Institution (Woods Hole, MA, USA) ~ 3 months after the field expedition. Each specimen was photographed using a camera in conjunction with a dissecting microscope (Leica), identified to morphotype, and counted.

Some common morphotypes could be identified to species based on previous investigator experience (i.e., *Hiatella*

arctica, *Margarites helycinus*). For morphotypes which could not be readily identified, molecular methods were used for identification. DNA was extracted using Insta-Gene (Bio-Rad) following Hiebert et al. (2013). We amplified ~ 500 bp sequences of mitochondrial COI and 16S rRNA, as well as nuclear 18S rRNA using “universal” and taxon-specific primers for PCR (see Online Resource 2). The PCR recipe was modified from Hare et al. (2000): 8 µL nuclease-free water (Ambion), 3 µL standard Taq buffer, 2.3 mM MgCl₂, 300 µM each dNTP, 1.5 U Taq polymerase (New England Biolabs), 1 µM primer, and 1 µL template DNA solution. PCR products were used for Sanger sequencing (Sequagen), and successful sequences were compared to the GenBank database using the blastn algorithm (blast.ncbi.nlm.nih.gov). We only report results for samples that had a reasonable match to a GenBank sequence (i.e., closest match was

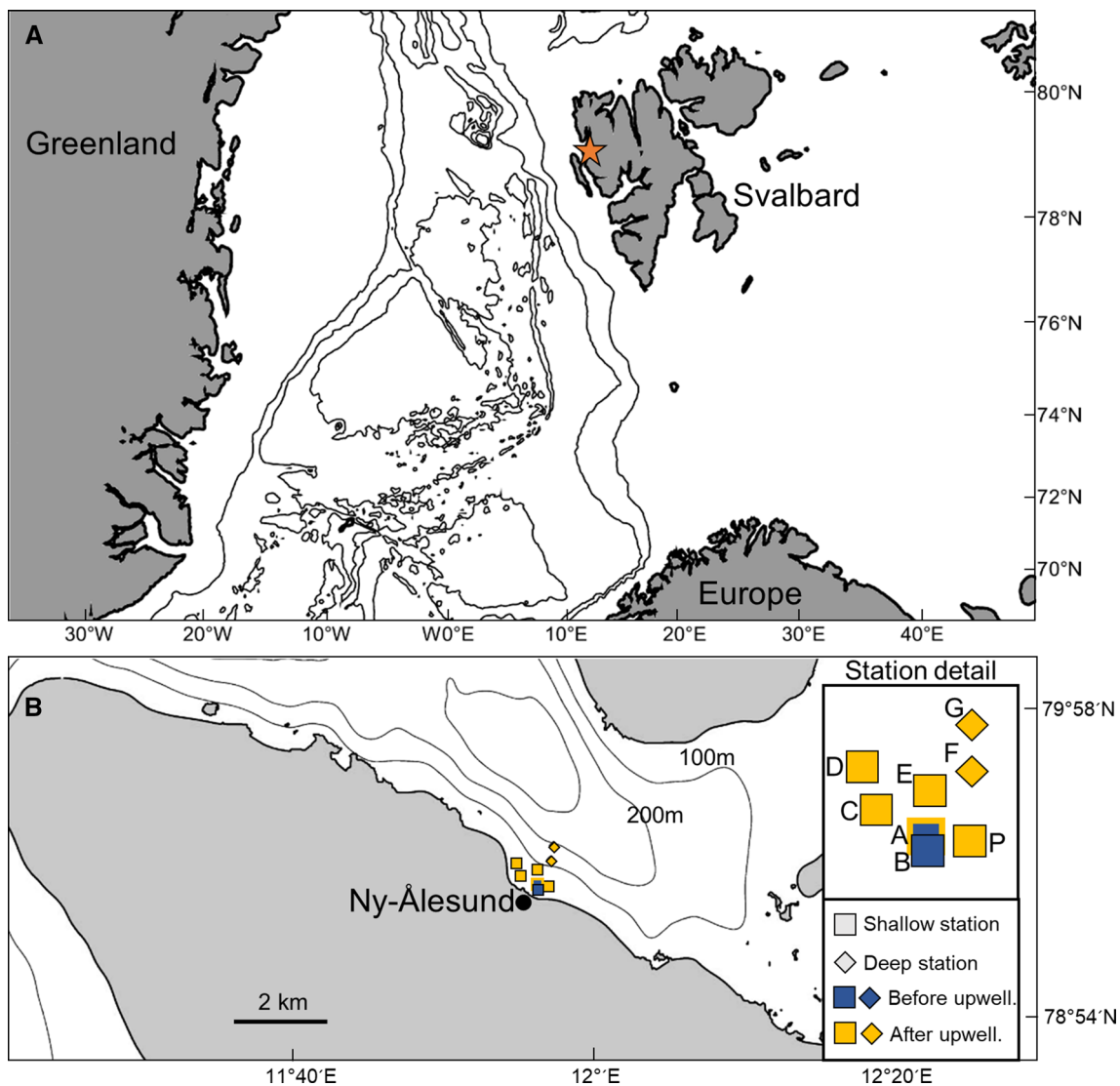


Fig. 1 Map of sampling sites. **A** Kongsfjorden location within Svalbard; **B** stations sampled in Kongsfjorden near Ny-Ålesund. Station A was sampled both before and after upwelling

a marine species, E -value < 0.05). Out of 44 total PCRs, 13 failed to produce a sequence, and another 27 sequences did not have a reasonable match in GenBank (i.e. closest match was not a marine species or was not in the correct phylum).

Statistical analysis

Each zooplankton sample represents a different volume of water filtered, so for statistical analysis, we normalized abundances of each taxon m^{-3} . All replicates were treated as independent samples (rather than using average values per station) in order to increase statistical power. Statistical analyses were conducted for all stations, for shallow stations only (excluding stations F and G), and for stations sampled after upwelling (to investigate differences between shallow

and deep stations). We tested for a significant difference in larval community structure before and after upwelling using PERMANOVA with unrestricted permutation of the raw data and type III partitioning sum of squares in Primer 7 (Anderson et al. 2008). In order to explore the influences of temperature, salinity, and depth on larval community structure, we used the DISTLM and dbRDA procedures in Primer 7. We also tested for differences in the average temperature and salinity of each station sampled before and after upwelling, densities of the most common larval taxa before and after upwelling, and larval densities at shallow v. deep stations using 2-sample t-tests in Matlab 2017. Homoscedasticity was tested using Bartlett tests, and in heteroscedastic cases, we used a non-parametric Mann–Whitney test instead of a t-test.

Results

Environmental conditions

When sampling began on 5 January 2020, dense sea-ice floes covered the surface of Kongsfjorden near Ny-Ålesund. Water temperatures were between -1 and -1.5°C , with the coldest temperatures occurring near the seafloor (Figs. 2, 3). Salinity ranged $34.0 - 34.2$ across the entire water column (Figs. 2, 3). Beginning on 6 January, strong down-fjord winds broke up the sea ice and moved floes out of Ny-Ålesund harbor. On 7 January, 8 m s^{-1} wind speeds were

measured in Ny-Ålesund (Fig. 4), with even stronger gusts over the exposed fjord waters (authors' pers. obs.). Strong winds persisted until 9 January and then began to subside (Fig. 4). Following the wind event, water temperatures in Kongsfjorden were significantly higher (Table 2). Temperatures ranged between -0.3 and -0.8°C through most of the water column and approached -1°C near the seafloor at some stations (Table 2, Fig. 2, 3). Salinity was also higher, approximately 34.2 throughout the water column at all stations, though this difference was not significant (Table 2, Figs. 2, 3). The strong winds, down-fjord transport of ice, and significant change in temperature of the water column suggest that an upwelling event occurred.

Fig. 2 Temperature and salinity data from each station in Kongsfjorden, Svalbard (5–200 m bottom depth). Each point represents one measurement. Water masses are indicated by boxes: *WCW* winter cooled water; *LW* local water; *ArW* Arctic water. Water mass definitions are from Cottier et al. (2005)

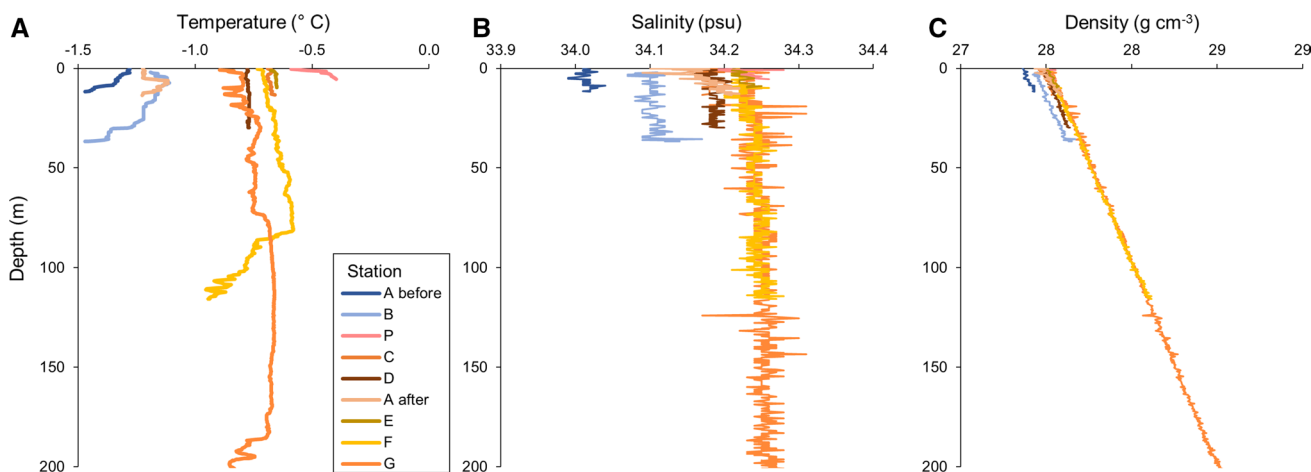
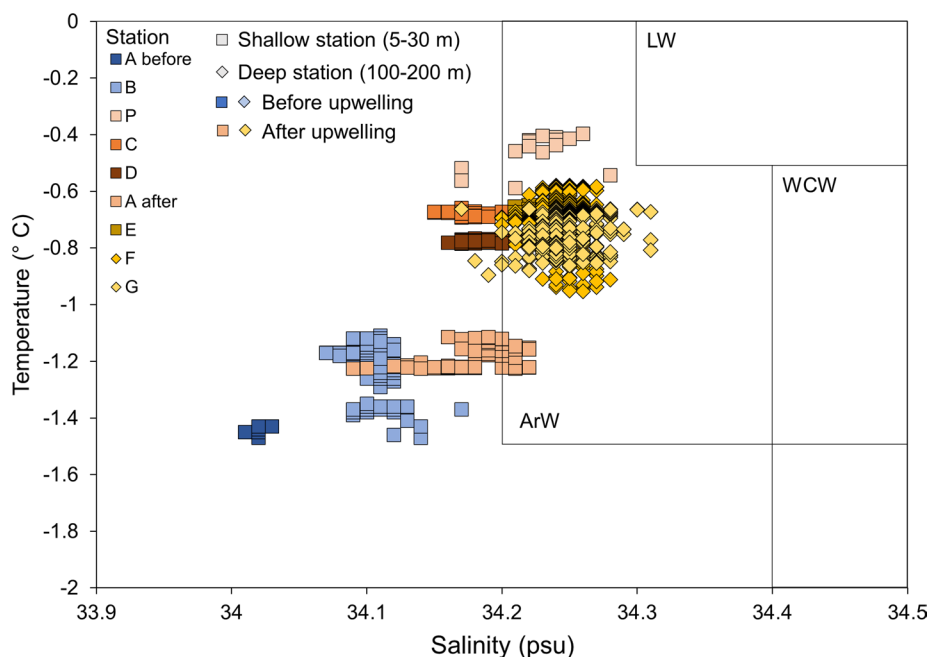


Fig. 3 **A**, temperature; **B**, salinity; **C**, density of seawater at each station in Kongsfjorden, Svalbard (5–200 m depth). Cool colors show stations sampled before upwelling; warm colors show stations sampled after upwelling

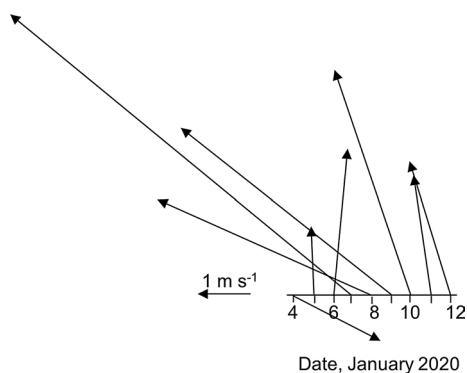


Fig. 4 Wind velocities during the sampling period in January 2020. Daily averages based on measurements 10 m above ground at the AWIPEV meteorological station in Ny-Ålesund

Embryos and larvae collected in Kongsfjorden

A total of 434 specimens were collected in zooplankton net samples. The specimens comprised 19 different morphotypes belonging to 10 different invertebrate phyla (Table 3,

Fig. 5). For taxa with uncertain identifications, we use the genus name or name of the larval form throughout this manuscript.

The most common morphotype collected was a small, green-gray embryo (Fig. 5). The COI sequence for this morphotype matched most closely to the sipunculan *Golfingia elongata* (E -value 1×10^{-7}). *Golfingia margaritacea* has previously been observed in Svalbard waters (Prestud et al. 2004), but the COI sequence of *G. margaritacea* was a slightly more distant match to our specimens (E value 5×10^{-6}).

A second embryo morphotype was identified using its 16S sequence as the hemichordate *Saccoglossus mere-schkowskii* (E value 5×10^{-26}). Our samples included some specimens that appeared to be juvenile hemichordates (Fig. 5) as well as juvenile nemerteans with approximately the same size, shape, and color. Nemerteans and hemichordates could be differentiated by proboscis morphology (Fig. 5), but it is possible that some embryos included in the *Saccoglossus* morphotype were in fact nemertean embryos. Therefore, we counted embryos separately from

Table 2 Results of statistical tests conducted in this study

Dependent variable	Independ. var	Test	Test stat	<i>P</i>
Temperature	B/A upwelling	<i>t</i> test	-3.36	0.012
Salinity	B/A upwelling	Mann-Whitney	3.00	0.055
Community structure (all)	Temperature	DISTLM	1.85	0.057
Community structure (all)	Salinity	DISTLM	2.20	0.012
Community structure (all)	Depth	DISTLM	3.28	0.002
Community structure (shallow)	B/A upwelling	PERMANOVA	2.13	0.019
Community structure (shallow)	Temperature	DISTLM	1.25	0.244
Community structure (shallow)	Salinity	DISTLM	1.88	0.041
Community structure (shallow)	Depth	DISTLM	1.47	0.134
<i>Golfingia</i> m ⁻³ (shallow)	B/A upwelling	Mann-Whitney	27.5	0.058
Embryo m ⁻³ (shallow)	B/A upwelling	Mann-Whitney	52.0	0.684
<i>Saccoglossus</i> m ⁻³ (shallow)	B/A upwelling	Mann-Whitney	50.0	0.661
<i>Nipponemertes</i> m ⁻³ (shallow)	B/A upwelling	Mann-Whitney	37.5	0.467
<i>Margarites</i> m ⁻³ (shallow)	B/A upwelling	Mann-Whitney	51.5	0.677
Nudibranch m ⁻³ (shallow)	B/A upwelling	Mann-Whitney	30.0	0.078
<i>Alcyonidium</i> m ⁻³ (shallow)	B/A upwelling	<i>t</i> test	-1.35	0.194
Asteroid m ⁻³ (shallow)	B/A upwelling	Mann-Whitney	40.0	0.701
<i>Parenchymella</i> m ⁻³ (shallow)	B/A upwelling	Mann-Whitney	45.0	0.999
<i>Golfingia</i> m ⁻³ (after upwell.)	Shallow v. deep	Mann-Whitney	71.0	0.362
Embryo m ⁻³ (after upwell.)	Shallow v. deep	Mann-Whitney	43.5	0.134
<i>Saccoglossus</i> m ⁻³ (after upwell.)	Shallow v. deep	Mann-Whitney	59.5	0.912
<i>Nipponemertes</i> m ⁻³ (after upwell.)	Shallow v. deep	Mann-Whitney	76.5	0.125
<i>Margarites</i> m ⁻³ (after upwell.)	Shallow v. deep	Mann-Whitney	42.0	0.126
Nudibranch m ⁻³ (after upwell.)	Shallow v. deep	Mann-Whitney	32.0	0.010
<i>Alcyonidium</i> m ⁻³ (after upwell.)	Shallow v. deep	Mann-Whitney	42.0	0.099
Asteroid m ⁻³ (after upwell.)	Shallow v. deep	Mann-Whitney	76.0	0.144
<i>Parenchymella</i> m ⁻³ (after upwell.)	Shallow v. deep	Mann-Whitney	78.0	0.041

Significant *p* values (<0.05) are shown in bold. B/A, before and after

Table 3 Larval and adult feeding modes for invertebrate taxa collected in this study

Larval taxon	Phylum	Larval feeding mode	Adult feeding mode	References
<i>Golfingia elongata</i>	Sipuncula	Lecithotrophic	Deposit feeder	Rice 1976, Grall et al. 2006
<i>Saccoglossus</i> sp.	Hemichordata	Lecithotrophic	Deposit feeder	Burdon-Jones 1952
<i>Nipponemertes pulchra</i>	Nemertea	Lecithotrophic	Predator	Maslakova 2010
<i>Margarites helicinus</i>	Mollusca	None	Herbivore	Holyoak 1988, Zmudczyńska-Skarbek and Bałazy 2017
<i>Buccinum</i> sp.	Mollusca	None	Predator	Smith and Thatje 2013
Nudibranch veliger	Mollusca	Suspect planktotrophic	Unknown	
<i>Hiatella arctica</i>	Mollusca	Planktotrophic	Suspension feeder	Flyachinskaya and Lesin 2006
Bivalve veliger	Mollusca	Suspect planktotrophic	Unknown	
<i>Alcyonidium</i> sp.	Bryozoa	Suspect lecithotrophic	Suspension feeder	Porter et al. 2002
<i>Cerianthis lloydii</i>	Cnidaria	Planktotrophic	Predator	Conway 2012, Eleftheriou and Basford 1983
Asteroid	Echinodermata	Unknown	Unknown	
Parenchymella	Porifera	Lecithotrophic	Suspension feeder	Maldonado 2006
Platyhelminth	Platyhelminthes	Suspect lecithotrophic	Suspect predator	
Polychaetes (3 morphotypes)	Annelida	Unknown	Unknown	

hemichordate and nemertean juveniles for statistical analysis. Based on the presence of a stylet, the nemerteans can be identified as Hoplonemertea, and we suspect these specimens belong to *Nipponemertes pulchra*, a hoplonemertean that has previously been observed in Svalbard fjords in winter (Moen and Svendsen 2004).

We collected juvenile benthic gastropods *Margarites helicinus* and a singleton cf. *Buccinum* sp. Our samples also included the veliger larvae of a nudibranch. Bivalve veliger larvae in our samples belonged to *Hiatella arctica* and an unidentified morphotype.

Our samples included a cyphonautes larva whose COI sequence matched most closely to *Alcyonidium mamillatum* (E value 1×10^{-31} ; Fig. 5). We also collected a cerinula larva that resembled *Cerianthis lloydii*, a cerianthid species which occurs in Svalbard (Prestud et al. 2004). Other taxa in our samples included a juvenile asteroid, three polychaetes, a parenchymella larva, a direct-developing platyhelminth, and an unknown (Fig. 5).

Six of the larval taxa we collected are likely lecithotrophic, and four are likely planktotrophic (Table 3). The two benthic gastropods, *Margarites helicinus* and *Buccinum* sp., develop by crawl-away larvae that complete their development in an egg case and do not have a pelagic stage (Table 3). Consequently, the individuals collected in this study may possibly have been disturbed from their substrata by the motion of the plankton net or scraped off kelp blades at shallow stations. The taxa we collected have a range of feeding modes as adults, including suspension feeders, deposit feeders, herbivores, and predators (Table 3).

Oceanographic influence on larval abundance and community structure

Larval community structure for all stations was significantly related to salinity and depth (Table 2). The best DISTLM model included all three variables but only explained about 22% of the variation in community structure ($R^2 = 0.22$). These relationships can be visualized in the dbRDA (Fig. 6a). Samples from the two deep stations, F and G, are aligned to the depth axis, indicating that depth explains most of the difference between these samples and shallower stations. Points representing shallow stations A-E and P aligned with the axes for temperature and salinity. Samples collected before upwelling at stations A and B were spatially separated from the other samples in the dbRDA (Fig. 6a).

Because of the strong influence of depth, we tested for significant differences in larval community structure before and after upwelling using shallow stations only (excluding deep stations F and G, which were only sampled after upwelling). Larval community structure at shallow stations was significantly different before and after upwelling (PERMANOVA, $p = 0.019$; Table 2). A DISTLM of the shallow stations showed a significant influence of salinity on community structure (Table 2). The best model included all 3 variables and explained about 21% of the variation in community structure ($R^2 = 0.21$). The dbRDA plot of the shallow stations shows that samples collected before upwelling are more scattered but cluster by station, indicating patchiness in the larval community, whereas samples collected after upwelling are more homogenous (Fig. 6b).

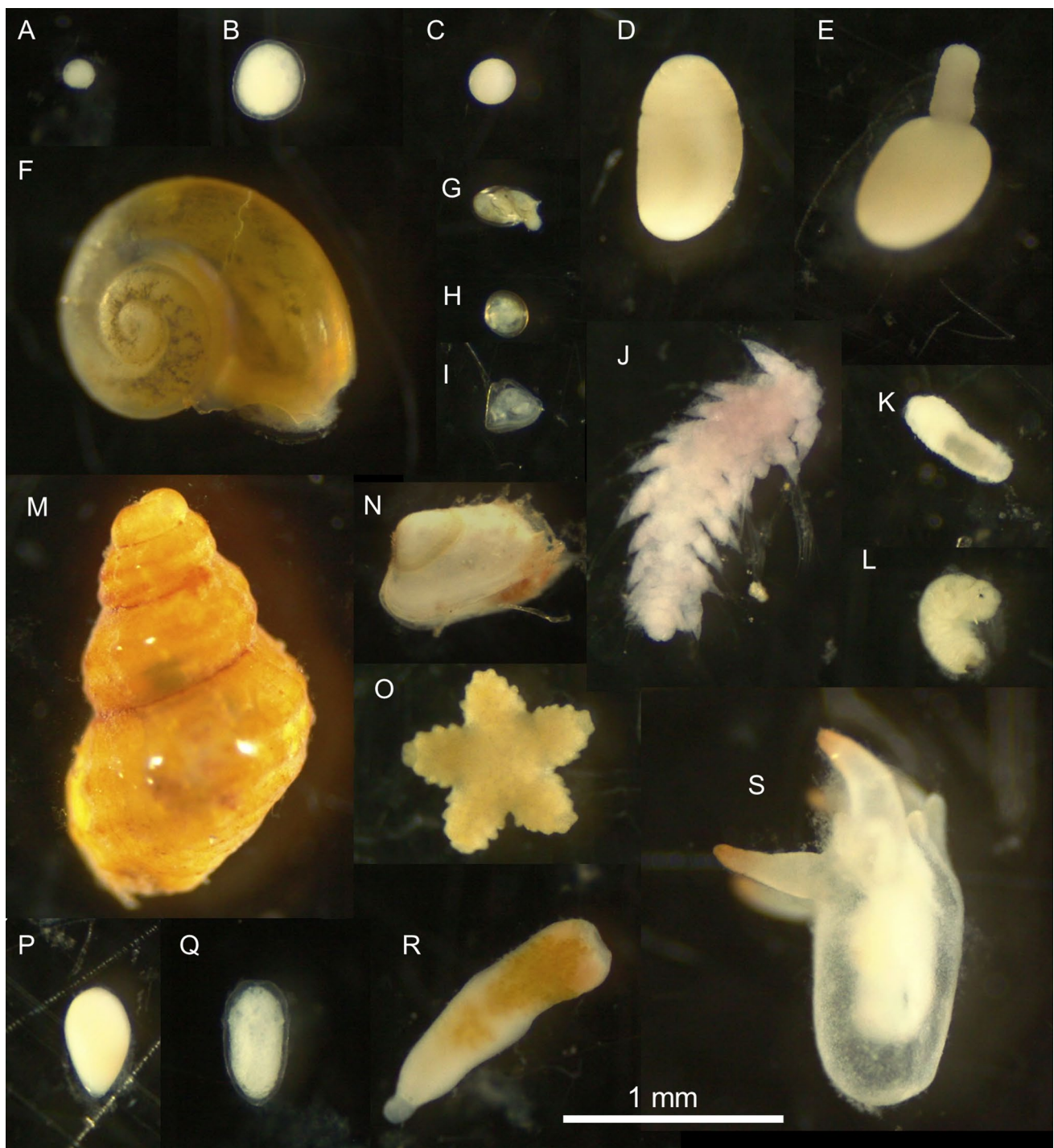


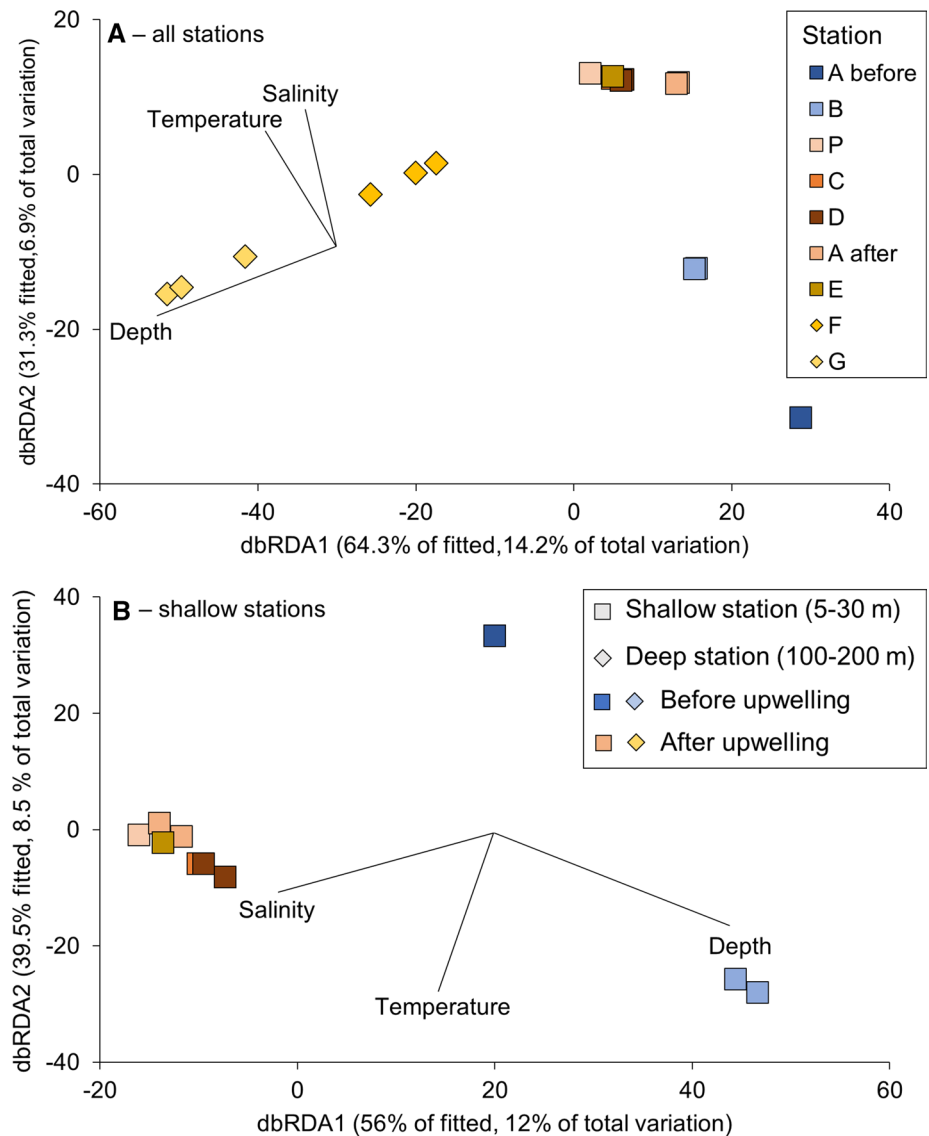
Fig. 5 Early life-history stages of benthic invertebrates collected in January 2020 in Kongsfjorden, Svalbard. **A**, *Golfingia* sp. embryo; **B**, *Saccoglossus* sp. embryo; **C**, embryo 3; **D**, *Saccoglossus* sp.; **E**, *Nipponemertes pulchra*, with everted proboscis; **F**, *Margarites helacinus*;

G, nudibranch veliger larva; **H**, bivalve veliger; **I**, *Alcyonidium* sp.; **J** polychaete 1; **K**, polychaete 2; **L**, polychaete 3; **M**, cf. *Buccinum* sp.; **N**, *Hiatella arctica*; **O**, asteroid juvenile; **P**, parachyrella larva; **Q**, platyhelminth; **R**, unknown; **S**, *Cerianthus lloydii*

Total larval densities ranged 0.02–2.9 m⁻³ in our samples. The densities for each larval taxon were not significantly different before and after upwelling at the shallow stations (Table 2, Fig. 7a). In order to further explore the distribution

of larvae, we compared densities for each taxon at shallow and deep stations sampled after upwelling (Table 2, Fig. 7b). The nemertean larva occurred at significantly higher density at shallow stations, while the parachyrella larva

Fig. 6 dbRDA plot showing influence of environmental factors on larval community structure in Kongsfjorden, Svalbard (5–200 m depth). Each point represents one larval sample. **A**, all stations; **B**, shallow stations only, stations F and G excluded. Both legends apply to both plots



had significantly higher density at deep stations (Table 2, Fig. 7b).

Discussion

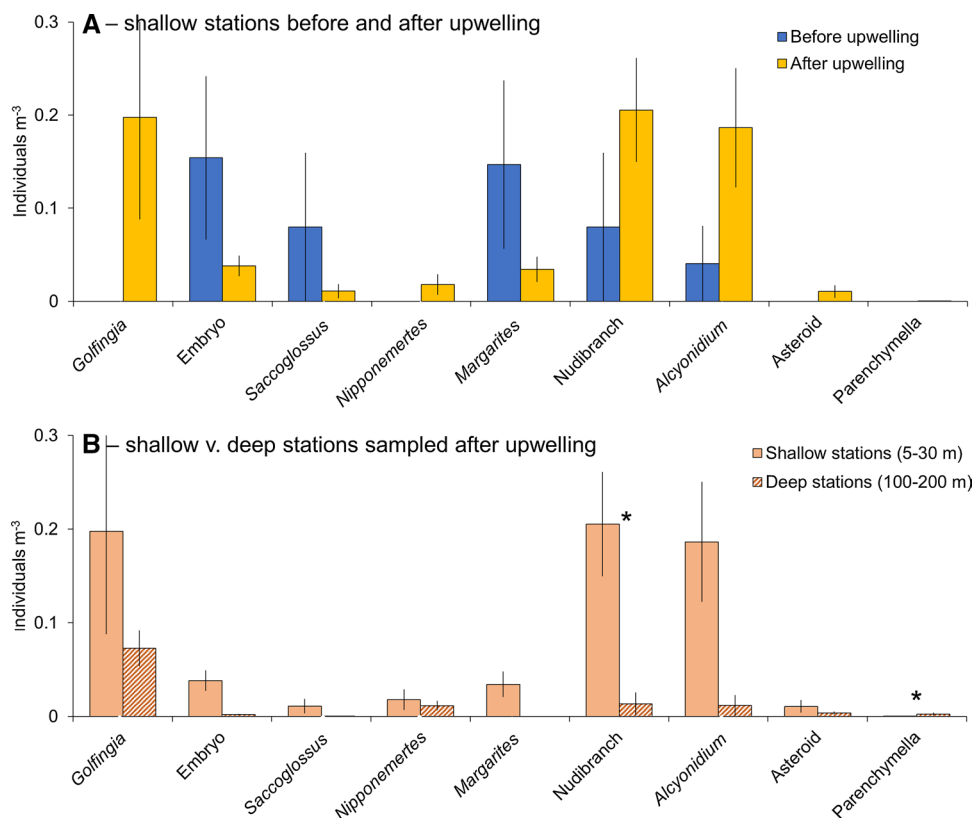
The major finding of this study is that many species of marine invertebrates have pelagic larvae or other early life-history stages present in the polar night. Our samples included 19 species or morphotypes belonging to ten different phyla. We even collected three morphotypes of embryos, which indicates multiple species are reproducing in early January, just hours or days before being collected in our samples.

In the polar night, phytoplankton are scarce and so pelagic larvae could have difficulty locating food sources. Studies from Antarctica have shown that at least some species of

larvae can feed on bacteria in the water column or absorb dissolved organic matter (Rivkin et al. 1986; Shilling and Bosch 1994). We were unable to determine the pelagic larval durations of the planktotrophic species we observed, but some larval taxa have durations on the order of weeks or months (Shanks 2009). The individuals we collected could have been spawned earlier in autumn, prior to the polar night, but these individuals are still likely to have experienced low-food conditions for the majority of the pelagic duration. Between December and March in Kongsfjorden, primary production is close to zero, and the majority of the organic matter in the water column is detritus (Hegseth et al. 2019). Our observations suggest that food sources for planktotrophic larvae during the polar night require more investigation and should be addressed through future research.

Our observations also provide motivation for further study into the role of lecithotrophy in these systems.

Fig. 7 Densities of larval taxa in Kongsfjorden, Svalbard (5–200 m depth). **A**, densities of the most common taxa at shallow stations before and after upwelling (deep stations F and G excluded), before upwelling $n=5$, after upwelling, $n=19$; **B**, densities of the most common taxa at shallow and deep stations after upwelling (samples collected before upwelling excluded), shallow station $n=13$, deep station $n=6$. Error bars denote standard error. *denotes a significant difference



Lecithotrophic development could be adaptive for species reproducing in winter, in order to prevent larval starvation and ensure settlement success. For taxa that have a stable, relatively non-seasonal food source as adults (i.e. scavengers), energetic costs incurred by the mother while provisioning lecithotrophic larvae could be recuperated through foraging. Reproduction in the winter months could be adaptive for some species, such as inferior competitors, so they can settle and grow prior to the arrival of other species in the spring bloom (Kukliński et al. 2013; Meyer et al. 2017).

Oceanographic events such as upwelling are associated with shifts in the zooplankton community in high Arctic fjords (Willis et al. 2006, 2008), and our study reveals significant differences in the meroplanktonic community structure before and after a wind-driven upwelling event. The temperature and salinity values observed after this upwelling event most closely match the characteristics of oceanic water that may have entered the fjord from the shelf (temperature -1 – 1 °C, salinity 34.2–34.7, Cottier et al. 2005). Strong down-fjord winds set up Ekman transport that moves surface waters to the right of the wind (in this case in Svalbard, to the north). This is compensated by upwelling along the south side of the fjord, where our stations were located (Cottier et al. 2010). The most likely scenario to explain our observations is that wind-driven transport of surface waters to the north side of Kongsfjorden led to upwelling of Arctic shelf water along the south side of the fjord. An improved

understanding of how fjord hydrography responds to wind forcing will be an important component for future investigations of such perturbations on larval ecology in Arctic fjords.

Meroplanktonic larvae can be advected by oceanographic currents and so sub-Arctic species can potentially be introduced to high Arctic habitats from lower latitudes (Ershova et al. 2019). The larval species that we observed have biogeographic affinities in the North Atlantic and Arctic, and many have previously been found in Svalbard. For example, *Golfingia elongata* has a distribution throughout the North Atlantic (Hayward and Ryland 1990). *Alcyonidium mamillatum* is a gelatinous bryozoan that has previously been observed in Svalbard (Prestud et al. 2004), and *A. gelatinosum* has been found on recruitment panels deployed in Kongsfjorden (Meyer et al. 2017). *Saccoglossus mereschkowskii* was originally described from the White Sea (Wagner 1885), and *Hiatella arctica* has a pan-Arctic distribution (Ershova et al. 2019; Sejr et al. 2002). While it does not appear that the upwelling we observed introduced new species of larvae to Kongsfjorden, there is at least one prior report of strong evidence that Atlantic water brings larvae into a western Svalbard fjord in summer (Berge et al. 2005). Our study area may be relevant in this respect given that Svalbard may be particularly vulnerable to invasion by lower-latitude taxa because of the rate of warming and level of ship traffic (van den Heuvel-Greve et al. 2021). Future research is required to determine if oceanographic currents

could bring new species of larvae into Kongsfjorden in winter.

Observed differences in the meroplankton community within a relatively confined area (nearshore in a single fjord) and short sampling window (one week) suggest a high level of patchiness in the larval community both spatially and temporally. Moreover, given that our samples were integrated through the whole water column, any presence of additional vertical patchiness would not be seen. Stratified sampling would be required to explore that additional dimension of patchiness and identify variability as a function of depth and in turn, water masses in these fjords. Repeated sampling is also necessary to capture the variation in meroplankton communities.

Observed larval densities ($0.02\text{--}2.9\text{ m}^{-3}$) were notable in this field study, roughly 4 orders of magnitude less than those reported by other meroplankton studies in Svalbard waters in summer ($43,900\text{ m}^{-3}$ in June, Kukliński et al. 2013; $83,900\text{ m}^{-3}$ in July, Stübner et al. 2016) and on the low end of density ranges reported in other polar regions ($0.03\text{--}84\text{ m}^{-3}$, Clough et al. 1997; $1.6\text{--}21\text{ m}^{-3}$, Freire et al. 2006; $100\text{--}10,000\text{ m}^{-3}$, Michelsen et al. 2017; 2.6 m^{-3} , Stanwell-Smith et al. 1999; $> 4000\text{ m}^{-3}$, Weydmann-Zwolicka et al. 2021). These low observed larval densities could stem in part from the mesh size used ($150\text{ }\mu\text{m}$), which is likely to miss many of the smallest zooplankton present. Nevertheless, despite methodological differences, comparison of different studies with order-of-magnitude estimations can indicate general patterns and merit further exploration. Our findings join a small number of studies that observed low densities of larvae in January in Svalbard (Brandner et al. 2017; Kukliński et al. 2013) and strong seasonal patterns in Arctic meroplankton (Stübner et al. 2016; Weydmann-Zwolicka et al. 2021).

While larval densities in the polar night are low, our results suggest that targeted sampling may reveal more taxa of meroplankton than may have been previously assumed. Increased research in the polar night will help increase our understanding of the actual seasonal patterns in this broader range of meroplankton taxa and therefore baseline ecosystem processes in the rapidly-changing polar regions.

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Data availability Raw data are provided in Online Resource 1.

Declarations

Conflict of interest The authors declare they have no conflicts of interest.

Human and animal rights statement This research did not involve any human subjects. Animal (zooplankton) specimens were collected and handled according to ethical best-practices for marine biology.

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