



FEATURE ARTICLE

Origin of marine invertebrate larvae on an Arctic inflow shelf

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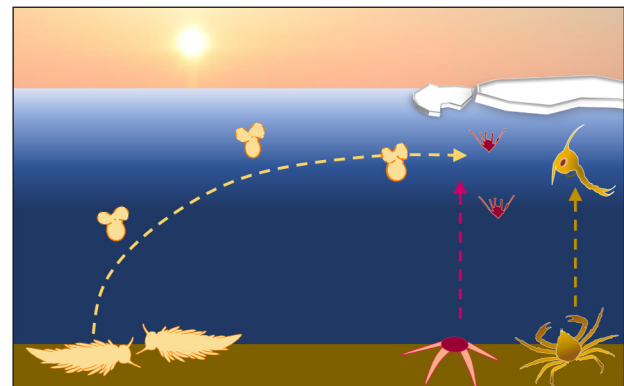
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ABSTRACT: Many benthic invertebrate taxa possess planktonic early life stages which drift with water currents and contribute to dispersal of the species, sometimes reaching areas beyond the current ranges of the adults. Until recently, it had been difficult to identify planktonic larvae to species level due to lack of distinguishing features, preventing detection of expatriate species. Here, we used DNA metabarcoding of the COI gene to obtain species-level identification of early life stages of benthic invertebrates in zooplankton samples from the Barents Sea and around Svalbard, where, regionally, large volumes of warm Atlantic Water enter the Arctic from the south. We compared the larval community in the water column to the adult community on the seafloor to identify mismatches. In addition, we implemented particle tracking analysis to identify the possible areas of origin of larvae. Our results show that 30–45% of larval taxa—largely polychaetes and nudibranchs—were not local to the sampling area, though most were found nearby in the Barents Sea. In the particle tracking analysis, some larvae originating along the Norwegian coast were capable of reaching the northwest coast of Svalbard within 3 mo, but larvae found east of Svalbard had a more constrained possible area of origin which did not extend to the Norwegian coast. This study highlights largely regional-scale larval connectivity in the Barents Sea but demonstrates the potential for some long-lived larval taxa to travel to Svalbard and the Barents Sea from further south.



Most Barents Sea larvae are of local or regional origin, but some are drifting into the Arctic from further south.

Graphic: Raphaëlle Descôteaux

KEY WORDS: Meroplankton · Larval dispersal · Barents Sea · Arctic benthos · Species distributions · Climate change

1. INTRODUCTION

Climate change and Atlantification of the Arctic are transforming the Barents Sea shelf ecosystem (Ingvaldsen et al. 2021). The Barents Sea is already warmer now compared to recent decades (Lind et al. 2018, Skagseth et al. 2020) and is expected to continue warming, with surface waters reaching up to 5°C above the long-term average by the end of the

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century (Drinkwater et al. 2021), although some models predict a more modest change (Long & Perrie 2017). The Barents Sea is an Arctic inflow shelf (Carmack & Wassmann 2006), where warm and saline Atlantic Water flowing northwards meets cold and relatively fresh Arctic Water flowing towards the south (see Fig. 1) (Oziel et al. 2016). The convergence of these 2 water masses occurs at the Polar Front, the location of which is strongly tied to the bathymetry, at least in the western Barents Sea where the front largely follows the northern edge of Bear Island Trough and Hopen Trench (Oziel et al. 2016). The Arctic-dominated northern Barents Sea is seasonally ice-covered but is predicted to become ice-free year-round by the end of the century (Onarheim & Årthun 2017). Since the flow related to the Polar Front is strongly linked to the topography, the flow regimes will likely persist. However, the loss of sea ice facilitates enhanced vertical mixing, so that some of the surface heat can be redistributed towards deeper layers (Polyakov et al. 2017, Lind et al. 2018). As such, the seafloor will not be sheltered from surface heating and is expected to warm concurrently, albeit at a slower pace (Renaud et al. 2015). Models predict bottom water temperatures on Arctic shelves to increase on average by $2.3 \pm 1.0^\circ\text{C}$ by 2100 (Heuzé et al. 2015), with the biggest changes, up to 6°C in some regions, occurring in the Barents Sea (Renaud et al. 2019).

As a result of changing environmental conditions, many species are expected to move poleward. The Arctic, and the Barents Sea in particular, will become increasingly habitable for a range of potential aquatic invasive species (Goldsmit et al. 2020). In addition, the surface speed of the Atlantic Water has increased in recent years, potentially strengthening the bio-advection of southern species into these regions (Oziel et al. 2020). Barents Sea benthic communities comprise a mix of Arctic, boreal (Atlantic) and boreal-Arctic taxa (Jørgensen et al. 2019, Zakharov et al. 2020) which have shifted with climate, with boreal taxa becoming relatively more abundant in warmer periods, both on glacial timescales as well as interannual timescales in the recent past (Blacker 1965, Jørgensen et al. 2019). In recent decades, Barents Sea fish communities have started transitioning into a more boreal assemblage, with more warm-water species moving north and the range of typical Arctic species retracting (Renaud et al. 2012, Berge et al. 2015, Fossheim et al. 2015). In the Barents Sea, the new, more boreal fish assemblage is characterized by larger, faster-growing and more omnivorous/generalist taxa compared to the

previous, more Arctic community (Frainer et al. 2017), with potentially important consequences for trophic connections in the ecosystem (Kortsch et al. 2015). While most benthic invertebrates are not as mobile as fish, at least at the adult stage, some cases of northward expansions have also been reported, such as blue mussels expanding their range to the Svalbard coast (Berge et al. 2005), several gastropod taxa extending into the Barents Sea (Zakharov & Jørgensen 2017) and Barents Sea peracarids assemblages shifting to increasingly boreal composition (Zimina et al. 2019). These changes in species composition can alter ecosystem functioning.

For many benthic invertebrate taxa, the adult stage has limited mobility, so it is up to the planktonic early life stages (from here on, referred to as meroplankton) to disperse. For some, the dispersal stage is short, lasting from minutes to a few hours and resulting largely in recruitment to the parent population, while others disperse for up to several months (Shanks 2009) and, in rare cases, years (Strathmann & Strathmann 2007). In a previous seasonal study in the Barents Sea, most meroplanktonic taxa were found at discrete time points suggesting a larval phase of no more than a few months, though a minority of taxa showed evidence of longer dispersal periods (though still shorter than a year; Descôteaux et al. 2021). Those taxa with the potential for long-distance dispersal may be better adapted to finding new habitat following periods of change (Wares & Cunningham 2001, Hardy et al. 2011). Unfortunately, larval duration is only known for a very small subset of benthic invertebrate taxa, and cold Arctic temperatures may extend the larval period as well (O'Connor et al. 2007). Without this information, it may be difficult to predict which taxa have the potential for long-distance dispersal and hence which boreal species currently have the means of reaching the Arctic Ocean within their larval phase. Instead, one can look directly in the Barents Sea for larvae of boreal origin. Such a strategy relies on species-level identification of larvae, which has historically been challenging because of the general lack of species-specific features at the larval stage for most taxa. New molecular methods, however, now enable reliable identification of planktonic early life stages of benthic invertebrates (Ershova et al. 2019, Descôteaux et al. 2021).

Here, we aimed to determine the likely origin of benthic invertebrate larvae that are found in the Barents Sea and around Svalbard. We used metabarcoding of zooplankton samples, a fast and efficient way to process large sample volumes, to identify the lar-

val community in 3 oceanographically different areas: (1) north of Svalbard and, in the Barents Sea, east of Svalbard, (2) north and (3) south of the Polar Front (Fig. 1). The areas north of Svalbard and south of the Polar Front are highly influenced by inflowing Atlantic Water, whereas the area north of the Polar Front is more Arctic in character (Lind & Ingvaldsen 2012, Smedsrud et al. 2013, Renner et al. 2018). We then compared the larval pool with the adult community on the seafloor to evaluate which species are local and which may be drifting in from other seas. Compared with other Arctic Seas, the Barents Sea benthos is relatively well studied (e.g. Cochrane et al. 2009, Jørgensen et al. 2015, Zakharov et al. 2020), offering a robust data set against which to compare the larval community. We hypothesized that the majority of the collected larvae belong to taxa that are known to inhabit the region. We then implemented particle tracking analysis to highlight which regions could realistically supply larvae to the Barents Sea within a 3 mo drift. We hypothesized that the areas north of Svalbard and south of the Polar Front would receive particles (larvae) from the Norwegian coast but that the area north of the Polar Front would be more isolated. This information can provide some indication of which boreal taxa currently have the means of reaching the Barents Sea during their larval stage and therefore may be some

of the first to settle once conditions there become favorable for establishment of a new population. Finally, based on our previous observation of a larva of *Bohuslania matsmichaeli* in the Barents Sea (Descôteaux et al. 2021), a nudibranch species otherwise only known from one fjord in southern Norway (Korshunova et al. 2018), we performed an additional particle tracking analysis where particles were released from a single point in southern Norway and allowed to drift for 1 yr. We hypothesized that a few of those particles would reach the Barents Sea and Svalbard within 1 yr, though fewer in the northern Barents Sea north of the Polar Front where the influence of the northward-flowing Atlantic Water is comparatively low.

2. MATERIALS AND METHODS

2.1. Collection and preparation of meroplankton samples

Zooplankton samples were collected in August, September and November 2017 as well as in January, April, June and August 2018 in the 3 study regions: north of Svalbard (11 samples), and north (28 samples) and south (22 samples) of the Polar Front (Fig. 1). Samples were collected using a WP2 or

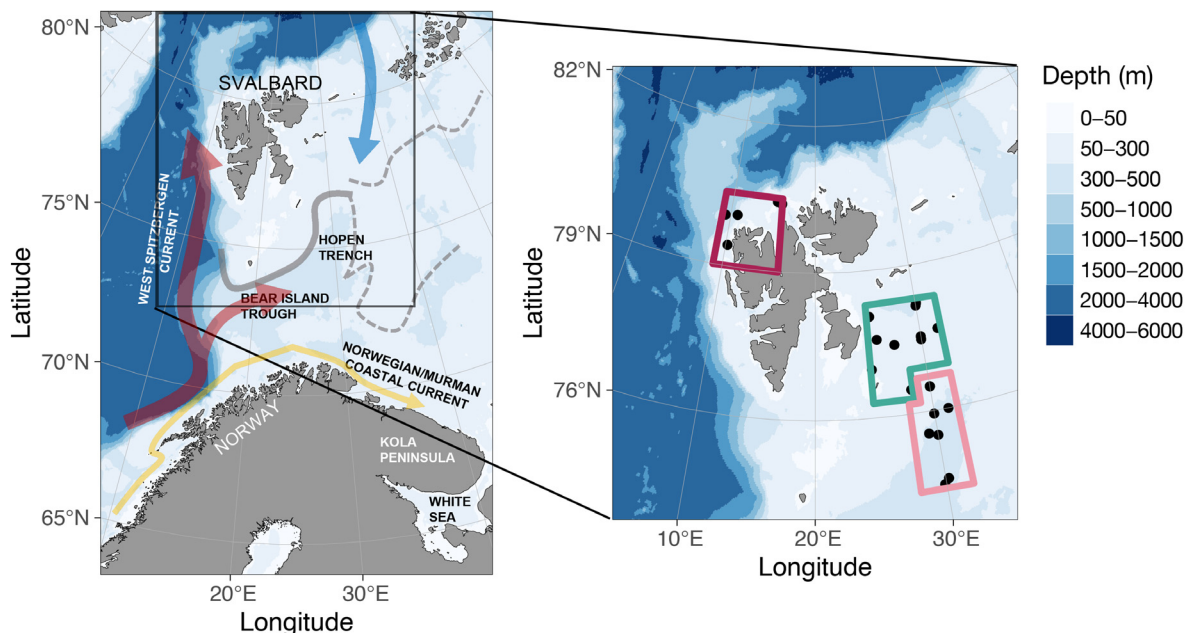


Fig. 1. Study area with Atlantic (red arrows) and Arctic (blue arrow) water inflows, Norwegian/Murman Coastal Current (yellow arrow) and Polar Front (gray lines). Inset: locations of zooplankton sampling (black dots) and the 3 areas of adult community analysis and particle tracking target (polygons): north of Svalbard (red), north of the Polar Front (green) and south of the Polar Front (light pink). All maps presented here were produced with package ggOceanMaps (Vihtakari 2022) in R

MultiNet (Hydro-Bios) with 64 or 180 μm mesh from near bottom to surface (Table S1 in the Supplement at www.int-res.com/articles/suppl/m699p001_supp.pdf) and preserved in 96% ethanol. When phytoplankton was abundant and clogging the 64 μm mesh, the 180 μm was used acknowledging that it could miss the smallest larvae retained in the 64 μm mesh. Hence, the total biodiversity may be underestimated when using the 180 μm mesh. Complete net-haul zooplankton samples were split in half using a Motodo box-type plankton splitter. While most samples were complete prior to splitting, some had a sub-sample removed for use in a different research project, resulting in metabarcoded fractions varying from 0.19–0.5 of the initial sample (Table S1). One of the 2 fractions was used for metabarcoding (see below), while the other was kept as a voucher for future reference. The portion of the zooplankton sample dedicated to metabarcoding was blended in a high-power blender (Nutribullet Max 1200) for at least 1 min until the sample appeared homogeneous. The blended sample was then transferred into a jar to settle overnight. The next day, the sample was decanted to remove as much of the supernatant ethanol as possible before transferring it to a 50 ml Falcon tube. The samples in Falcon tubes were centrifuged at $3000 \times g$ for 5 min to further separate the ethanol from the sample. The ethanol was then decanted out and discarded and the remaining sample weighed inside its Falcon tube (wet weight). For particularly large samples, some of the material was removed to keep the weight below 10 g for subsequent DNA extraction, as per the manufacturer's recommendation. The plankton splitter, blender container, jars, etc. were all soaked in 10% bleach for a few minutes and then rinsed in tap water in between samples to prevent cross-contamination.

2.2. DNA metabarcoding

DNA was extracted from the decanted zooplankton samples using the DNeasy PowerMax Soil Kit (Qiagen) according to manufacturer protocol, except that in step 4, the tubes were shaken in a shaking incubator (Infors HT, Microtron) at 65°C for 2 h at 200 rpm and in step 18 the DNA was eluted in 3 ml of solution C6 instead of 5 ml and run over the spin column twice to increase DNA concentration. The PowerMax Soil Kit was selected for its ability to process large sample volumes so as to obtain an extract as representative of the whole sample as possible, though its ability to extract efficiently across all meroplanktonic

phyla remains to be confirmed. We amplified the Leray-XT fragment of the COI gene (~313 bp), selected based on its ability to amplify across all our phyla of interest and to discriminate across species as well as on the completeness of its reference databases (Andújar et al. 2018, Wangenstein et al. 2018). Use of this fragment is extremely effective for identification of meroplankton (Ershova et al. 2019, Descôteaux et al. 2021). Each PCR reaction consisted of 10 μl AmpliTaq Gold polymerase, 0.16 μl bovine serum albumin $20 \mu\text{g} \mu\text{l}^{-1}$, 5.84 μl nuclease-free water, 1 μl individually tagged forward primer (5 μM , mlCOIntF-XT 5'-GGW ACW RGW TGR ACW ITI TAY CCY CC-3'), 1 μl individually tagged reverse primer (5 μM , jgHCO2198 5'-TAI ACY TCI GGR TGI CCR AAR AAY CA-3') as well as 2 μl undiluted DNA template for a total reaction volume of 20 μl . The PCR protocol consisted of a denaturation step for 10 min at 95°C followed by 35 cycles of 94°C for 1 min, 45°C for 1 min and 72°C for 1 min and a final extension of 5 min at 72°C (Wangenstein et al. 2018). The same tag was used on the forward and reverse primers to facilitate detection of chimeras. All samples were combined into a library, then cleaned (fragments below 70 bp removed) and concentrated using MinElute columns. The final DNA concentration was measured using a Qubit fluorimeter with broad-range dsDNA BR Assay Kit (Qubit). The NEXTflex PCR-free DNA sequencing kit (BIOO Scientific) was used to prepare the library for sequencing according to the manufacturer's instructions, omitting the second bead cleaning round in step B to improve yield. The library was quantified by qPCR using the NEBNext Library Quant Kit (New England Biolabs) and sequenced on an Illumina MiSeq platform with v3 2×250 bp kit spiked with 1% PhiX used as an internal control to calculate error rates.

2.3. Bioinformatics

Bioinformatics were carried out using the OBITools v1.01.22 pipeline (Boyer et al. 2016). Paired-end sequences were aligned with 'illumina-paired-end', and sequences with a score of <40 were removed. Samples were identified via primer tags, and primer sequences were removed from the data using 'ngsfilter'. Unique reads of lengths between 299 and 320 were selected using 'obigrep' and 'obiuniq', and chimeras were identified and removed from the data set using the 'uchime_denovo' algorithm (Edgar et al. 2011) from vsearch v1.10.1 (Rognes et al. 2016). SWARM 2.1.13 (Mahé et al. 2015) was used to cluster the sequences

into molecular operational taxonomic units (MOTUs) using a distance value of $d = 13$. A preliminary taxonomic assignment was done using 'ecotag' (Boyer et al. 2016) against DUFA-Leray v.2020-06-10, a custom reference database (publicly available from www.github.com/uit-metabarcoding/DUFA), which includes Leray fragment sequences extracted from the Barcode of Life Database (BOLD)/Genbank and in-house-generated sequences. Likely pseudogene sequences were then removed from the resulting data set using the algorithm LULU (Frøslev et al. 2017).

Only the MOTUs that made up at least 0.01 % of at least one sample were retained for further analysis. These sequences were then searched in BOLD (Ratnasingham & Hebert 2007) for taxonomic identification using package 'bold' (Chamberlain 2021) in R v4.2.1 (R Core Team 2021). When BOLD did not produce a match >97 %, we used the Ecotag assignment or identified the sequence using NCBI's basic alignment search tool (BLAST; Altschul et al. 1990). Sequences for which no match >97 % was found, for which the match was not at species-level and those belonging to fish, holoplanktonic taxa (e.g. copepods, chaetognaths, pteropods, etc.) or suspected contaminants (terrestrial or freshwater taxa) were not included in subsequent analyses. Our analysis focused exclusively on benthic invertebrate taxa with planktonic early life stages.

2.4. Comparison to adult community

Adult (and settled juvenile) benthic invertebrate community data for each of our 3 areas of interest were compiled from large data sets, including Norwegian–Russian Ecosystem Surveys (Jørgensen et al. 2015) and an Akvaplan-niva data set (Andrade et al. 2017). The Norwegian Institute of Marine Research, the Polar branch of the Russian Federal Research Institute of Fisheries and Oceanography (VNIRO) and the Murmansk Marine Biological Institute have been conducting annual trawl surveys of the Barents Sea megafauna since 2005 (Jørgensen et al. 2015, Zakharov et al. 2020). For this paper, we used data from the 2010, 2012, 2013 and 2015 samplings on the Norwegian side of the Barents Sea shelf, which totaled 694 sampling events and 805 taxa. The Akvaplan-niva data set consists of a compilation of macrofauna abundance data collected by Van Veen grab at 138 stations across the Barents, Pechora and Kara Seas from 1992–2005, including 1380 taxa, most of which were identified to species level. The boundaries of each area of

interest encompass the 3 geographical clusters of zooplankton sampling (Fig. 1). The list of meroplanktonic taxa found in each of the 3 areas from all seasons and depths combined was then compared to the list of adults compiled above. Meroplanktonic taxa that were not found as adults in one of those data sets were then investigated further in the Global Biodiversity Information Facility (GBIF) database for each of the 3 areas of interest, using the R package 'rgbif' (Chamberlain et al. 2022, GBIF.org 2022a). Taxa which still did not match any adult records were then investigated further in the literature to ensure that no occurrence records were missed (additional occurrence records were found in Kukliński 2002, Hansen et al. 2019, Dvoretzky & Dvoretzky 2021). Those taxa for which no evidence of the adults living in the same area was uncovered were considered 'non-local'. We counted the number of samples in which the taxon was present (frequency of occurrence) as a measure of prevalence. Finally, we calculated the distance of the closest known adult record (GBIF.org 2022b) to the center of each of the 3 areas of interest using function 'distGeo' in the R package 'geosphere' (Hijmans 2019). This function calculated the shortest distance between 2 points on a WG84 ellipsoid (a highly accurate representation of the earth's surface) but did not account for land or any other obstacle, resulting in an underestimation of the true minimum distance travelled. The boundaries of our 3 areas of interest were relatively small compared to the size of the overall oceanographic regions in which they each lay (see Fig. 1). Accordingly, in our interpretation, we placed less emphasis on the taxa for which the nearest known adult resides just outside the boxes but within the same oceanographic regions compared to the taxa for which the nearest known adult is known only from distant seas.

2.5. Particle tracking

A particle tracking analysis was used to determine the possible areas of origin of larvae found in the Barents Sea and around Svalbard. The hydrodynamic model used to represent the ocean currents in the study area was based on the Regional Ocean Modeling System (ROMS), a free-surface, hydrostatic, primitive equation ocean general circulation model (Shchepetkin & McWilliams 2005). ROMS was run with a horizontal resolution of 4×4 km in an orthogonal, curvilinear grid covering parts of the North Atlantic, all the Nordic seas and the Barents Sea (see

Lien et al. 2013 for details on model set-up and e.g. Lien et al. 2014 for a similar application).

To model the advection of particles in the horizontal plane, we applied the fourth-order Runge-Kutta scheme Lagrangian Advection and Diffusion Model (LADiM; Ådlandsvik 2021) coupled with the velocity fields from ROMS. Here, particles were released in a regular grid (every 4 km) across the model domain, initialized at 20 and 130 m on 23 August 2017 (called 'fall' for arrival of larvae by fall) and 10 May 2018 (called 'summer' for arrival by summer), and drifted at the depth set at initiation until the end of the drift period (3 mo). If at any time during the 3 mo drift period a particle entered one of the 3 polygons representing the 3 areas of interest, its release site was considered a possible area of origin. Three months represents a conservative estimate of the larval duration for the majority of benthic invertebrates (Shanks 2009), though, unfortunately, larval period is unknown for most taxa in our region. The times of release were chosen so that the end of the 3 mo drift would coincide with our previous observation of peak larval abundance (as well as high species richness) in August and November (Descôteaux et al. 2021). Drifts at 20 and 130 m accounted for differences in water mass and current properties through the water column.

Finally, to explore possibilities for long-range dispersal of particles, a separate drift experiment was initialized from a single point in Skagerrak, south of Norway/Sweden. A total of 1000 particles released each day of January 2018 (for a total of 31 000 particles) were allowed to drift for 1 yr (until 31 December 2018) at 20 m depth. We then checked whether any

of the particles entered one of the 3 areas of interest during their year-long drift period.

3. RESULTS

3.1. Meroplankton diversity

Metabarcoding uncovered a total of 2480 MOTUs across all zooplankton samples, of which 643 made up at least 0.01 % of at least one sample. Of those, a total of 213 obtained >97 % similarity match in BOLD, Eco-tag or BLAST, 171 (80 %) of which were identified to species level. Approximately half of the sequences identified to species level belonged to meroplanktonic taxa (91 sequences), while the rest (80 sequences) belonged to non-meroplanktonic taxa. Only meroplanktonic taxa identified to species level with >97 % sequence match were retained for further analysis.

3.2. Match to benthos settled at seafloor

We found a total of 42 meroplanktonic species with a mismatch to the adult communities on the seafloor. Possible non-local taxa made up about one-third of the meroplanktonic taxon richness north of Svalbard and north of the Polar Front and 45 % south of the Polar Front (Fig. 2A). In all 3 areas, the majority of non-local larvae belonged to polychaetes (Annelida) and nudibranchs (Mollusca), but, in total, we found taxa belonging to 6 phyla (Annelida, Arthropoda, Bryozoa, Echinodermata, Mollusca and Nemertea; Table 1, Fig. 2B). The adults of the majority of these 42

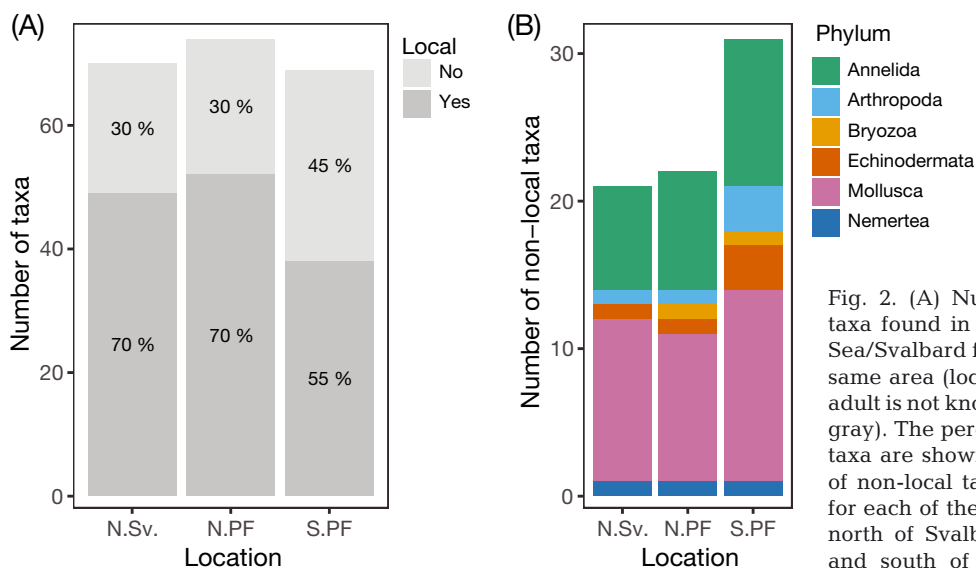


Fig. 2. (A) Number of benthic invertebrate taxa found in the larval pool of the Barents Sea/Svalbard for which the adult inhabits the same area (local, dark gray) or for which the adult is not known in the area (non-local, light gray). The percentages of local and non-local taxa are shown inside each bar. (B) Number of non-local taxa belonging to each phylum for each of the 3 areas. N.Sv, N.PF and S.PF: north of Svalbard, north of the Polar Front and south of the Polar Front, respectively

non-local taxa are found relatively close by in the Barents Sea itself, around Svalbard or along the northern Norwegian coast, but 7 of the taxa are only known to occur in more distant locations (Figs. 3 & 4). The closest known adults of *Serripes laperousii*, for instance, reside in the Canadian Arctic, while *Cephalothrix iwatai* is only known from the Sea of Japan (Chernyshev 2013), over 5000 km away in a straight line. Other notable examples include the nudibranchs *Dendronotus elegans* and *D. patricki*, found on the coasts of the Russian Kara and/or the White Sea, as well as *Doto maculata*, *Coryphella gracilis* and *Dendronotus yrjargul*, further south along the Norwegian coast

(Fig. 3A). For the area north of Svalbard, most taxa had adults residing on the shelf west of Svalbard or along the northern Norwegian coast (Fig. 3B). The adults of most larvae in the area north of the Polar Front, on the other hand, were found around Svalbard, in the northern Barents Sea or along the northern Norwegian coast. The closest adults to several taxa south of the Polar Front were also found on the northern Norwegian coast, but none came from around Svalbard. Instead, most were located in the southwestern Barents Sea. Distance to closest adult ranged from 77–5730 km, with 2 peaks in number of taxa around 100 and 1000 km (Fig. 3C).

Table 1. Non-local larval species for the 3 areas of interest, including frequency of occurrence (number of zooplankton samples in which a taxon was detected within each area). **Bold**: larval taxa whose closest known adults occur further than 1000 km away; n: total number of samples per region

Phylum Class	North of Svalbard (n = 11)	North of the Polar Front (n = 28)	South of the Polar Front (n = 22)
Annelida			
Polychaeta	<i>Dodecaceria concharum</i> 1 <i>Eunice pennata</i> 2 <i>Laonice blakei</i> 2 <i>Paramphinome jeffreysii</i> 4 <i>Praxillella praetermissa</i> 1 <i>Proclea malmgreni</i> 3 <i>Terebellides gracilis</i> 2	<i>Eunice pennata</i> 3 <i>Eunoe oerstedii</i> 1 <i>Harmothoe fragilis</i> 10 <i>Laonice blakei</i> 1 <i>Nereis pelagica</i> 3 <i>Paranaitis wahlbergi</i> 1 <i>Polycirrus arcticus</i> 3 <i>Polyphysia crassa</i> 7	<i>Eunice pennata</i> 1 <i>Eunoe nodosa</i> 4 <i>Gattyana cirrhosa</i> 9 <i>Harmothoe fragilis</i> 9 <i>Laonice blakei</i> 2 <i>Nereimyra woodsholea</i> 2 <i>Nereis zonata</i> 1 <i>Nothria conchylega</i> 4 <i>Proclea malmgreni</i> 3 <i>Thelepus cincinnatus</i> 6
Arthropoda			
Malacostraca	<i>Bopyroides hippolytes</i> 2	<i>Bopyroides hippolytes</i> 5	<i>Bopyroides hippolytes</i> 1 <i>Eualus gaimardii</i> 2
Thecostraca			<i>Balanus balanus</i> 21
Bryozoa			
Gymnolaemata		<i>Alcyonidium mamillatum</i> 13	<i>Alcyonidium mamillatum</i> 12
Echinodermata			
Echinoidea			<i>Gracilechinus acutus</i> 1
Holothuroidea			<i>Psolus phantapus</i> 3
Ophiuroidea	<i>Ophiocten gracilis</i> 11	<i>Ophiocten gracilis</i> 28	<i>Ophiocten gracilis</i> 22
Mollusca			
Bivalvia	<i>Serripes laperousii</i> 1	<i>Serripes laperousii</i> 5	<i>Serripes laperousii</i> 2
Gastropoda	<i>Coryphella gracilis</i> 6 <i>Cuthonella concinna</i> 1 <i>Dendronotus elegans</i> 3 <i>Dendronotus yrjargul</i> 7 <i>Doto coronata</i> 6 <i>Doto maculata</i> 4 <i>Eubranchus rupium</i> 2 <i>Onchidoris muricata</i> 4 <i>Placida dendritica</i> 4 <i>Scaphander punctostriatus</i> 2	<i>Coryphella gracilis</i> 5 <i>Cuthonella concinna</i> 3 <i>Dendronotus elegans</i> 11 <i>Dendronotus patricki</i> 7 <i>Dendronotus yrjargul</i> 14 <i>Diaphana hiemalis</i> 10 <i>Doto coronata</i> 1 <i>Eubranchus rupium</i> 8 <i>Placida dendritica</i> 2	<i>Coryphella gracilis</i> 6 <i>Cuthonella concinna</i> 1 <i>Dendronotus elegans</i> 8 <i>Dendronotus frondosus</i> 4 <i>Dendronotus patricki</i> 9 <i>Dendronotus robustus</i> 3 <i>Dendronotus yrjargul</i> 12 <i>Diaphana hiemalis</i> 5 <i>Doto coronata</i> 9 <i>Eubranchus rupium</i> 3 <i>Onchidoris muricata</i> 1 <i>Placida dendritica</i> 1
Nemertea			
Paleonemertea	<i>Cephalothrix iwatai</i> 10	<i>Cephalothrix iwatai</i> 23	<i>Cephalothrix iwatai</i> 19

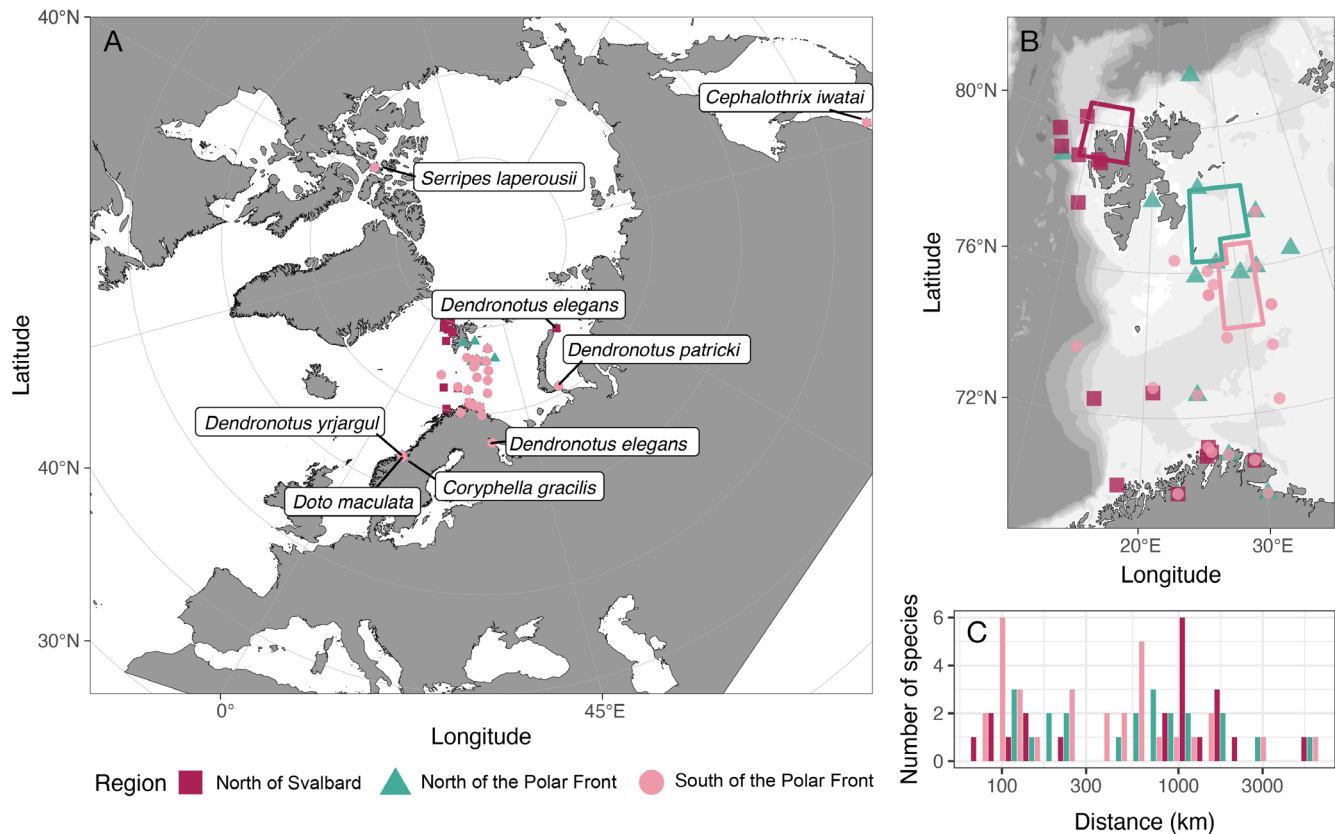


Fig. 3. Nearest adult record for each larval taxon that was not found as adults in each of the 3 areas of interest in (A) a broad ocean view including labels for the taxa that are found particularly far away and (B) a close-up of the Barents Sea, Svalbard and northern Norwegian coast. (C) Distribution of distances (shortest distance between 2 points on an ellipsoid) from the center of each area of interest to the nearest known adults (20 bins) with a log₁₀ x-axis to improve readability of lower-distance values. Positions on the map and the histogram are color-coded according to the 3 areas of interest

3.3. Particle tracking

The particle tracking analysis revealed different possible areas of larval origin depending on time of release, drift depth and location (Fig. 5). East of Svalbard, the majority of particles found north of the Polar Front originated within the same region or from nearby (largely within 300 km, maximum around 500 km), both in fall and summer. Some particles could have come from as far south as Bear Island in the fall at 20 m depth (Fig. 5A), but not at 130 m depth (Fig. 5C). In summer, particles originating from that area, both shallow and deep, also moved north along Bear Island Trough and Hopen Trench (Fig. 5B,D). Several particles also drifted in from the north, around the northeastern coast of Svalbard in fall (Fig. 5A,C) and from the northeast in summer, particularly at 20 m (Fig. 5B,D). Most particles found south of the Polar Front originated from well within the Barents Sea itself, largely within Hopen Trench or

along the southern and northern edges of Bear Island Trough. Some particles crossed the Polar Front from the north but only at 20 m. Compared to particles in the other two areas of interest, those that drifted north of Svalbard had the broadest probable area of origin, especially during summer (Fig. 5). Indeed, some particles released along the coast of Norway around 69° N (>1000 km away) were able to drift north of Svalbard within the 3 mo drift period, following the West Spitsbergen Current flowing north along the shelf break. In the fall, however, particles originated no further south than ~72° N. In both seasons, the majority of particles flowed northward along the shelf break. In this region, depth of release had minimal impact on the distribution of particles.

The majority of particles released in the Skagerrak in January 2018 at 20 m for a 1 yr drift followed the coastline of mainland Norway and eventually that of the Kola Peninsula in Russia (Fig. 6). A minority of

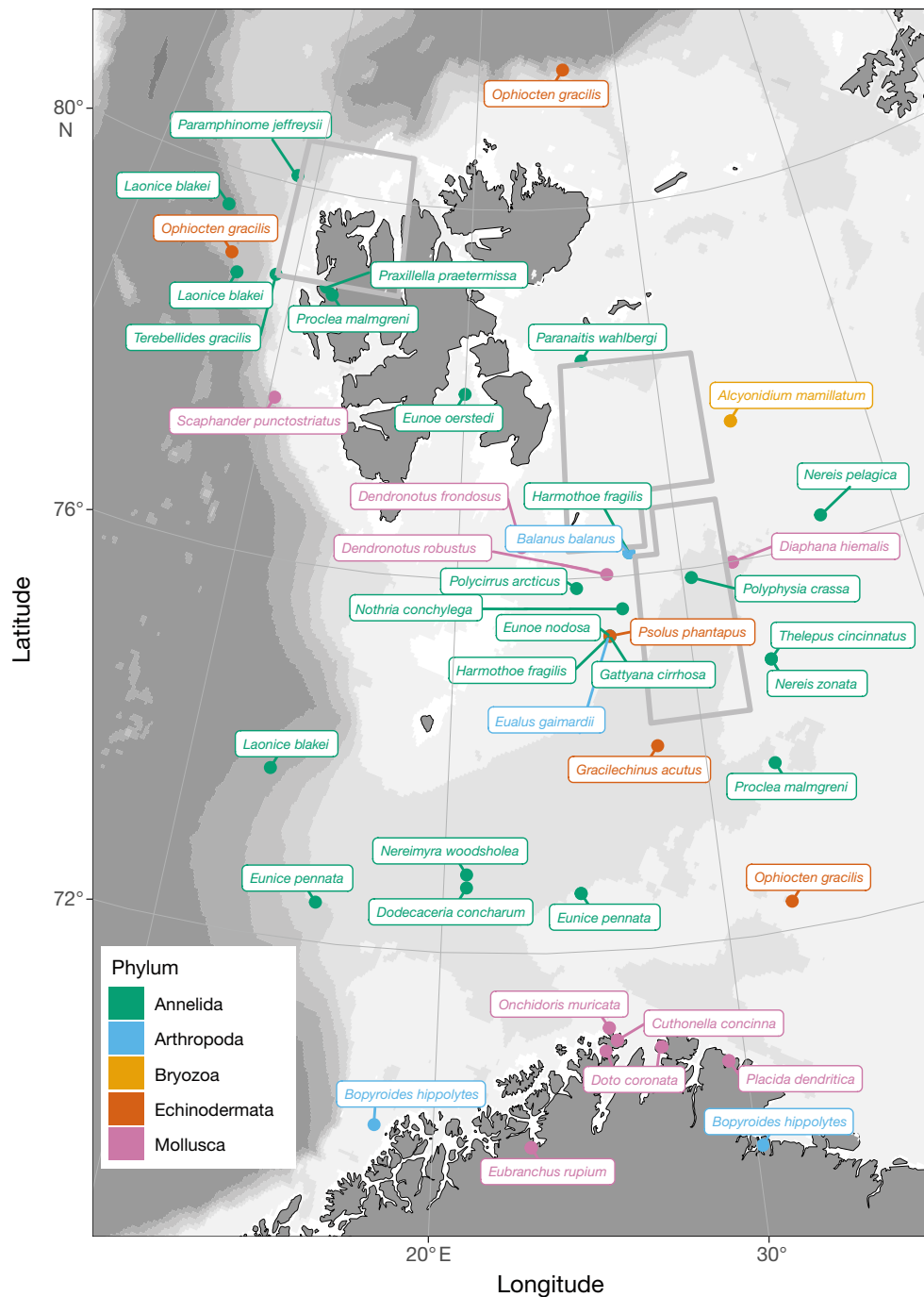


Fig. 4. Nearest known adults to the larval taxa that were found to be non-local to one of the 3 areas of interest (gray polygons). Taxa are color-coded by phylum. This figure omits the taxa for which the nearest known adult was located in more distant locations which are presented in Fig. 3A. Note that the presence of a taxon on this map does not necessarily mean that it is non-local to all 3 areas of interest. Refer to Table 1 for a list of non-local taxa for each area of interest

particles, however, diverged away from the coast and headed northward along the western edge of the Barents Sea then west of Svalbard along the slope. Out of the 31 000 particles released, only 2 eventually drifted into the area north of Svalbard

within 1 yr, with one particle arriving on Day 313 and the second on Day 328 after release. The 2 particles took very similar trajectories except for a section along mid-Norway, from around 63–67°N, where one stayed close to shore while the other drifted fur-

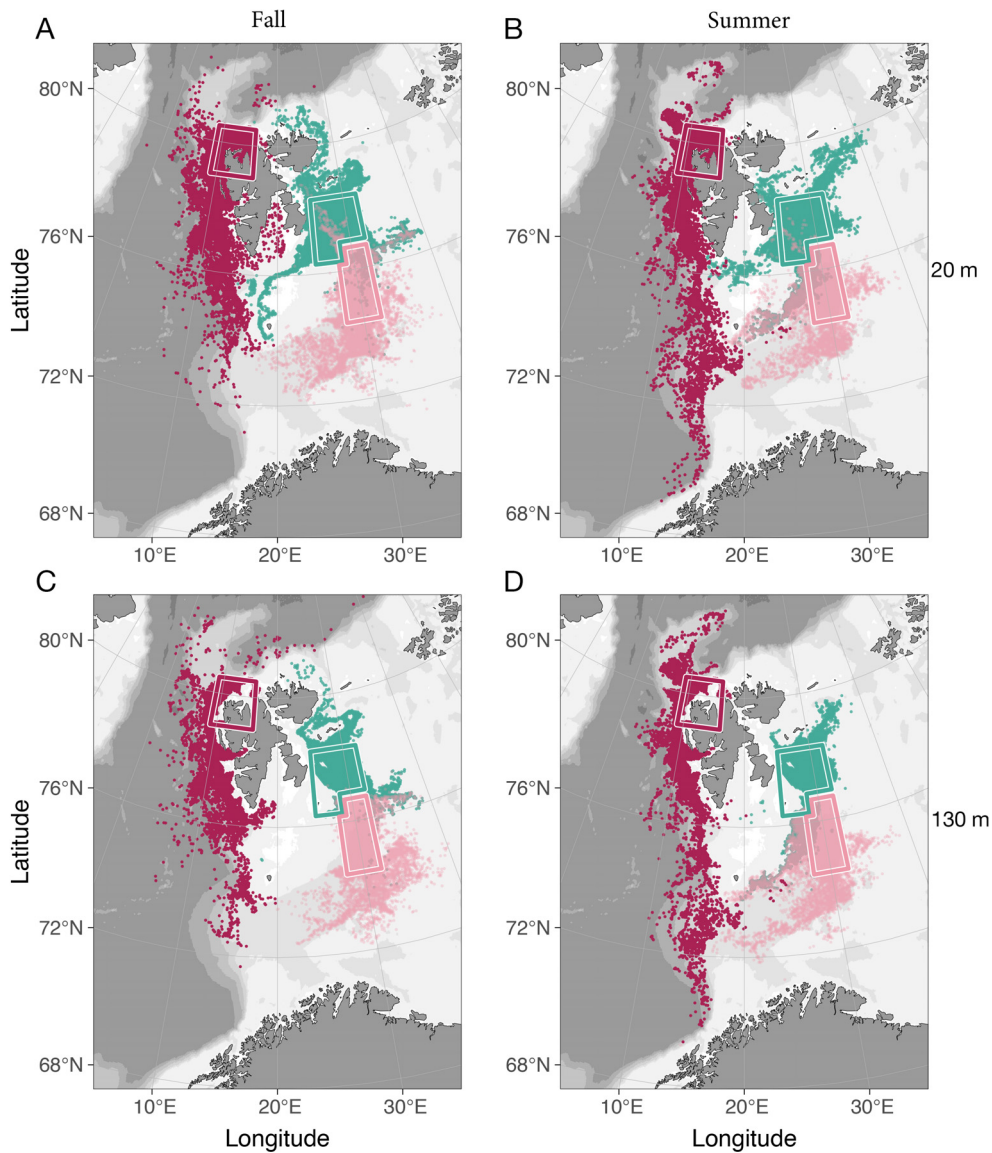


Fig. 5. Possible origins of particles (colored dots) drifting into one of 3 areas of interest (colored polygons): north of Svalbard (red), north of the Polar Front (green) and south of the Polar Front (light pink), anytime during a 3 mo period starting on (A,C) 23 August 2017 (fall) and (B,D) 10 May 2018 (summer) at (A,B) 20 m and (C,D) 130 m depth

ther offshore along the slope before their tracks came together again. A single particle reached the area south of the Polar Front on the Barents Sea shelf. This particle followed a similar trajectory to that of the previous 2 particles, except that it took a marked detour offshore around 62°N before heading back inshore and then northward along-shore like the others. This particle diverged westward around 72°N , following the Bear Island Trough and Hopen Trench into the area south of the Polar Front, arriving on Day 308 after release. No particles reached the area north of the Polar Front in the Barents Sea within the 1 yr drift period.

4. DISCUSSION

4.1. Origin of larvae

The Barents Sea, as an Atlantic gateway to the Arctic, has the potential to be the first introduction point of new species to the Arctic, along with the Chukchi Sea on the Pacific side (Ershova et al. 2019). Given that the mass transport from the south is much greater on the Atlantic side compared to the Pacific (Hunt et al. 2013), boreal imports may be particularly frequent in the Barents Sea. In this study, however, we found largely regional-scale larval connectivity,

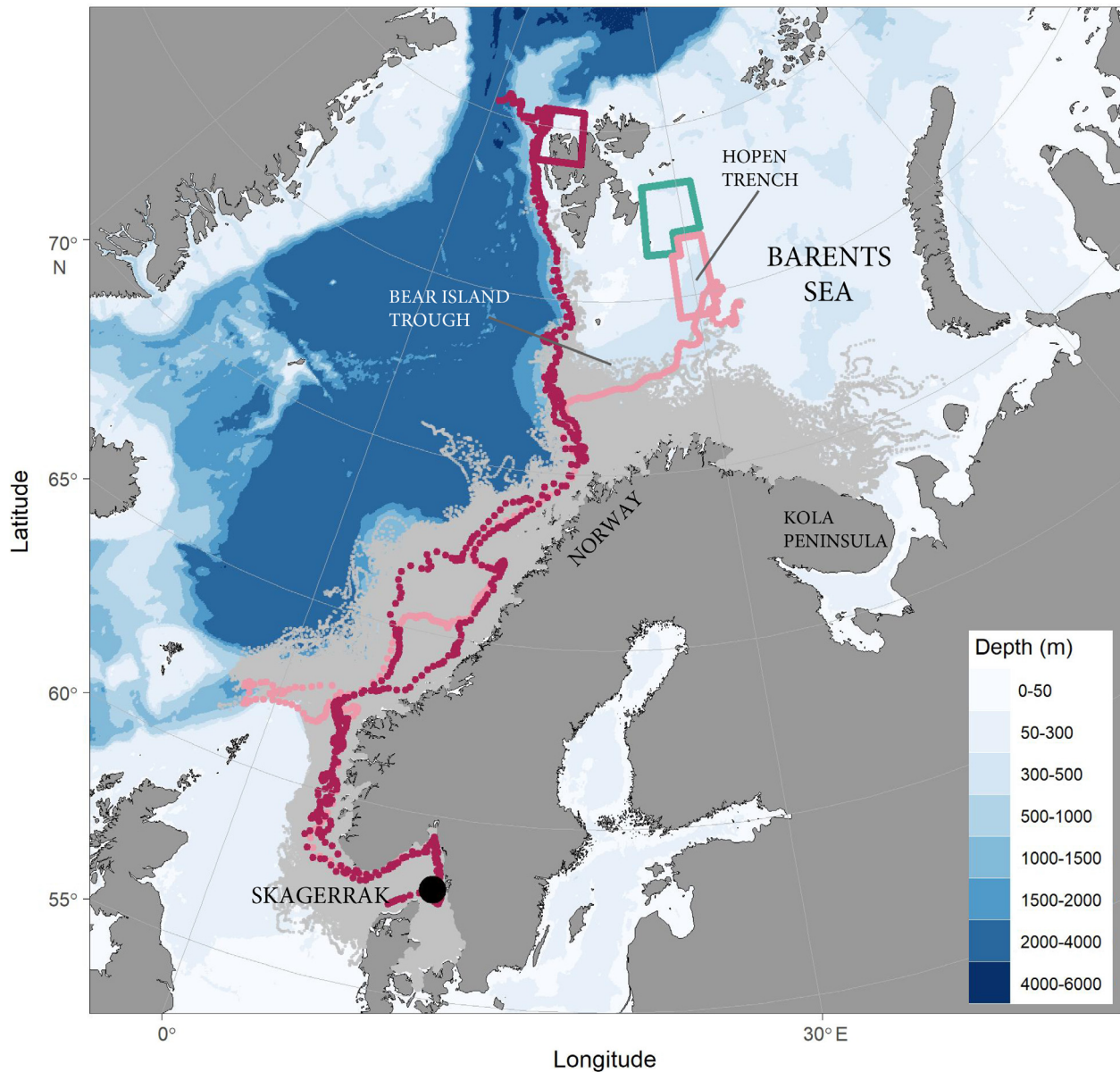


Fig. 6. Drift trajectories of simulated particles released in Skagerrak in January 2018 at 20 m depth and allowed to drift for 1 yr. Black dot: location where all particles were released; colored polygons: 3 areas of interest: north of Svalbard (red), north of the Polar Front (green) and south of the Polar Front (light pink). All drift trajectories are shown in light gray, but the trajectories of the 2 particles that eventually drifted into the area north of Svalbard are highlighted in red and that of the single particle that reached the area south of the Polar Front in pink

similarly to another meroplankton study further south along the Norwegian coast (though particles there were only drifting for 28 d; Silberberger et al. 2016). We demonstrated that 30–45% of meroplanktonic taxa were not local to the individual areas where they were collected, but most were native to the Barents Sea and Svalbard as a whole. This contrasts with the adjacent Kara Sea, where 47% of larval taxa were not known to the region at the time (Fetzer & Arntz 2008). For those species whose closest adult was

found around Svalbard or on the Barents Sea shelf, a 3 mo drift would be sufficiently long to supply the larvae into our 3 areas of interest. For the 6 taxa for which the closest adult was located along the northern Norwegian coast (Fig. 4), however, a larval duration greater than 3 mo would be required to account for our observations. Indeed, in this region, the Norwegian/Murman Coastal Current would entrain larvae released nearshore northeastward along the coast into the Russian Arctic (Sakshaug et al. 2009, Fig. 1). It is,

therefore, likely that more southern specimens of the species (e.g. found along the continental slope of the Norwegian Sea) would supply the larval pool to the Barents Sea and around Svalbard despite being located further away. Though such dispersal would be more realistic, it would still take longer than 3 mo.

4.2. Pelagic larval duration

The larval duration period is known only for a small subset of benthic taxa with a meroplanktonic stage. In a review across taxonomic groups, Shanks (2009) found larval drifts up to 3–4 mo, though most taxa had much shorter durations. In the Shanks (2009) review, most taxa dispersing for weeks or more belonged to Mollusca, Echinodermata, Polychaeta and Crustacea. In our study, most taxa identified in fact belonged to these groups. Our choice to run particle tracking analysis for 3 mo was based on the fact that few taxa are known to disperse for longer (though see Descôteaux et al. 2021). Teleplanic larvae have the ability to survive as a larva for years (Strathmann & Strathmann 2007), but they are presumably rare. According to our particle tracking analysis, larvae of the nudibranch *Bohuslania matsmichaeli* (to date only known from southern Norway/Sweden; Korshunova et al. 2018) would require more than 1 yr to reach the northern Barents Sea, where they have been previously recorded (Descôteaux et al. 2021).

Many living organisms do not behave as passive particles and tend to drift slower than models would suggest (Shanks 2009). Several taxa with weeks- to months-long larval duration disperse less than 1 km in that period while passive dispersal would have predicted 10s to 100s of km covered (Shanks 2009). Indeed, by remaining close to the seafloor where currents are slower, by vertically migrating or even, for more active taxa, by swimming against the currents, larvae may be retained closer to their area of origin (Shanks 2009). Vertical migration behaviour has been observed in some species of decapod crustaceans (Queiroga & Blanton 2004), barnacles (Bonicelli et al. 2016), molluscs (Rawlinson et al. 2004) and other groups. Our particle tracking analysis did not take into account any of these possible behaviours, so likely represents a maximum possible distance of origin for a 3 mo drift.

4.3. Potential drivers of larva–adult mismatches

A mismatch between larval and adult distribution can be artificial, created by an incomplete picture of

the benthic diversity in a region or differences in species identification. Thanks in part to an extensive annual survey carried out since 2006, there is comparatively strong knowledge of the benthic megafauna (here defined as fauna caught in trawls) of the Barents Sea shelf (Jørgensen et al. 2015, Zakharov et al. 2020). Information on benthic macrofauna (those animals caught on a 0.5 or 1 mm sieve) also exists for the study region (Denisenko 2001, Carroll et al. 2008, Cochrane et al. 2009, Carroll & Ambrose 2012, Kędra et al. 2013), though not as spatially and temporally extensive as for the megafauna. The absence of adults of a particular species, and consequent mismatches between larval and adult distributions, is therefore more likely to be driven by lack of data (or different taxonomic naming) in the macrofaunal taxa (largely polychaetes and bivalves) compared to the larger megafauna. Some taxa like nudibranchs (discussed below) may be too rare to be reliably caught by grabs or box cores used to sample macrofauna and too small to be retained in the trawl nets used to sample megafauna. Except for a few comparatively well-studied fjords, the benthic fauna of shallow coastal waters of Svalbard is poorly resolved (Renaud et al. 2015), again potentially leading to artificial mismatches between adult and larval distributions.

The lack of data on adult nudibranch distributions could partially explain the dominance of this group in our non-local larval fauna. For some of these taxa, the adults may inhabit the Barents Sea shelf but have remained undetected. The nudibranch *Dendronotus patricki* was first discovered near a whalefall at 1820 m depth in the Pacific Ocean off of California (Stout et al. 2011) and more recently found in the Arctic Kara Sea at 216 m depth (Ekimova et al. 2019). Given its affinity for deeper, soft-bottom habitats (Ekimova et al. 2021), this species could realistically inhabit the Barents Sea shelf. Many nudibranch (and other heterobranch gastropods) taxa identified here, however, appear to have a shallow coastal distribution (including *Microchlamyella gracilis*, now accepted as *Coryphella gracilis*, Korshunova et al. 2017; *Cuthonella concinna*, *Eubranthus rupium* and *Placida dendritica*, Svendsen & Moen 2020) and would therefore be unlikely to inhabit the Barents Sea shelf. Indeed, in our study, the nearest known adults to most non-local nudibranch taxa were found in coastal regions, especially along the northern Norwegian coast (Figs. 3A & 4). In these taxa, a long dispersal stage seems likely. Most nudibranch species have planktotrophic development, and many require a cue from the adult prey (e.g. hydroids) to settle (e.g. Sisson 2005), potentially leading to long dispersal

duration when such cues are lacking. Our data (not shown here) suggest that several of the so-called non-local nudibranchs were present as larvae in the Barents Sea during most of the year. Assuming one single reproductive period per year, as for many nudibranchs (including *D. yrjargul*; Korshunova et al. 2021a), their extended presence in the Barents Sea could indicate a long dispersal phase. In the laboratory, larvae of *D. frondosus* metamorphose after 63–86 d at 10°C (Sisson 2005). Larval duration lengthens with decreasing temperature (O'Connor et al. 2007) so that larval duration in the Barents Sea, where our modeled larvae experienced sea surface temperatures between –2 and 10.4°C (Barents Sea temperature range: 0–8°C in Barton et al. 2018), could reach well beyond durations observed at higher temperatures in the laboratory. Therefore, we hypothesize that the dominance of nudibranch taxa in the non-local pool is in part driven by their potential for long-distance dispersal in addition to being biased by our lack of knowledge of true geographical distribution of individual taxa. A third unexplored possibility—that nudibranch larvae have a greater tolerance to low temperatures and reduced mortality when entering the Arctic compared to other groups—cannot be excluded. Indeed, nudibranch larvae figure prominently in winter zooplankton samples in the Barents Sea (Hirche & Kosobokova 2011, Descôteaux et al. 2021). Recent taxonomic and molecular work has highlighted the complexity and diversity of the Arctic nudibranch fauna (Ekimova et al. 2015, Korshunova et al. 2021a,b), and our study emphasizes the need for continued taxonomic, molecular and ecological studies on this group.

4.4. Very distant taxa

The nemertean *Cephalothrix iwatai* was highly abundant in the larval pool, appearing in the majority of samples in all 3 areas of interest. To date, the adults of the species are only known from the Sea of Japan in the North Pacific, living in deep soft sediments (Chernyshev 2013). The larvae of palaeoneurteans (to which *C. iwatai* belongs) are usually planktotrophic (Maslakova 2010), though other authors have speculated that a shorter-lived lecithotrophic larval form exists (Fernández-Álvarez & Machordom 2013). Larval *Cephalothrix* sp. can survive up to 8 wk in the absence of food, but it is unknown how long they could survive if provided with adequate nutrition (Smith 1935). In this case, contrary to nudibranchs, a long larval duration can-

not in itself explain our observations, as it seems extremely unlikely that the larvae would have drifted all the way from the North Pacific, especially in such high numbers. While the molecular identification of *C. iwatai* was based on a single specimen sequence archived in BOLD, the source of that specimen is reliable (Chernyshev 2013) and consistent with the tree-based identification. Two species of the *Cephalothrix* genus, *C. rufifrons* and *C. linearis*, are common in the North Atlantic (GBIF Secretariat 2021b), including the Barents Sea for *C. linearis* (Buzhinskaja 2011). Neither closely matches our larval sequences despite being well-represented in BOLD. Our larval specimens, therefore, either belong to a yet non-barcoded species closely related to *C. iwatai* or truly belong to *C. iwatai*, which would therefore be presumed to have a much wider distribution range than is currently recognized.

The bivalve *Serripes laperousii* was also found in all 3 areas of interest, appearing in a total of 8 samples. It is considered a Pacific species, but it also has some recorded occurrences in the Canadian Arctic (GBIF Secretariat 2021a). The larvae's DNA-based identification was again based on a match with only 2 sequenced adults, but these sequences appear reliable (Layton et al. 2014). Another *Serripes* species, *S. groenlandicus*, is well known from the Barents Sea, but its DNA was not a direct match to our larval samples. A drift from the Canadian Arctic to the Barents Sea seems improbable, so we postulate that *S. laperousii* has a more widespread distribution than current records show.

Human activity can also facilitate the dispersal of species and may have contributed to some of our observations here. Transport in ballast waters, for example, has the potential to introduce new taxa to the Barents Sea despite mitigation protocols such as mid-ocean exchange (Rosenhaim et al. 2019). While mid-ocean exchange might reduce the transport of organisms from port to port, it may in fact contribute to transport to the Barents Sea if the exchange were to take place there. In the case of *C. iwatai* and *S. laperousii*, however, both taxa were found in several samples (52 and 8, respectively) spanning all 3 areas of interest, so it is unlikely that recent transport in ship ballast waters alone could account for their presence in the Barents Sea. Plastic debris floating in the oceans can also serve as a vector for dispersal, sometimes acting on intergenerational timescales so as to enable dispersal over greater distances than would be possible within the lifespan of a single larva (Haram et al. 2021). In fact, there is evidence that plastic debris has contributed to the dispersal of the

blue mussel back to Svalbard after a 1000 yr absence (Kotwicki et al. 2021). Similar to ship ballast waters, this mechanism is unlikely to explain our very frequent observations of *C. iwatai* in larval samples of the Barents Sea and Svalbard but could certainly have contributed to some of the dispersal.

4.5. Outlook

This study highlights the potential for larval stages of benthic invertebrates to drift into the Barents Sea and around Svalbard from further south despite the bulk of the larval community being of local or regional origin. Continued surveys of both benthic adults and pelagic early life stages in the region, but also along the Norwegian coast, will be critical to track the northward progress of boreal taxa. Most of these non-local larvae, however, likely represent a 'dead end', as the conditions in the Arctic seas are, for now, presumably inhospitable (in terms of temperature, food availability, etc.) to the growth of a viable population. Indeed, while larval supply is the critical first step in establishment of a viable population, the larvae must settle successfully, grow to reproductive maturity and produce enough young to compensate for mortality. Rising temperatures associated with climate change and Atlantification of the Barents Sea (Renaud et al. 2019, Polyakov et al. 2020) will likely allow some of these taxa to settle and reproduce successfully in the future (Renaud et al. 2015) as has been the case for the blue mussel (Berge et al. 2005) and other species. While this warming will likely be sufficient to enable some taxa to settle and reproduce, other factors, such as bottom substrate, availability of specific prey items, etc., may limit the expansion of others. Those taxa that specialize in rocky, shallow-water environments, for example, would be unlikely to colonize the deeper, soft-bottom Barents Sea shelf but could potentially settle on the coast of Svalbard. Additionally, new taxa may not be able to colonize the Barents Sea as long as local taxa occupy the same niche (so-called priority effects; Fraser et al. 2015). It should also be noted that increased temperatures are expected to speed up larval development (O'Connor et al. 2007) in a way that may reduce dispersal distance, potentially counteracting, at least in part, the rate of expansion. The effects of climate change on the benthic communities of the Arctic are therefore complex to predict, but we show that some boreal taxa with long-duration larvae have the means of reaching the Arctic during their planktonic phase.

Data availability. The data and code used in this article are available at Dataverse.no <https://doi.org/10.18710/DVYBTY>.

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