Spatial and temporal structure of the meroplankton community in a sub-Arctic shelf system

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ABSTRACT: The early development of many benthic invertebrates involves planktonic larval stages enabling larvae to disperse over large distances and to utilize food from the productive upper water layers. Although many past studies have recognized the importance of this period in the benthic life cycle, knowledge of larval distribution in time and space remains limited, especially for high-latitude regions with pronounced seasonal variability in environmental conditions. Here, we present the first inventory of meroplankton over the continental shelf in the Lofoten–Vesterålen region, northern Norway, over a full annual cycle. Six stations were sampled during 8 sampling events between September 2013 and August 2014. We recorded a total of 65 taxa, a considerably higher diversity than reported in studies from more northern regions. We observed a distinct seasonal pattern with characteristic meroplankton communities defining the seasons: spring, summer, and winter. Abundance and diversity during winter was low, with higher values in spring, and maximum abundances for most taxa in summer. Meroplankton community patterns did not reflect weak environmental spatial structure. Particle tracking was used to identify source and settlement locations of spring and summer communities. Spring and summer communities originated from shore and shelf areas, respectively. Larvae were generally transported toward Andfjord and adjacent shelf regions, irrespective of season. This spatially restricted dispersal and larval settlement highlights the importance of the local benthic communities for the resilience of the ecosystem.

KEY WORDS: Planktonic larvae · Larval dispersal · Seasonality · Invertebrate larvae · Norwegian waters · Environmental factors · High latitude

INTRODUCTION

The majority of benthic invertebrates are sedentary during their adult life, therefore limiting their dispersal largely to their early life stages. Consequently, many species have planktonic larvae to enable local and regional dispersal of their offspring (Becker et al. 2007). The planktonic phase also provides access to food in the productive upper water column, reduces intra- and interspecific competition, avoids predation by abundant benthic omnivores, and reduces inbreeding (Pechenik 1999, Palumbi 2003). At the same time, pelagic larvae risk being carried away from favorable settlement locations by the prevailing currents and expose themselves to high predation pressure in the plankton (Pechenik 1999).

Larval duration in the water column varies among species (hours to several weeks), but substantial intraspecific variation also occurs depending on water temperature and food availability (Thorson 1950, Hadfield & Strathmann 1996, O'Connor et al. 2007). Furthermore, successful larval recruitment may hinge on the timing of spawning, and some species spawn in synchrony with phytoplankton blooms or increased spring temperatures (Crisp & Spencer 1958, Highfield et al. 2010). Seasonal variation in hydrodynamics also interacts with the timing of larval release because encounter with a suitable benthic habitat ultimately influences larval success

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(Metaxas 2001, Ayata et al. 2011). Although a substantial literature discusses reproductive strategies and larval nutrition in holoplankton (taxa spending their entire lives in the water column) (Varpe et al. 2009, Daase et al. 2013), the transferability of all of these conceptual models directly to studies of the pelagic developmental stage of benthic organisms (meroplankton) remains unclear.

Historically, aside from early studies indicating a decreasing importance of planktonic larvae for benthic reproduction with increasing latitude (Thorson 1950, Mileikovsky 1971), few studies have examined meroplankton in polar regions. Several recent studies have put this gap into perspective. Fetzer & Arntz (2008) provided detailed estimates on the relative importance of different developmental modes for the dominant benthic species in the Kara Sea, showing many species with benthic development (about 30%) driven almost exclusively by the large number of peracarid crustaceans in the study area that lack pelagic development. Their analysis showed a predominance of pelagic development outside this group. Furthermore, recent studies of Arctic meroplankton have shown that planktonic larval stages of benthic organisms comprise a considerable fraction of the total zooplankton community (Clough et al. 1997), and may dominate during productive seasons in terms of abundance and biomass (Stübner et al. 2016). Furthermore, meroplankton diversity observed in Arctic and sub-Arctic regions points to the importance of a bentho–pelagic life cycle in these regions (Andersen 1984, Schlüter & Rachor 2001) that can provide insight into adult distributions and potential range extensions for benthic species in the context of climate change (e.g. Renaud et al. 2015).

Distinct knowledge gaps about the spatio-temporal distribution of larvae remain. Kuklinski et al. (2013) and Stübner et al. (2016) investigated an Arctic meroplankton community over a 12 mo period, and detected a strong seasonal pattern with meroplankton present nearly year-round in a high Arctic fjord. Plankton community studies have provided limited additional information on the seasonality of Arctic and sub-Arctic meroplankton (Willis et al. 2006); however, these studies all investigated temporal patterns in enclosed fjord environments, with no studies specifically addressing open-shelf meroplankton seasonality. This lack of knowledge juxtaposes the importance of meroplankton dispersal and subsequent recruitment for the resilience of benthic ecosystems in response to natural and anthropogenic disturbances, including climate change (Kirby et al. 2008).

In this study, we present the first inventory of the meroplankton community at 6 stations in a sub-Arctic shelf system over a 12 mo period from September 2013 to August 2014. The main objectives were to (1) describe the spatial and temporal distribution of meroplankton in relation to large-scale benthic habitats and water mass properties; and (2) to further evaluate the importance of environmental variables and the spatial and temporal characteristics of the sampling regime in structuring the meroplankton community. Furthermore, we used a particle-tracking approach to identify possible source and settlement locations of the meroplankton sampled in this study.

MATERIALS AND METHODS

Study area

Although our study location on the continental shelf off the coast of the Vesterålen Islands in northern Norway (Fig. 1) occurs north of the Arctic Circle, and therefore experiences pronounced seasonality in day length with periods of complete darkness (polar night) and permanent light (midnight sun), the strong influence of the North Atlantic Current results
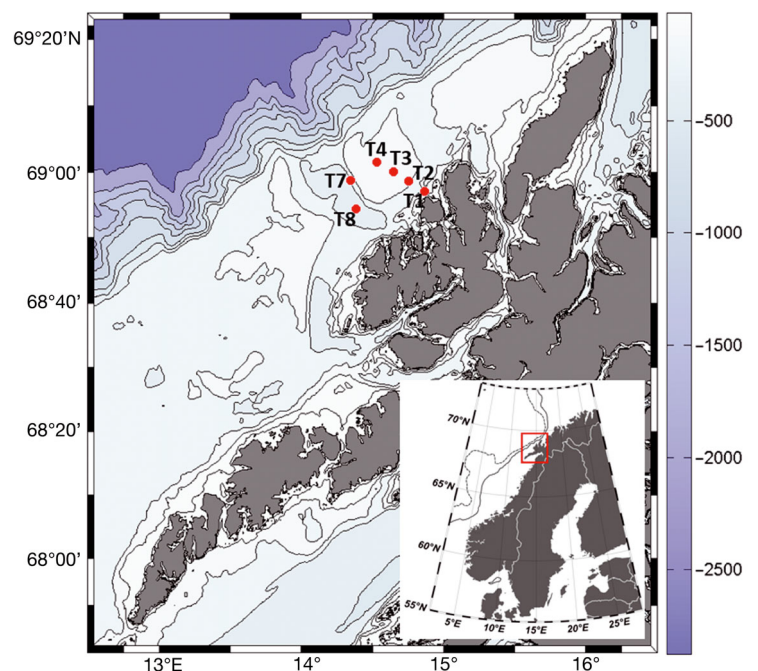

Fig. 1. Study area with bathymetry indicated by the color scale (unit: m). Sampling stations are indicated by red points. Inset: location of the study area in Norway, indicated by a red rectangle

in a permanently ice-free environment. Two major features comprise the narrow continental shelf in the area: shallow banks with hard substrate of bedrock and boulders contrast deep cross-shelf trenches with sandy or gravelly substrate (Buhl-Mortensen et al. 2012). Two northward-flowing currents characterize the regional hydrography. The low-salinity Norwegian Coastal Current flows over the shelf along the coast, whereas the warm and saline Norwegian Atlantic Current travels along the continental slope and frequently flushes onto the shelf (Bøe et al. 2009).

Sampling and sample processing

Plankton samples were collected at 6 stations (Fig. 1, Table 1) during 8 sampling events between September 2013 and August 2014 (see Table 2 for sampling dates). The 6 stations were selected to represent the major marine landscapes in the study area (Mortensen et al. 2009) and to cover most of the shelf width, with distance from shore between 1 and 20 km (Table 1). A WP2 closing net (opening = 0.25 m², mesh size = 200 μm), equipped with a CTD profiler with fluorescence sensor (Saiv A/S, CTD/CSD – model SD 204), sampled the complete water column at shallow stations (T1–T4, depth <100 m) in a single vertical tow. At deeper stations (T7 and T8, depth >100 m), we collected plankton from 2 depth intervals: estimated maximum mixed-layer depth (50–0 m) and deeper water (bottom–50 m). At each of these stations, we also collected a separate CTD profile of the entire water column. We chose a mesh size commonly used for sampling larger and relative mobile meroplankton, such as decapod zoea (e.g. Highfield et al. 2010, Koettker & Lopes 2013). However, this sampling gear may under-represent small larvae and early stages of some groups (e.g. Bivalvia). Samples were fixed in 4% buffered formaldehyde until further processing. Unfavorable weather conditions precluded sampling at station T8 on 10 September 2013 and a malfunctioning CTD resulted in no CTD data at station T7 on 1 May 2014.

CTD data (practical salinity, temperature, and pressure) were transformed following recommendations of the Intergovernmental Oceanographic Commission (IOC et al. 2010). All seawater properties were calculated using the Gibbs SeaWater package in R (Kelley et al. 2015). Absolute salinity (S_A), conservative temperature (Θ), fluorescence (F), and the potential density anomaly referenced to 0 dbar (σ_θ) were then averaged for 2 m depth bins, starting at 1 m depth, to smooth the data. The mixed-layer depth was defined as the depth where the difference between σ_θ and the surface value was 0.03 kg m⁻³ (Talley et al. 2011).

Samples were split in the laboratory consecutively with a Motoda plankton splitter until a minimum count of 400 individuals or one-quarter of the total sample was processed. Meroplankton were identified to the lowest feasible taxonomic level. We standardized the original count data for the analyzed fraction to individuals per m² surface area (ind. m⁻²) and integrated the 2 depth intervals for stations T7 and T8 to represent the whole water column.

Statistical analysis

All statistical analyses were performed in R, version 3.2.0 (R Core Team 2015).

We calculated the number of taxa, total abundance, the Shannon index ($H'_{\log e}$) (Shannon 1948), and Pielou's evenness (J') (Pielou 1977) for every sample to compare diversity between samples.

Although we report only results from log-transformed data unless otherwise stated, we ran multivariate analyses with 3 different transformations to explore all quantitative aspects of the data: (1) no transformation (raw), (2) natural logarithm (log), and (3) presence and absence data.

A triangular dissimilarity matrix was created using Bray-Curtis dissimilarities (Bray & Curtis 1957). Global nonmetric multidimensional scaling (GNMDS) ordinations were run with 100 restarts from random starting positions. The maximum number of iterations was set to 500 and the convergence criterion to 10⁻⁷. Rescaling of the axes in half-change units was applied (Gauch 1973). Similarity profile analysis (SIMPROF) (average link-

Table 1. Geographic position, bottom depth, distance from shore, and marine landscape of the sampling stations

Station	Longitude (°E)	Latitude (°N)	Depth (m)	Distance from shore (km)	Marine landscape
T1	14° 51.9846′	68° 57.0048′	40	1.389	Fjord and coast
T2	14° 45.2226′	68° 58.6056′	75	6.360	Bank
T3	14° 38.7630′	69° 00.0378′	75	10.583	Bank
T4	14° 31.7700′	69° 01.5690′	80	16.201	Bank
T7	14° 20.6526′	68° 58.7430′	215	18.669	Shelf trench
T8	14° 23.1450′	68° 54.4638′	260	11.927	Shelf trench

age; p < 0.01) verified patterns observed in the GNMDS ordinations. A species contribution analysis, as described by van Son & Halvorsen (2014), was performed to identify taxa contributing to observed differences in season patterns.

For variation partitioning, we created 4 matrices with explanatory variables. The first matrix contained 9 spatial variables: x, y, x^2, xy, y^2, x^3, x^2y, xy^2, and y^3. Universal Transverse Mercator (UTM) grid coordinates x and y of the sampling stations (5 digits for each coordinate) were used as the principal geographic information. Following Legendre (1990) and Anderson & Cribble (1998), we included all terms of a cubic trend surface regression in the matrix to allow more complex structures such as patches. The second matrix contained 11 environmental variables: depth, marine landscape, distance from shore (all constant over the study period), surface and bottom temperature, surface and bottom salinity, mean and maximum fluorescence, depth of maximum fluorescence, and mixed-layer depth. The marine landscape for each station was assigned following Mortensen et al. (2009). To determine the distance from shore of each sampling station, we used the gDistance function in the rgeos package (Bivand et al. 2015) together with the National Geospatial-Intelligence Agency's Prototype Global Shoreline Data (NGA 2009). All other parameters were based on individual CTD casts. Bottom CTD values were averages of the deepest 2 m bin, ending approximately 5 m above bottom. We included depth, marine landscape, and distance from shore in the matrix of environmental variables, even though they are not typical environmental variables in plankton research, because of their importance for local benthic communities. These measures also provide surrogates for other environmental variables not measured in our study (e.g. inputs of fresh water and terrigenous material decrease with distance from shore). The other 2 matrices contained a single temporal variable each: the sampling date expressed as day of year and sampling season, defined according to season-groups identified in the GNMDS ordinations. Two temporal matrices were used, since the season-groups were defined *a posteriori*. Including these 2 temporal sets of explanatory matrices allowed us to quantify additional variation in the meroplankton explained by knowledge of local seasons.

Each of the 4 matrices was subjected to forward selection using a series of constrained and partially constrained canonical correspondence analyses (CCA) followed by unrestricted permutation tests (999 permutations, p < 0.01). In each selection round, we selected the variable with the highest significant explanatory power for use as a conditioning variable for all the following selection rounds. Variables were selected until none added significantly to the explanation of the variation in the meroplankton data. In this way, we avoided artificially inflating the explained variation by including co-variables in the analysis.

Given the lack of explanatory power in any spatial variables (see 'Results'), we performed a variation partitioning through constrained and partially constrained CCA with all possible combinations of the 2 temporal and the environmental datasets. Variation explained by environmental variables only (E), sampling date only (D), season only (S), environment and season combined (ES), environment and sampling date combined (ED), sampling date and season combined (DS), and a combination of all 3 (EDS) were determined following Anderson & Cribble (1998) for variation partitioning on 3 sets of explanatory variables. To visualize the results of the variation partitioning, we generated a Euler diagram with the eulerAPE software (Micallef & Rodgers 2014).

We tested for autocorrelation between the meroplankton community, the environmental dataset, and space using Mantel and partial Mantel tests (Legendre & Legendre 1998), removing the factor variable marine landscape from the environmental variables.

All multivariate analyses used the vegan package version 2.3-0 (Oksanen et al. 2015).

Particle tracking

For tracking of larval dispersal pathways, we simulated velocity fields using the ocean modeling system NorKyst-800 (Albretsen et al. 2011). NorKyst-800 is based on the public domain Regional Ocean Modeling System, a 3D free-surface, hydrostatic, primitive equation ocean model using terrain-following s-coordinates in the vertical (Shchepetkin & McWilliams 2005, Haidvogel et al. 2008). In summary, we combined bathymetric data (50 m resolution) from the Norwegian Mapping Authority Hydrographic Service with lateral boundary conditions from the Norwegian Meteorological Institute (MET)'s Nordic4km, atmospheric forcing from MET's weather forecast model HIRLAM10km, tidal forces from a global inverse barotropic model of ocean tides (TPXO7.2), and Norwegian river discharge modeled by the Norwegian Water Resources and Energy Directorate. Recent studies have used the NorKyst-800 model

with success, showing relatively good agreement with field data (e.g. Myksvoll et al. 2014, Skarðhamar et al. 2015). The model domain covered the whole Norwegian Sea from 55.8° to 73.8° N and 0.5° W to 34.8° E, with 820 × 2420 grid cells in the horizontal, each 800 × 800 m in size.

Larval dispersal and origin were simulated using the individual-based model ICHTYOP (Lett et al. 2008), by tracking particles released inside an area around station T3. Hourly velocity fields from NorKyst-800 were used to simulate Lagrangian particle transport. A patch of 1000 particles was uniformly distributed in a 10 km diameter circular area between 20 m depth and the surface, and passively advected for 28 d, both forward and backward in time. Our simulation allowed transport of particles throughout the water column. We chose a duration of 28 d because the planktonic period for the majority of taxa in the study area (see Supplement 1 at www.int-res.com/articles/suppl/m555p079_supp.pdf) ranges from 3–6 wk (Mortensen 1927, Johannesson 1988, Shanks et al. 2003, Conway 2015). To account for the presence of different stages of larvae, we acquired weekly results in the simulations. Our simulation contrasted 2 periods during which typical spring (1 May 2014) or summer (22 July 2014) meroplankton communities were present.

RESULTS

Oceanography

Surface temperature and salinity in the study area varied seasonally, with high temperatures during summer and low salinity in late summer and autumn (Fig. 2). Surface temperature varied little spatially at any sampling date. Surface salinity, however, differed among sampling stations, but with no clear reoccurring pattern. Pronounced surface salinity outliers occurred, particularly at the deep stations T7 and T8, potentially indicating short-lived local high and low salinity patches over the shelf trench. Bottom temperature also showed distinct seasonality, with the highest temperatures in late summer and autumn. The strongest seasonality at the shallower stations (T1–T4; temperature range: 4.5–11.7°C) contrasted the weaker seasonality at the deeper stations (T7 and T8; temperature range: 6.1–8.0°C). In contrast to the other variables, bottom salinity varied spatially but not seasonally. Salinities above 35 characterized bottom waters at stations T7 and T8 throughout the year, with a single outlier at station
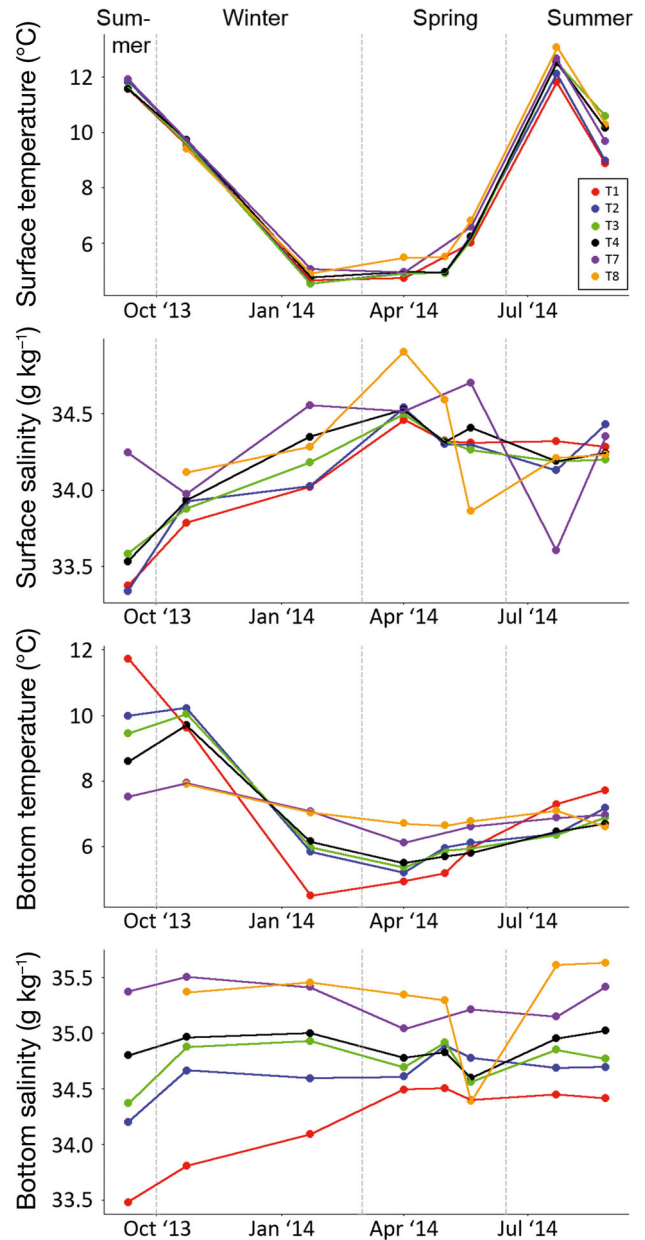

Fig. 2. Surface and bottom temperature and salinity at each sampling station over the whole study period. Sampling stations are indicated by different colors; identified seasons are separated by vertical lines

T8 in May. This high salinity over 35 assigns this bottom water to a Norwegian Atlantic Current origin. Salinities below 35 throughout the year, typical for the Norwegian Coastal Current, characterized bottom water at the shallower stations. The mixed-layer depth in the study area indicated deeper mixing from October to early May and a more stable surface layer in late spring and throughout the summer. The fluorescence values indicate mid-May and August phytoplankton blooms.

Meroplankton community

All samples analyzed contained planktonic larvae of benthic invertebrates, which we assigned to 65 different taxa in 11 phyla (see Supplement 1 at www.int-res.com/articles/suppl/m555p079_supp.pdf). On average, samples contained 14 041 ind. m^{-2} (range: 32–79 392 ind. m^{-2}) in 15 different taxa (range: 1–35). Mean number of taxa, abundance, $H'_{\log e}$ and J' varied seasonally, with low abundances and diversity in October and January and a peak in the summer months (Table 2). Spatial variation was low relative to seasonal variation. Abundances were highest at stations closest to shore (T1 and T2). Lower average numbers of taxa occurred at the stations farthest offshore (T4 and T7). $H'_{\log e}$ and J' did not vary spatially.

The 5 most abundant taxa in this study were the polychaete family Amphinomidae (mean abundance: 3724 ind. m^{-2}), the bryozoan *Membranipora membranacea* (2114 ind. m^{-2}), the barnacle *Verruca stroemia* (1642 ind. m^{-2}), echinoderms of the class Ophiuroidea (1048 ind. m^{-2}), and gastropods assigned to the group Littorinimorpha type (979 ind. m^{-2}). These 5 taxa accounted for 67.7 % of the total meroplankton abundance.
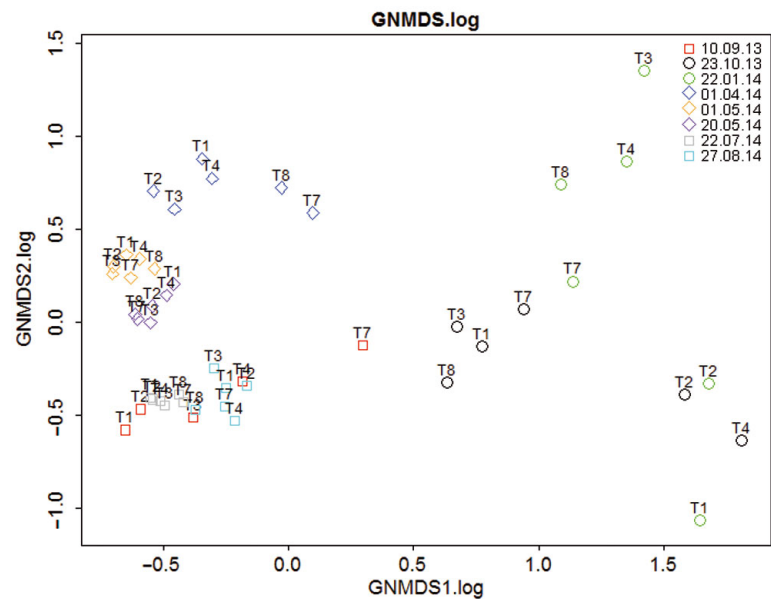

Fig. 3. Global nonmetric multidimensional scaling (GNMDS) results of logarithmic (log)-transformed meroplankton data. Sampling dates are indicated by different colors; labels are station numbers; symbols show season cluster according to similarity profile analysis: circles = winter; diamonds = spring; squares = summer

Multivariate community structure exhibited 3 distinct seasons (winter: 23 October 2013; 22 January 2014; spring: 1 April 2014; 1 May 2014; 20 May 2014; summer: 22 July 2014; 27 August 2014, 10 September 2013) in the GNMDS ordinations of the log-transformed data (Fig. 3), presence and absence data, and untransformed data. The SIMPROF analysis (not presented) supported this pattern, preserving these 3 season groups irrespective of transformations. The GNMDS ordinations also separated spring samples, where the sampling dates arranged chronologically, indicating a gradual development of the community towards the summer.

The GNMDS ordination revealed a spatial pattern in late summer (September) and a very weak pattern in early spring (April) only. In both months, samples from stations T7 and T8 were more similar to winter samples than all other spring and summer samples. In September, station T1 had the highest abundance and highest diversity of all samples (79 392 ind. m^{-2}; 35 taxa). Abundance decreased substantially with distance from shore

Table 2. Number of taxa, total abundance, Shannon index ($H'_{\log e}$) and evenness (J'). Data shown are mean values ± SD for each station and each sampling date

	Taxa (n)	Abundance (ind. m^{-2})	$H'_{\log e}$	J'
Station				
T1	16.6 ± 10.4	20 780 ± 31 310	1.63 ± 0.48	0.66 ± 0.18
T2	15.6 ± 9.6	19 388 ± 28 079	1.56 ± 0.79	0.62 ± 0.16
T3	17.0 ± 8.6	12 408 ± 15 016	1.70 ± 0.56	0.69 ± 0.17
T4	12.3 ± 7.5	12 772 ± 20 718	1.49 ± 0.79	0.73 ± 0.14[b]
T7	13.5 ± 7.7	9690 ± 15 307	1.64 ± 0.37	0.72 ± 0.17
T8[a]	15.6 ± 7.2	8491 ± 9896	1.58 ± 0.42	0.63 ± 0.18
Date				
01.09.2013[a]	23.0 ± 9.4	29 395 ± 34 898	2.19 ± 0.12	0.73 ± 0.13
23.10.2013	5.2 ± 3.1	403 ± 201	0.95 ± 0.68	0.63 ± 0.20[b]
22.01.2014	2.7 ± 0.8	72 ± 30	0.88 ± 0.29	0.93 ± 0.11
01.04.2014	10.5 ± 2.5	3029 ± 1801	1.37 ± 0.41	0.59 ± 0.18
01.05.2014	19.5 ± 3.0	9373 ± 2740	2.02 ± 0.08	0.69 ± 0.05
20.05.2014	20.8 ± 3.4	11 677 ± 3822	1.93 ± 0.22	0.64 ± 0.08
22.07.2014	19.8 ± 2.5	52 869 ± 16 993	1.69 ± 0.19	0.57 ± 0.08
27.08.2014	20.5 ± 2.6	8037 ± 4953	1.86 ± 0.38	0.62 ± 0.14

[a]Station T8 was not sampled on 1 September 2013. The presented results omit this sample; [b]Station T4 contained only 1 taxon on 23 October 2013 and therefore J' could not be calculated. The presented J' results omit this sample

(T4: 4016 ind. m^{-2}; 18 taxa) and even more to the deep trough (T7: 400 ind. m^{-2}; 11 taxa). In April, we observed a difference in abundance between deep (T7 and T8: 1064 ind. m^{-2}) and shallow stations (T1–T4: 4012 ind. m^{-2}). In addition, we observed spatial patterns for some taxa. *Balanus balanus* and *Semibalanus balanoides* occurred almost exclusively at shallow stations, whereas most individuals of *Munida* spp. occurred at deep stations. In contrast, Amphinomidae were equally distributed throughout the study area during their peak abundance in July, but were only present in samples from the deep stations on 20 May.

Seventeen taxa contributed to at least 5% of the difference between at least one season pair for at least one transformation (Table 3). All 17 taxa were virtually absent from the winter samples (Fig. 4). Accordingly, the taxa with the highest spring and summer abundances contributed most to separating winter samples from those from other seasons. *S. balanoides* was the taxon that reached its annual maximum abundance earliest (in April), followed by *B. balanus*, Spionidae, and Ophiuroidea in early May. These 4 taxa were representative of the spring meroplankton community and disappeared almost completely before the summer. The remaining taxa were abundant during the summer, and of these, only bivalves with *Mya* type larvae were equally high in abundance in spring and summer.

Most taxa appeared suddenly in the plankton and disappeared again after a short abundance peak. In contrast, the 2 bryozoans (*M. membranacea* and *Electra pilosa*) occurred in high numbers from early May until September, increasing gradually over the season.

Although many taxa contributed to spring and summer differences, the dominant barnacle separated these seasons most clearly. Though present in all samples during the spring, *S. balanoides* and *B. balanus* effectively disappeared during the summer. In contrast, another barnacle, *V. stroemia*, occurred in very high abundances in all samples during summer, following low presence during spring. Furthermore, the ratio of *S. balanoides* to *B. balanus* changed from early spring to mid- and late spring, contributing to intraseasonal differences.

Variables structuring the meroplankton community

Forward-selection CCA showed that variables from the environmental and both temporal datasets explained significant variation in the meroplankton data, whereas spatial variables did not (see Supplement 2 at www.int-res.com/articles/suppl/m555p079_supp.pdf). Therefore, we applied the variation partitioning method only for the 3 datasets with significant explanatory variables. After forward selection, the datasets included the following variables: environmental data (surface temperature, bottom tem-

Table 3. Results of the species contribution analysis for spring, summer, and winter for presence and absence (Qual.), logarithmic (Log.), and untransformed (Raw) meroplankton data. The average contribution of a taxon is 1.54% (= 100% / 65 taxa). Taxa contributing over 5% to the difference between a cluster pair for one transformation are shown. Contributions over 5% given in bold and contributions over 10% are given in bold italic. Values are rounded to 2 decimals

| Taxa	Spring vs. summer			Spring vs. winter			Summer vs. winter		
	Qual.	Log.	Raw	Qual.	Log.	Raw	Qual.	Log.	Raw
Galathea spp.	0.03	0.03	0.01	0.03	0.02	0.00	**0.05**	0.05	0.01
Verruca stroemia	0.01	0.04	***0.14***	**0.05**	0.05	0.02	**0.05**	**0.08**	***0.15***
Balanus balanus	0.05	**0.06**	0.03	**0.07**	**0.08**	***0.12***	0.01	0.01	0.00
Semibalanus balanoides	**0.06**	**0.06**	0.03	**0.07**	**0.08**	**0.09**	0.00	0.00	0.00
Membranipora membranacea	0.01	0.03	***0.12***	0.02	0.04	***0.12***	0.03	**0.06**	***0.16***
Electra pilosa	0.01	0.02	0.03	**0.06**	**0.07**	**0.09**	**0.05**	**0.07**	0.04
Amphinomidae	0.05	**0.05**	***0.32***	0.01	0.02	0.04	**0.05**	**0.06**	***0.33***
Chaetopteridae	**0.06**	0.05	0.02	0.00	0.00	0.00	**0.05**	0.05	0.02
Spionidae	0.02	0.02	0.00	**0.06**	**0.06**	0.02	0.04	0.03	0.00
Hiatella type	**0.05**	**0.06**	0.03	0.01	0.01	0.00	0.04	**0.05**	0.03
Mya type	0.04	0.04	0.01	0.02	0.03	**0.07**	**0.05**	**0.06**	0.03
Mytilidae type	**0.06**	**0.06**	0.02	0.01	0.00	0.00	**0.06**	**0.06**	0.02
Anomiidae type	**0.05**	0.04	0.01	0.00	0.00	0.00	0.05	0.04	0.01
Littorinimorpha type	0.01	0.03	**0.07**	0.01	0.03	0.03	0.02	**0.05**	**0.08**
Nudibranchia	0.02	0.04	**0.07**	0.01	0.02	0.01	0.01	0.02	**0.07**
Ophiuroidea	0.00	0.02	**0.06**	**0.06**	**0.09**	***0.28***	0.05	0.05	0.02
Echinoidea	0.02	0.02	0.00	**0.07**	**0.07**	0.04	0.04	0.04	0.01
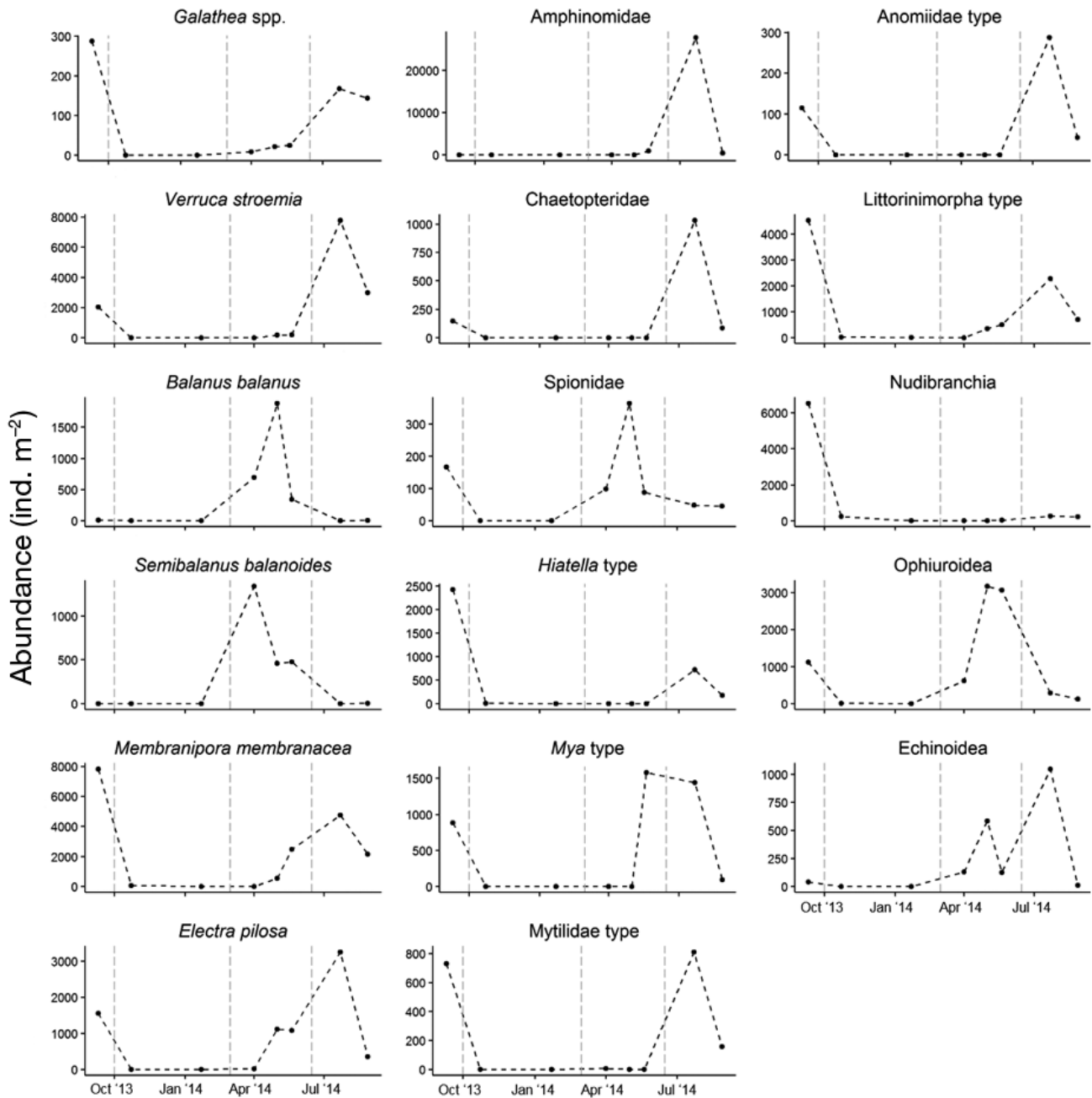
Fig. 4. Average abundances (ind. m⁻²) of the taxa contributing over 5% to the separation of 2 season clusters according to species contribution analysis results. Identified seasons are separated by vertical lines

perature, fluorescence maximum, bottom salinity), temporal 1 (season), and temporal 2 (sampling date). In total, these variables explained 35.5% of the total variance (TVE), leaving 64.5% unexplained. Variation explained exclusively by the environmental data accounted for the largest portion of the TVE, followed by variation explained by season alone and variation explained by all 3 sets of explanatory vari-

ables (Fig. 5). The remaining 4 combinations of the datasets explained negligible variance.

Mantel and partial Mantel statistics (Table 4) support the results of the forward-selection CCA, indicating no significant correlations between the geographic distance matrix and the dissimilarity matrix of the log-transformed meroplankton data, but the environmental data correlated significantly with both.
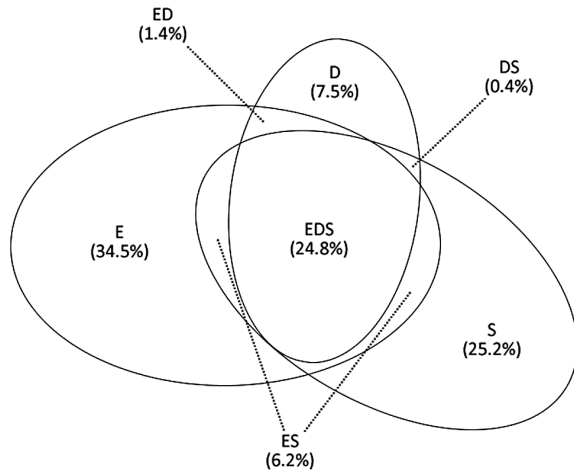
Fig. 5. Euler diagram showing the results of the variation partitioning for the logarithmic-transformed meroplankton data. The percentages indicate the relative contribution of each explanatory data set (E = environment; D = sampling date; S = season) and all combinations of them to the total variation explained (TVE = 35.5%)

Larval dispersal and origins

The May model advected a fraction of the particles northward relatively quickly along the continental slope, with some reaching 70.5° N latitude within just 2 wk and 9.7% of particles advected north of 71° N after 4 wk (Fig. 6A). The July simulation advected comparatively few particles along the slope, transporting particles northeastward onto the shelf and closer to the coast; 5.1% of the particles moved over 20° E by the end of the simulation. In both May and July, a significant percentage of the particles ended up in Andfjord (41.9% and 34.6%, respectively). Backward simulations showed different patterns for May and July (Fig. 6B). The May simulation advected a large fraction of the particles into the study area from the near coastal area all along the northwestern coast of the Lofoten Islands, in contrast to few particles from the off-shelf area farther south (5%). In July, most of the particles originated from the continental shelf adjacent to the release area, with 73.9% of the particles remaining north of 68° N 4 wk prior to sampling (compared with 11.9% in May).

Table 4. Mantel (upper triangle) and partial Mantel statistics (lower triangle) for logarithmic-transformed meroplankton data, environmental data, and space. p-values are given in parentheses

	Meroplankton (log)	Environment	Space
Meroplankton (log)	–	0.159 (0.029)	−0.014 (0.589)
Environment	0.182 (0.020)	–	0.426 (<0.001)
Space	−0.091 (0.969)	0.434 (<0.001)	–

DISCUSSION

Our results showed that diverse planktonic larvae of benthic invertebrates contribute to the planktonic community on the Lofoten-Vesterålen shelf from at least April until September, with maximum abundances during summer. Although we identified 65 taxa in 11 phyla, indicating a considerably higher meroplankton diversity than reported for other northern polar regions (44 taxa in the Kara Sea [Fetzer & Arntz 2008] and 42 in a north Greenland fjord [Andersen 1984]), this number nonetheless falls short of the diversity reported for temperate waters (~160 taxa in the Danish Øresund [Thorson 1946]). We offer 3 possible explanations for this difference in diversity. (1) The meroplankton diversity may directly reflect local benthic diversity, because regional benthic communities ultimately determine meroplankton diversity (Mileikovsky 1968). (2) Following Thorson's rule (Mileikovsky 1971) that postulates fewer planktotrophic species with increasing latitude, meroplankton diversity may reflect the sub-Arctic environment of the Lofoten-Vesterålen region. (3) Differences in sampling protocols and taxonomic resolution may contribute to between-study differences. Presumably, all 3 explanations contribute in some way. The particularly heterogeneous benthic habitats that characterize the Lofoten-Vesterålen region (Buhl-Mortensen et al. 2012) provide niches for a diverse benthic community. Although recent studies refute Thorson's rule for the whole benthic community and instead suggest a shift from planktotrophy to lecitotrophy with increasing latitude, the rule apparently holds for Prosobranchia (Clarke 1992), which were represented by 9 taxa in our present study despite total absence in Kara Sea plankton samples (Fetzer & Arntz 2008). Furthermore, the higher diversity of bivalves (5 morphotypes in our study vs. 28–33 species in Thorson [1946]) reflects Thorson's taxonomic expertise for molluscs. Additionally, our 200 μm mesh size may have underestimated the diversity of bivalve larvae.

Nonetheless, studies of (sub-)Arctic meroplankton from Svalbard and the Barents Sea report the same major components of the meroplankton community as our study. Schlüter & Rachor (2001), for example, described a community from the central Barents Sea in May and June characterized by echinoderm, polychaete, and *Mya truncata* larvae. These taxa mirror the meroplankton community in our study on 20 May 2014, but lack abundant barnacles (*Semibalanus balanoides*, *Balanus balanus*)
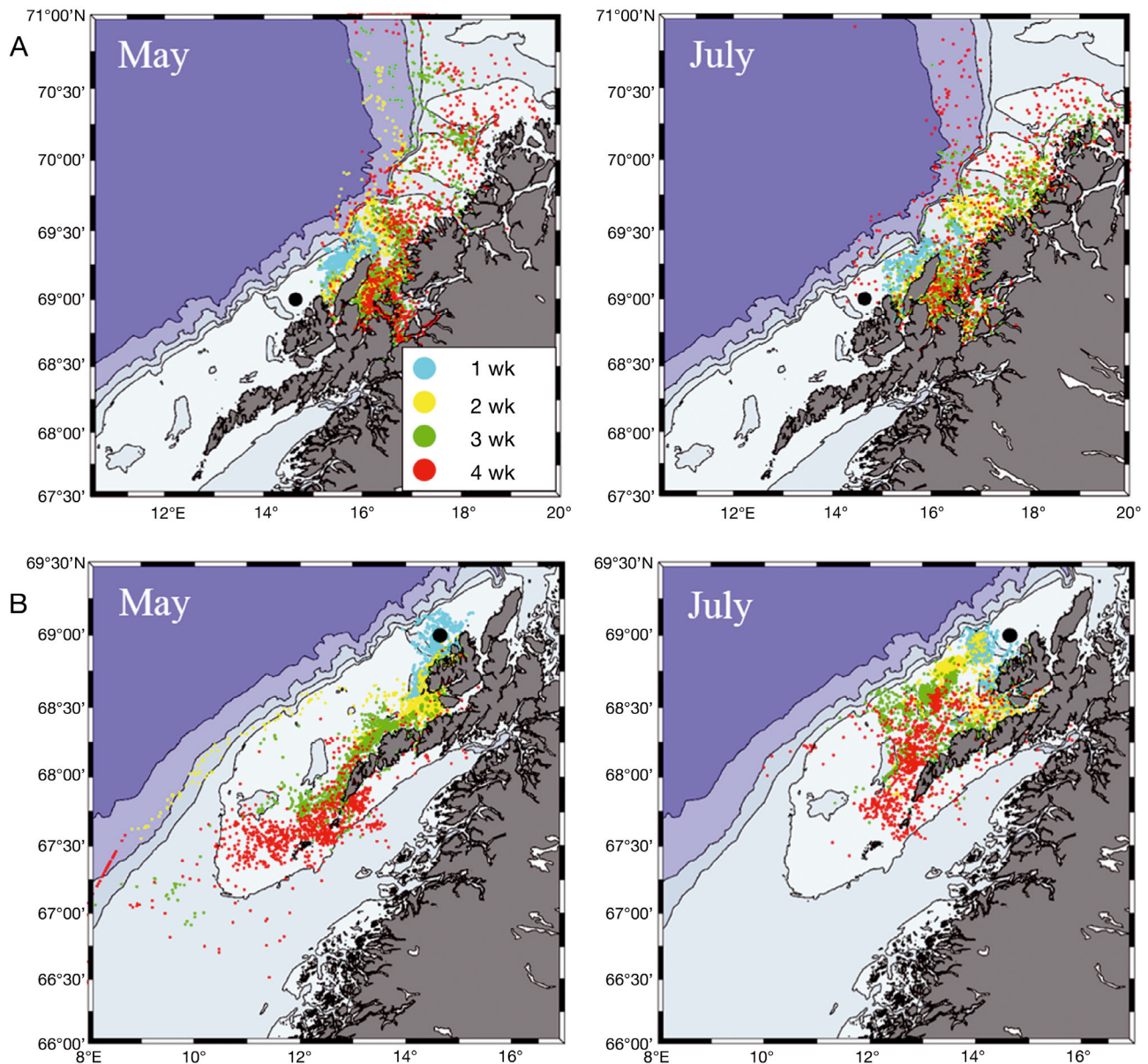
Fig. 6. Particle-tracking results. Forward (A) and backward (B) simulations of larval transport for the meroplankton community on 1 May 2014 (left) and 22 July 2014 (right). Particle distributions are presented in 1 wk steps (see color scale) following (A) or before (B) being observed at the black circle

and bryozoans (*Membranipora membranacea*, *Electra pilosa*), typically associated with hard substrates and shallow depth. In contrast, studies from Svalbard fjords reported peak abundances of barnacle larvae in May–June (Willis et al. 2006, Kuklinski et al. 2013, Stübner et al. 2016).

Only Kuklinski et al. (2013) and Stübner et al. (2016) have reported on a meroplankton community over a full annual cycle in an area similar to the Lofoten-Vesterålen region with respect to the physical environment. Like the Lofoten-Vesterålen region, their

Adventfjord study location on Svalbard experiences strong seasonality in day length and a short period of high primary production. In addition, the absence of winter sea-ice, the strong influence of Atlantic water, and increased freshwater input during the melting season in late summer characterize Adventfjord. Species with low-Arctic, boreal-Arctic, Arctic-boreal, and Atlantic biogeographic origin occur commonly in Adventfjord (Różycki 1993). Although the Adventfjord studies (Kuklinski et al. 2013, Stübner et al. 2016) used different sampling schemes to characterize the

meroplankton community over a 1 yr period, both studies nonetheless identified similar seasonal development, with meroplankton present in larger numbers from mid-April to the end of July. Within this period, they identified a spring community dominated by barnacles and a summer community dominated by molluscs. We report similar spring and summer communities in Lofoten-Vesterålen, characterized by the same groups. Two barnacle species dominated the spring community in contrast to abundant bivalve and gastropod taxa during the summer. The occurrence of other abundant taxa resulted in reduced dominance by the previously mentioned taxa in Lofoten-Vesterålen. Amphinomid polychaetes *Verruca stroemia* and the 2 bryozoan species occurred in lower numbers in Svalbard. This amphinomid, quite likely *Paramphinome jeffreysii*, occurs frequently and in high abundances in fjords of mainland Norway and on the continental shelf. No study has reported adults of *P. jeffreysii* in Svalbard. Regarding bryozoans, Stübner et al. (2016) reported a very different seasonal pattern than that in Kuklinski et al. (2013) or in our study. Stübner et al. (2016) observed very few bryozoans and exclusively during winter months, when virtually all other larvae were absent. In contrast, our samples contained high numbers of bryozoans almost throughout the complete spring and summer. Species with different larval types may explain this result (Temkin & Zimmer 2002). The planktivorous cyphonautes larvae of the species in our study spend a relatively long time in the plankton. Although Stübner et al. (2016) did not mention larval type, they likely observed small lecithotrophic larvae with a short planktonic period that do not require food while in the pelagic zone. Kuklinski et al. (2013) reported a high number of non-cyphonautes bryozoans, but also very low numbers of cyphonautes larvae. However, in their study the non-cyphonautes larvae appeared in April right after the spring phytoplankton bloom and disappeared from the water again in June.

Spatial and seasonal structure

Our analysis identified seasonal as well as spatial structure in the environment. However, our results also showed strong seasonal structure in the meroplankton community with little spatial structure other than the spatial patterns described for *B. balanus*, *S. balanoides*, Amphinomidae, and *Munida* spp.

Studies that sample single time periods often report spatial structure in meroplankton communities, frequently relating patterns to observed water

mass properties on a regional scale (Belgrano et al. 1995a,b, Ayata et al. 2011) or to differences in marine landscape (coast vs. shelf vs. oceanic) on a larger scale (Koettker & Lopes 2013). Year-round studies of meroplankton communities (Kuklinski et al. 2013, Weidberg et al. 2013) have not reported such spatial structure, perhaps relating to study design and the highly dynamic nature of pelagic ecosystems. Sampling campaigns for seasonal studies require extensive, repetitive sampling cruises. Therefore, the limited spatial coverage and number of samples make it impossible to detect weak spatial structure. However, the lack of spatial structure in the meroplankton community in our study could well be related to the particularly dynamic pelagic system in the study area (Røed & Kristensen 2013). A strong cross-shelf mixing in the study area is also in accordance with the particle-tracking results in this study. In each simulation, the particles were evenly distributed over the width of the shelf 1 wk before and after their release.

The strong seasonal changes in meroplankton in our study coincide with past studies of Arctic (Willis et al. 2006, Kuklinski et al. 2013, Stübner et al. 2016) and Antarctic (Stanwell-Smith et al. 1999) waters, as well as studies of temperate waters in Britain (Highfield et al. 2010) and northern Spain (Weidberg et al. 2013). We identified a winter period with very low abundances of meroplankton, as commonly reported in previous Northern Hemisphere temperate (~2 mo) and Arctic (~8 mo) studies.

The absence of early and late spawning species, or delayed and advanced spawning of early and late spawning species, respectively, may explain the shortened period of larval presence at high latitudes. The recurring dominance of barnacle larvae in spring characterizes meroplankton communities all along the European coast (Pyefinch 1948, Crisp 1962, Kuklinski et al. 2013, Weidberg et al. 2013). In British waters, early naupli of *S. balanoides*, *B. balanus*, and *V. stroemia* more or less co-occur in February–March (Pyefinch 1948, Crisp 1962), when the spring phytoplankton bloom triggers larval release (Crisp & Spencer 1958, Barnes & Stone 1973). Crisp (1962) showed a similar delay in larval release with increasing latitude for *S. balanoides* and *B. balanus*. In our study, however, *V. stroemia* appeared later in the season than the other barnacles. Stone (1989) showed experimentally that *S. balanoides* naupli feed on large diatoms, whereas *V. stroemia* develops better when fed small flagellates. Therefore, although the temporal succession of barnacle species in Lofoten-Vesterålen suggests adaptation to the regional tem-

poral succession of the phytoplankton community in northern Norway (Tande 1991), the causes for the longer delay in *V. stroemia* remain unclear.

Mytilidae larvae vary seasonally with environmental conditions on spatial scales of 100s–1000s of km (Philippart et al. 2012). Accordingly, Mytilidae abundance in our summer community strongly resembles the pattern in the White Sea (Günther & Fedyakov 2000), but differs from temperate regions in Europe (Philippart et al. 2012). Such large-scale similarities apparently hold for other bivalve species as seen by similarity in *Mya* spp. occurrence in Lofoten-Vesterålen and the Barents Sea (Schlüter & Rachor 2001).

Parental populations and settlement locations

Our particle-tracking simulation indicated very different origins of spring (coast) and summer (shelf) meroplankton communities, but advection of a large proportion of the larvae into Andfjord in both seasons. Unfortunately, a lack of information on the distributions of adult benthic populations in the Lofoten-Vesterålen region precludes any validation of possible spawning or settlement locations. We assumed particles in our simulations behaved passively without behavior, though previous studies have shown that vertical migration can reduce transport distances and risk of offshore transport (Robins et al. 2013). Therefore, our simulation may overestimate dispersal distances for some taxa, and we assume that the fraction of larvae that settled in Andfjord and adjacent shelf areas may represent underestimates in both seasons. This high local settlement points to the importance of the meroplankton community for the resilience of local benthic assemblages. Furthermore, perhaps even fewer larvae were transported offshore than our simulations suggested. Therefore, we propose a minimal risk of offshore transport for meroplankton in the Lofoten-Vesterålen region, as proposed by Mileikovsky (1968) based on his observation of low larval abundances in Norwegian Sea offshore waters.

Species composition on 1 May 2014 supports a coastal origin for larvae. Given its intertidal distribution, we can easily presume a coastal origin for *S. balanoides* larvae (Hayward & Ryland 1995). *B. balanus* occurs on, though is not restricted to, hard substrates in shallow coastal waters. Various brittle stars with ophiopluteus larvae commonly occur in northern Norway (Mortensen 1927), including *Ophiopholis aculeata*, and several *Ophiura* species, which are very common on the Lofoten-Vesterålen and Nordland

County coasts (M. J. Silberberger pers. obs.). Similar transport pathways were described for a 2011 early spring simulation (Espinasse et al. 2016). A simulated particle release in Vestfjorden on 15 March 2011 resulted in advection along the Lofoten coast and some particles reaching our study location within 3 wk.

Amphinomidae (*P. jeffreysii*), *V. stroemia*, and Mytilidae, all abundant taxa in samples from 22 July 2014, support the hypothesis of a dominant shelf origin of the summer community. However, these taxa occur beyond the shelf. *P. jeffreysii* also commonly occurs in north Norwegian fjords. *V. stroemia* occurs from the low littoral zone to several hundred meters depth (Stone & Barnes 1973). Likewise, the common Mytilidae species *Modiolus modiolus* occurs in northern Norway from a few meters to over 200 m depth. In contrast, the bryozoans *M. membranacea* and *E. pilosa* commonly associated with kelp and shallow waters originate from shore (Hayward & Ryland 1995). Although this observation contradicts our hypothesis of the summer community originating on the shelf, our particle-tracking simulation nonetheless showed a fraction of the particles originated from the coast in July as well.

Variability in circulation at small timescales can strongly influence generalizations drawn from the simulations regarding seasonal patterns in larval transport. Especially in the surface layer, changes in wind conditions can significantly alter transport. However, the 2 simulations identify some clear differences in seasonal patterns. Early in the year, prevailing southwest winds push water masses transported by the Norwegian Coastal Current towards the coast, thus strengthening the current. During summer, the prevailing northerly winds decrease Norwegian Coastal Current flow, producing lower advection and shorter transport pathways in summer compared with spring.

We conclude that a distinctly seasonal sub-Arctic meroplankton community, which is considerably more diverse than documented in previous Arctic studies, characterizes the Lofoten-Vesterålen region. Nonetheless, the diversity of meroplankton clearly reflects only a subset of the entire local benthic diversity. Low taxonomic resolution for some meroplankton may partly explain this discrepancy, but it may also indicate a high proportion of benthic organisms with direct development, short planktonic duration, or near-bottom larval distributions, which our sampling campaign did not capture. Our study revealed surprisingly little spatial variation across the continental shelf, despite large-scale differences in benthic habitats at the sampling locations. Particle tracking revealed some interesting transport patterns,

particularly given that water column properties at our sampling locations did not satisfactorily explain the observed variation in the meroplankton community. The simulated transport pathways indicate that meso- and large-scale oceanographic processes in the study area must be considered when estimating the potential of benthic communities for recovery from disturbances. At the same time, our study demonstrated the need for detailed knowledge of adult distributions and a better understanding of the mechanisms triggering larval release. Furthermore, assessment of the potential impacts of natural and anthropogenic disturbances on the resilience of Arctic and sub-Arctic benthic communities will likely require the use of new molecular methods that offer better taxonomic resolution than morphological approaches.

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