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Year-round meroplankton dynamics in high-Arctic Svalbard

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Meroplankton is often neglected in Arctic zooplankton studies, so our knowledge about their seasonal dynamics is limited. To investigate the highly dynamic nature of meroplankton, we sampled the zooplankton community in a high-Arctic fjord in West-Spitsbergen bi-weekly from December 2011 to December 2012. Five significantly different seasonal meroplankton assemblages were identified, representing winter, early spring, spring, summer and autumn. Meroplankton persistently dominated the zooplankton community during the productive seasons in both abundance (41–91%) and biomass (54–98%). Cirripedia and Bivalvia larvae occurred in particularly high numbers and dominated during spring and summer respectively. In the remaining seasons, the meroplankton diversity and abundance were comparatively poor, but interestingly Bryozoa larvae were present mainly during winter. Chlorophyll *a* and day length were identified as the main environmental variables structuring the meroplankton assemblage, followed by hydrography. Timing of the spring bloom determined the onset of the “meroplankton-boost” and from the observed hydrography, local rather than advective processes shaped the meroplankton community. Our investigation suggests that benthic invertebrate larvae play a significant role in the pelagic ecosystems in Arctic coastal regions, tightly linking the pelagic and benthic realms, thus deserving more attention in future studies.

KEYWORDS: benthic invertebrate larvae; zooplankton; seasonal; fjord; timing

INTRODUCTION

Meroplankton are organisms that spend only a part of their life cycle as plankton, and are mostly larvae of benthic invertebrates. A planktonic life stage enables

benthic invertebrates with limited motility to disperse their young to areas suited for colonization or recolonization (Mileikovsky, 1971; Fetzer, 2004), before settling on the sea floor. They are also important for recruitment of

new individuals to an existing benthic community or population (Mileikovsky, 1971). These larvae or early juvenile stages might be either feeding (heterotroph) or non-feeding (lecitotroph), and their duration in the plankton can vary from hours to months depending on the taxonomic group, species and environmental conditions (Thorson, 1950; Ockelmann, 1965; Mileikovsky, 1971). Depending on the time their larvae spend in the plankton, hydrography and sea currents, benthic invertebrates may colonize areas far from their mother colony (Mileikovsky, 1968; Scheltema, 1986) and extend their biogeographic range under favourable conditions (Berge *et al.*, 2005).

Meroplankton exhibit strong seasonality due to their often short-term residency in the plankton combined with distinct seasonal reproduction patterns (Thorson, 1946, 1950; Mileikovsky, 1970). The spawning period of adults can be either spread over longer periods, or occur in one or several short, intense spawning events (Thorson, 1950; Mileikovsky, 1971; Norden Andersen, 1984; Young *et al.*, 2002). Huge numbers of larvae may be released during these events (Giese and Kanatani, 1987) leading to extremely high abundances, which can comprise a substantial part of the zooplankton community (Smidt, 1979; Kulikova *et al.*, 2000; Pedersen *et al.*, 2005) and it has been argued that those peaks can be used to roughly estimate the timing of spawning (Mileikovsky, 1970). In the Arctic, pulsed occurrence with high abundances has been reported for larvae of cirripedes, bivalves, gastropods and echinoderms (Smidt, 1979; Fetzer, 2003; Pedersen *et al.*, 2005; Walkusz *et al.*, 2009). Especially cirripede nauplii can be very numerous (Smidt, 1979; Muxagata *et al.*, 2004), and it has been suggested, that these relatively large larvae can consume a significant part of the total particulate organic carbon (POC) during their mass occurrence (Pasternak *et al.*, 2008; Zajaczkowski *et al.*, 2010). Thus, meroplankton organisms may have a very important trophic role as grazers, competitors for food or as a potential food source for larger zooplankton and fish (Thorson, 1950; Young and Chia, 1987).

The number of dedicated meroplankton studies in the Arctic is limited. Although the meroplankton abundance at higher taxonomic levels is recorded in most zooplankton community studies also around Svalbard (Weslawski *et al.*, 1988; Willis *et al.*, 2006; Weydmann *et al.*, 2013), these are not specially designed to study meroplankton dynamics. For instance, most meroplankton are part of the smaller zooplankton fraction, which is substantially under-sampled in the most common, standard 180–200 μm mesh size plankton nets (Turner, 2004; Madsen *et al.*, 2008; Svensen *et al.*, 2011). Combined with the short residence time of meroplankton in the water column and

low sampling frequency in most Arctic studies, our knowledge of meroplankton seasonality, abundances and contribution to the zooplankton community in the arctic pelagic realm is limited.

This study was specially designed to capture the seasonal meroplankton dynamics in a high-Arctic fjord in West Spitsbergen, Svalbard. Throughout an entire year, we sampled the zooplankton community in the 80 m deep Adventfjorden bi-weekly with a fine-mesh plankton net (WP2, 63 μm mesh size). The overall objective with this intensive seasonal study was to establish a “meroplankton-baseline” to help close some of our current knowledge-gaps on these temporary guests in coastal Arctic plankton communities. We aimed to (i) estimate the proportion of meroplankton in the zooplankton community on a bi-weekly to seasonal to yearly basis, (ii) identify the timing of key meroplankton taxa, and (iii) identify distinct meroplankton assemblages and the main environmental factors driving these seasonal changes in meroplankton composition.

METHOD

The study area

Adventfjorden is a small side-fjord of Isfjorden, Spitsbergen’s largest fjord system. Adventfjorden is directed NW-SE and is around 7 km long and 3–5 km wide, with a maximum depth of ~ 100 m close to the mouth. It is situated at 78° North (Fig. 1) and thus has a high-Arctic light climate with almost 4 months of darkness (sun under the horizon) and 4 months of midnight sun. According to hydrography and seasonal ice cover, however, Isfjorden

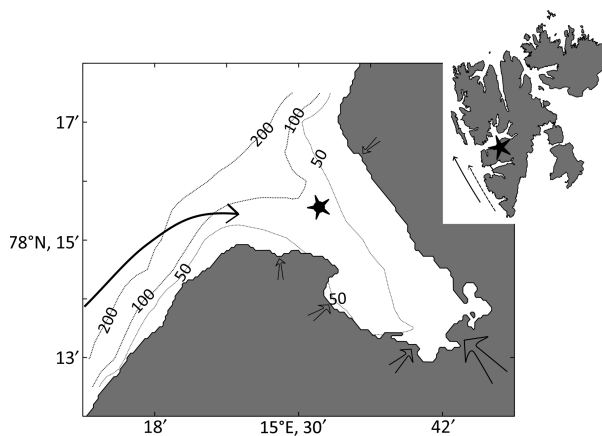


Fig. 1. Map of the sampling station Isfjorden/Adventfjorden (IsA), close to Longyearbyen, Spitsbergen. The sampling station (star) with general influences of Atlantic (single line arrow) and Arctic water masses (stippled arrow). Open arrows indicate fresh water influences from rivers into Adventfjorden.

and Adventfjorden resemble more a sub-Arctic fjord (Wiedmann *et al.*, 2015) with no winter sea ice cover the last decade (<http://polarview.met.no>). Both Isfjorden, and Adventfjorden, are open fjords that are seasonally influenced by warm and saline Atlantic (AW) and/or transformed Atlantic water (TAW) transported northwards along the continental shelf break with the West Spitsbergen Current (WSC) and advected into the fjord system (Nilsen *et al.*, 2008; Leikvin and Evenset, 2009). The time-series Isfjorden-Adventfjorden sampling station (IsA, 78.261 N 15.535 E, Fig. 1), near the mouth of Adventfjorden has a bottom depth of ~80 m. Two larger and several smaller rivers discharge freshwater and sediments from a catchment area of ~630 km² (based upon www.svalbardkartet.npolar.no) with several land locked glaciers into Adventfjorden. Thus, Adventfjorden is strongly influenced by brackish water and fine sediment particles during the main melting season in summer (Leikvin and Evenset, 2009).

The meroplankton seeding populations may either originate from the path of the main inflow into Adventfjorden, where hard bottom substrates support Cirripedia, Bivalvia, Decapoda, Ophiuroidea and Gastropoda or from within Adventfjorden, where hard bottom organisms are found on natural substrates along the edges or on port installations (pers. observation). The deeper and inner areas in Adventfjorden are mainly comprised of soft sediments and are generally dominated by Polychaeta, followed by Mollusca, with the two groups Gastropoda and Bivalvia as numerous components (Cochrane *et al.*, 2001; Wlodarska-Kowalczyk *et al.*, 2007). Due to the influence of AW, species with a low-Arctic, boreal-Arctic, Arctic-boreal or Atlantic biogeographic origin are common in the Isfjorden system (Rozycki, 1993).

Environmental conditions

This study was part of a larger collaborative sampling campaign (Adventfjorden field campaign, UNIS), investigating different aspects of the planktonic system. A mooring (moored oceanographic underwater observatory) was deployed at the IsA station from September 2011 until August 2012 with the same instrumentation and similar design as in Wallace *et al.* (Wallace *et al.*, 2010). SeaBird Electronics MicroCats at 25 and 76 m depth recorded temperature, conductivity, and pressure. At 25 m, a sensor for photosynthetic active radiation (PAR, Satlantic, PAR-LOG ICSW) and a SeaPoint fluorometer were deployed for combined physical and biological monitoring. Measurements were saved hourly at 25 m and every 20 min at 76 m depth. Temperature, salinity and fluorescence profiles were also recorded at each sampling event from the whole water column using a

hand-held CTD with a fluorometer attached (SAIV SD204).

Water samples for estimation of chlorophyll *a* (chl *a*) were taken weekly to bi-weekly at 5, 15, 25 and 60 m with a 10 L Niskin bottle. During the bloom period, chl *a* was sampled with a higher frequency, but due to time constraints, only one depth (25 m) was sampled. For chl *a*, three replicates of 200–400 mL, depending on the density of phytoplankton in the water column, were filtered through glass microfiber filters (GF/F, 0.7 μm, Whatman, England). Filters were either stored frozen (–80°C) or chl *a* was extracted immediately in 10 mL methanol (~99%) for 20–24 h at 4°C in darkness (Holm-Hansen and Riemann, 1978). Chl *a* concentrations were measured with a calibrated fluorometer (10-AU-005-CE Fluorometer, Turner, USA; chl *a* standard: Sigma S6144).

Day-length was calculated using the NOAA solar calculator available at <http://www.esrl.noaa.gov/gmd/grad/solcalc/calcdetails.html>, using the hours per day where the sun was above the horizon.

Meroplankton sampling and taxonomic analysis

Meroplankton was sampled one to three times per month (2 × 23 samples in total) from December 2011 until December 2012 during daytime (Supplementary data, Table SI). The attempted bi-weekly sampling scheme was adjusted according to weather conditions and logistical restraints. From the beginning of March until end of May, sampling took place more frequent, with highest sampling frequency during the spring bloom in May. A closing WP2 net (UNESCO, 1968) with 63 μm mesh size and an opening area of 0.25 m² was hauled at 0.25–0.5 ms^{–1} for quantitative sampling of meso- and the larger fraction of micro-zooplankton. Standard sampling depths were set to the core euphotic zone from 25–0 m and the remaining water column 65–25 m. Samples for taxonomic identification were preserved immediately on board or max. 2 h after sampling in the laboratory back at UNIS in 4% formaldehyde-seawater solution buffered with hexamine.

Community samples were analysed at the Institute of Oceanology Polish Academy of Science under an Olympus SZX 7 stereomicroscope (40× magnification) equipped with an ocular micrometre. Organisms, including both holoplankton and meroplankton, in subsamples were analysed until at least 200 meroplanktonic organisms were counted and identified. If specimens belonging to one taxon dominated the zooplankton community, i.e. during an event of mass occurrence, a minimum 200 individuals of other meroplanktonic organisms were

counted. Zooplankton were identified to the lowest possible taxonomic level. Larger organisms (>5 mm) like Euphausiacea, fish larvae, and gelatinous plankton belonging to Ctenophora and Cnidaria were counted for the whole sample, but not included in the analysis since they were not representatively sampled with the net used (WP2, 63 μm). Meroplankton and holoplankton abundances (ind. m^{-3}) were calculated from sample counts for each sampling layer (65–25 m and 25–0 m) and integrated for the whole water column sampled (65–0 m) assuming 100% filtration efficiency.

Data analyses

Temperature, salinity (from hand-held CTD) and chl *a* measurements were interpolated linearly with time and depth and presented in a Hovmöller plot. All interpolations were done using the *akima* package (Akima *et al.*, 2013) in R (R Core Team, 2014). Water masses were characterized according to Nilsen *et al.* (Nilsen *et al.*, 2008). PAR-measurements were normalized between 0 and 1 from the sensors voltage output.

Mean total annual abundances and biomass (dry weight) for groups of zooplankton were calculated from daily values, inferred from linear interpolation between sampling dates. Mean relative annual abundances and biomass were compared between total holo- and total meroplankton. Dry weight was measured directly for the most abundant group *Bivalvia* (6*100 ind., sampled 8.7.2014), since no representative dry weight estimate was available for these small larvae. Individuals were picked under a Leica stereo-microscope, measured and dried at 50°C in pre-weighed tin-cups. For other zooplankton, literature values were used to estimate dry weight (Supplementary data, Table SII).

For further analysis of meroplankton community composition, organisms were grouped into Polychaeta, Echinodermata, Bryozoa, Cirripedia, Decapoda, *Bivalvia* and Gastropoda. Pteropoda were grouped together with other holoplanktonic species. For holoplankton, organisms were divided into groups of adult and pre-adult stages (e.g. copepodid stages for copepods) and larval forms (e.g. nauplii stages for copepods). A root transformation was chosen to reduce the influence of very high abundances during mass occurrences of some groups. A series with root transformation (2nd, 4th, 6th, 8th root) was done for the whole dataset. A correspondence analysis (CA) (Oksanen *et al.*, 2013) was run for each transformation (not shown). The results showed that a fourth root transformation was sufficient to allow meaningful analysis.

To determine the date for the transition from one season to the next can be difficult, since calendar dates might not correspond well with biological seasons in

Arctic environments. Therefore, temporal breaks within the meroplankton composition were identified using a multivariate regressions tree (MRT) (De'ath, 2002) with the *mvpart* package in R (De'ath *et al.*, 2013; R Core Team, 2014). To distinguish breaks along a gradient, the method splits the data repeatedly along one or several pre-set, constraining parameters, trying to minimize the dissimilarity within groups. In subsequent runs, both a pre-made dissimilarity matrix, using Bray Curtis similarity, as well as a species-sample matrix was used as input, since slightly different results may be produced in each case. Analyses were made for meroplankton data constrained by time (Julian day) for (i) the integrated water column and (ii) per sample layer, with 500 cross validations. The number of breaks in each model run was selected manually, choosing the tree with the lowest combination of relative error and cross-validation error below 1 SE. Dates that occurred consistently in different model-runs, were used to define transition dates between seasons and only the tree best representing the final seasonal division is presented and discussed. The resulting divisions between grouped seasonal meroplankton assemblages and seasonal differences for each of the taxa were tested with ANOSIM and ANOVA respectively with the *vegan* package in R (Oksanen *et al.*, 2013; R Core Team, 2014). Differences in meroplankton composition between sampling layers in each season were tested with a two-way ANOVA. Two additional MRT-analysis were run on the taxa-sample matrix for meroplankton per sampling layer constrained by all environmental variables except either day length or chl *a* respectively (Figure not shown) to explore which parameters influenced meroplankton composition the most. Two separate models were run, since chl *a* and day length were highly correlated ($r = 0.71$, $P < 0.001$, Spearman rank for non-linear correlations).

To show the distribution of samples, a non-metric multi-dimensional scaling (nMDS) was performed using Bray-Curtis similarities. Seasons from MRT analysis were indicated in the plot by colours, and environmental factors were fitted (9999 permutations). Both nMDS and vector fitting were done in the *vegan* package in R (Oksanen *et al.*, 2013; R Core Team, 2014).

Spearman rank correlations between chl *a* as an estimate of food availability and a) total meroplankton abundance and b) abundances of the different taxa were calculated.

RESULTS

Environmental conditions

In 2012, the sampling station IsA, was influenced by both colder local water (LW) and warmer transformed Atlantic water (TAW) (Fig. 2 and Supplementary data,

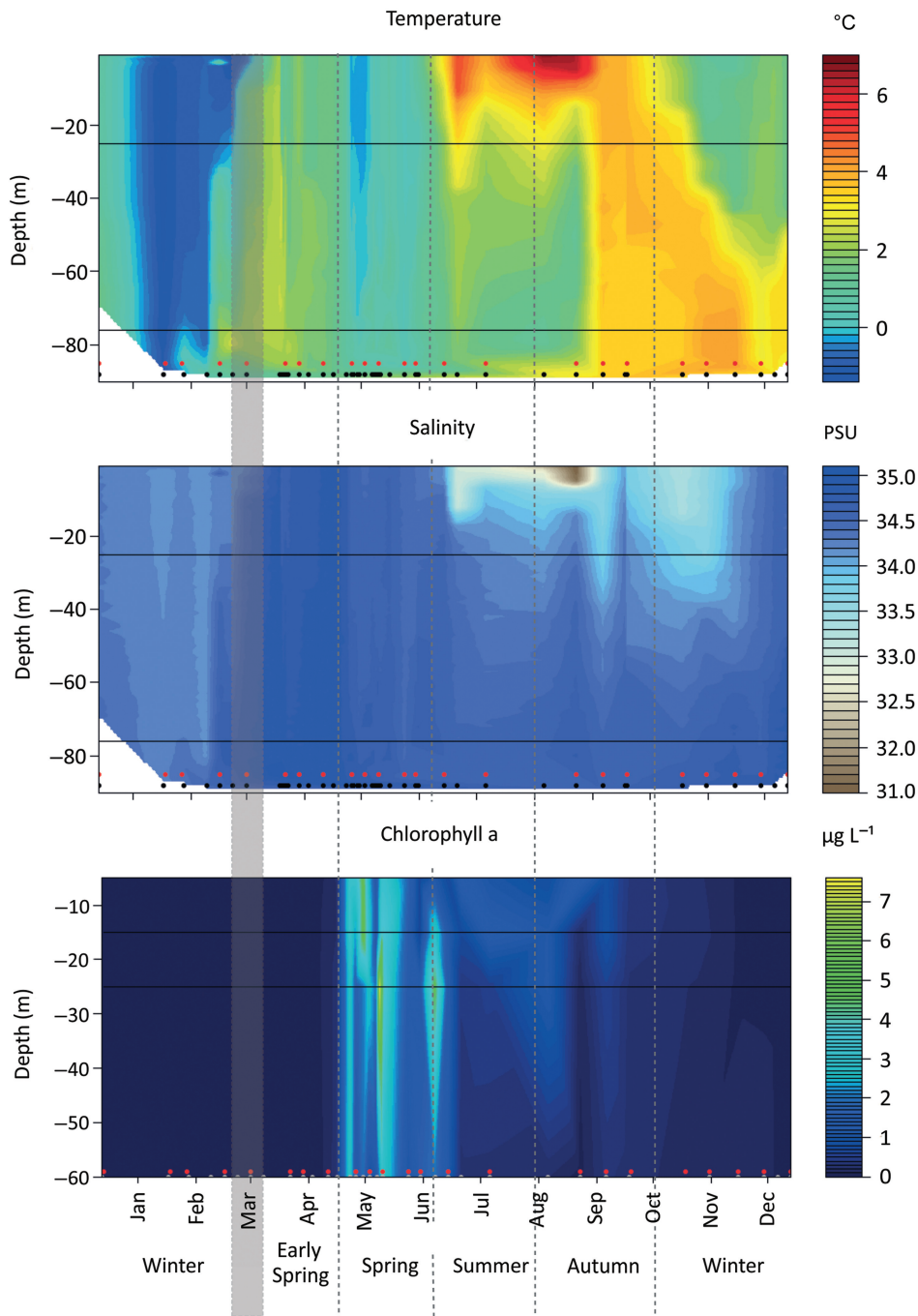


Fig. 2. Contour plots of environmental variables. Temperature (upper panel), salinity (middle panel) and chlorophyll *a* (lower panel) were interpolated linear between measurements (black dots in the upper two panels/grey dots in the lower panel). Horizontal lines indicate depth of CTDs deployed on the mooring and depth of sampling for CTD and chl *a* measurements, respectively. Red dots indicate dates for zooplankton sampling. Vertical lines indicate transitions between seasonal communities as identified by the MRT analysis. Pay attention to different depth ranges for the upper two plots compared to the chl *a* plot.

Table SI), and no sea ice formed. Local water prevailed from the beginning of the year, but was in February replaced by an inflow of warmer and more saline TAW, which remained until April. At the end of April, wind conditions (www.met.no) led to reduced influence of

TAW and LW re-entered the station. At the same time, chlorophyll *a* levels increased (see below). From June to August, freshwater river run-off led to a distinct fresher, warmer surface layer (SW), but below LW remained. During September, stronger wind (www.met.no) led to

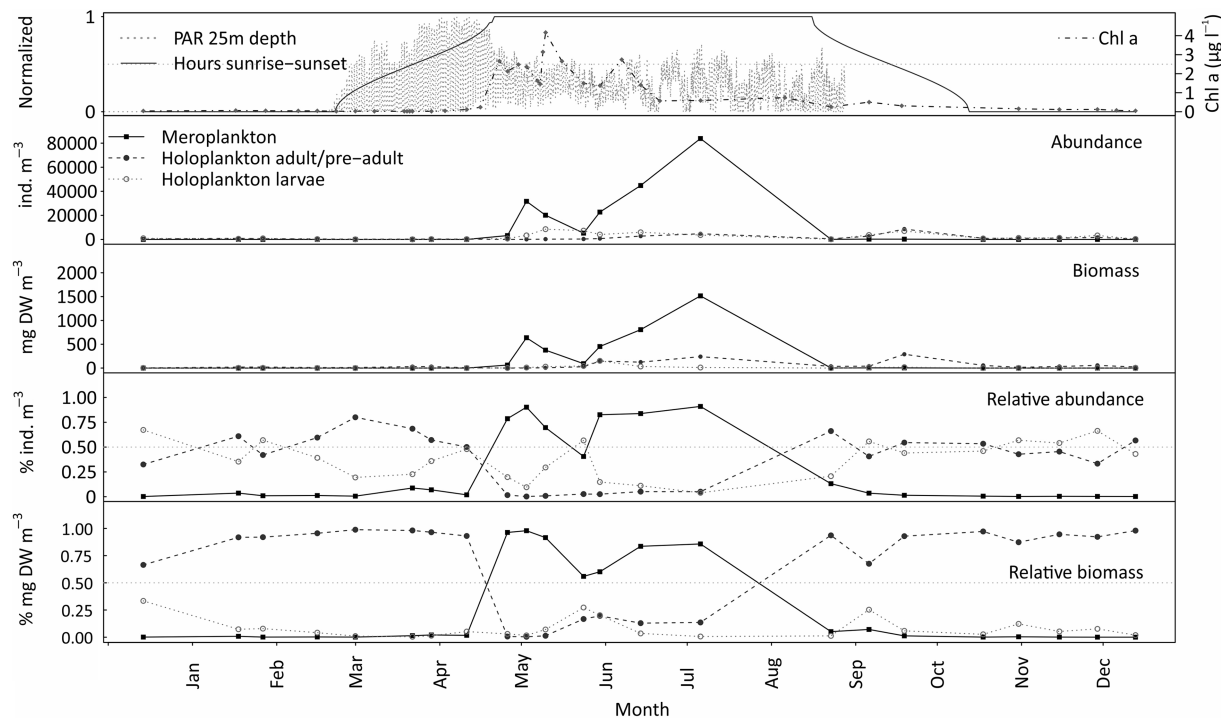


Fig. 3. Zooplankton pattern across the year in relation to light, chlorophyll *a* and day length. Upper panel: Normalized photosynthetic active radiation (PAR, dotted line) from moored sensor at 25 m depth, day length (full line, data from www.met.no) and mean chlorophyll *a* concentration for 65–0 m (stippled line). The other panels show meroplankton (full line) versus adult holoplankton (stippled line) and juvenile holoplankton (dotted line). Abundance (2nd panel), biomass (3rd panel), relative abundance (4th panel) and relative biomass are shown. Dots indicate sampling dates. Biomass is given as dry weight (DW) in mg m^{-3} , abundance in ind. m^{-3} .

mixing of the entire water column. Combined with a new inflow of warmer and more saline water at depth, continuing until the end of the sampling period, intermediate water (IW) formed (Nilsen *et al.*, 2008), concurrent with a cooling of surface waters. CTD-measurements from the mooring generally agreed with the hand-held CTD measurements (not shown).

Measured PAR levels at 25 m were low until February and reached a maximum between end of March and mid-April (Fig. 3). High loads of terrigenous particles could be observed at the station during the main melting season from June to September, but varied strongly with tides and wind conditions (pers. observations).

Chl *a* concentrations were very low throughout winter and early spring and increased first in mid-April (Fig. 3; Marquardt *et al.*, in 2016). The first indication of a bloom was observed at the end of April ($>2 \mu\text{g L}^{-1}$) and chl *a* concentrations reached the highest annual concentration in May ($\sim 4 \mu\text{g L}^{-1}$, Figs 2 and 3 and Supplementary data, Table SIII). Chl *a* concentrations stayed high throughout the water column during May and the first half of June ($>1 \mu\text{g L}^{-1}$). From July through September moderate to low chl *a* values prevailed, while from October on, low winter concentrations ($<0.2 \mu\text{g chl } a \text{ L}^{-1}$) were reached again.

Zooplankton dynamics

Total zooplankton abundances, including both holoplankton and meroplankton, varied from lowest in March (260 ind. m^{-3}) to highest in July ($92\,200 \text{ ind. m}^{-3}$). Meroplankton was found year-round with highest abundance in early July ($83\,800 \text{ ind. m}^{-3}$), dominating in abundance during the productive spring and summer period (41–91%) (Fig. 3 and Table I). Outside the main productive seasons, meroplankton occurred in low numbers ($0\text{--}240 \text{ ind. m}^{-3}$) (Figs 3 and 4, Supplementary data, Table SIII) and contributed little to the total zooplankton abundance ($0\text{--}13\%$) (Fig. 3 and Table I). Among holoplankton, Copepoda was the most abundant taxon ($250\text{--}13\,860 \text{ ind. m}^{-3}$), occurring in higher numbers from beginning of the productive season until the end of the year. They were followed by mostly juvenile Pteropoda ($0\text{--}1\,590 \text{ ind. m}^{-3}$) and Euphausiacea ($0\text{--}580 \text{ ind. m}^{-3}$), which showed high abundances in autumn and spring/summer respectively.

Across the year, the meroplankton contributed 76% to the mean total annual zooplankton abundance. Most of these (88%) were small bivalve veliger larvae ($0.1\text{--}0.4 \text{ mm}$), followed by the larger cirripede nauplii ($0.4\text{--}0.8 \text{ mm}$, 12%). Other meroplankton taxa contributed little

Table I: Seasons with averages of relative abundances (relative biomass) of the most abundant meroplankton phyla, holoplankton and total mesozooplankton abundances

Seasons	Dates	Meroplankton [%]			Holoplankton [%]		Tot. abundance [ind/m ³]
		Bivalvia	Cirripedia	Other	Ad and pre-ad	Larvae	
Winter	4.10.-23.2./11.3.	0 (0)	0 (0)	1 (0)	47 (91)/51 (91)	52 (9)/48 (8)	1926/1760
Early spring	24.2./11.3.-18.4.	3 (1)/4 (1)	0 (0)	2 (0)	64 (97)/59 (96)	31 (2)/36 (2)	440/499
Spring	19.4.-6.6.	25 (26)	46 (53)	2 (0)	2 (8)	26 (12)	21 702
Summer	7.6.-30.7.	85 (83)	2 (2)	0 (0)	5 (13)	8 (2)	72 851
Autumn	1.8.-3.10.	6 (4)	0 (0)	0 (0)	54 (85)	40 (11)	7728

Seasons according to MRT analysis of the meroplankton community. Values for both adult and pre-adult as well as larvae holoplankton are given. For the unsure transition between winter-early spring, values are given for both possible division dates (where differing).

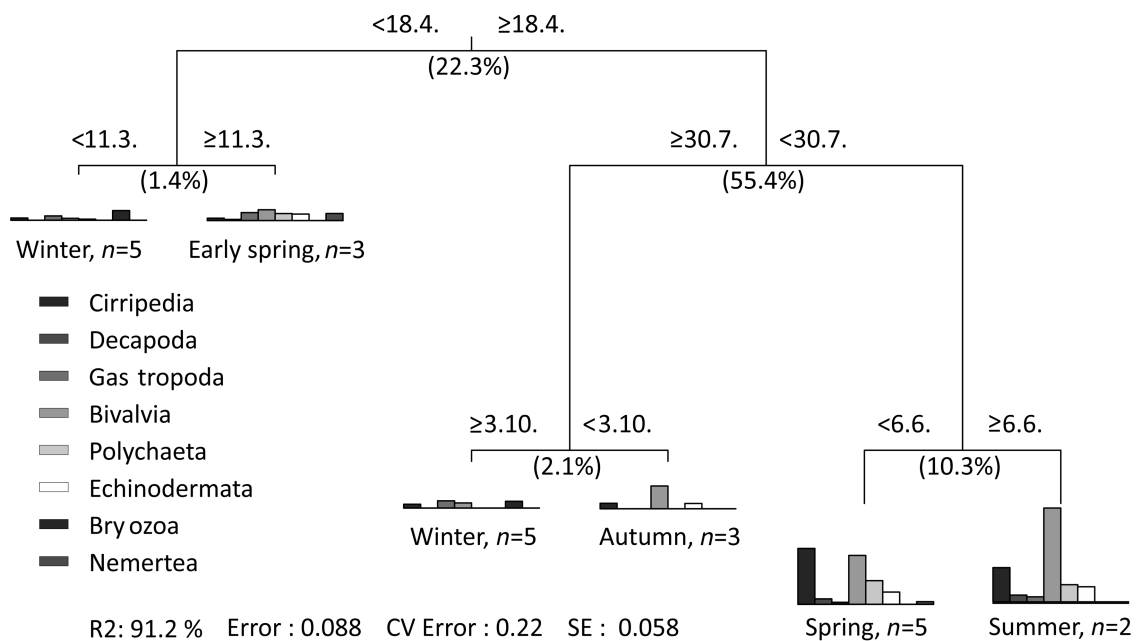


Fig. 4. Multivariate regression tree (MRT) on 4th root transformed meroplankton abundance data integrated over the whole water column, constraint by time. Bar plots indicate characteristic community composition for identified seasons. Total variance explained by the model is 91.2%. For each node, the variance explained by the respective split is given in brackets as well as the estimated date of the community shift. N = number of sampling days in each leaf of the tree.

(<1%) to the mean total annual zooplankton abundance. The two major peaks in zooplankton abundance in 2012 were largely driven by dynamics in meroplankton abundance (Fig. 3). The first peak occurred end of April – beginning of May and comprised mainly of Cirripedia larvae (65–68%), while the second, extending from the end of May to the beginning of July, was largely dominated by small Bivalvia larvae (30–88%) (Fig. 5). Later in the year, two smaller zooplankton peaks were apparent, but were mainly caused by an increase in holoplankton abundance (Fig. 3). All major meroplankton groups showed a minimum two abundance peaks during the year (Fig. 5).

Patterns in holoplankton and meroplankton biomass largely followed those seen for abundance (Fig. 3 and Table I). Across the year, meroplankton contributed 74%

of the mean total annual zooplankton biomass, and from 41 to 98% of the total zooplankton biomass during the productive spring and summer seasons (Fig. 3). Bivalvia contributed the most to the mean total meroplankton biomass (86%), followed by Cirripedia (14%). The contribution of other meroplankton taxa was low (<1%).

Meroplankton dynamics and relation to environmental conditions

There was no statistically significant difference in meroplankton composition between depth layers when tested across the year (2-way ANOVA including sampling layer and seasons and Table II), so seasonal patterns are discussed for values integrated over the whole water column. Five

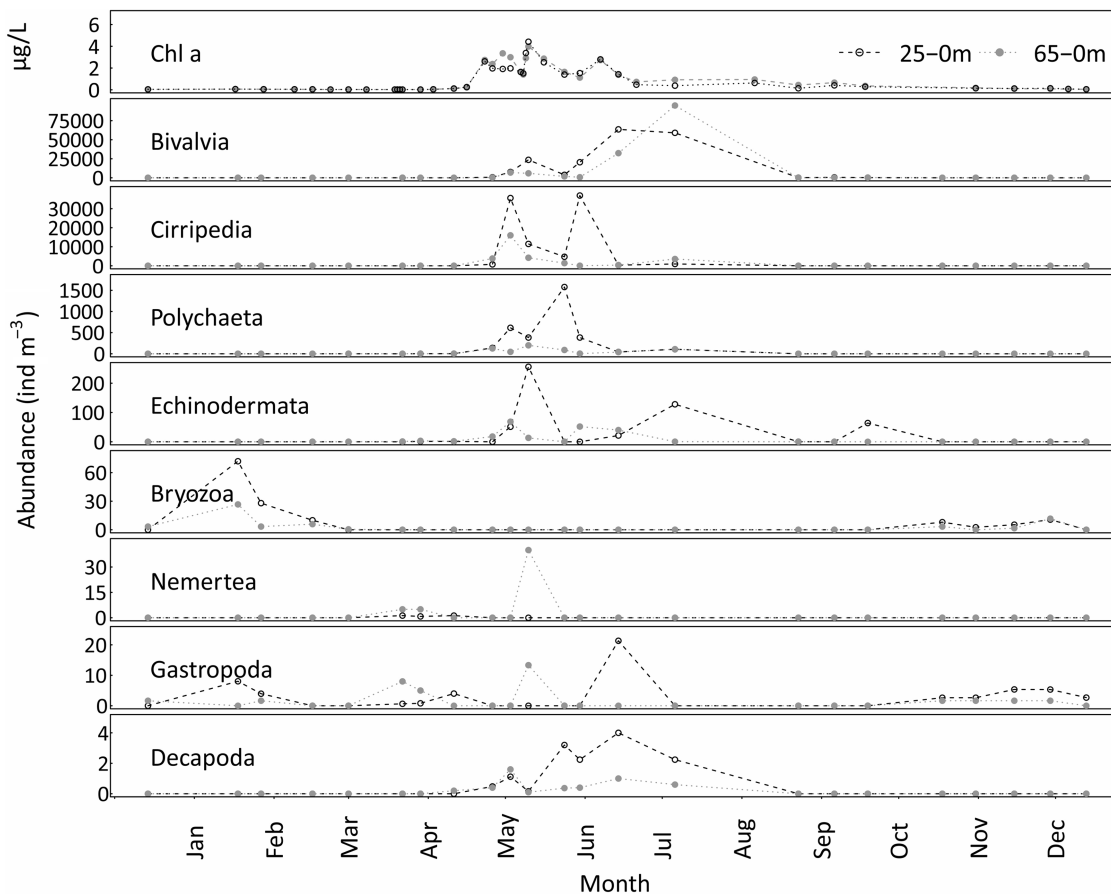


Fig. 5. Abundance of different groups of meroplankton for the upper (stippled line) and lower (dotted line) layer sampled, given in ind. m^{-3} . The upper panel shows mean chlorophyll a [$\mu\text{g L}^{-1}$] for the respective layers. The following panels give abundances for Bivalvia, Cirripedia, Polychaeta, Echinodermata, Bryozoa, Nemertea, Gastropoda and Decapoda in the order of their abundance. Note the varying scales for the different plots.

Table II: Results from environmental data fitted to the nMDS plot

Envifit for continuous variables			Goodness of fit for factors			
	r^2	$\text{Pr}(> t)$		r^2	$\text{Pr}(> t)$	
Julian day	0.088	0.151	Layer	0.004	0.839	
Salinity	0.250	0.002	**	Season	0.766	0.001
Temperature	0.027	0.562		Watermass	0.092	0.247
Chl a	0.460	0.001	***			
Density	0.216	0.007	*			
Daylength	0.834	0.001	***			

Significance indicated by * = 0.5, ** < 0.01 *** < 0.001,

distinct meroplankton assemblages (ANOSIM, $P = 0.001$, $r = 0.647$) were identified through MRT analysis and were termed according to five corresponding seasons (Fig. 4 and Table I). Differences in abundance among seasonal assemblages were highly significant for all identified taxa (ANOVA, $P < 0.001$), except for the low abundance taxa Nemertea and Gastropoda (ANOVA, $P < 0.01$ and $P < 0.05$ respectively). Winter assemblages were generally poor in meroplankton, except for Bryozoa and Gastropoda

larvae. In the early spring assemblage, the meroplankton abundances were higher and more diverse, but the meroplankton outburst was first observed in spring when the spring bloom occurred, with the particularly abundant Cirripedia. The summer assemblage was also rich in meroplankton abundance and taxa, and Bivalvia larvae strongly dominated. In autumn, meroplankton abundances dropped markedly and only some Echinodermata larvae were found in relatively high numbers. Transitions from one season to the next coincided with shifts in either chl a concentration and/or changes in water mass properties (Fig. 1 and Supplementary data, Table SI). The transitions between the low-productive seasons (winter–early spring and autumn–winter) were less distinct than the transitions between low-productive seasons and the productive seasons spring and summer (Figs 4 and 6).

In the MRT analysis constrained by environmental factors, chl a explained 67% of the observed variability in meroplankton composition and hydrography, either as temperature or the factor water mass, an additional 8% (overall error: 0.25, standard error: 0.18, cross validation error:

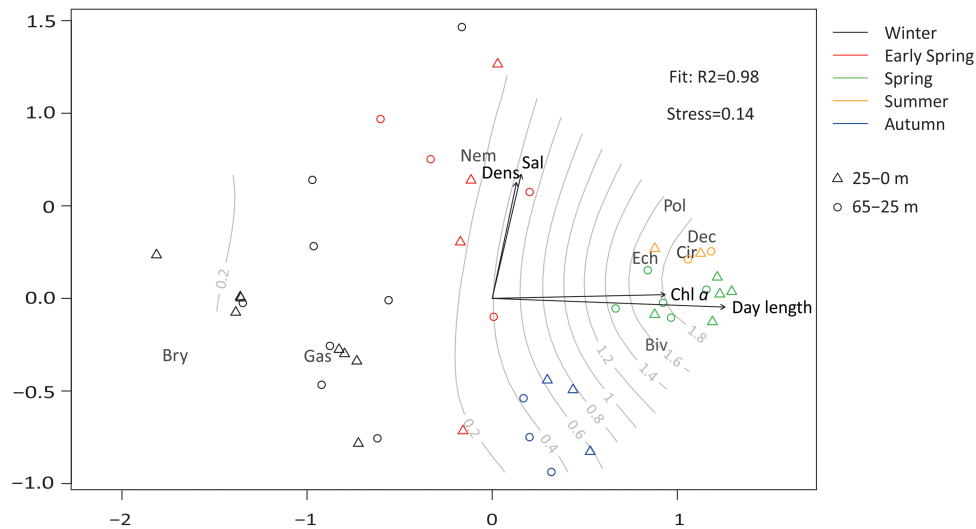


Fig. 6. Non-metric Multidimensional scaling (nMDS) plot on 4th root transformed meroplankton data for each depth layer and date. Colours indicate seasons assigned according to MRT-results; symbols indicate which depth-layer samples were taken in. Grey lines indicate superimposed chl *a* isolines and black arrows indicate fitted environmental variables. Only significant continuous environmental variables ($p_{max} \leq 0.05$) are shown.

0.65; delineations [Supplementary data, Table SI](#)). Day length explained slightly less variability (62%) in the corresponding analysis (delineations [Supplementary data, Table SI](#)). Results from environmental variables fitted to the nMDS diagram were in accordance with the MRT results (Table II and Fig. 6), with day length, chl *a* and the hydrographic parameters significantly explaining the observed meroplankton variability. Day length and chl *a* were also here highly positively correlated, as were salinity and density (Fig. 6). The MRT-defined seasons were highly significant, when fitted as environmental factor (Table II) and clustered together in the nMDS, with a clear cut division between high productive and low productive seasons (Fig. 6). Spearman rank correlations showed that the abundance of the three taxa Cirripedia, Decapoda and Bivalvia were all highly positively correlated to chl *a* ($r > 0.7$, $P < 0.01$), Polychaeta and Echinodermata were positively correlated to chl *a* ($r = 0.56$, $P = 0.01$) and Bryozoa and chl *a* were slightly negatively correlated ($r = -0.45$, $P = 0.03$). Species scores in the nMDS analysis largely agree with the assemblages delineated through the MRT analysis (Fig. 6).

DISCUSSION

Meroplankton composition and contribution to the zooplankton community

High meroplankton numbers and even dominance of meroplankton over holoplankton during shorter periods have been recorded regularly in Arctic coastal regions,

but the meroplankton numbers in our study were two- to more than 10-fold higher than reported elsewhere (Smidt, 1979; Weslawski *et al.*, 1988; Coyle and Paul, 1990; Kulikova *et al.*, 2000; Arendt *et al.*, 2013). Also such a long prevalence of meroplankton dominance, observed as a shift from a zooplankton community dominated by holoplankton during the less productive times to a community totally dominated by meroplankton during the productive season, was unexpected. Whether this was a result of frequent sampling enabling us to capture the several peaks in meroplankton, combined with use of a fine mesh net can be discussed. The extremely high meroplankton numbers in Adventfjorden were largely due to the small bivalve larvae (Fig. 5), which are more representatively caught in fine mesh nets like the one employed in this study. The meroplankton dominance over holoplankton on the other hand, could not only be explained by use of finer nets in our study, since also small copepods or younger copepodite stages are more representatively sampled by these finer nets (Turner, 2004; Madsen *et al.*, 2008; Svendsen *et al.*, 2011). The copepod abundances in this study were not unusual high, but within or below the copepod abundances reported in other seasonal studies in coastal Arctic regions using similar fine mesh nets (Smidt, 1979; Arendt *et al.*, 2013) (Fig. 3). Meroplankton abundances and contributions to the total zooplankton are higher in estuaries (Fetzer, 2003) or inlets (Kulikova *et al.*, 2000), and highest abundances are found in the upper 50 m (Smidt, 1979; Norden Andersen, 1984; Weydmann *et al.*, 2013). This likely affects comparisons of our relatively shallow sampling site with deeper stations, especially if

located further away from the coastline. Another important factor accounting for high meroplankton numbers in Adventfjorden may be the presence of benthic species of temperate and sub-Arctic origin (Rozycki, 1993), due to the relatively strong influence of Atlantic water that also prevent the fjord from freezing in winter (Cottier *et al.*, 2005; Nilsen *et al.*, 2008). According to Thorson's rule, benthic species with a non-Arctic origin are more likely to have planktonic larvae than Arctic ones (Thorson, 1936; Ockelmann, 1965; Mileikovsky, 1971). The high meroplankton numbers in our study may therefore partly be due to the more "temperate" biogeographic origin of many benthic species present in the area compared to many other high-Arctic regions.

Grazing impacts of meroplankton are believed to be negligible, since they have low clearance rates and are assumed to seldom occur in very high numbers (Strathmann, 1996). For example, Bivalve larvae are not known to efficiently graze down the algal standing stock (Sommer *et al.*, 2000; Lindeque *et al.*, 2015), but these meroplankton grazing rate estimates have been calculated for situations when abundances were much lower than those found in our study. The very high numbers of Cirripedia and particularly Bivalvia larvae found for a significant part of the year in the present study, suggest these meroplankters to be important trophic components in the plankton both as grazers and as prey. Meroplankton is therefore likely to be a very important component of the plankton community in West Spitsbergen coastal regions, which definitely needs more research attention in the future. Estimates of meroplankton grazing impacts in regions with particularly high meroplankton concentrations are needed to fully explore the importance of this temporary visitor in the pelagic environment.

Meroplankton composition, with Bivalvia, Cirripedia and Polychaeta as the most abundant groups in this study, is in accordance with other studies from Arctic fjords and inlets (Coyle and Paul, 1990; Kulikova *et al.*, 2000). Unfortunately, little information on the hard bottom fauna within and in the direct inflow area to Adventfjorden is available and no direct correlation between adult population and meroplankton abundance can be made. Adult bivalve and cirripede populations are established in Adventfjorden (pers. observation) and these local populations may potentially produce the large larval abundance peaks observed in this study, since those taxa can potentially release huge amounts of larvae/gametes at times (Barnes and Barnes, 1954; Ockelmann, 1958; Giese and Kanatani, 1987). Even though the relative abundances of Polychaete larvae were low, they had high total abundances during their peak occurrences in our study (Fig. 5), which agrees with their strong presence in the Adventfjorden bottom

community (Cochrane *et al.*, 2001; Wlodarska-Kowalczyk *et al.*, 2007). Echinodermata, which are often one of the main meroplankton components (Norden Andersen, 1984; Timofeev, 1998; Schlüter and Rachor, 2001; Fetzer, 2003), were poorly represented in Adventfjorden (Kuklinski *et al.*, 2013; this study) which agrees with Echinodermata not being very numerous at least in the soft bottom communities in Adventfjorden (Cochrane *et al.*, 2001; Wlodarska-Kowalczyk *et al.*, 2007).

In addition to the distribution of adult populations (Mileikovsky, 1968; Kulikova *et al.*, 2000; Pedersen *et al.*, 2005), advective transport of larvae (Mileikovsky, 1968; Scheltema, 1986) is recognized as an important factor influencing the distribution of benthic invertebrate larvae. According to flow simulations supported by *in situ* measurements (Leikvin and Evenset, 2009), benthic larvae from inside Adventfjorden as well as Isfjorden can be advected to our sampling station. Atlantic Water needs ~2 weeks to travel from the entrance of Isfjorden to IsA (Ragnheid Skogseth, Longyearbyen, personal communication) and both Cirripedia (Barnes and Barnes, 1958), Decapoda (Anger, 1984), Echinodermata (Byrne and Selvakumaraswamy, 2002) and most likely Bivalvia (Ockelmann, 1958) have representatives in the Arctic with larval durations exceeding this time. Thus, larvae might be advected from adult populations living on the shelf and along the coast outside Isfjorden during periods of strong AW-inflow. Even though, only small proportions of larval populations are transported far (Mileikovsky, 1968; Scheltema, 1986), so that abundance peaks occurring at the sampling station are rather expected to be produced locally or at least close to the inflow area towards Adventfjorden than at a large distance. Even though larvae transported from afar might not contribute to locally observed abundance peaks, the potential of long-lived larvae to be transported over very long distances (Mileikovsky, 1968), can lead to colonization or re-colonization of habitats under changing climate conditions, as seen for the blue mussel re-establishment in Svalbard after thousand year of absence (Berge *et al.*, 2005). If conditions in newly colonized areas allow reproduction, this will in turn influence the number and types of meroplankton larvae released into the water column and have implications for zooplankton dynamics. Accordingly, under a warmer ocean climate regime, we could expect more species with a boreal distribution to be able to establish and reproduce in higher latitudes. Those would, according to Thorson's rule (Ockelmann, 1965; Mileikovsky, 1971), be more likely to produce long-lived larval stages, so that the contribution of meroplankton to the zooplankton community might even increase.

Seasonal meroplankton dynamics and main environmental drivers

This study revealed a strong seasonal meroplankton dynamic in a high-latitude coastal ecosystem. The rather poor meroplankton assemblages in the low-productive seasons winter, early spring and autumn contrasted clearly with the rich and abundant assemblages during the high-productive spring and summer (Figs 4–6). Chl *a* levels, a proxy for phytoplankton food availability (Fig. 6 and Table II), were identified together with day length as the main environmental drivers for the meroplankton presence in the pelagic ecosystem in Adventfjorden. Since daylight is a pre requisite for primary production, especially in Arctic areas with a polar day and night, the larval phase can be timed to the main productive season via light regimes. The timing of the spring phytoplankton bloom and the first meroplankton-outburst were in our study closely synchronized, and that was after about a month with relatively long day lengths. We therefore argue that food availability rather than day length in itself was the main environmental driver shaping the timing of meroplankton presence, even though seasonally changing day-length in itself can be a spawning-trigger for benthic invertebrates (Giese and Kanatani, 1987).

The onset of spawning in several benthic phyla can be induced by phytoplankton or substances produced by phytoplankton (Starr *et al.*, 1990), although triggering factors or required combinations thereof vary between species (Giese and Kanatani, 1987). It has been suggested, that most benthic invertebrate larvae feed on phytoplankton (Thorson, 1950), also including several omnivorous larvae, which prefer phytoplankton as their main food source (Turner *et al.*, 2001; Vargas *et al.*, 2006; Pasternak *et al.*, 2008). To time reproduction to the spring bloom is therefore particularly advantageous for planktotrophic larvae and ensures the offspring access to large quantities of high quality food (Søreide *et al.*, 2010), e.g. demonstrated in northern Greenland as a “burst of growth” in benthic invertebrate larvae during the bloom period (Norden Andersen, 1984). For non-primarily herbivorous larvae such as Decapoda, which are, especially during later stages, carnivorous (Anger, 2001), the advantage of being present during the productive seasons lies most likely in the high general zooplankton abundance as prey.

Cirripedia have been shown to start larval release with increased food availability (Crisp and Spencer, 1958), which agrees well with the first Cirripedia larval peak observed right after the onset of the spring bloom (Fig. 5). A second peak in Cirripedia larvae abundance was observed ca. 2 weeks later, but was likely comprised of a different species (pers. observation). Besides others,

Balanus balanus, *Semibalanus balanoides* and *Balanus crenatus* are common in Svalbard (Palerud *et al.*, 2004), and these species may have slightly different timing in larval release (Korn and Kulikova, 1995). Alternatively, the second Cirripedia peak might have originated from an adult population located at a distance. Cirripedia nauplii prefer diatoms and small flagellates in their diet (Turner *et al.*, 2001). The Cirripede nauplii in our study had clearly visible green guts and were likely feeding on the large sized diatoms *Thalassiosira* spp. and *Fragilariopsis* spp. and possibly also the flagellate *Phaeocystis* sp., which were dominant parts of the spring bloom in Adventfjorden in 2012 (Kubiszyn *et al.*, submitted).

Interestingly, small Bivalvia larvae occurred in highest numbers after the peak spring bloom when the chl *a* biomass was mainly dominated by small (<10 µm) algal cells (Marquardt *et al.*, 2016). Bivalvia larvae have highest clearance rates on algae sized below 10 µm (Sommer *et al.*, 2000), suggesting that Bivalvia timed the peak presence of their larvae to the larvae’s most preferable algal food size. Bivalvia are known to spawn in summer and autumn in Arctic seas (Thorson, 1936; Norden Andersen, 1984), which agrees with our observations. Most bivalve species release gametes into the water column (Thorson, 1950; Zardus and Martel, 2002), and a time lag between the onset of spawning and peak larval abundances can be expected. However, some bivalve species in cold areas have brood protection, releasing developed veliger larvae (Ockelmann, 1965), but since veliger larvae were not identified to species level, we have no knowledge of their reproduction strategy. Still, the presence of planktonic food has been mentioned as a spawning trigger in this group, but might also be important at an earlier stage in reproduction, namely for gonad growth (Giese and Kanatani, 1987).

Larvae of Polychaeta and Echinodermata, were also correlated to increasing chl *a* biomass (Fig. 5), even though Echinodermata peaked several times, with some peaks even month after the spring bloom. Several Polychaeta and many Echinodermata release gametes and not larvae into the water column (Thorson, 1950; Giese and Kanatani, 1987). Therefore, some organisms of those two taxa, with larvae present during abundance peaks in spring, might have released gametes prior to the spring bloom, using different spawning cues. Day length and temperature seem important in Echinoderm reproductive cycles, especially for sea stars (Giese and Kanatani, 1987), while phytoplankton is a spawning trigger for at least some sea urchins (Starr *et al.*, 1990). The multiple abundance peaks observed for most taxonomic groups (Fig. 5) can be caused through distinct spawning events of certain parent-populations or species (Kulikova *et al.*, 2000; Schlüter and Rachor, 2001), or by

one species with disjunctive spawning (several periods of intense spawning) (Thorson, 1950; Mileikovsky, 1968; Norden Andersen, 1984). To be able to draw appropriate conclusions about spawning times and in turn spawning cues, higher taxonomic resolution and more knowledge on reproduction types and development times from egg to larvae is needed.

Distinct spawning events were limited and/or little pronounced during low productive periods. Water temperature can act as a timing cue (Thorson, 1936) and has to be above a certain necessary minimum for many benthic organisms to be able to spawn. Even though temperature was not identified as a statistically important factor (Table II), the lowest number of meroplankton coincided with the lowest recorded seawater temperatures during winter. Gastropoda and Bryozoa have often larvae that are little or not at all dependent on phytoplankton food availability, which fits nicely with Gastropoda and Bryozoa occurring in winter/early spring. Arctic Gastropoda often have lecithotrophic larvae or feeding larvae supported by empty nursing, with none or a short pelagic life (Thorson, 1936). Bryozoan larvae have either a lecithotroph form or a planktotrophic cyphonaut larvae (Temkin and Zimmer, 2002), which has been suggested to be able to feed on bacteria (Strathmann, 1987). Also several Echinodermata larvae seem able to use non-phytoplankton food sources (Rivkin *et al.*, 1986). One major advantage for larvae not dependent on phytoplankton may be a lower predation-pressure during winter and early spring.

Even though hydrography is recognized as one of the main structuring factors for the distribution of invertebrate larvae in the plankton (Schlüter and Rachor, 2001; Fetzer, 2003; Fetzer and Arntz, 2008), our statistical analysis did not identify hydrography as the main driver of meroplankton dynamics in this study (Table II and MRT). This could support the conclusion, that local reproduction strategies rather than large advective processes drive the meroplankton dynamics in Adventfjorden. Although shifts in the meroplankton assemblage mostly concurred with changes in water mass properties (Supplementary data, Table SI and Fig. S4), only one season, namely early spring, was clearly associated with a larger advective process. Meroplankton could have been transported into Adventfjorden with the TAW influx, but the change in meroplankton composition was only minor. The transition from early spring to spring coincided with the return of local colder water masses in Adventfjorden, simultaneously with an increase in chl *a* values, which makes it difficult to separate the influence of both factors on the meroplankton assemblage (Figs 2 and 3 and Supplementary data, Table SI). From the onset of the spring bloom until end of summer, local water masses dominated Adventfjorden. The change in water mass

properties in summer (Fig. 2 and Supplementary data, Fig. S4) was a local, non-advective process created by melt water run-off from land and heating through solar radiation (Fig. 2). Mixing of the entire water column occurred in autumn, with a smaller influx of warmer water below the sampling depth. The smaller peak in Echinodermata larvae in autumn could therefore potentially be advected into Adventfjorden, but for other taxa, no great changes in abundances were seen at that time, suggesting that advective impacts on the meroplankton assemblage was low.

Inter-annual variation in meroplankton composition and abundance peaks reveal some variation in timing between years (Smidt, 1979; Highfield *et al.*, 2010; Arendt *et al.*, 2013). This is most likely related to inter-annual variability in biological or physical environmental cues triggering gamete and/or larval release, such as the timing of the spring bloom, ensuring favourable conditions for the offspring (Philippart *et al.*, 2014). A continued time series including several years covering inter-annual variability would reveal clearer trends and allow stronger conclusions to be drawn.

CONCLUSIONS AND OUTLOOK

Our study demonstrated a high and persistent occurrence of meroplankton in the coastal zooplankton community in the western Svalbard region during the productive seasons, spring and summer. Meroplankton are therefore likely to be an important trophic component in the pelagic, both as grazers and as prey items for others. The release of large amounts of larvae/gametes into the water column, followed by pelagic grazing of meroplankton and subsequent settling as benthos also represent a strong pelagic-benthic coupling in coastal regions that is not often accounted for. The study of meroplankton seasonal dynamics could help us to better understand basic biology such as the timing of reproduction in benthic species if lower taxonomic resolution can be achieved for instance by molecular methods. We therefore argue that meroplankton deserves more focus in Arctic studies, also to provide a better knowledge base for management of coastal resources in Arctic areas. We showed that a high sampling frequency is crucial to capture short duration and multiple peaks within meroplankton groups, which is important for evaluating their relative importance throughout the year and illustrates the importance of a proper sampling design.

With temperatures generally above zero and lack of winter sea ice formation in recent years, Adventfjorden may be a representative model system for how the coastal high-Arctic ecosystems and zooplankton communities will be in a future warmer Arctic. Increased establishment of

sub-arctic species may result in similar or even larger contribution of meroplankton in coastal Arctic zooplankton communities. The tight coupling of most meroplankton taxa to phytoplankton availability implies that potential changes in the timing and magnitude of the bloom will have a major impact on benthic invertebrate reproduction and subsequent meroplankton occurrence in the plankton. In future studies, it would be of interest to integrate benthic surveys including several aspects of the benthic invertebrate reproductive cycle like the timing of gonad growth and environmental conditions required as well as the observation of larvae in the plankton, to get a better understanding of controlling and regulating factors that result in the observed pattern of meroplankton dynamics.

SUPPLEMENTARY DATA

Supplementary data can be found online at <http://plankt.oxfordjournals.org>.

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