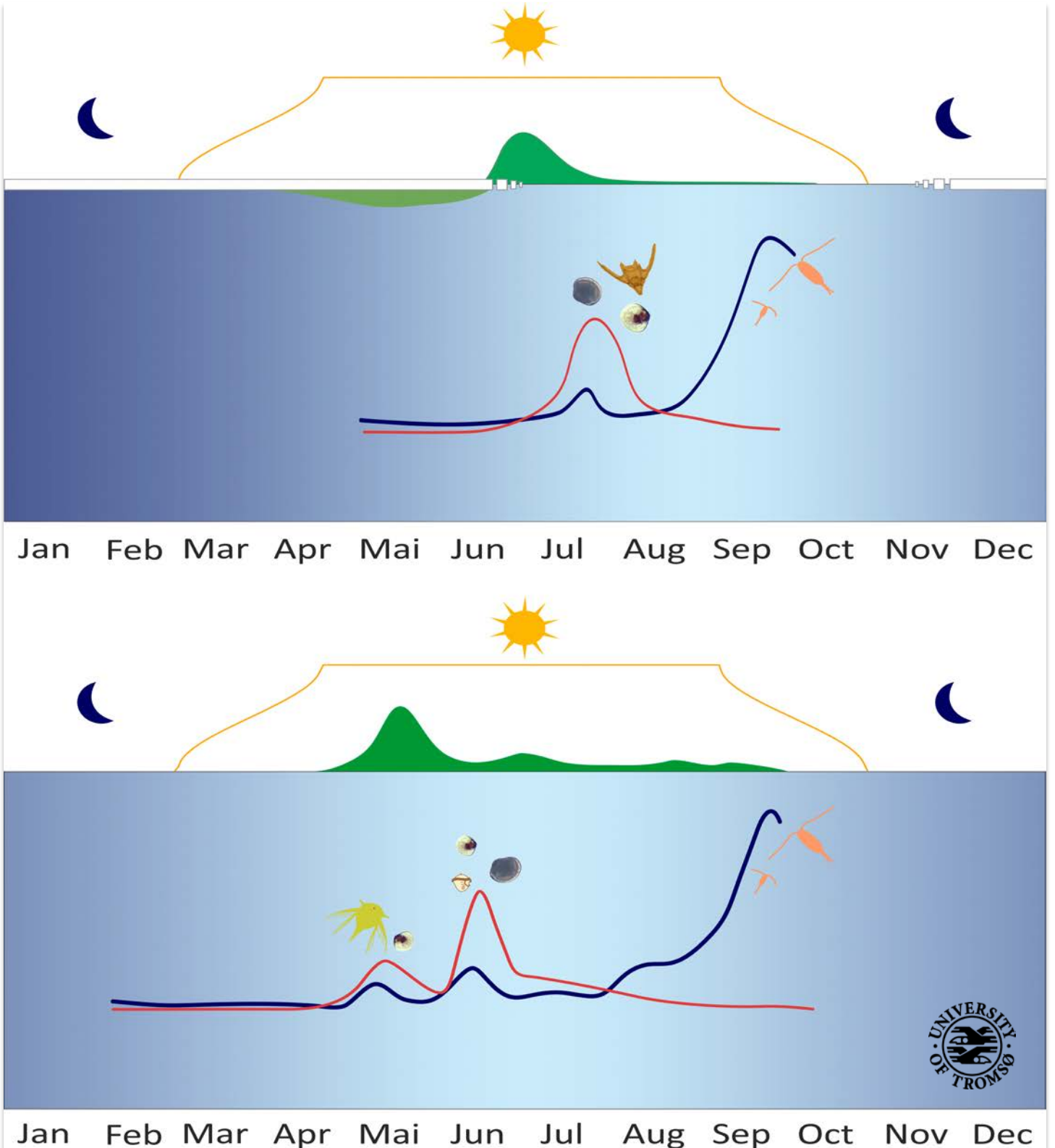


Seasonality of Meroplankton in Svalbard Waters

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Eike Stübner

A dissertation for the degree of Philosophiae Doctor – September 2016



Seasonality of Meroplankton in Svalbard Waters

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“The crucial lesson was that the scope of things I didn’t know wasn’t merely vast; it was, for all practical purposes, infinite. ... If our ignorance is infinite, the only possible course of action is to muddle through as best we can.... Focusing on important questions puts us in the awkward position of being ignorant. One of the beautiful things about science is that it allows us to bumble along, getting it wrong time after time, and feel perfectly fine as long as we learn something each time.” (MA Schwartz, “The importance of stupidity in scientific research”)

Acknowledgments

A PhD takes several years; in some cases a few more than originally planned since life might come up with other things that can't be ignored. Throughout those years, I wouldn't have managed without the many people around that shared their time and knowledge, their friendship and smiles.

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Summary

Meroplankton, mainly comprised of larvae of benthic organisms that only temporarily inhabit the pelagic environment, are an important part of the Arctic marine coastal environment. Since the life cycle of many marine benthic invertebrates includes a larval stage, they are also important for benthic community ecology. They mainly occur during certain time periods of the year, have relatively short residence times in the water column and due to their small size they usually escape the standard 180µm meshed nets. Their identification is difficult and their peak-occurrences can easily be missed during the mostly infrequent sampling regime in Arctic seasonal studies. Good temporal resolution in annual studies is rare, and the temporal and spatial distribution of meroplankton of high latitudes is poorly understood.

The main objective of this thesis was to increase our knowledge on meroplankton dynamics and their ecological role in the Arctic marine coastal ecosystem. Three different approaches including field sampling, molecular identification and experiments were applied to answer the main objectives of meroplankton ecology raised in this thesis. To investigate the highly dynamic nature of meroplankton and how they relate to biological and environmental drivers, we frequently sampled the zooplankton community in several fjords at Svalbard Archipelago with different primary productive regimes and hydrographic conditions. The general taxonomic resolution in our investigation was low, but in order to identify contributions of single species to the bulk of meroplankton groups, as well as identify potential species-specific differences in timing, a combination of DNA barcoding of mitochondrial 16S ribosomal RNA and morphological analysis was applied on bivalve larvae found within the zooplankton. And finally, feeding experiments using natural prey concentrations and composition, incubated under close to natural conditions in the fjord, were conducted to assess the feeding impact of the abundant cirripede larvae during spring.

Bi-weekly sampling was carried out in the sub-arctic influenced Adventfjorden throughout two consecutive years, and gave important information on the timing and duration of meroplankton presence and activity. The high sampling frequency was possible due to the close proximity to Longyearbyen. For 2012, the meroplankton dynamics were investigated in detail. Meroplankton data for three more annual series were gathered from two other fjords, Billefjorden and Rijpfjorden, with more Arctic conditions, where sampling was conducted monthly. We found that the strong correlation of meroplankton abundance with phytoplankton biomass observed in Adventfjorden was a general pattern, and the timing of the bloom and timing of meroplankton abundance was correlated Cirripedia and Bivalvia. Our data showed that meroplankton persistently dominated the zooplankton community during most of the productive seasons in both abundance and biomass at the shallow sampling station in Adventfjorden. Contributions to the total zooplankton abundance was lower in the deeper fjords, but still considerable (<30%) during spring. Cirripedia and Bivalvia larvae occurred in particularly high numbers and dominated during spring and summer respectively in Adventfjorden and Billefjorden. Interestingly Bryozoa larvae were present mainly during

winter and Gastropoda throughout the year in low numbers. In Rjipfjorden, Bivalvia and Echinodermata were the two dominating groups of meroplankton with one period of peak-abundance shortly after sea-ice break-up. Chlorophyll a and day length were the main environmental variables structuring the meroplankton assemblage, with hydrography being of less importance. We found that the timing of the spring bloom determined the onset of the “meroplankton-boost”. Strong seasonality was also found in the occurrence of the different bivalve larval species, largely coinciding with periods of primary productivity. For 3 out of 4 identified bivalve species similar spawning pattern and reproductive timing was indicated, with several potential spawning periods. Those three species, *Hiatella arctica*, *Mya truncata* and *Mya* sp., had all wider distributional ranges. The fourth species, *Serripes groenlandicus*, has a circum-Arctic distribution and only one slightly later spawning period was indicated. But due to low sample size, those conclusions need to be regarded with care. *Serripes groenlandicus* larvae had the most pronounced response to seasonality, with the shortest presence in the water column, which might be an adaptation to the highly seasonal Arctic environment.

The feeding experiments gave limited results, since the experimental set-up needs some improvements. Still, they indicated that Cirripedia nauplii on their own are not capable of controlling the phytoplankton biomass during their mass occurrences in spring, as had been suggested earlier. But further experiments are recommended, since their trophic role in the food-web is far from clear. Our investigation suggests that benthic invertebrate larvae play a significant role in the pelagic ecosystems in Arctic coastal regions, linking the pelagic and benthic realms. The different reproductive strategies of benthic invertebrates with planktonic larvae are discussed and some speculations about potential changes in a warming Arctic climate are made.

List of papers

Paper I

E.I. Stübner, J.E. Søreide, M. Reigstad, M. Marquardt, K. Blachowiak-Samolyk 2016 “Year-round meroplankton dynamics in high-Arctic Svalbard”, *Journal of Plankton Research* 38 (3): 522-536

Paper II

M. Bradner, E.I. Stübner, A.J. Reed, T.M. Gabrielsen, S. Thatje 2016 “Seasonality of bivalve larvae within a high Arctic fjord”, *Polar Biology*: doi:10.1007/s00300-016-1950-x

Paper III

E.I. Stübner, P. Renaud, J. Berge, T.M. Gabrielsen, M. Reigstad, S. Kwasniewski, R. Boehnke, K. Blachowiak-Samolyk, J.E. Søreide “Timing of meroplankton in different Arctic primary production regimes”, manuscript in preparation for submission

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1. Introduction

The life cycle of most marine invertebrates – pelagic as well as benthic - includes a larval stage, which differs morphological, in life-style and food requirements from the adult organisms (B. K. Hall and Wake, 1999; Young, Sewell and Rice, 2002). This is called indirect reproduction or indirect development. Larvae found in the water column usually belong to the plankton, mainly drifting in the water column with limited swimming ability. The term meroplankton refers to organisms, which spend only a certain part of their lives drifting as plankton through the water column, before they either settle at the sea floor or become part of the actively swimming nekton. The majority of meroplankton are planktonic larvae of marine benthic invertebrates. For the purpose of this thesis, the term meroplankton will be used when referring collectively to the investigated planktonic larvae of marine benthic invertebrates.

Historically, planktonic larvae of marine benthic invertebrates are considered to be of limited importance in the Arctic pelagic systems since the number of benthic organisms having planktonic larvae has been considered to be low at high latitudes ("Thorson's rule"; Thorson, 1936, 1950; Mileikovsky, 1971). They mainly occur during certain times of the year and usually have relatively short residence times in the water column (Thorson, 1950). Although they can be released in enormous numbers, they are dispersed quickly and mortality is assumed to be high (R. Scheltema, 1986; Giese and Kanatani, 1987; Morgan, 1995a). Coupled with a size that usually escapes the standard 180µm meshed nets and irregular sampling usual for Arctic seas, meroplankton is likely underestimated in planktonic surveys. Difficulties with identification are also in issue, since larvae of different species can be very similar, with few morphological distinct features. For some larval types, it can even be difficult to decide which phylum they belong to. All those factors combined make this temporary group of plankton particularly understudied in the Arctic marine environment.

Thorson's rule has been challenged and revised (Pearse, 1994; Marshall *et al.*, 2012) since by now, many marine benthic invertebrate species with planktonic larvae are known from both the Arctic (Norden Andersen, 1984; Fetzer and Arntz, 2008) and especially the Antarctic (Stanwell-Smith *et al.*, 1999; Sewell and Jury, 2011). There are regular reports of high numbers of meroplankton from Arctic coastal areas (Smidt, 1979; Coyle, Chavtur and Pinchuk, 1996; Walkusz *et al.*, 2009), but there are very few year-round studies in the Arctic with frequent sampling, and species identification is difficult. We therefore lack information to verify and assess their importance and role within the Arctic marine ecosystem. Simply due to their high numbers, they are likely to impact the pelagic system both as grazers, competitors and prey items. They are also important for benthic community ecology (Morgan, 2001; Marshall and Morgan, 2011). Several studies have noted changes in benthic communities due to a changing climate in the Svalbard region (Berge *et al.*, 2005; Kortsch *et al.*, 2012). Dispersal takes place during the larval phase, when mortality is highest. Therefore, studies of meroplankton are important to increase our knowledge on benthic reproduction patterns and strategies in Arctic marine coastal environments.

To evaluate changes over time, which becomes more and more pressing in the light of a changing climate, we need to increase our knowledge on seasonal fluctuations and normal year-to-year variations. Comparing samples between years is only meaningful, if samples were taken at equivalent points within the yearly cycle, which are determined by a variety of environmental and biological factors and can be shifted in time between years (Highfield *et al.*, 2010; Arendt *et al.*, 2013; Philippart *et al.*, 2014). This is especially important for organisms like meroplankton, which exhibit extreme seasonal variation with short periods of peak-abundances. Besides the deep ocean, the Arctic marine environment is one of the least known systems on our planet. Seasonal variations like variations in sea ice cover, primary production and following secondary production are especially strong in high-Arctic marine systems, driven by the extreme changes in light climate between polar night and polar day. The harsh and cold climate and remoteness makes regular observations and sampling difficult and logistically challenging – especially during winter and spring. As a result, we still lack important knowledge on the seasonal variations in the Arctic marine environment. This limits our ability to differentiate between natural seasonal variations and actual changes, which in turn inhibit valid future predications.

My interest was sparked while observing incredible numbers of cirripede larvae during a sampling campaign in an ice covered fjord in Svalbard during spring. Some of the immediate questions were: Is this normal? Which other larval groups have this type of mass-occurrence? How much do they contribute to the total zooplankton number throughout the year? Are they an important component in the Arctic planktonic system? I found limited updated information in the literature and my questions largely remained, resulting in the presented PhD-thesis. In the light of climate change and effects on Arctic marine ecosystems, this thesis was aimed at gathering basic knowledge on seasonal variation of meroplankton, a diverse and occasionally very numerous group of short term pelagic inhabitants, and re-evaluating their importance within the Arctic pelagic system.

2. Objectives

The main objective of this PhD project was to increase our knowledge on meroplankton dynamics and their ecological role in high-Arctic coastal marine ecosystems, moving a step towards closing our vast knowledge gap about those organisms in Arctic areas. More precisely the following topics and research questions were addressed:

- a) **Duration and contribution** to the zooplankton community: When and in what numbers do planktonic larvae of marine invertebrates occur in the plankton and how much do they contribute to the total zooplankton abundance and biomass? What is the importance of meroplankton in the zooplankton of Arctic coastal regions and fjord environments?
- b) **Timing**: What are the **driving environmental forces** behind the observed **seasonal variations** in meroplankton abundances and composition (Paper I & II) and can those be generalized (Paper III)?
- c) **Species identification**: To which degree can a combined approach of morphological and molecular tools help us resolve the meroplanktonic diversity better? How do single species contribute to the general pattern observed in the most abundant group Bivalvia and what reproductive timing do we find in species of this group (Paper II)?
- d) What is the estimated **feeding impact** of meroplankton organisms and can they exert top-down control on their prey during times of mass occurrences (synthesis, example cirripede nauplii)?

3. Background

3.1. Short historical background

Marine benthic invertebrate larvae were first recognized as such around the 18th century. Some of the oldest drawings of marine invertebrate larvae picture oyster larvae (Brach, 1689) and polychaete larvae, barnacle cypris and crustacean megalopa and zoeas observed by Martinus Slabber (Slabber, 1778; fig. 1). Many larval forms were described thereafter and their importance and connection with the adult organisms recognized, even though they were not always correctly classified in the beginning (e.g. Thomson, 1828; Müller, 1846, 1855). The discovery of larvae as part of an indirect development helped answer many zoological and evolutionary questions and many important ecological ideas were proposed in the 19th century (discussed and summarized in Young, 1990; Young, Sewell and Rice, 2002). In the early 20th century, research focused on questions about larval feeding, swimming and orientation, as well as comparative embryology and mortality (Young, 1990). The definition of larvae is not straight forward because of the great diversity in invertebrate larval forms, with many degrees of discreet or gradual transformation, as well as differences between structural, ecological and morphogenetic definitions (Brian K. Hall and Wake, 1999). A general and relative simple definition sees larvae as one or several consecutive postembryonic stages, which differ morphologically from the adult organisms and/or inhabit a different habitat than the adults (structural definition) and need to go through metamorphosis to become or be replaced by an adult (parts of the morphogenetic definition) (Brian K. Hall and Wake, 1999). With Thorson's work in the 20th century summarizing previous work and adding considerable amounts of new data (Thorson, 1936, 1946, 1950), the term "larval ecology" started to exist (Young, 1990). The ecological definition sees the larvae as a free-living life-history stage and as an agent for dispersion and does not include life stages that show morphological structures of larvae, but are not released like e.g. encapsulated larvae (Brian K. Hall and Wake, 1999). The pelagic larvae of marine invertebrates investigated in this thesis have a profound different life-style and food requirements than the benthic adult organisms.



Figure 2: Early drawing of a *Semibalanus balanoides* nauplii and a *Carcinus maenas* megalopa, P.M Brassier in M. Slabber (1778), extracted from plate 06 and 18. Licensed under a Creative Commons Attribution-Noncommercial-Share Alike 4.0 License

Thorson's work on Greenland (Thorson, 1936) combining benthic and planktonic surveys to gain knowledge about reproductive modes and seasonality in benthic species, together with Mileikovsky's extensive studies on spawning ecology and dispersal in the White Sea and Barents Sea (e.g. Mileikovsky, 1965, 1966, 1968, 1970), today still represent some of the most detailed and in-depth ecological studies on benthic invertebrate larvae undertaken in the Arctic. According to Thorson (Thorson, 1936, 1950) and later also Mileikovsky (Mileikovsky, 1971), pelagic invertebrate larvae are of limited importance to benthic invertebrate reproduction in colder climates, even though they recognized that they can occur in high numbers at times. Mileikovsky (Mileikovsky, 1971) coined the term "Thorson's rule", which predicts that while pelagic development dominates in general, it is rare in polar areas, becoming less important at higher latitudes while direct development (without larval stage, offspring resemble miniature-adults), vivipary (giving birth to developed young) or demersal (non-planktonic, free-living larvae) development becomes more frequent. Today, it is recognized that Thorson's rule is only valid with modification – non-feeding larvae are predominant at the poles and deep sea and feeding larvae in warm and temperate waters, but this is not uniform for all groups (Clarke, 1992; Pearse, 1994; Pearse and Lockhart, 2004). There is evidence that temperature and ocean productivity are the driving forces for gradients in reproductive modes (O'Connor *et al.*, 2007; Marshall *et al.*, 2012). It has also been shown, that environmental conditions can influence the larval type produced by the adult organisms (Krug, Gordon and Romero, 2012) or the breeding seasonality (Mileikovsky, 1971; Von Oertzen, 1972).

Mileikovsky showed that short term and seasonal variation are considerable (Mileikovsky, 1970) and that seasonal dynamics are shaped by differences in spawning periods between species. He related spawning periods of species with certain zoogeographical origin to water temperatures. Several seasonal studies from the Russian Arctic and sub-Arctic (Beer, 2000; Günther and Fedyaikov, 2000; Kulikova, Solokhina and Samatov, 2000), Greenland waters (Thorson, 1936; Norden Andersen, 1984), Canadian Arctic (Grainger, 1959) as well as Alaska (Coyle and Paul, 1990) described the strong seasonality of meroplanktonic organisms, with high abundances commonly occurring during late spring and summer. Others studies describe more spatial pattern within the meroplankton community found in Arctic waters and demonstrate the importance of hydrological regimes for larval occurrence (Clough *et al.*, 1997; Schlüter and Rachor, 2001; Fetzner, 2003). Several studies have been undertaken by Russian scientists, but those are largely not available to non-Russian speakers. Nevertheless, the information we have on meroplankton in Arctic regions is still scarce and insufficient compared to other plankton like for instance larger copepods, especially those of the genus *Calanus*.

3.2. Larval ecology and connections with benthic invertebrate ecology

Pelagic larvae are an important stage in the reproductive cycle and life history of many marine invertebrates. Indirect development is found in most species of 23 of in total 31 marine phyla

(Young, Sewell and Rice, 2002). This means most of the marine animals do develop indirectly. The larval stage is only one part of the reproductive cycle. A reproductive cycle in marine invertebrates with indirect development includes: embryonic development, a larval stage, metamorphosis to a juvenile stage, growth of the juvenile to an adult, storage of nutrients in the gonads, activation of gonads and multiplication of gametogenic cells, activation of gametogenesis (sexual maturity), maturation of gametes, potential behaviour changes and then – finally - spawning and fertilization (Giese and Kanatani, 1987). Between closely related species, very different types of development may occur (Thorson, 1950; Levin and Bridges, 1995) and in a few species both indirect and direct development can occur (Levin and Bridges, 1995; Chia, Gibson and Qian, 1996). Larval types can be divided according to nutritional mode, development type, dispersal potential and morphogenesis (Levin and Bridges, 1995). The main types of nutrition are for example feeding (heterotrophy) or non-feeding, depending on nutrients supplied by the mother organism (lecitotrophy) or mixed types or variants of those (Levin and Bridges, 1995). Benthic invertebrates with planktonic larvae either release gametes which are fertilized in the water column, or might release already developed larvae into the water column (Giese and Kanatani, 1987). Depending on species and environmental conditions, vast amounts of gametes or larvae can be released into the water column during spawning (Giese and Kanatani, 1987), but it is generally assumed that mortality of embryos and larvae is high (Thorson, 1950; Morgan, 1995a). Factors like environmental stressors (temperature and salinity changes and extremes, UV, pollutants and food limitation) are potential causes of mortality, but predation is likely the most important one (reviewed in e.g. Thorson, 1950; Morgan, 1995). Also transportation by water current to unsuitable locations can challenge survival, but larval behaviour can influence transportation and dispersal and reduce risks, e.g. through vertical movements in and out of currents or layers (Young, 1995; Pineda, Hare and Sponaugle, 2007; Shanks, 2009).

It has become clear, that understanding reproductive modes and larval ecology is necessary to understand population ecology of benthic species and communities (Morgan, 2001; Marshall and Morgan, 2011). For example, it seems that populations of species with planktonic larval forms show less fluctuation than populations of species without planktonic larvae (Eckert, 2003) and latent effects from conditions experienced by the larvae influence juvenile and adults even after metamorphosis and show the importance of the larval life for adult organisms (Pechenik, 2006; Marshall and Morgan, 2011). A planktonic, free living life stage enables recruitment of new individuals to populations and communities of benthic organisms, which are otherwise sedentary or have a limited action radius compared to pelagic species (Mileikovsky, 1971). Free living larval stages also make dispersion of young individuals to areas with suitable habitat possible, sometimes over very large distances (Mileikovsky, 1971; R. S. Scheltema, 1986; Fetzer, 2004). The distribution distances are dependent on their residence time in the plankton, hydrography and currents (Mileikovsky, 1971; R. Scheltema, 1986) and can allow species to extend their biogeographic range under favourable conditions (Berge *et al.*, 2005). The duration time of larvae in the plankton can vary greatly from hours to months depending on taxonomic group, species and environmental conditions (Thorson, 1950; R. Scheltema, 1986). Larvae may delay metamorphosis if they do not encounter a

suitable habitat, which can be recognized by a variety of cues, increasing chances of survival for the post settlement stage (Pechenik, 1990; Steinberg, De Nys and Kjelleberger, 2002).

3.3. Seasonal cycles

Each step in the reproductive cycle, starting from the storage of nutrients in gonads, needs activation – either through environmental conditions or internal mechanisms and is part of the breeding season (Giese, 1959; Giese and Kanatani, 1987). This means, that many conditions have to be met, before the adult organism is able to spawn and larvae can be observed (Giese, 1959). Thorson, working in Greenland waters (Thorson, 1936) recognized that many species reproduce in times of high primary productivity, namely in summer, where also surface water temperatures are higher. Even though he recognized the potential advantage for larvae feeding on planktonic food sources (planktotrophic) to occur in times of high primary production, he also saw temperature as a main factor for timing.

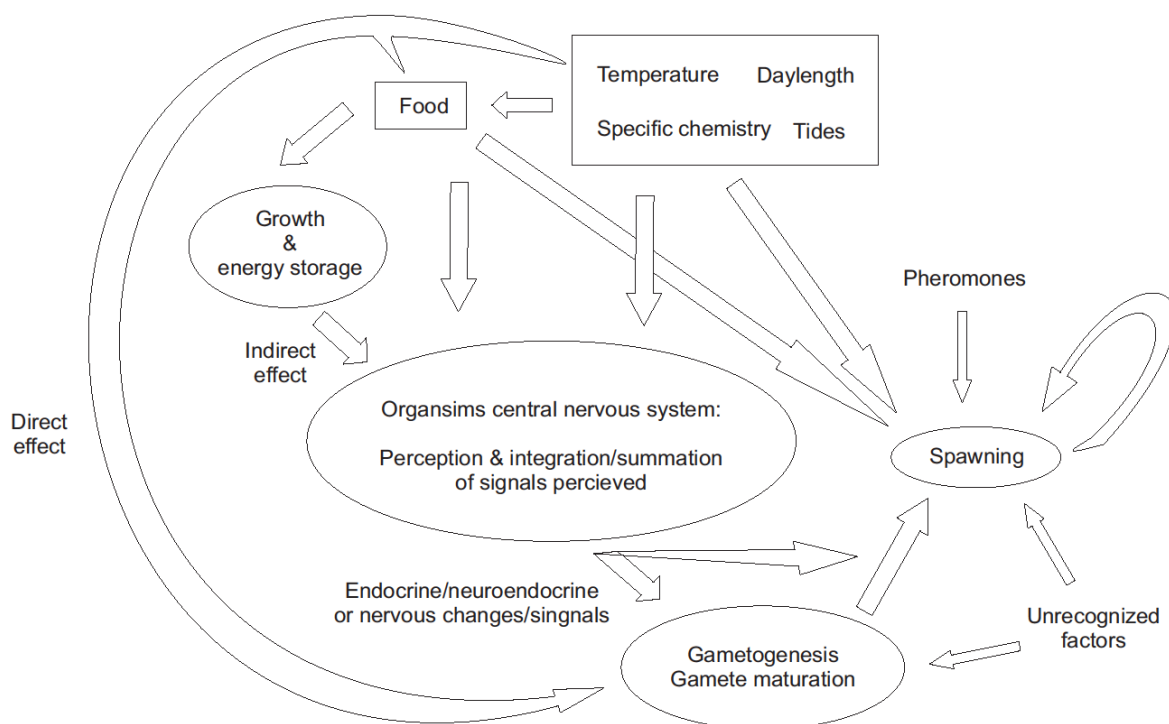


Figure 2: "Chain of control" for externally synchronized reproductive cycles with multiple external factors leading to a spawning event (Adapted after Giese and Kanatani, 1987 and Barnes *et al.*, 2009).

Many factors have been mentioned in literature to trigger spawning, and there are differences between animal groups, but also among species within the same group. External factors

include lunar cycles, light intensity or light-dark cycles (day light regime), temperature (either changes or above or below a certain threshold), tidal periodicity, presence of planktotrophic food, and chemical interactions as well as combinations of factors all seem to play a role in coordinating spawning in marine benthic invertebrates (Orton, 1920; Himmelman, 1975; Giese and Kanatani, 1987; Starr, Himmelman and Therriault, 1990; Morgan, 1995b; Olive, 1995). Besides external triggering factors, endocrine signals like hormones or gametes can help to coordinate spawning events, increasing the probability of fertilization (Watson, Williams and Bentley, 2000; Watson *et al.*, 2003). In general, a complex combination of an endogenous internal clock and external cues seems to determine the annual reproductive cycles (Giese and Kanatani, 1987; Barnes *et al.*, 2009; fig 2).

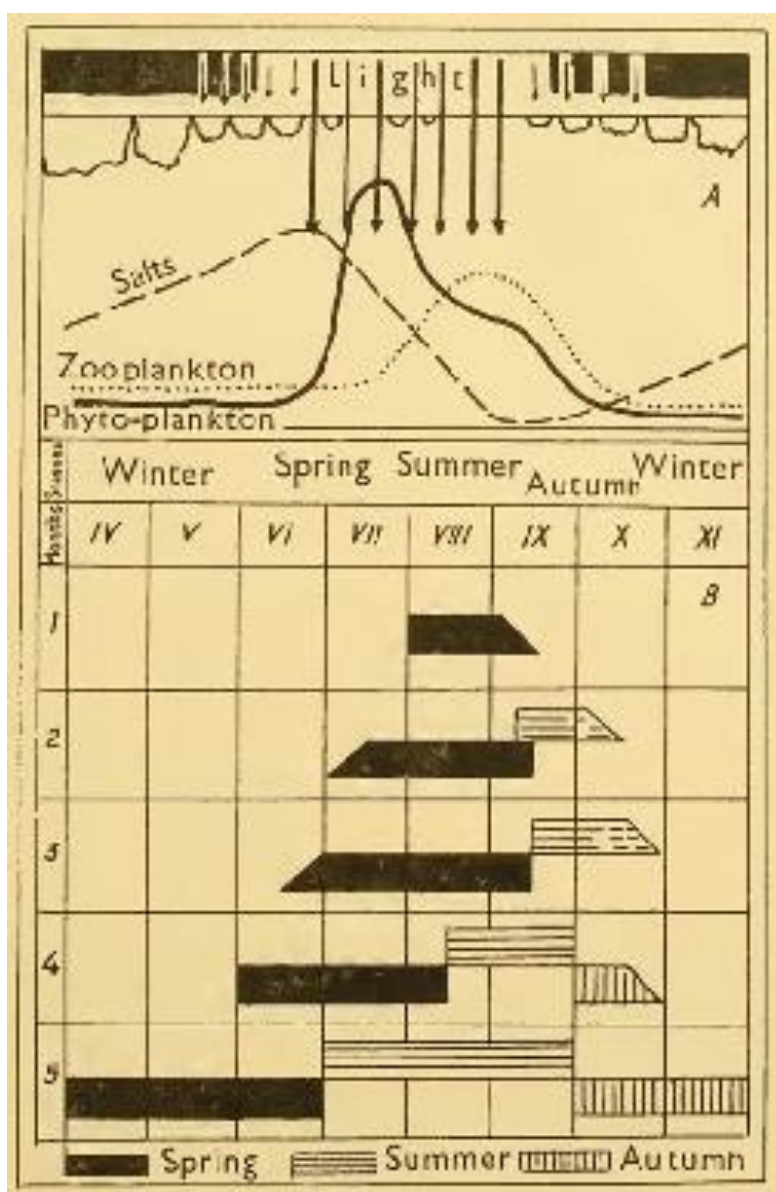


Figure 3: Seasonality of the plankton in different parts of the Arctic Seas. Taken from (Zenkevitch, 1963). 1) Circumpolar Arctic Ocean, 2) Central Kara Sea, 3) Laptev Sea, 4) Northern Barents Sea, 5) Southwestern Barents Sea.

Marine invertebrates might either spawn 1) partial, releasing a portion of gametes at several consecutive times, 2) continuously, releasing small amounts over a prolonged time period, or 3) complete in a single outburst. Spawning might also occur several times throughout a breeding season if conditions are favourable (Giese and Kanatani, 1987). While species in tropical waters commonly breed continuously with some more intense periods, organisms living in seasonal environments normally show a seasonal breeding behaviour (Giese, 1959). Coordinated mass-spawning events, where many species release gametes during a few days have been observed in many marine habitats (Barnes *et al.*, 2009). Several species with a wide biogeographic distribution seem to be able to adapt their breeding behaviour to local conditions, with compressed spawning periods in extreme seasonal environments like the Arctic (Mileikovsky, 1970). In Arctic areas, the strong difference in light regime from 24 hours of darkness during the polar night and 24 hours of light during the polar day lead to extreme differences in the primary productive regime (Zenkevitch, 1963; fig 3). Even though the polar night is not bare of biological activity (Berge *et al.*, 2015; Vader *et al.*, 2015), most organisms exhibit highest activity and occur in far greater abundances during the lighter parts of the year. The term season following calendar dates might hold limited information in the Arctic, and it might be better to talk about biological seasons. The exact seasonal timing varies throughout the Arctic, depending on latitude and local sea ice conditions (Zenkevitch, 1963; illustrated in fig. 3), and in the following, seasons always refers to biological seasons. It has been suggested that primary productivity has higher importance in timing of marine benthic invertebrate reproduction in the extremely seasonal Arctic environment than elsewhere (Mileikovsky 1970).

3.4. Trophic linkages

Many planktonic larvae of marine benthic invertebrates are now assumed to be feeding in some way and at some point during their time in the plankton and many are able to switch between feeding modes and type of nutrition (Boidron-Métairon, 1995; Levin and Bridges, 1995). In general, larvae feed on a wide variety of food sources – both with respect to size as well type, and requirements can change throughout larval life (Boidron-Métairon, 1995). The main classical division between larval types has been between non-feeding and feeding larvae. Non-feeding larvae are dependent on a nutritional supply provided by their mothers through the egg (lecitotroph), while feeding larvae feed on other planktonic organisms or material (planktotrophic) (Thorson, 1950; Mileikovsky, 1971). While later research showed a considerable wider variety, including mixed modes and variations, osmotrophy using dissolved organic matter (DOM) and even some forms of partial autotrophy using endosymbiotic algae or bacteria (Levin and Bridges, 1995). This makes potential trophic interaction with the rest of the planktonic community quite complex. The majority of zooplankton are omnivores, with a preference for either carnivory or herbivory and are able to ingest both phytoplankton and protozoa (Paffenhofer, 1988). Planktotrophy is found in larvae of many if not most marine invertebrate phyla – both benthic and pelagic (Strathmann, 1987; Levin and Bridges, 1995). Several larvae of e.g. Echinodermata, Polychaeta (Spionidae),

Mollusca and Cirripedia seem to prefer phytoplankton as their main food source (Turner *et al.*, 2001; Vargas, Manriquez and Navarrete, 2006; Pasternak *et al.*, 2008) and most larvae reared in laboratory studies are fed and survive on a combination of phytoplankton, DOM and bacteria (Boidron-Métairon, 1995). For many, DOM as well as bacteria seems to be a valuable nutritional addition and part of larval food (Boidron-Métairon, 1995) and *Mytilus edulis* larvae can actually compete effectively with bacteria for DOM (Manahan and Richardson, 1983). It is not clear, which influence meroplankton has on potential prey organisms in nature or as competitors for resources. Impact on prey is believed to be negligible, because of generally low clearance rates and low abundances (Strathman 1996). This seems questionable, since high abundances and mass occurrences are regularly encountered (Zenkevitch, 1963; Smidt, 1979; paper I), and at least for Arctic areas, good clearance rate estimates are not available.

Meroplankton can also serve as prey. A wide range of predators on meroplanktonic larvae are known, like fish larvae and smaller planktivorous fish, Cnidaria (Hydromedusae and Scyphomedusae), Ctenophora, Siphonophora, Chaetognatha, Copepoda, Euphausiacea, shrimps, hyperiid amphipods and predatory meroplanktonic larvae as well as adult benthic organisms (Young and Chia, 1987; Morgan, 1995a). Among them, the gelatinous predators and fish larvae/planktivorous fish are some of the most important ones (Morgan, 1995a). Since many planktonic predators are opportunistic, they likely utilize meroplankton organisms during times of high abundances, that means seasonally, and depending on encounter rates (Young and Chia, 1987). In some studies, low predation rates on meroplanktonic larvae have been observed, but this varies with larval type and background plankton affects predation rates (Johnson, 1998; Johnson and Shanks, 2003). Other studies found selective feeding on larvae of benthic invertebrates by some predators but not others (Short, Metaxas and Daigle, 2013). Predators also exhibit size-preferences and thus different larval stages likely experience different predation pressure (Allen, 2008). Predation rates on meroplanktonic larvae by benthic organisms is largely unknown and difficult to discern (Young and Chia, 1987), but seems to be considerably larger than by planktonic predators (Allen and McAlister, 2007). Also benthic organisms might show differential predation on incoming larvae (Cowden, Young and Chia, 1984; Mercier, Doncaster and Hamel, 2013). All in all, trophic connections of meroplankton organisms with either the rest of the planktonic community or the benthos are not well understood but likely to be complex.

4. Approach

A combination of extensive seasonal field sampling, feeding experiments and genetic bar-coding was applied to investigate seasonal variation (Paper I & III) and diversity (mainly Paper II) of meroplankton, and potential trophic implications (experimental results only presented in this synthesis). Fjord-environments were chosen for sampling, since they represent a coastal environment where meroplankton abundance can be high and are more readily accessible year-round than more exposed waters outside the fjords. Field activities for this study were part of the collaborative Adventfjorden field campaign and several other projects (MicroFun, MeroSeason, CLEOPATRA I & II, CIRCA). Environmental and abundance data from four years and three fjords are used in this PhD work, representing 5 one-year seasonal series: 2007 in Rijpfjorden, 2011 in Billefjorden, 2012 in Adventfjorden and 2013 in both Adventfjorden and Billefjorden. In Adventfjorden, in close vicinity to Longyearbyen and thus easily accessible, sampling was conducted on a roughly bi-weekly interval. The other fjords, where access is more restricted due to remoteness, were sampled on a roughly monthly basis.

4.1. Study Area

For the present study, three fjords in Svalbard Archipelago; Adventfjorden, Billefjorden and Rijpfjorden, with different primary production regimes due to differences in sea ice cover and following underwater light climate were chosen (fig. 4). Svalbard Archipelago with the two main islands Spitsbergen and Nordaustlandet is a group of islands located between 74° N and 81° N and 10° E and 35° E, bordering the Barents Sea to the South and East, the Fram Strait to the West and the Arctic ocean to the North. All three locations experience a high Arctic light climate with up to 4 month of polar night (sun below the horizon) and midnight sun. Adventfjorden (paper I-III) and Billefjorden (paper III) are small side-fjords of Spitsbergens largest fjord system, Isfjorden. Isfjorden is an open fjord, opening westwards and influenced by warmer and more saline Atlantic water advected into the fjord from the West Spitsbergen Current flowing northwards along the shelf break (Berge *et al.*, 2005; Nilsen *et al.*, 2008).

Adventfjorden is NW-SE directed and only around 7 km long and 4 km wide. Its maximum depth is around 100 m close to the mouth and several rivers discard freshwater into it. Adventfjorden is lacking a sill and is influenced by Atlantic water in form of transformed Atlantic water and advective processes, as well as local processes due to river run-off and atmospheric cooling and warming (Leikvin and Evenset, 2009). The time-series Isfjorden-Adventfjorden sampling station (IsA, 78.261°N, 15.535°E) is located near the mouth of Adventfjorden with a bottom depth of ~80 m. In recent years, sub-Arctic hydrographic conditions have been the norm in Adventfjorden, with no sea-ice formation in winter (Wiedmann *et al.*, 2016). Commonly a spring bloom forms in April/ early May with potentially a small autumn bloom later in the year (pers. obs.). Billefjorden is also part of the

Isfjorden-system, located far inside the main-fjord to the northeast. It has an outer (maximum depth ~230 m) and an inner (maximum depth ~190 m) basin. An outer (ca. 70 m deep) and inner (ca. 45 m deep) sill restrict water exchange with the main fjord system and local water masses are predominant (Nilsen *et al.*, 2008) and mostly influenced by internal processes (Arnkværn, Daase and Eiane, 2005). Billefjorden is usually ice-covered 3 to 6 month during winter and spring. During summer and autumn, sediment loaded melt water from the big Nordeskiöld-glacier runs into the fjord. The sampling station in Billefjorden, Adolfbukta (BAB, 78.662°N, 16.739°E), is ~190 m deep within the inner basin.

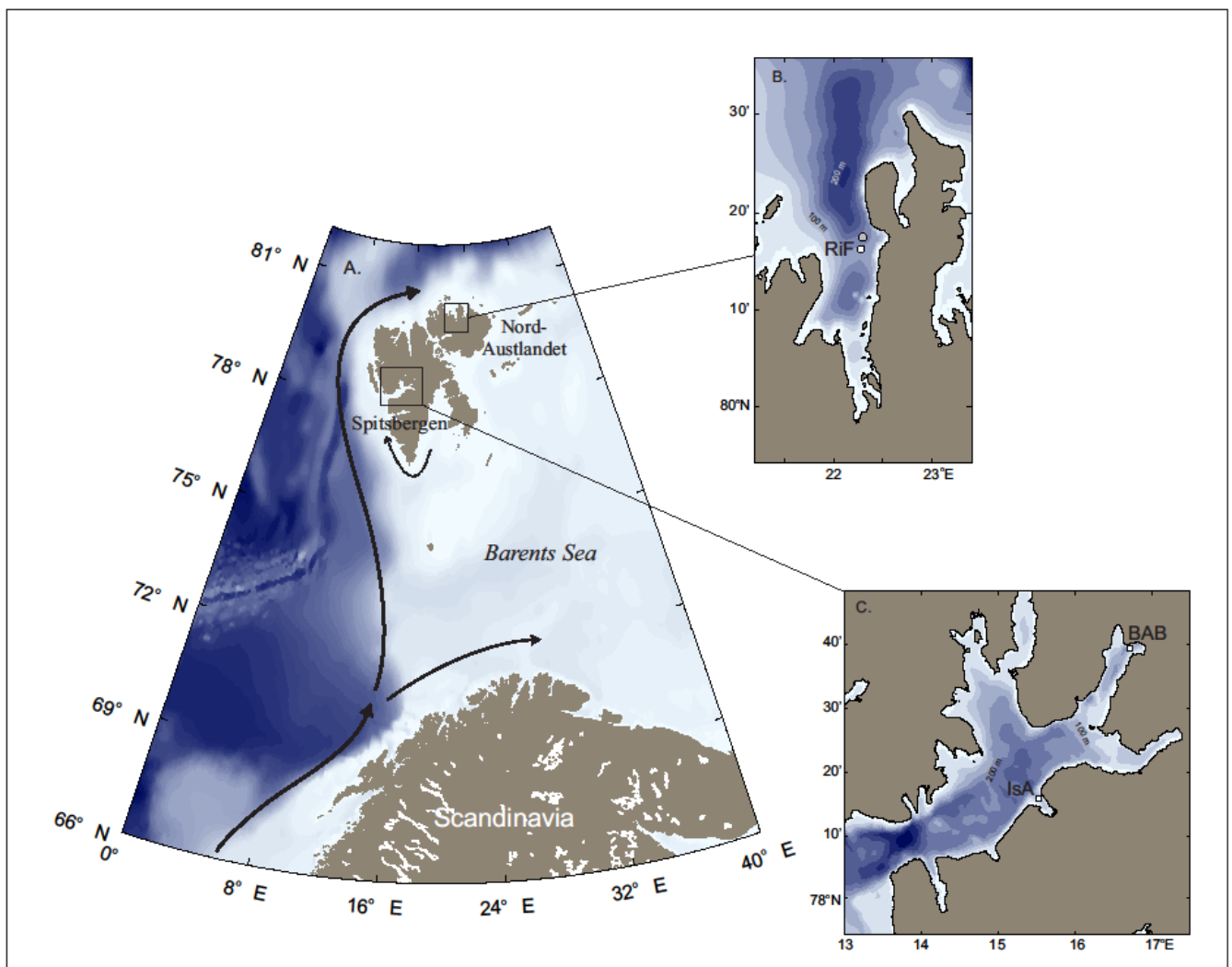


Figure 4: Map of the sampling area showing Svalbard archipelago and its location relative to the Norwegian mainland, as well as the sampled fjords Rijpfjorden (right, above) and Adventfjorden and Billefjorden within the Isfjorden system (right, below). Sampling stations are indicated by white squares, the mooring placement in Rijpfjorden as grey square. Arrows indicate movements of main current systems.

Rijpfjorden (paper III), on Nordaustlandet, opens to the North onto a broad shallow shelf that is in direct contact with the Arctic Ocean (Søreide *et al.*, 2010). The maximum depth of the fjord is around 240m. Of the fjords investigated, this is the most Arctic one, with ice cover up to 9 month a year and predominantly Arctic water masses (Ambrose *et al.*, 2006; Søreide *et al.*, 2010). Due to logistical challenges, sampling was undertaken at slightly different stations throughout the sampling period (collectively termed RiF: BS 80.219° N, 22.372° E and SH 80.265° N, 22.29° E), with the main station (SH) having a bottom depth of ~145m.

4.2. Methods

4.2.1. Environmental parameters

Physical background data in this study has been collected in collaboration with (Adventfjorden & Billefjorden) or primarily for other projects (Rijpfjorden) and has also been published in connection with other studies (Berge *et al.*, 2009; Søreide *et al.*, 2010; Leu *et al.*, 2011; Weydmann *et al.*, 2013) (Marquardt *et al.*, 2016; Wiedmann *et al.*, 2016; Boissonnot *et al.*, submitted). In Adventfjorden, several parameters like nutrients were measured additionally to the ones used in this study, but only the parameters likely to be relevant for the timing of meroplankton occurrence in the water column were used here. Those were temperature, salinity, in-situ fluorescence, chlorophyll *a*, day-length, Photosynthetic active radiation (PAR) and sea ice cover. Temperature, salinity and fluorescence were measured both with CTD casts and with data loggers and CTD's mounted on moorings (moored oceanic underwater observatory) at each station. For more details see paper I & III. Photosynthetic active radiation (PAR) was measured at the mooring. Water masses were characterized according to Nilsen et al (Nilsen *et al.*, 2008) and PAR and in-situ fluorescence were normalized between 0 and 1 from sensor voltage output. Fluorescence was used to estimate the start and peaks of phytoplankton blooms as specified in paper III. Samples for chl *a* were taken in context of several different studies and since hydrographic properties differ between stations, water samples for chl *a* measurements originated from somewhat varying depth (paper III for details). Chl *a* values were interpolated linearly with time and depth and the resulting values for each meter averaged for the upper 50 m (60 m in Adventfjorden) with the akima package in R (Akima, Petzoldt and Maechler, 2013; R Core Team, 2014). Those depth intervals were chosen to be in accordance with standard sampling depth at the different stations. To be able to look for correlations between the timing of the bloom and the occurrence of peaks in meroplankton abundance (paper III), the week of the beginning of the bloom and the peak bloom were identified for each year and fjord. Day-length as hours per day when the sun is above the horizon was calculated with the NOAA solar calculator (<http://www.esrl.noaa.gov/gmd/grad/solcalc/calcdetails.html>) and periods of sea-ice cover were determined from sea ice charts provided by the Norwegian Meteorological Institute (www.met.no).

4.2.2. Zooplankton composition and seasonality

In this study, zooplankton sampling was designed to target meroplankton specifically. While e.g. Cirripedia nauplii are comparable in size to some of the small calanoid copepods, many others are smaller organisms and easily missed with nets using the standard 180 μm mesh size (Turner, 2004; Svensen *et al.*, 2011). Therefore, a WP2 net (UNESCO, 1968) with the mesh size of 63 μm was chosen, which also retains smaller species and stages like small bivalve larvae. Benthic invertebrate larvae show high variability in numbers (Mileikovsky, 1970) and sampling regularity needs to be sufficiently high to be able to observe abundance peaks. Many seasonal studies in the Arctic are based on a few sampling dates throughout the year, due to remoteness and logistical restraints. Often, they also exclude winter sampling. At IsA, samples were collected in bi-weekly intervals year-round. With this, we hoped to both cover important changes in the meroplankton community, get an overview of the full annual cycle as well as having a realistic chance to overcome the workload of sample analysis. At BAB and RiF, which are more remote, samples were taken approximately monthly (paper III). Sampling schemes were adjusted to weather conditions and logistical constraints.

Zooplankton samples for community composition were analysed at the Institute of Oceanology, Polish Academy of Science and for most analysis, grouped into higher taxonomical units (Cirripedia, Bivalvia, Gastropoda, Polychaeta, Bryozoa, Decapoda and Nemertea). Identification of marine invertebrate larvae is very difficult, since they are small and clear morphological traits are often missing. Thus, grouping into higher taxonomical units to be able to analyse large numbers of samples is the most feasible procedure. Total and relative abundances of meroplankton, as well as biomass estimates, were used to analyse seasonal pattern and evaluate meroplankton contribution to the total zooplankton community. Since very few benthic invertebrate larvae were found below 100 m in the two deeper sampling stations, the upper 65 m (Adventfjorden) and 100 m (Billefjorden and Rjipfjorden) were used in comparisons. Organisms roughly larger than 0.5 mm were not included in the analysis since they were not representatively sampled with the sampling nets used. Both univariate (Spearman Rank correlations, ANOVA) and multivariate (ANOSIM, MANOVA, nMDS, hierarchical clustering, MRT) methods were applied in R (R Core Team, 2014) to analyse influence of the environment on the occurrence of meroplankton and timing. Both constraint and model based (MRT) and unconstrained distant based (nMDS) multivariate methods were used and compared to assure robust results.

Box 1: MRT

MRT is an effective multivariate statistical method, which finds breaks in the data along one or several gradients to partition/divide the data along those variables. It is a constraint approach related to models, that can handle multivariate environmental and response variables. The analysis can be run both on a data matrix (transformed or untransformed) as well as on a distance matrix and those can yield slightly different results. MRT is a divisive technique in contrast to e.g. RDA/CCA (De'ath, 2002). Further, the MRT does not assume any particular relationship between species abundances and environmental variables – also in contrast to e.g. RDA/CCA. This makes it valuable for datasets that do not fulfil the requirements of other multivariate methods with respect to data distributions. Resulting divisions can be analysed further with supplementary tests or compared to results from different multivariate approaches to verify and ensure robustness of results.

4.2.3. Genetic identification of bivalve larvae using DNA barcoding

The generally small size and absence of clear morphological features makes species identification of meroplankton larvae very difficult or impossible. To investigate species diversity of the most abundant group – Bivalvia – in detail, samples from IsA collected bi-weekly between December 2011 and January 2013 and preserved on ethanol were analysed combining genetic and morphological methods. Individuals sorted from the samples were categorized into larval stages (D-shape veliger, transitional veliger, eyed pediveliger) and morphological measurements were taken from photomicrographs for each individual. Besides a diagram created from photomicrographs, morphological features for D-shaped larvae were further analysed. To test if genera can be distinguished on the basis of morphometric features, a multiple analysis of variance (MANOVA) was run in R (R Core Team, 2014). A model for identification of D-shaped larvae was created using a linear discriminant analysis (hinge length, shell length and width) and the data from genetic identification.

Amplification success of gene-regions suitable for genetic barcoding varies between genes and organism groups. To decide on a suitable gene region for our Arctic marine bivalve larvae, amplification of several mitochondrial (mt) genes previously used in studies on Bivalvia (ribosomal 12S & 16S DNA, cytochrome oxidase subunit I = COI, and cytochrome b = cytB) were tested following Plazzi & Passamonti (Plazzi and Passamonti, 2010). Only amplification of the mt 16S rDNA worked satisfactorily on DNA from crushed larvae (primer designed by Palumbi, 1994). In total 110 positive larval amplicons and 26 positive adult amplicons were obtained. After purification, Sanger sequencing at either GATC Biotech AG or Centre of Ecological and Evolutionary Synthesis (CEES) at the University of Oslo, and quality control, 74 larvae sequences were available for further analysis. Very few DNA-sequences of bivalve species found around Svalbard are registered in the GenBank database. Additionally, as COI is the most commonly used barcoding gene, using the 16S-sequences reduced the amount of available sequences even more. Therefore, adult bivalve specimens were collected at several locations around Svalbard and identified using morphological traits followed by DNA-extraction and sequencing (mt 16 S rDNA). The material did far from cover all species recorded in Svalbard waters, but extended the number of available reference sequences. A searchable local database was created using both own adult Bivalve sequences and Bivalve sequences from GenBank (downloaded July 15th, 2015).

The acquired DNA sequences were manually quality screened, and contigs were built from forward and reverse sequences when both were available. Sequences from the local database and the acquired larval sequences were globally aligned followed by manual optimization of the alignment. Unique sequences were blasted against database and against the local database. When pairwise sequence identity was 99% or higher (Feng, Li and Kong, 2011) a species name was assigned. The genetic distances were evaluated applying the Kimura 2-parameter model and a neighbour-joining tree was built for verification (Tamura *et al.*, 2013). The unique sequences identified were submitted to GenBank.

Box 2: Genetic barcoding

Genetic barcoding describes the process of using a standardized short sequence of DNA to identify a species. The gene sequence used as reference is usually deposited in a major gene-databank and attached to a voucher specimen of the species. Other sequences can then be matched to the sequences available at the database. The gene chosen needs enough variability to distinguish between species. It also needs to produce a robust result under repeated sequencing and amplification. It is useful for identification of e.g. larvae of species that do not have the morphological traits to be readily identified, but depends on the availability of good reference sequences in databases. If sequences cannot be matched to existing sequences, the construction of a phylogenetic tree can help to place the specimen

4.2.4. Feeding experiments

The trophic position of planktonic larvae of marine invertebrates is largely unknown in the Arctic system. Therefore, feeding experiments on some of the most abundant groups present during the spring bloom were conducted. These experiments were run on natural food assemblages and under natural conditions, to be able to evaluate their impact in the field.

Feeding experiments were run 4 times with a total of 7 sets à 5 replicates each for cirripede nauplii and 1 set of replicates for polychaete larvae (tab. 1). The method described here, was used for the last two runs after several set-backs and methodological adjustments with earlier trial, resulting in a total of 3 replica-sets of cirripede nauplii feeding experiments usable for further analysis. Cirripedia nauplii and water for the feeding experiments were collected at IsA (expm. 1) or BAB (expm. 2) during times of high cirripede abundance. Samples were taken with a 10 L Niskin water sampler (KC Denmark) from 15 m depth and kept in the cooling room at 4°C close to in-situ temperature over night before the experiment. The following day, the sample was filtered through a 150 µm mesh, separating larger organisms including cirripede nauplii for the experiments, and other potential grazers and the sea water solution. A t0 sample was collected as 100 ml of filtered sea water, preserved on 1% (final solution) acidic lugol with formaldehyde buffered with hexamine (final concentration of 2%) for community analysis. The rest was used as natural feeding solution for the experiments. Cirripede nauplii were picked under a stereomicroscope, and 20 or 40 individuals (tab. 1) were kept in 50 ml GF/F filtered seawater for each replicate until the start of the experiment (up to 1 hour at 4°C). Since the aim was to distinguish the grazing-impact of cirripede nauplii on the system under conditions resembling natural conditions, consumer concentrations close to the natural abundances encountered in the field were used (paper I). At the same time, grazer concentrations needed to be low enough as not to risk food depletion towards the end of the 24 h experiment.

Table 1: Details about the feeding experiments conducted. Grey colour indicates experiments conducted but invalid because of technical problems. Black colour indicates experiments conducted and analysed.

Date	Taxa	Nr. of ind.	Volume [ml]	Duration [h]	Nr. of repl.	conc. Feeding solution
03.05.2012	Cirripedia	20	1000	24	5	100 %
	Cirripedia	20	1000	24	5	50 %
	Controll	0	1000	24	3	100 %
11.05.2012	Cirripedia	20	1000	25	5	100 %
	Cirripedia	40	1000	25	5	100 %
	Controll	0	1000	25	3	100 %
31.05.2012	Cirripedia	20	1250	26	5	100 %
	Cirripedia	40	1250	26	5	100 %
	Polychaeta	20	1250	26	4	100 %
	Controll	0	1250	26	3	100 %
06.06.2012	Cirripedia	20	1250	25	5	100 %
	Controll	0	1250	25	3	100 %

For each series of experimental runs, five controls with no animals were run in parallel to 5 experimental replicates with cirripede nauplii added. Acid washed glass bottles (Duran, 1250 ml) were filled with 1200 ml feeding solution. To start the experiment, the 50 ml GF/F filtered water containing the nauplii were added and if needed, filtered sea water added until the bottles were topped to avoid disturbing bubbles. To keep conditions for both cirripede nauplii as well as organisms in the feeding solution as close as possible to conditions in their natural environment, the filled bottles were attached to a rope in groups of 5 bottles and gently lowered into the sea water. They were incubated at 3m depth in the fjord for around 25hrs (tab. 1, hanging from a pier (fig. 5)). The filled bottles were just slightly negatively buoyant and moved by waves, which prohibited organisms from sinking to the bottom of the bottles. Temperature, salinity and light were recorded using HOBO Micro Station Logger attached to the setup. Experiments were stopped by sieving the water through a 150 μ m mesh to retrieve the cirripede nauplii. They were counted again and checked for their condition and preserved in ethanol. The total volume of water was measured to check for leakages. 100ml of the feeding solution both from controls and replicates (t_{end}), was preserved on 1% lugol (final concentration), and after 24h formaldehyde buffered with hexamine was added (2% final concentration).

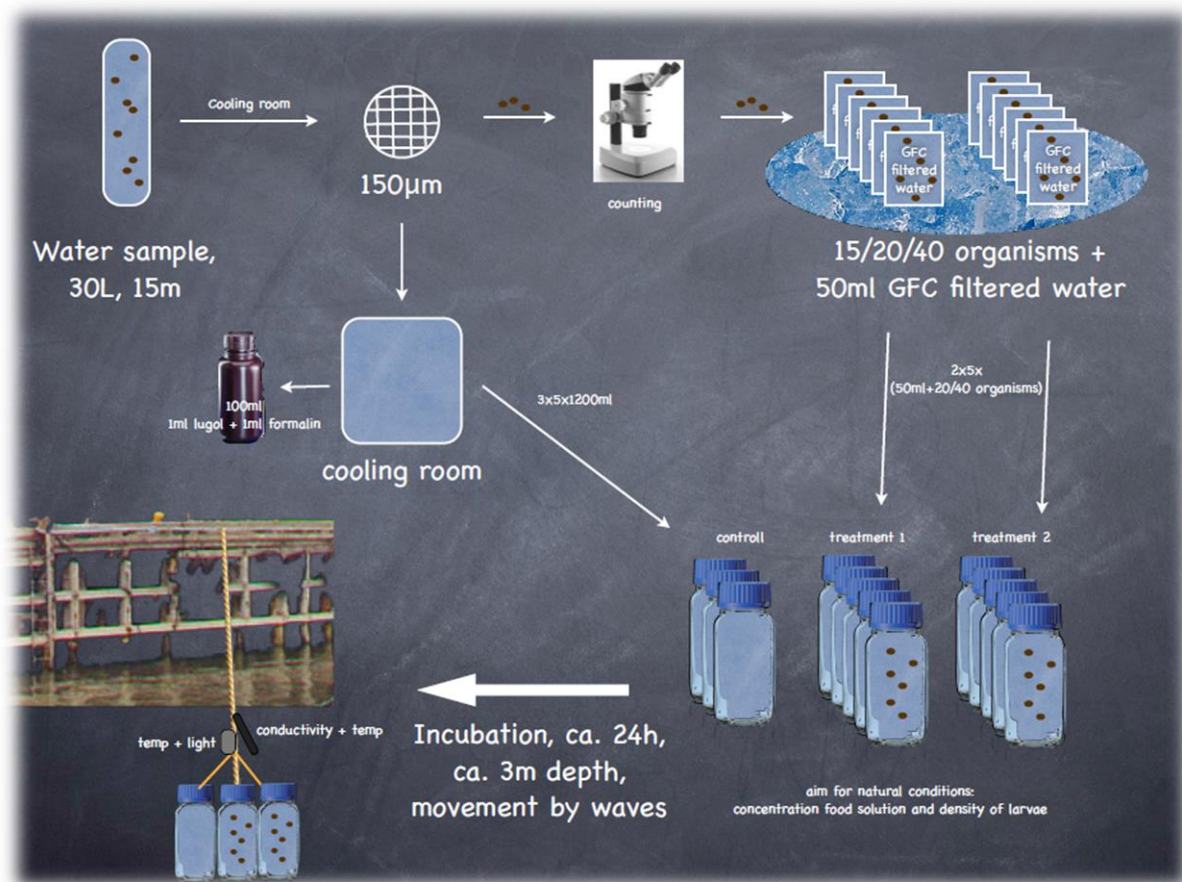


Figure 5: Schematics of the experimental set-up used for feeding experiments with preparative work-flow. Brown dots indicate experimental organisms.

Feeding-solution samples were analysed at the Institute of Oceanology, Polish Academy of Science, for community composition and abundances. The identification process followed the method from Kubiszyn *et al.* (in review) and is briefly outlined below. Protists were counted from 10-50 mL subsamples, which were placed in a settling chamber for 24h, using an inverted microscope with phase and interference contrasts (Nikon 120 Eclipse TE-300). Microplankton (>20 µm) were counted from the entire chamber under 100x magnification, while nanoplankton (3–20 µm) were counted over the length of three transverse transects at 400x magnification. Up to 50 specimens of the most numerous were counted, deciding on the number of fields counted individually. Both literature and the Nordic Microalgae web base (<http://nordicmicroalgae.org>) was used to place organisms into the trophic groups phototroph or heterotroph (Kubiszyn *et al.*, 2014). For individuals that could not be identified to species level, the classification “undetermined” was used.

A student t-test was used to test for differences between controls and experiments for each taxonomic group (class) and size class (10µm-spacing), assuming equal starting conditions in all bottles. Boxplots were used for visual evaluation. As multivariate test a one-way ANOSIM was chosen both on species level, taxonomic group level and for size classes to check for differences between experimental runs and controls. To visually evaluate differences of the community composition on species level between controls and experimental samples, an nMDS was run and plotted. A SIMPER analysis provided information about the species that contributed most to the differences between controls and treatments in each experimental run. All statistical analysis were done in R with either the base package or the vegan package (Oksanen *et al.*, 2013; R Core Team, 2014).

5. Summary of main findings

5.1. Timing of meroplankton, duration and contribution to the zooplankton community - Paper I & III

Paper I was a baseline study of meroplankton seasonality in Adventfjorden, in close vicinity to UNIS to be able to sample frequently year-round. Meroplankton organisms comprised a considerable proportion of the total number of zooplankton organisms over the year at our relatively shallow sample site within Adventfjorden. They dominated the zooplankton community during the productive time of the year both in number and biomass and entirely outnumbered other groups during peak occurrences in spring and summer. During the rest of the year, meroplankton occurred sparsely. The meroplankton assemblages could be divided into 5 significantly different seasonal communities. Winter and early spring communities were poorest, while spring and summer showed exceptionally high dominance of meroplankton and most groups occurred during this time. Autumn meroplankton composition kept an intermediate position. The most numerous groups were Cirripedia in spring, and Bivalvia in spring and summer. Bryozoans were the only taxonomic group with larvae mainly found during winter, and Gastropoda larvae were encountered throughout the year. All other groups had their main occurrence in the plankton during spring through autumn, and all groups showed multiple abundance peaks. Day length and chlorophyll *a* were the best predictors for meroplankton composition on this coarse taxonomic resolution, followed by hydrography.

To test if seasonal meroplankton patterns found at IsA in 2012 are general features, paper III extends the study from paper I both in space and time, including 2 more fjords and years. The main goal was to test if the strong positive correlation between meroplankton occurrence and primary production found at IsA is a common feature in Svalbard fjords and if the timing of the spring bloom could be steering the timing of maximum meroplankton occurrences. The positive correlation of chl *a*/fluorescence and day length with abundances of most groups was confirmed. Like in the first study, Bryozoa and Gastropoda were the exceptions. Correlations between the timing of larval abundances (measured as week of the year with maximum abundance) and the peak of the bloom, (measured as week of the year with maximum chl *a*/fluorescence values) and start of the bloom (when chl *a*/fluorescence values started to increase significantly), were tested. Peak Cirripedia larval abundance was positively correlated to the start of the bloom, while peak Bivalvia larval abundance and total meroplankton were positively correlated to the peak phytoplankton bloom. For all other groups, no significant relationships were found. Including literature data, significant positive relationships between the timing of the bloom and maximum abundances were also found for Polychaeta and Echinodermata. Only at least bi-weekly sampling showed to be sufficient to catch dynamics in the meroplankton community properly, even though monthly sampling still showed some general trends.

Marine invertebrate larvae comprised a significant part of the zooplankton community during the productive time of the year in all locations and years, even though their contribution was lower in the deeper fjords, especially below 100 m depth. Both contribution to total zooplankton numbers and which groups dominated varied. Bivalvia was the most abundant group in all fjords and years and Cirripedia (IsA, BAB) and Echinodermata (RiF) were the second most abundant groups in the respective fjords.

5.2. Species composition and seasonality of the dominating meroplanktonic Bivalvia larvae - Paper II

To investigate the meroplankton composition with higher taxonomic resolution, Bivalvia, as the most abundant group, was chosen for more in-depth investigation at the IsA sampling station in Adventfjorden. Four different species of bivalve larvae (*Hiatella arctica*, *Mya truncata*, *Mya* sp., *Serripes groenlandicus*) were successfully identified by DNA-barcoding (16S ribosomal DNA) and 11 new adult bivalve sequences (mt 16S rDNA) not previously available were added to the NCBI GenBank database. Through the combination of genetic barcoding and measurements of size relationships as morphological traits, a model for D-shaped larvae and a description for the identified larvae could be developed. Only the 2 *Mya* species could not be separated morphologically from each other. All 4 identified species occurred during the productive time of the year, and total bivalve abundance was positively correlated with chl *a* concentrations, but not hydrography. Reproductive seasonality and length of occurrence in the water column varied between species. *Hiatella arctica* and the two *Mya* species had similar seasonal dynamics with seemingly two spawning periods – one during spring and one later in summer. The occurrence of their D-shaped larvae coincided with 2 different peaks in bivalve larval abundance. *Serripes groenlandicus* appeared to have only one spawning period in early summer during a main peak in bivalve larvae. A comparison with literature data showed that the seasonality of the bivalve larvae identified in this study (paper II) varies throughout their geographic range.

5.3. Potential trophic impact of marine invertebrate larvae on the zooplankton community - Feeding experiments with Cirripedia nauplii

Results obtained from the feeding experiments did not allow calculations of clearance rates or observe prey preferences. Differences between pre-experiment samples, controls and experimental bottles with nauplii were nearly absent (experimental run 2) or not significant. The student's t-test showed no significant differences between controls and experiments for size classes or higher taxonomic groups (class) (tab. 2). Even though the results were not significant, prey-item numbers for some phytoplankton and protozoan groups and size classes

were slightly higher in the bottles with nauplii compared to the controls in experimental run 1. Also, for some prey-organism groups and size classes numbers of prey-organisms were higher after the experiments compared to pre-experimental values, both in control bottles as well as experimental bottles with cirripede nauplii. Since experiments were not run in darkness, primary production continued during the experiments and removal of other potential grazers/predators likely reduced the predation pressure on prey organisms. Besides potential flaws and set-backs in experimental set-up, a possible conclusion is that Cirripede larvae alone cannot control primary production in a late bloom scenario even during mass occurrences as suggested earlier (Kuklinski *et al.*, 2013). Their excretion might even facilitate microorganism growth (Seuthe, Rokkan Iversen and Narcy, 2010). The nMDS-analysis, using non-aggregated data (species resolution with size classes), indicated slight differences in species composition between controls and feeding experiments for the first experimental run, but not the second (fig. 6). Surprisingly, differences in species composition on non-aggregated data between experimental bottles and controls were still significant for all 3 experimental runs (ANOSIM, $p \leq 0.05$), even though they were not for data aggregated to higher taxonomic groups or size classes (ANOSIM). A SIMPER analysis identified *Phaeocystis pouchettii* (5-10 μm), and small (3-7 μm) unidentified flagellates and monoflagellates as the organisms mostly responsible for the differences between controls and treatments in all experimental runs. No further analysis was undertaken with the obtained experimental results. Using natural concentrations of both nauplii and potential prey-organisms under near-natural conditions, the results still indicate that cirripede nauplii do not exert top down control on phytoplankton during the late bloom period. During the last experimental run, several nauplii metamorphosed into the non-feeding cypris-state, which might be a reason while even less response on any taxonomic group or size class was found during experiment 2. For further experiments, parallel incubations or all incubation in the darkness and nutrients-measurements could yield better results.

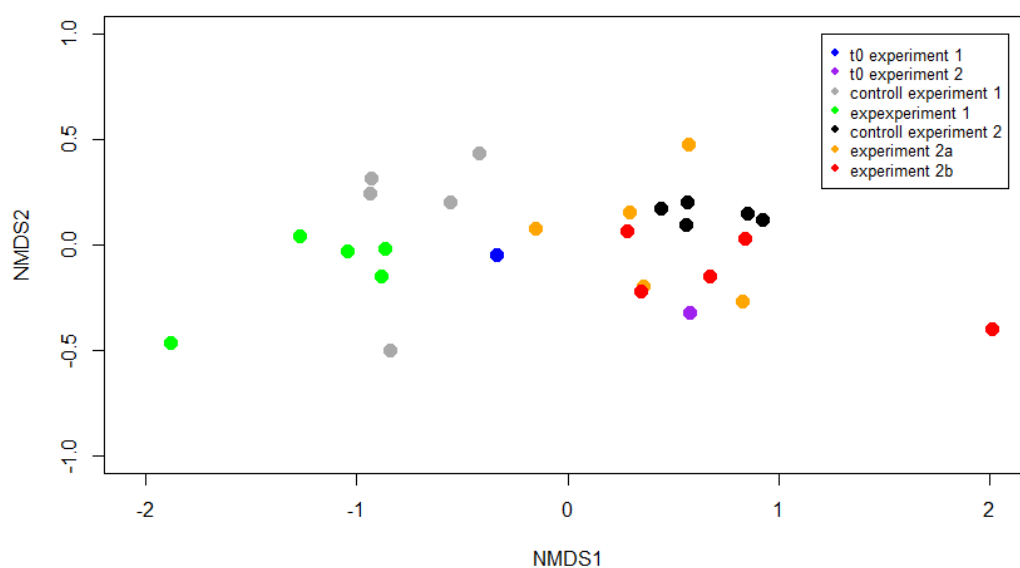


Figure 6: MDS plot for community data (species) of the feeding experiments. Stress = 0.051.

Table 2: Results from student t-test for taxon classes and size classes between experiment and control of the experiments per experimental run.

Experiment 1			Experiment 2a			Experiment 2b		
Class	p	df	Class	p	df	Class	p	df
Bacillariophyceae	0,12	4,01	Bacillariophyceae	0,18	4	Bacillariophyceae	0,18	4
Choanozoa	0,59	7,89	Choanozoa	NA	NA	Choanozoa	NA	NA
Chrysophyceae	0,31	7,36	Chrysophyceae	0,37	4	Chrysophyceae	NA	NA
Ciliophora	0,32	4,03	Ciliophora	0,73	6,51	Ciliophora	0,36	4,64
Cryptophyta	0,38	5,39	Cryptophyta	0,37	4	Cryptophyta	0,66	5,82
Dinoflagellata	0,17	4,41	Dinoflagellata	0,17	6,3	Dinoflagellata	0,73	6,88
Flagellata	0,37	4,14	Flagellata	0,34	5,32	Flagellata	0,68	5,91
Haptophyta	0,16	7,91	Haptophyta	0,33	4,68	Haptophyta	0,94	6,7
<10µm	0,24	4,66	<10µm	0,29	4,9	<10µm	0,84	5,88
10-20µm	0,45	6,58	10-20µm	0,16	7,51	10-20µm	0,91	7,03
20-30µm	0,34	6,44	20-30µm	0,36	4,02	20-30µm	0,18	5,87
30-40µm	0,21	5,94	30-40µm	0,32	4	30-40µm	0,21	4
40-50µm	0,63	6,58	40-50µm	0,59	4,17	40-50µm	0,21	7,37
50-60µm	0,11	4,00	50-60µm	0,6	5,43	50-60µm	0,49	4,65
60-70µm	0,18	4,02	60-70µm	0,97	7,98	60-70µm	0,53	7,79
70-80µm	0,37	4,00	70-80µm	0,18	4	70-80µm	0,18	4
80-90µm	0,73	6,56	80-90µm	0,37	4	80-90µm	0,37	4

6. Discussion

This thesis represents one of few Arctic year-round studies of marine benthic invertebrate larval occurrence in the plankton. From one high-frequency time series throughout a whole year in Adventfjorden (paper I), it extends the study spatially and temporally with 2 further locations and a second year of sampling in two of those testing for generality of patterns found earlier (paper III) and investigates the most abundant group Bivalvia on a more detailed taxonomic level (paper II). Even though taxonomic resolution does not match some of the other available seasonal studies (Thorson, 1936; Smidt, 1979; Norden Andersen, 1984), observations over more than one year and the large area included made it possible to test if pattern in meroplankton occurrence and timing were local or general features. For at least some of the most abundant forms, larval occurrence and with that the reproductive cycle is timed to the compressed time of primary productivity in the Arctic. The advantage for planktotrophic larvae is obvious, but also other aspect like energy input to the adult organisms for gonad maturation, conditions for settling juveniles or predation pressure could be important factors and are discussed below. Also potential advantages and disadvantages for different reproductive strategies are discussed briefly, focusing on the most abundant groups, as well as potential influences of climate change on the meroplankton community.

6.1. Seasonality and variability in meroplankton occurrence

Within year variation in meroplankton occurrence are generally very pronounced (Thorson, 1950; Coyle, Chavtur and Pinchuk, 1996; Sewell and Jury, 2011) and reflect to a large extend seasonality in reproductive cycles of the benthic adult individuals (Mileikovsky, 1970). Seasonal variations in abundance of meroplankton around Svalbard were strongly correlated to chl *a* and/or fluorescence as estimated for photosynthetically active biomass and day-length (paper I, II, III). For some groups, the timing of the bloom and the timing of main larval abundances was correlated (paper III). Even though hydrographical processes like advection and dispersion can influence larval abundances at local scales (Pedersen, Ribergaard and Simonsen, 2005), the present study showed that observed meroplankton abundances were only to a very limited extend correlated to the hydrographical parameters measured (discussed in paper I & III).

Meroplankton dynamics within the zooplankton community

Total meroplankton dynamics and seasonality following phytoplankton bloom dynamics, had strong implications for the total zooplankton composition throughout the year. Both in ice-covered fjords as well as fjords with no ice cover, a pattern with low abundances of both holoplankton and meroplankton during winter (dominance of holoplankton organisms), were followed by a faster increase in meroplankton abundances during the bloom compared to

holoplanktonic organisms, and were dominating in 2 of the 3 investigated fjords during this time. Holoplanktonic organisms reach their maximum abundances later during summer/autumn, when meroplankton abundances had already decreased (schematics shown in fig. 7).

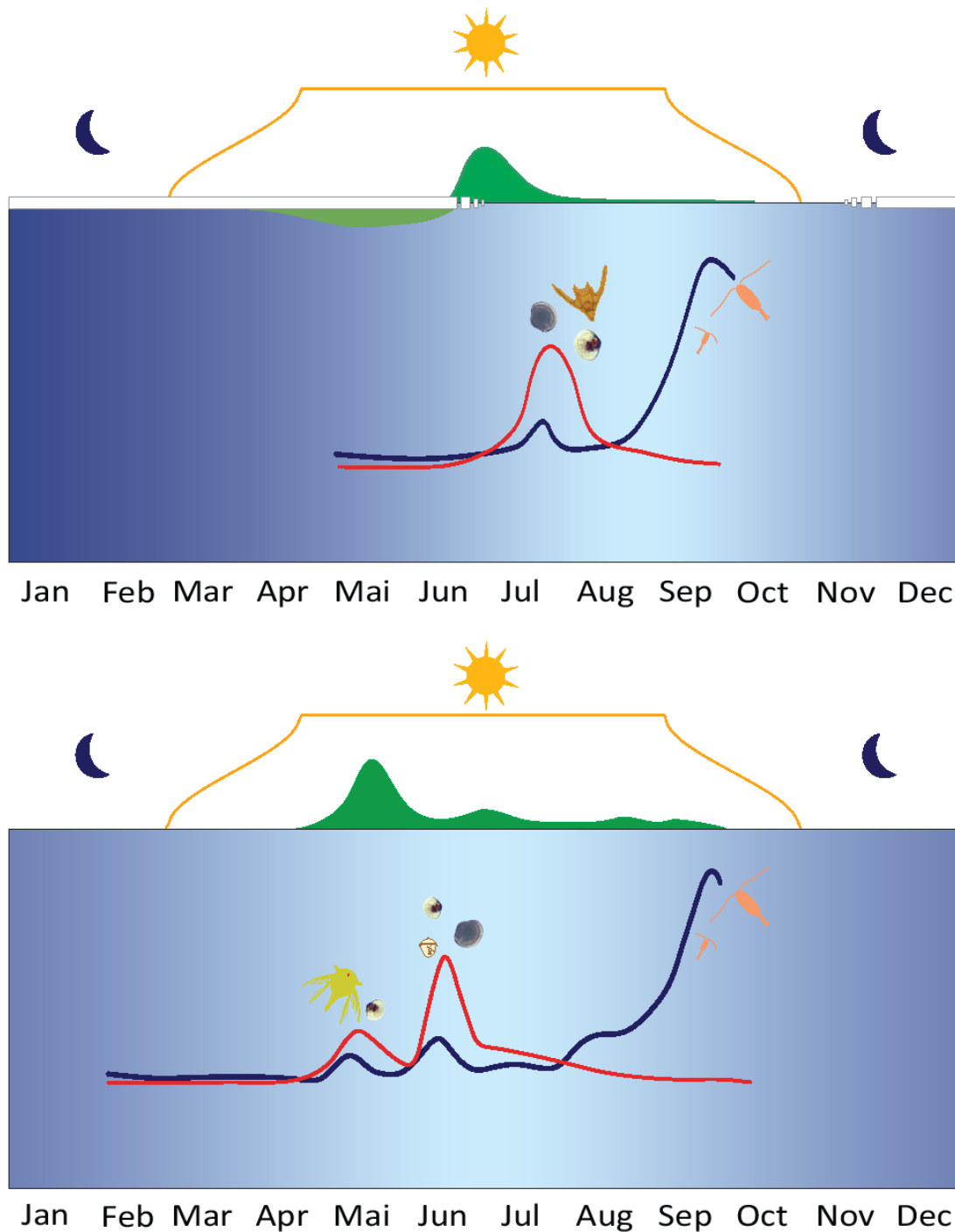


Figure 7: Simplified schematics depicting the annual succession within the plankton community for an ice-covered (upper) and ice-free (lower) fjord in the Arctic. Included are abundances of ice-algae (light-green), phytoplankton (dark-green), meroplankton (red line)

and holoplankton (blue line). Figures show the most abundant groups, dominating each abundance peak.

Comparison of the seasonal zooplankton dynamics in Svalbard waters (summarized in figure 7) with other Arctic regions shows that there are several agreements but also some differences in patterns between areas. In the Bering Sea Coyle et al. (Coyle, Chavtur and Pinchuk, 1996) found that neritic zooplankton during spring was dominated by meroplankton forms, agreeing well with the presented data. Summarized for the Russian Arctic Seas (Zenkevitch, 1963), a somewhat different seasonal development of the zooplankton community was described on the basis of biomass. During spring, when the phytoplankton blooms around the time of ice break up, many eggs and larvae of pelagic forms were found in the increasing zooplankton biomass, but no large numbers of meroplankton. Also in our data, juvenile forms of holoplankton were found during spring, but in low numbers compared to meroplankton. The only exception was observed at the northernmost locality Rijpfjorden. But here we missed the time of the phytoplankton spring bloom with our sampling regime, and therefore we might have missed the early increase in meroplankton. Generally, meroplankton was the zooplankton component that responded stronger to the increased productivity compared to holoplankton. During summer in the Russian Arctic Seas, total zooplankton biomass increased further with more copepods, which were predominant together with larval forms of benthic organisms (Zenkevitch, 1963). This was similar to what was observed at the shallow IsA sampling station in Adventfjorden, even though there meroplankton kept its dominance until the end of summer when holoplankton increased strongly. Holoplankton dominated at the deeper stations from summer on. In the Russian Arctic Seas during winter, as it was found in Svalbard waters, the low zooplankton biomass mainly consisted of adult overwintering stages. The Arctic Seas comprise a variety of different habitats, with their specific hydrographical regimes, difference in sea ice dynamics and zooplankton and benthic community compositions (e.g. Zenkevitch, 1963) and it would be surprising if no regional differences were found.

Seasonal meroplankton pattern and primary production

The link between the timing of planktotrophic larvae of benthic invertebrates and times of high primary production has been proposed earlier for the Arctic (Thorson, 1936; Ockelmann, 1958) and also temperate regions (Barnes, 1962). This study was able to demonstrate this connection in different Arctic locations with different primary productive regimes for bulk meroplankton and most large taxonomic groups (paper I & III). The timing of larval occurrence and spawning can differ throughout a species biogeographical range (paper II; Mileikovsky, 1970; Von Oertzen, 1972), and general pattern for larval release and reproductive cycles differ between latitude, with the productive season having especially high importance in the highly seasonal environment of polar areas (Giese, 1959). High chl *a* and fluorescence values only occur when productivity is higher than mortality (due to grazing or sinking) and a biomass build-up defined as a bloom develops. Primary productivity and thus availability of food for the planktonic food web can therefore still be high while chl

a/fluorescence values are low if the predation pressure is high (Rokkan Iversen and Seuthe, 2010). Meroplankton peaks and high contributions to zooplankton might occur at somewhat different times throughout the productive season (discussed next paragraph), but still within time periods of elevated primary productivity (Zenkevitch, 1963; Coyle, Chavtur and Pinchuk, 1996).

Why are meroplankton organisms so abundant during the productive time of the year? Why is it beneficial for benthic invertebrates with planktonic larvae to time reproduction with the productive time of the year? And how do they time spawning? Observations showed that several bivalve species match larval occurrence in the plankton with optimum environmental conditions for their larvae, which were either optimal food or temperature conditions (Philippart *et al.*, 2014), both which are likely to occur during spring/summer in the Arctic (Thorson, 1936). Larvae are supposedly seldom or never affected by starvation in nature (Vance, 1973), but indirect effect on survival may occur through impact on development time which is dependent on food availability (Bayne, 1965; Vance, 1973; Pechenik *et al.*, 1990). Also, it has been suggested that food-availability and optimal timing for early juvenile stages can be critical for mobile benthic taxa (Bowden, Clarke and Peck, 2009, Antarctica). This would give an advantage to species that release their larvae early during the productive season, so they can utilize a longer part of the productive season, with both larvae and juveniles having access to high food availability before winter. A high downward flux of biogenic material in autumn observed in Adventfjorden (Wiedmann *et al.*, 2016) could be important in supporting both settled juveniles as well as adults who can start gathering energy reserves for new re-production next spring (Giese, 1959; Ockelmann, 1965). With the extreme differences in primary productivity resulting from the Arctic light regime, it is likely more important to time reproduction with the short times of high food availability in the Arctic compared to less seasonal primary productive regimes further south (Mileikovsky, 1970; discussed in paper III). Besides potential food availability (discussed in detail in paper I), there might be an advantage in coordinating larval occurrence with high abundances of other zooplankton organisms. In experiments, predation rates on meroplankton organisms were markedly reduced or disappeared when background zooplankton was present (Johnson and Shanks, 2003), which – in contrast to the increased predation pressure one might expect – decreases predation pressure during times of high zooplankton occurrence. This was attributed to encounter rates of predators with meroplankton or holoplankton organisms (Johnson and Shanks, 2003). Meroplankton proportions in the zooplankton found in this study, were however much higher than used in the experiments, which would lead to higher encounter rates and higher predation.

Timing is not solely defined by what is best for larvae or juveniles, but also by the requirements of the adult organisms and several other aspects of the reproductive strategy (Giese, 1959; Marshall and Morgan, 2011). Cirripede of the species *Balanus balanoides* for example, are a capital breeders and assimilate energy during the productive season after releasing their young. They mate through internal fertilization during winter and brood their young in the mantle cavity until the next spring (Pyefinch, 1948). They are very fast in responding to increased phytoplankton availability during spring by releasing their larvae,

which to a large degree feed on algae present during this time (discussed in paper I). Some Bivalvia on the other hand will assimilate energy, but do not finish their maturation of gonads before they receive fresh energy and nutrients during spring (Ockelmann, 1958), and can therefore be regarded as income breeder or partial income breeder. Following energy input, they spawn large amounts of gametes freely into the water column (broadcast-spawning) where external fertilization takes place, and fertilized gametes develop into larvae feeding on both DOM and small phytoplankton cells before settling in late summer or autumn (Manahan, 1990; Boidron-Métairon, 1995; Lindeque *et al.*, 2015). In the present study on Svalbard, both bivalve and cirripede larvae were found during the productive time of the year, but the main bulk of bivalve larvae occurred later than the bulk of cirripede larvae. In Antarctic water, no seasonality was found in taxonomic diversity of meroplankton, but seasonal changes in larval abundance were apparent (Sewell and Jury, 2011). Those abundance peaks during the productive time are most likely related to the numerous planktotrophic larvae that might originate from only a few species, while less numerous lecithotrophic or short lived demersal larvae from other species can easily also occur during non-productive times of the year, since they are not dependent on high food availability and can take advantage of reduced predation pressure during winter and early spring, when total zooplankton abundances are low. Reproductive strategies with lecithotrophic or demersal larvae are not discussed further here; since those larval types are less abundant than planktotrophic larvae or do not occur in plankton samples (demersal larvae) and will thus very likely not contribute to a large extent to the observed meroplankton pattern in this study.

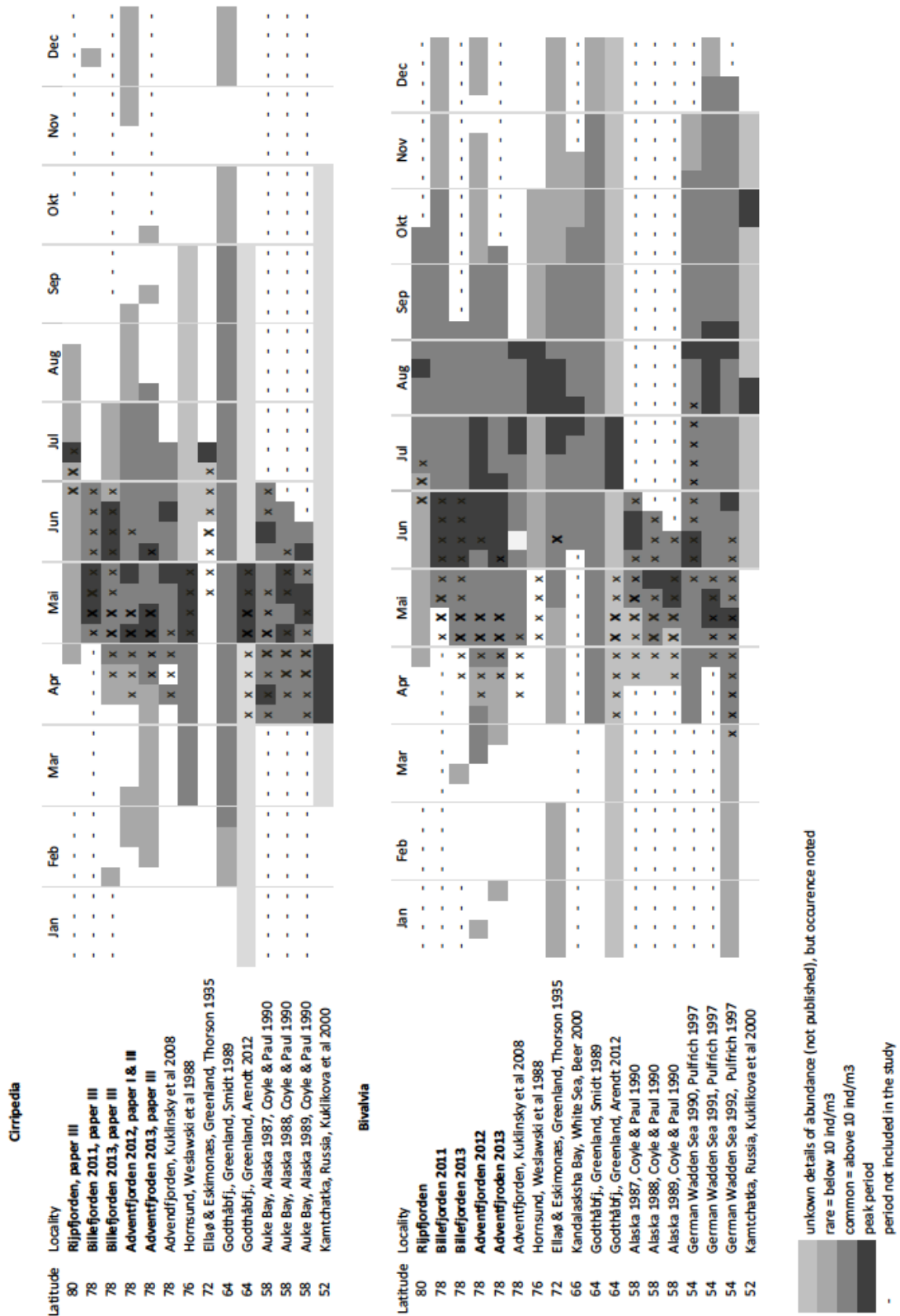
A mechanism for timing is required to be able to coordinate spawning of gametes to ensure good fertilization success and to be able to release larvae during times which are advantageous for those or later stages. These mechanisms can be very complex and rely on one or more often several triggering cues (see background, also discussed in paper I & III). Experimental work has demonstrated direct coupling between spawning and phytoplankton occurrence in the water column for barnacles, sea urchins and mussels, triggering larval release or spawning either through direct contact or through extracellular phytoplankton-metabolites (Starr, Himmelman and Therriault, 1990, 1991).

Based on the close correlation between abundances of most groups and chl *a*/fluorescence and not with hydrographical factors, we conclude that phytoplankton is likely involved as trigger in the timing of larval/gamete release in the Svalbard region (for discussion see paper I & III). The downward flux of material observed at IsA during early spring (Wiedmann *et al.*, 2016) can supply energy to adult organisms, as well as working as a signal. The day-light regime might either be directly involved in timing the spawning process or indirectly as facilitating factor for primary production (discussed in paper I). Most larvae disappeared from the water column until autumn.

Variability of reproductive timing

There seems to be a certain variation in timing of groups both between latitudes and locations within the Arctic (tab. 3, paper II). Bivalve larvae showed mostly one main abundance peak

Table 3: Occurrences of Cirripedia and Bivalvia larvae found in different studies from the Arctic and sub-Arctic. Periods of high primary productivity (x) and bloom situations (X) are indicated as well as abundances of larvae where this information was available.



under Arctic conditions, and two abundance peaks in more temperate conditions, where the first peak generally occurred earlier and the second later compared to the peak occurrence in Arctic waters (see tab. 3, paper II). A multi-year study in Plymouth waters also found multiple peaks, with large numbers of bivalve larvae both in spring and then again during late summer and autumn after the autumn bloom (Lebour, 1938, 1947). The maximum abundances of bivalve larvae within the Arctic occurred with several weeks of time lag after the spring bloom, but the length of the time lag differed between locations. Unfortunately, data on the timing of the bloom was not available for all studies, especially for studies with delayed bivalve larval abundance peaks. The timing of spawning periods varies with species (Lebour, 1938; Günther and Fedyakov, 2000) and different benthic community compositions together with different timing of the spring bloom might explain local differences within the Arctic. Cirripedia larval abundance maxima are much closer timed with the spring bloom and variations in this connection are much smaller for this group compared to the bivalves, most likely due to different reproduction strategies as discussed earlier. Both timing and larval output can vary somewhat between years (Smidt, 1979; Coyle and Paul, 1990; Pulfrich, 1997). This can be related to variation in environmental conditions leading to changes in timing or reproductive output of the present species (Loosanoff and Nomejko, 1951). The two years investigated at IsA showed both some inter-annual differences in timing and differences in larval abundances (fig. 8). Even though the timing of the beginning of the bloom was similar, bloom dynamics differed greatly. This might have affected larval output from the adult organisms as well as the timing. Also, even with bi-weekly sampling, strong short term periodicity in spawning and larval abundances (Loosanoff and Nomejko, 1951; Mileikovsky, 1970), might not have been caught properly. A bi-weekly sampling regime might be enough, if intervals of more frequent, very intense sampling are included especially during the spring time, to be able to evaluate such potential short term periodicities and potential triggering effects better.

Limitations due to taxonomic resolution

General seasonality pattern for groups of marine benthic invertebrates with planktonic larvae were investigated. The low taxonomical resolution is a large set-back when trying to relate meroplankton dynamics to benthic invertebrate life cycles and reproductive strategies. One has to keep in mind that within each group, many species with different reproductive timing and strategies can be present, and it is not possible to distinguish between them with the taxonomic resolution in our dataset. With the taxonomic resolution chosen, little can be said about seasonality in meroplankton diversity and the following discussion will only be applicable for those species with high numbers of planktotrophic larvae, creating the main abundance peaks within each group. Further complicating is that main peaks in each group might be either created by several species having overlapping spawning periods or by one or very few species producing very large numbers of larvae. Also it is not possible to know if multiple abundance peaks, apparent in the high-resolution time series in Adventfjorden for all

groups in both years (fig. 8 for the most abundant groups each year), are attributed to several species, stages or several spawning periods of the same species.

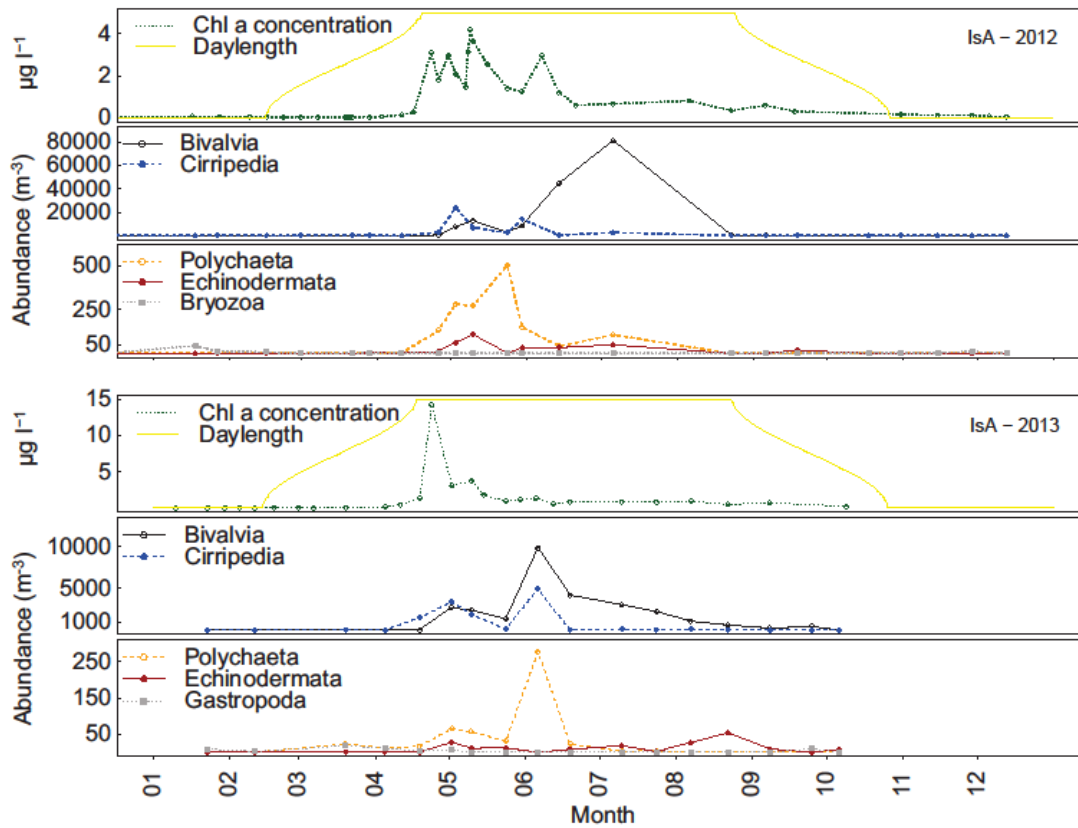


Figure 8: Abundances (ind./m³) of the 5 most common groups of meroplankton found at IsA in 2012 and 2013, chl *a* biomass (µg/l) and day-light regime.

Species specific reproduction strategies

For *Bivalvia* in Adventfjorden 2012, the identified species had largely overlapping spawning periods, and the early stage D-shaped larvae occurred during abundance peaks (paper II). Thus, here several species created the peaks together. Since only few larvae were genetically identified each time and not randomly picked, no statement about relative abundances can be made, but both *Hiatella arctica* and *Mya truncata* are two of the most common larval bivalve species found e.g. in Greenland waters (Smidt, 1979) and are also common within the bivalve meroplankton in the White Sea (Beer, 2000; Günther and Fedyaikov, 2000). In Plymouth waters, a single species of Bivalves was often dominating at a time (Lebour, 1938, 1947) and it could well be that *H. arctica* had this role at IsA, since by far the most sequences belong to this species, and colonies are present not far from the IsA station (pers. observation). *Hiatella arctica*, *M. truncata* and *Mya* sp. D-shaped larvae occurred more or less simultaneously in the water column during two time periods, corresponding quite well with bivalve peak occurrences. Those separate occurrences of early stage larvae likely represent 2 spawning

occasions for each of the species. If those are entirely separated or just represent discontinuous spawning cannot be said. For both *Mya* species, the low number of individuals found also makes it likely that not the whole reproductive period was captured with the number of individuals analysed. Multiple spawning events for *H. arctic* were also found in Greenland waters, with 3 reproductive periods (Norden Andersen, 1984), while more continuous spawning was indicated for both *H. arctica* and *M. truncata* in the White Sea (Beer, 2000). *Serripes groenlandicus* D-shaped larvae started too occurred a month later than the other 3 species, but overlapped with the occurrence *H. arctica* and *M. truncata* D-shaped larvae during their likely first spawning period. Only one spawning was found for this species, but the low number of individuals found, makes it also here possible that not the whole reproductive period was covered. So, 3 out of the 4 genetically identified species had very similar reproductive patterns and differences could be related to the biogeographical range of the species (paper II). To infer spawning times from larval occurrence in the plankton has its limitations, but is still a valuable method to provide a rough estimate of spawning times for those species that do have planktonic larvae (Loosanoff and Nomejko, 1951; Giese, 1959; Mileikovsky, 1970). Also the duration of larval periods is difficult to estimate since not necessarily the same clutch is observed during successive samplings instances. If we assume we sample the same clutch with successive development stages, the development from D-shaped larvae to a pediveliger for *H. arctica* takes between 2 and 3 months. This means that knowledge about stage or age of the larvae is important in order to be able to estimate spawning times. Surprisingly few bivalve larval species were detected using genetic methods (paper II), considering that 47 bivalve species are registered in Isfjorden (Rozycki, 1993, 1995; Wlodarska-Kowalczyk, Szymelfenig and Zajickowski, 2007). Many of those might have a very short or absent pelagic phase (Ockelmann, 1958, 1965) and are therefore unlikely to be found in zooplankton samples. Still the number of species is low. The absence of larvae of e.g. *Macoma calcaria*, *Ciliatocardium ciliatum* which both are known from the Isfjorden system (Rozycki, 1993) is surprising, since their larvae otherwise occur in larger numbers throughout late spring to early autumn (Norden Andersen, 1984) or June and earlier (Günther and Fedyakov, 2000) respectively. *Macoma calcaria* larvae show strong inter-annual variations, potentially because this species might not reproduce annually or larval development might fail during certain years (Ockelmann, 1958; Von Oertzen, 1972). But more likely, those two and several other larval species were missed with the sample size taken for genetic analysis. A sample-size of at least 50, if possible 100 randomly picked individuals per sampling date, preferably at least every second week should be able to cover the species diversity better.

Keeping in mind the many steps of the reproductive cycle leading to a spawning events at the end of each breeding season, conclusions based solely on larval occurrence in the plankton need to be drawn with care and need further verification in follow-up studies. Using the presented data as a basis and background knowledge, those should ideally include benthic sampling looking at gonad development in some selected species and focus on certain groups with a higher taxonomic resolution. To cover the whole larval phase, would also provide a valuable addition about the length of the larval phase and development time.

6.2. Prevalence of meroplankton in the Arctic coastal plankton, trophic interactions and benthic-pelagic coupling

Prevalence of meroplankton

Marine benthic invertebrate larvae were revealed to occur persistently in high abundances during the productive season in the plankton, contributing an important fraction to the total zooplankton numbers and biomass (paper I & III) in 3 fjords around the Svalbard archipelago. Maximum abundances found in the shallow Adventfjorden in 2012 (up to 98 000 ind./m³) were surprisingly high and above values recorded elsewhere in the Arctic. Abundance peaks found in the other years and fjords are more common for Arctic waters, where some hundreds to thousands of individuals per m³ are regularly reached depending on season and area. More seldom, a few tenth of thousands per m³ are reached when small-meshed nets are used, like in this study (Smidt, 1979; Coyle, Chavtur and Pinchuk, 1996; Arendt *et al.*, 2013; Questel, Clarke and Hopcroft, 2013). The high abundances reached in Adventfjorden compared to the deeper stations are likely due to the shallow depth (paper I). Additionally, more frequent sampling in Adventfjorden likely allowed us to capture abundance peaks better than the coarser sampling scheme applied in Billefjorden and Rijpfjorden. Numbers and relative abundances in the zooplankton were very variable both within (paper I&III) as well as between years and locations (Paper III) in accordance with earlier studies from the Arctic, where variability was attributed to multiple factors like productivity and blooms, which again are linked to seasonality and hydrographical processes, degree of fresh-water input, coastal. vs. non-coastal environment, bottom depth and species composition (Smidt, 1979; Coyle, Chavtur and Pinchuk, 1996; Fetzer, 2003; Pedersen, Ribergaard and Simonsen, 2005; Arendt *et al.*, 2013). In the Svalbard region, Bivalvia were important as the main component in all 3 locations and years. While Cirripedia were abundant in the more southern location, Echinodermata were important in the northernmost and most Arctic location. In different areas around the Arctic, groups recorded to contribute noticeably to the total zooplankton community differ (Zenkevitch, 1963; Smidt, 1979; Coyle and Paul, 1990; Walkusz, Kwaśniewski and Dmoch, 2004). How much the different groups contribute is influenced by the local benthic standing stock releasing larvae and gametes into the water column and their condition (Loosanoff and Nomejko, 1951; Clough *et al.*, 1997; Kulikova, Solokhina and Samatov, 2000). We do not have benthic data that is good enough to compare the 3 fjords investigated here and to relate patterns to observed larvae abundances, but can assume that the benthic communities that can release larvae vary among the fjords.

Bivalvia, the most abundant larval group in this study, is regularly reported to be a significant part of the total zooplankton all around coastal Arctic regions; e.g. in Greenland (Pedersen, Ribergaard and Simonsen, 2005), the Kara Sea, Leptav Sea (Bogorov & Jashnov in Zenkevitch, 1963) and Alaska (Coyle, Paul and Ziemann, 1990). Here species like *Hiatella arctica*, *Macoma* spp., *Mya* spp., *Serripes groenlandicus* and *Ciliatocardium ciliatum*, which have a wide distributional range in the Arctic, contribute larvae. In areas where they exist, also *Mytilus edulis* can contribute considerable numbers of larvae (Smidt, 1979; Beer, 2000; Günther and Fedyaikov, 2000). Since bivalve larvae are small, sampling with a small-meshed

net is especially important to catch their dynamics (paper I). Polychaeta larvae played a minor part in this study (paper I & III) and a study from Canadian N.W. Fox Basin (Grainger, 1959), but comprised a very common and sometimes dominating meroplanktonic part in zooplankton in most other Arctic areas like the shallow Kara Sea, Leptav Sea and Chukchi Sea (Bogorov & Jashnov in Zenkevitch, 1963), but also Greenland (Norden Andersen, 1984), Alaska (Coyle and Paul, 1990) and the Canadian Beaufort Sea (Walkusz, Williams and Kwasniewski, 2012). Polychaeta are abundant part of the benthic fauna in Arctic seas with several species producing planktonic larvae, especially within Polynoidae and Phyllodocidae (Smidt, 1979). Even though Polychaeta larvae reached common abundances of several hundreds to over thousand in Adventfjorden, they were very sparse or absent in the 2 deeper locations. Polychaete larvae are often highly abundant in shallow locations (Kulikova, Solokhina and Samatov, 2000), and the depth of the sampling location might play an important role. High numbers and contributions of Cirripedia larvae have been documented in Svalbard waters (Weslawski *et al.*, 1988; Walkusz *et al.*, 2009), the Barents Sea (Manteufel in Zenkevitch, 1963), Greenland (Pedersen, Ribergaard and Simonsen, 2005), the Bering Sea (Coyle, Chavtur and Pinchuk, 1996) and Canadian north-west Foxe Basin (Grainger, 1959). Cirripedia nauplii were clearly less abundant in the northernmost locality. This group has short peak occurrences, which are linked to the spring bloom. In Rijpfjorden, the limited sampling frequency missed the bloom, and might also have missed high cirripede nauplii abundances. Echinodermata larvae are abundant in several places in Spitsbergen waters (Timofeev, 1998; Walkusz *et al.*, 2009), the Kara Sea (Fetzer, 2003) and the Bering Sea (Coyle, Chavtur and Pinchuk, 1996). Abundances of Echinodermata larvae were similar in Adventfjorden and Rijpfjorden, even though they comprised a much higher proportion in the latter one. Only in Billefjorden, abundances of this group were very low, but it is unclear why.

In summary, the strong contribution of meroplankton to the zooplankton community in coastal areas in the Arctic during certain times is quite common. But to our knowledge, we demonstrate for the first time, that meroplankton can dominate the zooplankton abundance over most of the productive season in shallow Arctic fjords (paper I & III).

Trophic interactions and benthic-pelagic coupling

Particles and biogenic material sinking to the sea floor for “recycling” comes immediately to mind when thinking about pelagic-benthic coupling. In this case, energy flows passively from the pelagos to the benthos. Many meroplanktonic larvae feed at some point on planktonic organisms or material (Boidron-Métairon, 1995; Turner *et al.*, 2001; Vargas, Manriquez and Navarrete, 2006; Pasternak *et al.*, 2008), removing biological material – energy - from the pelagic to the bottom through active transport when they migrate to the sea floor, where they either settle or are eaten by other benthic organisms. This adds to the energy-flow towards the sea floor. From the feeding experiments with Cirripedia nauplii (abundances: field= 36 ind/L; experiments= 20 or 40 ind/L), it seems that this group alone is not able to graze down primary production and control spring bloom dynamics as proposed earlier (Kuklinski *et al.*, 2013), even though they contributed considerably to total zooplankton numbers (paper I) during peak abundances. This agrees well with earlier studies, concluding that meroplankton

has negligible effect on their food source (Strathmann, 1996, Almeda et al 2011). Still, nauplii collected were observed to have green guts and thus were feeding. Small flagellates were responsible for the main differences between control and experimental runs (SIMPER). Nanoflagellates, like *Phaeocystis* sp. which was an abundant spring bloom component at the IsA-station in Adventfjorden (Kubiszyn *et al*, submitted) are known prey for cirripede nauplii (Turner et al 2001, Almeda et al 2011), which agrees well with the experiment results. The experimental set-up had some flaws and for a new experimental set-up, dark controls parallel with feeding experiments or placing the whole experiment in the dark to remove the effect of photosynthetic activity with reproduction of those organisms might be helpful. In 1970, the Russian scientist, S.A. Mileikovsky, referring back to work done as early as the 1890s, wrote "... to regard the shallow shelf benthos and neritic plankton of all nearshore areas as part of one complex biological system characterized by certain ecological patterns and regularities common to both components". Relative abundances of marine invertebrate larvae vs. copepods increase towards the shore both in Arctic and sub-Arctic areas (Chukchi Sea, Bogorov & Jashnov in Zenkevitch, 1963; Vesterålen, Norway in Silberberger *et al.*, 2016). To which degree meroplankton organisms are able to influence dynamics within the coastal Arctic plankton communities is often poorly addressed and unclear. The high and persistent presence during longer periods of the year demonstrated here and by others, should make us consider this link more in the future.

Pelagic larvae or gametes, released from their benthic parents in vast numbers into the water column can also represent a reversed flow of energy: they are a food source for a variety of pelagic organisms (Thorson, 1950; Cowden, Young and Chia, 1984; Young and Chia, 1987; Johnson and Shanks, 2003) – an energy source supplied by the benthic community to the plankton – a trophic link and energy transfer direction less commonly considered and studied. In Svalbard waters Chaetognatha, Ctenophora, Amphipoda, Hydromedusae and Euphausiacea are common zooplankters (ref), which can be important predators on invertebrate larvae (Young and Chia, 1987). E.g. *Parasagitta elegans* feeds on cirripede nauplii, *Parathemisto/Euthemisto* nauplii on decapod larvae and *Thysanoessa* sp. on echinoderm and decapod larvae (Young and Chia, 1987). Even microorganisms, like the dinoflagellate *Noctiluca scintillans* can feed on meroplankton, in this case bivalve veliger (Johnson and Shanks, 2003).

So, even if the importance of meroplanktonic organisms as prey is not well understood, their biomass and extreme high numbers, combined with the wide range of organisms feeding on them, make meroplankton likely to fulfil an important trophic role as a link between the benthic and pelagic realm and for the energy transfer within and between these two systems. Also a different form of coupling between the two realms, potential signalling effect of material from the plankton to the benthos has been discussed above and in paper I & III, and contribute to linking the two often separated habitats or realms, plankton and benthos, to each other.

6.3. Meroplankton in changing climate

Changes in climate are likely to lead to changes of both abundance and timing of marine benthic larvae, as shown e.g. for echinoderm larvae in the North Atlantic and North Sea (Kirby and Lindley, 2005) and the lamellibranch *Macoma balthica* in the Wadden Sea (Philippart *et al.*, 2016). This reflects changes in reproductive output and reproductive timing. Both numeric as well as relative abundances of echinoderm larvae increased and the seasonal peak occurrence advanced with warmer ocean climate. For *M. balthica* on the contrary, warmer seawater temperatures seemed to lower the number of larvae produced but also advanced the spawning period. The discussion presented in paper I - III mainly focuses around a more or less direct connection between triggering mechanisms and larval release, but the timing of reproductive cycles of marine benthic invertebrates are complex, and factors functioning as spawning-triggers differ from those facilitating and inducing gonad maturation and growth – a pre-requisite for being able to spawn (Giese, 1959; Giese and Kanatani, 1987). Changes in temperature and primary productive regime can influence those earlier stages in the reproductive cycle and through that, influence timing of larval release indirectly as well as directly through triggering mechanisms for spawning itself (). Changing spawning periods to winter and early spring times for Arctic or psychrophilic species, meaning species capable of reproducing under cold conditions, has been demonstrated (Von Oertzen, 1972). Plasticity and adaptability of reproductive and breeding cycles might enable species to survive under different environmental conditions (Von Oertzen, 1972; Philippart *et al.*, 2014). In some cases even the larval type produced can vary with environmental conditions (Krug, 2009; Krug, Gordon and Romero, 2012), which also provides a potential way to adapt to changing conditions for those species. Increased sea temperature can also shorten larval development-times and with that increase survival of larvae but reducing larval dispersal distance, which will influence the benthic community structure (O'Connor *et al.*, 2007). Following, the frequency of different reproductive modes found within the benthic community might change (Marshall *et al.*, 2012). All those mentioned aspects and potential ways of benthic invertebrates to alter and adapt their reproductive strategy would change dynamics not only for benthic communities, but also the zooplankton community. With our current knowledge, it is very difficult to make predictions about future zooplankton dynamics, since also the holoplankton will be affected by the same changes and need to respond. Complicating this even further, reaction and sensitivity to changing environment differ between adult and larval stages, with larval stages likely being more sensitive than the adult life stages (Marshall *et al.* 2016), and changes in the benthic community will be determined by the combined effect. Still, species with planktotrophic larvae are expected to become more common at high latitudes and expand their ranges towards the poles, as a strong connection between ocean temperature and productivity with the occurrence of planktonic larvae has been observed (Marshall *et al.*, 2012). This would alter the contribution of meroplankton to the zooplankton community and its role in the planktonic food web. To be able to understand reproductive strategies of marine benthic invertebrates in the Arctic and the way they may react to climatic changes properly, more multidisciplinary studies including benthic and planktonic research, laboratory studies and field investigations need to be carried out and combined.

7. Conclusions

This PhD thesis has contributed new information about meroplankton dynamics in Svalbard waters on several aspects of their presence, dynamics and role in the pelagic ecosystem.

Duration and contribution

The study revealed that meroplankton can contribute considerable to the zooplankton community in coastal areas during the productive period, which greatly influences the total zooplankton dynamics. Contributions between 30 and 90 % to total zooplankton abundance during peak occurrences, with prolonged dominance of the zooplankton community during most of the productive season at the shallowest location were quite remarkable and unexpected. In the shallow Adventfjorden they did not only dominate abundances during spring and parts of the summer, but also in terms of biomass. This suggests that meroplankton is an important component in the zooplankton community of Arctic coastal regions and fjord environments and that more attention should be given to these temporary visitors. Seasonal studies with high sampling frequency, which are hitherto very rare in the Arctic, are required to capture the meroplankton dynamics and assess their contributions to the zooplankton communities correctly.

Timing and driving environmental forces

Based on the close correlation between abundances of most groups and chlorophyll *a*/fluorescence and not with hydrographical factors such as temperature and salinity, we conclude that phytoplankton is likely involved as trigger in the timing of larval/gamete release of benthic invertebrates with planktonic larvae in the Svalbard region (for discussion see paper I & III) and that hydrography is less important. This was concluded based on investigations in three fjords with different timing and dynamics in primary production. Strong correlation might either be related to the increased light intensities facilitating primary production, or the light regime exhibiting a more direct effect on the benthic parental organisms. Due to the low taxonomical resolution, those conclusions are only valid for benthic invertebrates that produce large numbers of planktotrophic larvae, since other larval types which are produced in smaller number likely contributed little to the observed general pattern of the higher taxonomic groups. Also within the groups, different species with varying timing will be present with different reproductive strategies. Keeping in mind the complexity of reproductive cycles with one or several spawning events at the end of each breeding season, conclusions on reproductive timing based just on larval occurrence in the plankton need to be drawn with care and further studies are needed. The presented data can serve as valid baseline to design later, more targeted follow-up studies, which should aim for a higher taxonomic resolution and also include studies on the gonad development in adult benthic populations.

Species identification

The combined morphological and molecular method applied, helped to resolve the diversity within the chosen group Bivalvia on a better resolution, but only 4 species were identified. DNA barcoding used to identify marine benthic invertebrate larvae found in the plankton. The resolution and applicability depends to a large degree and the availability of reference sequences accessible in a database, and those are limited for species from remote habitats such as the Arctic or Antarctic. That so few species were found in this study might also be influenced by the relatively low number of individuals taken from each zooplankton sample. For further studies, a larger sample set is recommended to capture the present diversity better. The 4 identified bivalve species had largely overlapping spawning periods, and contributed to the total bivalve abundance peaks together. *Hiatella arctica* was likely dominating, but this is uncertain. Three out of the 4 species with a wide biogeographical distribution seemed to have several spawning events, while the one Arctic species had only one. But low sample size makes conclusions uncertain.

Feeding impact

Only limited conclusions can be drawn from the feeding experiments, since the experimental set-up needs some improvement. Still, they indicate that cirripede nauplii on their own were not able to exert top-down control on the primary producer stock. The importance of meroplanktonic organisms in the food web is not well understood, but we do know that they both feed and are fed on by numerous organisms. Their high biomass and numbers found throughout this study, especially in shallow Adventfjorden, make meroplankton likely to fulfil an important trophic role and further, improved experiments should be conducted. They also represent a link between the benthic and pelagic realm transferring energy within and between these two systems, and they might rather be seen as two segments of the same realm in shallow coastal areas and be treated as such. Also here more research is recommended.

Considering the potential changes within the timing and production of planktonic larvae of benthic invertebrates, as well as the demonstrated influence on zooplankton dynamics, this group clearly deserves a renaissance of interest and more focus in Arctic marine research.

8. References

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