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Seasonal and spatial dynamics of meroplankton in a sub-Arctic fjord

With additional focus on larvae of the invasive red king crab

—
Helena Kling Michelsen

A dissertation for the degree of Philosophiae Doctor – September 2017



Front page clockwise from top left:

Stage I red king crab larvae, red king crab glaucothoe stage, Spionid polychaete larvae, Cirripede
Cypris larvae

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“Many of these creatures so low in the scale of nature are most exquisite in their forms & rich colours”

- Charles Darwin, written when working with plankton on board the Beagle

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SUMMARY

Many benthic marine organisms produce pelagic larvae, meroplankton, which spend from hours to months in the pelagic before settling on the sea floor. During this time, meroplankton form an important part of the pelagic community. The survival of meroplankton is important for maintaining benthic population and community structure and is hinged on larvae being released at a time with suitable environmental variables in the water column. In polar waters, seasonal fluctuation in the environment are strong, thus meroplankton dynamics vary temporally and spatially. Few field studies have focused on the year round dynamics of meroplankton or identified meroplanktonic larvae with a high taxonomic resolution. Therefore, many aspects of meroplankton dynamics remain poorly understood in sub-Arctic and Arctic waters. In the 1960s one of the largest benthic decapods in the world, the red king crab, was intentionally introduced into Russian coastal waters of the southern Barents Sea. Today they are continually expanding their range along the Norwegian coast and fjords. They cause changes to the benthic community through predation, but also provide a valuable fishery. Like many benthic invertebrates, the red king crab have a pelagic larval stage. Yet there is no knowledge on when and where larvae are released nor how larval release correlates with favorable environmental variables in Norwegian waters. The objectives of this thesis were to increase our understanding on the seasonal and spatial dynamics of meroplankton in sub-Arctic waters and identify the environmental variables responsible for these dynamics. The potential role of meroplankton in the pelagic was investigated by identifying their numerical contribution to the zooplankton community. Finally, the temporal and spatial dynamics of red king crab larvae was investigated to see how larvae are timed with favorable environmental variables in Norwegian waters. The study area, the sub-Arctic Porsangerfjord, Norway (70 – 71 °N), has a productive benthic community and was recently invaded by the red king crab. It displays strong gradients in environmental variables and therefore represents an ideal field laboratory for investigating aspects of meroplankton dynamics.

Sampling monthly to bi-monthly over a 1.5-year period, showed that meroplankton abundance and assemblage separate into significantly different seasonal communities (winter, spring, early summer and late summer). Meroplankton were present in the water column year around but the highest abundance and greatest number of meroplanktonic taxa were found in spring and summer and correlated with increased chlorophyll *a* and temperature in the water column. Meroplankton was periodically the dominant numerical component in the

mesozooplankton community these seasons (particularly in April). Spatial patterns in meroplankton was investigated by sampling transects along the fjord in spring (April). Significantly different meroplankton assemblages were found in three separate basins along the fjord. The assemblages correlated with environmental variables and followed a downfjord succession in seasonal communities. A community typical of winter characterized the inner basin and an early summer community the outer basin. A high abundance and numerical dominance of meroplankton in the mesozooplankton community was found in shallow bays and the middle basin. Larvae of the red king crab were first recorded in late winter and were continually released over a period of four months resulting in a larval period of six months (January to June). The greatest densities of larvae on both a temporal and spatial scale was found at shallow protected stations. Having a prolonged larval release is advantageous for recruitment success of this invasive species because it ensures that at least some larvae will coincide with favorable food concentrations and warmer temperatures in the water column. Releasing larvae at protected sites may also increase the chance that larvae remain close to suitable settlement localities. These findings coupled with a wide tolerance to temperature and salinity during their larval and adult phase means that they are well suited for life in the southern Barents Sea and that they have the potential of continuing their range along the coast to southern Norway and north into Svalbard coastal waters. The findings on meroplankton dynamics in this study provide evidence that larval release by benthic invertebrates is tightly coupled with seasonal and spatial variations in environmental variables and that an organism's response to these variables result in complex seasonal and spatial dynamics of meroplankton. In a warming ocean this coupling could cause a shift in larval release timing and a range expansion for organisms. A periodical seasonal and spatial dominance of meroplankton in the mesozooplankton community suggest that they are an important component of the pelagic food web.

LIST OF PAPERS

Paper I

Michelsen, H. K., Svensen, C., Reigstad, M., Nilssen, E. M., Pedersen, T. (2017) Seasonal dynamics of meroplankton in a high-latitude fjord. *Journal of marine systems* 168:17-30

Paper II

Michelsen, H. K., Nilssen, E. M., Pedersen, T., Reigstad, M., Svensen, C. Spatial patterns of spring meroplankton along environmental gradients in a sub-Arctic fjord. Accepted for publication in *Aquatic Biology*

Paper III

Michelsen, H. K., Nilssen, E. M., Pedersen, T., Svensen, C. Temporal and spatial dynamics of the invasive Red King Crab zoea and co-existing native decapods in Norwegian waters. Manuscript

1 BACKGROUND

1.1 EARLY LIFE-CYCLE AND LIFE HISTORY TRAITS OF BENTHIC MARINE INVERTEBRATES

A majority of animals on earth display a complex life cycle, meaning that they pass through two or more discrete phases during their lifetime (Moran 1994). These phases can differ from each other in a number of ways, including morphologically, behaviorally and/or physiologically (Moran 1994). The passage through a life cycle is governed by an organisms life history traits such as: size at birth, growth rate, age and size at maturity, number of offspring and reproduction events and lifespan (Stearns and Hoekstra 2005). The exact combination of these traits characterize a species and are imperative for their present and future survival and reproduction (Stearns and Hoekstra 2005). Some life history traits can be plastic in nature and vary between individuals and populations of the same species. These include size and age at maturity, fecundity, hatching timing, larval duration and size (Nylin and Gotthard 1998). The plasticity of these traits is usually an effect of external forces acting on an organism, such as food availability, environmental variables, competition and predation (Nylin and Gotthard 1998). Life history traits can thus vary within a species over both geographical and temporal scales.

Marine benthic invertebrates display a wide range of life cycles. One prevalent and highly complex life cycle is the production of larvae that hatch, swim into the water column, metamorphose and settle back to the benthos as juveniles that mature and finally reproduce (Levin and Bridges 1995). Other life cycles include the production of larvae that hatch and metamorphose close to or on the sea floor, brooding of larvae until metamorphosis to the juvenile state, and production of eggs that hatch directly as juveniles (Levin and Bridges 1995). Marine invertebrates that produce larvae are usually termed as having an indirect development whereas those that brood or produce juveniles have a direct development. Within many benthic invertebrate families and genera, one can often find examples of species belonging to each of the life cycle types. Moreover, some populations of the same species can even vary between an indirect development with pelagic larvae or benthic larvae (Bhaud and Duchêne 1995). Yet, an indirect development with pelagic larvae is the predominant life-cycle type for marine benthic invertebrates and is displayed by approximately 70 % of species (Thorson 1950; Young et al. 2002). The complexity in both early life cycle and life history traits of marine benthic

invertebrates sparked its own field of study, marine larval ecology, which aims at identifying patterns in life history traits, ecological niches and the ecological role of larval stages (Marshall et al. 2012). Increasing our insight into such patterns is essential for understanding, managing and predicting the abundance, distribution, potential dispersal and range expansion of benthic invertebrate populations (Steidinger and Walker 1984). The focus of the present study is on the larval stages of benthic invertebrates with an indirect reproduction and free-living larva in the water column.

1.2 SEASONAL AND SPATIAL DYNAMICS OF BENTHIC INVERTEBRATE LARVAE

For life history and thereby life-cycle events to happen at an optimal time for survival and future reproduction, organisms are often entrained and triggered by external as well as internal forces. For benthic as well as pelagic invertebrates in marine environments, these external factors include photoperiod, temperature, salinity, lunar cycles, tidal periodicity, food availability and chemical cues; while internal factors include hormonal secretion and gamete maturation (Giese 1959; Olive 1995; Morgan 1995). In reproductive cycles the events are often timed with the optimal survival of either or both the reproducing adult and their released offspring (Mercier and Hamel 2009).

Due to the axial rotation and elliptical orbit around the sun, the earth experiences daily and annual variations in photoperiod, light intensity and temperature (Hut et al. 2013). Moreover, because the earth's axis is tilted relative to its orbit around the sun, the seasonal (annual) variation and amplitude in photoperiod and temperature increases with increasing latitude from the equator (Hut et al. 2013). Consequently, both poles experience continuous darkness during winter and continuous light in summer, while the equator experiences a more or less constant light to dark ratio (Hut et al. 2013). These geographical differences in light regimes in turn affect temperature and the timing and intensity of primary production, the latter of which is dependent on sufficient irradiation. Thus, an increased seasonality in environmental variables is found with increasing latitude in marine environments. As a consequence, reproductive events and larval release by many benthic marine invertebrates becomes more seasonal with increased latitude. Despite the knowledge that such recruitment phenology i.e. reproductive seasonality is operating, only a modest number of studies have focused on the year around seasonality of benthic invertebrate larvae in sub-Arctic and high-Arctic waters (Thorson

1936; Mileikovsky 1970; Smidt 1979; Falk-Petersen 1982; Kuklinski et al. 2013; Silberberger et al. 2016; Stübner et al. 2016; Kulikova et al. 2011; **Paper I**). These studies have been conducted with varying sampling frequencies, sampling methods and have identified larvae to a varying degree (some to phylum others to family, genus and/or species level). Thus, many aspects on the timing of spawning, larval duration in the water column and timing of settlement still remain unknown for many benthic organisms at these latitudes.

Benthic invertebrates that produce pelagic larvae often differ in the number of gametes produced and their spawning habits. Some benthic invertebrates produce large amounts of small sized eggs while others produce large eggs in low numbers. These gametes may be released into the water column with consequent fertilization, embryology and egg hatching happening freely (Levitan 1995). Others fertilize and brood their eggs until they are ready for release or when the optimal environmental variables are met (Levin and Bridges 1995). Moreover, spawning and larval release may happen in one large burst, over a prolonged period of time or portions are released several consecutive times (Levin and Bridges 1995). These differences make the study of benthic invertebrate phenology and thereby meroplankton dynamics even more complex.

Benthic invertebrate larvae released into the water column are small in size (micrometers to a few millimeters) giving them a limited ability of deciding their horizontal distribution (Shanks 1995). Although some larvae are capable of migrating vertically in the water column, their horizontal distribution mainly depends on water currents in the area of release. Consequently, larvae may be advected or retained close to their release site. The ability to advect can be an important recruitment and distribution mechanism for benthic populations, as it ensures that sessile adults have the opportunity of exchanging genetic material with other subpopulations and to colonize new areas (Scheltema 1986). The amount of time these larvae spend in the water column varies from hours to months, some even remain years before settling on the sea floor (Shanks 1995). Thus, larvae have the potential for dispersing vast distances. Understanding the spatial variability in marine invertebrate larvae may aid in developing optimal marine protected areas (Shanks et al. 2003), understanding the spread of invasive species (Neubert and Caswell 2000; Pedersen et al. 2006) and the potential northward expansion of benthic populations with warming sea temperatures (Berge et al. 2005; Renaud et al. 2015).

1.3 LARVAL LIFE IN THE WATER COLUMN

When benthic marine invertebrate larvae are released into the water column they form a temporary part of the zooplankton community termed meroplankton (Greek: *meros* = part + *plankt* = drifter). They reside here together with holoplankton (Greek: *holo* = entire/whole + *plankt* = drifter), which are permanent members that spend their entire life cycle in the water column. Holoplankton display seasonal variation in abundance, biomass and reproductive events at high-latitudes (e.g. Hopkins et al. 1984; Weydmann et al. 2013). Because holoplankton are permanent members in the zooplankton community they are usually the most prevalent and dominant component. Yet, a growing number of high-latitude zooplankton studies in fjord and coastal areas are now showing a periodic high contribution of meroplankton in the zooplankton community (e.g. Kwasniewski et al. 2013; Stübner et al. 2016).

During their time in the water column, meroplankton display different nutritional modes. Some larvae are dependent on food for survival (planktotroph), feeding on phytoplankton, bacteria, microorganisms, other pelagic organisms and even dissolved organic matter (Boidron-Fétaïron 1995). Other meroplankters are dependent on food supplies in the form of lipids and yolk derived from their mothers and thus do not feed (lecitotrophic). The exact feeding mode, prey preferences and feeding rates is still unknown for many boreal and Arctic species. Thus, the potential feeding pressure by meroplankton at high-latitudes remains difficult to assess. A wide array of pelagic organisms prey upon meroplanktonic larvae (Thorson 1950). Thus, meroplankton can also have an inverse trophic position by acting as a food source for other pelagic organisms (Anger 2006; Short et al. 2013).

One of the most central paradigms in marine benthic larval biology at high-latitudes is “Thorson’s Rule” (Mileikovsky 1971). This paradigm states that the number of benthic adult species producing non-pelagic larvae increases with latitude and depth, i.e. pelagic larvae becomes rarer at high-latitudes and deep seas (Mileikovsky, 1971). The paradigm has, and still does, receive a considerable amount of attention, resulting in a growing number of contradictory observations of high proportions of pelagic development at both poles (e.g. Clarke, 1992; Fetzer and Arntz, 2008; Pearse, 1994). Today the paradigm receives less support and has been modified to include the observation of higher proportions of lecitotrophic larvae with increasing latitude (Clarke, 1992; Marshall et al., 2012). This modification is based on

studies from mainly Antarctic waters (summarized by Marshall et al. 2012), but a growing number of studies in the Arctic and on selected taxonomic groups are suggesting that the increase in lecithothophy with latitude may not always be the rule (Clarke 1992; Fetzer and Arntz 2008).

1.4 INVASIVE SPECIES

In a world that is progressively being effected by human expansion and movement with ships, anthropogenic disturbances and global change, the translocation of marine species to new areas is increasing rapidly (Molnar et al. 2008). Although this translocation may be intentional or unintentional, some species establish self-sustaining populations well outside their native range (deRivera et al. 2007). Many of these new populations become invasive meaning that they cause considerable ecological and/or economic damage in their new home. They are thus one of the threats to global biodiversity today (Bax et al. 2013). Consequently, a large and increasing body of research and legislative efforts have been put on understanding and preventing new and further range expansion of such organisms (e.g. Molnar et al. 2008). For invasive organisms to establish, persist and expand their range, a complex life cycle and high plasticity in life history traits has been identified as important factors (Anger 2006). Thus in order to eradicate, predict and prevent further expansion of these organisms it is crucial to understand timing of life cycle events, life history traits and tolerances in their native as well as non-native range. Yet, as previously mentioned such knowledge is still lacking for many boreal and Arctic benthic species. Complicating matters further is the fact that the biology of a species in its native range may not always be applicable to their new area (deRivera et al. 2007).

One invasive benthic organism in Norwegian coastal waters with a complex life cycle is the red king crab (*Paralithodes camtschaticus*). Russian scientists intentionally introduced them to the Barents Sea from the North Pacific Ocean in the early 1960s, with the intension of establishing a population of a new harvestable species (Orlov & Ivanov 1978). In the late 1970s, the first crabs were caught in Russian and Norwegian waters and the introduction was deemed successful (Orlov and Ivanov 1978). The crab spread rapidly along the coast and not until the 1990s did the Norwegian and Russian governments start a joint research and management cooperation. In 2002, commercial fishing for the crab was opened to local

fishermen (Sundet and Hoel 2016). Due to concerns about their potential effects to the benthic ecosystem, a western distribution limit was set at 26°E, which is on the northernmost tip of Norway (Figure 1). West of 26°E, an open access fishery and decimation fishery was implemented while east of 26°E the population was – and currently is – managed as a harvestable resource. Despite these efforts the crab has, as of 2013, increased their distribution from Kapp Kanin, Russia in the east to Sørøya (22 °E), Norway in the west (stippled line in Figure 1) (Britayev et al. 2010, Jørgensen and Nilssen 2011). However, recent research cruises in Tromsø (19 °E), Norway have found adult and juvenile crabs (red dot in Figure 1), indicating that a reproducing population has established this far south (E. M. Nilssen pers. com. 2017).

Due to concerns that this invasive crab can have a negative effect on local benthic ecosystems, the Norwegian government expressed - in a white paper on the management of red king crab - a need for an increased research effort on population surveys, understanding their life cycle and their potential effect on the local benthic ecosystem (Anon. 2007). In the same white paper, the government expressed a desire to use such knowledge to both implement further eradication efforts and to keep the crab as a resource (Anon. 2007). Currently, most of the research in Norwegian waters has focused on dynamics of the large juvenile and adult portion of the population, focusing on individual growth (Windsland et al. 2013), migration patterns (Windsland et al. 2014) and mortality (Windsland 2015), feeding habits (Jørgensen and Primicerio 2007; Fuhrmann et al. 2015, Mikkelsen et al. 2012), temperature preferences (Christiansen et al. 2015) and size and fecundity of adult females (Hjelset et al. 2008; 2012). In contrast, the only work done on their zoeal (larval) phase in Norwegian waters is modeling work and one laboratory experiment. The former focused on potential spread with surface currents and possible settlement localities along the coast (Pedersen et al. 2006), while the latter looked at temperature and salinity tolerances of the larvae (Larsen 1996). Thus, many aspects of their temporal and spatial patterns in egg hatching and larval stage composition remain unknown in Norwegian waters. This leads to uncertainties as to what role reproductive phenology and the larval phase has had for the successful crab invasion, how well larval release is timed with favorable environmental variables and how the timing of larval release compares with other native Anomuran and Brachyuran crabs.

1.5 HIGH-LATITUDE FJORD SYSTEMS AS FIELD LABORATORIES

Despite the seasonal variation in environmental variables, benthic communities in sub-Arctic and high-Arctic fjord and estuarine systems are some of the most diverse and productive on earth (Nilsen et al. 2006). This is due to a heterogeneous coastal and seafloor topography, varied sediment types, strong environmental and hydrographical gradients, high sedimentation rates and thereby benthic food supply, which provides a rich environmental landscape for benthic invertebrates of different ecological niches to occupy. Unlike temperate and boreal fjords on the southern and south western coast of Norway where benthic sediments can be periodically or permanently anoxic, sub-Arctic north Norwegian fjords experience yearly vertical mixing of the water column and have a frequent exchange of water masses with the coast (Wassmann et al. 1996). The frequency of such exchange varies through the year and depends on the presence or absence of a fjord sill (Svendsen 1995) and can affect not only temporal but also spatial gradients in environmental variables within a fjord. This in turn can impact both the pelagic and benthic community. Typically communities are more stable in silled fjords due to predictable hydrodynamics, environmental variables and less frequent advection of pelagic organisms into or out of the fjord (Nilsen et al. 2006; Renaud et al. 2007). In contrast, hydrodynamics and hydrographics are more variable in fjords without sills making the composition and advection of organisms more susceptible to change over time and space (Basedow et al. 2004; Renaud et al. 2007).

One of the largest fjords in northern Norway is the sub-Arctic Porsangerfjord (70 – 71 ° N) located adjacent to the Barents Sea (Figure 1). As with other high-latitude fjords, it displays a strong along fjord gradient in temperature, salinity, depth and sediment types. This is in part caused by a deep sill at the fjord entrance, characterizing a majority of Porsangerfjord as sillless while a shallow sill separates the innermost part of the fjord from the rest (Myksvoll et al. 2012). This has led to the formation of different benthic communities along the fjord, consisting of a mix of cosmopolitan, boreal and Arctic organisms (Oug and Høisæter 2000; Oug and Fuhrmann 2013; Fuhrmann et al. 2015). In particular, the innermost part of the fjord provides a unique refuge area for benthic populations of truly Arctic species (Fuhrmann et al. 2015; Wassmann et al. 1996). Porsangerfjord is located at the westernmost edge of the quota regulated area for red king crab and today it has become one of the most important harvestable species in the fjord (Fuhrmann et al. 2015). The fjord also provides an important nursing ground for fish and contains populations of birds, seals and whales that feed on the rich benthic and pelagic

communities. Strong gradients in environmental variables, hydrodynamics, benthic communities and as well as the presence of red king crabs make Porsangerfjord an ideal field laboratory to study larval timing, duration and spatial patterns of benthic marine invertebrates sub-Arctic waters.

2 MAIN OBJECTIVES

In this study we investigated the seasonal and spatial dynamics of benthic invertebrate larvae residing in the water column (meroplankton) in the sub-Arctic Porsangerfjord, Norway (70 – 71 °N). Special focus was put on the red king crab (*Paralithodes camtschaticus*) to elucidate reproductive patterns and early life cycle characteristics responsible for the successful introduction of this invasive species. The main objectives were:

- I. to investigate the abundance, seasonality and spatial pattern in the meroplankton community by identifying larvae to the lowest taxonomical level (**Paper I, II, III**),
- II. to identify environmental drivers responsible for seasonal and spatial patterns in meroplankton community structure (**Paper I, II and III**),
- III. to assess the relative abundance of meroplankton in the mesozooplankton community on a seasonal (**Paper I**) and spatial (**Paper II**) scale,
- IV. to investigate the timing and spatial patterns in red king crab zoeal stage composition in order to understand possible causes for their successful invasion (**Paper III**).

3 MATERIALS AND METHODS

3.1 PORSANGERFJORD

Porsangerfjord is located on the northernmost coastal part of Norway (70.0 – 71.0 °N, 25 – 26.5 °E). It is a broad fjord of 15 – 20 km with a length of approximately 120 km and a mean depth of 200 m. Based on bathymetry and water exchange, the fjord can be separated into three main basins: Outer, Middle and Inner (Figure 1) (Svendsen 1991; Myksvoll et al. 2012; Mankettikkara 2013). A shallow 60 m sill delineates the Inner-basin, while the Middle-basin is separated from the Outer-basin by the large island Tamsøya (Figure 1). Finally, the Outer-basin is separated from the coast by a deep sill at 180-200 m, which is in the same depth range as the surrounding basin (Mankettikkara 2013; Myksvoll et al. 2012) (for location of basins and sills see Figure 1). Due to the deep sill, the Outer-basin is open to the coast while the Middle-basins is classified as semi-enclosed. The basins thus experience a continuous or frequent exchange of deep water with the Norwegian Coastal Current (NCC) and Atlantic water (Svendsen 1995; Wassmann et al. 1996; Eilertsen and Skarðhamar 2006). The Inner-basin has little contact with the coast and experiences a moderate amount of freshwater runoff during spring and summer. This basin is characterized as Arctic, due to annual ice-coverage in late winter and early spring, temperatures reaching as low as -1.7 °C in late winter and remaining around 0 °C through summer.

Circulation patterns in the fjord is influenced by prevailing wind direction and strength, which is strongest in un-stratified waters during winter and spring (Svendsen 1991, 1995). The prevailing wind direction in the fjord is southerly and northerly (Wassmann et al. 1996). Southerly winds in combination with rotational effects result in the main circulation pattern of the fjord, forming an outflowing current with winter cooled fjord-waters along the eastern side and an incurrent of warmer coastal waters along the western side of the Middle-basin (Myksvoll et al. 2012; Svendsen 1991). In summer stratified water (May – October) a wind-induced upwelling and downwelling system sets up on the western and eastern side of the fjord, respectively. This often causes a cross fjord gradient in environmental variables and stratification. In the Outer-basin, a large eddy is often formed mixing water from the NCC and cold water originating from within the fjord (Pedersen et al. 2005; Myksvoll et al. 2012).

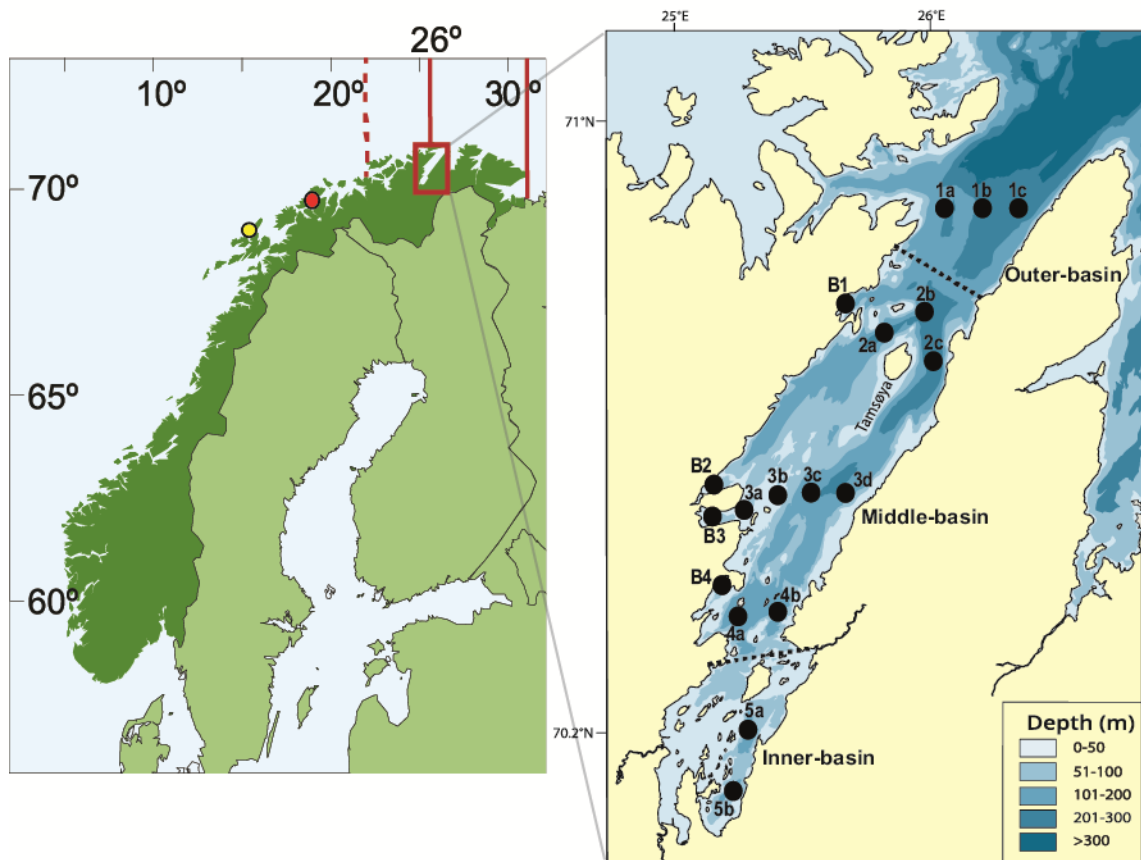


Figure 1. Map of the study area: Norway and Porsangerfjord, Norway. Red solid lines delineates the area of commercial fishery for red king crabs (*Paralithodes camtschaticus*), red stippled line shows the current distribution of red king crabs, black stippled lines show the location of fjord sills. Red circle shows the location of a newly discovered red king crab stock and yellow circle pinpoints the Lofoten and Vesterålen area.

The limited exchange of surface waters between the Inner- and Middle-basin results in a strong down-fjord gradient in environmental variables, with the water column becoming warmer and more saline moving from the fjord head toward the mouth. Recently, The Norwegian Geological Survey produced detailed maps of the bottom sediments in the Middle-basin and Inner-basin (Anon. 2015). Generally, the deep basins have a muddy and sandy sediment type while gravel, cobbles, boulders and hard bottom are found on the western part of the fjord, around islands and in bays along the western shoreline.

Porsangerfjord is located at the westernmost limit of the quota-regulated area for the red king crab (*P. camtschaticus*) (Figure 1) and was one of the last fjords to be invaded by the crab. In 2002, the first crabs were recorded within the fjord (Fuhrmann et al. 2015) and by 2008, a quota-regulated fishery for crabs in the Outer- and Middle-basin was established. In 2012, juvenile crabs started being caught in the Inner-basin, while a few adult crabs have been detected in 2014 (E. M. Nilssen).

3.2 FIELD PROCEDURES

The temporal dynamics of meroplankton and decapod zoeal release was examined by collecting zooplankton samples monthly or bi-monthly between February 2013 and August 2014 (11 sampling dates in total) from RV Johan Ruud. Zooplankton samples were collected at six fixed stations along the eastern side fjord (1c, 2c, 3d, 4a and 4b) and in a shallow protected Bay on the western side (B4) (Figure 1). All samples from all stations were analyzed and used in **Paper III** when focusing on decapod zoea (a total of 72 samples). This way spatial and temporal dynamics of zoeal stage composition could be studied simultaneously and possible hotspots for crab zoea identified. For **Paper I**, we selected two contrasting stations. This was done because identifying meroplankton to the lowest taxonomic level from all the samples proved to be complicated (see next section 3.3 for details). Previous seasonal studies on meroplankton in fjord and coastal areas usually select stations in shallow protected areas. Therefore, one shallow station that was protected and surrounded by mixed sediment types (B4) and one deep station influenced by eddies and surrounded by mainly soft sediments (3d) was selected (Figure 1). Between April 11th and 17th, 2013 zooplankton samples was collected at 18 stations within the fjord. Stations were arranged in transects across the fjord: one transect was located in the Outer-basin (1a-c), three transects in the Middle-basin (2a-c, 3a-d and 4a-b) and two stations in the Inner-basins (5a-b), and four stations in Bays (B1, B2, B3, B4) along the western side of the Middle-basin (Figure 1). This way it was possible to identify possible along-fjord and cross-fjord differences in meroplankton (**Paper II**) and decapod zoeal stage (**Paper III**) composition and abundance.

All zooplankton samples were collected using a standard WP2 equipped with a 180- μ m mesh size net (Hydrobios, Kiel, 0.57 m mouth opening) and a filtering cod-end. The net was towed vertically from approximately 5 m above the seafloor to the sea surface at a speed of 0.5 m s⁻¹. One to three hauls were taken at each station and fixed with 4 % buffered formaldehyde

in seawater. Environmental variables were provided by the University of Tromsø Sea Monitoring Program, which collects CTD-data from fixed stations all along the north-Norwegian coast including Porsangerfjord. Within the fjord, stations 1c, 2c, 3d, 4a and 4b are established monitoring stations and our seasonal zooplankton samples were collected as part of this cruise regime. A CTD-profile was collected prior to each zooplankton sample. The CTD-profiles were cast using a Sea-Bird Electronics SBE9 and a Sea-Bird Electronics SBE25 (Seabird Electronics Inc., USA). Due to loss of instrumentation during one cruise, we were not able to provide CTD-profiles for June 2014. In April 2013 CTD-profiles were collected at all stations (**Paper II, III**). Only environmental variables important for timing of meroplankton in the water column were included in the papers. These variables included water column temperature, salinity and *in situ* fluorescence. *In situ* fluorescence was calibrated to provide an approximate chlorophyll *a* concentration in the water column.

3.3 TAXONOMIC IDENTIFICATION AND STATISTICAL ANALYSIS

Zooplankton samples were analyzed in the laboratory at UiT, The Arctic University of Norway and the two main zooplankton components, meroplankton and holoplankton, were counted and identified (**Paper I and II**). First, the whole sample was sorted through and all decapod crab zoea were removed and stored for identification and reference (**Paper III**). Large macrozooplankton were also removed at this stage. Decapod zoea were first identified to genus (Figure 2a) or species (Figure 2b) level and then to zoeal stage using available identification literature. Anomuran decapods pass through four zoeal stages and a final glaucothoe stage that settles on the seafloor while brachyuran decapods have two zoeal stages and a settling megalopa stage (see Figure 2a and 2b for examples of stage I zoeae). Because the literature available for species and stage identification is based on larvae originating from other geographical localities, they differed slightly in size (one of the key ways of separating some species) from the zoea identified in this study. Therefore several repeated rounds of identification was needed to identify zoeae from Porsangerfjord. If key features separating two very similar species were absent (e.g. length of rostral spines on *Hyas araneus* vs. *Hyas coarctatus* in Figure 2c and 2d, respectively) zoeae were grouped in their respective higher taxon.

Second, randomized subsample aliquots were extracted from the zooplankton sample until approximately 300 individuals of each zooplankton component (meroplankton and holoplankton) were counted (600 individuals in total) using a stereomicroscope equipped with

a calibrated micrometer (**Paper I** and **II**). The aim was to identify all meroplankton to the level of genus or species using available identification keys. However, many soft-bodied meroplankton undergo big changes in morphology from the time they enter the water column to the time they are ready to settle (e.g. polychaete larvae in Figure 2f) and closely related species can often be very similar in morphology (e.g. bivalve and gastropod veligers in Figure 2g,h), making species identification difficult. Moreover, there is a scarcity in identification literature available for many marine invertebrate larval species and stages. The identification of larvae to a low taxonomic level of genus and species therefore proved to be highly complex for many taxa. To compensate for this, unidentifiable larvae were pooled according to their respective higher taxa or developmental stage (e.g. Prosobranchia veliger, Bivalvia veliger in Figure 2g,h).

Holoplankton were identified to the level of phylum or order (**Paper I**). Copepods were separated by order into cyclopoid and calanoid copepods and the calanoid copepods were further divided according to size, smaller and larger than 2 mm prosome length. Copepod nauplii were considered as a single group. Due to low representation the remaining holoplanktonic mesozooplankton and macrozooplankton were identified but designated as one group in results and discussion. With this identification scheme, we could describe general temporal and spatial trends in the holoplanktonic composition within the fjord.

Total and relative abundance of both zooplankton components were used in the analysis of temporal and spatial dynamics. This way the relative abundance of meroplankton in the zooplankton community could be evaluated. In **Paper I** and **Paper II**, total abundances were presented as individuals per cubic meter (ind. m⁻³). Because of a low number of individuals per sample, decapod zoea were presented as individuals per square meter (ind. m⁻² in **Paper III**). This is the main presentation method used in decapod zoea studies and makes comparisons easier. In the studies we used both univariate statistics: Kruskal-Wallis test; and multivariate statistics: Canonical Correspondence Analysis (CCA), Multivariate non-Parametric Permutation ANOVA (PERMANOVA), hierarchical clustering and Similarity Percentages Analysis (SIMPER). These methods were used to identify temporal and spatial differences in meroplankton composition and to pinpoint possible environmental variables responsible. R version 2.14.2 (R Development Core Team, 2012) using the vegan (Oksanen 2015) and pvclust (Suzuki and Shimodaira 2015) libraries, were used for statistical analysis. Graphs were

produced in SigmaPlot Version 13.0 (Systat Software, San Jose, CA), R version 2.14.2 and Windows Excel.

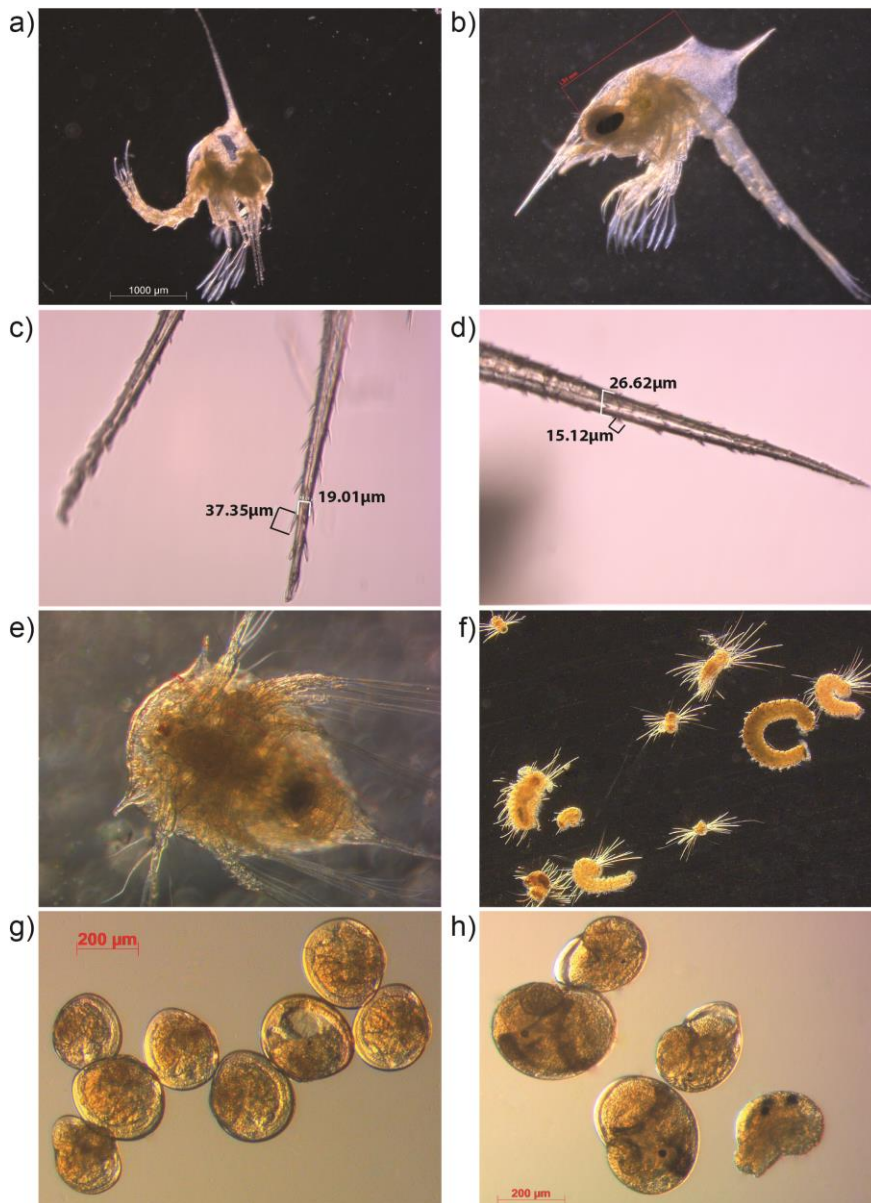


Figure 2. Photographs of meroplankton collected over the course of this study: a) *Hyas* sp. stage I zoea, b) stage I zoea of the red king crab *Paralithodes camtschaticus*, c) rostral spines of *Hyas araneus* zoea (spines are longer than the width of rostrum), d) rostral spines of *Hyas coarctatus* zoea (spines are shorter than the width of rostrum), e) cirripede *Balanus crenatus* nauplii, f) polychaete larvae of various stages and species (mainly Spionids), g) various bivalve veligers and h) various gastropod veligers.

4 SUMMARY OF RESULTS

Paper I: Seasonal dynamics of meroplankton in a high-latitude fjord

From the 21 samples collected at two stations (B4 and 3d) over a 1.5 year period, we identified 56 distinct morphological larval forms belonging to 41 benthic taxa and eight phyla. The two stations did not differ significantly in terms of meroplankton composition nor abundance. Multivariate analysis indicated that there were significantly different meroplankton compositions through the year separating into winter, spring, early summer and late summer assemblages. The winter composition of main meroplanktonic taxa was composed of mainly gastropod veligers and bryozoa cyphonautes, while the composition during spring was dominated by cirripede nauplii and polychaete larvae (Figure 3). In early summer a wide variety of meroplankton taxa were present, belonging primarily to polychaeta and echinodermata (Figure 3). Finally, late summer comprised of bivalve veligers and bryozoan cyphonautes larvae (Figure 3). The highest abundances of larvae appeared during spring and summer, forming two peaks in meroplankton abundance in April and August (Figure 3). The spring peak was dominated by cirripede nauplii, while the late summer peak was dominated by bivalve veligers. Meroplankton were the principal component in the zooplankton community in spring. By contrast, winter had a very low abundance of meroplankton and their relative abundance in the zooplankton community was negligible. The presence of a majority of meroplankton correlated with primary production and temperature in the water column. The fact that meroplankton were present in the water column through the whole year and at times were the dominant component in the zooplankton community, suggests that they, in addition to being important for benthic recruitment, are important in the pelagic ecosystem as grazers on phytoplankton and as prey for other organisms.

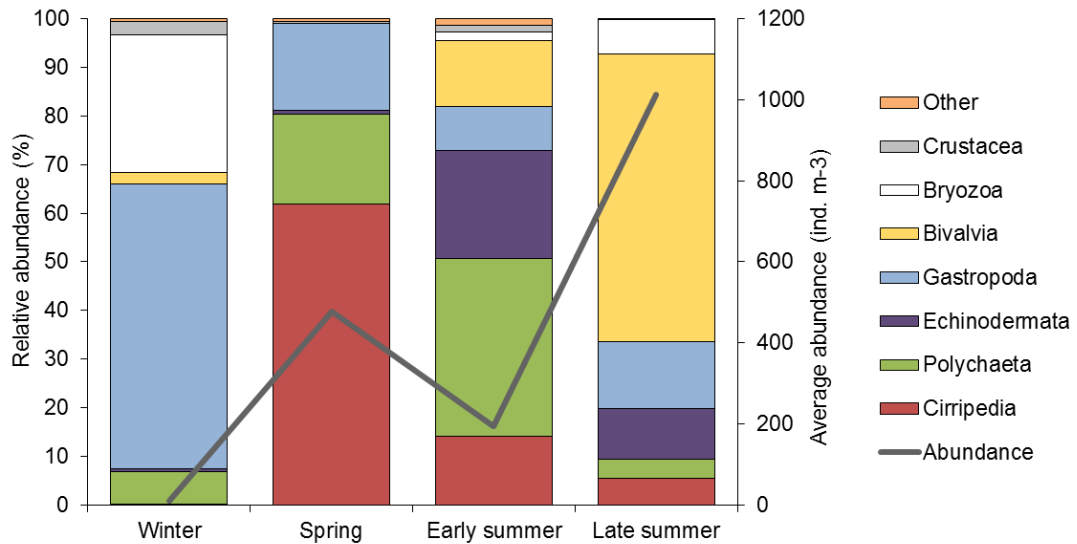


Figure 3. The seasonal relative abundance of the main meroplanktonic groups and the total abundance of meroplankton in Porsangerfjord, Norway (based on mean abundances from the two stations B4 and 3d).

Paper II: Spatial patterns of spring meroplankton along environmental gradients in a sub-Arctic fjord

Because April was one of the spring months that experienced a peak in meroplankton abundance and relative abundance in the zooplankton community, their spatial patterns, relationship with environmental variables and their relative abundance in the mesozooplankton community was investigated in April 2013. In this part of the study, a total of 32 morphologically different larval forms were identified belonging to 23 taxa and eight phyla. Meroplankton were found at all stations and their community structure and total abundance differed significantly along the fjord (Figure 4). The abundance in the Inner-basin and Outer-basin was low and dominated by gastropoda and echinodermata, respectively (Figure 4). The highest abundances were recorded in the Bays and the Middle-basin where cirripedia and polychaeta were dominant (Figure 4). Numerically meroplankton contributed highly to the zooplankton community in the Bays (30-90 %) and Middle-basin (13-48 %). Changes in community structure were attributed to spatial gradients in environmental variables such as chlorophyll *a*, salinity and temperature. When these results were compared with the seasonal communities found in Paper I, the different communities suggested a down-fjord seasonal succession in reproductive events where the Inner-basin had a community typical for late winter (dominated by gastropods), the Middle-basin typical of spring (dominated by cirripede nauplii)

while the Outer-basin was more typical for late spring to early summer (dominated by echinoderms).

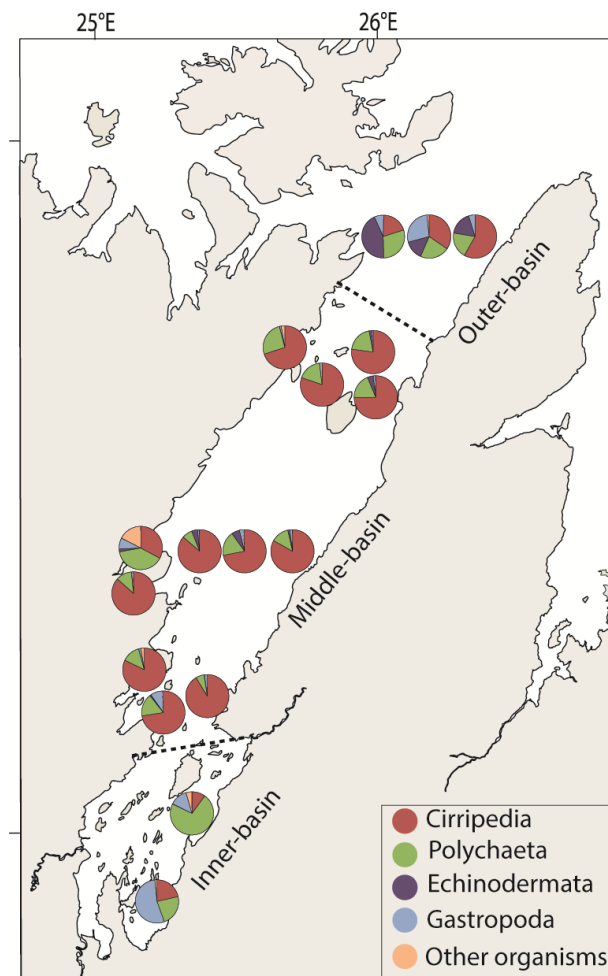


Figure 4. The spatial relative abundance of the main meroplanktonic groups in April 2013 in Porsangerfjord, Norway.

Paper III: Temporal and spatial dynamics of invasive Red King Crab larvae and co-existing decapods in north Norwegian waters

Temporal and spatial patterns in larval stages belonging to the invasive red king crab (*Paralithodes camtschaticus*) and co-existing native decapods was investigated at 6-18 stations over the whole study period (1.5-years). To explain the spawning behavior of the red king crab population in Norwegian waters, the degree of egg hatching was determined from females collected at selected stations in April 2013 and 2014. Larvae of the red king crab were the first to be released into the water column and display a prolonged larval release (Figure 5), where hatching starts in January and terminates in late April or early May. This is likely due to several peculiarities in their spawning behavior - like a protracted hatching that lasts 30 days for

individual females and a later shift in timing with each successive reproduction - together with the environmental effects influencing both the adults and their zoea. Two native larval decapods, *Pagurus pubescens* and *Hyas araneus*, displayed a similar behavior, appearing in the water column in February and March, respectively and residing there for three to four months (Figure 5). Finally, three native decapods, *Pagurus bernhardus*, *Hyas coarctatus* and *Munida* sp., were observed later in spring and summer and had a comparably shorter larval duration. The highest density of decapod larvae was located in shallow areas of the fjord and in locations with mixed sediment types of hard bottom and gravel, and may reflect aggregative behaviors displayed by spawning females. Based on the biogeographical origin of the decapod species, the differences in timing and duration in the water column is due to various tolerances to environmental variables. Moreover, findings from this study could help explain how high-latitude species such as the red king crab have successfully invaded the southern Barents Sea and how they may spread further along the Norwegian coast.

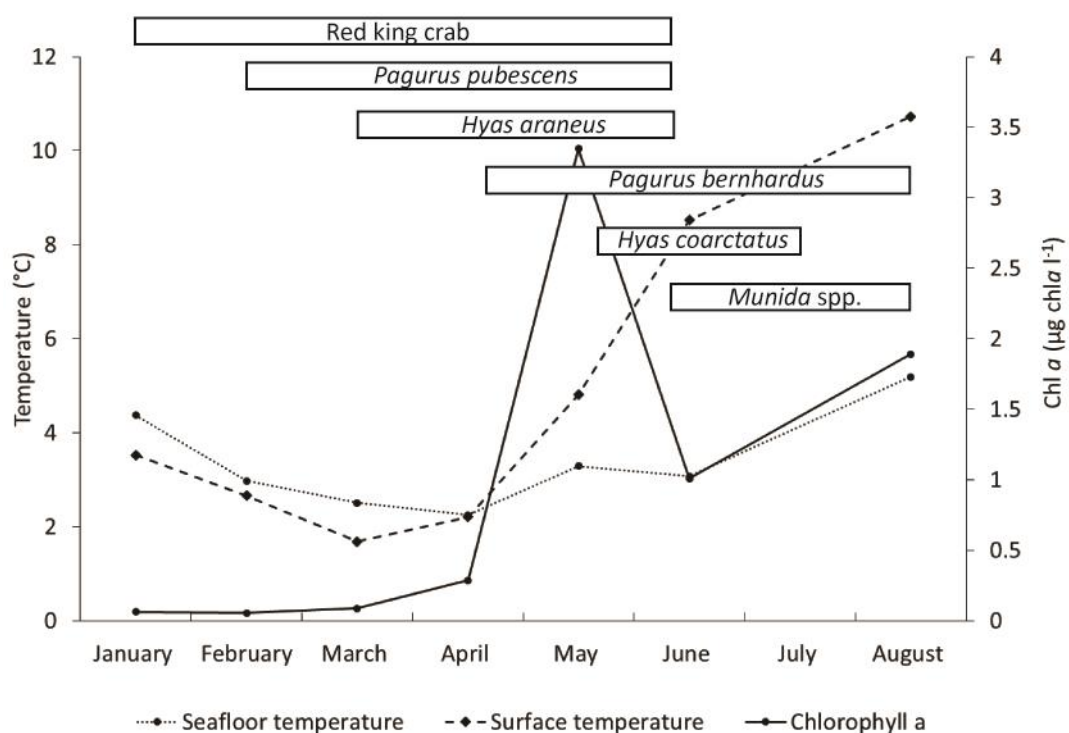


Figure 5. Timing and duration decapod zoeae various decapod species are found in the water column and the monthly average environmental variables – seafloor and surface temperature (°C) and Chlorophyll a ($\mu\text{g chla l}^{-1}$) in Porsangerfjord, Norway.

5 DISCUSSION

5.1 MEROPLANKTON COMPOSITION AND SEASONALITY

By sampling the sub-Arctic Porsangerfjord over a 1.5-year period, we found a strong seasonal variation in larval timing, duration and abundance in the water column (**Paper I, III**). The peak abundance and highest number of meroplanktonic taxa were found in spring and summer (**Paper I, II**). This appears to be a prominent feature across the whole sub-Arctic and Arctic (e.g. Eastern Greenland by Thorson 1936; Andersen 1984; Western Greenland by Smidt 1979; Arendt et al. 2013; the Chukchi Sea by Hopcroft et al. 2010; Questel et al. 2013; the Northeast Atlantic by Falk-Petersen 1982; Silberberger et al. 2016; Stübner et al. 2016; Kamchatka by Kulikova et al. 2000) and demonstrates that these seasons are important for spawning and reproduction of many benthic organisms at these latitudes.

Currently, only a handful of meroplankton studies have focused on identifying the entire meroplanktonic community to a high taxonomic level in sub-Arctic (**Paper I, II**; Falk-Petersen 1982; Shlüter and Rachor 2001; Silberberger et al. 2016) and high-Arctic waters (Thorson 1936; Smidt 1979; Andersen 1984; Fetzer and Arntz 2008). In Porsangerfjord, 41 benthic taxa and 75 distinct larval stages belonging to eight phyla were identified on a temporal and spatial scale (**Paper I, II, III**). Although this number of taxa is lower than that found in temperate waters (e.g. 160 taxa by Thorson 1946) and a recent sub-Arctic shelf study (65 taxa by Silberberger et al. 2016), it is within a comparable range to that of other high-latitude coastal areas and suggests that similar benthic compositions and reproductive strategies are operating in the sub-Arctic and Arctic (**Paper I**). The level of taxonomic resolution and identification of larval stage varies between studies due to the difficulty in identifying some larvae to a low taxonomic level and the scarcity of identification literature available for larvae of many boreal and a majority of Arctic species. Therefore, a higher number of taxa are most likely present at high-latitudes (**Paper I**). Morphological identification of mollusk larvae in particular has been fraught with difficulty regardless of latitude, as closely related species are indiscernible at early stages (summarized by Pulfrich 1997). Yet, in a recent study from Svalbard, bivalve veligers were identified to species level and larval stage by using a combination of morphological identification and molecular techniques (Brander et al. 2016). Combining classical morphological taxonomy with modern molecular methods are proving to be a promising future

within meroplankton biology and has been used in an increasing number of studies in Antarctic waters (e.g. Webb et al. 2006; Bowden et al. 2009).

Other year-round meroplankton studies at high-latitudes report a very similar but also somewhat different seasonal composition and development in the main meroplanktonic groups found in this study (**Paper I**). For example, a pulse of cirripedia nauplii is a common feature in spring, followed by multiple peaks of echinoderm and polychaete larvae through spring and summer, high abundance of bivalve veligers and bryozoan cyphonautes in late summer and fall and finally a low abundance of mainly gastropod veligers in winter appears to be a common scenario in the sub-Arctic and Arctic (e.g. **Paper I**; Smidt 1979; Kuklinski et al. 2013; Silberberger et al. 2016; Stübner et al. 2016). This pattern is also observed for polychaete and echinoid larvae, while bivalve veligers are only recorded in late summer in sub-Antarctic and high-Antarctic waters (Stanwell-Smith et al. 1999; Bowden et al. 2009; Sewell and Jury 2011). In contrast to the seasonal assemblages found in this study, Thorson (1936) did not record any gastropod veligers during winter in Franz Joseph Fjord, Greenland while Stübner et al. (2016) reported bivalve veligers and bryozoa cyphonautes in mid-winter in Adventfjord, Svalbard. Finding comparable seasonal compositions of the main meroplanktonic groups suggest that benthic adults belonging to these groups respond in similar ways to external and internal forces over broad geographical scales. At the same time, dissimilarities between studies are expected as various regions exhibit different hydrographics, hydrodynamics, substrate types and benthic adult compositions.

Identifying larvae to the lowest taxonomic level demonstrated that a seasonal succession of taxa, larval stages, abundance and durations are operating through the year in Porsangerfjord (**Paper I, III**). Three co-occurring mass spawning cirripede species were responsible for the peak meroplankton abundance in spring. This is similar to findings from sub-Arctic shelf seas outside Lofoten-Vesterålen, Norway, however unlike our finding they also detected a slight temporal succession in the timing of peak abundance for these species through spring and early summer (Silberberger et al. 2016). Interestingly, although the greatest variety of taxa had their peak larval abundance in the early summer months the total bulk of meroplankton decreased this season. This feature has also been found in Greenland fjords (Smidt 1897; Andersen 1984) and in another north Norwegian fjord (Balsfjord, Norway by Falk-Petersen 1982) and demonstrates that these taxa are not mass spawners to the same degree as cirripedes and bivalves. The duration different larvae were present in the water column varied, ranging from

six months for red king crab zoea to single observations of *Anomia* sp. in August (**Paper I, III**). Other organisms like gastropods were found year around but due to the lack of high taxonomic resolution on this taxon, it is unknown if this consists of one or several species with continued or successive spawning. It is important to note that by sampling monthly to bi-monthly we have likely missed some larval dynamics, as some larvae may have appeared and settled between our sampling dates (**Paper I, II**). Moreover, by using a coarse mesh size of 180 μm many young larval stages of bivalves, polychaetes and trochophores have escaped the net (**Paper I, II**). Despite this by comparing findings between meroplankton studies using various sampling frequencies and methods we are steadily getting closer to understanding the full scope of meroplankton seasonality at high-latitudes.

5.2 ENVIRONMENTAL VARIABLES CORRELATES WITH MEROPLANKTON SEASONALITY

The meroplankton assemblage is affected by environmental variables in boreal (Thorson 1946), sub-Arctic (Silberberger et al. 2016) and Arctic waters (Brander et al. 2016; Kuklinski et al. 2013; Stübner et al. 2016). In the present study, correlations between the environment and meroplankton were detected on both a temporal (**Paper I**) and spatial scale (**Paper II**). The majority of meroplankton in Porsangerfjord are planktotrophic (**Paper I**) and their ability to locate an adequate quantity and quality of food is vital for development and survival (Thorson 1950). Thus timing larval release to phytoplankton availability greatly increases the chance of propagules surviving to settlement. Mazzuco and Kasten (2017) argued that releasing larvae at a time when food is abundant in the water column is a strong evolutionary driver for benthic invertebrates with feeding larvae. This likely explains why the greatest number and variety of planktotrophic cirripede, polychaete, decapod, echinoderm and bivalve larvae are present during the spring and summer phytoplankton bloom in sub-Arctic (**Paper I, II, III**; Falk-Petersen 1982; Silberberger et al. 2016) and Arctic waters (Smidt 1979; Stübner et al. 2016). Some benthic invertebrates also have temperature requirements during their larval phase (Mileikovsky 1968). For example, larvae of many boreal organisms need warmer sea surface temperatures to successfully grow, feed and survive (e.g. the boreal hermit crab *P. bernhardus* in **Paper III**). Increased temperatures will ultimately accelerate larval development and thereby shorten the time larvae are exposed to pelagic predators and potential adverse advection with currents.

For invertebrates to synchronize spawning and larval release with the phytoplankton bloom and favorable sea surface temperatures, they rely on external cues like chlorophyll *a* concentration, temperature and photoperiod as triggers (**Paper I, II**; Kuklinski et al. 2013; Silberberger et al. 2016; Stübner et al. 2016). In this study, the identification of larvae to the lowest taxonomic level made it possible to discern when and possibly why certain taxa are present in the water column through the year. Cirripedes, such as *Semibalanus balanoides*, release their nauplii when they come into direct contact with substantial concentrations of diatom cells (Barnes 1962). Waiting for this direct cue is a strong signal that an adequate amount of suitable food is available as soon as their larvae enter the water column in spring (**Paper I, II**). The boreal-Arctic spider crab *H. araneus* and polychaetes belonging to genus *Dipolydora* require a combination of cooling temperatures and increasing photoperiod prior to and during egg hatching in late winter and early spring (**Paper I**; Petersen 1995). This early spawning mechanism is advantageous at high-latitudes where the onset of the phytoplankton bloom can occur while temperatures are low but photoperiod is increasing (Eilertsen and Frantzen 2007). In contrast, many polychaetes (Blake and Arnofsky 1999), echinoderms (Mercier and Hamel 2009), bivalves (Günther and Fedyaikov 2000) and decapods (**Paper III**; Lindley 1998) require a combined increase in temperature, photoperiod and/or nutrients. Larvae belonging to these groups are released through summer, thereby coinciding with peak phytoplankton bloom and sea surface temperature (**Paper I, III**). These findings suggest that benthic invertebrates are well adapted to the temporal dynamics in phytoplankton and temperature in Porsangerfjord.

Interestingly, some meroplankters appear to be unsynchronized with favorable environmental variables and reside in the water column in fall and winter (**Paper I**; Hirche and Kosobokova 2011; Silberberger et al. 2016; Stübner et al. 2016). It has been suggested that many of these larvae are lecithotrophic and can thus utilize a larger part of the year for spawning, even when there is no phytoplankton available (Thorson 1950). However, in this study some larvae present this season could be planktotrophic and likely utilize alternative food sources (**Paper I**). The advantage to releasing larvae in winter could be less competition for space when settling on the seafloor (Kuklinski et al. 2013; Meyer et al. 2017). Moreover, newly settled recruits potentially receive sinking nutrients in the form of phytoplankton cells and detritus during the phytoplankton bloom, providing them with a good start to the benthic phase (Thorson 1946). These findings add to the evidence that benthic invertebrate reproduction and

biological processes are operating during the polar night in not only Arctic waters (Berge 2015), but also in sub-Arctic waters (**Paper I**; Silberberger et al. 2016).

5.3 ENVIRONMENTAL GRADIENTS CAUSE SPATIAL VARIATIONS IN MEROPLANKTON ASSEMBLAGE

Spatial patterns of planktonic larvae is influenced by the local adult community, environmental variables, adult spawning behavior, larval behavior, larval duration and hydrodynamics (Shanks 2009; Pineda et al. 2010). In this thesis, I provide some of the first evidence that down-fjord gradients in environmental variables influence spawning and larval release of benthic invertebrates (**Paper II**). In the Inner-basin, sub-zero temperatures and low chlorophyll *a* concentrations may have inhibited spawning for some benthic adults, thereby causing the meroplankton community to be of a late winter and early spring assemblage in April 2013. In contrast, the community in the Outer-basin consisted of taxa that are more typical of a spring and early summer assemblage, and correlated with the highest seafloor salinities and temperatures recorded in April. A similar reproductive delay has been found for the holoplanktonic copepod *Calanus finmarchicus* in the Inner-basin of Porsangerfjord. They release their nauplii one month later and have a longer developmental time than those residing in the Outer-basin (Priou 2015). Spatial studies in other Atlantic influenced sub-Arctic and high-Arctic fjords have shown a similar up-fjord delay in reproduction and development by holoplanktonic organisms (e.g. Falkenhaus et al. 1997). Thus, reproductive patterns in both the benthic community and the holoplanktonic are influenced by along fjord gradients in environmental variables of high-latitude fjords.

Two general features of potential larval origin and settlement in the fjord became apparent: first, because the larval assemblage reflected the benthic adult composition and there was a significant difference in meroplankton community and abundance between the three basins it could be suggest that larvae were, to some extent, locally produced. Second, shallow protected bay stations had the greatest abundances of larvae both on a temporal and spatial scale and likely act as hotspots and retention areas for propagules of intertidal and subtidal adults. The benthic invertebrate community within the fjord may therefore be self-recruiting depending on area of release. Recent evidence indicate that local retention close to the release site may actually be a common feature for many pelagic larvae in coastal, fjord and embayment waters (Archambault et al. 1998; Levin 2006; Silberberger et al. 2016). Current systems within parts

of Porsangerfjord are however strong, water exchange between the Mid-basin and Outer-basin is frequent and larval duration in high-latitudes can last between 2-8 weeks, thus larval transport out of the fjord and intrusion of propagules originating from outside the fjord cannot be entirely excluded. A recent study on the mesozooplankton community in Porsangerfjord found that advection is occurring due to the presence of holoplanktonic organisms originating from outside the fjord in the Outer-basin and the outer parts of the Middle-basin (Varela 2015). In contrast, the Inner-basin is more enclosed and experience less larval advection due to the shallow sill (Myksvoll et al. 2012), which may aid in the maintenance of a unique refuge area of Arctic benthic species in this basin.

5.4 MEROPLANKTON IN THE MESOZOOPLANKTON COMMUNITY AND THE FOOD WEB

In Porsangerfjord meroplankton was periodically a high contributor (summer) and a dominant (spring) component in the mesozooplankton community on both a temporal (**Paper I**) and spatial scale (**Paper II**). This agrees well with other studies on seasonal dynamics of zooplankton in high-latitude coastal and fjord studies, which have shown a periodic (e.g. Smidt 1979; Willis et al. 2006; Kwasniewski et al. 2013; Questel et al. 2013) or even a continuous (Stübner et al. 2016) dominance and high contribution of meroplankton through spring and summer. In contrast to coastal waters, meroplankton are a negligible component in the water column of the deep open ocean (Longhurst 1998) and is linked with a predominantly direct benthic reproduction and development at great depths. The spring dominance of meroplankton at high-latitudes typically appear at the start of the phytoplankton bloom prior to the increase in copepods and is predominantly due to the pulse of planktotrophic cirripede nauplii (**Paper I**; Smidt 1979; Kwasniewski et al. 2013; Stübner et al. 2016). Similar to our study, Walkusz et al. (2009) found that cirripede nauplii and echinoderm larvae caused a pulsed and patchy dominance of meroplankton thorough spring and summer in Kongsfjord, Svalbard. A dominance due to cirripedes was however not found in Young Sound east Greenland (Nilsen et al. 2007) and is likely caused by prolonged ice scouring causing adults to become dislodged from the sea floor (Kwasniewski et al. 2013). A recent study in Adventfjorden, Svalbard found that bivalve veligers caused a prolonged dominance of meroplankton through mid to late summer (Stübner et al. 2016). Although meroplankton abundance, distribution, seasonality and composition in fjords and coastal areas is variable in nature, their periodic high contribution to

the mesozooplankton community during the productive seasons could point to an important role in the pelagic food web.

Currently, the general consensus is that feeding pressure exerted by meroplankton is negligible due to low abundances and clearance rates (Strathmann 1996; Hansen et al. 1997). Yet, many dominant meroplankton found in this (**Paper I**) and a recent Arctic study (Fetzer and Arntz 2008) appear to be planktotrophic and can feed on a mixture of diatoms, flagellates, ciliates, bacteria, detritus and dissolved organic materials (Young et al. 2002). Currently, literature on larval nutritional mode (planktotrophic vs. lecithotrophic), ingestion rates and food selectivity for many benthic invertebrates are scarce (**Paper I**). The studies that have looked into these mechanisms show that feeding often change with larval ontogeny and differ between taxa and larvae of similar size (e.g. Cirripedes by Stone 1989; Echinoderms by Hart 1996; Opisthobranchs by Hansen 1991; Polychaetes by Hansen et al. 2010) making the potential role of meroplankton in the pelagic food web difficult to determine. In general, crustacean larvae have higher ingestion rates, compared to ciliated filter-feeding larvae due to a more efficient feeding behavior and morphology of feeding structures (Strathmann 1971; Hansen et al. 1997). Yet, ciliated larvae like polychaetes, mollusks and echinoderms display an omnivorous diet (Young et al. 2002) and their feeding pressure can be substantial depending on their abundance and prey field. Jørgensen (1981) found an abundant veliger cohort of the bivalve *Mytilus edulis* to have a daily clearance rate of $0.25 - 1.39 \text{ ml larva}^{-1} \text{ d}^{-1}$ on nanophytoplankton, in Isefjord, Denmark, which resulted in a loss of 40 – 50 % nanophytoplankton in local waters. Since crustacean and ciliated meroplankton of different species and sizes occur simultaneously in high abundances in fjords and estuaries they should not be overlooked as part of the food-web structure. Meroplanktonic larvae can also serve as prey for a wide range of pelagic predators such as chaetognaths, ctenophores, hydromedusae, scyphomedusae, euphausiids, shrimp, fish larvae and juveniles and other predatory meroplanktonic larvae (Thorson, 1950), and many of these predators overlapped with meroplankton in time and space in the present study (**Paper I**). Juvenile capelin and herring caught at the mouth of Porsangerfjord have been found to have bivalve veligers, polychaete larvae, cirripede nauplii and bryozoa cyphonautes in their stomachs (Fossheim et al. 2006; Pedersen and Fossheim 2008). Thus during spring and summer, meroplankton is an important food source for pelagic predators. The periodic dominance of meroplankton in the water column certainly warrants further research on what trophic role meroplankton may have in high-latitude coastal waters.

5.5 CAN LARVAL DYNAMICS SHED LIGHT ON THE INVASIVE SUCCESS OF RED KING CRABS?

For an invasive species to persist and survive in a new environment they need to recruit successfully on a consistent basis (Anger 2006). Hence, invasive marine invertebrates with planktotrophic larvae must release their propagules at a time when they experience favorable conditions in the water column. The present study, showed that larval release by red king crabs in Porsangerfjord is prolonged over a period of approximately 4 to 5 months, starting in winter (January) and ending in early summer (May). Disseminating larval release over such a long period is a highly advantageous reproductive behavior because it increases the chance that at least some zoea will encounter favorable conditions. That zoea of the red king crab can tolerate a broad range of temperatures and salinities make them even more suited for life in fluctuating environments (Larsen 1996). However, duration of the zoeal phase is highly sensitive to food availability and temperature in the water column (Paul and Paul 1980; Shirley and Shirley 1990). In north Norwegian and native Alaskan waters, larval release by red king crabs appeared to be uncoupled with the phytoplankton bloom (**Paper III**; Shirley and Shirley 1989; Shirley and Shirley 1990). Therefore, zoeae residing in the water column in January and February may experience a suboptimal availability of food, leading to a prolonged larval phase and subsequent reduced survival (**Paper III**; Shirley and Shirley 1990). Those present in the water column from March will encounter favorable conditions as the phytoplankton bloom builds and the pulse of suitable meroplanktonic larval prey becomes available (**Paper III**).

When the final pelagic stage of the red king crab is ready to settle on the seafloor they actively chose shallow (< 27 m) structurally complex habitats with heterogeneous hard bottom and communities of bryozoans and hydrozoans and thus plenty of hiding places from predators and availability of food (Stevens and Kittaka 1998). Having a long individual residence time in the water column (two months) coupled with a protracted hatching period leaves zoeae of the red king crab at the risk of dispersing vast distances and potentially away from favorable places to settle. In a 3 year modelling study on advection of red king crab zoea in fjords and along the coast of northern Norway, Pedersen et al. (2006) found that zoeae released within fjords and semi-enclosed areas generally stayed close to their release site each year while those released in less protected areas on the coast were transported into the Barents Sea or along the shelf with the Norwegian coastal current depending on the wind systems. The present study suggested that some degree of retention was operating within Porsangerfjord, as zoeae were only found in the

Middle-basin and the bay stations retained the greatest abundance of zoeae (e.g. stations B4 and B3 in **Paper III**). Zoeae released or transported into the Outer-basin of Porsangerfjord may be subject to a higher level of advection (**Paper II**), which based on advection modeling mainly travel east with the Norwegian coastal current (Pedersen et al. 2006). However, a small fraction are transported west and thus outside the quota regulated area. Having a migratory spawning behavior where larvae are released at shallow protected sites, semi-enclosed areas and within fjords is highly advantageous for this species as it increases the chance that zoeae are retained in close proximity to suitable settlement areas. This coupled with the complex coastal and seafloor topography with numerous fjords and semi-enclosed areas along the Norwegian coast increases the chance that red king crab zoeae do not travel far (Shanks 2009), can locate favorable settlement habitats and thus survive their larval phase.

Although the open fishery and decimation fishery for red king crabs has slowed their spread west of 26 °E (Sundet and Hoel 2016), young crabs have recently been caught in fjords around Tromsø (red circle in Figure 1) indicating that a local stock has established in the area (E. M. Nilssen pers. comm.). Given their wide tolerance to environmental variables and their potential for further spread there is concern that the red king crab could also establish north in Svalbard waters (Christiansen et al. 2015). It is unlikely that adult migration will be responsible for any northward migration given that the deep depth between the continental shelves of Norway and Svalbard is outside the depth range utilized by adults. However, if a crab stock establishes around Vesterålen, Norway (yellow circle in Figure 1), larvae could be advected with the strong Norwegian Atlantic Current that passes this area before moving into Svalbard waters (Loeng 1991). A recent study modelling the drift of bivalve veligers from Vesterålen to Svalbard showed that surface-layer transport takes between 47 to 80 days in May and that transport is likely faster earlier in spring (Berge et al. 2005). A protracted larval release through spring (**Paper III**) and a larval duration that lasts on average two months, could thus provide plenty of opportunities for northward advection of king crab zoeae. For these zoeae to successfully recruit and establish a new Svalbard stock there needs to be an adequate prey field available in the water column as they advect and that they need to locate suitable settlement localities once they reach Svalbard. Future research on king crab zoea should therefore also model a potential northward advection. The findings in this study ultimately provides further evidence that a strong fishery on particularly female red king crabs is vital when aiming at decreasing and restricting the spread of crab outside the quota regulated area in northern Norway.

It is clear that for the red king crab as population and from an economic standpoint, the introduction has been successful and that a combination of different life history traits and life cycle mechanisms have contributed to this success. These include high individual investments in eggs (Stevens 2014), high female fecundity (Hjelset et al. 2012), a large size at maturity (Hjelset et al. 2008), a migratory spawning behavior to shallow protected areas (**Paper III**; Sundet and Hjelset 2010), a protracted zoeal release (**Paper III**), a temporal match between favorable pelagic conditions and zoeae (**Paper III**), zoeal and adult stages that are tolerant to a wide range of temperatures (Larsen 1996; Christiansen et al. 2015), an omnivorous diet (Paul et al. 1979; Fuhrmann et al. 2015; Fuhrmann et al. 2017) and the ability to migrate great distances into new areas (Windsland et al. 2014). Moreover, characteristics of the southern Barents Sea and Porsangerfjord contribute to the success by providing favorable environmental variables for both the pelagic and benthic phase, a rich prey field (Fuhrmann et al. 2015), few natural enemies (Sundet 2014) and little competition during their adult life (Fuhrmann et al. 2017) and a complex coastal topography with a wide range of suitable areas for feeding, spawning and larval settlement coupled with hydrodynamics that keep some larvae close to suitable settlement locations (Pedersen et al. 2006). Combined, these factors show that the red king crab have the potential to continue their spread south along the Norwegian coast and potentially north to Svalbard waters.

5.6 BENTHIC INVERTEBRATE REPRODUCTION IN A WARMING OCEAN

In this study we show that shifts in timing of larval release due to changes in temperature and phytoplankton bloom occur at the level of individual species and main meroplanktonic groups on broad latitudinal scales (**Paper I, III**), over short spatial scales (**Paper II**) and interannually (**Paper I**). For example, cirripeds nauplii appear later in regions with delayed bloom situations (**Paper II**). Boreal organisms such as the hermit crab *Pagurus bernhardus* require warm temperatures in the water column to hatch their eggs and for their larvae to survive, therefore a later larval release is observed with increased latitude and subsequent later warming of the water column (**Paper III**; Lindley 1987; Lindley et al. 1993). This demonstrates how reproductive phenology of benthic invertebrates is fine-tuned with local environmental variability in the various regions they inhabit. Temperature has a strong influence on benthic invertebrate reproduction. In a warming ocean due to climate change, long term temperature

increase may have consequences for reproductive phenology, recruitment success, range expansion of benthic organisms and benthic community structure in sub-Arctic and Arctic waters. Changes in timing of spawning has already been demonstrated for echinoderms in the North Atlantic and North Sea, which in a 44 year time series appear progressively earlier in the year as temperatures in the water column have gradually increased (Edwards and Richardson 2004; Kirby and Lindley 2004; Kirby et al. 2008). Shifts in phenology have been proposed to cause a potential mismatch in time between larvae and the food and environment they require (Atkinson et al. 2015). How larval survival and reproductive cycles of benthic organisms will respond to higher temperatures in the future, will depend on their niche breadth, plasticity and ability to adapt (Philipart et al. 2014; Slayter et al. 2013). Here an organism's niche can be defined, in the widest sense, as the range of tolerance for multiple environmental factors like temperature and salinity, their dietary requirements and their utilization of these both in time and space (Hutchinson 1957; Slayter et al. 2013). Species with a broad generalist niche during their adult and larval stage could be expected to be more tolerant to increased temperatures. Examples of such species are the red king crab which are tolerant to a wide array of temperatures during a majority of their life and disseminates larval release over time in order to optimally utilize food resources in the water column (**Paper III**). Specialist species with a narrower niche are likely to be less tolerant to increased temperatures and may experience periods that are suboptimal for successful reproduction. Research therefore needs to continue looking at environmental tolerances, larval timing in the water column and how timing corresponds with favorable environmental variables.

The north Norwegian coast lies at the transition between sub-Arctic and high-Arctic waters and serves as a biogeographical transitional zone for many benthic organisms, which reside at their northernmost and southernmost distribution limit (Mileikovsky 1968). Temperate and boreal species requiring warm temperatures for reproduction could find a warming Arctic more favorable and thus move northward. A northward shift from sub-Arctic Norwegian to Arctic Svalbard waters has already been noted for the boreal bivalve *Mytilus edulis* and has been attributed to periodically warm years (Berge et al. 2005). Similar expansions could be expected for other organisms. For example, females of the hermit crab *P. bernhardus*, require late fall and winter temperatures of between 6 to 8 °C to produce eggs (Lancaster 1990), while the larval stage require temperatures above 6 °C to survive in spring (Dawirs 1979). Currently these temperature requirements are too high for this crab to establish a viable population in Svalbard waters where temperatures are generally lower than 6 °C in fall and winter (Loeng

1991). In contrast, Arctic species that require cold winter temperatures for reproduction will likely respond in the opposite way by retreating north. Thus, a predicted temperature increase of 2 to 4 °C during winter in high-latitude waters by the end of the century (IPCC 2001), will certainly cause changes in local reproductive phenology and distribution patterns of benthic invertebrates.

6 CONCLUSIONS AND FUTURE PERSPECTIVES

This thesis provided new knowledge on meroplankton dynamics in sub-Arctic waters, including their temporal and spatial abundance, assemblage and relative abundance in the mesozooplankton community. Moreover, it was shown that reproductive strategies of the red king crab makes them well suited for life in the southern Barents Sea and that they are equipped to continue their spread westward and potentially north into Svalbard waters.

The composition and abundance of meroplankton formed four distinct seasonal assemblages caused by a complex succession of taxa and larval stages through the year. Larvae varied in the duration they resided in the water column, some benthic invertebrates were mass spawners producing large quantities of larvae causing the bulk of meroplankton to peak some months. These finding provides strong evidence that benthic invertebrates are tuned to release their larvae at different parts of the year and shows various reproductive strategies and life history traits are operating in sub-Arctic waters. Because a majority of larvae correlated with the phytoplankton bloom through spring and summer it can be concluded that phytoplankton is involved in governing when spawning and larval release should take place for many benthic organisms and may act as a direct trigger for some species. Strengthening notion is the fact that many of these larvae were identified as planktotrophic and thus need to be released when food is available in the water column. Meroplankton also correlated with temperature, where some species wait for an increase in temperature before spawning. This can increase larval survival by shortening the time they reside in the water column. Finding an up-fjord delay in the seasonal succession of meroplankton communities which correlated with the up-fjord decrease in temperature and chlorophyll *a* provides further evidence that timing of some benthic larvae is coupled with temperature and phytoplankton. The significantly different communities in the three basins and high concentration of larvae in protected bays suggests that larvae are locally produced and may add to increasing evidence that local retention is a common feature in fjord and coastal waters. Yet some degree of larval transport into and out of the fjord cannot be entirely excluded. To elucidate the origin of larvae in the fjord requires studying spatial patterns in larval supply, juvenile settlement localities and adult compositions. A periodic dominance of planktotrophic meroplankton in the mesozooplankton community both in space and time suggests that they are an important part of the pelagic food web, both as grazers on phytoplankton and as potential prey for other pelagic predators. This therefore warrants further

studies on larval feeding type (planktotrophic vs. lecithotrophic), diet and potential predators on meroplankton at high-latitudes.

Red king crabs released their larvae over a period of four to five months and larvae were present in the water column for six months. Having a protracted larval release acts as a successful reproductive strategy for this high-latitude invasive species, ensuring that at least some larvae will match the variable phytoplankton bloom and thus survive to settlement. This coupled with a complex and favorable coastal topography with plenty of shallow protected areas to release larvae, retain larvae and for juveniles to settle makes the red king crab well equipped for life in the southern Barents Sea. It also makes them able to continue their westward spread along the Norwegian coast and potentially advect north into Svalbard waters. Therefore, to restrict its spread it is vital that the Norwegian government continue the free fishery and decimation fishery on female crabs outside the quota restricted area. Further research is needed to model potential northward drift of zoeae, to identify their predator-prey relationship with phytoplankton and other prey organisms and identify potential predators in the water column of Norwegian waters.

There is still a strong need to better understand various reproductive strategies and the temporal and spatial patterns in spawning and larval release displayed by benthic invertebrates and how this structures benthic populations. Moreover, predicting how species may respond to warmer temperatures due to climate change and how this may change benthic community structure calls for a more holistic research effort on both the pelagic and benthic phase. This will require the identification of meroplankton in spatial and temporal zooplankton studies together with benthic studies that incorporates juvenile settlement dynamics with adult population patterns in sub-Arctic and high-Arctic waters. Identification of larvae to the level of species, genus and larval stage should become a central part when working with meroplankton and can be done by combining morphological identification with molecular techniques. Moreover, field and laboratory experiments on reproductive strategies and tolerances to various environmental variables during the adult and larval phase of benthic invertebrates needs to be continued.

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