



Seasonal dynamics of meroplankton in a high-latitude fjord



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ABSTRACT

Knowledge on the seasonal timing and composition of pelagic larvae of many benthic invertebrates, referred to as meroplankton, is limited for high-latitude fjords and coastal areas. We investigated the seasonal dynamics of meroplankton in the sub-Arctic Porsangerfjord (70°N), Norway, by examining their seasonal changes in relation to temperature, chlorophyll *a* and salinity. Samples were collected at two stations between February 2013 and August 2014. We identified 41 meroplanktonic taxa belonging to eight phyla. Multivariate analysis indicated different meroplankton compositions in winter, spring, early summer and late summer. More larvae appeared during spring and summer, forming two peaks in meroplankton abundance. The spring peak was dominated by cirripede nauplii, and late summer peak was dominated by bivalve veligers. Moreover, spring meroplankton were the dominant component in the zooplankton community this season. In winter, low abundances and few meroplanktonic taxa were observed. Timing for a majority of meroplankton correlated with primary production and temperature. The presence of meroplankton in the water column through the whole year and at times dominant in the zooplankton community, suggests that they, in addition to being important for benthic recruitment, may play a role in the pelagic ecosystem as grazers on phytoplankton and as prey for other organisms.

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1. Introduction

Many benthic organisms have an indirect development, producing pelagic larvae, termed meroplankton, which go through several distinct phases before settling on the sea floor. Meroplanktonic larvae are important for benthic organisms, as their survival and ability to locate a suitable habitat for settlement determines the success of recruitment to the adult population. The balance between mortality and settlement is complex and may be influenced by temperature and salinity, transportation to unfavorable habitats, food availability and predation (Todd, 1998).

In tropical waters, benthic invertebrates display a continuous spawning behavior through the year, whereas a more pronounced seasonal reproduction is common at higher-latitudes (Giese and Pearse, 1977). Strong seasonal variability in environmental variables such as temperature, salinity, light availability and primary production characterize high-latitude coastal waters. These factors in turn influence reproduction, abundance and distribution of both permanent pelagic residents, holoplankton (Fossheim and Primicerio, 2008; Tande, 1989), and meroplankton (Morgan, 1995). For benthic invertebrates, changes in photoperiod and primary production are thought to be the

strongest spawning cues, with temperature and salinity acting as additional triggers (Olive, 1995). Thus, the spawning times of benthic organisms and the resulting composition of meroplanktonic communities vary through the year.

Meroplanktonic larvae can spend intervals from hours to years in the upper water column, where a wide range of predators may prey upon them (Thorson, 1950). During their time there meroplankton display two nutritional modes: some are planktotrophic, feeding as herbivores, carnivores or detritivores, while others are lecithotrophic, not feeding but surviving on yolk and lipid supplied in the egg (Mileikovskiy, 1971). A majority of planktotrophic larvae feed on phytoplankton and are dependent on locating food for survival. Thus, spawning just prior to or during the spring and summer phytoplankton bloom provides the best feeding condition for such larvae. High densities of meroplankton have been found in high-latitude coastal waters at the onset of the phytoplankton spring bloom (Kuklinski et al., 2013; Smidt, 1979; Stübner et al., 2016). In contrast, lecithotrophic larvae are not dependent on being spawned during the food-rich periods of spring and summer.

Meroplankton are drifters in the watercolumn and their horizontal distribution is primarily shaped by local adult populations and advective dispersal (Mileikovskiy, 1968). Dispersal to new areas not only allows population expansion to suitable new sites, it ensures that sessile adults have the opportunity of exchanging genetic material with other populations (Scheltema, 1986). The distance a propagule may disperse depends on current speeds and directions and on the vertical swimming

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behaviour and developmental time of individuals before settlement (Scheltema, 1986).

Strong latitudinal trends in benthic reproductive strategies were observed by early polar researchers (Thomson, 1876; Thorson, 1936, 1946, 1950) and led to the formulation of one of the main paradigms in meroplankton research, Thorson's rule. It states that the number of benthic adults producing non-pelagic larvae increases with latitude and depth (Mileikovsky, 1971). The paradigm has received considerable 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; Stanwell-Smith et al., 1999). Today the paradigm receives less support and has been modified to include the observation of higher proportions of lecithotrophic pelagic larvae at high-latitudes (Clarke, 1992; Marshall et al., 2012). However, since some meroplanktonic larvae are found in high abundances during spring and summer they could, depending on their nutritional mode, be important phytoplankton grazers as well as prey in the water column.

Studies of seasonal changes in zooplankton at high-latitudes have mainly focused on holoplankton, while meroplankton are typically registered to the level of phylum (e.g. Arashkevich et al., 2002; Hopkins et al., 1989). A modest number of studies have focused on the year around seasonality of meroplankton within Arctic (Smidt, 1979; Falk-Petersen, 1982a; Kuklinski et al., 2013; Silberberger et al., 2016; Stübner et al., 2016; Thorson, 1936) and Antarctic waters (Bowden et al., 2009; Freire et al., 2006; Sewell and Jury, 2011; Stanwell-Smith et al., 1999). More short-term surveys looking at the spatial distribution, abundance, biomass and composition in connection to environmental and biological conditions have been conducted in the Arctic (e.g. Andersen, 1984; Clough et al., 1997; Fetzer, 2003; Mileikovsky, 1968, 1970; Schlüter and Rachor, 2001).

Here we present a 1.5-year study of the seasonal dynamics of meroplankton in the sub-Arctic Porsangerfjord, Norway. This fjord is located adjacent to the Barents Sea and has a high biomass and active production of benthic invertebrates (Fuhrmann et al., 2015). The main objectives for the study were i) to investigate the seasonal changes in meroplankton abundance, composition and nutritional modes, ii) to identify the environmental drivers responsible for changes in meroplankton composition and iii) to estimate the seasonal proportion of meroplankton in the zooplankton community. Furthermore, the local benthic community and hydrography within the fjord are discussed in relation to meroplankton dynamics. Two contrasting stations were examined in order to explore the effects of depth and distance from shore on meroplanktonic dynamics.

2. Materials and methods

2.1. Study area

Porsangerfjord is a broad fjord that is oriented in a north-south direction between 70–71°N and 25–26.5°E, with a length of 100 km and a width of 15–20 km (Fig. 1) (Myksvoll et al., 2012). There is little freshwater runoff from land and based on bathymetry and water exchange, the fjord is separated into outer, middle and inner basins (Mankettikkara, 2013; Svendsen, 1991). A shallow (60 m) sill approximately 30 km from the head of the fjord delineates the inner basin; a sill at 180 m separates the middle basin from the outer fjord. The outer basin is open to the coast (Myksvoll et al., 2012). The outer and middle basins are classified as semi-enclosed with frequent exchanges of deep water with the Norwegian Coastal Current (NCC) and the Barents Sea (Eilertsen and Skarðhamar, 2006; Svendsen, 1995; Wassmann et al., 1996). The water in the inner basin has little contact with the coast and is characterized as Arctic, with temperatures reaching $-1.7\text{ }^{\circ}\text{C}$ (Wassmann et al., 1996). The eastern side of the fjord is characterized by a northward outflow current of water from the fjord, with low temperature and salinity. A southerly inflowing current of warmer, saline coastal water characterizes the western side (Myksvoll et al., 2012).

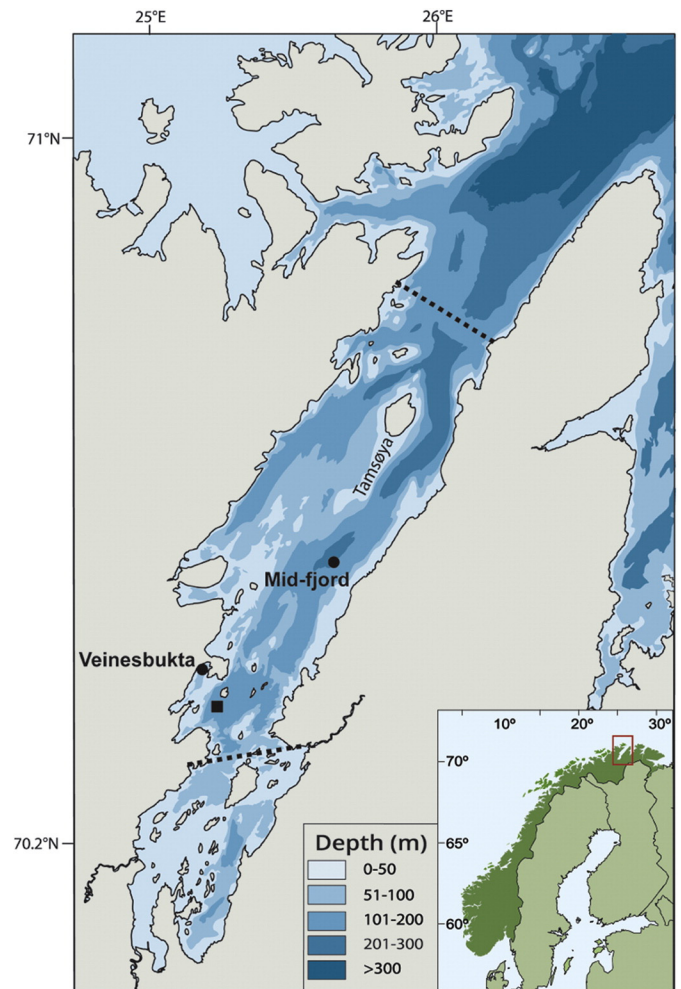


Fig. 1. Map of Porsangerfjord, northern Norway. With location of the three sampling stations Veinesbukta and Mid-fjord (circles), and the CTD station Inner-west (square). Sills are indicated by dashed lines and sub-basins by names. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Plankton sampling and hydrography

Mesozooplankton was sampled at two contrasting stations in the middle basin (Fig. 1 and Table 1). One station, Mid-fjord, was deep (190 m) and located on the eastern side of the fjord. The other, Veinesbukta, was shallow (60 m) and protected, located on the western side of the fjord. Zooplankton samples were collected bi-monthly or monthly between February 2013 and August 2014 from RV *Johan Ruud* (Table 1). Samples were collected using a WP2 plankton net with a mesh size of 180 μm (Hydrobios, Kiel, 0.57 m^{-2} mouth opening) and a filtering cod-end. The net was towed vertically from about 10 m above the seafloor to the sea surface at a speed of 0.5 m s^{-1} , filtering a mean volume of 120 m^3 ($\pm 34\text{ m}^3$) at Mid-fjord and 38 m^3 ($\pm 11\text{ m}^3$) at Veinesbukta. One to three hauls were obtained at each station and preserved in 4% buffered formaldehyde in seawater for later analysis. Mid-fjord was not sampled in April 2014 and clogging of the net by the algae *Phaeoystis pouchetii* reduced sampling efficiency at Veinesbukta in April 2014.

CTD-data were provided by the University of Tromsø Sea Monitoring Program, which carries out regular surveying at fixed stations (Mankettikkara, 2013). The Mid-fjord station is located at a fixed site, and a CTD-profile was taken there prior to each WP2 sampling. The closest CTD-station to Veinesbukta was Inner-west, located 2.7 nautical miles southeast of Veinesbukta and was used as a proxy for this station

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