



Secondary production at the Polar Front, Barents Sea, August 2007

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ABSTRACT

To investigate spatial patterns of secondary production we sampled four core hydrographical regions of the Polar Front in the Barents Sea (Arctic Water, ArW; Polar Front Water, PFW; Atlantic Water, AtW; and Melt Water, MW) by towing an undulating instrument platform along a transect crossing the front from August 8–9, 2007. Sensors mounted on the platform provided data on the hydrography (CTD), fluorescence (Fluorometer, F) and zooplankton abundance in the size range between 0.1 and 30 mm (Laser Optical Plankton Counter, LOPC). These continuous, biophysical data with high-spatial resolution were supplemented by discrete water and zooplankton net samples at stations for sensor calibrations. After in depth quality assessments of the biophysical data, estimates were made of the vital rates based on biovolume spectrum theory. Five size groups were distinguished from the LOPC data: small (S), mainly *Oithona* spp. and the appendicularian *Fritillaria* sp.; medium (M), mainly *Pseudocalanus* spp. and *Calanus* spp. CI–CIII; large (L), mainly *Calanus* spp. CIV–CV; and extra large (XL and 2XL), juvenile and adult euphausiids. Size groups were further divided based on transparency of organisms. Vital rates based on the biophysical in situ data in combination with biovolume spectrum theories agreed generally well with data from empirical and numerical models in the literature. ArW was characterised by subsurface maxima of chlorophyll *a* (chl *a*), and an estimated population growth of ca. $13 \text{ mg C m}^{-3} \text{ d}^{-1}$ for CI–CIII *Calanus* spp. and some older *Pseudocalanus* within the chl *a* maxima. Frontal waters were characterised by low chl *a* concentrations, but high abundances and production (around $1 \text{ g C m}^{-3} \text{ d}^{-1}$) of small copepods (*Oithona* spp.) and appendicularians (*Fritillaria* sp.). The estimated production of small-size zooplankton was an order of magnitude higher than the production of all other size groups combined, including large copepods. The high loss rates (-166 to $-271 \text{ mg C m}^{-3} \text{ d}^{-1}$) of small zooplankton may contribute a substantial amount of carbon to the benthos and to pelagic predators such as young capelin. AtW was the most productive water mass, with surface chl *a* maxima and an estimated population growth of $134 \text{ mg C m}^{-3} \text{ d}^{-1}$ for small zooplankton, $3.6 \text{ mg C m}^{-3} \text{ d}^{-1}$ for medium-sized copepods and $0.9 \text{ mg C m}^{-3} \text{ d}^{-1}$ for CIV–CVI *Calanus*. For those *Calanus* spp. in the surface layer, the estimated specific mortality rates were up to -0.35 d^{-1} , partly due to high predation pressure by hydrozoans and chaetognaths.

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1. Introduction

Secondary production in the pelagic zone, i.e. the increase in biomass of zooplankton over a period of time, constitutes the base for the largest fisheries in the world. It has therefore been a priority research question for biological oceanographers since the onset of marine research. Despite the major interest, spatio-temporal patterns of secondary production remain largely unresolved, due to a lack of adequate methods to estimate secondary production.

Among the approaches that have been tried for estimating secondary production in marine systems are the ecological method, the cohort

method, the physiological method, the egg production method, empirical models and more recently biochemical methods (see also Poulet et al., 1995; Runge and Roff, 2000). The ecological method is based on the trophodynamic concept (Lindemann, 1942), where the production of any trophic level is estimated based on primary production and transfer efficiencies between trophic levels (Lalli and Parsons, 1997). The cohort method has been very much in use in those situations where age or stage information of a population can be analysed with a minimum degree of uncertainty (Aksnes and Magnesen, 1988; Kimmerer, 1987; Kimmerer and McKinnon, 1987). Some decades ago the physiological method was extensively explored in experimental systems, using the energy budget of an individual to calculate growth and secondary production by taking into account all input to and output from the individual (Ikeda and Motoda, 1978; Le Borgne, 1982). In response to the high degree of uncertainty in many earlier methods (Miller, 2004), the egg production method was proposed as a means to obtain globally comparable production estimates by a simplified method (Poulet et al., 1995). Production estimates are limited to female copepods, allowing for

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relatively high resolution on large spatial scales (e.g. [Jonasdottir et al., 2005](#); [Stenevik et al., 2007](#)).

In the 1990s and early 2000s, several empirical models aggregating research on vital rates of the preceding decades were introduced to provide global analyses of growth and mortality based on locomotion of animals, food availability and energy balance ([Hirst and Bunker, 2003](#); [Hirst and Lampitt, 1998](#); [Huntley and Boyd, 1984](#); [Huntley and Lopez, 1992](#)). The latest empirical analysis of a large data set revealed that growth in juvenile copepods is strongly temperature-dependent, and that juveniles reach half-saturation of growth at food concentrations an order of magnitude lower than adults ([Hirst and Bunker, 2003](#)). This globally confirmed earlier findings that juveniles in nature are growing much closer to food saturation than adults ([Vidal, 1980](#)).

More recently, biochemical methods have been developed that can provide production estimates for the whole zooplankton community, not only copepods. These methods use the rate of nucleic acids (RNA/DNA), enzyme activity (specific aminoacyl-tRNA-synthetases, spAARS), or a combination of both to estimate overall metabolic activity and then growth and production (e.g. [Yebra and Hernández-León, 2004](#)). Biochemical methods might become more widely used in the future for obtaining reliable production estimates of mesozooplankton. However, spatial resolutions of any method that involves net tow sampling at stations are too low to resolve the spatial variability of mesozooplankton population processes.

Also, the knowledge on mortality rates in marine systems is limited because of the difficulties in measuring these rates ([Ohman, 2012](#), and references therein). Most commonly vertical or horizontal life tables have been applied, which assume either a stable age-structure of a population, or repeated sampling of the same population ([Aksnes and Ohman, 1996](#); [Aksnes et al., 1997](#)). Though many problems in relation to estimating mortality rates of a population at a particular location can be minimised by optimal sampling design ([Ohman, 2012](#)), observing spatio-temporal patterns of mortality rates remains a challenge. To our knowledge, the only global approximation of natural rates of mortality has been provided by [Hirst and Kiørboe \(2002\)](#). Their empirical analysis of field data predicts that mortality rate in copepods increases with temperature and declines with body weight. Furthermore, the analysis reveals that small copepods seem to be able to avoid some agent of mortality that other similar-sized pelagic animals do not ([Hirst and Kiørboe, 2002](#)).

These previous studies have contributed to a valuable synthesis of empirical information on vital rates in copepods and have provided new understanding on the underlying patterns with regard to growth and mortality. We may have reached a stage where we have extracted what is possible from a clearly under-sampled system, and where further progress will come only after using new approaches that allow for high-resolution sampling ([Bi et al., 2011](#); [Hirst and Bunker, 2003](#)). The present study uses the latest models based on biovolume spectrum theories to estimate vital rates in a spatially heterogeneous area, and is thus a response to the repeated call for improved methods to measure spatial patterns of growth, mortality and production of marine zooplankton (e.g. [Hirst and Bunker, 2003](#); [Miller, 2004](#); [Ohman, 2012](#); [Plourde et al., 2009](#); [Skarðhamar et al., 2011](#)).

Biovolume spectrum theories are ecological theories tailored to optical instruments that observe plankton distribution in size classes. They were developed as an alternative approach to the classical modelling of the marine food web when it was realised that plankton biomass is distributed systematically along size classes, and that energy fluxes through the spectrum can be described by size-dependent physiological and vital rates ([Platt and Denman, 1978](#); [Sheldon et al., 1972](#); [Silvert and Platt, 1978](#)). In the early mathematical formulations by [Platt and Denman \(1978\)](#) and [Silvert and Platt \(1978\)](#), the flow of energy was restricted from small to larger size classes. [Zhou and Huntley \(1997\)](#) developed a general mathematical approach, which includes all sinks and sources contributing to the energy flow through the spectrum, and described energy fluxes based on the distribution function of

abundance and the law of the conservation of mass (see also [Basedow et al., 2010b](#)). Later, [Zhou et al. \(2010\)](#) refined the equations describing growth to avoid an overestimation of growth at high food concentrations and temperature, and developed a mortality model based on assimilation efficiencies and the slope of the biovolume spectrum. Applications of biovolume spectrum theories to field data are scarce, but have yielded realistic estimates of trophic levels ([Basedow et al., 2010b](#); [Tarlind et al., 2012](#)), and of growth and mortality rates of zooplankton in an enclosed fjord ([Edvardsen et al., 2002](#)). The later growth and mortality models by [Zhou et al. \(2010\)](#) have not been applied to field data to date.

The present study has been outlined to cover three core hydrographical regions of the Polar Front in the Barents Sea, where high spatial variability in vital rates has been predicted by biophysical models ([Skarðhamar et al., 2011](#)). For adequate resolution in sampling, this study rests on high resolution data obtained by new technology platforms (see [Basedow et al., 2010b](#)) which, after in depth quality assessments, are followed by estimates of vital rates in the zooplankton community based on biovolume spectrum theories ([Zhou et al., 2010](#)). The combined use of conductivity–temperature–depth–fluorescence sensors (CTD-F) and laser optical plankton counter (LOPC) has been proven to be a powerful tool in generating environmental and plankton data with high spatial resolutions based on semi-automatic sampling. The quantitative nature of the LOPC has been further ascertained by an intercalibration study of video plankton recorder and LOPC ([Basedow et al., 2013](#)).

The objectives are (i) to compare rates estimated based on biovolume spectrum theories with literature values, (ii) to present spatial patterns of vital rates along a transect crossing the front, and (iii) to provide growth, mortality and production rates for the mesozooplankton community within the main hydrographical regimes at the Polar Front: Atlantic Water, Arctic Water, Polar Front Water and Melt Water.

2. Methods

2.1. Study area

The Barents Sea is a highly productive Arctic shelf sea with marked differences between the Atlantic influenced areas in the south and the Arctic influenced areas in the north ([Loeng, 1991](#)). The ecosystem is fuelled by an annual gross primary production of about 120 g C m^{-2} in Atlantic influenced areas, and ca. 60 g C m^{-2} in seasonally ice-covered areas according to a recent modelling study ([Reigstad et al., 2011](#)). The topography of the Barents Sea includes many deep channels ($>300 \text{ m}$) and shallow banks. An inflow of Atlantic water from the Norwegian Sea brings in heat and salt and during spring and summer, zooplankton biomass ([Edvardsen et al., 2003](#)). The influx of zooplankton is largely controlled by climatic forcing, but when it enters the Barents Sea the zooplankton are utilised mainly by planktivorous fish, which can exert strong predation pressure masking the effect of climatic forcing ([Stige et al., 2009](#)). The biomass of higher trophic levels, e.g. capelin (*Mallotus villosus*), cod (*Gadus morhua*) and herring (*Clupea harengus*), in the Barents Sea is an order of magnitude higher than in comparable subarctic ecosystems that lack the influx of zooplankton ([Hunt et al., 2013](#)).

The Polar Front in the Barents Sea separates warmer, more saline Atlantic Water (AtW) from colder, less saline Arctic Water (ArW) ([Loeng, 1991](#)). It is tightly coupled to topography in the western part, while less so in the eastern part of the Barents Sea where the position of the front is more variable.

2.2. Field sampling

Data presented here stem from an area of the Polar Front in the west, close to Storbanken, which was visited during a cruise with R/V “Jan Mayen” as part of the International Polar Year project NESSAR in August 2007 ([Fig. 1](#)). The NESSAR project focused on biophysical interactions at frontal systems in the Norwegian and Barents Sea. During two crossings

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