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Corresponding Author: Mrs. Emilia Trudnowska,

Corresponding Author's Institution:

First Author: Emilia Trudnowska

Order of Authors: Emilia Trudnowska; Sünnje L Basedow; Katarzyna Blachowiak-Samolyk

Abstract: Improved quantification of marine constituents is needed to parameterize ecological processes for ecosystem modelling so as to comprehend environmental and climatic impacts on the sustainability of Arctic ecosystems. The combination of high-resolution automatic measurements with a Laser Optical Plankton Counter (LOPC) and size spectrum analyses was utilized to estimate the secondary production of a high Arctic fjord system during a summer post bloom situation in 2012. The dataset comprised 28 vertical and extensive horizontal hauls of a LOPC-CTD-fluorometer platform plus four zooplankton net sampling stations for taxonomic composition designation. A clear gradient in the distribution of hydrographic properties, chlorophyll a concentrations as well as mesozooplankton abundance, biomass and production was demonstrated along Hornsund fjord axis. The outer fjord part was under the influence of advection of Atlantic Water and had the highest chlorophyll a concentrations, numerous opaque mesozooplankton individuals and flat slopes of size spectra, pointing to long food chains in which biomass is recycled several times. The opposite state was found in the innermost parts, where the glaciers melt water discharge led to low chlorophyll a concentrations but high abundance of amorphous particles. It resulted in steep slopes indicating more herbivorous or detritivorous feeding mode of highly abundant C. glacialis specimens. The model of mesozooplankton production demonstrated that Hornsund fjord is a highly productive ecosystem (> 500 g C m-3 day-1), where the bulk of secondary production is concentrated within the upper 50 m layer (72%) and in the fjord's interior.

1  *Estimation of mid-summer mesozooplankton production in a glacial Arctic fjord (Hornsund,*
2  *Svalbard)*

3  Trudnowska, E. [1], Basedow, S.L.[2], Blachowiak-Samolyk, K.[1],

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5  [1] Marine Ecology Department, Institute of Oceanology, Polish Academy of Sciences,
6  Powstancow Warszawy 55, 81-712 Sopot, Poland

7  [2] Faculty of Biosciences and Aquaculture, University of Nordland, N-8049 Bodø, Norway

8  Corresponding author: Emilia Trudnowska, emilia@iopan.gda.pl; tel. (+48 58) 731 17 83;
9  fax. (+48 58) 551 21 30

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## 1. <u>Introduction</u>

Quantitative parameterisations of marine processes have increased rapidly over the past decades owing to the development of new methods and tools that enable mapping and modelling the biogenic state and flux of ecosystems at extensive scales (Carlotti and Poggiale, 2009). Specifically in the case of zooplankton ecology the application of *in situ* optical counters and hydro-acoustics (Checkley et al., 2008; Möller et al., 2012; Trudnowska et al., 2012; Basedow et al., 2013) along with statistical modelling (Carlotti and Poggiale, 2009; Zhou et al., 2010; Reigstad et al., 2011; Slagstad et al., 2011) and trait-based approaches (Litchman et al., 2013) have given the possibility to advance the characterization of pelagic systems complexity as well as to estimate growth, mortality, trophic levels and production of zooplankton (Zhou and Huntley, 1997; Zhou et al., 2009; Zhou et al., 2010). Thus it is now time to ask new and broader questions in marine studies, questions that have not been feasible to address using conventional sampling technology.

Consequently, it might be possible to reduce the large amount of measures and diverse observations characterizing ecosystem complexity and functioning into a single number. The estimation of secondary production is such an integrating proxy and powerful tool that enables the assessment of ecosystem status, its various functions as well as its response to environmental stressors (Dolbeth et al., 2012). Secondary production combines static and dynamic processes involved in the transfer and cycling of energy and material, and thus provides more information on ecosystem status than measures derived from traditional basic assessments such as biomass estimations. Body size is another example of a useful surrogate for the extensive biological diversity, because it provides information on comprehensive properties of ecosystems without studying the amazing variety of organisms (Woodward et al., 2005; Barnes et al., 2010; Heckmann et al., 2012).

Previous research on Arctic zooplankton has mostly focused on the estimation of abundance and biomass (e.g. Kosobokova and Hirche, 2000; Auel and Hagen, 2002), on biodiversity (e.g. Kosobokova and Hopcroft, 2010; Kosobokova et al., 2011), reproduction (e.g. Hirche and Kwasniewski, 1997; Hagen, 1999), migration (e.g. Blachowiak-Samolyk et al., 2006; Berge et al., 2009) and on distribution (e.g. Lane et al., 2008; Trudnowska et al., 2012). Most of the investigations were concentrated on single key-species, especially on copepods of the genus of *Calanus* (e.g. Falk-Petersen et al., 2007; Søreide et al., 2010). Apart from few studies that analyzed plankton size structure in the Arctic ecosystems (e.g. Basedow

et al., 2010; Forest et al., 2012), very little is still known on zooplankton production in the Arctic.

The Arctic region has unique conditions for biological production, as it is characterized by a dramatic seasonality, generally low water temperatures, multi-year and seasonal ice cover as well as fresh water input from rivers and ice melt. The strictly seasonal pulse of primary production is represented by both ice algae and phytoplankton (Søreide et al., 2010; Leu et al., 2011). Arctic waters tend to be dominated by large, lipid-rich and long-living zooplankton taxa in contrast to Atlantic waters, in which primary production is mostly utilized by smaller, faster-growing species (Kosobokova and Hirche, 2009; Weslawski et al., 2009). Arctic secondary production has been predicted to increase in the future (Slagstad et al., 2011), but the individual body-size of organisms is foreseen to decrease in response to global warming (Daufresne et al., 2009, Weslawski et al., 2009; Gardner et al., 2011). However, higher growth rates and shorter life spans in response to higher temperatures will not necessarily lead to increased productivity due to the increased metabolic demands, high mortality and habitat loss of some key species. Warming is also expected to increase the steepness of the plankton community size spectrum and the zooplankton to phytoplankton biomass ratios (Yvon-Durocher et al., 2011).

Hornsund fjord is the European Marine Biodiversity Research Site and represents a typical Arctic marine environment (Warwick et al., 2003). Ice cliffs of fourteen tidewater glaciers constitute a substantial part of the Hornsund coastline (Błaszczyk et al., 2013). These glaciers strongly modify the physical environment and cause various disturbances, such as the outflow of melt waters transporting high concentrations of mineral suspensions, which influences light conditions and primary production. The marine fauna is represented largely by species of Arctic origin, but due to the influence of Atlantic waters also boreal fauna is found there. The most common fish species, *Myoxocephalus scorpius* L. along with *Boreogadus saida* serve as the main food source for sea birds and as a predator of pelagic crustaceans (Weslawski and Kulinski, 1989). Hornsund area is also an important breeding site for ten bird species, among which little auk and Arctic tern are the most common and abundant (e.g. Wojczulanis-Jakubas et al., 2008).

Our study is the first evaluation of zooplankton size spectra from a Svalbard fjord system. The observed differences in water characteristics along the fjord's axis point to their substantial impact on the potential secondary production, which provides groundwork data for the assessment of future environmental and climatic impacts on the sustainability of a typical Arctic ecosystem.

99      The main aim of this study was to estimate the mesozooplankton production of the unique

100 Hornsund fjord ecosystem during mid-summer. Our specific objectives were i) to present the

101 first high resolution measurements of the bio-physical condition of Hornsund waters in mid-

102 summer, namely the distribution of temperature, salinity and chlorophyll *a* together with

103 zooplankton abundance, composition and biomass, ii) to examine the along fjord

104 heterogeneity in various Hornsund ecosystem components iii) to analyze the biovolume

105 spectra and trophic indexes of plankton assemblages and iv) to investigate the state and

106 potential capacity of summer secondary production in Hornsund waters.

107      **2.    <u>Material and Methods</u>**

108      **2.1 Study site**

109      Hornsund is the southernmost fjord on the west coast of Spitsbergen (Fig. 1). It is a

110 medium sized (264 km$^2$ area; 34 km long; Błaszczyk et al., 2013) fjord connected with the

111 open sea through a wide opening without a sill at the entrance, which facilitates its penetration

112 by oceanic waters (Swerpel, 1985). It has a complicated coastline with numerous bays; the

113 greatest are Brepollen and Burgerbukta situated in its interior. Brepollen is isolated from the

114 main basin by an underwater sill and is a reservoir of Winter Cooled Water (Swerpel, 1985).

115 Fourteen tidewater glaciers enter directly into the fjord causing a complicated structure of

116 waters in the coastal zone (Swerpel, 1985). Thus the innermost part of Hornsund has

117 completely different hydrographical conditions compared to the central basin. Intense

118 freshwater discharge results in strong water stratification restricting vertical exchange of

119 energy and matter (Görlich et al., 1987).

120      The warm West Spitsbergen Current enters the fjord in the intermediate layers and flows

121 along a through. Cold waters are advected into the fjord by the Sørkapp Current as a surface

122 stream or persist as a form of coastal waters that develop locally and seasonally (Swerpel,

123 1985). The main water masses found within the fjord system are: Transformed Atlantic Water

124 (T>1.0°C, S>34.7), Surface Water (T>1.0°C, S<33.25), Intermediate Water (T>1.0°C,

125 33.25>S<34.5), Local Water (T<0°C, S>34.7) and Winter Cooled Water (T<-1.7°C, S>35.0)

126 (Weslawski et al., 1991).

127      Simultaneous inflow of Atlantic waters from the mouth of the fjord and runoff of fresh

128 and turbid water from the glaciers result in steep horizontal gradients in temperature, salinity

129 and light regime along the fjord's axis, which strongly impact phytoplankton assemblages

130 (Keck et al., 1999; Piwosz et al., 2009). The substantial impact of glacier meltwater during

131     spring can result in high amounts of inorganic suspension (Hop et al., 2002; Svendsen et al.,

132     2002; Zajaczkowski, 2008), which in turn controls the depth of the euphotic zone as well as

133     the spectral composition of penetrating radiation (Urbanski et al., 1980; Svendsen et al.,

134     2002).

135     **2.2 Field sampling**

136     Data were collected by an instrument platform equipped with a LOPC (Laser Optical

137     Plankton Counter, Brooke Ocean Technology Ltd., Canada), CTD (SBE 911plus, Seabird

138     Electronics Inc., USA) and a fluorometer (Seapoint Sensors Inc., USA). The platform was

139     lowered vertically from surface (2.5 m) to a few meters above the bottom at 28 stations and

140     towed horizontally at approximately 20-25 m depth along extensive transects (Fig. 1, Table

141     1). Traditional zooplankton net samples were collected by a MPS (Multi Plankton Sampler,

142     180 μm mesh, 0.25 $m^2$ mouth opening, Hydrobios, Kiel, Germany) in vertically stratified

143     hauls from bottom to surface at four stations. The location of all stations and transects were

144     set so as to cover evenly the whole fjord (Fig. 1).

145     The dataset was divided *a priori* into four consecutive zones of Hornsund fjord: Outer,

146     Central, Inner and Glacial on the basis of their geographic location (Fig. 1). The water column

147     was divided into the upper (50 m to 2.5 m) and lower (near bottom to 50 m) layers at vertical

148     profiles sampling stations. The horizontal hauls of the LOPC-CTD-F platform were

149     performed in the mid depth (20-25 m) of the defined upper layer as a representative of the

150     most productive zone of the water column where high zooplankton and phytoplankton activity

151     occurs, contrary to the very surface and the deep layers. To compare the independence of the

152     upper and lower layers the nonparametric Mann–Whitney U-test was used. The comparisons

153     of different parameters among defined zones of Hornsund fjord were performed by the non-

154     parametric Kruskal-Wallis and *post-hoc* Dunn tests.

155     **2.3 LOPC-CTD-F data processing**

156     The measurements of a LOPC-CTD-F platform on plankton abundance and biomass,

157     hydrography (temperature and salinity) and chlorophyll *a* fluorescence were processed using

158     especially developed Matlab routines and averaged over 1 m depth and 5 m distance intervals.

159     The digitized voltage of the fluorometer (F) was calibrated based on filtered chlorophyll *a*

160     (*chl a*) [mg $m^{-3}$] from different Svalbard waters (Kongsfjorden, Fram Strait, Sørkapp

161     Current). The resulting calibration equation was:

162     *chl a* = 0.1972 * F + 0.2907, (correlation coefficient $r^2 = 0.78$).

163  Unfortunately, the sensitivity of the sensor was not adjusted properly; it should have been

164  strengthened by the 10X jumper cable to obtain higher resolution measurements in waters of

165  low chlorophyll *a* concentrations such as those found in Hornsund. As a result an unnaturally

166  small variance of chlorophyll *a* values was obtained, so we re-scaled the chlorophyll *a* values

167  to more realistic values, taking minimum obtained value as 0 mg m$^{-3}$ and maximum value as 5

168  mg m$^{-3}$, based on long-term monitoring database (Józef Wiktor personal communication,

169  IOPAS) as well as on two additional profiles sampled in 2012 in the Outer part of Hornsund

170  fjord (data not shown).

171  The LOPC is an *in situ* sensor, which autonomously counts and measures plankton

172  particles passing its beam path in the sampling tunnel (7×7 cm wide; 49 cm$^2$ cross section).

173  The portion of light blocked by the particle is measured and recorded as digital size, which is

174  converted to Equivalent Spherical Diameter (ESD) - a diameter of a sphere that would present

175  the same cross-sectional area as the particle being measured, using a semi-empirical formula

176  based on calibration with spheres of known diameters (Herman, 1992; Herman et al., 2004).

177  The technical specifications allow for counting and size-fractioning of particles in the

178  size-range of 0.1 to 35.0 mm ESD. However, it is recommended to restrict the size ranges for

179  the analysis of the mesozooplankton, for which LOPC is suited for, as the particles of the

180  lower and upper ends of the size range are undersampled. Moreover the upper end of the

181  spectrum is highly influenced by randomness, as the occasional sampling of big organisms

182  can have a substantial effect on the parameters of the spectrum (Blanco et al., 1994).

183  Therefore in this study the size range for the mesozooplankton was limited to 0.3 – 3.2 mm

184  ESD. Additionally, separate analyses were performed for the whole plankton size spectrum

185  (0.1 – 28.2 mm ESD) and for older life stages (CIV – CVI F) of *Calanus* spp. (1.0 – 2.5 mm

186  ESD, Jakubas et al., 2013).

187  Zooplankton abundance was calculated as the total number of detected particles divided

188  by the volume of water passing through the LOPC sampling tunnel. Data with abnormally

189  low and high water volume estimates were eliminated. The ESD diameter (mm) was

190  converted to biovolume (mm$^3$) according to the equation for a sphere: $\pi ESD^3/6$ (Heath, 1995).

191  Biomass was computed from the biovolume using relation of 0.0475 mg of carbon (C) per

192  unit of biovolume (Reigstad et al., 2008). In addition, we tested the sensitivity of production

193  estimates to the biovolume to carbon conversion by applying also a newly developed equation

194  of:

195  $\qquad$ biovolume-to-carbon = $0.0125*(biovolume)^{1.3217}$ $\qquad$ (Forest et al., 2012)

196    that is based on Arctic copepods (1 - 6 mm ESD) sampled by an underwater video profiler.

197    Such production estimates were on average 45% (± 3%) higher than estimations using the

198    widely used conversion of Reigstad et al., 2008.

## 2.4. Net samples analysis

200    Depth layers of the MPS sampling were determined according to preceeding CTD

201    profiles. Zooplankton collected within each of five discrete layers was preserved as individual

202    samples in 4% formaldehyde-in-seawater solution buffered with borax. Qualitative-

203    quantitative examinations were done in the laboratory following recommendations in Postel,

204    (2000). First, all larger zooplankters (total size > 5 mm) were picked out, identified and

205    counted. The remaining zooplankton sample was examined by a sub-sampling method under

206    stereo-microscope. The number of examined subsamples was determined so as to count and

207    identify at least 300 zooplankton individuals per sample. *Calanus* identification was based on

208    the criteria given in Weydmann and Kwasniewski (2008). The rest of the sample was scanned

209    in order to enumerate other, less numerically important taxa that were not caught in sub-

210    samples. The zooplankton abundance was expressed as number of individuals in cubic meter

211    (ind. $m^{-3}$) using filtered water volume estimation. Data was integrated into two layers, upper

212    (50/40 m to surface) and lower (underneath 50/40 m) to match the layers of LOPC profiles

213    and to simplify data display and interpretation (Table 1).

## 2.5. Calculations of biomass spectra, trophic indices and production

215    The shape of the biomass spectrum is a useful tool to assess energy fluxes within

216    aquatic ecosystems (Sprules and Munawar, 1986; Thiebaux and Dickie, 1992; Zhou, 2006).

217    The biomass and biovolume spectra were computed by normalizing the concentration of

218    biomass/biovolume to the width of the 50 individual body size classes (intervals on an equal

219    $\log_{10}$ step) (Platt and Denman, 1978; Zhou and Huntley, 1997; Kerr and Dickie, 2001). The

220    biovolume size spectra of the community were assessed through consideration of their slope,

221    the y-intercept, and the coefficient of the linear regression determination $R^2$ fitted to the log-

222    transformed data within the whole community as well as the size-separated

223    (mesozooplankton, older stages of *Calanus* spp.) fractions. The biovolume and biomass

224    spectra were firstly calculated for 1 m depth and 5 m distance binning and then averaged for

225    the stations, the upper and lower layers and consecutive geographic zones of Hornsund fjord.

226    A steeper slope of a biomass spectrum generally indicates communities dominated by

227    herbivorous species and of higher potential productivity (Zhou and Huntley, 1997; Zhou,

7

228  2006). Also the high intercept of the biomass spectrum, namely the high abundance of

229  herbivorous zooplankton, directly reflects the higher potential secondary production (Zhou et

230  al., 2009). The slope of a biomass spectrum becomes flatter when there is more recycling of

231  biomass by carnivorous-omnivorous zooplankton (Dickie et al., 1987; Zhou, 2006), which

232  can be reflected as waves propagating along the biomass spectrum (Zhou and Huntley, 1997).

233  Trophic interactions depend rather on size constraints than on taxonomy (Badosa et al., 2007;

234  Rall et al., 2011). The relative number of trophic levels (Trophic Index, TI) was estimated on

235  the basis of the slope of the biomass spectrum and the mean assimilation efficiency (70%,

236  commonly used for copepods, Basedow et al., 2010) of the community following Zhou et al.,

237  2009, eq. 3.

238      The production of plankton communities refers to the rate of biomass generation,

239  determined by rates of body growth and abundance change. The estimations of body growth

240  have been found to depend on temperature (Huntley and Lopez, 1992), temperature and body

241  mass (Ikeda, 1985; Hirst and Lampitt, 1998) and chlorophyll *a*, temperature and body weight

242  (Hirst and Bunker, 2003). The growth rate (G) [g day$^{-1}$] in this study was calculated in

243  relation to chlorophyll *a* (*chl a*) [mg m$^{-3}$], temperature (T) [°C] and body weight (*w*) [µg C

244  ind.$^{-1}$] separately for each size class from 50 body size classes with intervals on an equal $\log_{10}$

245  step according to equation:

246      $G = 10^{0.0186*T} * w^{-0.288} * chl\ a^{0.417} * 10^{-1.209}$          (Hirst and Bunker, 2003).

247      Among many existing approaches for zooplankton production estimations, such as

248  ecological, physiological and biochemical methods or empirical models, the zooplankton

249  closure model based on high-resolution data on biomass size spectrum, temperature and

250  phytoplankton biomass (Zhou et al., 2010) to calculate the secondary production of marine

251  zooplankton seems to be the most accessible and reliable (Basedow et al., 2014). Therefore

252  the secondary production [mg C m$^{-3}$ day$^{-1}$] in this study was calculated on the basis of the

253  growth rate (G) [g day$^{-1}$] and the accumulated biomass within the mesozooplankton size

254  fraction (Zhou et al., 2010, Basedow et al., 2014 eq. 3).

255      **2.6. Particle characteristics**

256      Two different methods were applied to estimate the transparency of multi element

257  particles (that occlude more than 3 laser elements). The first approach was to calculate the

258  attenuation index (AI), which is the ratio between mean DS (digital size) of middle diodes

259  (first and last diodes excluded to ensure that the occluded area is completely covered by the

particle; Basedow et al., 2013) and the maximum DS. The AI has been introduced as an index to enable the distinction between copepods and non-copepod particles (Checkley et al., 2008). The application of the AI to distinguish particle types varies among regions and zooplankton communities, e.g. ranges for copepods: AI > 0.6 (Checkley et al., 2008), 0.2 – 0.5 (Gaardsted et al., 2010), AI > 0.4 (Basedow et al., 2013) indicating that copepods can vary from quite translucent to relatively opaque (Basedow et al., 2013). An additional analysis to distinguish between relatively opaque animals and relatively transparent aggregates is the ratio of ESD ($d_{esd}$) to the OD (occluded diameter $d_{od}$ – the width of the beam intercepted) (Jackson and Checkley, 2011; Petrick et al., 2013), with the assumption that aggregates have much larger ratios of OD to ESD because of their amorphous nature (Jackson et al., 1997).

## 3.  Results

### 3.1. Hydrographical and biological features of Hornsund waters measured by LOPC-CTD-F platform

The hydrographical and biological features of Hornsund waters were heterogeneous both vertically (upper vs. lower layer) and horizontally (along the fjord's axis) (Figs. 2&3). Generally, the upper layer (50-0 m) was warmer and less saline than the deeper layer (Mann–Whitney U-test; Z=6.2, Z=-6.3 p<0.0001 (Table 1, Fig. 2B) and the peaks of chlorophyll fluorescence occurred primarily within the upper 50 m layers (Mann–Whitney U-test (Z=6.23, p<0.0001, Fig. 2B)). A characteristic feature of the vertical water stratification was a temperature gradient (peaks within 20-40 m layer) and increasing salinity with depth. The outflow of glacial waters was marked as a surface (up to 20 m) low salinity layer at almost all stations, except for those situated in the Outer zone. The abundance of the mesozooplankton size fraction was the highest in the upper layers, with some exceptions at the Glacial stations, where it was distributed relatively evenly within the whole water column.

Temperature, salinity and chlorophyll *a* decreased along the fjord's axis, from the entrance to the inner bay (Figs. 2&3). The warmest and most saline waters were observed in the Outer and Central parts of the fjord, the Inner part was cooler and less saline, and the Glacial part was the coolest and freshest. Temperatures below zero were noted at stations close to the glaciers, especially in Brepollen bay. Contrary to chlorophyll *a* concentration, which was the highest at the Outer stations and the lowest in the glacial bays, the amount of the mesozooplankton size fraction increased along the fjord's axis (Figs. 2&3).

### 3.2. Zooplankton composition

According to net results, the highest zooplankton abundance was noted at the Outer station (Table 2), and it was represented mainly by abundant copepods (*Pseudocalanus* spp., *Metridia longa*, *Calanus finmarchicus* and *Oithona similis*). Also the Glacial station was associated with highly abundant zooplankton assemblages, with *Pseudocalanus* spp., *C. glacialis* and Bivalvia veligers being numerously important taxa (Table 2). Generally *Pseudocalanus* spp. accounted for more than 30% of total zooplankton abundance at each station and it was represented mainly by younger copepodid stages, which stayed in great numbers in upper layers. *C. finmarchicus* and *Acartia longiremis* were most abundant at the Outer station and stayed primarily in the upper layer. *Calanus glacialis* was very abundant in the upper layer of the Outer station. Almost half of the older copepodids (CIV-CVI) of *C. glacialis* found within the Hornsund stations stayed below 50 m at the Glacial station (Table 2). This depth stratum was characterized also by high numbers of copepod nauplii. The Central and Inner stations had slightly lower zooplankton abundances. Our category 'others' included rather rare copepods (e.g. *Bradyidius similis*, *Scolecithricella minor*, *Triconia* spp.), meroplankton (e.g. larvae of Cirripedia, Decapoda, Pteropoda, Gastropoda, Polychaeta, Echinodermata, Bryozoa) and soft-bodied zooplankters (*Mertensia* spp., Chaetognatha, Appendicularia).

### 3.3. Biovolume spectra, biomass and trophic levels of zooplankton

The biovolume spectrum parameters reflected the horizontal along fjord's axis gradient in the amount of mesozooplankton biomass (Table 3, Fig. 3). The intercepts increased from the lowest at the Outer stations, intermediate at the Central and Inner parts to the highest at the Glacial stations for each zooplankton size fraction (Table 3, Fig. 3). The slope that was fitted to the biovolume spectra of the whole zooplankton community was close to -1 at all stations, but when the fit was restricted to the mesozooplankton and *Calanus* size fractions, the slope was steeper at the Inner and Glacial stations and flatter at the Outer and Central ones (Table 3). An especially flat slope was obtained for *Calanus* at the Outer stations, which was also associated with the increase of biomass within this size fraction (Table 3, Fig. 4). The bulk of mesozooplankton biomass was represented by *C. glacialis* (Fig. 4). The highest biomass of zooplankton individuals caught with the MPS net was found at the Glacial station, but it was also relatively high at Outer station, where along with *C. glacialis*; *C. finmarchicus, Metridia longa, C. hyperboreus* and chaetognaths contributed greatly to the overall zooplankton biomass (Fig. 4). At each station the TIs of the whole zooplankton community were on average 2.5. Within the mesozooplankton size fraction the highest TIs

were computed for the Outer stations and the lowest in the Inner and Glacial fjord parts (Table 3). TIs of *Calanus* were very high at the Outer stations and decreased significantly along the fjord's axis.

### 3.4. Mesozooplankton production

The secondary production was generally the highest in the interior and much lower in the external parts of Hornsund fjord (Figs. 3&5). Vertically, on average 72 % (41-95 %) of the estimated production for the mesozooplankton size fraction was concentrated in the upper 50 m layer. The continuous survey of the 20-25 m layer showed that mesozooplankton production was extremely low in the Outer zone, the highest in the Inner zone and intermediate in Brepollen Bay (Fig. 5).

### 3.5. Transparency of particles

The attenuation index (AI) as well as the relationship between two different measures of particle diameter ($d_{esd}$ and $d_{od}$) indicated that two types of particles occurred within Hornsund fjord; relatively opaque zooplankton animals and relatively amorphous and transparent aggregates (Fig. 6). Aggregates and transparent animals were an important component of the mesozooplankton size fraction inside the fjord, whereas higher contribution of opaque particles was noted in the Outer part of Hornsund fjord.

## 3. **Discussion**

The marked ecological gradient along Hornsund fjord axis that was observed in this study clearly reflected the interplay between two important processes shaping the pelagic environment in typical Arctic glacial fjords (Weslawski et al., 2000, Basedow et al., 2004, Willis et al., 2006). The outer fjord part was influenced by advection while the inner parts were affected by the freshwater and suspension discharge from several glaciers. High-spatial resolution measurements of hydrographic properties, chlorophyll *a* concentrations as well as mesozooplankton biomass, community structure and production indicated a progressive increase or decrease trend of those parameters along Hornsund fjord axis (Figs. 2&3). Thus four consecutive geographic zones were clearly distinguished: Outer, Central, Inner and Glacial (Fig. 1). This highlights the importance to address the spatial heterogeneity of a system characterized by complex and dynamic environmental settings, especially in food web studies (Pinel-Alloul, 1995; Tamelander et al., 2006). The influence of glacier-derived environmental gradients on species distributions and community structures along the Arctic

356  glacial fjords has previously been stated for phytoplankton (Wiktor and Wojciechowska,

357  2005; Piwosz et al., 2009), zooplankton (Weslawski et al., 2000; Weydmann and

358  Kwasniewski, 2008), foraminifera (Wlodarska-Kowalczuk et al., 2013) and various benthic

359  assemblages (Wlodarska-Kowalczuk and Pearson, 2004; Grzelak and Kotwicki, 2012; Kędra

360  et al., 2013). To our knowledge this study is the first to present the high-resolution pelagic

361  measurements along the fjord gradient and it is a pioneering attempt in modelling

362  mesozooplankton production in Arctic fjords.

363    The along fjord ecological gradient was characterized by a gradual decrease in water

364  temperature, salinity and chlorophyll *a* concentration accompanied by a progressive increase

365  of the plankton biomass from the fjord's entrance to the inner basin (Figs. 2&3). The Outer

366  part of Hornsund fjord was under the influence of advection of relatively saline and warm

367  waters, in which highest chlorophyll *a* values were noted. This corresponds to the high

368  primary production that previously has been found in the outer part of Hornsund fjord

369  (Piwosz et al., 2009). The water masses of Atlantic origin that flow along the west coast of

370  Spitsbergen carry large amounts of copepods of the genus *Calanus* (Daase et al., 2007). These

371  are advected into fjords along the west coast (Basedow et al., 2004; Willis et al., 2006) and

372  likely were responsible for the high zooplankton biomass observed at the Outer stations.

373  Consecutive parts along Hornsund fjord axis, the Central and Inner zones were under the

374  influence of both glacial activity from several glaciers and advected waters from the fjord

375  entrance. These combined influences were associated with the most sustainable conditions

376  within the fjord, providing optimum and stable environment for zooplankton to thrive. In

377  contrast, at the Glacier stations low chlorophyll *a* concentrations, but high abundances and

378  biomass of zooplankton were observed in our study (Fig. 2). These findings agree well with

379  previously observed trend of decreasing phytoplankton biomass towards the fjord's inner part

380  caused by decreasing light penetration and increasing zooplankton abundance (Piwosz et al.,

381  2009).

382    Our analyses of the ecological gradient along the fjords axis was based on data collected

383  vertically in the upper 50 m layer as well as horizontal high spatial resolution measurements

384  performed at 20-25 meters depth. This mid-part of the upper water layer was selected *a priori*

385  as the most representative depth level of the productive euphotic zone, and reflected well the

386  overall pattern in the upper 50 m of the water column. A typical pattern of vertical

387  zooplankton distribution for the Arctic summer season is characterized by the maximum of

388  biomass in the surface layer (up to 90%) and its rapid decrease below 50 m (Kosobokova et

389  al., 1998; Blachowiak-Samolyk et al., 2007). Also the investigation of Weydmann and

390 Kwasniewski (2008) indicated considerably higher numbers of *C. glacialis* in the surface

391 Hornsund waters (up to 70 m) in comparison to deep waters, except for the distinctive station

392 in Brepollen. This is in line with our study showing markedly higher zooplankton biomass in

393 the upper layer (50-0 m) than in the lower layer (bottom-50 m) apart from the Glacial stations.

394     The optical method measurements provided high spatial resolution data, but were not

395 suited to resolve the taxonomy of the zooplankton community. They were therefore supplied

396 by net samples (Table 2). When comparing mesozooplankton (0.3-3.2 mm ESD) abundances

397 obtained from the LOPC with those gained from 180 μm mesh size nets, we got divergent

398 results, e.g. the highest (net samples) and lowest (LOPC) mesozooplankton abundances in the

399 Outer part of Hornsund fjord. This is not surprising, as the LOPC measures a wider size range

400 than the 180 μm net (Nichols and Thompson, 1991, Herman et al., 2004), including small

401 zooplankton that often is very abundant. When comparing abundances of larger copepods

402 (mainly older stages of *Calanus* spp., 1.0-2.5 mm ESD), both methods yielded comparable

403 results. This is in agreement with previous calibration studies showing that absolute

404 abundances obtained from analogous nets and the LOPC closely correspond for the size range

405 of larger *Calanus* stages (Herman and Harvey, 2006, Gaardsted et al., 2010). A substantial

406 part of plankton particles were relatively opaque in the waters of the Outer zone (Fig. 6),

407 which is an additional indicator of the numerical importance of older stages of *Calanus* spp.

408 individuals, that have filled up their lipid sacks at this time of the year (Falk-Petersen et al.,

409 2009; Søreide et al., 2010), likely resulting in a higher opacity (Basedow et al., 2013). The

410 high biomass detected by the LOPC at the Glacial stations was most probably caused by both

411 highly abundant *Calanus* individuals and an additional biomass supply from glacier melt

412 waters. The last fraction, identified as relatively amorphous and transparent particles in the

413 LOPC data, included mineral particles known as 'glacial milk' (Fig. 6). The entrapment of

414 zooplankton due to the estuarine circulation driven by glacial meltwater discharge might

415 explain the high zooplankton biomass that was observed in the inner fjord basins at the

416 Glacier stations (Weslawski et al., 2000).

417     The slope of the regression line that was fitted to the biovolume spectra of the whole

418 zooplankton community (0.1-28.2 mm ESD) within the entire water column was close to -1

419 (Table 3), which is in accordance to the theoretical principles of the normalized biomass size

420 spectra theory (Platt and Denman, 1978) and confirms the striking regularity of body size

421 distributions of aquatic systems. Looking at the slopes in more detail, by selecting size ranges

422 of the biovolume spectra, and regions in the fjord, allowed us to analyze the trophic flow

423 within the mesozooplankton community in relation to the environmental gradient observed. In

424 the Outer zone, a relatively flat slope of the mesozooplankton community (0.3-3.2 mm ESD),

425 and of older *Calanus* spp. stages (1.0-2.5 mm ESD) indicated a higher strength of top-down

426 control there compared to the Inner and Glacial zones (Ye et al., 2013). The steep slopes and

427 the high intercepts of the mesozooplankton biovolume spectrum in the Inner and Glacial parts

428 of Hornsund (Table 3) points to the higher occurrence of additional plankton material such as

429 aggregates and detritus material (Herman and Harvey, 2006). Furthermore, it suggests also a

430 relatively high loss of energy from primary producers to secondary consumers (Boudreau et

431 al., 1991; Thiebaux and Dickie, 1992; Sprules and Goykie, 1994). Although it is hypothesized

432 that long food chains favour ecosystem stability (Jennings and Warr, 2003), it has been also

433 proposed that stable systems should be characterized by steep slopes of their size spectra

434 (Jennings and Mackinson, 2003). This would suggest that the Inner and Glacial zones within

435 Hornsund fjord constitute a stable ecosystem during summer, despite the high seasonal

436 variation in glacial runoff. Generally, the slopes obtained in this study for Hornsund pelagial

437 in summer season were steeper than those calculated for Barents Sea waters in spring time

438 (Basedow et al., 2010) and the slopes obtained for northern Norwegian shelf waters in spring

439 and summer seasons (Zhou et al., 2009), but comparable to slopes obtained for Melt and Polar

440 Front Waters of Barents Sea in August (Basedow et al., 2014). This implies that Arctic melt

441 waters as well as the mixture of Arctic and Atlantic waters in a post bloom situation

442 characterize with a relatively steep slopes specifying shorter food chains.

443     The shape of the biovolume spectra is determined by the trophic flow and recycling within

444 zooplankton community, so it can indicate the trophic position of the mesozooplankton

445 (Zhou, 2004, Basedow et al., 2010). The trophic indices (TIs) calculated for the whole

446 plankton spectrum were on average 2.5 in Hornsund fjord regardless of its zone (Table 3).

447 Compared to the TIs calculated for mesozooplankton community in the Barents Sea during

448 spring (Basedow et al., 2010) TIs detected in Hornsund in summer were much lower. The

449 trophic structure of the mesozooplankton community differed along the observed ecological

450 gradient in Hornsund fjord waters: TIs were higher in the Outer and Central parts (2.2 and

451 2.1, respectively) than at the Inner and Glacial stations (TIs = 1.8) indicating a more

452 herbivorous or detritivorous feeding mode in the interior. However, individual zooplankton

453 species play many functional roles at different developmental stages of their lifespan. Some

454 species can also rapidly change their food preferences depending on the food availability in

455 the environment. Trophic indices from whole communities from different regions and seasons

456 are thus not directly comparable. Studies of the trophic structure of Arctic zooplankton

457 species revealed that pure herbivory and carnivory are very rare (Søreide et al., 2006;

458    Blachowiak-Samolyk et al., 2007; Søreide et al., 2008). The very high trophic position of

459    older stages of *Calanus* spp. (TI = 5.5) that was observed in Outer waters suggests a more

460    carnivorous feeding mode on biomass that has been recycled several times. TIs calculated for

461    *Calanus* spp. size fraction decreased progressively along the fjord's axis with the lowest TIs

462    (2.1) at the Glacial stations, indicating a feeding on less recycled material there. Although

463    *Calanus* species are predominately herbivorous (e.g. Falk-Petersen et al., 2007), they have

464    been shown to display a flexible diet in relation to food availability and phytoplankton bloom

465    stage, feeding also on fecal detritus, microzooplankton, protozooplankton, and *Calanus*

466    nauplii (Ohman and Runge, 1994; Levinsen et al., 2000; Basedow and Tande, 2006; Cambell

467    et al., 2009).

468        Estimates of secondary production were based on a few easily measurable parameters

469    such as temperature, chlorophyll *a* and size-distributed biomass, which enabled production

470    estimates with high spatial resolution and provided a holistic view of the mesozooplankton

471    community along the Hornsund fjord axis (Fig. 5). Even though this seems to be a rough

472    model of secondary production, and specific values have to be treated with some caution,

473    uncertainty of this approach is relatively low compared to other empirical approaches

474    (Basedow et al., 2014 and references therein). Due to the uncertainty associated with a

475    species-based approach of estimating secondary production, it has been proposed that

476    generalizing biological dynamics into a biomass spectrum is a more appropriate approach for

477    production estimates than estimates based on individual species classification level (Kerr and

478    Dickie, 2001; Jennings et al., 2002). Our approach showed that mesozooplankton production

479    was not evenly distributed horizontally and vertically, but was clearly concentrated in the

480    fjord's interior and within the upper 50 m layer (Fig. 5). This mesozooplankton production

481    calculated within Hornsund fjord in mid-summer was much higher than at the polar front in

482    the Barents Sea during spring time (Basedow et al., 2014). The estimated production of

483    *Calanus* spp. in the pelagic ecosystem of Hornsund fjord was also much higher than in Disko

484    Bay, Western Greenland (Madsen et al., 2001). However, the attempts to confront different

485    estimates of secondary production are unreasonable, as until now no specific method has been

486    universally adopted over all regions. Indeed, a number of methods and zooplankton size

487    fractions have so far been utilized to measure secondary production and resulted in a great

488    variety of autonomous results (Rey-Rassat et al., 2004).

489        The mesozooplankton production estimated during a post bloom state within Hornsund

490    fjord could be both over- and underestimated. The extremely abundant amorphous particles

491    from the glacier melt waters, especially at the Glacial stations, were an important source of

overestimation in the calculation of the mesozooplankton size fraction biomass. Whereas underestimation could be caused by not including the microbial food web (microzooplankton and bacteria) in our estimates (Forest et al., 2011). Moreover, even if small copepods generally do not contribute significantly to the overall zooplankton biomass, their potential growth rates indicate that they might significantly contribute to the overall zooplankton production (Hopcroft et al., 2005; Lischka and Hagen, 2005; Reigstad et al., 2011), as small species exhibit shorter generation time and more constant reproduction (Ashijan et al., 2003). Numerically small copepods (*Oithona* spp., *Pseudocalanus* spp. and *Acartia* spp.) dominated zooplankton assemblages in Hornsund fjord (Table 2), but in terms of biomass *C. glacialis* was the most important zooplankton contributor in the fjord (Fig. 4), which is consistent with several previously performed studies in the Arctic (e.g. Kosobokova and Hirche, 2000; Auel and Hagen, 2002; Hopcroft et al., 2005).

The combination of high resolution automatic measurements and the size spectrum analysis proved to be essential to comprehend the structure and function of the zooplankton community in response to the heterogeneous environment. Our results revealed a clear ecological gradient within the waters of Hornsund fjord, with the highest production in the fjords interior. As there is an increasingly urgent need to study ecological responses, e.g. structures of communities and ecosystem functioning in response to climate warming in the Arctic (Wassmann, 2011), our data on zooplankton productivity provide a groundwork for future Arctic ecosystem management and modelling.

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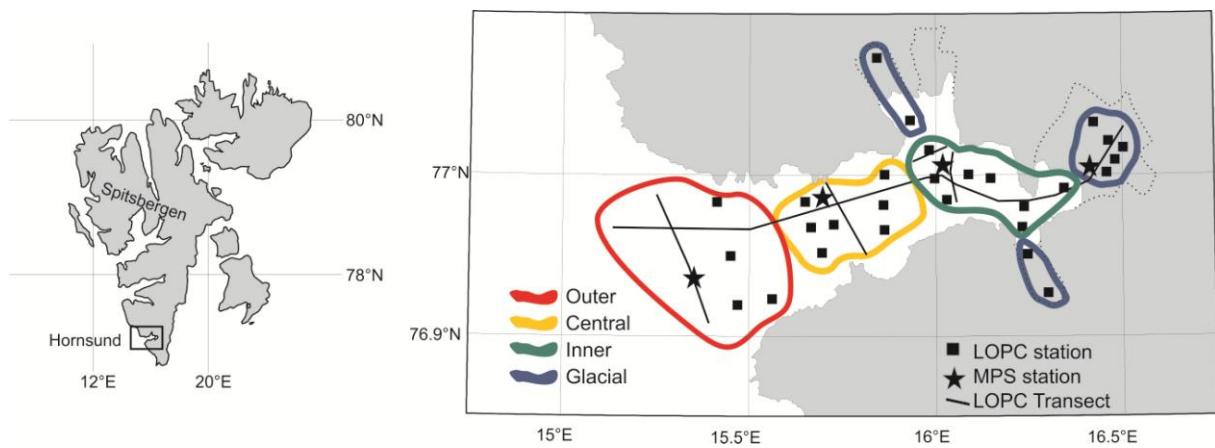837

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**Figures and Tables**



Fig. 1. Map of the survey area, Svalbard Archipelago (left) and the sampling grid in Hornsund fjord (right). Lines indicate the location of horizontal transects of LOPC-CTD-F platform at 20-25 m depth, square points indicate vertical profiles of LOPC-CTD-F platform from surface to the bottom and stars indicate stations of vertical hauls of MPS net. Colours indicate groups of stations in defined zones of Hornsund fjord.

Table 1. List of stations and transects, sampling date, time and locations. The depth of the vertical profiles together with mean water temperature and salinity in the upper 50 m and underneath (Upper / Lower) for stations. Mean and standard deviations of depth, temperature and salinity along the transects within different zones of Hornsund fjord.

| | | | | Stations | | | Mean: Upper / Lower | |
|---|---|---|---|---|---|---|---|---|
| Zone | Name | Date | Time [UTC] | Latitude | Longitude | Depth [m] | Temperature [°C] | Salinity |
| Glacial | G1 | 30.07.2012 | 11:30 | 77 01.91 N | 016 25.54 E | 61 | 2.1 / | 32.8 / |
| Glacial | G2 | 30.07.2012 | 14:10 | 77 01.23 N | 016 27.78 E | 112 | 2.3 / 0.0 | 32.8 / 34.3 |
| Glacial | G3 | 30.07.2012 | 15:45 | 77 00.48 N | 016 29.62 E | 131 | 2.4 / -0.2 | 32.8 / 34.3 |
| Glacial | HB1 | 30.07.2012 | 16:40 | 77 00.11 N | 016 27.46 E | 122 | 2.1 / -0.1 | 32.6 / 34.3 |
| Glacial | Inner | 31.07.2012 | 17:15 | 77 00.99 N | 016 29.90 E | 106 | 2.3 / -0.1 | 33.0 / 34.3 |
| Outer | A5 | 1.08.2011 | 08:15 | 76 55.17 N | 015 28.13 E | 147 | 3.5 / 2.1 | 33.8 / 34.6 |
| Outer | Outer | 1.08.2011 | 10:15 | 76 55.39 N | 015 33.59 E | 101 | 3.4 / 1.5 | 33.8 / 34.4 |
| Central | B3 | 1.08.2011 | 18:00 | 76 57.97 N | 015 40.59 E | 112 | 3.0 / 1.1 | 33.6 / 34.5 |
| Central | B4 | 2.08.2012 | 06:15 | 76 57.10 N | 015 41.73 E | 122 | 3.1 / 1.5 | 33.7 / 34.4 |
| Central | HB3 | 2.08.2012 | 08:00 | 76 58.16 N | 015 43.62 E | 198 | 3.1 / 1.3 | 33.5 / 34.5 |
| Central | B2 | 2.08.2012 | 09:10 | 76 58.92 N | 015 38.83 E | 112 | 3.1 / 1.2 | 33.3 / 34.4 |
| Outer | A1 | 2.08.2012 | 12:00 | 76 59.00 N | 015 24.78 E | 103 | 3.0 / 1.3 | 33.4 / 34.4 |
| Outer | A3 | 2.08.2012 | 16:00 | 76 56.97 N | 015 26.93 E | 127 | 3.3 / 2.0 | 33.7 / 34.6 |
| Central | C1 | 3.08.2012 | 06:10 | 77 00.04 N | 015 51.81 E | 159 | 2.6 / 1.1 | 33.1 / 34.5 |
| Central | C2 | 3.08.2012 | 06:50 | 76 58.99 N | 015 51.67 E | 188 | 3.0 / 1.2 | 33.2 / 34.5 |
| Central | C3 | 3.08.2012 | 07:50 | 76 57.97 N | 015 51.73 E | 193 | 3.1 / 1.3 | 33.6 / 34.5 |
| Inner | D4 | 3.08.2012 | 08:35 | 76 59.04 N | 016 01.86 E | 102 | 2.8 / 1.2 | 33.0 / 34.3 |
| Inner | D3 | 3.08.2012 | 09:05 | 77 00.01 N | 016 00.09 E | 101 | 2.9 / 1.0 | 33.1 / 34.4 |
| Inner | D2 | 3.08.2012 | 09:45 | 77 00.89 N | 015 58.81 E | 112 | 2.6 / 1.0 | 33.0 / 34.4 |
| Glacial | D0 | 3.08.2012 | 13:00 | 77 04.33 N | 015 50.47 E | 132 | 1.8 / 1.4 | 33.2 / 34.1 |
| Glacial | D1 | 3.08.2012 | 13:50 | 77 01.98 N | 015 55.87 E | 51 | 2.0 / | 33.2 / |
| Inner | HB2 | 3.08.2012 | 14:30 | 77 00.02 N | 016 05.01 E | 79 | 2.9 / 1.2 | 33.0 / 34.2 |
| Inner | F3 | 4.08.2012 | 06:05 | 76 59.48 N | 016 20.56 E | 111 | 2.5 / 0.0 | 33.2 / 34.3 |
| Inner | E3 | 4.08.2012 | 07:10 | 76 58.81 N | 016 14.17 E | 101 | 2.2 / 0.3 | 33.2 / 34.3 |
| Glacial | E6 | 4.08.2012 | 08:15 | 76 55.58 N | 016 17.93 E | 122 | 2.3 / 0.0 | 33.3 / 34.3 |
| Glacial | E5 | 4.08.2012 | 08:50 | 76 57.02 N | 016 14.91 E | 101 | 2.5 / 0.3 | 33.4 / 34.3 |
| Inner | E4 | 4.08.2012 | 09:15 | 76 58.05 N | 016 13.89 E | 106 | 2.6 / 0.7 | 33.2 / 34.3 |
| Inner | E2 | 4.08.2012 | 09:50 | 76 59.91 N | 016 08.75 E | 46 | 2.9 / | 33.2 / |

| | Transects | | Longitude | | | Mean  (SD) | |
|---|---|---|---|---|---|---|---|
| Zone | Date | | Start | End | Depth [m] | Temperature [°C] | Salinity |
| Outer | 31.07.2012 | | 015.13 - 015.67 E | | 22.3 (0.9) | 3.5 (0.1) | 33.8 (0.0) |
| Central | 31.07 - 1.08. 2012 | | 015.67 - 15.90 E | | 22.1 (1.9) | 3.3 (0.4) | 33.8 (0.1) |
| Inner | 31.07.2012 | | 015.90 - 016.33 E | | 23.1 (1.9) | 3.0 (0.3) | 33.6 (0.2) |
| Glacial | 31.07.2012 | | 016.33 - 016.51 E | | 21.5 (0.6) | 2.3 (0.2) | 33.2 (0.1) |
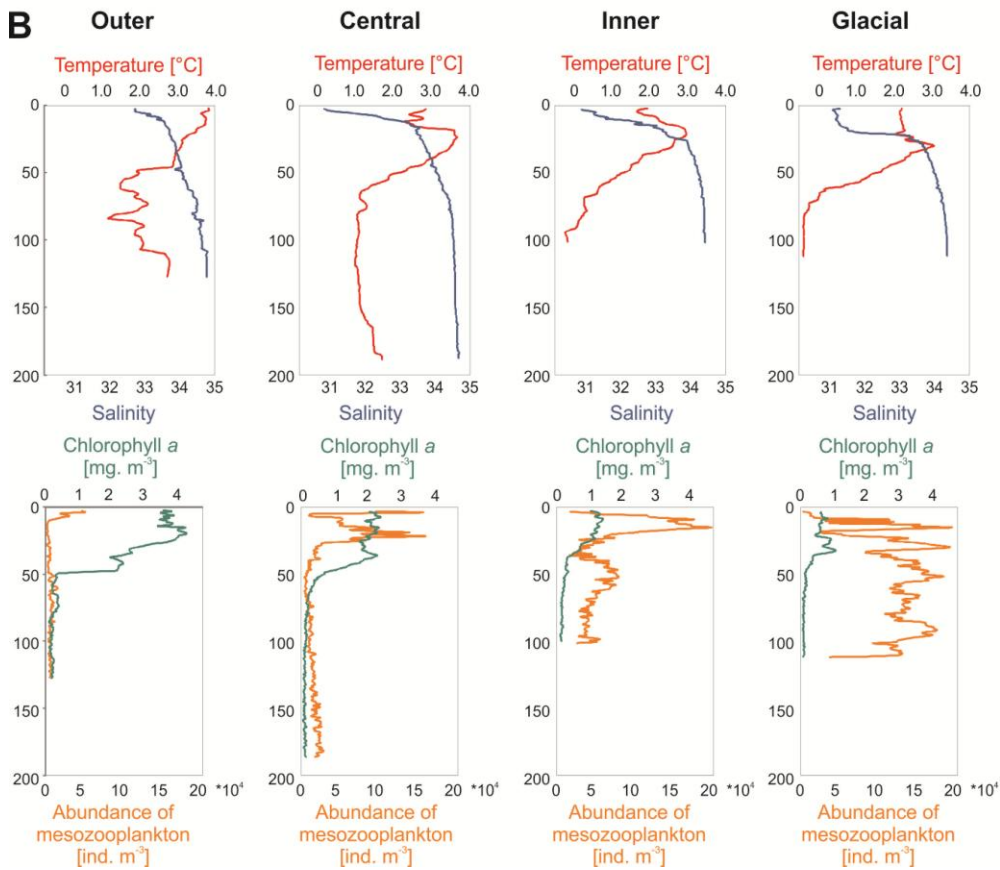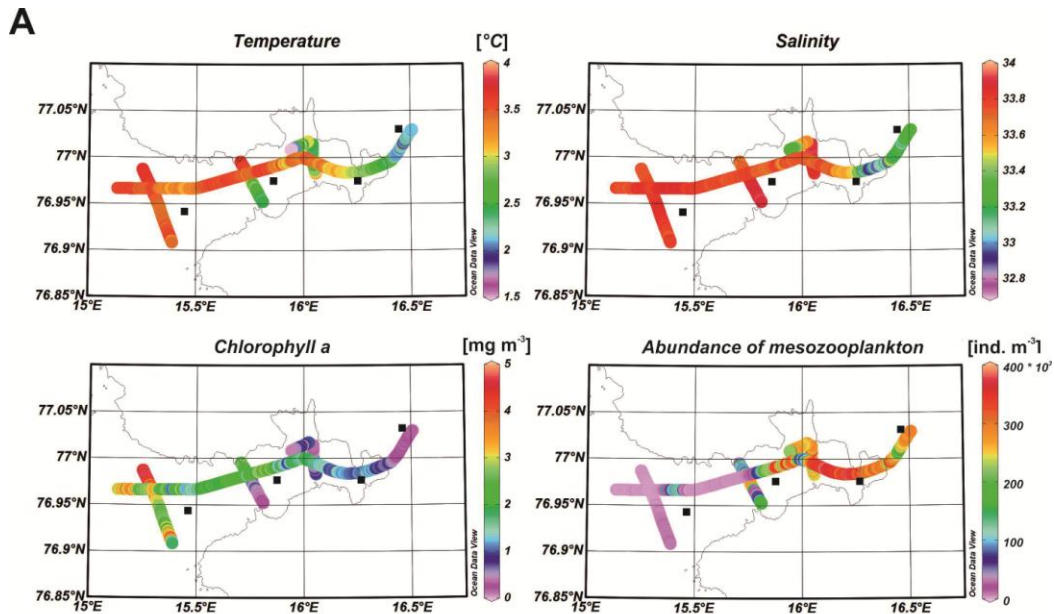
Fig. 2. **A:** maps of horizontal transects of LOPC-CTD-F platform in Hornsund fjord at 20-25 m depth **B:** vertical profiles of selected stations (their locations indicated by black square markers on the maps). Results of hydrography showed in upper panels of A&B. Chlorophyll *a* and the mesozooplankton size fraction abundance showed in lower panels of A&B.
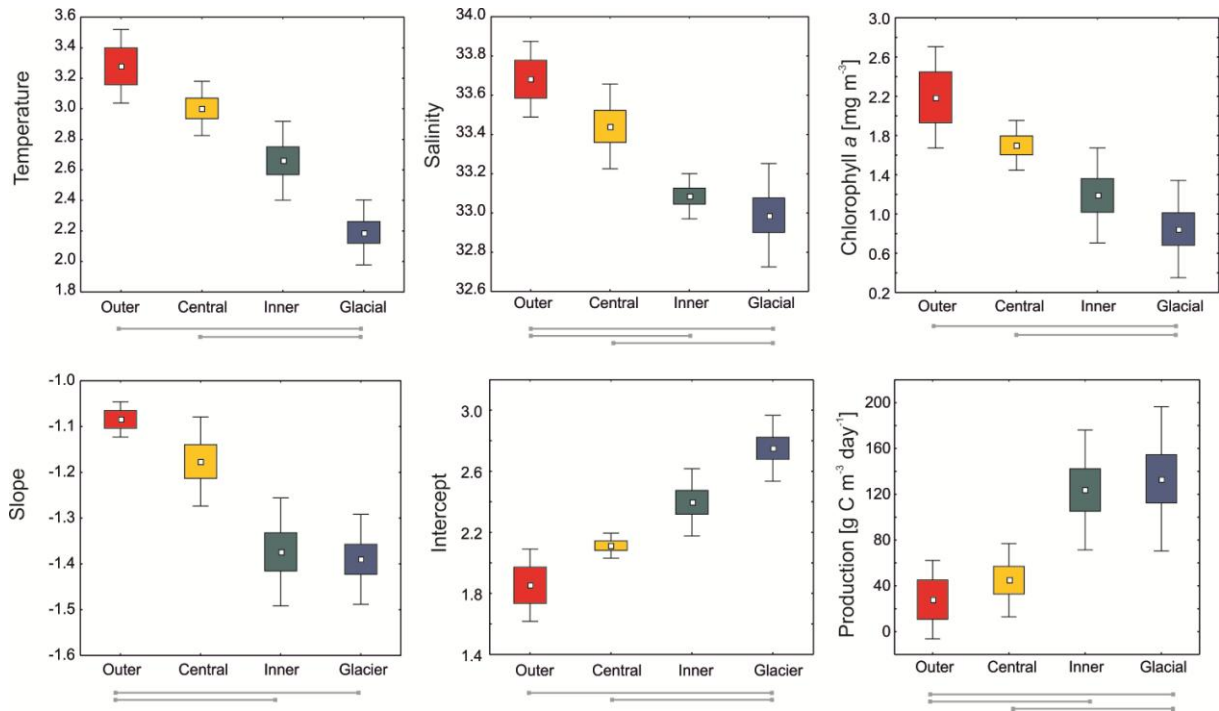
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885 Fig.3. Comparison of mean values of different parameters measured along vertical profiles at
886 stations sampled by a LOPC-CTD-F platform within upper layers (50-0 m) of defined zones
887 of Hornsund fjord. Upper panel: temperature, salinity and chlorophyll *a*. Lower panel: size
888 spectra slopes, intercepts and production of mesozooplankton. Figures presents means (white
889 squares), quartiles (boxes) and standard deviations. The statistically important differences
890 between zones are indicated by grey lines underneath the individual graphs (p<0.001;
891 Kruskal-Wallis test, *post hoc* Dunn test).

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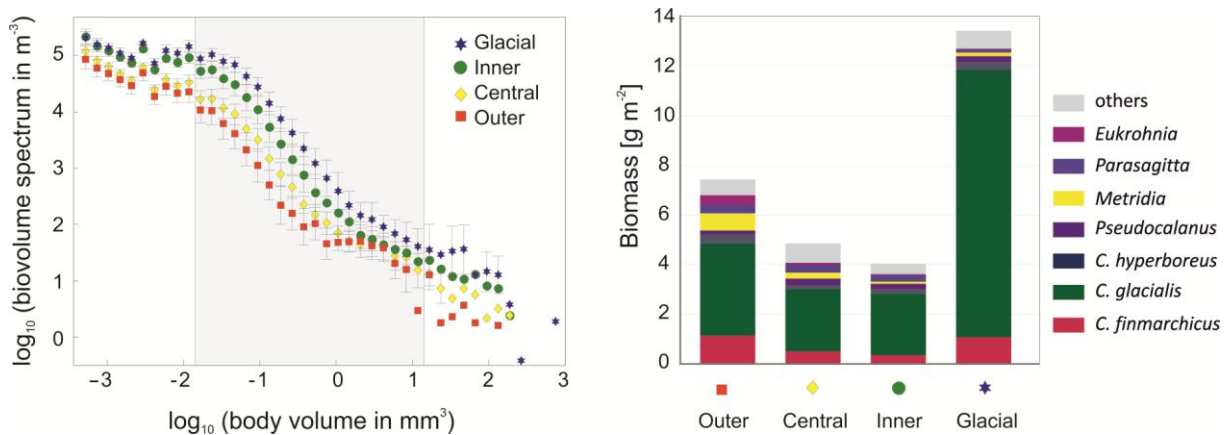


893

894 Fig. 4. Biovolume spectra of Hornsund fjord zooplankton communities measured by the
895 LOPC within its four zones (Outer, Central, Inner, Glacial) indicated by different markers and
896 colours (left panel). The grey shadow indicates the mesozooplankton size fraction. The
897 biomass of zooplankton collected by MPS net at four stations within different zones of
898 Hornsund fjord, colours indicate the contribution of different taxa (right panel).

899

27

900    Table. 2. Net results of zooplankton abundance [ind. m$^3$] in upper and lower layers of
901    Hornsund zones.

|  | Outer | | Central | | Inner | | Glacial | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Lower | Upper | Lower | Upper | Lower | Upper | Lower | Upper |
|  | 95-40 | 40-0 | 140-50 | 50-0 | 90-50 | 50-0 | 120-50 | 50-0 |
| C. finmarchicus CI-CIII | 11 | 149 | 9 | 24 | 3 | 40 | 6 | 40 |
| C. finmarchicus CIV-CVI | 51 | 93 | 17 | 13 | 13 | 31 | 32 | 60 |
| C. glacialis CI- CIII | 9 | 200 | 4 | 9 | 4 | 32 | 33 | 19 |
| C. glacialis CIV - CVI | 22 | 154 | 27 | 24 | 26 | 74 | 182 | 107 |
| Pseudocalanus spp. CI - CIII | 121 | 455 | 111 | 549 | 54 | 793 | 135 | 433 |
| Pseudocalanus spp. CIV - CVI | 126 | 147 | 94 | 231 | 48 | 177 | 62 | 190 |
| Oithona similis | 55 | 193 | 105 | 185 | 14 | 181 | 60 | 184 |
| Copepoda Nauplii | 8 | 48 | 16 | 39 | 4 | 37 | 52 | 22 |
| Acartia longiremis | 17 | 211 | 51 | 46 | 28 | 64 | 32 | 53 |
| Bivalvia veligers | 8 | 17 | 9 | 86 | 2 | 72 | 1 | 236 |
| Microcalanus spp. | 88 | 1 | 50 | 61 | 28 | 33 | 60 | 40 |
| Metridia longa | 253 | 7 | 69 | 10 | 71 | 17 | 84 | 16 |
| others | 114 | 51 | 83 | 60 | 65 | 94 | 120 | 63 |
|  |  |  |  |  |  |  |  |  |
| Total | 882 | 1726 | 644 | 1337 | 358 | 1645 | 858 | 1463 |

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903    Table 3. Parameters of linear functions fitted to the biovolume spectra of four geographic
904    zones of Hornsund fjord to different zooplankton size fractions (all – whole plankton size (0.1
905    – 28.2 mm ESD), meso - mesozooplankton (0.3 – 3.2 mm ESD) Calanus - older stages of
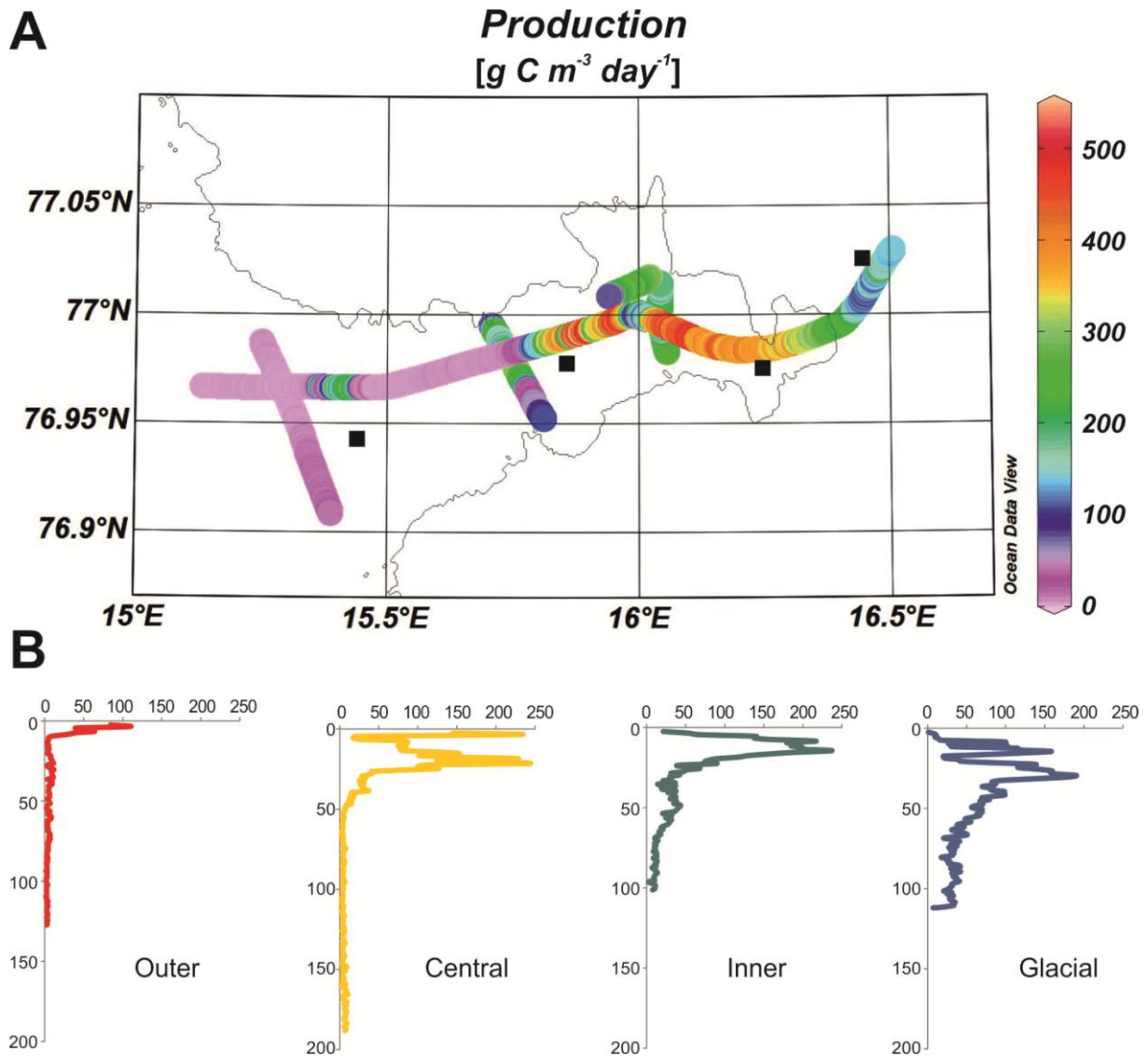906    *Calanus* spp. (1.0 – 2.5 mm ESD).

| Area | Type | Slope | Intercept | Tis | $r^2$ | p |
| --- | --- | --- | --- | --- | --- | --- |
| Outer | all | -1.0 | 2.0 | 2.5 | 0.97 | < 0.001 |
|  | meso | -1.1 | 1.9 | 2.2 | 0.93 | < 0.001 |
|  | Calanus | -0.4 | 1.8 | 5.5 | 0.69 | 0.010 |
| Central | all | -0.9 | 2.3 | 2.6 | 0.99 | < 0.001 |
|  | meso | -1.2 | 2.2 | 2.1 | 0.96 | < 0.001 |
|  | Calanus | -0.6 | 1.9 | 3.8 | 0.93 | < 0.001 |
| Inner | all | -1.0 | 2.6 | 2.5 | 0.96 | < 0.001 |
|  | meso | -1.4 | 2.5 | 1.8 | 0.98 | < 0.001 |
|  | Calanus | -1.0 | 2.2 | 2.5 | 0.97 | < 0.001 |
| Glacial | all | -1.0 | 2.8 | 2.5 | 0.94 | < 0.001 |
|  | meso | -1.4 | 2.8 | 1.8 | 0.98 | < 0.001 |
|  | Calanus | -1.2 | 2.6 | 2.1 | 0.97 | < 0.001 |

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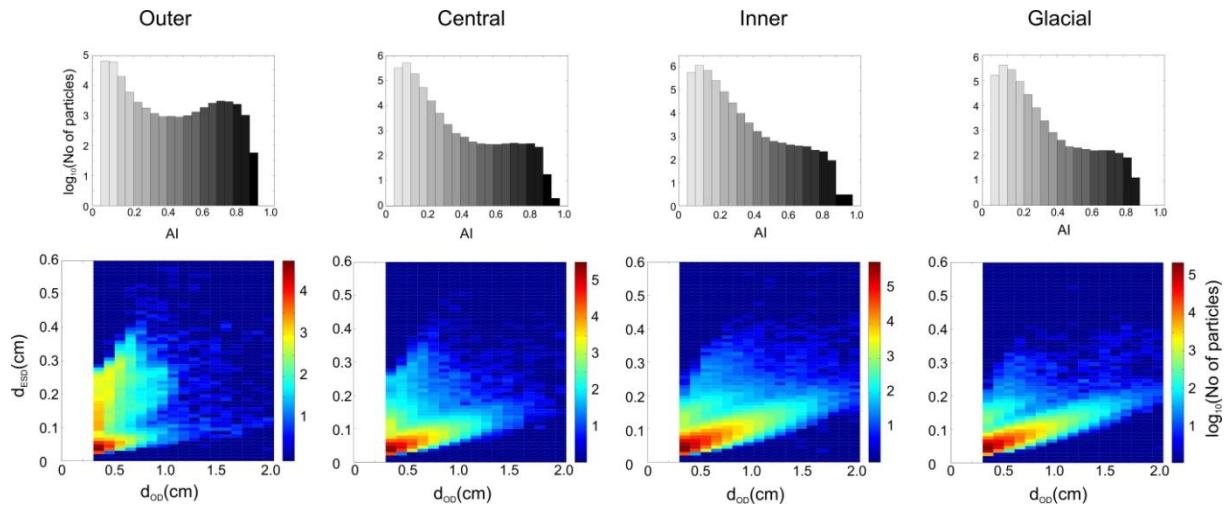
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Fig. 5. The modelled secondary production in Hornsund fjord. **A:** maps of horizontal transects of LOPC-CTD-F platform in Hornsund fjord at 20-25 m depth (5 m averaged) **B:** vertical profiles of selected stations (their locations indicated by black square markers on the map).

Fig. 6. Upper panel: Histograms of the $\log_{10}$(number of particles) within different ranges of attenuation index (AI), the lighter colours refers to the higher transparency ranges whereas the darker the colour the more opaque particle represent. Lower panel: Relationship between equivalent spherical diameter ($d_{esd}$) and occluded diameter ($d_{od}$). Colour scale indicates the $\log_{10}$(number of particles) in a size bin. Each separate plot represents the data of LOPC-CTD-F platform horizontal hauls (20-25 m depth) within four different zones of Hornsund fjord.

1. The model of mesozooplankton production within high Arctic fjord is presented.

2. High-resolution measurements showed bio-physical gradient along fjord's axis.

3. Secondary production was high and concentrated mainly in Hornsund interior.

4. The feeding modes (trophic indices) of *Calanus* spp. differed along fjord's axis.

5. Different types of particles (opaque/amorphous) were distinguished in LOPC data.