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# Zooplankton distribution and feeding in the Arctic Ocean during a *Phaeocystis pouchetii* bloom

Enric Saiz[*,1], Albert Calbet[1], Stamatina Isari[1], Meritxell Antó[1], Eva M. Velasco[1,2], Rodrigo Almeda[1], Juancho Movilla[1] and Miquel Alcaraz[1]

[1]Institut de Ciències del Mar (CSIC), Ps. Marítim de la Barceloneta 37-49, E-08003 Barcelona, Catalunya, Spain

[2]Present address: Centro Oceanográfico de Gijón (IEO), Avenida Príncipe de Asturias 70 bis, E-33212 Gijón, Spain

*corresponding author, enric@icm.csic.es. Phone: INT+34-932309521, Fax: INT+34-932309555

ABSTRACT

In early summer 2007 we determined the vertical distribution of mesozooplankton (>200 μm) and assessed the copepod feeding rates in 19 stations distributed along the East Greenland Current and the Fram Strait. The study coincided with a bloom of the haptophyte *Phaeocystis pouchetii* in the colonial form. Copepods dominated the zooplankton community numerically, and were mainly distributed within the upper 150 m (except for *Metridia longa* and *Oithona spp.*, that inhabited deeper waters), without showing a clear avoidance of the *P. pouchetii* layer. Copepod diet was diverse, ciliates having a relevant share (40% of the diet). Copepods also displayed active grazing upon the colonies of *P. pouchetii*. In general, feeding rates were low (on average, daily ration was 1.6% of body carbon), likely due to the scarcity of nano and microplankton during the study (<100 μg C $L^{-1}$). Consequently, the trophic impacts on both the nano- and microplankton standing stocks and on primary production were negligible. These results suggest that during the period of study the transfer of carbon and energy from lower trophic levels towards copepods was low.

KEYWORDS

Arctic; Fram Strait; Spitsbergen; Greenland; Zooplankton; Copepod; Feeding; Diet; Vertical distribution; Phaeocystis; ZooImage

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## 1. INTRODUCTION

The Arctic Ocean is currently one of the most sensitive marine ecosystems confronted with global change (Wassmann, 2011). Warming and ice loss will affect the radiative balance of polar waters, resulting not only in a presumable disruption of the global conveyor belt (Spielhagen et al., 2011), but also in likely changes in the phenology and species composition of the autotrophic and zooplankton communities. Such changes would result in alterations of the functioning of the planktonic Arctic food webs, affecting as a whole the biological and biogeochemical processes in the water column (Agustí et al., 2011). In spite of this relevance, our knowledge of the structure and, especially, the functioning of Arctic planktonic food webs is still scarce, limiting our ability to detect ecological changes related to climate variability (Daase & Elane, 2007; Wassmann et al., 2011). This lack of knowledge extends to the zooplankton level as well, and, in particular, to copepods. Copepods are key organisms responsible for the transfer of primary production to upper trophic levels (either directly or via microzooplankton; Calbet & Saiz, 2005), and they are also involved in the recycling of nutrients in the upper layer and in the downward export of biogenic carbon to the deep ocean.

Here we present data from a multidisciplinary cruise conducted in the framework of the Spanish Project ATOS (Aportes atmosféricos de carbono orgánico y contaminantes al océano polar: tasas, significación y perspectivas), and the International Polar Year. The survey took place in early summer 2007 on board the Spanish R/V Hespérides and covered waters along the East Greenland Current and the Fram Strait. The Fram Strait is a region of confluence of North-Atlantic waters and the export of Arctic Sea ice through the East Greenland current (Hop et al., 2006); therefore, it is considered particularly important and very sensitive to any effects induced by global change. In this

study we determined the vertical distribution of mesozooplankton and experimentally assessed copepod feeding rates on autotrophic and heterotrophic prey, with a two-fold goal: i) to evaluate the contribution of protozooplankton to the diet of Artic copepods and compare it to those reported at lower latitudes, and ii) to establish the flux of carbon through the copepod community and evaluate the impact on their prey populations.

Contrarily to the still widely accepted view that polar copepods are mainly herbivorous (e.g. Blachowiak-Samolyk et al., 2007; Saunders et al., 2003; Søreide et al., 2008), the limited number of available studies analyzing the diet composition of Arctic copepods suggest that in occasions the contribution of protozooplankton can be high (e.g. Levinsen et al., 2000; Møller et al., 2006), similar to the general pattern found in most of the oceans (Saiz & Calbet 2011). Generally, with the exception of the extensive data set provided by Campbell et al. (2009) in the Beaufort and Chuckchi Seas, reports on copepod diet composition and daily rations in most areas of the Artic are either lacking, based only on gut contents fluorescence, or are relying on too few observations to withdraw general conclusions or patterns. In particular for the Fram Strait area, most of the previous copepod feeding studies were based on the gut fluorescence method (e.g. Båmstedt, 1984; Tande & Bamstedt, 1985), which neglects the heterotrophic components of the diet (Saiz & Calbet, 2011). To our knowledge, only the works by Barthel (1988; 1990) or Smith (1988), restricted to few observations, contemplated microscopic counts. As a consequence, there are no thorough studies on the carbon fluxes mediated by zooplankton in the Fram Strait, despite being one of the most studied and sensitive zones in the Arctic. During the study we benefitted from the fact that the cruise was coincident with the late phase of a bloom of the colonial form of the haptophyte *Phaeocystis pouchetii*, a recurrent phenomenon in the area (Schoemann et al., 2004). This phenomenon broadened the range of scenarios to be

faced by zooplankton during our study. In addition, instead of focusing on a copepod stage- and species-specific approach (typically limited to a few species and/or stages), to obtain a better picture of the fluxes at the community level we conducted the experiments using the natural copepod assemblages.

Parallel studies conducted during the ATOS-Arctic cruise have focused on the metabolic activity of mesozooplankton (Alcaraz et al., 2010) and the grazing of microzooplankton (Calbet et al., 2011), and will be considered in the Discussion section.

## 2. MATERIAL AND METHODS

### *2.1 Study site, CTD casts and water samples for chlorophyll profiles*

The ATOS-Arctic cruise took place in the Greenland Sea, the Fram Strait and an area north of Spitsbergen from the 1st to the 25th of July 2007, onboard the research vessel "BIO Hespérides'' (Fig. 1). It included stations located in ice-free open waters, as well as stations close to the sea ice edge (Table 1). The sea ice extent observed that year was a minimum (Zhang et al., 2008) and allowed the ship to sail up to 80º 50'N. At each station, profiles of temperature, salinity and fluorescence were obtained in the morning with a Seabird CTD911, fitted with a Rosette with 12-L Niskin bottles. Water samples for chlorophyll *a* (chl *a*) analysis were taken from 5 depths (including the fluorescence maximum) during the CTD ascent. Aliquots of water were low-pressure (<100 mm Hg) filtered onto both Whatmann GF/F and 5-µm polycarbonate filters, and frozen (-80ºC); filters were later extracted with 90% acetone and analyzed using a Turner Designs fluorometer before and after acidification.

### *2.2 Composition and standing stocks of zooplankton*

At each station (except 3 cases in which it was not possible), a Longhurst-Hardy Plankton Recorder net (LHPR) fitted with 200 µm gauze was deployed to 350 m depth

(or shallower when not possible), and 9 depth intervals (nominally, 0-25, 25-50, 50-75, 75-100, 100-150, 150-200, 200-250, 250-300, 300-350 m; occasionally an extra interval had to be intercalated) were sampled during the descent cast. Zooplankton samples were preserved with 4% formaldehyde (final concentration) buffered with borax.

Zooplankton samples were scanned in the lab, and later analyzed using the software ZooImage (www.sciviews.org/ZooImage), which has proved to be a useful tool for automatic analysis of zooplankton samples (e.g. Grosjean et al. 2004; Bell and Hopcroft, 2008; Gislason and Silva, 2009). When necessary, the samples were first either concentrated, or diluted with a Folsom splitter to ensure a suitable concentration that would not result in significant overlapping of individuals. Aliquots were stained with a drop of 1% yellow eosin in glass vials, and left overnight in darkness at room temperature. Later, they were transferred to a square polystyrene Petri dish (12 cm x 12 cm), filtered seawater was added to fill up to approximately 50% of the volume of the dish, and a dab of soap was used to break surface tension and avoid organisms sticking to the surface. The aliquot was then distributed homogenously in the dish with a plastic comb, checked visually and, when necessary, individuals were separated with a dissecting needle. Occasionally, when the number of individuals in the aliquot was still too high or very large zooplankters appeared, the aliquot was distributed (and scanned) in several dishes. The samples were scanned in color, transparency mode, at 2400 dpi using an Epson 4990 scanner controlled by the Vuescan software, and saved as jpeg files to be processed by ZooImage. Two areas, each one of 10.5 cm x 4.8 cm (10144 x 4548 pixels), were scanned per dish (aliquot), covering in total 74.6 % of the dish area; these two scanned areas were subsequently analyzed together. A training set of objects including up to 20 categories of objects (different zooplankton groups, debris, etc.) was defined, comprising 13 groups of zooplankton. Images were classified according to the

established training set with the Random Forest algorithm (see Web Appendix for further information on automatic classification accuracy and manual verification procedures followed). Major and minor axes of each particle (fitted to an ellipse of the same area) were determined, and then biovolume was calculated using the minor axis to build an ellipsoid.

We used multivariate analysis, i.e. hierarchical agglomerative average-linkage clustering and non-metric multidimensional scaling (NMDS), to compare the copepod community structure among stations (Field et al., 1982; Clarke & Warwick, 1994). Using PRIMER v6 package (Clarke & Gorley, 2006) a sample-to-sample matrix was calculated as Bray Curtis similarity index, based on copepod square-root transformed abundance values integrated for the 0-100 m layer (standardized to $m^3$).

*2.3 Grazing experiments*

Live zooplankton samples were collected with a double 200-μm WP-2 net fitted with ca. 5-10 L plastic bags as cod ends. Nets were deployed to 75 or 100 m depth, and towed vertically at low speed (10 m $min^{-1}$) to avoid organism damage. Once on deck, the plastic bags containing zooplankton were kept in coolers filled with surface seawater and plastic ice packs. As on most occasions the presence of *Phaeocystis pouchetii* colonies was conspicuous, the live zooplankton samples were diluted with filtered seawater and gently screened several times through a submerged 500-μm sieve to remove the *P. pouchetii* colonies, and finally were transferred to 1.5 L of *in situ* water. This was done repeatedly until the concentration appeared visually sufficient, and then the live zooplankton was divided into aliquots (100-250 ml) for seeding the experimental bottles. Any large carnivorous zooplankters (e.g. amphipods, chaetognaths) were individually removed or screened off (2000 μm sieve) before making the aliquots. Later

analysis confirmed that the aliquots were mainly composed of copepods (on average, 94.1% of individuals; see Web Appendix).

Water for the grazing experiments was collected from the fluorescence maximum depth with the CTD Niskin bottles. Six 9-L Nalgene polycarbonate bottles were used as incubation bottles; two additional 2.3-L Nalgene polycarbonate bottles were also filled in order to be sampled immediately and assess the initial concentration values of chl *a* and phyto- and protozooplankton (see below). Incubation bottles were filled simultaneously from three different Niskin bottles to ensure homogeneity. Bottles were filled slowly and carefully, to avoid water bubbling and turbulence, which is particularly harmful to microzooplankton, and may also result in the breaking of diatom chains. Three of the 9-L incubation bottles were intended as grazing bottles, in which the concentrates of zooplankton were added (on average, 157±9.7 SE individuals per bottle). Extra aliquots from the zooplankton concentrate were either preserved in 4% buffered formaldehyde or filtered onto GF/A filters and oven dried (60ºC), for later analysis in the laboratory and calculation of biovolume-biomass conversion factors (Alcaraz et al., 2003; see Section 2.4 and the Web Appendix). The remaining three 9-L incubation bottles had no addition of concentrated zooplankton and served as control bottles. To ensure similar conditions between experimental and control bottles (added nutrients from zooplankton, small zooplankton and phytoplankton, etc.), the same amount of water from the “zooplankton concentrate” that was used in the aliquots was sieved through 500-µm and added to the control bottles. Nutrients (180 µmols of $NH_4Cl$ and 12 µmols of $Na_2HPO_4$ per bottle) were added to compensate for any differences in nutrients between grazing and control bottles due to excretion (Broglio et al., 2004; Calbet et al. 2009; Almeda et al. 2011). Bottles were incubated on deck in a large (600 L), plastic incubator with open-circuit seawater running from 5-m depth, providing

temperature similar to *in situ* (see Table 1 in Calbet et al., 2011). Light was dimmed with a dark plastic mesh to mimic the light intensity at the fluorescence maximum. The bottles were incubated for 24-30 h, and turned upside down several times during the incubation to reduce settling of non-motile prey.

After the incubation, the bottle contents were homogenized by repeatedly turning upside down, and samples for chl *a* analysis (500 ml) and for Lugol's fixation (500 ml, 1% acidic Lugol's solution) were carefully siphoned with silicone tubing. Special care (visually) was taken to avoid sucking out copepods when taking the samples. After the water samples were taken, the remaining water of each grazing and control bottle was filtered onto a 200 μm sieve, concentrated into a volume of 50 ml and preserved with buffered formaldehyde (4%). Samples to estimate total and >5-μm chl *a* concentration were filtered onto Whatmann GF/F and >5-μm polycarbonate 25-mm diameter filters respectively (50 to 250 ml, depending on the station and the type of filter), and kept frozen until analysis by fluorometry according to the procedures mentioned above (Section 2.1).

For microscopic counts, 100 ml of the Lugol samples were settled in Utermöhl chambers for 48 h, and either the whole chamber or a fraction of it was counted under an inverted microscope (XSB-1A) at magnification 100, 250, and 400 x, depending on cell size. As the abundance of prey was expected to be lower in the grazing bottles (as compared to the controls), the entire 500 ml samples were settled for 72 h and then the supernatant was carefully and slowly siphoned out until the volume was reduced to one half; the concentrate was then resuspended, and 100 ml of it were then transferred to the Utermöhl chambers for counting as mentioned above. A total of 78 taxa and/or groups of phyto- and microzooplankton were distinguished, 20 cells of each were sized, and then converted to carbon using the equations of Menden-Deuer & Lessard (2000).

Details on the full taxonomic composition of phyto- and microzooplankton community can be found in Calbet et al. (2011). For the purposes of this study, phyto- and microzooplankton were grouped into the following categories: diatoms, dinoflagellates (<20 and >20 µm, respectively), ciliates (<20 and >20 µm, respectively), *Phaeocystis* (*Phaeocystis pouchetii*), and *others* (composed mainly of nanoflagellates). Data on ciliates (both biomass and ingestion rates upon) were increased by 30% to correct for losses in cell numbers during fixation according to Broglio et al. (2004) and Calbet & Saiz (2005). Regarding dinoflagellates, we assumed that 50% were heterotrophic (Lessard & Swift, 1986). Further detailed information on the composition of phytoplankton and microzooplankton during the cruise and other additional information can be found in Calbet et al. (2011) and Lasternas & Agustí (2010).

Clearance and ingestion rates, either based on chl *a* concentration or microscopic counts, were calculated according to the equations provided by Frost (1972). No corrections for microzooplankton grazing were applied (Nejstgaard et al., 2001) (see Discussion). Statistically significant grazing was determined by comparing the prey growth rates between the respective replicated control and experimental bottles by t-tests. When grazing for a certain prey was not significant, the respective clearance and ingestion rates were rectified to zero.

The abundance, composition, biovolume and biomass of the zooplankton added in the grazing experiments were estimated using the ZooImage software, similarly to the LHPR net samples. Due to the lower abundance of the zooplankton present in the grazing bottles, the whole sample had to be scanned instead of aliquots; a single area of 10 cm x 10 cm (9448 x 9449 pixels) was scanned per dish, and all zooplankters close to the walls were moved towards the center to ensure they were within the scanned area. As the seawater used for the experiments may already have had some naturally

present zooplankton, the zooplankton biomass in the control bottles was subtracted from the zooplankton biomass measured in the grazing bottles to assess the actual added zooplankton biomass.

*2.4 Biomass conversion*

Biovolume was converted into ash-free dry weight (AFDW) using the conversion factor of 0.132 mg AFDW $mm^{-3}$ obtained with the zooplankton samples used in the grazing experiments (see detailed explanations in the Web Appendix). As the zooplankton aliquots used for the grazing experiments were essentially composed of copepods (on average: 94.1%, range: 80.7-99.7), we opted to apply this conversion factor only to this group. For this reason, data on field distribution of other zooplankters is presented only as abundance and biovolume.

## 3. RESULTS

*3.1 Hydrography*

During the present study, the physical properties of the water column showed a high spatial variability, reflecting the hydrodynamic complexity of the Greenland Sea - Fram Strait system. Profiles of temperature (Fig. 2A) and salinity (not shown here) revealed notable thermohaline variability, especially in the upper 50 m; average temperature and salinity in the upper 50 m ranged from -1.5°C to 6.9°C and from 33.2 to 35, respectively. In contrast, the deeper part of the water column (50-400 m) was less structured, with mean temperature and salinity ranging from -0.1 to 4.8°C and from 34.8 to 35.1, respectively; both parameters remained almost constant with depth.

According to the T-S diagram of average temperature and salinity in the 0-50 m stratum (Fig. 2B), three groups of stations were defined in relation to the physical

properties of the prevailing water masses in the area (i.e. Polar Water, Atlantic Water, and a mixture of the two). Stations located at the western boundary of Fram Strait (Stns 46, 49) along with one site off the northern part of Spitsbergen (Stn 42) and another in the southwestern part of the sampling grid (Stn 2) showed a remarkable combination of low values of surface temperature (<0 $^{o}$C) and salinity (<34.4) (Group I). The presence of a cooler and less saline water mass at these locations, extending from the subsurface down to the depth of 50 m, suggests either the influence of Polar Surface Water (PSW) arrested by the Greenland current (PSW has been defined as T<0°C, S<34.4 by Hirche et al., 1991), or the influence of ice melting. The 0-50 m layer of the remaining stations showed higher temperature and salinity values, being presumably under the influence of the warmer and saltier mass of intermediate Atlantic water. Stations with a combination of T>0°C and S>34.4 were considered to be under a strong influence of Atlantic Water (Schlichtholz & Houssais, 1999). This group (labeled Group III) comprised mainly stations situated on the west of the Spitsbergen as well as those on the northern sites of the latitudinal transect. In the Group II stations the surface layer was occupied by water of intermediate temperature and salinity (T>0°C and S<34.4), likely reflecting mixing between the two previously mentioned water masses. Although the stations had been initially classified according to their proximity to the ice (see Table 1), this ice was always drifting ice, and such classification did not appear related to the station specific hydrographic features.

Well-developed fluorescence maxima were identified over almost the entire sampling grid (profiles not shown), at depths ranging mainly within the 12-36 m stratum (Fig. 2C). Most of the stations in the Greenland Sea (i.e. Stns: 1, 2, 3, 4, 6) had overall lower fluorescence maxima, than the others situated north and western of the Spitsbergen.

*3.2 Standing stocks of phyto- and protozooplankton*

The integrated (upper 100 m) standing stocks of chl *a* were variable (Fig. 3), and in general tended to be lower at stations of the longitudinal transect and those influenced by Polar water (Group I stations). Hence, maximum standing stocks were found at stations 5, 18, 23 and 42, reaching values up to 207 mg chl *a* $m^{-2}$. At those stations, chl *a* concentrations at the fluorescence maximum (from CTD-rosette vertical profile, data not shown) were respectively 7.52, 7.04, 6.13 and 6.26 µg chl a $L^{-1}$, consistent with bloom situations. Overall, about 50% of the chl *a* was in the >5 µm fraction (Fig. 3), with minimum values at Stn 49 (18%) and maximum ones at Stn 9 (76%). Lowest contributions were found within the stations influenced by Polar water (Stns 42, 46 and 49).

The biomass and composition of phyto- and protozooplankton in the grazing incubations (initial values) varied considerably among stations (Fig. 4). *Phaeocystis pouchetii* was the main phytoplankter, on average contributing to 35% of phytoplankton biomass; at some stations *P. pouchetii* was scarce or absent (Stns 3, 27, and 36). Diatoms were the next major contributor to phytoplankton biomass, accounting for 24% on average, closely followed by autotrophic dinoflagellates (23%). Diatoms were particularly relevant at the stations 27, 1 and 23 (66%, 57% and 51%, respectively, of the autotrophic biomass), whereas the autotrophic dinoflagellates (mostly on the <20-µm fraction) consisted up to 62% of the phytoplankton biomass (i.e. Stn 5). Total chl *a* was positively correlated with the total phytoplankton biomass ($r=0.68$, $p<0.004$, $n=16$), the diatom biomass ($r=0.60$, $p<0.015$, $n=16$) as well as the biomass of *P. pouchetii* ($r=0.54$, $p<0.032$, $n=16$).

Regarding microheterotrophs, 69% of their biomass consisted of ciliates (mainly in the >20 µm class). Ciliate biomass was on average ca. 4 times higher than the estimated biomass of heterotrophic dinoflagellates (16.1 vs 4.4 µg C $L^{-1}$, respectively).

Taking into account the whole phyto- and protozooplankton community, on average ciliates contributed to 33% of the total biomass, followed by dinoflagellates (25%), and by *Phaeocystis pouchetii* (21%). More information on the taxonomical composition of the phyto- and protozooplankton community and the relationships between them can be found in Calbet et al. (2011).

*3.3 Zooplankton composition, distribution and standing stocks*

The average zooplankton abundance ranged from 80 (Stn 23) to 661 (Stn 18) ind $m^{-3}$ throughout the surveyed area, whereas in terms of zooplankton biovolume values ranged from 121 (Stn 12) to 604 (Stn 2) $mm^3$ $m^{-3}$ (Fig. 5). The copepod category (encompassing only copepodite and adult stages) dominated the community, with average contributions of 67% and 40% of, respectively, the zooplankton abundance and biovolume (Fig. 5). Copepod nauplii were classified as a separate category, and numerically was an important contributor to zooplankton (on average 23%, range 9-48%); however, in biovolume their contribution was <1%. Amphipods and chaetognaths were also relevant groups (respectively, 4.2 and 3.5% of mean abundance, and 21% and 21% of mean zooplankton biovolume), whereas other taxons like euphausiids and cnidarians only showed occasional relevance of in terms of biovolume. Caution should be taken, however, with the non-copepod biovolume estimates, because in certain groups their relative contribution could be overestimated because their shape certainly might differ much from an ellipsoid.

The vertical distribution patterns of the zooplanktonic groups identified during the ATOS-Arctic cruise are shown in Figure 6. Most of the zooplankton was concentrated above 200 m, which contained from 48 to 87% (average: 65%) of total zooplankton abundance in the water column. Within the 0-200 m layer copepods were the dominant component of the zooplankton community both in terms of abundance (Fig. 6) and

biovolume (data not shown), with an average contribution of 70% and 45% of the standing stock in that layer, respectively.

Figure 7 shows the vertical distribution of copepod abundance and biomass and the concurrent depth profile of fluorescence (from LHPR net). Typically the maximum of copepod abundance and biomass coincided with the fluorescence maximum (or was located below this). This pattern did not appear to be influenced by the presence of *Phaeocystis pouchetii*. For instance, at stations 6, 23, 39, 42 and 46 there was high abundance of *P. pouchetii* (Fig. 4) and both patterns can be found, either coincidence of peaks (Stns. 6, 42 and 46) or a deeper distribution of copepods (Stns. 23 and 39). At stations 3 and 18 the peaks of copepod abundance and biomass were clearly below the fluorescence maximum in spite of the absence (Stn. 3) or very scarce (Stn. 18, see Calbet et al., 2011 for the *P. pouchetii* abundance at that station) presence of *P. pouchetii*.

A total of six copepod groups were identified during the present work and their size characteristics have been summarized in Table 2. Three "calanoid" groups dominated the copepod community, both numerically and in terms of biomass (Fig. 8). Although we did not perform any taxonomic identification of these three groups, visual observations indicated that they were mainly made up of adults and copepodites of the three typical *Calanus* species in the area (*Calanus hyperboreus*, *Calanus glacialis* and *Calanus finmarchicus*; Hirche et al., 1991; Blachowiak-Samolyk et al., 2007). These calanoid groups were generally concentrated in the upper 150 m (Fig. 8), and mainly comprised the small (mean abundance: 56 ind $m^{-3}$, maximum: 615 ind $m^{-3}$; values per sampling layer, not integrated) and medium (mean abundance: 30 ind $m^{-3}$, maximum: 491 ind $m^{-3}$) size classes. The large-sized calanoids, presumably corresponding to individuals of *Calanus hyperboreus*, had much lower abundance (mean abundance: 2 ind $m^{-3}$,

maximum: 30 ind $m^{-3}$). In terms of biomass the more relevant group of copepods corresponded to the medium-sized calanoids.

The cyclopoid genus *Oithona* was also very relevant in terms of abundance (mean abundance: 52 ind $m^{-3}$, maximum: 495 ind $m^{-3}$) with a vertical distribution more widespread compared with those of the calanoid categories, showing also significant numbers in deeper strata (Fig. 8A). *Metridia longa* was present at all stations (mean abundance: 18 ind $m^{-3}$), but only showed high abundance at the southwesternmost stations (i.e., Stns. 2, 3, 4; Fig. 8), where they reached concentrations up to 196 ind $m^{-3}$ (Stn. 2).

Multivariate analyses based on the abundance of the 3 major copepod categories (calanoids, *Oithona* spp, *Metridia longa*) computed over the 0-100 m layer (ind $m^{-3}$) revealed a strong spatial differentiation in the copepod community structure of the sampling area (Fig. 9A). Three groups of stations (Group 1, 2, 3) were distinguished with significant differences in the total copepod abundance (on average, Group 1: 190 ind $m^{-3}$, Group 2: 369 ind $m^{-3}$, Group 3: 108 ind $m^{-3}$) but also in the relative (%) density of the copepod categories (Fig. 9B). Calanoids (especially the small-sized individuals) were the dominant component in all the groups of stations. Notably, five stations (Group 1) had a higher contribution of *Metridia longa* in the copepod community and lower of the genus *Oithona,* compared to rest of the sites. It is worth mentioning that most of the Group 1 stations were characterized by low temperature and low salinity values, and were assumed to be under the influence of Polar water masses (see Fig. 2B, Stn 3 had also similar characteristics with the Polar waters Group). The 11 remaining locations formed two distinct groups (Group 2 and 3) with similar species composition but significant differences in their copepod stock. Group 2 included stations with very high copepod densities, however this could not be associated to the topographic or

hydrological features (apart from Stn 18, i.e. shallow station with high chl *a* stock). The rest of the sites (Group 3) had lower copepod stocks and were overall affected by higher temperature and higher salinity waters either of Atlantic origin or deriving from mixing processes.

*3.4 Zooplankton grazing rates based on* chl *a removal*

Zooplankton clearance rates ranged from non-significant grazing (i.e. nil) to close to 400 ml mg $AFDW^{-1}$ $d^{-1}$ (Fig. 10). Except for Stns 3, 12 and 23, clearance rates were significantly higher on >5 µm chl *a* (t-tests, $p<0.05$, Fig. 10), and averaged 99 and 205 ml mg $AFDW^{-1}$ $d^{-1}$, respectively, on total (GF/F) and >5 µm chl *a*. No significant correlation was found between clearance rate and chl a concentration for any of the GF/F and >5- µm size fractions (respectively, $r=-0.40$, $p>0.2$; and $r=-0.16$, $p>0.6$).

Taking into consideration that the aliquots used in the incubations were mainly composed of copepods (see Section 2.3), we assessed the zooplankton grazing impact on phytoplankton based on copepod standing stocks. We explored different possibilities using either: 1) the average copepod standing stock in the upper 100 m, 2) the average copepod standing stock in the upper 200 m, 3) the maximum copepod biomass recorded in the water column, and 4) the actual copepod biomass at the depth of fluorescence maximum (Table 3). In all cases the grazing impact on the chl *a* maximum (initial values) was negligible, with maximum impacts <2% $d^{-1}$ for both GF/F and >5 µm chl *a*.

*3.5 Zooplankton grazing rates based on cell removal (microscopic counts)*

Zooplankton ingestion rates on the different phyto- and protozooplankton are shown in Figure 11. Overall ingestion rates were low, averaging 8 µg C mg $AFDW^{-1}$ $d^{-1}$ (1.6% of body carbon ingested daily, assuming 49% carbon content for Arctic copepods; Conover & Huntley, 1991). Very low rates were observed at stations 9 and 49 (ca. 1 µg

C mg AFDW$^{-1}$ d$^{-1}$, daily ration: 0.2% d$^{-1}$), characterized by low initial phyto- and protozooplankton biomass, whereas maximum rates (ca. 30 µg C mg AFDW$^{-1}$ d$^{-1}$, daily ration: 6% d$^{-1}$) were observed at station 3 coincidence with an exceptionally high abundance of ciliates in the water and the absence of *Phaeocystis pouchetii*. The effect of prey density on feeding rates is illustrated by the significant positive relationship between ingestion rates and total prey availability (Fig. 12).

Regarding clearance rates (Fig. 13), there were significant differences among prey types (ANOVA test, $p<0.001$). A posteriori test (Tukey-Kramer HSD) showed that the highest clearance rates were exhibited on ciliates >20 µm and diatoms (Table 4). However, further analysis comparing the contribution (as % biomass) of each prey type to the phyto- and protozooplankton community with its contribution to the zooplankton diet did not evidence strong patterns of prey selection (Fig. 14). Although for some groups (i.e. ciliates >20 µm, dinoflagellates <20 µm) observations tended to be above the 1:1 line, linear regression analysis showed that, except for dinoflagellates <20 µm, no significant differences in intercept or slope from the 1:1 line were found; regarding dinoflagellates <20 µm, the removal of the highest value also resulted in the lack of significant differences.

Trophic impact on the different prey types was assessed as described in Section 3.4 for chlorophyll, based on the concentrations at the fluorescence maximum, i.e. the initial values in experiments. Again, trophic impact on phyto and microzooplankton stocks was negligible in all the scenarios contemplated (Section 3.4), accounting for average removal rates of <1.9% d$^{-1}$ for any of the prey considered (maximum removal rates were always <4.1% d$^{-1}$).

## 4. DISCUSSION

### *4.1 Phytoplankton and microzooplankton standing stocks*

A remarkable feature of this study was the particularly dense blooms of *Phaeocystis pouchetii* at some stations, mainly in the colonial form (Lasternas & Agustí, 2010), which forced us to screen the zooplankton to be used in the incubations through a 500-µm sieve, therefore omitting the smaller-sized zooplankton (see below). *P. pouchetii* comprised on average 35% of the phytoplankton carbon, in some stations reaching ca. 60-70% of carbon. As these values are based on cell counts and do not take into account the mucilaginous matrix in the colonial form (Rousseau et al., 1990), they must be taken as underestimates; unfortunately, we have no information about the colony size, since many colonies disaggregate after fixation. The blooming of *P. pouchetii* in the Arctic is quite common (Schoemann et al., 2005; Hop et al., 2006). In the Fram Strait and nearby areas, Spies (1987) reported an extended presence of *P. pouchetii* during July and August. At the nearby Barents Sea, Eilertsen et al. (1989) and Estep et al. (1990) also reported the dominance of *P. pouchetii* in summer. During our cruise we did not find any clear association between the abundance of *P. pouchetii* and the different hydrographic areas, although it appeared to be negatively correlated with temperature (Lasternas & Agustí, 2010; Calbet et al., 2011). Concurrent dilution experiments during the cruise indicated a low microzooplankton grazing activity in the area (Calbet et al., 2011), which was attributed to the presence of the *P. pouchetii* bloom in colonial form and senescing phase (Lasternas & Agustí, 2010).

### *4.2 Zooplankton standing stocks and vertical distribution*

The abundance and biomass of zooplankton and copepods found during the cruise ATOS-Arctic are within the range of values found previously in the area (see the review by Hop et al., 2006). Copepods were concentrated in the upper layers, in agreement

with previous works on Arctic copepods during summer. For instance, Smith (1988) and Hirche & Mumm (1992) also found that in the Fram Strait and the Nansen Basin the bulk of zooplankton during summer (composed by three *Calanus* species) was located in the upper 100 m. Similarly, in the Svalbard region Søreide et al. (2008) reported that in May and August the vertical distribution of the three *Calanus* species usually coincided with the chlorophyll peak in the water column. Their data for the month of May, which was coincident with a *Phaeocystis* bloom, showed the overlapping distribution of copepods and *Phaeocystis*, indicating the lack of avoidance behavior by copepods. Similarly, Hansen et al. (1990) found in the Barents Sea in July that high copepod biomass overlapped with the phytoplankton maximum, dominated by colonial *Phaeocystis pouchetii* and *Dinobryon pellucidum*. Norrbin et al. (2009), studying high-resolution vertical profiles during different phases of the Arctic spring bloom, also observed that zooplankton did not avoid *P. pouchetii* colonies. All these studies agree with our observation that the depth of maximum copepod biomass was often close to the fluorescence maximum (presumably coincident with the *P. pouchetii* peak). Chaetognaths and Amphipods, the other major groups found in the nets, were also within this stratum, as expected because copepods constitute their major prey (Falkenhaug, 1991; Noyon et al., 2009).

Within the copepod group, nauplii and the small calanoid category, likely composed of young copepodites of *Calanus* spp. and *Pseudocalanus* spp., were the most abundant; in terms of biomass, however, the medium-sized calanoids were more relevant. The large-sized calanoids were generally very rare, with average abundances in the order of ca. 2 ind $m^{-3}$, and due to their size (Table 2) they were probably *Calanus hyperboreus*. Reported abundances of *C. hyperboreus* in the area (e.g. 4-20 ind $m^{-3}$,

see review by Hop et al., 2006) fall within the range of values we found for this size-class category.

Although negligible in terms of biomass, *Oithona* spp. was numerically very abundant during our study, in spite of the fact that our estimates are biased by the use of the 200-µm mesh size. In recent years several studies have pointed out the numerical importance of the genus *Oithona* in the Arctic (e.g. Walkusz et al., 2003; Daase & Eiane, 2007) and emphasized their likely relevant, but still unknown, role at high latitudes, especially at those times of the year when *Calanus* disappears from the upper water column for overwintering (Hopcroft et al., 2005; Svensen et al., 2011). Interestingly, during the ATOS-Arctic cruise *Oithona* spp. were more broadly distributed in the water column than calanoid copepods, suggesting either a weaker dependence on the phytoplankton peak (in agreement with their ambush behavior, Svensen & Kiørboe, 2000), or perhaps an avoidance of potential predators in the top layers. *Metridia longa* was only relevant at the Stns 2, 3 and 4, and showed a deeper distribution than the other calanoids, as reported in previous studies (e.g. Hirche & Mumm, 1992; Blachowiak-Samolyk et al., 2006; Rabindranath et al., 2010).
The application of multivariate analyses to identify any spatial differentiation in the 0-100 m copepod community structure over the sampling grid revealed 3 groups of stations with differences in the copepod stock and taxonomic composition. This pattern, however, can be only slightly associated with the hydrological variability in the upper water column and the influence of the distinct water masses (Polar Surface water, Atlantic water, water of intermediate characteristics). The lack of detailed knowledge on the taxonomic and stage composition of the copepod community probably did not allow us to get further insights on the relationship between copepod composition and the water masses (polar versus Atlantic) during the cruise. The review by Hop et al. (2006)

and references therein provide detailed reports on zooplankton composition and distribution in the area.

*4.3 Copepod feeding rates and trophic impact on nano- microplankton communities*

Overall, the copepod feeding rates found during the cruise were quite low, with maximum values up to 6% body carbon $d^{-1}$. Due to the presence of *Phaeocystis pouchetii*, one might consider the possibility of an inhibitory or deterrent effect of *P. pouchetii* on the zooplankton community at the time of our experiments. Although in the past there has been some controversy on the inhibitory effect of *Phaeocystis* spp. upon zooplankton (Huntley et al., 1987), nowadays there is clear evidence of ingestion of *P. pouchetii* colonies, especially for the large calanoid copepods of the genus *Calanus* (see review in Nejstgaard et al., 2007). Indeed, the statistically significant relationship found between the relative ingestion of *P. pouchetii* and its relative presence in the water (Fig. 12) suggests active feeding upon it. At those stations where the contribution of *P. pouchetii* was highest (Stns 12 and 46), *P. pouchetii* actually contributed to 40-52% of the copepod-ingested carbon. As mentioned in Section 4.2, our estimates of *P. pouchetii* biomass do not take into consideration the carbon content of the colony mucilage, although such organic carbon appears to be of low nutritional quality (Rousseau et al., 1990; Thingstad & Billen, 1994). Estep et al. (1990) found that predation by copepods on *P. pouchetii* colonies was a function of the physiological state of the colonies; whereas the unhealthy ones were consumed at high rates, healthy colonies were not consumed, likely due to the production of grazing deterrents. Regarding the physiological state of the *P. pouchetii* bloom during the ATOS-Arctic cruise, Lasternas & Agustí (2010) and Calbet et al. (2011) provided evidence of phytoplankton senescence, which would agree with our observations of active consumption by the large copepods used in our experiments.

A comparison with the available data in the area or nearby ones indicates, however, that our copepod feeding rates although low are well within the typical values observed for Arctic copepods. Thus, Barthel (1988) reported daily rations <1% $d^{-1}$ for the three *Calanus* species in the same area and similar season, and Smith (1988) also in Fram Strait, but in June, reported daily rations <2% $d^{-1}$. Off the western part of Greenland, Levinsen et al. (2000) reported daily rations between 0.1 and 16% $d^{-1}$ for the same three *Calanus* species, whereas Mayor et al. (2006) in the Irminger Sea found feeding rates up to 4.7% $d^{-1}$. Similarly, Eilertsen et al. (1989) reported maximum daily rations (based on gut fluorescence) ca. 7-8% $d^{-1}$ in the Arctic Barents Sea near Spitsbergen during summer with dominance of colonies of *P. pouchetii* in the phytoplankton. In East Greenland waters (Disko Bay), Dünweber et al. (2010) also reported very low copepod daily rations after the spring bloom. All these values are below the maximum feeding capability we would expect for the dominant copepods in the area. According to the empirical equation for maximum copepod feeding rates provided by the review of Saiz & Calbet (2007), we would expected a maximum daily ration of 45% body carbon $d^{-1}$ for copepods of a similar body mass as the average copepod in our incubations (ca. 109 µg C). Such high daily rations have actually being reported in the large Arctic copepods, either in other areas or under different seston composition. For instance, Thibault et al. (1999) reported daily rations (based on the gut fluorescence method) between 4 and 30% body carbon $d^{-1}$ in the Chukchi Sea and central Arctic basic during summer. Similarly, with the same method Tande & Bamstedt (1985) reported daily rations in the Barents Sea ranging from 0.5 to 32%, and from 0.5 to 54% body carbon $d^{-1}$ for *Calanus finmarchicus* and *Calanus glacialis* adult females, respectively. Comparing different methods, Dünweber et al. (2010) also estimated high daily rations (up to 74% body carbon $d^{-1}$) for *Calanus* spp during the spring bloom.

We cannot discard that the presence of *Phaeocystis pouchetii* colonies in our incubations, in spite of being actively grazed, might mechanically hamper copepod feeding and be partially responsible for the low rates found, mediated by either increased prey handling time or by an increase in water viscosity due to the mucilaginous colonies of *P. pouchetii*, although Seuront & Vincent (2008) did not observed any effects of the latter in *Temora longicornis*. Most likely, however, the low feeding rates found were just a consequence of the low biomass of phytoplankton and protozooplankton found during the cruise, with ensemble biomass concentrations <100 μg C $L^{-1}$ in all stations, far below the expected critical satiating concentrations for such large copepods (e.g. Frost, 1972). The spring bloom in the area occurs earlier in the season (Hop et al., 2006), and during the ATOS-Arctic cruise we were in the senescent phase of the *P. pouchetii* bloom, explaining the low prey availability conditions for copepods and the feeding limitation. The low metabolic C:N ratios (respiration versus excretion) found by Alcaraz et al. (2010) for mesozooplankton during the same cruise are indicative of protein metabolism, very likely as a consequence of such low feeding rates and starving conditions, and are also consistent with the close match between the daily rations found here and the zooplankton respiratory demands reported by Alcaraz et al. (2010) (on average 2% $d^{-1}$). It does not seem likely, either, that the low feeding rates could be attributed to the copepods being in or close to diapause during our cruise, because several studies report active *Calanus* in the area until later in the year (e.g. Falk-Petersen et al., 2008; Søreide et al. 2010).

The present study is one of the few studies in the Arctic where ciliates have been considered as a component of copepod diet (Disko Bay and Young Sound, Greenland: Levinsen et al., 2000, Turner et al., 2001; Greenland Sea: Møller et al., 2006; Beaufort and Chukchi Seas: Campbell et al., 2009; Fram Strait: Barthel, 1988). In our study on

average ciliates contributed 40% to the copepod ingestion (range: 16-94%); comparatively, diatoms only comprised on average 14% of the diet. These findings contrast with the common belief that polar copepods, specifically the three large *Calanus* (*Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus*) are essentially herbivorous (e.g. Blachowiak-Samolyk et al., 2007; Saunders et al., 2003). Evidence from stable isotope analysis on polar *Calanus* spp. also seems to miss the importance of the heterotrophic component in the diet, at least on some occasions (Søreide et al., 2008). The inclusion of heterotrophic dinoflagellates, which also comprised a relevant component of the diet (on average, 12%), would certainly increase the contribution of the microheterotrophic fraction to the diet. Indeed, the contribution of ciliates to copepod diet in our experiments is similar to the global average determined in the review on the diet composition of copepods by Saiz & Calbet (2011), and falls within the range of available values for Arctic copepods (Table 5). Therefore, our results suggest that after the spring diatom bloom the heterotrophic component of the diet of Arctic copepods can be very important, and as Levinsen & Nielsen (2002) pointed out, higher relevance should be given to protozooplankton at high latitudes to better understand the functioning of the planktonic system.

We did not find strong patterns of prey selectivity as expected. In copepods, most studies taking into consideration protozoans have shown a strong selection for them (e.g. Fessenden & Cowles, 1994; Broglio et al., 2004; Saiz & Calbet, 2011). In this regard, although we found significant differences among clearance rates on the different prey types, these are rather small compared to what would be expected due to differences in prey size. We think that the low food levels together with the presence of *P. pouchetii* probably have masked or disrupted the evidence of strong patterns of

selection for protozoans, which were cleared at rates comparatively similar to the other prey types.

Regarding the significant contribution of microheterotrophs to copepod diet in our study, Nejstgaard et al. (2001) warned of the likely bias in copepod feeding incubations due to the disappearance of microheterotrophs in incubation bottles with copepods compared with the control bottles. When planning the experiments, we aimed to do such a correction and parallel dilution grazing experiments were conducted in most stations (Calbet et al., 2011). Grazing activity by microzooplankton during the cruise was quite low and proved significant only in 6 out of 16 experiments. For this reason, we did not attempt any correction of copepod feeding rates. A recent study by Saiz & Calbet (2011) shows that the boundary of uncertainty is up to 30% when such a correction is not applied and also warns of the risks when applying it indiscriminately.

Our low trophic impacts on phytoplankton standing stocks are at the very low end of typical values reported in the Arctic. Had they been computed on primary production and assuming 0.93 g C $m^{-2}$ $d^{-1}$ as average integrated primary production during the cruise (Alcaraz et al., 2010), copepod grazing impact would be higher but still low (average removal rates <4% $d^{-1}$). It could be argued that our estimations are low because they are based on the total copepod biomass obtained from the LHPR nets (see Table 3), whereas in our feeding incubations we had to constrain to the >500 µm fraction to get rid of *Phaeocystis pouchetii* in the grazing incubations. The smaller zooplankters omitted with our procedure might had increased the trophic impact due to their higher metabolic rates (per unit weight). We have evaluated this potential underestimation assuming that 1) the copepods used in the feeding incubations (with body mass of 0.223 mg AFDW) were representative of the categories "large calanoids", "medium calanoids" and "*Metridia longa*", and 2) the copepods not retained by the 500

μm sieve fall in the categories "small calanoids" and "Oithona spp" (with a weighted average body mass of 0.032 mg AFDW). Assuming a power scaling of 0.75 for copepod feeding rates on a per individual basis, it can be estimated that the feeding rates of small copepods in our samples would have been (theoretically) 1.62 times higher than the ones from the copepods we used in the incubations. A further calculation taking into account the contribution of small copepods to the total copepod biomass (15%±2.3SE) indicates that we may have underestimated the trophic impact of the entire community (captured by our 200 μm nets) by 8.5% (±1.16SE). This argument could also be extended to the relevance of the even smaller zooplankton not captured by the 200 μm mesh size in our sampling device (Hopcroft et al., 2005; Svensen et al., 2011), which can be relevant numerically but not in terms of biomass during the summer season (Hopcroft et al., 2005; Møller et al. 2006). In addition, the copepods not captured by a 200 μm mesh net are largely composed of non-calanoid species (e.g. *Oithona*), which have typically much lower feeding and metabolic rates (Paffenhöfer, 1993; Saiz & Calbet, 2007). From this analysis we conclude that the potential bias and underestimation are low, and therefore our low trophic impacts are reliable.

Dünweber et al. (2010) also reported fairly low impacts on phytoplankton standing stocks by copepods (<6% $d^{-1}$) in Disko Bay, both during the spring bloom and after the bloom. Similarly, Campbell et al. (2009) in the western Arctic Ocean reported low average grazing impacts on both chlorophyll standing stock (0.6% $d^{-1}$ and 5% $d^{-1}$ in spring and summer, respectively) and primary production (13% $d^{-1}$ and 28% $d^{-1}$ in spring and summer, respectively). Saunders et al. (2003), in the North Water Polynya during summer, also observed that the copepod impact on daily primary production was usually less than 10% (except at those stations where a high copepod standing stock was coupled to low daily primary production). Low to moderate grazing impacts on

primary producers by copepods have been also estimated by Hirche et al. (1991) and Møller et al. (2006) in, respectively, the Fram Strait and the Greenland Sea.

Much higher grazing impacts are not infrequent in the Arctic literature. For instance, Thibault et al. (1999) reported, from gut contents experiments, high copepod grazing impacts on phytoplankton biomass and primary production in different regions of the Arctic Ocean, from ca. 7% to >100%. Eilertsen et al. (1989) estimated that 65-90% of primary production could be grazed by copepods in the Arctic Barents Sea in summer. Similarly, Hansen et al. (1990) in the Barents Sea, under post-bloom conditions (July) and with a phytoplankton community dominated by the colonial alga *Phaeocystis pouchetii* and *Dinobryon pellucidum*, found that the copepod community grazed from 10 to 400% of daily primary production. As the copepod standing stocks found during the ATOS-Arctic cruise fell well within the typical values reported for the area and season, it seems reasonable to conclude that, therefore, the low trophic impact of the copepod community on primary producers must be a consequence of the low feeding rates observed (the latter driven by the low prey availability at the time).

### *4.4 Conclusions*

The lack of proper species taxonomic identification and stage composition of the copepod community (e.g. the distinction of the three *Calanus* species in the area) has probably obscured a deeper distinction of copepod assemblages in relation to the different water masses sampled. However, as counterpart, the use of a "whole copepod assemblage", instead of a species-specific and a stage-specific approach, permitted a fast processing of a large number of samples using automatic counting, sizing and classification software (ZooImage), and also allowed the experimental determination of the carbon fluxes through the whole copepod community and not just a few stages

and/or species as most studies do. We have found very low copepod feeding rates during the study period. These low feeding rates were not a consequence of the presence of high abundance of *Phaeocystis pouchetii* in the colonial form, as they were actively grazed on, but of the overall low abundance of phyto- and protozooplankton. This result coupled with the low metabolic C:N ratios (respiration versus excretion) reported by Alcaraz et al. (2010) during the same cruise suggest that the copepod community during the ATOS-Arctic cruise was on a transitional phase towards late summer-autumn conditions, when food availability is actually scarce and eventually overwintering will be triggered. Our feeding experiments have also shown that the diet of polar copepods is more diverse than usually considered, at least during post-spring bloom situations such as the one we studied, in which on average protozooplankton contributed 52% to copepod daily rations. This suggests that in the Arctic the transfer of carbon and energy from primary producers to copepods through microzooplankton can be more important, at least on occasion, than usually believed.

FIGURE CAPTIONS

Figure 1. Sampling grid of the study.

Figure 2: (A) Temperature profiles in the water column along the sampling grid. Three distinct line patterns have been assigned according to the station temperature-salinity characteristics in the upper 50 m (solid black: low temperature–low salinity values, solid grey: high temperature–high salinity values, dashed black: intermediate temperature–intermediate salinity values) (B) Mean temperature and salinity in the layers 0-50 m and deeper than 50 m in the total sampling grid. Station labels are indicated only for the surface layer, along with their distinction in Groups (Group I: $T<0^{o}C$ and $S<34.4$; Group II $T>0^{o}C$ and $S<34.4$; Group III: $T>0^{o}C$ and $S>34.4$) (C) Maximum values of fluorescence ($F_{max}$) at every station in relation to the depth of appearance (Depth of $F_{max}$). Labels indicate the station names.

Figure 3. Integrated (upper 100 m) standing stock of total chl *a* (GF/F filter; bars) at the sampled stations. Line corresponds to the percentage of >5 μm chlorophyll *a*. Station numbers have been marked according to water mass grouping from Figure 4. *: Group I ; $^{+}$: Group III; no mark for Group II stations.

Figure 4. Initial values of biomass (μg C $L^{-1}$) of phyto- and protozooplankton in the grazing incubations, corresponding to water from the fluorescence maximum. Station numbers have been marked according to water mass grouping from Figure 4. *: Group I ; $^{+}$: Group III; no mark for Group II stations. nd: not determined.

Figure 5. Average abundance (A) and biovolume (B) of zooplankton (integrated over the sampling depth) during the cruise. Numbers on top of stacked bars are the respective sampling depth (m). Station numbers have been marked according to water mass grouping from Figure 4. *: Group I ; $^{+}$: Group III; no mark for Group II stations.

Figure 6. Vertical distribution of abundance (ind $m^{-3}$) of copepods ("Copepods") and the other dominant groups. Station numbers have been marked according to water mass grouping from Figure 4. *: Group I ; $^{+}$: Group III; no mark for Group II stations. Notice that "Copepods" refers only to the copepodite and adult stages, and copepod nauplii were taken as a separated category (see text).

Figure 7. Depth profiles of copepod abundance (ind $m^{-3}$), copepod biomass (mg AFDW $m^{-3}$) and fluorescence (relative units). Station numbers have been marked according to water mass grouping from Figure 4. *: Group I ; $^{+}$: Group III; no mark for Group II stations. Notice that the fluorescence profile shown is the one provided by the LHPR net (i.e. concurrent with the zooplankton collection), not the one from the CTD vertical casts.

Figure 8. Vertical distribution pattern of the different copepod groups identified with Zooimage, both in terms of abundance (A, ind $m^{-3}$) and of biomass (B, mg AFDW $m^{-3}$). Station numbers have been marked according to water mass grouping from Figure 4. *: Group I ; $^{+}$: Group III; no mark for Group II stations.

Figure 9. Ordination plots of the comparison between stations (for the integrated 0-100 m layer) using non-metric multidimensional scaling and Bray–Curtis similarity index. (A) Respective cluster groups (at 78% similarity level) are indicated (i.e., Group 1, 2, 3) and number of stations have been provided. (B) total copepod abundance of each station has been superimposed on the ordination plot along with the mean relative (%) density of each copepod taxon for each group of stations (pies).

Figure 10. Clearance rates of zooplankton (average±SE) on respectively GF/F and >5 µm chl *a* along the sampled stations. Station numbers have been marked according to water mass grouping from Figure 4. *: Group I ; $^{+}$: Group III; no mark for Group II stations. nd: grazing not determined. 0: clearance rates were nil. ns: not significant

differences between the rates for GF/F and >5-µm chl. s: significant differences at $p<0.05$ between the rates for GF/F and >5-µm chl.

Figure 11. Zooplankton ingestion rates (based on microscopic counts) on the different phyto- and protozooplankton items. Station numbers have been marked according to water mass grouping from Figure 4. *: Group I ; $^{+}$: Group III; no mark for Group II stations. nd: not determined.

Figure 12. Relationship between the ingestion rate of zooplankton (based on microscopic counts) and prey availability (the ensemble phyto- and protozooplankton biomass) in the cruise ATOS-Arctic. Intercept was not significantly different from 0

Figure 13. Relationship between prey availability and clearance rate of zooplankton. Average cell size (equivalent spherical diameter, EDS) for each prey type is provided. Notice that in the case of *Phaeocystis pouchetii* we do not provide colony size. In order to pool the data from the different stations, clearance rates were computed for an "standard" individual ($ind_{STD}$), with biomass equal to the average copepod biomass in the incubations (0.223±0.0229 SE mg AFDW), and assuming a 0.75 power scaling in the calculation (Saiz & Calbet, 2011). The empty circle highlights an extreme value out of scale.

Figure 14. Prey selectivity plot. The contribution (as percentage) of each prey item to the ensemble biomass of phyto- and protozooplankton is plotted against its contribution to diet (as % of total ingested biomass). The continuous line indicates the 1:1 relationship (i.e. no selection). Linear fits for each prey category are shown, except for the category "others", which was not significant ($p>0.1$).

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