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Mesozooplankton structure and functioning during the onset of the Kerguelen phytoplankton bloom during the KEOPS2 survey

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Abstract. This paper presents results on the spatial and temporal distribution patterns of mesozooplankton in the naturally fertilized region to the east of the Kerguelen Islands (Southern Ocean) visited at early bloom stage during the KEOPS2 survey (15 October to 20 November 2011). The aim of this study was to compare the zooplankton response in contrasted environments localized over the Kerguelen Plateau in waters of the east shelf and shelf edge and in productive oceanic deep waters characterized by conditions of complex circulation and rapidly changing phytoplankton biomass.

The mesozooplankton community responded to the spring bloom earlier on the plateau than in the oceanic waters, where complex mesoscale circulation stimulated initial more or less ephemeral blooms before a broader bloom extension. Taxonomic compositions showed a high degree of similarity across the whole region, and the populations initially responded to spring bloom with a large production of larval forms increasing abundances, without biomass changes. Taxonomic composition and stable isotope ratios of size-fractionated zooplankton indicated the strong domination of herbivores, and the total zooplankton biomass values over the survey presented a significant correlation with the integrated chlorophyll concentrations in the mixed layer.

The biomass stocks observed at the beginning of the KEOPS2 cruise were around 1.7 g C m⁻² above the plateau and 1.2 g C m⁻² in oceanic waters. Zooplankton biomass in oceanic waters remained on average below 2 g C m⁻² over the study period, except for one station in the Polar Front zone (F-L), whereas zooplankton biomasses were around 4 g C m⁻² on the plateau at the end of the survey. The most remarkable feature during the sampling period was the stronger increase in abundance in the oceanic waters (25 × 10³ to 160 × 10³ ind m⁻²) than on the plateau (25 × 10³ to 90 × 10³ ind m⁻²). The size structure and taxonomic distribution patterns revealed a cumulative contribution of various larval stages of dominant copepods and euphausiids particularly in the oceanic waters, with clearly identifiable stages of progress during a Lagrangian time series survey. The reproduction and early stage development of dominant species were sustained by mesoscale-related initial ephemeral blooms in oceanic waters, but growth was still food-limited and zooplankton biomass stagnated. In contrast, zooplankton abundance and biomass on the shelf were both in a growing phase, at slightly different rates, due to growth under sub-optimal conditions. Combined with our observations during the KEOPS1 survey (January–February 2005), the present results deliver a consistent understanding of patterns in mesozooplankton abundance and biomass from early spring to summer in the poorly documented oceanic region east of the Kerguelen Islands.
1 Introduction

The eastern part of the Kerguelen Plateau sustains one of the most important local foraging areas for land-based marine predators (birds, penguins, seals and elephant seals) and for whales (Hindell et al., 2011; Blain et al., 2013). Satellite-based chlorophyll images of this region highlight the intensive seasonal Kerguelen bloom and its south-east extension off the archipelago (Schlitzer, 2002; Thomalla et al., 2011; Blain et al., 2013; Trull et al., 2015). During the KEOPS1 survey (Kerguelen Ocean and Plateau compared Study), the origin and fate of the elevated phytoplankton biomass over the Kerguelen Plateau were addressed (Blain et al., 2008), with a focus on the mechanisms supplying the surface waters with iron. The Kerguelen Plateau, oriented along the 70° E meridian, forms a large north-west/south-east topographical barrier of the Antarctic Circumpolar Current, forcing the Polar Front (PF) to pass above the plateau south of the Kerguelen Islands in a meandering course (Fig. 1). The PF flow on the shelf induces entrainment and mixing of Fe-enriched shelf waters from plateau sediments in the oceanic upper layer in the area east of Kerguelen, and is a driver of relatively high phytoplankton bloom concentrations, with a strong increase from October to December (Blain et al., 2007, 2013), initially dominated by diatoms of high growth rates (Quéguiner, 2013) contrasting with the generally high-nutrient low-chlorophyll (HNLC) surface oceanic waters of the Southern Ocean. This enhanced biological productivity in the eastern area fuels the trophic level of zooplankton and micronekton, which are potential prey of fish and squid forage required to meet the demand of top predators. During the KEOPS1 cruise (January–February 2005), the mesozooplankton populations, mainly copepods, were already well established without significant spatial and temporal changes in species composition and biomass, around 10.6 g C m$^{-2}$ above the plateau and around 5 g C m$^{-2}$ in HNLC oceanic waters (Carlotti et al., 2008). The KEOPS1 survey occurred during the decline phase of a natural long-term spring bloom initiated in November.

How the zooplankton populations increase from overwintering stocks by exploiting new primary production in early spring is still poorly documented because descriptions of seasonal variations of mesozooplankton standing stocks in oceanic Antarctic regions are scarce. The implementation of the Southern Ocean CPR survey delivers consistent information regarding the seasonal succession of zooplanktonic communities in the Southern Ocean south of Australia (Hosie et al., 2003; Hunt and Hosie, 2006a, b). In the PF zone, a relatively strong increase in zooplankton abundance occurs in spring, from October to November (see Hosie et al., 2003; their Fig. 3), mainly due to changes in density of all common taxa from average winter levels still maintained until October (Hunt and Hosie, 2006b). The largest copepods of the region (Rhincalanus gigas, Calanoides acutus, Ctenocalanus citer) are seasonal migrants which arrive in the surface layer from winter diapause depths when Chl a concentrations increase (October to November). Overwintering females may spawn reserves even before the full bloom, whereas overwintering stages other than adult stages resume their growth in surface water up to mature adults which produce new cohorts during the full bloom period (Atkinson, 1998; Hunt and Hosie, 2006b). Other smaller species (Calanus similimus, Oithona sp., etc.) resume their population development from survivors from the previous year and start reproduction earlier in spring (Atkinson, 1998). There are no historical CPR data around the Kerguelen Islands, but some pieces of the puzzle suggest similar patterns. Zooplankton distribution patterns observed by Semelkina (1993) during the SKALP cruises around the Kerguelen Islands (46–52° S, 64–73° E) from February 1997 to February 1998 showed a change in biomass (fourfold higher) from winter (July–August) to mid-summer (February), but did not describe this early spring period. It is also worth noting that the seasonal zooplankton abundances recorded from February 1992 to January 1995 at the KERFIX station, located around 60 miles south-west of the Kerguelen Islands in 1700 m of water, show a major increase in copepod densities from September to January (Razoul et al., 1998).

The main objective of the KEOPS2 study was to investigate the early phase (October–November 2011) of the seasonal marine productivity in this Kerguelen region in order to gain new insights into the biogeochemistry and ecosystem response to iron fertilization. The study was conducted in contrasted environments differently impacted by iron availability, i.e. on the plateau waters, in areas common with KEOPS1, and in productive oceanic deep waters with strong mesoscale activity to the east of the Kerguelen Islands. The focus of the present paper is to document the responses of zooplankton in terms of species diversity, density and biomass in the mosaic of blooms observed during the survey, and to characterize the trophic pathways from primary production to large mesozooplanktonic organisms.

2 Material and methods

2.1 Study site and sampling strategy

The KEOPS2 survey was performed east of the Kerguelen Islands in the Indian sector of the Southern Ocean, on board R.V. Marion Dufresne, between the 15 October and the 20 November 2011. It firstly consisted of predefined stations along two transects (Fig. 1) the first oriented north-south between 46°50’ and 49°08’ S, and subsequently referred to as the TNS transect (stations TNS1 to TNS10, blue dots in Fig. 1), and the second oriented east-west between 69°50’ and 74°60’ E, referred to as the TEW transect (stations TEW1 to TEW8, green dots on Fig. 1). Along these two transects, zooplankton samples were collected once at each station. The TEW transect crossed the Polar Front (PF) twice, first be-
tween TEW3 and TEW4 where the southern branch of the PF flows northwards along the shelf break, and secondly between TEW6 and TEW7, where the PF is directed southwards after a semicircle trajectory maintaining a large stationary meander in this area. The most westerly stations were located over the inner (TEW1) and outer (TEW2) parts of the Kerguelen plateau. The most easterly stations (TEW7 and TEW8) were situated in Subantarctic Mode Water whereas the central section (TEW4 to TEW6) within the stationary meander was covered by mixed Antarctic surface water (Farías et al., 2015; Trull et al., 2015).

In addition, intensive sampling (24 h) was performed at nine strategic stations (Fig. 1) located in the eastern bloom in the Polar Front zone (F-L station), in the north-eastern bloom (set of E stations), in the south-eastern bloom above the Kerguelen Plateau (A3 station) and in the deep waters southwest of the Kerguelen Islands considered as a HNLC reference station (R station). Station A3 (common with KEOPS1) was sampled twice during KEOPS2: at the winter (A3-1) stage and the spring stage (A3-2). The patterns of change over time of the north-eastern bloom, located in a complex recirculation area inside the stationary meander of the Polar Front (Park et al., 2014; Zhou et al., 2014), was studied by a quasi-Lagrangian survey including five stations (E1-E2-E3-E4-E5).

Real-time-satellite images (chlorophyll and altimetry) in combination with trajectories of 50 drifters released during the first part of the cruise were used to carefully decide the positions of these five stations (Trull et al., 2015, their Fig. 2). In addition, we visited a productive station (E4W, red dot in Fig. 1) located in the plume of chlorophyll observed downstream of the plateau and close to the jet induced by the PF.

### 2.2 Mesozooplankton sampling

Zooplankton collection was conducted at 27 stations with a double Bongo (60 cm mouth diameter) with one 330 μm mesh net and a 120 μm mesh net mounted with filtering cod ends. Hauls were done from a 250 m depth to the surface at 0.5 ms⁻¹. The stations of the TNS transect (stations TNS 1 to TNS10) and the stations of the TEW transect (stations TEW1 to TEW8) were each sampled once. During the intensive stations study (including A3 – which was visited twice – R2, F-L, and the set of E stations), zooplankton samples were taken twice daily, by day and by night (stations were named R2-d and R2-n, for instance).

For each sampling station, two successive net hauls at each station were done: the first net haul was taken for ZOOSCAN processing, taxonomy study and dry weight measurements, and a second net haul was taken for isotope analysis. The cod-end contents of the first haul were kept fresh and split into two parts with a Motoda box (Motoda, 1959). The first part was preserved in 4 % borax-buffered formalin seawater for further laboratory study of zooplankton community structure (taxonomy, abundance and size structure) and for biomass estimates from organism biovolume (see be-
low). The second half of the sample was preserved for dry weight measurements. As many of the 120 µm size nets were clogged with phytoplankton cells and aggregates, we could not finally use the sample for dry weight measurements and ZOOSCAN processing. However we used the 120 µm mesh net samples for isotope analysis (as described in the following paragraph).

To prepare samples for isotope analysis, size fractions were obtained as follows. Samples from the second 330 µm net haul at each station were passed sequentially through five sieves arranged in a column (2000, 1000, 500, 200 and 80 µm meshes). The three largest sizes were then collected, and for the largest size (2000 µm) large organisms such as salps and euphausiids were separated into additional containers. To provide more material for the two smallest sizes (200, 80 µm), these materials were retained on the sieves and the contents of the 120 µm net haul were passed through the entire set of five sieves (with the overlying 2000, 1000 and 500 µm sieves serving to block larger organisms and aggregates, but without those materials being collected). All samples were placed in small containers and immediately deep-frozen (−80 °C).

2.3 Abundance and biomass using the ZOOSCAN

For each station, the cod-end content of a 330 µm mesh size net was processed using ZOOSCAN (www.zooscan.com) to determine the zooplankton community size structure. ZOOSCAN has recently been used to study the zooplankton community in various areas and has been validated by comparisons with traditional sampling methods (Grosjean et al., 2004; Schultes and Lopes, 2009; Gorsky et al., 2010). Our ZOOSCAN setup is similar to the one described by Gorsky et al. (2010), and our sample processing protocol is fully presented in Nowaczyk et al. (2011), following the recommendations of Gorsky et al. (2010).

After homogenization, each sample was quantitatively split with a Motoda box once back in the laboratory and a fraction of each preserved sample containing a minimum of 1000 particles (in general 1/32 or 1/64 of the whole sample) was placed on the glass plate of the ZOOSCAN. Organisms were carefully separated one by one manually with a long wooden needle, in order to avoid overlapping. Each image was then run through the ZooProcess plug-in using the image analysis software Image J (Grosjean et al., 2004; Gorsky et al., 2010). Several measurements of each organism were then computerized. Organism size is given by its equivalent circular diameter (ECD) and can then be converted into biovolume, assuming each organism is an ellipsoid (more details in Grosjean et al., 2004). The lowest ECD detectable by this scanning device is 300 µm. To discriminate between aggregates and organisms, we used a training set of about 1000 objects which were selected automatically from 40 different scans. This protocol allows discrimination between aggregates and organisms by building the initial training set of images. The biovolume (BV; mm³) was calculated from the organism image areas and morphometric parameters. In order to estimate the biomass of each organism, we used the same conversion as in Carlotti et al. (2008); each measured biovolume (BV; mm³) of a zooplankton individual was converted into biomass (W, in units of mg dry weight, DW) using the following relationship: log (W) = 0.865 log (BV) − 0.887 (Riandey et al., 2005). Carbon content was assumed to be 50 % of body dry weight.

In this article, the terms “ZOOSCAN abundance” and “ZOOSCAN biomass” will designate the values derived from the laboratory ZOOSCAN processing. The abundance and biomass of organisms were then grouped into four size fractions (< 500, 500–1000, 1000–2000 and > 2000 µm) based on their ECD, and summed to deliver the total abundance and biomass per sample over the upper 250 m.

The choice of the net haul sampling depth was based on mixed layer depth found at the first station of the cruise, and maintained afterwards. Abundance and biomass values are normalized to the volume of water filtered in situ. An ANOVA test (5 % significance level) was used to test differences of abundance and biomass between stations or oceanic areas.

2.4 Taxonomic determination

Common taxa were counted with the binocular microscope for taxonomy. For the 330 µm mesh size net, around 600 organisms were counted from subsamples 1/32 or 1/64. For the 120 µm mesh size net, around 400 organisms were counted from diluted samples (dilution from one to ten thousandths). The whole sample was examined for either rare species and/or large organisms (i.e. euphausiids, amphipods). Identification of the copepod community was done down to species level and groups of developmental stage when possible. Species/genus identification was done according to Rose (1933), Tregouboff and Rose (1957) and Razouls et al. (2014). Organisms other than copepods as well as meroplankton were identified down to taxa levels. Identifications were done to genus level for copepods, amphipods, pelagic molluscs, polychaetes, Thaliacea and Cnidarians; and to taxa level for other major holoplanktonic and meroplanktonic groups. To identify which taxonomic groups contribute to the four size fractions defined from ZOOSCAN measurements done on the 330 µm mesh net samples (see above), each observed organism was classified as small, medium, large or very large mesozooplankton, which approximately corresponds to the four size fractions determined by ZOOSCAN (see above). Similarly, the organisms observed and counted from the 120 µm mesh size net samples were also classified into small and medium size fractions. Distribution in larger size fractions was not considered from the 120 µm mesh size net samples, the large organisms being undersampled.
2.5 Biomass measurement

The subsample of the 330 µm mesh net for bulk biomass measurement was filtered onto a pre-weighed and pre-combusted GF/F filter (47 mm) which was quickly rinsed with distilled water and dried in an oven at 60 °C for 3 days on board. The dry weight (mg) of 19 samples was calculated from the difference between the final weight and the weight of the filter, and biomass (mg DW m⁻²) was extrapolated from the total volume sampled by the net.

2.6 Stable isotope analysis

Before processing, identification of the broad taxonomic composition of each sample preserved for isotopic measurements was performed under a binocular microscope. When possible, the main group of organisms in the largest > 2000 µm size fraction were sorted out and processed separately. Then, zooplankton fractions were freeze-dried and ground into a homogeneous powder. As they may contain carbonates, an acidification step was necessary to remove ¹³C-enriched carbonates (DeNiro and Epstein, 1978; Søreide et al., 2006). A subsample was acidified with 1% HCl, rinsed, dried and used for determination of δ¹³C values, while the other untreated subsample was used for determination of nitrogen isotopic composition. Three replicates were performed on each plankton fraction per sampled station for both δ¹³C and δ¹⁵N values. Stable isotope measurements were performed with a continuous-flow isotope-ratio mass spectrometer (Delta V Advantage, Thermo Scientific, Bremen, Germany) coupled to an elemental analyzer (Flash EA1112 Thermo Scientific, Milan, Italy). Results are expressed in parts per thousand (‰) relative to Vienna Pee Dee Belemnite and atmospheric N₂ for δ¹³C and δ¹⁵N, respectively, according to the equation: \[ \delta X = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \times 10^3, \]
where \( X \) is ¹³C or ¹⁵N, and \( R \) is the isotope ratio ¹³C/¹²C or ¹⁵N/¹⁴N, respectively. Calibration was performed using certified reference materials (USGS-24, IAEA-CH6, -600 for carbon; IAEA-N2, -NO-3, -600 for nitrogen). Analytical precision based on repeated analyses of acetanilide (Thermo Scientific) used as an internal standard was < 0.15 ‰. Percentage of organic C and organic N were obtained using the elemental analyzer and were used to calculate sample C / N ratios.

Lipids are depleted in δ¹³C relative to proteins and carbohydrates, and variation in lipid content between organisms can introduce considerable bias into carbon-stable isotope analyses (Bodin et al., 2007; Post et al., 2007). Like most polar marine organisms (Lee et al., 2006), KEOPS2 zooplankton fractions could present a high lipid content (up to 20% dry mass, data not shown), reflected by high C / N values. Thus, δ¹³C acidified sample values of fractions > 200 µm were corrected according to the formula calculated by Post et al. (2007) for aquatic organisms, using the C / N ratio of each sample: \[ \delta^{13}C_{\text{normalized}} = \delta^{13}C_{\text{acidified}} - 3.32 + 0.99 \times C / N. \]
Acidified δ¹³C values of the lowest size fraction (80–200 µm) were not lipid-corrected due to their low lipid content (< 5%, data not shown). The resulting δ¹³Cnormalized provides an estimate of δ¹³C corrected for the effects of
lipid concentration. Lipid correction calculated by Smyntek et al. (2007) for zooplankton give $\delta^{13}C$ values $0.63 \pm 0.01\%$ lower than those of Post et al. (2007). As $\delta^{13}C$ values provided by Trull et al. (2015) were not lipid-normalized, acidified $\delta^{13}C$ values for all zooplankton size fractions are indicated in Table 2, along with lipid-normalized $\delta^{13}C$ values, to allow comparisons between the two data sets.

To consider the relationships between zooplankton and phytoplankton, we used the groups of stations (T-groups) defined by Trull et al. (2015) based on chemometric measurements of phytoplankton. The HNLC reference station R2 belonged to T-group 5. Trull’s two most easterly stations, located in the open ocean near the Polar Front (F-L and TEW8), belonged to T-group 2 and T-group 3, respectively. The two most easterly stations, located in the open ocean near the Polar Front (F-L and TEW8), belonged to T-group 5. Trull’s T-group 4 corresponded to coastal stations not sampled for zooplankton analysis.

2.7 Data analysis

The effect of stations and dates ($n = 12$) on zooplankton abundance and biomass was tested statistically using one-way ANOVA with the statistical software Statistica v7. The statistical significance was tested at the 95% confidence level. Community patterns for taxa abundance were explored using the Primer (V6) software package which has been shown to reveal patterns in zooplankton communities (e.g. Clarke and Warwick, 2001; Wisnher et al., 2008). Data sets were power-transformed (fourth root), and the Bray–Curtis dissimilarity index between stations (Bray and Curtis, 1957) was calculated employing all taxonomic categories that contributed at least 1% to any sample in that data set. Different groups of zooplankton (BC groups) were individualized based on their taxonomic composition. Mean C- and N-stable isotope values among size fractions and between day and night within each fraction were compared by one-way ANOVAs followed by Tukey post-hoc tests, after testing for normality by a Levene test.

3 Results

3.1 Hydrology and trophic conditions

The KEOPS2 campaign was characterized by conditions of complex circulation and rapidly changing phytoplankton biomass (see Trull et al., 2015, their Figs. 1 and 2 and Suppl.). During the survey, the horizontal circulation pattern was dominated by the northernmost branch of the PF (Park et al., 2014) flowing across the plateau in the narrow, mid-depth (1000 m) channel just to the south of Kerguelen Island (Fig. 1). After passing to the east of the plateau, the jet flows outside the shelfbreak northwards and enters in a bathymetrically trapped cyclonic recirculation system (d’Ovidio et al., 2015; Park et al., 2014, Trull et al., 2015). The variations of the PF position during the KEOPS2 survey are documented in Trull et al. (2015, in supplement). The PF jet separated the central plateau and offshore stations to the south (A3, TNS 10 to TNS 3, TEW3 to TEW6, and E stations) from those to the north and east (TNS1, TNS2, TEW7, TEW8, F-L) and those stations close to the coast (TEW1 and TEW2).

At the beginning of our study (during the visit to station A3-1 and to the TNS transect), slight chlorophyll accumulation was visible from satellite images (see complementary information on satellite-image-derived primary production supplied by Trull et al. (2015), their Fig. 2 and Supplement), but the sampling on the first visit to station A3 (A3-1, on 20 October) revealed pre-bloom conditions on the plateau and some stations (TNS9, TNS4) of oceanic waters (Jouandet et al., 2014; Lasbleisz et al., 2014). The bloom started in earnest in early November, first massively on the plateau and in coastal waters, and secondly in spatially heterogeneous low biomass oceanic waters (during our TEW transect and stations E1-E3), with higher chlorophyll values at stations (TEW 7, TEW 8, F-L) downstream from the Polar-Front bloom (Lasbleisz et al., 2014; Trull et al., 2015). In mid-November, the central plateau bloom was well-developed (station A3-2) and afterwards started to decrease slightly, whereas downstream in the Polar Front, bloom was most extensive south of PF and showed its highest biomass there (stations E4–5).

The vertical depth stratification was variable over both space and time (see Trull et al. (2015), their Table 4a). Station R2 presented a MLD around 117 m. At station A3, the water column was characterized by a deep mixed layer (around 150 m) during the pre-bloom (station A3-1) and early bloom (station A3-2) surveys, with a range of 120 to 171 m (Jouandet et al., 2014). The Chl $a$ concentrations showed a fourfold increase from A3-1 (21 October) to A3-2 (15–17 November), with Chl $a$ concentrations at the surface increasing from 0.5 to 2 mg m$^{-3}$ (Jouandet et al., 2014, their Figs. 1 and 2). The mixed layer depth of the TNS stations south of the PF decreased northward from around 150 m (TNS10) to 100 m (except TNS6), with accompanying chlorophyll $a$ concentrations between 0.5 and 1.5 mg m$^{-3}$ (Lasbleisz et al., 2014, their Fig. 3). During the following visits to the region within the recirculation system in the PF meander (square zoom in Fig. 1), the MLD progressively decreased from 100 to 50 m (stations E1, TEW4 to TEW5), and then below 50 m (stations TEW6, E2 to E5, – except E4 decreasing slightly around 70 m) with similar chlorophyll $a$ concentrations between 1.0 and 1.5 mg m$^{-3}$ (Lasbleisz et al., 2014, their Fig. 4). The highest chlorophyll $a$ concentrations (values up to 4.7 mg m$^{-3}$) were found in the 40 upper metres of the 100 m water column of the coastal stations (TEW1 and TEW2, Lasbleisz et al., 2014), whereas the TEW3 above the shelf break presented lower chlorophyll $a$ concentrations ($<1.0$ mg m$^{-3}$) in its 60 m mixed layer, possibly due to its proximity to the PF jet.
3.2 Temporal and spatial variations of zooplankton abundance and biomass

Zooplankton abundances and biomass from ZOOSCAN processed samples of the 330 µm mesh net varied from $14 \times 10^3$ to $200 \times 10^3$ ind m$^{-2}$ (Fig. 2) and from 0.25 to 4.94 g C m$^{-2}$ (Fig. 3), respectively. Comparisons of abundance (ind m$^{-2}$) and biomass (g C m$^{-2}$) between ZOOSCAN-derived data and direct measurements showed that ZOOSCAN-derived data slightly overestimated direct measurements from regression forced through the origin: slope equal to 1.0015 for abundance ($R^2 = 0.75$, $n = 37$, $p < 0.01$) and slope equal to 1.1246 for dry weight ($R^2 = 0.803$, $n = 19$, $p < 0.01$).

Abundance values followed a normal distribution pattern with an average of $7310^3$ ind m$^{-2}$ (SD: 42). ANOVA with main effects (stations and dates) without interaction showed clear effects for dates ($p < 0.05$) but not for stations. All abundance values plotted against dates (Fig. 4a) showed a general increase, and the linear regression ($R^2 = 0.42$, $n = 37$) predicted a ratio of 3.7 between abundance at the beginning and at the end of the survey. Highest abundance (above the regression line on Fig. 4a) was observed for oceanic stations within the PF meander, both for the stations of the two transects (stations TNS4, 5, 7, 8, and TEW 4, 6, 7, 8, and stations E, except for E4-West). By contrast, the lowest abundance was found to the east and north of this PF meander, as well as for the first visit to A3. One exception was station TEW5, which presented the lowest abundance, whereas nearby spatial and temporal sampling stations presented much higher abundance. Between the two visits to sta-
tion A3 at the beginning and the end of the survey, the total abundance had multiplied by 3.5.

The fraction 500–1000 µm (see Fig. 3) presented the most abundant number of organisms (62.0% on average), followed by the <500 µm fraction (18.8% on average), the 1000–2000 µm fraction (14.2% on average) and the >2000 µm fraction (5.0% on average). The contribution of the smaller size fraction (<500 µm) increased with time from the beginning to the end of the survey (8.1% on average), whereas the 500–1000, 1000–2000, and > 2000 µm decreased to 5.0, 0.8 and 2.3%, respectively. However, these temporal changes were not significant in any of the four regressions due to the variability in size distribution between the stations. In addition, no clear diurnal pattern was observed from the day/night samplings performed at nine sampling dates.

Log-transformed biomass values followed a normal distribution pattern. As for the abundance, ANOVA with main effects (stations and dates) without interaction for biomass values showed an effect for dates \((p < 0.05)\) but not for stations. Average biomass was 2.32 g C m\(^{-2}\) (SD: 1.33), and the linear regression against time (not significant) predicted a ratio of 1.7 between biomass values at the beginning and the end of the survey (Fig. 4b). However, the biomass ratio between the two visits at station A3 showed an increase of 2.9, whereas the biomass values at station E (the Lagrangian survey) showed a slightly decreasing trend (with the exception of E4-En). The fraction > 2000 µm represented the highest biomass of organisms (57.1% on average), followed by the 1000–2000, 500–1000 and <500 µm fractions with 22.8, 18.2 and 1.9% on average, respectively (see Fig. 2). None of the regressions between the percentage value and dates presented a significant correlation, and the slopes of the regression were all near to zero for the intermediate size fractions. From the beginning to the end of the survey, the largest size fraction (> 2000 µm) decreased in its contribution to the biomass (~1.5%), whereas the contribution to the biomass increased with time by 0.1, 0.5 and 0.9%, respectively, for the 1000–2000, 500–1000 and <500 µm fractions.

The total zooplankton biomass values presented a significant correlation \((p < 0.01)\) with the average chlorophyll concentrations in the 100 upper metres, as well as with the integrated chlorophyll concentrations in the mixed layer depth (Fig. 5). Only stations TEW1 and TEW2 presented low zooplankton biomass for relatively high fluorescence concentrations (>1 µg Chl a L\(^{-1}\), Fig. 5a), but not versus the integrated Chl a biomass in their shallow (<80 m) mixed layers (Fig. 5b).

### 3.3 Metazooplankton community composition and distribution

From the 330 µm mesh size net, 65 taxa were identified for the 37 stations of this study (Table 1) with 26 genera/species of copepods. Copepods contributed the bulk of the zooplankton community abundance with 78.4% (SD = 13.13%) of the counted organisms over the whole area, and copepodites represented a little more than half of the counted copepods (mean = 52.5%, SD = 8.2%). ANOVA with main effects (stations and dates) without interaction showed no effect either for dates or for stations, either for the percentage of copepods against the whole zooplankton abundance, or for the percentage of copepodites stages against the total copepods abundance. Nauplii represented an average 2% of the total abundance, and showed an increasing abundance with time up to 4%, although they were undersampled with our net. The copepod communities were dominated by *Ctenocalanus citer*, followed by *Oithona similis* and *O. frigida*, *Metridia lucens*, *Scolecidicrilla minor*, *Calanus simililimus*, *Paraeuchaeta spp.*, *Rhincalanus gigas*, and near the coastal area *Drepanopus pectinatus*. Other dominant taxa were the different larval stages of euphausiids (eggs, nauplii, metanauplii, proto et metazoee), appendicularians (*Oikopleura spp.*, *Fritillaria spp.*), chaetognaths, pteropods (*Limacina retroversa*) and amphipods (*Themisto gaudiaudii*, *Hyperia spp.*). Radiolarians and foraminifera were regularly sampled as well. In some stations, other taxa occurred in low numbers, such as salps.

With the 120 µm mesh size net, the number of identified taxa for the 37 stations was reduced to 28 taxa (Table 1), strongly dominated by copepod species. Copepod larval forms as nauplii, undetermined copepod nauplii and copepodites, and copepodid stages of *Oithona sp.*, *Oncoea sp.*, and *Ctenocalanus citer* represented 20.4% of organisms in 120 µm mesh size nets. Adult forms (73% of the organisms in nets) were mainly from small and medium size copepods such as *Oithona similis* and *O. frigida*, *Microsetella rosea*, *Oncaea spp.*, *Trichona sp.*, *Microcalanus pygmaeus* and *Scolecidicrilla minor*. Other dominant taxa in this net were the different larval stages of euphausiids, appendicularians, chaetognaths, pteropods (*Limacina antarctica*), as well as, at a few stations, echinoderm larvae.

Comparison between the community compositions in the two nets clearly showed that some key groups were undersampled in the 330 µm mesh net: mainly the larval stages of many copepods, small copepods such as *Oithona sp.* Mi-
Table 1. List of zooplanktonic taxa collected and identified during the 2011 KEOPS2 cruise (average values for the 37 stations, in ind m$^{-3}$). Samples from the 330 µm (left) and 120 µm mesh size (right) nets.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>330 µm mesh size net</th>
<th>120 µm mesh size net</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult forms</td>
<td>Copepodites stages</td>
<td>Nauplii stages</td>
</tr>
<tr>
<td><strong>Copepods</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oithona similis</td>
<td>8.1</td>
<td>2.8</td>
</tr>
<tr>
<td>Oithona frigida</td>
<td>14.8</td>
<td>2.8</td>
</tr>
<tr>
<td>Microsetella rosea</td>
<td>1.9</td>
<td></td>
</tr>
<tr>
<td>Oncaea spp.</td>
<td>1.3</td>
<td>0.1</td>
</tr>
<tr>
<td>Triconia sp.</td>
<td>8.7</td>
<td>2.0</td>
</tr>
<tr>
<td>Clausocalanus laticeps</td>
<td>3.9</td>
<td>0.8</td>
</tr>
<tr>
<td>Centocalanus citter</td>
<td>35.8</td>
<td>56.5</td>
</tr>
<tr>
<td>Microcalanus pygmaeus</td>
<td>0.7</td>
<td></td>
</tr>
<tr>
<td>Mertidia lucens</td>
<td>9.6</td>
<td>8.9</td>
</tr>
<tr>
<td>Calanus propinquus</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>Calanus similimus</td>
<td>6.45</td>
<td>1.9</td>
</tr>
<tr>
<td>Calanoides acutus</td>
<td>1.1</td>
<td>1.6</td>
</tr>
<tr>
<td>Scolecithricella minor</td>
<td>9.2</td>
<td>6.4</td>
</tr>
<tr>
<td>Scaphocalanus spp.</td>
<td>0.7</td>
<td>2.5</td>
</tr>
<tr>
<td>Drepanopus pectinatus</td>
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<td>2.7</td>
</tr>
<tr>
<td>Pleuromamma robusta</td>
<td>0.9</td>
<td>0.2</td>
</tr>
<tr>
<td>Candacia maxima</td>
<td>rare</td>
<td>rare</td>
</tr>
<tr>
<td>Heterorhabdus spp.</td>
<td>rare</td>
<td>rare</td>
</tr>
<tr>
<td>Aetideus armatus</td>
<td>rare</td>
<td>rare</td>
</tr>
<tr>
<td>Haloptilus oxycephalus</td>
<td>rare</td>
<td>rare</td>
</tr>
<tr>
<td>Parauchaeta spp.</td>
<td>0.54</td>
<td>14.29</td>
</tr>
<tr>
<td>Rhincalanus gigas</td>
<td>2.93</td>
<td>7.34</td>
</tr>
<tr>
<td>Subeucalanus longiceps</td>
<td>0.14</td>
<td>0.02</td>
</tr>
<tr>
<td>Euchirella rostramagna</td>
<td>rare</td>
<td>0.04</td>
</tr>
<tr>
<td>Gaetanus pungens</td>
<td>rare</td>
<td></td>
</tr>
<tr>
<td>Undeuchaeta incisa</td>
<td>rare</td>
<td></td>
</tr>
<tr>
<td>Undetermined nauplii</td>
<td>2.1</td>
<td></td>
</tr>
<tr>
<td><strong>Undetermined copepodes</strong></td>
<td>22.4</td>
<td></td>
</tr>
<tr>
<td>Adult forms</td>
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<td></td>
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<td><strong>Euphausiids</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Undetermined species</td>
<td>0.27</td>
<td>6.22</td>
</tr>
<tr>
<td>Ostracods</td>
<td>2.3</td>
<td></td>
</tr>
<tr>
<td>Isopods</td>
<td>0.05</td>
<td></td>
</tr>
<tr>
<td>Mysis</td>
<td>rare</td>
<td></td>
</tr>
<tr>
<td>Decapod</td>
<td>rare</td>
<td></td>
</tr>
<tr>
<td><strong>Amphipods</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Themisto gaudicaudii</td>
<td>0.26</td>
<td></td>
</tr>
<tr>
<td>Hyperia spp.</td>
<td>0.86</td>
<td></td>
</tr>
<tr>
<td>Primno macropa</td>
<td>0.10</td>
<td></td>
</tr>
<tr>
<td>Vibilia sp.</td>
<td>rare</td>
<td>0.04</td>
</tr>
<tr>
<td>Scina sp.</td>
<td>rare</td>
<td></td>
</tr>
<tr>
<td><strong>Molluscs</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Limacina retroversa</td>
<td>3.45</td>
<td></td>
</tr>
<tr>
<td>Limacina helicina</td>
<td>rare</td>
<td></td>
</tr>
<tr>
<td>Spongiobranchaea sp.</td>
<td>rare</td>
<td></td>
</tr>
<tr>
<td>Clio sp.</td>
<td>rare</td>
<td></td>
</tr>
<tr>
<td><strong>Polychaetes</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pelagobia sp.</td>
<td>0.22</td>
<td></td>
</tr>
<tr>
<td>Tomopteris spp.</td>
<td>rare</td>
<td></td>
</tr>
<tr>
<td>Travisiptis sp.</td>
<td>rare</td>
<td></td>
</tr>
<tr>
<td>Undetermined</td>
<td>rare</td>
<td>0.32</td>
</tr>
<tr>
<td><strong>Appendicularians</strong></td>
<td>8.45</td>
<td>149.1</td>
</tr>
</tbody>
</table>

www.biogeosciences.net/12/4543/2015/  Biogeosciences, 12, 4543–4563, 2015
The impact of 120 µm mesh size and clogging on the larger planktonic organisms was difficult to assess as many groups were in any case in low density in the 330 µm mesh size net, except for the copepods *Clausocalanus laticeps*, *Calanus simillimus* and *Calanoides acutus*.

The taxonomic distributions are presented in more detail for stations A3 (the two visits A3-1 and A3-2) and for stations E3 and E5 in Fig. 6 for the four size fractions from the 330 µm mesh size net sample, and only in the small and medium size fractions from the 120 µm mesh size net sample.

The distribution pattern from the 330 µm mesh size net samples is first presented below. The zooplankton community structure in A3-1 was numerically dominated by the medium size fraction (nearly comparable to the fraction 500–1000 µm in total abundance in Fig. 2) comprising more than 50 % of copepods, characterized by the abundant cyclopoid *Oithona similis*, along with unspecified calanoid copepodes, and the harpacticoid *Microsetella rosea*. The rest of this fraction included metanauplii of euphausiids, appendicularians, ostracods and small chaetognaths. The fraction of “large size” mesozooplankton, similar to the 1000–2000 µm fraction counted with ZOOSCAN and representing 10.7 % of the total abundance, was composed of 98 % copepods with some major taxa (*Ctenocalanus citer*, *Metridia lucens*, *Scoleithricella minor*, *Calanus simillimus*, *Scaphocalanus spp.*, *Clausocalanus laticeps*), and early copepodites of *Paraeuchaeta* and of *Calanidae*. The highest size fraction was dominated by more than 75 % by *Rhinocalanus gigas* and amphipods *Hyperia* spp. and *Themisto gaudicaudii*. It corresponds to the fraction > 2000 µm from the ZOOSCAN which contributes to two-thirds of the mesozoooplancton biomass at station A3-1 (see Fig. 2). The lowest size fraction was mainly composed of euphausiid eggs and nauplii, copepod nauplii, small forms of the pteropod *Limacina retroversa* and in small densities foraminifera and radiolarians.

As a whole, the mesozoooplancton community in A3-1 was mainly composed of herbivorous species in all fractions, such as the copepods *R. gigas*, *C citer*, *O. similis*, *M. rosea*, but also pteropod *Limacina retroversa* and in small densities foraminifera and radiolarians. During the second visit to station A3 (A3-2), the size distribution in abundance was dominated by fractions with ECD ≤ 1000 µm (up to 83 % of the total abundance, see in Fig. 3). The taxa distribution in A3-2 differed from the first visit (station A3-1) both in the “small” size fractions by an increase in...
copepod nauplii and euphausiid eggs, and in the “medium” size fraction by a large proportion of appendicularians and early copepodid stages of copepods. The two largest fractions (“large” and “very large”) were not very different at A3-1 and A3-2 in taxonomic composition and distribution (the only difference being the appearance of late larval stages of euphausiid in the “very large” fraction).

The major features in taxonomic changes between stations E3 (04 November) and E5 (18 November) (Fig. 6) were the increasing contribution of calanoid copepods in the medium and large size fractions, with the concomitant increase of contribution of these fractions to the total abundance (see also Fig. 2), and the increase of euphausiid larvae in the largest fraction. The smaller fraction presented a rather stable distribution of dominant taxa, with copepod nauplii and Limacina as dominant groups (Fig. 6). As a whole, while omnivores, carnivores and scavengers are present, the herbivorous component is strongly dominant with all these larval forms. It is of interest to note that the dominant species for the different fractions at E5 were quite similar to those at A3-1, but with the noticeable difference that many larval stages occurred in all size fractions, inducing the highest observed abundance during the survey (see Fig. 2), although finally representing a lower biomass (see Fig. 3).

In the 120 µm mesh size net samples, the taxonomic observation generally delivered the same dominant taxa in the medium size fraction as for the 330 µm mesh size net, but with larger proportions of small copepodid forms and small adult copepods, such as Oncoea spp. and Microsetella rosea.
Table 2. Isotopic composition of size-fractionated zooplankton (mean and standard deviation). Mean $\delta^{13}$C, values of acidified samples; mean $\delta^{13}$C-norm, lipid-normalized values (except for the lowest size fraction); mean $\delta^{15}$N, values of untreated samples.

<table>
<thead>
<tr>
<th>Station</th>
<th>Fraction</th>
<th>Mean $\delta^{13}$C</th>
<th>SD $\delta^{13}$C</th>
<th>Mean $\delta^{15}$N</th>
<th>SD $\delta^{15}$N</th>
<th>C / N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Date</td>
<td>µm</td>
<td>% PDB</td>
<td>% PDB</td>
<td>% PDB</td>
<td>% air</td>
</tr>
<tr>
<td>A3-1 day</td>
<td>06/11/2011</td>
<td>80  200  500  1000  2000</td>
<td>23.52 26.48 26.20 24.52 25.16</td>
<td>-25.52 -24.00 -23.10 -22.67 -22.97</td>
<td>0.10 0.05 0.05 0.14 0.03</td>
<td>0.06 0.08 0.07 0.12 0.03</td>
</tr>
<tr>
<td></td>
<td>20/10/2011</td>
<td>80  200  500  1000  2000</td>
<td>23.26 25.18 25.74 24.76 25.84</td>
<td>-23.26 -23.70 -23.29 -23.03 -23.21</td>
<td>0.06 0.03 0.06 0.01 0.03</td>
<td>0.07 0.02 2.00 0.00 0.06</td>
</tr>
<tr>
<td>TNS-7 day</td>
<td>22/10/2011</td>
<td>80  200  500  1000  2000</td>
<td>23.61 25.37 25.73 26.43 26.27</td>
<td>-23.61 -23.91 -23.26 -22.80 -22.75</td>
<td>0.05 0.04 0.03 0.05 0.03</td>
<td>0.06 0.03 0.11 0.05 0.08</td>
</tr>
<tr>
<td>R-2 day</td>
<td>26/10/2011</td>
<td>80  200  500  1000  2000</td>
<td>24.62 25.86 25.70 26.54 26.12</td>
<td>-24.62 -23.48 -22.77 -22.45 -22.74</td>
<td>0.04 0.02 0.04 0.02 0.02</td>
<td>0.12 0.09 0.08 0.01 0.14</td>
</tr>
<tr>
<td>E-1 night</td>
<td>30/10/2011</td>
<td>80  200  500  1000  2000</td>
<td>25.15 25.98 25.23 26.01 27.02</td>
<td>-25.15 -24.73 -23.39 -21.98 -21.52</td>
<td>0.01 0.01 0.02 0.03 0.06</td>
<td>0.05 0.02 0.02 0.04 0.04</td>
</tr>
<tr>
<td>E-2 day</td>
<td>01/11/2011</td>
<td>80  200  500  1000  2000</td>
<td>22.58 23.29 23.73 23.60 23.29</td>
<td>-22.58 -21.00 -21.62 -21.73 -21.61</td>
<td>0.05 0.03 0.04 0.07 0.05</td>
<td>0.04 0.04 0.08 0.08 0.05</td>
</tr>
<tr>
<td>TEW-4 day</td>
<td>01/11/2011</td>
<td>80  200  500  1000  2000</td>
<td>24.70 25.79 25.60 25.67 25.62</td>
<td>-24.70 -23.52 -23.24 -22.63 -23.20</td>
<td>0.02 0.02 0.02 0.03 0.04</td>
<td>0.03 0.03 0.03 0.11 0.03</td>
</tr>
<tr>
<td>TEW-8 day</td>
<td>02/11/2011</td>
<td>80  200  500  1000  2000</td>
<td>24.82 24.06 26.26 24.31 24.64</td>
<td>-24.82 -23.51 -22.79 -22.41 -21.48</td>
<td>0.04 0.01 0.02 0.03 0.01</td>
<td>0.07 0.06 0.05 0.03 0.04</td>
</tr>
<tr>
<td>F-L day</td>
<td>06/11/2011</td>
<td>80  200  500  1000  2000</td>
<td>23.69 24.06 24.59 24.31 24.64</td>
<td>-23.69 -21.42 -21.62 -21.58 -21.48</td>
<td>0.03 0.01 0.03 0.03 0.01</td>
<td>0.05 0.06 0.14 0.07 0.04</td>
</tr>
</tbody>
</table>
Copepod nauplii and early copepodid contributed with high abundance (see Table 1) to the small size fraction.

To compare the taxonomic composition between all stations, a cluster dendrogram quantifying the compositional similarity of taxa distributions between the different stations was constructed from the Bray–Curtis coefficient using the 330 µm mesh size net samples which presented the largest number of taxa. Figure 7 presents the cluster dendrogram and
Table 3. Mean (±SD) stable isotope values of the main groups of organisms sorted in the largest size fraction (> 2000 µm). *n* is the number of samples analysed.

<table>
<thead>
<tr>
<th>Groups</th>
<th><em>n</em></th>
<th>$\delta^{13}$C (‰)</th>
<th>$\delta^{15}$N (‰)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salps</td>
<td>12</td>
<td>-22.36 ± 0.82</td>
<td>3.87 ± 1.29</td>
</tr>
<tr>
<td>Copepods</td>
<td>15</td>
<td>-21.98 ± 0.95</td>
<td>4.40 ± 0.54</td>
</tr>
<tr>
<td>Euphausiacea</td>
<td>12</td>
<td>-21.03 ± 2.34</td>
<td>4.24 ± 0.63</td>
</tr>
<tr>
<td>Amphipods</td>
<td>9</td>
<td>-23.19 ± 0.24</td>
<td>4.14 ± 0.41</td>
</tr>
<tr>
<td>Pteropods</td>
<td>5</td>
<td>-23.44 ± 0.04</td>
<td>4.56 ± 0.09</td>
</tr>
<tr>
<td>Chaetognaths</td>
<td>5</td>
<td>-22.94 ± 0.18</td>
<td>5.93 ± 0.60</td>
</tr>
<tr>
<td>Polychaetes</td>
<td>3</td>
<td>-22.52 ± 0.03</td>
<td>7.72 ± 0.06</td>
</tr>
<tr>
<td>Fish larvae</td>
<td>3</td>
<td>-21.60 ± 0.05</td>
<td>5.99 ± 0.08</td>
</tr>
</tbody>
</table>

![Figure 7](image.png)

Figure 7. (a) Dendrogram and (b) MDS plot produced by the clustering of the 37 samples (28 stations, among them nine stations with day–night sampling) during KEOPS2 based on the density (ind m$^{-3}$) of mesozooplankton taxa. Density values were fourth-root-transformed prior to analysis of the Bray–Curtis similarity matrix. The stress statistic for the MDS plot is 0.12.

3.4 Isotopic composition of size-fractionated zooplankton and within zooplankton taxa

A wide range of $\delta^{13}$C (> 8 ‰) and $\delta^{15}$N (> 4 ‰) values were recorded among zooplankton size fractions and stations (Table 2). A slight general increase of $\delta^{13}$C with increasing size fraction was observed, while the difference was not significant due to wide differences between sites ($F = 1.818$, $p = 0.132$) (Fig. 8a). A significant increase in $\delta^{15}$N with increasing size was observed ($F = 11.67$, $p < 0.001$), particularly between the two smallest fractions (80–200 and 200–500 µm) and the three largest ones (Fig. 8b). However, no significant difference in mean $\delta^{15}$N was apparent between the 500–1000 and > 2000 µm fractions, while the 1000–2000 µm fraction exhibited a slightly lower $\delta^{15}$N than the two others. Within each size fraction, no difference was observed between mean day and night $\delta^{13}$C and $\delta^{15}$N values ($p > 0.05$ for both), in spite of differences at site level (Table 2). Thus, for both $\delta^{13}$C and $\delta^{15}$N values, the main difference occurred between the two smallest size classes (< 500 µm) and the three largest ones (> 500 µm).

At the station level, mean $\delta^{13}$C and $\delta^{15}$N values differed. Station R2 presented the lowest mean $\delta^{13}$C (~25.26 ‰) and the highest mean $\delta^{15}$N (4.49 ‰), while stations F-L, TEW-8 and E4-E were characterized by the highest $\delta^{13}$C (~21.2 ‰) and rather high $\delta^{15}$N values (~4 ‰). All the other stations exhibited mean $\delta^{13}$C values (from ~23.26 to ~21.76 ‰) and a wide range of mean $\delta^{15}$N values (from 3.63 to 4.25 ‰).

Differences in mean $\delta^{15}$N between small (< 500 µm) and large (> 500 µm) zooplankton size fractions were low in T-group 1 (0.3 ‰), increased in T-group 5 (0.6 ‰) and were highest at most stations located in the eddy (Fig. 9). This trend suggested higher food overlap among size fractions in zooplankton associated with phytoplankton T-group 1 and Tgroup 5, and more partitioned food resources in phytoplank-
Table 4. Seasonal variations of zooplankton abundance and biomass from KEOPS2 (15 October to 20 November 2011) and KEOPS1 (19 January to 13 February 2005) surveys with contribution of different size fractions (< 500, 500–1000; 1000–2000 and > 2000 µm). The reference stations were A3 (shelf waters) and C11 (oceanic waters) for KEOPS1 (see Carlotti et al. (2008), their Figs. 3 and 5), and A3 (shelf waters) and TNS6-TNS5 and E4E-E5 (oceanic waters) for KEOPS2.

<table>
<thead>
<tr>
<th>Area</th>
<th>Date</th>
<th>KEOPS2</th>
<th>KEOPS1</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>20–22/10</td>
<td>13–16/11</td>
<td>22–28/1</td>
</tr>
<tr>
<td>Shelf waters</td>
<td>Abundance</td>
<td>× 10^6 m^−2</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>Percentages of total abundance</td>
<td>&lt; 500 µm</td>
<td>10 %</td>
</tr>
<tr>
<td></td>
<td></td>
<td>500–1000 µm</td>
<td>60 %</td>
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<tr>
<td></td>
<td></td>
<td>1000–2000 µm</td>
<td>23 %</td>
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<tr>
<td></td>
<td></td>
<td>&gt; 2000 µm</td>
<td>7 %</td>
</tr>
<tr>
<td></td>
<td>Biomass</td>
<td>g C m^−2</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>Percentages of total biomass</td>
<td>&lt; 500 µm</td>
<td>&lt; 1 %</td>
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<tr>
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<td></td>
<td>500–1000 µm</td>
<td>12 %</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1000–2000 µm</td>
<td>23 %</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2000 µm</td>
<td>64 %</td>
</tr>
<tr>
<td>Oceanic waters</td>
<td>Abundance</td>
<td>× 10^6 m^−2</td>
<td>70</td>
</tr>
<tr>
<td></td>
<td>Percentages of total abundance</td>
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<td>18 %</td>
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<td>1000–2000 µm</td>
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<td>&gt; 2000 µm</td>
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<td>Biomass</td>
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<td>Percentages of total biomass</td>
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<td>2000 µm</td>
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Figure 8. Distribution of δ^{13}C (a) and δ^{15}N (b) of zooplankton across size fractions during KEOPS2. White symbols represent day; black symbols represent night.

T-group 2 and T-group 3, as indicated by a more even increase in δ^{15}N with zooplankton size at these stations. The smaller size fraction (80–200 µm) was differently composed according to stations, being dominated either by diatoms (A3-2, E-4W), foraminifera (A3-1), small copepods (R2), or a mixture of these groups (most stations). Copepods, eggs, thecosome pteropods foraminifera and small aggregates contributed to 200–500 µm fractions. The following size fractions (500–1000, 1000–2000 and > 2000 µm) were all dominated by copepods (60–95 %), but amphipods, euphausiids, appendicularians and chaetognaths increased in abundance from the 500–1000 to the 1000–2000 µm fractions. The largest size fraction (> 2000 µm) was dominated by *Rhincalanus gigas* and euphausiid larvae or juveniles. Large chaetognaths completed this large fraction.

Thus, differences in specific composition of size fractions, particularly the smallest and the largest, could result in isotopic differences between stations within a size fraction. For example, when diatoms dominated the 80–200 µm fraction, δ^{15}N values were lower than when composed of foraminifera or small copepods (2–3 and 4–4.5 ‰, respectively).
4 Discussion

4.1 Zooplankton development during the 2011 early spring bloom and comparison with other seasons

In high latitudes, zooplankton first increase in abundance more than biomass in response to initial phytoplankton spring bloom due to stimulated reproduction of overwintering adults of dominant copepods. This induces a lag-time in the grazing response of herbivorous zooplankton at the beginning of blooms, which further promotes the rapid phytoplankton accumulation. Higher phytoplankton concentrations then stimulate grazing by overwintering stages and new cohorts which results in build-up of zooplankton biomass. With the succession of new cohorts in full bloom conditions (> 0.8 mg Chl \textit{a} m\textsuperscript{−3}), continuous egg production and individual growth induce proportional increase of abundance and biomass.

Such a response of zooplankton to an early phase of the north-eastern Kerguelen bloom was observed during the Lagrangian survey within the stationary meander of the Polar Front (stations E1 to E5, except E4-W, Figs. 2, 3 and 4). The average integrated Chl \textit{a} concentrations were rather low (0.49 to 0.77 µg Chl \textit{a} m\textsuperscript{−3}) for these E stations and but slightly higher than the previous weeks – transects TNS and TEW (Lasbleisz et al., 2014). The POC was constant in the surface layer up to the time of E3, with an average of 83 mg C m\textsuperscript{−3}, and then slightly increased at E4 and E5 (with an average up to 109 mg C m\textsuperscript{−3}) (Lasbleisz et al., 2014). Zooplankton densities increased from 60 × 10\textsuperscript{3} ind m\textsuperscript{−2} (E1-d) to 200 × 10\textsuperscript{3} ind m\textsuperscript{−2} (E5-d) whereas biomass gradually decreased (excepted E4-E-n) from 2.3 g C m\textsuperscript{−2} (E1-d) to 1.7 g C m\textsuperscript{−2} (E5-n). Two processes may favour the shift towards smaller size classes. Firstly, the contribution of the larger size classes to biomass decreased with time (Fig. 3) due to the reduction of initial standing stock of overwintering zooplankton by mortality and by investment in egg production. The dominant overwintering copepods (\textit{Ctenocalanus citer}, \textit{Rhincalanus gigas}) are known to be strong seasonal migrants able to spawn in early spring even at low chlorophyll concentrations (Schneck-Schiel, 2001; Atkinson, 1998), i.e. before the full bloom conditions. Moreover, smaller copepod species and copepodids of large copepods may better exploit these low food concentrations (Atkinson et al., 1996), allowing individuals to develop and grow, whereas large copepods are food limited.

The response to chlorophyll increase in waters above the plateau (station A3 in Fig. 4c) was proportional in abundance and biomass (threefold higher at A3-2 than at A3-1). Lasbleisz et al. (2014) mention that the Chl \textit{a} increase at station A3-2 was accompanied by an increase of the Phaeo : Chl \textit{a} ratio, reflecting a potential higher grazing activity. The mesozooplankton at A3-2 (see Fig. 6) presented a grazer community structure able to feed on a wide spectrum of cells from small diatoms to phytodetritus aggregates, as observed.

Figure 9. Distribution of $\delta^{13}$C (left column, \textit{a}) and $\delta^{15}$N (right column, \textit{b}) values across zooplankton size fractions for four of the five T-groups of stations identified by Trull et al. (2015) for phytoplankton. Station E4-E is included here in T-group 5 instead of T-group 2. From top to bottom: a1 and b1, T-group 1 (diamonds); a2 and b2, T-group 2 (triangles); a3 and b3, T-group 3 (dots); and a4 and b4, T-group 5 (squares). T-group 4 included coastal stations not sampled in the zooplankton analysis.

Groups of organisms individualized in the > 2000 µm fraction presented highly different isotopic signatures according to their main feeding behaviours (Table 3). Filtering salps presented the lowest $\delta^{15}$N (< 4 %), the mostly herbivorous copepods, amphipods, euphausiids, and pteropods intermediate values (4 to 4.6 %), while predatory chaetognaths, fish larvae and polychaetes exhibited higher $\delta^{15}$N values (> 5 %). Thus, $\delta^{15}$N differences of the > 2000 µm fraction between stations resulted mainly from the relative contributions of these groups to bulk samples (e.g. higher proportion of salps and euphausiids at A3-2, and large chaetognaths at E5). Accordingly, differences in $\delta^{13}$C values could be linked to difference in both size and composition of the ingested food. The lower $\delta^{13}$C recorded in gymnosomes and copepods suggested the consumption of small phytoplankton particles, while the higher $\delta^{13}$C of euphausiids suggested a consumption of larger-sized phytoplankton. Higher $\delta^{13}$C in euphausiids compared to copepods was also observed in Arctic seas (Schell et al., 1998).
at this station (Lasbleisz et al., 2014; Laurenceau-Cornec et al., 2015), as well as small nano-/microzooplankton (Christi-
taki et al., 2014) and carnivorous zooplankton. Compared to
A3-1, the medium size and small size mesozooplankton frac-
tions had a much larger contribution of microphagous organ-
isms (appendicularians, copepod nauplii, etc.) which could
quickly remove the smaller planktonic forms (below 20 µm).
The larger zooplankton size fractions were a mixture of effi-
cient grazers on large diatoms (> 20 µm), omnivores and de-
tritivores able to feed on aggregates, and carnivores consum-
ing micro- and mesozooplankton.

The mesozooplankton biomass stocks observed at the
beginning of the KEOPS2 cruise (Table 4) were around
1.7 g C m\(^{-2}\) above the plateau (A3) and 1.2 g C m\(^{-2}\) in
oceanic waters (TNS transect). Oceanic biomass slightly in-
duced during the cruise, except the biomass observed in
the eastern bloom (station F-L) in the Polar Front zone
(above 4 mg C m\(^{-2}\)), and station A3 also presented biomass
around 4 mg C m\(^{-2}\) at the end of the survey. These differ-
et results during KEOPS2 suggest that the zooplankton
community is able to respond to the growing phytoplank-
ton blooms earlier on the plateau than in the oceanic waters,
where complex mesoscale circulation stimulates initial more
or less ephemeral blooms before a broader bloom extension.
Due to our constrained sampling for oceanic stations, it was
not possible to determine whether the observed zooplankton
biomass variability between oceanic stations was linked to
enhanced local production (except for stations near the per-
manent Polar Front sustaining high level of production). Our
results in the quasi-Lagrangian survey within the meander
suggests that the heterogeneous primary production linked
to oceanic mesoscale activity in the early bloom phase may
stimulate the production of new zooplankton cohorts, with-
out sustaining individual growth, slowing down the built-up
of new zooplankton biomass. In addition, potential predation
on mesozooplankton by euphausiid populations was ex-
pected, from observations of the increasing contribution of
euphausiid larval stages in our Bongo net samples (see Fig. 6)
and of long faecal pellets in gel traps (Laurenceau-Cornec et
al., 2015).

In contrast, stations F-L (06 November) and A3-2
(16 November) presented the highest biomass (maintained
below 5 g C m\(^{-2}\)) observed in November (Figs. 4 and 5) and
a similar ratio of abundance to biomass, around 20 \(\times 10^3\) ind
per g C (Fig. 4c) and a lower contribution of smaller size
fractions (ESD ≤ 1000 µm) to total biomass comparatively
to station E5. These characteristics could be the results of a
phytoplankton-sustained zooplankton development over the
previous weeks.

4.2 Comparison with previous results

If we group our observations of KEOPS1 and KEOPS2 (Ta-
ble 4), the zooplankton seems to continuously increase from
mid-October to early February, with a ratio higher on shelf
waters (abundance \(\times 20\) and biomass \(\times 9\)) than in oceanic wa-
ters (abundance \(\times 3\) and biomass \(\times 2.5\)). After early February,
the zooplankton community structure remained rather sta-
able (Carlotti et al., 2008). Over the whole spring to summer
seasons, the small size fractions (< 500 and 500–1000 µm)
significantly contribute to the increase in abundance (from
70 to 85 %), with the production of calanoid copepod lar-
val stages and large numbers of cyclopoid copepods, whereas
the increase in biomass is mainly due to the fraction 1000–
2000 µm with calanoid copepod late larval stages (with a con-
tribution doubling from spring to summer). The taxonomic
composition did not show major differences between shelf
and oceanic waters, except that the contribution of copepods
to the whole mesozooplankton was higher in oceanic waters
than on the shelf, and these taxonomic patterns were quite
similar between the KEOPS 1 (see Fig. 7 in Carlotti et al.,
2008) and KEOPS2 survey (Fig. 6).

The use of different laboratory technologies (Lab OPC
during KEOPS1 and ZOOSCAN during KEOPS2) to opti-
tically measure and size plankton organisms from net haul
samples must be considered. In their comparative study be-
tween LOPC and ZOOSCAN, Schultes and Lopes (2009)
found good agreement in the normalized biomass size spectra
(NBSS) for particles in the size range of 500 to 1500 µm in
equivalent spherical diameter (ESD). Several disparities for
smaller and larger particles size range in their study were due
both to in situ sampling (LOPC and net have different sam-
ping efficiencies), in situ vs. lab counting (LOPC counts any
particles, not only zooplankton, with potential overlapping
between particles, whereas ZOOSCAN samples are carefully
distributed on a scanned window), etc. Our present com-
parison of estimated abundance and biomass for KEOPS1
and KEOPS2 is based on similar sampling protocols with a
330 µm mesh net on the Bongo frame, and in both cases a
delicate laboratory protocol. The flow-through system used
with the Lab-OPC for KEOPS1 samples was controlled to
avoid coincidence of organisms counted by the laser (count
rate at 20 particles min\(^{-1}\); see Carlotti et al., 2008) and or-
ganisms were carefully separated on the ZOOSCAN window
for the KEOPS2 samples. In both studies, a large number of
individuals were counted (1000 particles per samples) to
correctly count and size larger organisms. Finally, the lower
and higher range of counted and measured zooplankton or-
ganisms are mainly due to the 330 µm mesh net efficiency,
and the abundance and biomass results of both studies might
be compared.

In addition to the recent survey of the CPR data for the re-
region (see in Introduction), which shows the strong develop-
ment of mesozooplankton abundance in October–November,
the overall results of KEOPS 1 and 2 in terms of seasonal
changes in abundance and biomass values are highly con-
sistent with the information provided by Semelkina (1993)
and Razouls et al. (1996, 1998). During the SKALP cruises,
all around the Kerguelen Islands (46–52° S, 64–73° E),
Semelkina (1993, her Table 1) observed an increase from
62 × 10³ ind m⁻² in July–August 1987 (average values between 0 and 200 m depth for the whole sampled area, nearly double from 0–1000 m) to 570 × 10³ ind m⁻² in February 1988 (values between 0 and 200 m, 100 × 10³ ind m⁻² more in the layer 200–400 m). In terms of biomass, assuming a carbon content to be 50 % of body dry weight, the biomass increase in the upper 200 m was from 2.2 g C m⁻² to 19 g C m⁻². The sampled areas during the SKALP cruises covered a much larger area than that studied during KEOPS2, but these average values corresponded to those observed on the eastern side of the Kerguelen Islands (see Semelkina (1993), her Fig. 2). Concerning the taxonomic composition of the mesozooplankton, this author mentioned no seasonal variations but differences in population development and distribution.

Razouls et al. (1998) presented the seasonal changes in copepod distributions at the KERFIX station, a fixed time-series station, situated 60 miles south-west of the Kerguelen Islands (50º40′ S, 68º25′ E), in 1700 m of water, characteristic of the Permanently Open Ocean Zone (POOZ). The copepod abundance sampled from vertical hauls (300 m – surface) ranged from less than 30 × 10³ ind m⁻² in winter and 45 × 10³ ind m⁻² in October up to 222 × 10³ ind m⁻² in January. The nearest station during KEOPS1 and 2 was station R2 which presented biomasses (respectively abundance densities) of 10.7 g C m⁻² (272 × 10³ ind m⁻²) in February 2005 and 4.5 g C m⁻² (80 × 10³ ind m⁻²) in November 2011. Abundances during KEOPS1 and 2 were largely dominated (> 80 %) by copepods (Carlotti et al., 2008, their Fig. 7; distribution not shown for KEOPS2). In addition, during a coastal annual survey in Morbihan Bay at the Kerguelen Islands, Razouls et al. (1996) found a ratio of 10 between winter and spring–summer mesozooplankton density (from 2 to 20 × 10³ ind m⁻³) and a ratio of 20 for the corresponding biomass (from 20 to 400 mg DW m⁻³).

4.3 Effects of primary production on trophic pathways through mesozooplankton

The KEOPS2 cruise illustrates the complexity of the phytoplankton bloom in spring in the oceanic waters of the Kerguelen Islands, linked to the intense mesoscale activity both in species diversity and spatial production. Comparatively, the mesozooplankton presents initial standing biomass stocks between 1 and 2 g C m⁻² everywhere in the region, ready to exploit any new phytoplankton production. When this occurs, the initial response is to produce new cohorts which grow further as the bloom builds up, delaying the major grazing impact when these cohorts reach the later stages. Sustained full blooms at plateau stations or permanent fronts favour the highest and longest secondary production rate. The spring period usually shows the greatest increase in grazing pressure on phytoplankton (Razouls et al., 1998).

The comparison of the sinking particle composition at early and advanced stages of the bloom at station A3 (Laurenceau-Cornec et al., 2015 for KEOPS2; Ebersbasch et al., 2008 for KEOPS1) shows that early bloom stage is characterized by particles dominated by phyto-aggregates due to relatively weak grazing pressure on phytoplankton stocks, whereas faecal aggregates characterized the vertical matter flux as soon as zooplankton grazing substantially affects the phytoplankton stock.

The qualitative composition of the bloom had a direct impact in terms of species dominance (mostly herbivorous species) and biochemical composition of the zooplankton organisms. The spatial differences observed in isotopic signatures of phytoplankton were tracked up to the higher zooplankton levels and showed the impact of the food source.

Differences in the isotopic ratios of zooplankton were observed between stations during the KEOPS2 survey. Station R2 exhibited a 2.2‰ lower δ¹³C than stations located on the plateau (A3) or in the eddy (E1 to E5), while δ¹³C of stations located in the open ocean (F-L) was increased by ~ 1.5‰ compared to them. A similar increase in carbon isotopic signature was observed by Trull et al. (2015) for phytoplankton, with the lowest δ¹³C at the HLNC reference station (R2) and the highest at stations located in the open ocean downstream near the Polar Front (F-L, TEW8) (Fig. 10). The trophic relationship between mesozooplankton and phytoplankton (Trull et al., 2015) was evidenced by the significant positive correlation of their δ¹³C values (δ¹³C Zooplankton = 0.745 δ¹³C Phytoplankton − 5.465, r = 0.85, p < 0.001). As shown in Fig. 10, mean δ¹³C values of zooplankton were related to those of phytoplankton, testifying to the consumption of phytoplankton by zooplankton at station level. The mean trophic fractionation factor from phytoplankton to zooplankton was 0.40 ± 0.71 ‰ for δ¹³C and 2.69 ± 0.65 ‰ for δ¹⁵N. These values corresponded to a mean increase lower than one trophic level, if we apply the commonly used trophic fractionation factors (1 ‰ for δ¹³C and 3.14 ‰ for δ¹⁵N) that are in agreement with previous studies on zooplankton (Fry and Quinones, 1994). Such low values again indicated a dominance of herbivory among zooplankton organisms, which confirmed the conclusions based on zooplankton composition.

The mean increase in δ¹⁵N in small zooplankton size classes (from 80–200 to 500–1000 μm) was higher than among larger size fractions (from 500–1000 μm to > 2000 μm) (1 ‰ and 0.28 ‰ respectively). This lower increase in mean δ¹⁵N from 500–1000 to > 2000 μm suggested a high food overlap among the three largest size fractions, with a dominance of herbivorous organisms. Within the largest size fraction (> 2000 μm), an increase in trophic level (δ¹⁵N) was observed from filtering (salps) and mostly herbivorous organisms (copepods, pteropods, etc.) to predatory carnivores (chaetognaths), as observed in other regions (Tarling et al., 2012; Banaru et al., 2014). While different feeding behaviours can be observed among euphausiids (Mauchline, 1980), most euphausiids collected during the KEOPS2 survey were mainly herbivores or omnivores.

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with a $\delta^{15}N$ varying between 3.5 and 5.0‰ for individuals > 2000 µm, a range value already observed in the Southern Ocean (Gurney et al., 2001; Schmidt et al., 2003). High feeding overlap across size-fractionated zooplankton is reported in most studies (Fry and Quiñones, 1994; Bode et al., 2007) and may increase during food shortage (Tarling et al., 2012; Banaru et al., 2014). During KEOPS2, the highest food overlap among zooplankton size fractions seemed to be associated with phytoplankton T-group 1 and T-group 5 in which small-sized cells dominated, while more partitioned food resources among size fractions seemed to occur in zooplankton associated with phytoplankton T-group 2 and T-group 3, where large phytoplankton cells dominated (Trull et al., 2015). The direct comparison between stable isotope values of size-fractionated zooplankton and their abundance or biomass in water masses is difficult. Zooplankton isotopic values are firstly related to those of the phytoplankton they feed on, themselves being linked to water characteristics and nutrient cycling (Trull et al., 2015). The stable isotope values recorded during the KEOPS2 survey suggest a general increase in herbivory in zooplankton during the bloom in accordance with the increase in the abundance of small-sized zooplankton, and corroborate the finding of Lasbleiz et al. (2015) based on the Phaeo : Chl $a$ ratio.

5 Conclusions

The complexity of the oceanic processes inducing the large-scale phytoplankton bloom in the eastern area of the Kerguelen Islands occurs over scales ranging from the very large (1000 s of kilometres) down to the submesoscales (10 s of kilometres), marked by intense oceanic–plateau interactions linked to the meandering circulation of the Polar Front (PF) and by a myriad of secondary circulations linked to circulations resulting in a patchy distribution of the new production with different intensity and duration. The KEOPS2 survey addressed the challenge of examining the large-scale phytoplankton bloom that forms over and downstream of the Kerguelen Plateau in the most productive season, but also of carrying out observations at a finer resolution in order to understand the influence of spatial and temporal variability of biogeochemical and biological processes on the overall regional ecosystem dynamics and carbon export.

Our results on the mesozooplankton dynamics during KEOPS2 suggest that the zooplankton community maintains relatively high winter stocks both on the plateau and in the oceanic waters, mostly distributed in mesopelagic waters, ready to exploit the early phytoplankton blooms. The timing and intensity of the bloom on the plateau allow an earlier and longer period favourable for zooplankton development and growth compared to the surrounding oceanic waters. A longer lag-time (several weeks) between an initial reproduction phase of the zooplankton organisms and the biomass increase, and thus their grazing impact, was clearly observed in oceanic waters.

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References


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