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2 **Mesozooplankton structure and functioning during the onset of the Kerguelen**  
3 **Phytoplankton Bloom during the Keops2 survey**  
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1 **Abstract.**

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

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

18 The biomass stocks observed at the beginning of the KEOPS2 cruise were around 1.7 g  
19 C m<sup>-2</sup> above the plateau and 1.2 g C m<sup>-2</sup> in oceanic waters. Zooplankton biomass in oceanic  
20 waters remained on average below 2 g C m<sup>-2</sup> over the study period, except for one station in  
21 the Polar Front Zone (F-L), whereas zooplankton biomasses were around 4 g C m<sup>-2</sup> on the  
22 plateau at the end of the survey. The most remarkable feature during the sampling period was  
23 the stronger increase in abundance in the oceanic waters (25 10<sup>3</sup> to 160 10<sup>3</sup> ind.m<sup>-2</sup>) than on  
24 the plateau (25 10<sup>3</sup> to 90 10<sup>3</sup> ind. m<sup>-2</sup>). The size structure and taxonomic distribution patterns  
25 revealed a cumulative contribution of various larval stages of dominant copepods and  
26 euphausiids particularly in the oceanic waters, with clearly identifiable stages of progress  
27 during a Lagrangian time series survey. The reproduction and early stage development of  
28 dominant species were sustained by mesoscale-related initial ephemeral blooms in oceanic  
29 waters, but growth was still food-limited and zooplankton biomass stagnated. In contrast,  
30 zooplankton abundance and biomass on the shelf were both in a growing phase, at slightly  
31 different rates, due to growth under sub-optimal conditions. Combined with our observations  
32 during the KEOPS1 survey (January-February 2005), the present results deliver a consistent  
33 understanding of patterns in mesozooplankton abundance and biomass from early spring to  
34 summer in the poorly documented oceanic region east of the Kerguelen Islands.

## 1        **Introduction**

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

26        How the zooplankton populations increase from overwinter stocks by exploiting new  
27 primary production in early spring is still poorly documented because descriptions of seasonal  
28 variations of mesozooplankton standing stocks in oceanic Antarctic regions are scarce. The  
29 implementation of the Southern Ocean CPR survey delivers consistent information regarding  
30 the seasonal succession of zooplanktonic communities in the Southern Ocean south of  
31 Australia (Hosie et al, 2003; Hunt and Hosie, 2006 a and b). In the PF zone, a relatively  
32 strong increase in zooplankton abundance occurs in spring, from October-November (see  
33 Hosie et al, 2003, their Fig. 3), mainly due to changes in density of all common taxa from  
34 average winter levels still maintained until October (Hunt and Hosie, 2006 b). The largest  
35 copepods of the region (*Rhincalanus gigas*, *Calanoides acutus*, *Ctenocalanus citer*) are

1 seasonal migrators which arrive in the surface layer from winter diapause depths when Chl *a*  
2 concentrations increase (October - November). Overwintering females may spawn reserves  
3 even before the full bloom, whereas overwintering stages other than adult stages resume their  
4 growth in surface water up to mature adults which produce new cohorts during the full bloom  
5 period (Atkinson, 1998; Hunt and Hosie, 2006 b). Other smaller species (*Calanus similimus*,  
6 *Oithona* sp., etc.) resume their population development from survivors from the previous year  
7 and start reproduction earlier in spring (Atkinson, 1998). There is no historical CPR data  
8 around the Kerguelen Islands, but some pieces of the puzzle suggest similar patterns.  
9 Zooplankton distribution patterns observed by Semelkina (1993) during the SKALP cruises  
10 around the Kerguelen Islands (46–52°S, 64–73°E) from February 1997 to February 1998  
11 showed a change in biomass (4-fold higher) from winter (July-August) to mid-summer  
12 (February), but did not describe this early spring period. It is also worth noting that the  
13 seasonal zooplankton abundances recorded from February 1992 to January 1995 at the  
14 KERFIX station, located around 60 miles southwest of the Kerguelen Islands in 1700 m of  
15 water, show a major increase in copepod densities from September to January (Razouls et al.,  
16 1998).

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

26

## 27 **2 Material and methods**

### 28 **2.1 Study site and sampling strategy**

29 The KEOPS2 survey was performed east of the Kerguelen Islands in the Indian sector  
30 of the Southern Ocean, on board R.V. Marion Dufresne, between the 15<sup>th</sup> of October and the  
31 20<sup>th</sup> of November 2011. It firstly consisted of predefined stations along two transects (Fig. 1)  
32 the first oriented north-south between 46°50 S and 49°08 S, and subsequently referred to as  
33 TNS transect (Stations TNS1 to TNS10, blue dots in Fig. 1), and the second oriented east-  
34 west between 69°50 E and 74°60 E, referred to as TEW transect (Stations TEW1 to TEW8,  
35 green dots on Fig. 1). Along these two transects, zooplankton samples were collected once at

1 each station. The TEW transect crossed the Polar Front (PF) twice, first between TEW3 and  
2 TEW4 where the southern branch of the PF flows northwards along the shelf-break, and  
3 secondly between TEW6 and TEW7, where the PF is directed southwards after a semicircle  
4 trajectory maintaining a large stationary meander in this area. The most westerly stations were  
5 located over the inner (TEW1) and outer (TEW2) parts of the Kerguelen shelf. The most  
6 easterly stations (TEW7 and TEW8) were situated in Sub-Antarctic Mode Water whereas the  
7 central section (TEW4 to TEW6) within the stationary meander was covered by mixed  
8 Antarctic surface water (Farias et al., 2015; Trull et al., 2015).

9 In addition, intensive sampling (24 hours) was performed at 9 strategic stations (Fig. 1)  
10 located in the eastern bloom in the Polar Front zone (F-L station), in the north-eastern bloom  
11 (set of E stations), in the south-eastern bloom above the Kerguelen plateau (A3 station) and in  
12 the deep waters south west of the Kerguelen Islands considered as a HNLC reference station  
13 (R station). Station A3 (common with KEOPS1) was sampled twice during KEOPS2: at  
14 winter (A3-1) and spring stage (A3-2). The patterns of change over time of the northeastern  
15 bloom, located in a complex recirculation area inside the stationary meander of the Polar  
16 Front (Park et al., 2014; Zhou et al., 2014), was studied by a quasi-lagrangian survey  
17 including 5 stations (E1-E2-E3-E4E-E5).

18 Real time satellite images (chlorophyll and altimetry) in combination with trajectories  
19 of 50 drifters released during the first part of the cruise were used to carefully decide the  
20 positions of these 5 stations (Trull et al, 2015, their Fig. 2). In addition, we visited a  
21 productive station (E4W, red dot in Fig. 1) located in the plume of chlorophyll observed  
22 downstream of the plateau and close to the jet induced by the PF.

23

## 24 **2.2 Mesozooplankton sampling**

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

32 For each sampling station, two successive net hauls at each station were done: the first  
33 net haul was taken for the ZOOSCAN processing, taxonomy study and dry weight, and a  
34 second net haul was taken for isotopes. The cod-end contents of the first haul was kept fresh  
35 and split into two parts with a Motoda box (Motoda, 1959). The first part was preserved in 4%

1 borax-buffered formalin seawater for further laboratory study of zooplankton community  
2 structure (taxonomy, abundance and size structure) and biomass estimates from organism  
3 biovolume (see below). The second half of the sample was preserved for dry weight  
4 measurements. As many of the 120  $\mu\text{m}$  size nets were clogged with phytoplankton cells and  
5 aggregates, we could not finally use the sample for dry weight and ZOOSCAN processing.  
6 However we used the 120  $\mu\text{m}$  net samples for the isotope analysis (as described in the  
7 following paragraph). .

8

9 To prepare samples for isotope analysis, size fractions were obtained as follows.  
10 Samples from the second 330  $\mu\text{m}$  net haul at each station were passed sequentially through  
11 five sieves arranged in a column (2000, 1000, 500, 200, and 80  $\mu\text{m}$  meshes). The three largest  
12 sizes were then collected, and for the largest size (2000  $\mu\text{m}$ ) large organisms such as salps and  
13 euphausiids were separated into additional containers. To provide more material for the two  
14 smallest sizes (200, 80  $\mu\text{m}$ ), these materials were retained on the sieves and the contents of  
15 the 120  $\mu\text{m}$  net haul were passed through the entire set of 5 sieves (with the overlying 2000,  
16 1000, and 500  $\mu\text{m}$  sieves serving to block larger organisms and aggregates, but without those  
17 materials being collected). All samples were placed in small containers and immediately  
18 deep-frozen ( $-80\text{ }^{\circ}\text{C}$ ).

19

### 20 **2.3 Abundance and biomass using the Zooscan**

21 For each station, the cod end content of a 330  $\mu\text{m}$  mesh size net was processed using  
22 ZOOSCAN ([www.zooscan.com](http://www.zooscan.com)) to determine the zooplankton community size structure.  
23 ZOOSCAN has recently been used to study the zooplankton community in various areas and  
24 has been validated by comparisons with traditional sampling methods (Grosjean et al., 2004;  
25 Schultes and Lopes, 2009; Gorsky et al., 2010). Our ZOOSCAN setup is similar to the one  
26 described by Gorsky et al. (2010), and our sample processing protocol is fully presented in  
27 Nowaczyk et al. (2011), following the recommendations of Gorsky et al. (2010).

28 After homogenization, each sample was quantitatively split with a Motoda box once  
29 back in the laboratory and a fraction of each preserved sample containing a minimum of 1000  
30 particles (in general 1/32 or 1/64 of the whole sample) was placed on the glass plate of the  
31 ZOOSCAN. Organisms were carefully separated one by one manually with a long wooden  
32 needle, in order to avoid overlapping. Each image was then run through the ZooProcess plug-  
33 in using the image analysis software Image J (Grosjean et al., 2004; Gorsky et al., 2010).  
34 Several measurements of each organism were then computerized. Organism size is given by  
35 its equivalent circular diameter (ECD) and can then be converted into biovolume, assuming

1 each organism is an ellipsoid (more details in Grosjean et al., 2004). The lowest ECD  
2 detectable by this scanning device is 300  $\mu\text{m}$ . To discriminate between aggregates and  
3 organisms, we used a training set of about 1000 objects which were selected automatically  
4 from 40 different scans. This protocol allows discrimination between aggregates and  
5 organisms by building the initial training set of images. The biovolume (BV,  $\text{mm}^3$ ) was  
6 calculated from the organism image areas and morphometric parameters. In order to estimate  
7 the biomass of each organism, we used the same conversion as in Carlotti et al. (2008), each  
8 measured biovolume (BV,  $\text{mm}^3$ ) of a zooplankton individual was converted into biomass (W,  
9 in units of mg dry weight, DW) using the following relationship:  $\log(W) = 0.865 \log(BV) -$   
10  $0.887$  (Riandey et al., 2005). Carbon content was assumed to be 50% of body dry weight.

11 In this article, the terms ‘ZOOSCAN abundance’ and ‘ZOOSCAN biomass’ will  
12 designate the values derived from the laboratory ZOOSCAN processing. The abundance and  
13 biomass of organisms were then grouped into four size fractions (<500, 500–1000, 1000–  
14 2000, and > 2000  $\mu\text{m}$ ) based on their ECD, and summed to deliver the total abundance and  
15 biomass per sample over the upper 250 meters.

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

20

## 21 **2.4 Taxonomic determination**

22 Common taxa were counted with the binocular microscope for taxonomy. For the 330  
23  $\mu\text{m}$  mesh size net, around 600 organisms were counted from subsamples 1/32 or 1/64). For the  
24 120  $\mu\text{m}$  mesh size net around 400 organisms were counted from diluted samples (dilution  
25 from one to ten thousandths). The whole sample was examined for either rare species and/or  
26 large organisms (i.e. euphausiids, amphipods). Identification of the copepod community was  
27 done down to species level and groups of developmental stage when possible. Species/genus  
28 identification was done according to Rose (1933), Tregouboff and Rose (1957) and Razouls et  
29 al. (2005–2014). Organisms other than copepods as well as meroplankton were identified  
30 down to taxa levels. Identifications were done to genus level for copepods, amphipods,  
31 pelagic molluscs, polychaetes, Thaliacea and Cnidarians; and to taxa level for other major  
32 holoplanktonic and meroplanktonic groups. To identify which taxonomic groups contribute to  
33 the four size fractions defined from ZOOSCAN measurements done on the 330  $\mu\text{m}$  mesh net  
34 samples (see above), each observed organism was classified as small, medium, large or very  
35 large mesozooplankton, which approximately corresponds to the four size fractions



1 determined by ZOOSCAN (see above). Similarly, the organisms observed and counted from  
2 the 120 µm mesh size net samples were also classified into small and medium size fractions.  
3 Distribution in larger size fractions were not considered from the 120 µm mesh size net  
4 samples, the large organisms being undersampled.

5

## 6 **2.5 Biomass measurement**

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

12

## 13 **2.6 Stable isotope analysis**

14 Before processing, identification of the broad taxonomic composition of each sample  
15 preserved for isotopic measurements was performed under a binocular microscope. When  
16 possible, the main group of organisms in the largest >2000 µm size-fraction were sorted out  
17 and processed separately. Then, zooplankton fractions were freeze-dried and ground into a  
18 homogeneous powder. As they may contain carbonates, an acidification step was necessary to  
19 remove <sup>13</sup>C-enriched carbonates (DeNiro and Epstein, 1978; Sørensen et al. 2006). A  
20 subsample was acidified with 1% HCl, rinsed, dried and used for determination of δ<sup>13</sup>C  
21 values, while the other untreated subsample was used for determination of nitrogen isotopic  
22 composition. Three replicates were performed on each plankton fraction per sampled station  
23 for both δ<sup>13</sup>C and δ<sup>15</sup>N values. Stable isotope measurements were performed with a  
24 continuous-flow isotope-ratio mass spectrometer (Delta V Advantage, Thermo Scientific,  
25 Bremen, Germany) coupled to an elemental analyzer (Flash EA1112 Thermo Scientific,  
26 Milan, Italy). Results are expressed in parts per thousand (‰) relative to Vienna Pee Dee  
27 Belemnite and atmospheric N<sub>2</sub> for δ<sup>13</sup>C and δ<sup>15</sup>N, respectively, according to the equation: δX  
28 = [(R<sub>sample</sub>/R<sub>standard</sub>)-1] x 10<sup>3</sup>, where X is <sup>13</sup>C or <sup>15</sup>N and R is the isotope ratio <sup>13</sup>C/<sup>12</sup>C or  
29 <sup>15</sup>N/<sup>14</sup>N, respectively. Calibration was performed using certified reference materials (USGS-  
30 24, IAEA-CH6, -600 for carbon; IAEA-N2, -NO-3, -600 for nitrogen). Analytical precision  
31 based on repeated analyses of acetanilide (Thermo Scientific) used as an internal standard was  
32 <0.15‰. Percentage of organic C and organic N were obtained using the elemental analyzer  
33 and were used to calculate sample C/N ratios.

34 Lipids are depleted in δ<sup>13</sup>C relative to proteins and carbohydrates, and variation in lipid  
35 content between organisms can introduce considerable bias into carbon stable isotope

1 analyses (Bodin et al. 2007; Post et al. 2007). Like most polar marine organisms (Lee et al.  
2 2006), KEOPS2 zooplankton fractions could present a high lipid content (up to 20% dry  
3 mass, data not shown), reflected by high C/N values. Thus,  $\delta^{13}\text{C}$  acidified sample values of  
4 fractions  $>200\ \mu\text{m}$  were corrected according to the formula calculated by Post et al. (2007) for  
5 aquatic organisms, using the C/N ratio of each sample:  $\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{acidified}} - 3.32 +$   
6  $0.99 \times \text{C/N}$

7       Acidified  $\delta^{13}\text{C}$  values of the lowest size-fraction (80-200  $\mu\text{m}$ ) were not lipid corrected  
8 due to their low lipid content ( $<5\%$ , data not shown). The resulting  $\delta^{13}\text{C}_{\text{normalized}}$  provides an  
9 estimate of  $\delta^{13}\text{C}$  corrected for the effects of lipid concentration. Lipid correction calculated by  
10 Smyntek et al. (2007) for zooplankton give  $\delta^{13}\text{C}$  values  $0.63 \pm 0.01\text{‰}$  lower than those of  
11 Post et al. (2007). As  $\delta^{13}\text{C}$  values provided by Trull et al. (2015) were not lipid normalized,  
12 acidified  $\delta^{13}\text{C}$  values for all zooplankton size-fractions were indicated in Table 2, along with  
13 lipid normalized  $\delta^{13}\text{C}$  values, to allow comparisons between the two data sets.

14 To consider the relationships between zooplankton and phytoplankton, we used the groups of  
15 stations (T-Groups) defined by Trull et al. (2015) based on chemometric measurements of  
16 phytoplankton. The HNLC reference station R2 belonged to T-Group 1, along with station  
17 TEW4. Stations located on the plateau (A3 and E4) and in the eddy (E1 to E5) are included in  
18 T-Group 2 and T-Group 3, respectively. The two most easterly stations, located in the open  
19 ocean near the Polar Front (F-L and TEW8), belonged to T-Group 5. Trull's T-Group 4  
20 corresponded to coastal stations not sampled for zooplankton analysis.

21

## 22 **2.7 Data analysis**

23       The effect of stations and dates ( $n=12$ ) on zooplankton abundance and biomass was  
24 tested statistically using one-way ANOVA with the statistical software Statistica v7. The  
25 statistical significance was tested at the 95% confidence level. Community patterns for taxa  
26 abundance were explored using the Primer (V6) software package which has been shown to  
27 reveal patterns in zooplankton communities (e.g. Clarke and Warwick, 2001; Wishner et al.,  
28 2008). Data sets were power transformed (4th root), and the Bray–Curtis dissimilarity index  
29 between stations (Bray and Curtis, 1957) was calculated employing all taxonomic categories  
30 that contributed at least 1% to any sample in that dataset. Different groups of zooplankton  
31 (BC-Groups) were individualized based on their taxonomic composition. Mean C and N  
32 stable isotope values among size-fractions and between day and night within each fraction  
33 were compared by one-way ANOVAs followed by Tukey post-hoc tests, after testing for  
34 normality by Levene test.

35

## 1 **3 Results**

### 2 **3.1. Hydrology and trophic conditions**

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

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

28 The vertical depth stratification was variable over both space and time (see Trull et al,  
29 their table 4a). Station R2 presented a MLD around 117 m. At station A3, the water column  
30 was characterized by a deep mixed layer (around 150 m) during the pre-bloom (station A3-1)  
31 and early bloom (station A3-2) surveys, with a range of 120 to 171 m (Jouandet et al., 2014).  
32 The Chl *a* concentrations showed a fourfold increase from A3-1 (21 October) to A3-2 (15–17  
33 November), with Chl *a* concentrations at the surface increasing from 0.5 to 2 mg m<sup>-3</sup>  
34 (Jouandet et al., 2014, their Figs. 1 and 2). The mixed layer depth of the TNS stations south of  
35 the PF decreased northward from around 150 m (TNS10) to 100 m (except TNS6), with

1 accompanying chlorophyll *a* concentrations between 0.5 to 1.5 mg m<sup>-3</sup> (Lasbleisz et al., 2014,  
2 their Fig 3). During the following visits to the region within the recirculation system in the PF  
3 meander (square zoom in Fig 1), the MLD progressively decreased from 100 to 50 m  
4 (Stations E1, TEW4 to TEW5), and then below 50 m (stations TEW6, E2 to E5, - except E4  
5 decreasing slightly around 70 m) with similar chlorophyll *a* concentrations between 1.0 to 1.5  
6 mg m<sup>-3</sup> (Lasbleisz et al., 2014, their Fig 4). The highest chlorophyll *a* concentrations (values  
7 up to 4.7 mg m<sup>-3</sup>) were found in the 40 upper meters of the 100 m water column of the coastal  
8 stations (TEW1 and TEW2, Lasbleisz et al., 2014), whereas the TEW3 above the shelf break  
9 presented lower chlorophyll *a* concentrations (<1.0 mg m<sup>-3</sup>) in its 60 m mixed layer, possibly  
10 due to its proximity to the PF jet.

11 The sampled stations in the Subantarctic Mode Water presented very low chlorophyll *a*  
12 concentration in TNS2 (0.6 5 mg m<sup>-3</sup> in the upper 60 m), but much higher 10 days later, in  
13 TEW-7 and TEW-8 (average above 3 mg m<sup>-3</sup> in the upper 60 m, with peak concentrations up  
14 to 5.0 mg m<sup>-3</sup>; Lasbleisz et al., 2014, their Fig. 4).

15

### 16 **3.2 Temporal and spatial variations of zooplankton abundance and biomass**

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

24 Abundance values followed a normal distribution pattern with an average of 7310<sup>3</sup> ind  
25 m<sup>-2</sup> (SD: 42). ANOVA with main effects (stations and dates) without interaction showed clear  
26 effect for dates (p<0.05) but not for stations. All abundance values plotted against dates (Fig.  
27 4A) showed a general increase, and the linear regression (R<sup>2</sup> = 0.42, n = 37) predicted a ratio  
28 of 3.7 between abundance at the beginning and at the end of the survey. Highest abundance  
29 (above the regression line on Fig. 4A) was observed for oceanic stations within the PF  
30 meander, both for the stations of the two transects (Stations TNS4, 5, 7, 8, and TEW 4, 6, 7, 8,  
31 and stations E, except for E4-West). By contrast, the lowest abundance was found to the east  
32 and north of this PF meander, as well as for the first visit to A3. One exception was station  
33 TEW5 which presented the lowest abundance whereas nearby spatial and temporal sampling  
34 stations presented much higher abundance. Between the two visits to station A3 at the  
35 beginning and the end of the survey, the total abundance was multiplied by 3.5.

1 The fraction 500-1000  $\mu\text{m}$  (see Fig. 3) presented the most abundant number of  
2 organisms (62.0 % on average), followed by the < 500  $\mu\text{m}$  fraction (18.8 % on average), the  
3 1000-2000  $\mu\text{m}$  fraction (14.2 % on average) and the > 2000  $\mu\text{m}$  fraction (5.0 % on average).  
4 The contribution of the smaller size fraction (< 500  $\mu\text{m}$ ) increased with time from the  
5 beginning to the end of the survey (8.1 % on average), whereas the 500-1000  $\mu\text{m}$ , 1000-2000  
6  $\mu\text{m}$ , and > 2000  $\mu\text{m}$  decreased to 5.0 %, 0.8 % and 2.3 %, respectively. However, these  
7 temporal changes were not significant in any of the four regressions due to the variability in  
8 size distribution between the stations. In addition, no clear diurnal pattern was observed from  
9 the day/night samplings performed at 9 sampling dates.

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

26 The total zooplankton biomass values presented a significant correlation ( $p < 0.01$ ) with  
27 the average chlorophyll concentrations in the 100 upper meters, as well as with the integrated  
28 chlorophyll concentrations in the mixed layer depth (Fig. 5). Only stations TEW1 and TEW2  
29 presented low zooplankton biomass for relative high fluorescence concentrations (>1  $\mu\text{g Chl } a$   
30  $\text{l}^{-1}$ , Fig. 5A), but not versus the integrated Chl  $a$  biomass in their shallow (<80 m) mixed layer  
31 (Fig. 5B).

### 33 **3.3 Metazooplankton community composition and distribution**

34 From the 330  $\mu\text{m}$  mesh size net, 65 taxa were identified for the 37 stations of this study  
35 (Table 1) with 26 genera/species of copepods. Copepods contributed the bulk of the

1 zooplankton community abundance with 78.4 % (SD = 13.13 %) of the counted organisms  
2 over the whole area, and copepodites represented a little more than half of the counted  
3 copepods (mean=52.5 %, SD = 8.2 %). ANOVA with main effects (stations and dates)  
4 without interaction showed no effect either for dates or for stations, either for the percentage  
5 of copepods against the whole zooplankton abundance, or for the percentage of copepodites  
6 stages against the total copepods abundance. Nauplii represented an average 2 % of the total  
7 abundance, and showed an increasing abundance with time up to 4 %, although they were  
8 undersampled with our net. The copepod communities was dominated by *Ctenocalanus citer*,  
9 followed by *Oithona similis* and *O. frigida*, *Metridia lucens*, *Scolecithricella minor*, *Calanus*  
10 *simillimus*, *Paraeuchaeta* spp., *Rhincalanus gigas*, and near the coastal area *Drepanopus*  
11 *pectinatus*. Other dominant taxa were the different larval stages of euphausiids (eggs, nauplii,  
12 metanauplii, proto et metazoe), appendicularians (*Oikopleura* spp., *Fritillaria* spp.),  
13 chaetognaths, pteropods (*Limacina retroversa*), amphipods (*Themisto gaudicaudii*, *Hyperia*  
14 spp.). Radiolarians and foraminifera were regularly sampled as well. In some stations, other  
15 taxa occurred in low numbers, such as salps.

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

25 Comparison between the community compositions in the two nets clearly showed that  
26 some key groups were under-sampled in the 330 µm mesh net: mainly the larval stages of  
27 many copepods, small copepods such as *Oithona* sp. *Microsetella rosea*, *Oncaea* spp  
28 *Triconia* sp., *Microcalanus pygmaeus*, *Ctenocalanus citer*. The impact of 120 µm mesh size  
29 and clogging on the larger planktonic organisms was difficult to assess as many groups were  
30 in any case in low density in the 330 µm mesh size net, except for the copepods  
31 *Clausocalanus laticeps*, *Calanus simillimus* and *Calanoides acutus*.

32

33 The taxonomic distributions are presented in more detail for stations A3 (the two visits  
34 A3-1 and A3-2) and for stations E3 and E5 in Figure 6 for the four size fractions from the 330

1  $\mu\text{m}$  mesh size net sample, and only in the small and medium size fractions from the 120  $\mu\text{m}$   
2 mesh size net sample.

3 The distribution pattern from the 330  $\mu\text{m}$  mesh size net samples is first presented below.  
4 The zooplankton community structure in A3-1 was numerically dominated by the medium  
5 size fraction (nearly comparable to the fraction 500-1000  $\mu\text{m}$  in total abundance in Fig.2)  
6 comprising more than 50 % of copepods, characterized by the abundant cyclopoid *Oithona*  
7 *similis*, along with unspecified calanoid copepodites, and the harpacticoid *Microsetella rosea*.  
8 The rest of this fraction included metanauplii of euphausiids, appendicularians, ostracods and  
9 small chaetognaths. The fraction ‘large size’ mesozooplankton, similar to the 1000–2000  $\mu\text{m}$   
10 fraction counted with the ZOOSCAN and representing 10.7 % of the total abundance, was  
11 composed of 98 % copepods with some major taxa (*Ctenocalanus citer*, *Metridia lucens*,  
12 *Scolecithricella minor*, *Calanus simillimus*, *Scaphocalanus* spp., *Clausocalanus laticeps*),  
13 and early copepodites of *Paraeuchaeta* and of *Calanidae*. The highest size fraction was  
14 dominated for more than 75 % by *Rhincalanus gigas* and amphipods *Hyperia* spp. and  
15 *Themisto gaudicaudii*. It corresponds to the fraction  $>2000$   $\mu\text{m}$  from the ZOOSCAN which  
16 contributes to two thirds of the mesozooplankton biomass at station A3-1 (see Fig. 2). The  
17 lowest size fraction was mainly composed by euphausiid eggs and nauplii, copepod nauplii,  
18 small forms of the pteropod *Limacina retroversa* and in small densities foraminifera and  
19 radiolarians. As a whole, the mesozooplankton community in A3-1 was mainly composed by  
20 herbivorous species in all fractions, such as the copepods *R. gigas*, *C. citer*, *O. similis*, *M.*  
21 *rosea*, but also pteropod *L. retroversa*, appendicularians and different nauplii stages of  
22 copepods and euphausiids. In lowest densities, omnivores and detritivores (such as the  
23 copepods *M. lucens*, *S. minor*, *C. simillimus*) and carnivores (such as chaetognaths and  
24 amphipods, and the copepod *Paraeuchaeta*) were found.

25 During the second visit to station A3 (A3-2), the size distribution in abundance was  
26 dominated by fractions with ECD  $< 1000$   $\mu\text{m}$  (up to 83 % of the total abundance, see in Fig  
27 3). The taxa distribution in A3-2 differed from the first visit (station A3-1) both in the “small”  
28 size fractions by an increase in copepod nauplii and euphausiid eggs, and in the “medium”  
29 size fraction by a large proportion of appendicularians and early copepodid stages of  
30 copepods. The two largest fractions (“large” and “very large”) were not very different at A3-1  
31 and A3-2 in taxonomic composition and distribution (the only difference being the  
32 appearance of late larval stages of euphausiid in the “very large” fraction).

33 The major features in taxonomic changes between stations E3 (4<sup>th</sup> November) and E5  
34 (18<sup>th</sup> November) (Fig. 6) were the increasing contribution of calanoid copepodids in the  
35 medium and large size fractions, with the concomitant increase of contribution of these

1 fractions to the total abundance (see also Fig 2), and the increase of euphausiid larvae in the  
2 largest fraction. The smaller fraction presented a rather stable distribution of dominant taxa,  
3 with copepod nauplii and *Limacina* as dominant groups (Fig. 6). As a whole, while  
4 omnivores, carnivores and scavengers are present, the herbivorous component is strongly  
5 dominant with all these larval forms. It is of interest to note that the dominant species for the  
6 different fractions at E5 were quite similar to those at A3-1, but with the noticeable difference  
7 that many larval stages occurred in all size fractions, inducing the highest observed abundance  
8 during the survey (see Fig. 2), although finally representing a lower biomass (see Fig.3).

9 In the 120  $\mu\text{m}$  mesh size net samples, the taxonomic observation generally delivered the  
10 same dominant taxa in the medium size fraction as for the 330  $\mu\text{m}$  mesh size net, but with  
11 larger proportions of small copepodid forms and small adult copepods, such as *Oncoea* spp.  
12 and *Microsetella rosea*. Copepod nauplii and early copepodid contributed with high  
13 abundance (see Table 1) to the small size fraction.

14

15 To compare the taxonomic composition between all stations, a cluster dendrogram  
16 quantifying the compositional similarity of taxa distributions between the different stations  
17 was constructed from the Bray-Curtis coefficient using the 330  $\mu\text{m}$  mesh size net samples  
18 which presented the largest number of taxa. Figure 7 presents the cluster dendrogram and its  
19 associated 2D multidimensional scaling plot. This analysis showed a high degree of similarity  
20 across the whole region related to the initial phase of zooplankton development. The shelf  
21 stations presented the highest level of dissimilarity compared to the other stations.

22 The cluster dendrogram sliced at 80 % similarity distinguished two BC-groups : a first one  
23 (BC-Group 1, with more than 80 % similarity) grouping the oceanic stations within the PF  
24 meander and including eastern stations east of PF (F-L and TW7), and a second group of  
25 dispersed stations (BC-Group 2, with less than 80 % similarity – differences in day-night  
26 samplings not being considered in this analysis), including the R2 station on the western side  
27 of the Kerguelen plateau characterized by higher abundance of large calanoid copepods such  
28 as *Rhincalanus gigas* and *Paraeuchaeta* spp., the TEW1 and TEW2 stations, near the  
29 Kerguelen coast and dominated by *Drepanopus pectinatus* and bivalvia meroplanktonic  
30 larvae, the TNS1 and TNS2 stations in Sub-Antarctic Surface Water waters dominated by  
31 medium size cyclopoid and calanoids and larval forms of euphausiids, the A3 and TNS10  
32 stations in the southern part (see detail below), and stations TEW3, TEW5, TEW8, which  
33 were characterized by relative differences in very few taxa compared to other stations of the  
34 TEW transect (high density of *Metridida lucens* in TEW3, relatively lower density of  
35 *Ctenocalanus citer* in TEW5, and high density of *Triconia* sp. in TEW8).



### 1 3.4 Isotopic composition of size-fractionated zooplankton and within zooplankton taxa

2 A wide range of  $\delta^{13}\text{C}$  ( $>8\text{‰}$ ) and  $\delta^{15}\text{N}$  ( $>4\text{‰}$ ) values were recorded among zooplankton  
3 size-fractions and stations (Table 2). A slight general increase of  $\delta^{13}\text{C}$  with increasing size-  
4 fraction was observed, while the difference was not significant due to wide differences  
5 between sites ( $F = 1.818$ ,  $p = 0.132$ ) (Fig. 8-A). A significant increase in  $\delta^{15}\text{N}$  with increasing  
6 size was observed ( $F = 11.67$ ,  $p < 0.001$ ), particularly between the two smallest fractions (80-  
7 200  $\mu\text{m}$  and 200-500  $\mu\text{m}$ ) and the three largest ones (Fig. 8-B). However, no significant  
8 difference in mean  $\delta^{15}\text{N}$  was apparent between the 500-1000  $\mu\text{m}$  and  $>2000$   $\mu\text{m}$  fractions,  
9 while the 1000-2000  $\mu\text{m}$  fraction exhibited a slightly lower  $\delta^{15}\text{N}$  than the two others. Within  
10 each size-fraction, no difference was observed between mean day and night  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$   
11 values ( $p > 0.05$  for both), in spite of differences at site level (Table 2). Thus, for both  $\delta^{13}\text{C}$  and  
12  $\delta^{15}\text{N}$  values, the main difference occurred between the two smallest size classes ( $<500$   $\mu\text{m}$ )  
13 and the three largest ones ( $>500$   $\mu\text{m}$ ).

14 At the station level, mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values differed. Station R2 presented the  
15 lowest mean  $\delta^{13}\text{C}$  ( $-25.26\text{‰}$ ) and the highest mean  $\delta^{15}\text{N}$  ( $4.49\text{‰}$ ), while stations F-L, TEW-8  
16 and E4-E were characterized by the highest  $\delta^{13}\text{C}$  ( $>-21.2\text{‰}$ ) and rather high  $\delta^{15}\text{N}$  values  
17 ( $>4\text{‰}$ ). All the other stations exhibited mean  $\delta^{13}\text{C}$  values (from  $-23.26\text{‰}$  to  $-21.76\text{‰}$ ) and a  
18 wide range of mean  $\delta^{15}\text{N}$  values (from  $3.63\text{‰}$  to  $4.25\text{‰}$ ).

19 Differences in mean  $\delta^{15}\text{N}$  between small ( $<500$   $\mu\text{m}$ ) and large ( $>500$   $\mu\text{m}$ ) zooplankton  
20 size-fractions were low in T-Group 1 ( $0.3\text{‰}$ ), increased in T-Group 5 ( $0.6\text{‰}$ ) and were  
21 highest at most stations located in the eddy (Fig. 9). This trend suggested higher food overlap  
22 among size-fractions in zooplankton associated with phytoplankton T-Group 1 and T-Group  
23 5, and more partitioned food resources in phytoplankton T-Group 2 and T-Group 3, as  
24 indicated by a more even increase in  $\delta^{15}\text{N}$  with zooplankton size at these stations.

25 The smaller size-fraction (80-200  $\mu\text{m}$ ) was differently composed according to stations,  
26 being dominated either by diatoms (A3-2, E-4W), foraminifera (A3-1), small copepods (R2),  
27 or a mixture of these groups (most stations). Copepods, eggs, thecosome pteropods  
28 foraminifera and small aggregates contributed to 200-500  $\mu\text{m}$  fractions. The following size-  
29 fractions (500-1000  $\mu\text{m}$ , 1000-2000  $\mu\text{m}$  and  $>2000$   $\mu\text{m}$ ) were all dominated by copepods (60-  
30 95 %), but amphipods, euphausiids, appendicularians and chaetognaths increased in  
31 abundance from the 500-1000  $\mu\text{m}$  to the 1000-2000  $\mu\text{m}$  fractions. The largest size-fraction  
32 ( $>2000$   $\mu\text{m}$ ) was dominated by *Rhincalanus gigas* and euphausiid larvae or juveniles. Large  
33 chaetognaths completed this large fraction.

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

5 Groups of organisms individualized in the  $>2000 \mu\text{m}$  fraction presented highly different  
6 isotopic signatures according to their main feeding behaviours (Table 3). Filtering salps  
7 presented the lowest  $\delta^{15}\text{N}$  ( $<4\text{‰}$ ), the mostly herbivorous copepods, amphipods, euphausiids,  
8 and pteropods intermediate values (4 to 4.6‰), while predatory chaetognaths, fish larvae and  
9 polychaetes exhibited higher  $\delta^{15}\text{N}$  values ( $>5\text{‰}$ ). Thus,  $\delta^{15}\text{N}$  differences of the  $>2000 \mu\text{m}$   
10 fraction between stations resulted mainly from the relative contributions of these groups to  
11 bulk samples (ex: higher proportion of salps and euphausiids at A3-2, and large chaetognaths  
12 at E5). Accordingly, differences in  $\delta^{13}\text{C}$  values could be linked to difference in both size and  
13 composition of the ingested food. The lower  $\delta^{13}\text{C}$  recorded in gymnosomes and copepods  
14 suggested the consumption of small phytoplankton particles, while the higher  $\delta^{13}\text{C}$  of  
15 euphausiids suggested a consumption of larger-sized phytoplankton. Higher  $\delta^{13}\text{C}$  in  
16 euphausiids compared to copepods was also observed in Arctic seas (Schell et al., 1998).

## 17 18 **4. Discussion**

### 19 **4.1 Zooplankton development during the 2011 early spring bloom and comparison with** 20 **other seasons**

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

29 Such a response of zooplankton to an early phase of the northeastern Kerguelen bloom  
30 was observed during the Lagrangian survey within the stationary meander of the Polar Front  
31 (stations E1 to E5, except E4-W, Fig. 2, 3 and 4). The average integrated Chl *a* concentrations  
32 were rather low (0.49 to 0.77  $\mu\text{g Chl } a \text{ m}^{-3}$ ) for these E stations and but slightly higher than

1 the previous weeks - transects TNS and TEW- (Lasbleisz et al, 2014). The POC was constant  
2 in the surface layer up to the time of E3, with an average of  $83 \text{ mg C m}^{-3}$ , and then slightly  
3 increased at E4 and E5 (with an average up to  $109 \text{ mg C m}^{-3}$ ) (Lasbleisz et al, 2014).  
4 Zooplankton densities increased from  $60 \cdot 10^3 \text{ ind m}^{-2}$  (E1-d) to  $200 \cdot 10^3 \text{ ind m}^{-2}$  (E5-d) whereas  
5 biomass gradually decreased (excepted E4-E-n) from  $2.3 \text{ g C m}^{-2}$  (E1-d) to  $1.7 \text{ g C m}^{-2}$  (E5-n).  
6 Two processes may favor the shift towards smaller size classes. Firstly, the contribution of the  
7 larger size classes to biomass decreased with time (Fig. 3) due to the reduction of initial  
8 standing stock of overwintering zooplankton by mortality and by investment in egg  
9 production. The dominant overwintering copepods (*Ctenocalanus citer*, *Rhincalanus gigas*)  
10 are known to be strong seasonal migrants able to spawn in early spring even at low  
11 chlorophyll concentrations (Schnack-Schiel, 2001; Atkinson, 1998), i.e. before the full bloom  
12 conditions. Moreover, smaller copepod species and copepodids of large copepods may better  
13 exploit these low food concentrations (Atkinson et al., 1996), allowing individuals to develop  
14 and grow, whereas large copepods are food limited.

15 The response to chlorophyll increase in waters above the plateau (station A3 in Fig. 4C)  
16 was proportional in abundance and biomass (3-fold higher at A3-2 than at A3-1). Lasbleisz et  
17 al. (2014) mention that the Chl *a* increase at station A3-2 was accompanied by an increase of  
18 the Phaeo:Chl *a* ratio, reflecting a potential higher grazing activity. The mesozooplankton at  
19 A3-2 (see Fig. 6) presented a grazer community structure able to feed on a wide spectrum of  
20 cells from small diatoms to phytodetritus aggregates, as observed at this station (Lasbleisz et  
21 al., 2014; Laurenceau-Cornec et al., 2014), as well as small nano- / microzooplankton  
22 (Christaki et al., 2014) and carnivorous zooplankton. Compared to A3-1, the medium size  
23 and small size mesozooplankton fractions had a much larger contribution of microphagous  
24 organisms (appendicularians, copepod nauplii, etc.) which could quickly remove the smaller  
25 planktonic forms (below  $20 \mu\text{m}$ ). The larger zooplankton size fractions were a mixture of  
26 efficient grazers on large diatoms ( $> 20 \mu\text{m}$ ), omnivores and detritivores able to feed on  
27 aggregates, and carnivores consuming micro- and mesozooplankton.

28 The mesozooplankton biomass stocks observed at the beginning of the KEOPS2 cruise  
29 (Table 4) were around  $1.7 \text{ g C m}^{-2}$  above the plateau (A3) and  $1.2 \text{ g C m}^{-2}$  in oceanic waters  
30 (TNS transect). Oceanic biomass slightly increased during the cruise, except the biomass  
31 observed in the eastern bloom (station F-L) in the Polar Front Zone (above  $4 \text{ mg C m}^{-2}$ ), and  
32 station A3 also presented biomass around  $4 \text{ mg C m}^{-2}$  at the end of the survey. These different  
33 results during KEOPS2 suggest that the zooplankton community is able to respond to the  
34 growing phytoplankton blooms earlier on the plateau than in the oceanic waters, where

1 complex mesoscale circulation stimulates initial more or less ephemeral blooms before a  
2 broader bloom extension. Due to our constrained sampling for oceanic stations, it was not  
3 possible to determine whether the observed zooplankton biomass variability between oceanic  
4 stations was linked to enhanced local production (except for stations near the permanent Polar  
5 Front sustaining high level of production). Our results in the quasi-Lagrangian survey within  
6 the meander suggests that the heterogeneous primary production linked to oceanic mesoscale  
7 activity in the early bloom phase may stimulate the production of new zooplankton cohorts,  
8 without sustaining individual growth, slowing down the built-up of new zooplankton biomass.  
9 In addition, potential predation on mesozooplankton by euphausiid populations was expected,  
10 from observations of the increasing contribution of euphausiid larval stages in our bongo net  
11 samples (see Fig. 6) and of long faecal pellets in gel traps (Laurenceau-Cornec et al., 2014).

12 In contrast, stations F-L (Nov. 6<sup>th</sup>) and A3-2 (Nov. 16<sup>th</sup>) presented the highest biomass  
13 (maintained below 5 g C m<sup>-2</sup>) observed in November (Figs 4 and 5) and a similar ratio of  
14 abundance to biomass, around 20 10<sup>3</sup> ind per g C (Fig. 4C) and a lower contribution of  
15 smaller size-fractions (ESD < 1000 µm) to total biomass comparatively to station E5. These  
16 characteristics could be the results of a phytoplankton-sustained zooplankton development  
17 over the previous weeks.

18

## 19 **4.2 Comparison with previous results**

20 If we group our observations of KEOPS1 and KEOPS2 (Table 4), the zooplankton  
21 seems to continuously increase from mid-October to early February, with a ratio higher on  
22 shelf waters (abundance x20 and biomass x9) than in oceanic waters (abundance x3 and  
23 biomass x2.5). After early February, the zooplankton community structure remained rather  
24 stable (Carlotti et al., 2008). Over the whole spring to summer seasons, the small size  
25 fractions (< 500 µm and 500-1000 µm) significantly contribute to the increase in abundance  
26 (from 70 % to 85 %), with the production of calanoid copepod larval stages and large  
27 numbers of cyclopoid copepods, whereas the increase in biomass is mainly due to the fraction  
28 1000-2000 µm with calanoid copepod late larval stages (with a contribution doubling from  
29 spring to summer). The taxonomic composition did not show major differences between shelf  
30 and oceanic waters, except that the contribution of copepods to the whole mesozooplankton  
31 was higher in oceanic waters than on the shelf, and these taxonomic patterns were quite  
32 similar between the KEOPS 1 (see Fig. 7 in Carlotti et al. 2008) and KEOPS2 survey (Fig. 6).

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

20           In addition to the recent survey of the CPR data for the region (see in Introduction),  
21 which shows the strong development of mesozooplankton abundance in October-November,  
22 the overall results of KEOPS 1 and 2 in terms of seasonal changes in abundance and biomass  
23 values are highly consistent with the information provided by Semelkina (1993) and Razouls  
24 et al. (1996, 1998). During the SKALP cruises, all around the Kerguelen Islands (46–52°S,  
25 64–73°E), Semelkina (1993, her Table 1) observed an increase from 62  $10^3$  ind  $\text{m}^{-2}$  in July-  
26 August 1987 (average values between 0 and 200 m depth for the whole sampled area, nearly  
27 double from 0-1000 m) to 570  $10^3$  ind  $\text{m}^{-2}$  in February 1988 (values between 0 and 200 m,  
28 100  $10^3$  ind  $\text{m}^{-2}$  more in the layer 200-400 m). In terms of biomass, assuming a carbon  
29 content to be 50 % of body dry weight, the biomass increase in the upper 200 meters was  
30 from 2.2 g C  $\text{m}^{-2}$  to 19 g C  $\text{m}^{-2}$ . The sampled areas during the SKALP cruises covered a much  
31 larger area than that studied during KEOPS2, but these average values corresponded to those  
32 observed on eastern side of the Kerguelen Islands (see Semelkina 1993, her Fig. 2).  
33 Concerning the taxonomic composition of the mesozooplankton, this author mentioned no  
34 seasonal variations but differences in population development and distribution.

1 Razouls et al. (1998) presented the seasonal changes in copepod distributions at the  
2 KERFIX station, a fixed time-series station, situated 60 miles southwest of the Kerguelen  
3 Islands (50°40'S, 68°25'E), in 1700 m of water, characteristic of the Permanently Open Ocean  
4 Zone (POOZ). The copepod abundance sampled from vertical hauls (300 m – surface) ranged  
5 from less than 30 10<sup>3</sup> ind m<sup>-2</sup> in winter and 45 10<sup>3</sup> ind m<sup>-2</sup> in October up to 222 10<sup>3</sup> ind m<sup>-2</sup> in  
6 January. The nearest station during KEOPS1 and 2 was station R2 which presented biomasses  
7 (respectively abundance densities) of 10.7 g C m<sup>-2</sup> (272 10<sup>3</sup> ind m<sup>-2</sup>) in February 2005 and 4.5  
8 g C m<sup>-2</sup> (80 10<sup>3</sup> ind m<sup>-2</sup>) in November 2011. Abundances during KEOPS1 and 2 were largely  
9 dominated (> 80 %) by copepods (Carlotti et al., 2008, their Fig. 7; distribution not shown for  
10 KEOPS2). In addition, during a coastal annual survey in Morbihan Bay at the Kerguelen  
11 Islands, Razouls et al. (1996) found a ratio of 10 between winter and spring-summer  
12 mesozooplankton density (from 2 to 20 10<sup>3</sup> ind m<sup>-3</sup>) and a ratio of 20 for the corresponding  
13 biomass (from 20 to 400 mg DW m<sup>-3</sup>).

14

#### 15 **4.3 Effects of primary production on trophic pathways through mesozooplankton**

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

25

26 The comparison of the sinking particle composition at early and advanced stages of the  
27 bloom at station A3 (Laurenceau-Cornec et al., 2014 for KEOPS2; Ebersbasch et al., 2008 for  
28 KEOPS1) shows that early bloom stage is characterized with particles dominated by phyto-  
29 aggregates due to relatively weak grazing pressure on phytoplankton stocks, whereas faecal  
30 aggregates characterized the vertical matter flux as soon as zooplankton grazing affects  
31 substantially the phytoplankton stock.

32 The qualitative composition of the bloom had a direct impact in terms of species  
33 dominance (mostly herbivorous species) and biochemical composition of the zooplankton

1 organisms. The spatial differences observed in isotopic signatures of phytoplankton were  
2 tracked up to the higher zooplankton levels and showed the impact of the food source.

3 Differences in the isotopic ratios of zooplankton were observed between stations during  
4 the KEOPS2 survey. Station R2 exhibited a 2.2‰ lower  $\delta^{13}\text{C}$  than stations located on the  
5 plateau (A3) or in the eddy (E1 to E5), while  $\delta^{13}\text{C}$  of stations located in the open ocean (F-L)  
6 was increased by  $\sim 1.5\%$  compared to them. A similar increase in carbon isotopic signature  
7 was observed by Trull et al. (2015) for phytoplankton, with the lowest  $\delta^{13}\text{C}$  at the HNLC  
8 reference station (R2) and the highest at stations located in the open ocean downstream near  
9 the Polar Front (F-L, TEW8) (Fig. 10). The trophic relationship between mesozooplankton  
10 and phytoplankton (Trull et al. 2015) was evidenced by the significant positive correlation of  
11 their  $\delta^{13}\text{C}$  values ( $\delta^{13}\text{C}_{\text{Zooplankton}} = 0.745 \delta^{13}\text{C}_{\text{Phytoplankton}} - 5.465$ ,  $r = 0.85$ ,  $p < 0.001$ ). As shown  
12 on Fig. 10, mean  $\delta^{13}\text{C}$  values of zooplankton were related to those of phytoplankton,  
13 testifying to the consumption of phytoplankton by zooplankton at station level. The mean  
14 trophic fractionation factor from phytoplankton to zooplankton was  $0.40 \pm 0.71 \%$  for  $\delta^{13}\text{C}$   
15 and  $2.69 \pm 0.65 \%$  for  $\delta^{15}\text{N}$ . These values corresponded to a mean increase lower than one  
16 trophic level, if we apply the commonly used trophic fractionation factors (1 ‰ for  $\delta^{13}\text{C}$  and  
17 3.14 ‰ for  $\delta^{15}\text{N}$ ) that are in agreement with previous studies on zooplankton (Fry and  
18 Quinones, 1994). Such low values again indicated a dominance of herbivory among  
19 zooplankton organisms, which confirmed the conclusions based on zooplankton composition.

20 The mean increase in  $\delta^{15}\text{N}$  in small zooplankton size classes (from 80-200  $\mu\text{m}$  to 500-  
21 1000  $\mu\text{m}$ ) was higher than among larger size-fractions (from 500-1000  $\mu\text{m}$  to  $>2000 \mu\text{m}$ ) (1‰  
22 and 0.28‰ respectively). This lower increase in mean  $\delta^{15}\text{N}$  from 500-1000  $\mu\text{m}$  to  $>2000 \mu\text{m}$   
23 suggested a high food overlap among the three largest size-fractions, with a dominance of  
24 herbivorous organisms. Within the largest size fraction ( $>2000 \mu\text{m}$ ), an increase in trophic  
25 level ( $\delta^{15}\text{N}$ ) was observed from filtering (salps) and mostly herbivorous organisms (copepods,  
26 pteropods, etc.) to predatory carnivores (chaetognaths), as observed in other regions (Tarling  
27 et al., 2012; Banaru et al., 2014). While different feeding behaviours can be observed among  
28 euphausiids (Mauchline, 1980), most euphausiids collected during KEOPS2 survey were  
29 mainly herbivores or omnivores with a  $\delta^{15}\text{N}$  varying between 3.5‰ and 5.0‰ for individuals  
30  $>2000 \mu\text{m}$ , a range value already observed in the Southern Ocean (Gurney et al., 2001;  
31 Schmidt et al., 2003). High feeding overlap across size-fractionated zooplankton is reported in  
32 most studies (Fry and Quiñones, 1994; Bode et al., 2007) and may increase during food  
33 shortage (Tarling et al., 2012; Banaru et al., 2014). During KEOPS2, the highest food overlap  
34 among zooplankton size-fractions seemed to be associated with phytoplankton T-Group 1 and  
35 T-Group 5 in which small-sized cells dominated, while more partitioned food resources

1 among size-fractions seemed to occur in zooplankton associated with phytoplankton T-Group  
2 2 and T-Group 3, where large phytoplankton cells dominated (Trull et al., 2015). The direct  
3 comparison between stable isotope values of size-fractionated zooplankton and their  
4 abundance or biomass in water masses is difficult. Zooplankton isotopic values are firstly  
5 related to those of the phytoplankton they feed on, themselves linked to water characteristics  
6 and nutrient cycling (Trull et al., 2015). The stable isotope values recorded during the  
7 KEOPS2 survey suggest a general increase in herbivory in zooplankton during the bloom in  
8 accordance with the increase in the abundance of small-sized zooplankton, and corroborate  
9 the finding of Lasbleisz et al. (2015) based on the Phaeo : Chl *a* ratio.

10

## 11 **5 Conclusions**

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

23

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

32



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**Table 1:** List of zooplanktonic taxa collected and identified during the 2011 KEOPS2 cruise (average values for the 37 stations, in ind.m<sup>-3</sup>). Samples from the 330 µm (left) and 120 µm mesh size (right) nets.

	330 µm mesh size net			120 µm mesh size net		
	Adult forms	Copepodites stages	Nauplii stages	Adult forms	Copepodites stages	Nauplii stages
<b>Copepods</b>						
<i>Oithona similis</i>	8.1	}2.8		489.8	}1362.5	
<i>Oithona frigida</i>	14.8			71.5		
<i>Microsetella rosea</i>	1.9			79.0		
<i>Oncaea spp.</i>	1.3	0.1		58.2	53.6	
<i>Triconia sp.</i>	8.7			20.7	11.4	
<i>Clausocalanus laticeps</i>	3.9	0.8		1.5	0.1	
<i>Ctenocalanus citer</i>	35,8	56.5		47.8	195.7	
<i>Microcalanus pygmaeus</i>	0.7			23.2		
<i>Metridia lucens</i>	9.6	8.9		4.6	39.3	
<i>Calanus propinquus</i>	0.02					
<i>Calanus simillimus</i>	6.45	1.9		1.4	1.62	
<i>Calanoides acutus</i>	1.1	1.6		0.2	0.41	
<i>Scolecithricella minor</i>	9.2	6.4		10.1	8.4	
<i>Scaphocalanus spp.</i>	0.7	2.5				
<i>Drepanopus pectinatus</i>	0.6	2.7		1.4	13.7	
<i>Pleuromamma robusta</i>	0.9	0.2		0.4		
<i>Candacia maxima</i>	rare	rare				
<i>Heterorhabdus spp.</i>	rare	rare				
<i>Aetideus armatus</i>	rare	rare				
<i>Haloptilus oxycephalus</i>	rare	rare				
<i>Paraeuchaeta spp.</i>	0.54	14,29			14.1	
<i>Rhincalanus gigas</i>	2.93	7.34	3.1	1.1	7.9	26.63
<i>Subeucalanus longiceps</i>	0.14	0.02		0.4		
<i>Euchirella rostramagna</i>	rare	0.04			0.04	
<i>Gaetanus pungens</i>	rare					
<i>Undeuchaeta incisa</i>	rare					
Undetermined Nauplii			2.1			1071.7
Undetermined Copepodites		22.4			253.5	

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1 **Table 1:** (continued)

	330 µm mesh size net			120 µm mesh size net		
	Adult forms	Larval forms	Eggs	Adult forms	Larval forms	Eggs
<b>Euphausiids</b>						
Undetermined species	0.27	6.22	32.23		6.8	32.2
<b>Ostracods</b>	2.3			7.9		
<b>Isopods</b>	0.05					
<b>Mysid</b>		rare				
<b>Decapod</b>		rare				
<b>Amphipods</b>						
<i>Themisto gaudicaudii</i>	0.26					
<i>Hyperia</i> spp.	0.86					
<i>Primno macropa</i>	0.10					
<i>Vibilia</i> sp.	rare	0.04				
<i>Scina</i> sp.	rare					
<b>Molluscs</b>						
<i>Limacina retroversa</i>	3.45			33.2		
<i>Limacina helicina</i>	rare					
<i>Spongiobranchaea</i> sp.	rare					
<i>Clio</i> sp.	rare					
<b>Polychaetes</b>						
<i>Pelagobia</i> sp.	0.22					
<i>Tomopteris</i> spp.	rare					
<i>Travislopsis</i> sp.	rare					
Undetermined	rare	0.32		rare	9.28	
<b>Appendicularians</b>	8.45			149.1		
<b>Thaliacea</b>						
<i>Salpa thompsoni</i>	0.07					
Pyrosomid	rare					
<b>Ctenophores</b>	rare					
<b>Cnidarians</b>						
Undetermined larvae		rare			rare	
Undetermined adult	rare					
<i>Bougainvillia</i> sp.	rare					
<i>Dimophyes arctica</i>	rare					
<i>Pyrostephos vanhoeffeni</i>	rare					
<i>Rosacea plicata</i>	rare					
<i>Muggiaea bargmannae</i>	rare					
<i>Solmundella bitentaculata</i>	rare					
<i>Pegantha</i> sp.	rare					
<b>Chaetognaths</b>	4.15			5.7		
<b>Radiolarians</b>	0.93					
<b>Foraminifera</b>	0.98					
<b>Meroplankton</b>						
Cirripedia		rare				
Echinodermata		rare			11.4	
Fish		0.05	rare			
Mysid		rare				
Polychaeta		rare				
Bivalvia		rare				

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1 **Table 2.** Isotopic composition of size-fractionated zooplankton (mean and standard  
2 deviation). mean  $\delta^{13}\text{C}$ : values of acidified samples, mean  $\delta^{13}\text{C}$ -norm.: lipid-normalised  
3 values (except for the lowest size-fraction), mean  $\delta^{15}\text{N}$ : values of untreated samples.

Station	Fraction	mean $\delta^{13}\text{C}$	sd $\delta^{13}\text{C}$	mean $\delta^{13}\text{C}$ - norm.	sd $\delta^{13}\text{C}$ - norm.	mean $\delta^{15}\text{N}$	sd $\delta^{15}\text{N}$	C/N
Date	$\mu\text{m}$	$\text{‰PDB}$	$\text{‰PDB}$	$\text{‰PDB}$	$\text{‰PDB}$	$\text{‰air}$	$\text{‰air}$	mass
<b>A3-1 day</b> 20/10/2011	80	-25.52	0.10	-25.52	0.06	4.01	0.05	5.31
	200	-26.48	0.05	-24.00	0.08	4.89	0.12	5.85
	500	-26.20	0.05	-23.10	0.07	4.87	0.02	6.48
	1000	-24.52	0.14	-22.67	0.12	3.21	0.07	5.22
	2000	-25.16	0.03	-22.97	0.03	3.58	0.05	5.57
<b>TNS-7 day</b> 22/10/2011	80	-23.26	0.06	-23.26	0.07	3.45	0.09	4.55
	200	-25.18	0.03	-23.70	0.02	3.41	0.15	4.85
	500	-25.74	0.06	-23.29	2.00	4.29	0.04	5.82
	1000	-24.76	0.01	-23.03	0.00	4.21	0.06	5.10
	2000	-25.84	0.03	-23.21	0.06	4.60	0.22	6.01
<b>R-2 day</b> 26/10/2011	80	-27.93	0.02	-27.93	0.03	4.36	0.08	4.87
	200	-27.69	0.07	-25.84	0.10	4.97	0.03	5.23
	500	-27.11	0.06	-24.93	0.15	4.79	0.19	5.55
	1000	-26.43	0.10	-24.52	0.11	3.24	0.06	5.28
	2000	-26.15	0.06	-24.59	0.03	5.09	0.10	4.93
<b>E-1 night</b> 30/10/2011	80	-23.61	0.05	-23.61	0.06	3.62	0.23	4.70
	200	-25.37	0.04	-23.91	0.03	3.04	0.05	4.83
	500	-25.73	0.03	-23.26	0.03	3.67	0.03	5.85
	1000	-25.26	0.05	-22.80	0.05	3.58	0.01	5.84
	2000	-26.27	0.03	-22.75	0.08	4.69	0.32	6.91
<b>E-2 day</b> 01/11/2011	80	-24.62	0.04	-24.62	0.12	3.93	0.19	4.89
	200	-25.86	0.02	-23.48	0.09	3.83	0.03	5.75
	500	-25.70	0.04	-22.77	0.08	4.38	0.08	6.32
	1000	-25.54	0.02	-22.45	0.01	3.65	0.11	6.47
	2000	-26.12	0.02	-22.74	0.14	5.48	0.15	6.77
<b>TEW-4 day</b> 01/11/2011	80	-25.15	0.01	-25.15	0.05	4.06	0.11	4.67
	200	-25.98	0.01	-24.73	0.02	3.61	0.23	4.62
	500	-25.23	0.02	-23.39	0.02	3.24	0.06	5.21
	1000	-26.01	0.03	-21.98	0.04	3.50	0.07	7.42
	2000	-27.02	0.06	-21.52	0.04	5.23	0.03	8.90
<b>TEW-8 day</b> 02/11/2011	80	-22.58	0.05	-22.58	0.04	3.88	0.03	5.24
	200	-23.29	0.03	-21.00	0.04	3.90	0.03	5.67
	500	-23.73	0.04	-21.62	0.07	4.28	0.08	5.48
	1000	-23.60	0.07	-21.73	0.08	4.30	0.04	5.24
	2000	-23.29	0.05	-21.61	0.05	3.78	0.02	5.05
<b>E-3 night</b> 03/11/2011	80	-24.70	0.02	-24.70	0.03	3.02	0.13	4.84
	200	-25.79	0.02	-23.52	0.03	3.50	0.04	5.65
	500	-25.60	0.02	-23.24	0.03	4.14	0.07	5.74
	1000	-25.67	0.03	-22.63	0.11	3.67	0.02	6.42
	2000	-25.62	0.04	-23.20	0.03	4.58	0.35	5.79
<b>E-3 day</b> 04/11/2011	80	-24.82	0.04	-24.82	0.07	2.98	0.10	4.71
	200	-25.99	0.02	-23.51	0.05	3.58	0.06	5.85
	500	-26.26	0.02	-22.79	0.05	3.90	0.04	6.86
	1000	-25.57	0.03	-22.41	0.03	3.68	0.06	6.54
	2000	-26.71	0.03	-22.19	0.06	5.23	0.48	7.92

<b>FL day</b>	80	-23.69	0.03	<b>-23.69</b>	0.05	<b>3.66</b>	0.09	<b>5.87</b>
06/11/2011	200	-24.06	0.01	<b>-21.42</b>	0.06	<b>4.20</b>	0.10	<b>6.02</b>
	500	-24.59	0.03	<b>-21.62</b>	0.14	<b>5.08</b>	0.08	<b>6.35</b>
	1000	-24.31	0.03	<b>-21.58</b>	0.07	<b>4.44</b>	0.10	<b>6.11</b>
	2000	-24.64	0.01	<b>-21.48</b>	0.04	<b>5.00</b>	0.17	<b>6.55</b>
<b>FL night</b>	80	-21.77	0.02	<b>-21.77</b>	0.01	<b>4.06</b>	0.10	<b>4.80</b>
06/11/2011	200	-23.41	0.03	<b>-20.96</b>	0.03	<b>3.54</b>	0.03	<b>5.83</b>
	500	-24.67	0.08	<b>-21.01</b>	0.12	<b>4.41</b>	0.09	<b>7.05</b>
	1000	-23.75	0.05	<b>-21.58</b>	0.06	<b>4.06</b>	0.05	<b>5.54</b>
	2000	-22.38	0.01	<b>-21.53</b>	0.02	<b>3.61</b>	0.06	<b>4.21</b>
<b>E-4W day</b>	80	-23.26	0.08	<b>-23.26</b>	0.02	<b>3.17</b>	0.12	<b>5.14</b>
11/11/2011	200	-24.66	0.05	<b>-22.93</b>	0.05	<b>3.43</b>	0.11	<b>5.10</b>
	500	-25.05	0.02	<b>-22.70</b>	0.02	<b>3.85</b>	0.07	<b>5.73</b>
	1000	-24.21	0.02	<b>-22.31</b>	0.08	<b>3.97</b>	0.08	<b>5.28</b>
	2000	-25.01	0.02	<b>-21.38</b>	0.01	<b>4.64</b>	0.17	<b>7.53</b>
<b>E-4W night</b>	80	-23.24	0.03	<b>-23.24</b>	0.05	<b>2.97</b>	0.29	<b>4.72</b>
11/11/2011	200	-24.83	0.07	<b>-23.10</b>	0.13	<b>3.33</b>	0.06	<b>5.09</b>
	500	-25.30	0.06	<b>-22.81</b>	0.06	<b>3.94</b>	0.02	<b>5.86</b>
	1000	-24.83	0.07	<b>-22.52</b>	0.04	<b>3.91</b>	0.04	<b>5.68</b>
	2000	-24.92	0.06	<b>-22.10</b>	0.07	<b>3.85</b>	0.12	<b>6.20</b>
<b>E-4E night</b>	80	-23.47	0.04	<b>-23.47</b>	0.04	<b>2.42</b>	0.14	<b>5.14</b>
12/11/2011	200	-25.24	0.04	<b>-22.59</b>	0.10	<b>3.77</b>	0.06	<b>6.03</b>
	500	-26.07	0.04	<b>-19.61</b>	0.06	<b>4.72</b>	0.14	<b>9.88</b>
	1000	-26.02	0.07	<b>-18.92</b>	0.45	<b>4.82</b>	0.20	<b>10.53</b>
	2000	-27.12	0.11	<b>-17.64</b>	0.26	<b>4.76</b>	0.59	<b>12.93</b>
<b>E-4E day</b>	80	-23.65	0.02	<b>-23.65</b>	0.03	<b>3.17</b>	0.52	<b>5.53</b>
13/11/2011	200	-25.32	0.06	<b>-21.90</b>	0.11	<b>4.02</b>	0.15	<b>6.81</b>
	500	-25.97	0.02	<b>-20.81</b>	0.17	<b>4.40</b>	0.08	<b>8.56</b>
	1000	-25.38	0.08	<b>-21.06</b>	0.21	<b>4.63</b>	0.08	<b>7.72</b>
	2000	-25.76	0.11	<b>-22.67</b>	0.09	<b>3.96</b>	0.49	<b>6.48</b>
<b>A3-2 day</b>	80	-22.82	0.09	<b>-22.82</b>	0.22	<b>1.71</b>	0.17	<b>4.49</b>
16/11/2011	200	-23.58	0.02	<b>-22.42</b>	0.05	<b>3.89</b>	0.02	<b>4.53</b>
	500	-24.19	0.04	<b>-22.38</b>	0.15	<b>5.45</b>	0.16	<b>5.19</b>
	1000	-23.44	0.05	<b>-21.91</b>	0.04	<b>4.66</b>	0.07	<b>4.89</b>
	2000	-23.09	0.04	<b>-21.42</b>	0.07	<b>3.71</b>	0.20	<b>5.04</b>
<b>A3-2 night</b>	80	-22.42	0.02	<b>-22.42</b>	0.06	<b>2.43</b>	0.09	<b>4.44</b>
16/11/2011	200	-23.47	0.04	<b>-22.31</b>	0.09	<b>3.98</b>	0.16	<b>4.53</b>
	500	-23.98	0.05	<b>-22.33</b>	0.16	<b>4.90</b>	0.06	<b>5.02</b>
	1000	-24.99	0.04	<b>-20.38</b>	0.10	<b>5.04</b>	0.04	<b>8.01</b>
	2000	-23.22	0.05	<b>-21.46</b>	0.04	<b>4.11</b>	0.06	<b>5.13</b>
<b>E-5 day</b>	80	-25.88	0.06	<b>-25.88</b>	0.09	<b>2.45</b>	0.01	<b>3.71</b>
18/11/2011	200	-26.64	0.36	<b>-23.91</b>	0.30	<b>3.10</b>	0.22	<b>6.11</b>
	500	-26.01	0.03	<b>-23.04</b>	0.04	<b>3.24</b>	0.17	<b>6.35</b>
	1000	-25.89	0.05	<b>-23.00</b>	0.09	<b>3.30</b>	0.02	<b>6.27</b>
	2000	-27.74	0.01	<b>-21.59</b>	0.20	<b>6.19</b>	0.14	<b>9.56</b>
<b>E-5 night</b>	80	-26.18	0.03	<b>-26.18</b>	0.07	<b>2.87</b>	0.27	<b>6.01</b>
19/11/2011	200	-25.90	0.02	<b>-22.64</b>	0.05	<b>3.45</b>	0.09	<b>6.64</b>
	500	-26.07	0.01	<b>-22.54</b>	0.04	<b>3.61</b>	0.02	<b>6.92</b>
	1000	-25.90	0.04	<b>-22.71</b>	0.09	<b>3.76</b>	0.05	<b>6.58</b>
	2000	-27.39	0.02	<b>-22.83</b>	0.10	<b>4.37</b>	0.38	<b>7.97</b>

1 **Table 3.** Mean ( $\pm$  SD) stable isotope values of the main groups of organisms sorted in the  
2 largest size fraction ( $>2000 \mu\text{m}$ ). n = number of samples analysed.

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

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1 **Table 4:** Seasonal variations of zooplankton abundance and biomass from KEOPS2 (15  
2 October – 20 November 2011) and KEOPS1 (January 19- February 13, 2005) surveys with  
3 contribution of different size fractions (<500 µm, 500-1000 µm; 1000-2000 µm; > 2000 µm).  
4 The reference stations were A3 (shelf waters) and C11 (oceanic waters) for KEOPS1 (see  
5 Carlotti et al., 2008, their Figs. 3 and 5), and A3 (shelf waters) and TNS6-TNS5 and E4E-E5  
6 (oceanic waters) for KEOPS2.

Area	Date		KEOPS 2		KEOPS 1		
			20 -22/10	13-16/11	22-28/1	4-5/2	12/2
Shelf waters	<b>Abundance</b>	<b>X 10<sup>6</sup> m<sup>-2</sup></b>	<b>26</b>	<b>90</b>	<b>600</b>	<b>700</b>	<b>450</b>
	Percentages of total abundance	< 500 µm	10 %	34 %	55%	46 %	41 %
		500-1000 µm	60 %	50 %	32 %	35 %	44 %
		1000-2000 µm	23 %	13 %	12 %	18 %	13.5 %
		>2000 µm	7 %	3 %	1 %	< 1 %	1.5 %
	<b>Biomass</b>	<b>g C m<sup>-2</sup></b>	<b>1,7</b>	<b>4</b>	<b>10</b>	<b>15</b>	<b>9</b>
	Percentages of total biomass	< 500 µm	<1 %	4 %	7.5 %	5 %	7 %
		500-1000 µm	12 %	17 %	21.5%	23%	26%
		1000-2000 µm	23 %	28 %	45 %	59%	46 %
		2000 µm	64 %	51 %	26 %	12%	21 %
Oceanic waters	<b>Abundance</b>	<b>X 10<sup>6</sup> m<sup>-2</sup></b>	<b>70</b>	<b>150</b>	<b>200</b>	<b>100</b>	<b>-</b>
	Percentages of total abundance	< 500 µm	18 %	15 %	50 %	47 %	-
		500-1000 µm	66 %	65 %	40 %	41 %	-
		1000-2000 µm	12 %	15 %	10 %	10 %	-
		>2000 µm	4 %	5 %	< 1 %	2 %	-
	<b>Biomass</b>	<b>g C m<sup>-2</sup></b>	<b>1,2</b>	<b>2</b>	<b>4</b>	<b>3</b>	<b>-</b>
	Percentages of total biomass	< 500 µm	1 %	2 %	10 %	5 %	-
		500-1000 µm	16 %	16 %	35 %	25%	-
		1000-2000 µm	18 %	24 %	40 %	40 %	-
		2000 µm	65%	58 %	15 %	30 %	-

7

1 **Figures**

2

3 **Figure 1:** Map of the KEOPS2 study area and station locations. The locations of the stations  
4 are marked by color dots. The southern station A3 (red dot) was visited twice at the beginning  
5 (station A3-1) and the end (station A3-2) of the KEOPS2 survey. This station A3 situated in  
6 the middle of the shelf was the reference station for the shelf bloom observed during KEOP1.  
7 The stations of the North-South transect in blue dots are located in oceanic waters and were  
8 sampled just after the first visit to A3, from south to north (stations TNS1 to TNS10), from  
9 the central plateau (TNS-10) across the recirculation feature (TNS7 to TNS3) and Polar Front  
10 (TNS3-TNS2) and into sub-antarctic waters (TNS-1). Station R-2 (black dot) in the west of  
11 the Kerguelen plateau represented a HNLC reference station. The transect TEW (transect  
12 east–west) was sampled from west to east from the near coast of Kerguelen Island (TEW1)  
13 above the shelf (TEW32) and shelf break (TEW3) across the middle of the recirculation  
14 system (TEW4 to TEW6), and beyond the southward meandering Polar Front (TEW7 and  
15 TEW8) in the extreme east of the study region. The survey ended with a quasi-Lagrangian  
16 time series (stations E1–E5 in orange dots in the zoom panel), during a progressive phase of  
17 the bloom within the recirculation system in the meander of the Polar Front. In addition, one  
18 station (Station F-L) situated in high-biomass waters in the extreme northeast of the study  
19 region, near the downstream location of the PF, was sampled within the period of the time  
20 series.

21

22 **Figure 2:** Integrated 0–200 m mesozooplankton abundance counted from ZOOSCAN for the  
23 different stations sampled during KEOPS2 with size fraction distributions. Size fractions:  
24 <500  $\mu\text{m}$ : black; 500–1000  $\mu\text{m}$ : dark gray; 1000–2000  $\mu\text{m}$ : light gray; >2000  $\mu\text{m}$ : white.

25

26 **Figure 3:** Integrated 0–200 m mesozooplankton biomass estimated from ZOOSCAN for the  
27 different stations sampled during KEOPS2 with size fraction distributions. Size fractions:  
28 <500  $\mu\text{m}$ : black; 500–1000  $\mu\text{m}$ : dark gray; 1000–2000  $\mu\text{m}$ : light gray; >2000  $\mu\text{m}$ : white.

29

30 **Figure 4. (a)** Abundance and **(b)** biomass values and **(c)** ratio abundance on biomass for the  
31 different stations visited during KEOPS2 over sampling dates.

32 Abundance and biomass values from Figures 2 and 3.

33

1 **Figure 5.** Zooplankton biomass values against average Chl *a* in the upper 100 m (a) and  
2 against the integrated Chl *a* in the mixed layer depth (b) for the different stations visited  
3 during KEOPS2. Biomass values from Figure 3.

4

5 **Figure 6.** Distributions of main taxa abundance at stations A3-1, A3-2, E3 and E5 from  
6 binocular observation. Distributions are presented from left to right for the four stations, and  
7 from top to bottom for the four size fractions (four upper bands: small, medium, large, and  
8 very large) observed in the 330  $\mu\text{m}$  mesh size net samples, and for the two lower size  
9 fractions (two lower upper bands: small and medium) for the 120  $\mu\text{m}$  mesh size net samples.  
10 Distributions are average values between day and night samples. For each size fraction (the  
11 four pie charts on the same horizontal band), the color labels for the different taxa are similar.

12

13 **Figure 7.** Dendrogram (A) and MDS plot (B) produced by the clustering of the 37 samples  
14 (28 stations, among them 9 stations with day-night sampling) during KEOPS2 based on the  
15 density ( $\text{ind m}^{-3}$ ) of mesozooplankton taxa. Density values were fourth-root transformed prior  
16 to analysis of the Bray-Curtis similarity matrix. The stress statistic for the MDS plot is 0.12.

17

18 **Figure 8:** Distribution of  $\delta^{13}\text{C}$  (A) and  $\delta^{15}\text{N}$  (B) of zooplankton across size-fractions during  
19 KEOPS2. White symbols = day; Black symbols = night.

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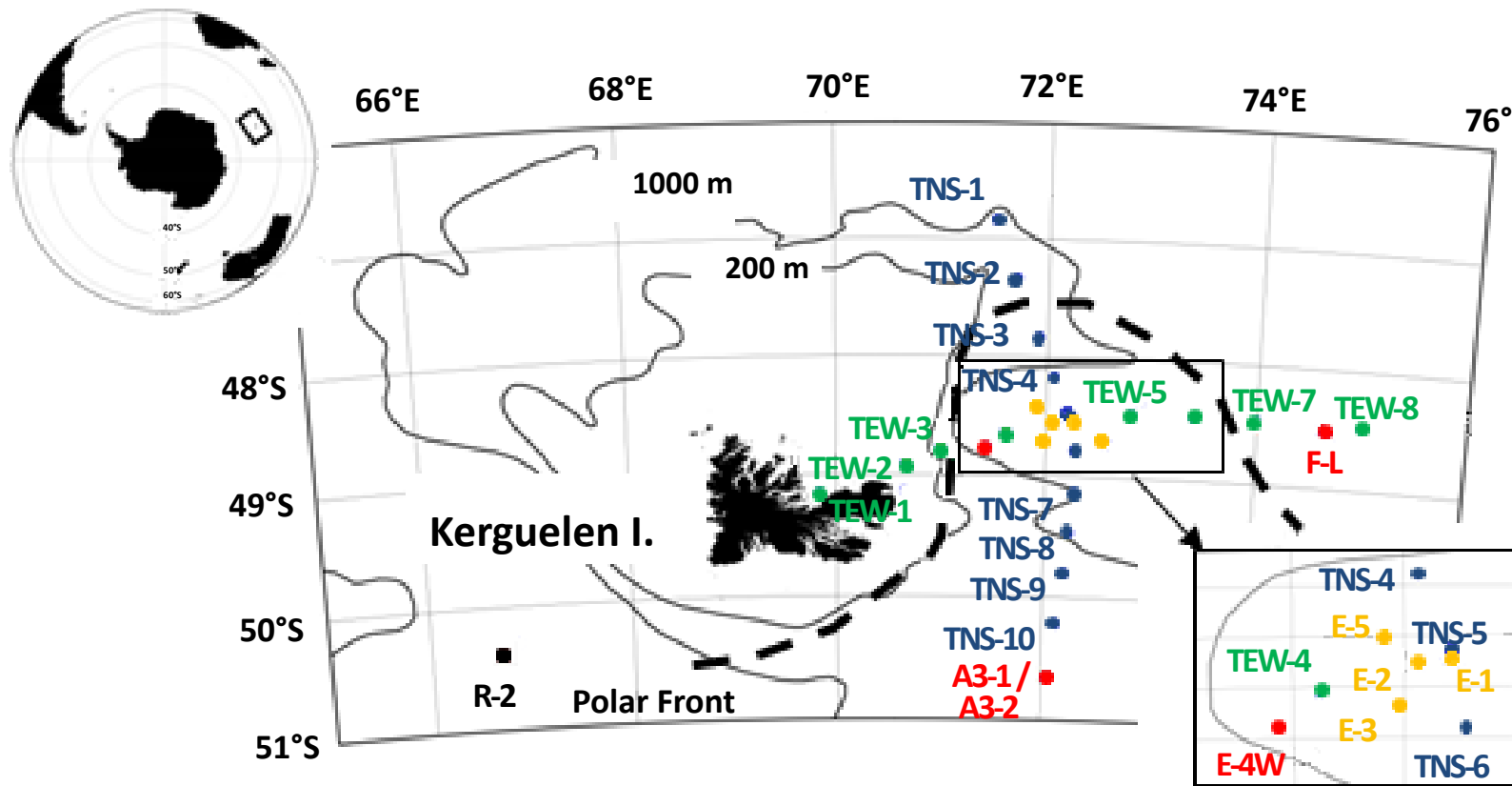
21 **Figure 9:** Distribution of  $\delta^{13}\text{C}$  (left column, a) and  $\delta^{15}\text{N}$  (right column, b) values across  
22 zooplankton size-fractions for 4 of the 5 T-Groups of stations identified by Trull et al (2015)  
23 for phytoplankton. Station E4-E is included here in T-Group 5 instead of T-Group 2. From top  
24 to bottom: a1 and b1 = T-Group 1 (diamond), a2 and b2 = T-Group 2 (triangle), a3 and b3 =  
25 T-Group 3 (dot), a4 and b4 = T-Group 5 (square). T-Group 4 included coastal stations not  
26 sampled for zooplankton analysis.

27

28 **Figure 10:** Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of phytoplankton (5-210  $\mu\text{m}$ ) (Trull et al. 2015) and  
29 zooplankton (200->2000  $\mu\text{m}$ ) (present study) for stations sampled during KEOPS2 cruise.  
30 Symbols correspond to the phytoplankton groups based on chemometric measurements  
31 identified by Trull et al. (2015). Diamond = T-Group 1; Triangle = T-Group 2; Dot = T-Group  
32 3; Square = T-Group 5.

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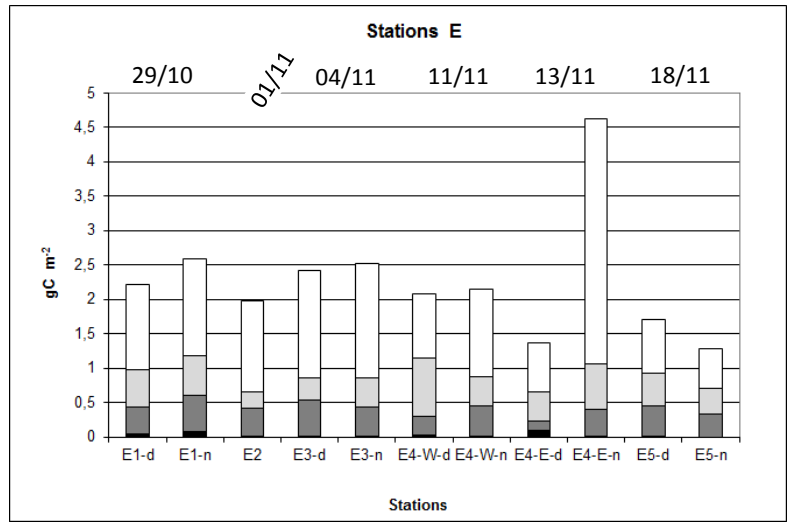
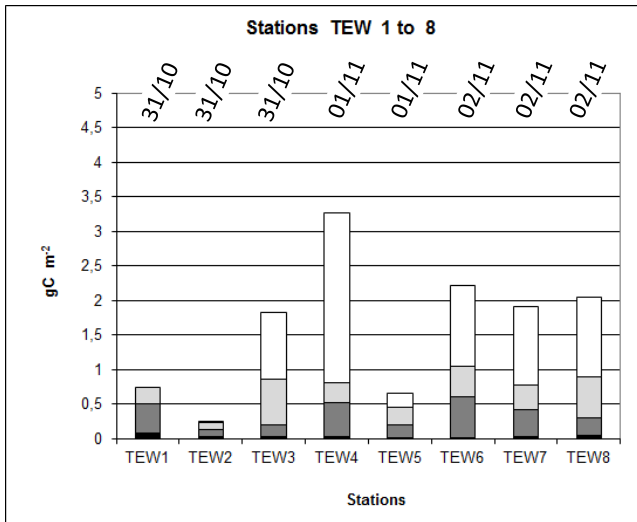
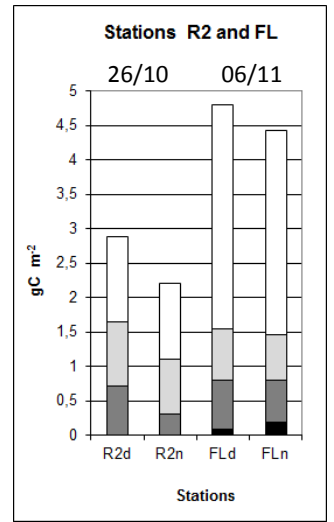
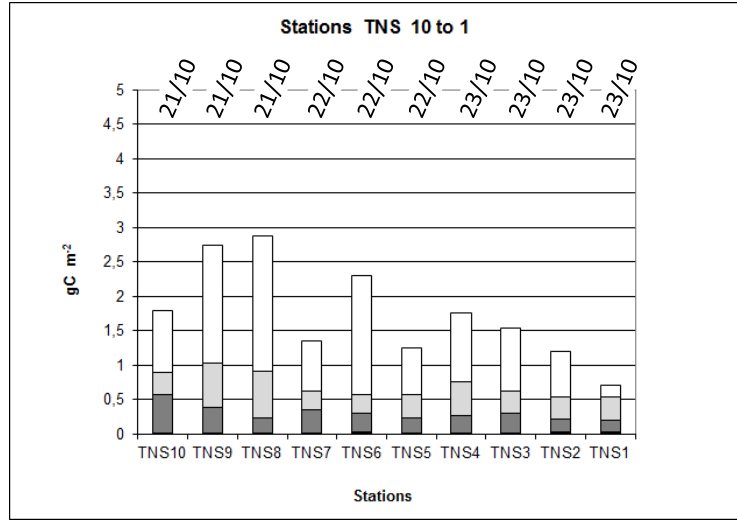
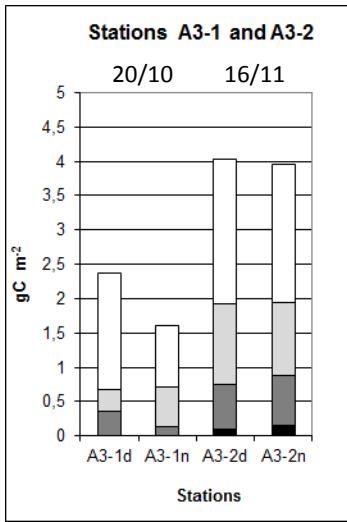
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2 **Figure 1**



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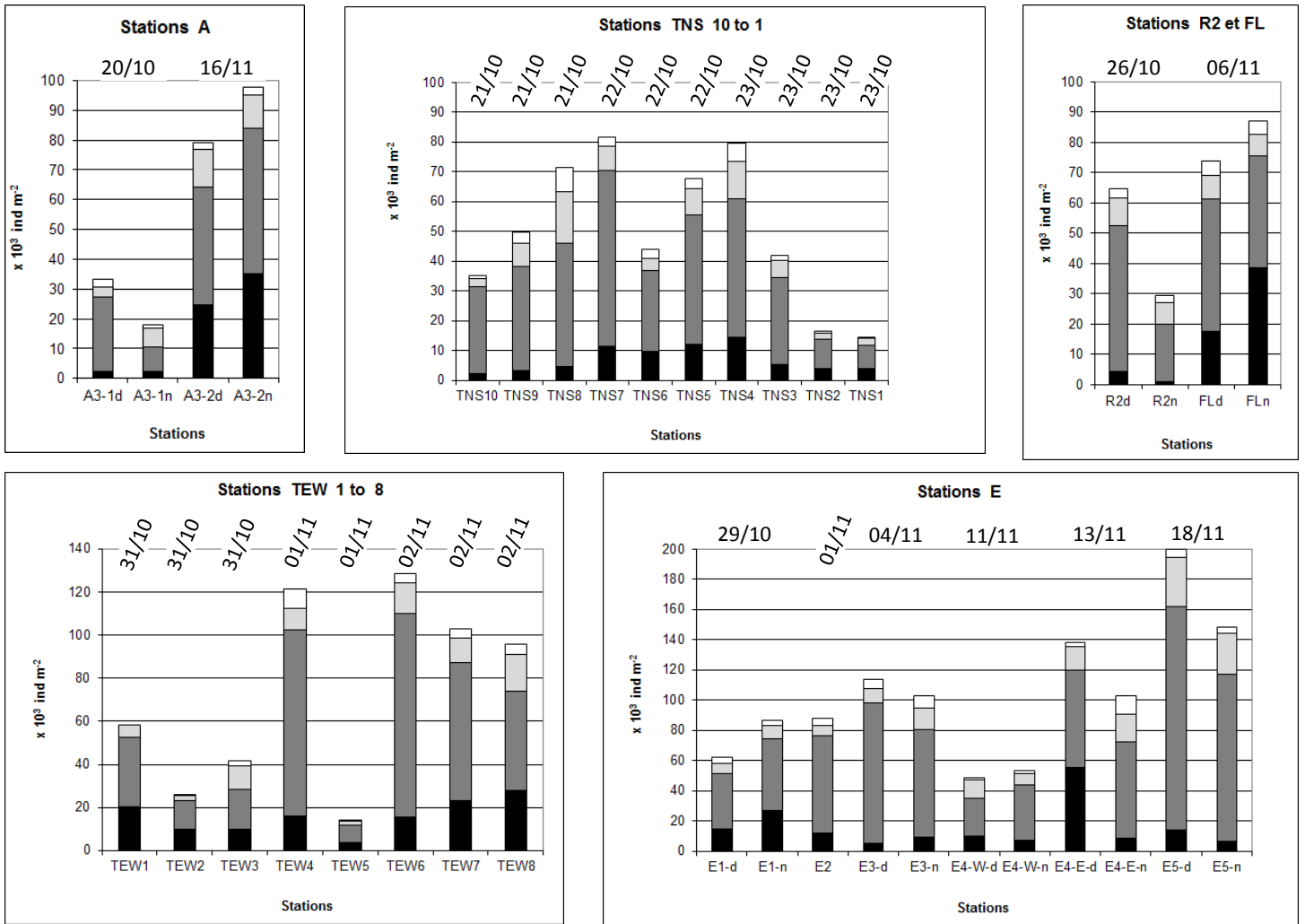


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2 **Figure 2**



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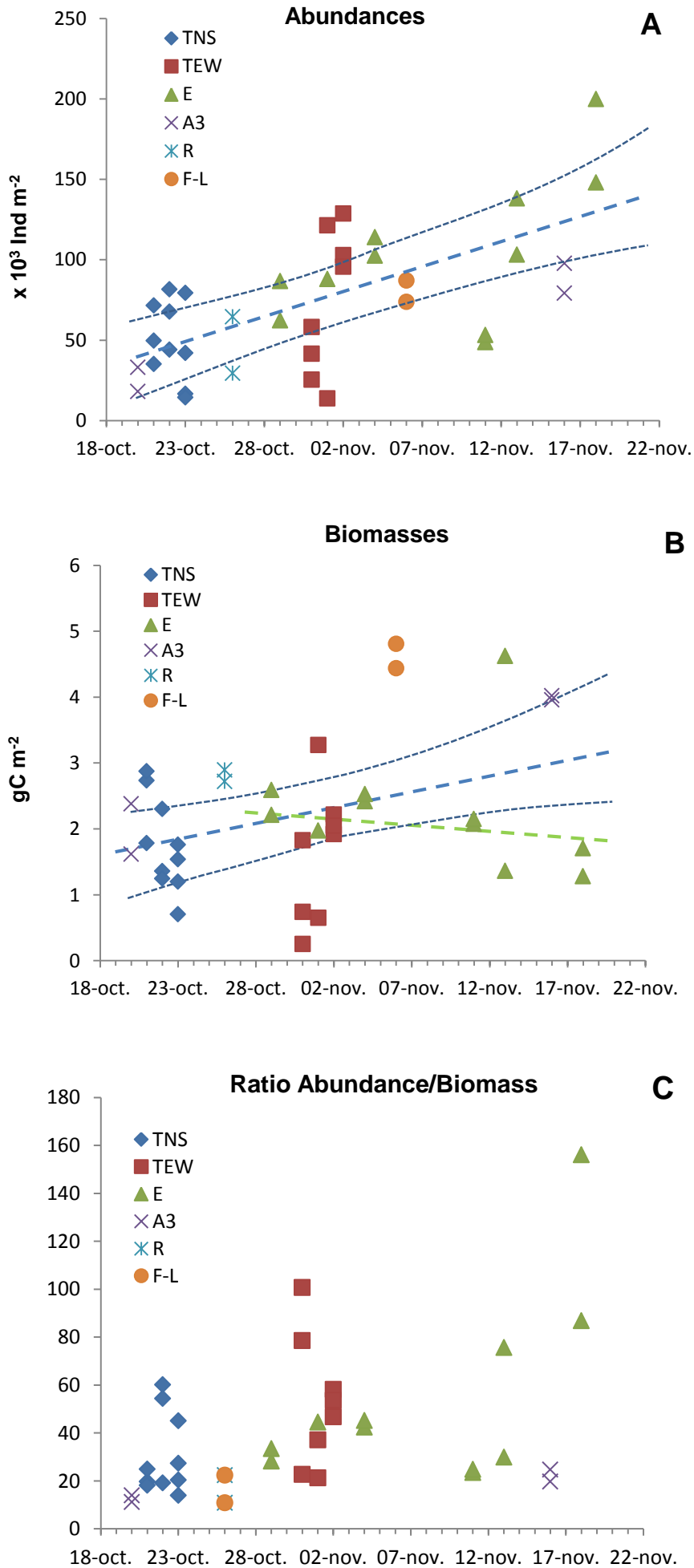
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2 **Figure 3**



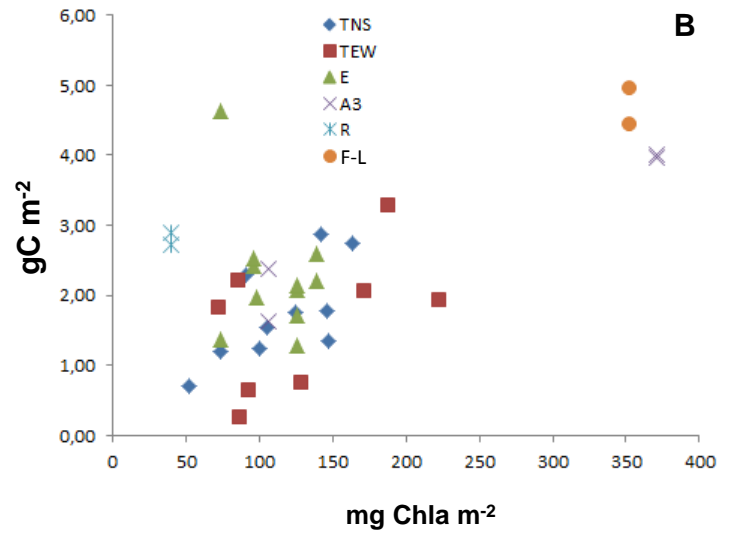
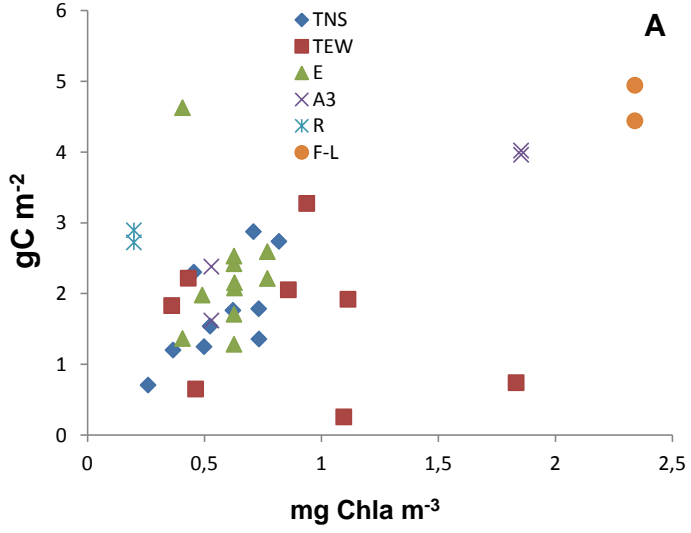
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Figure 4:



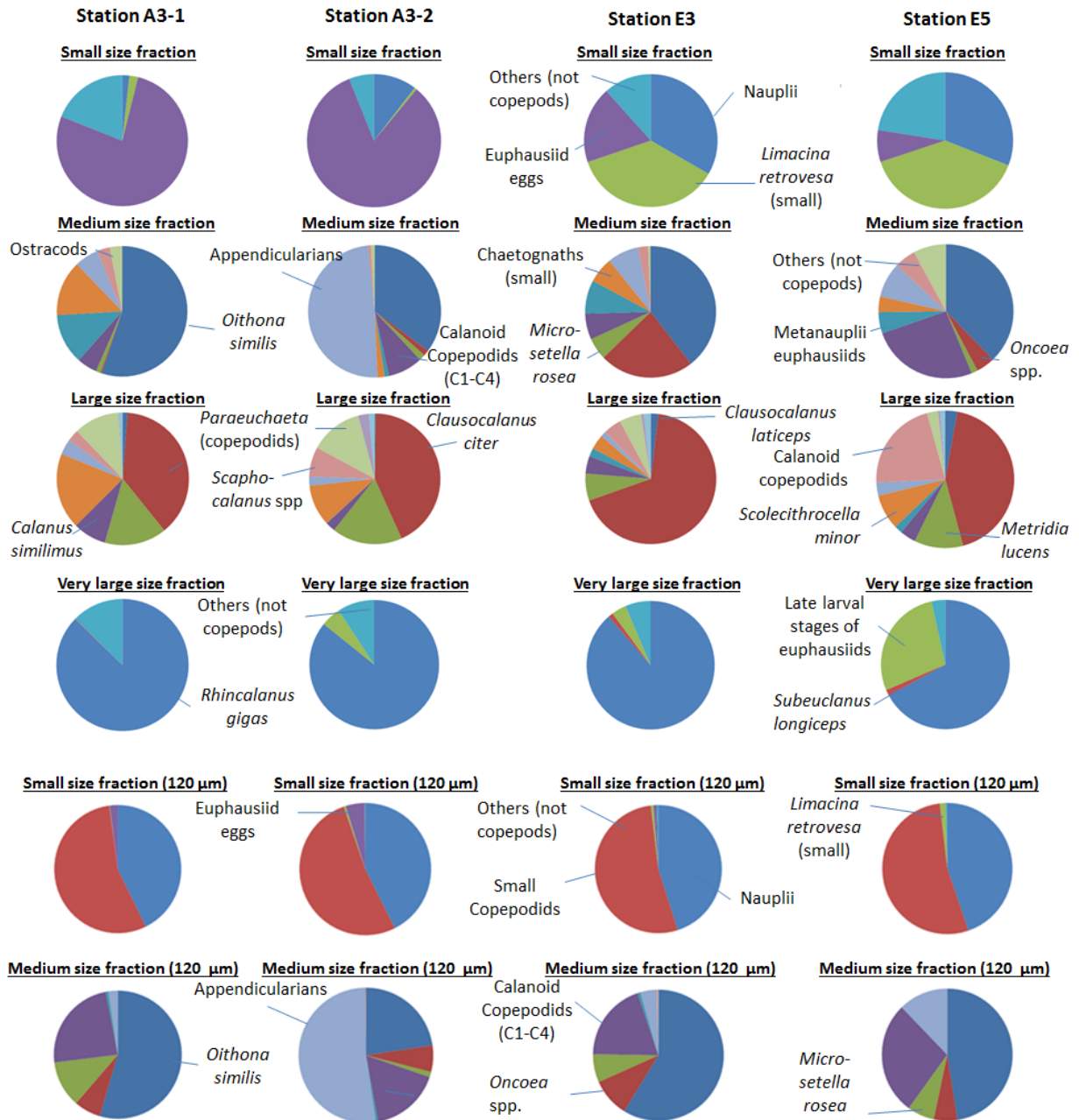
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2 **Figure 5**



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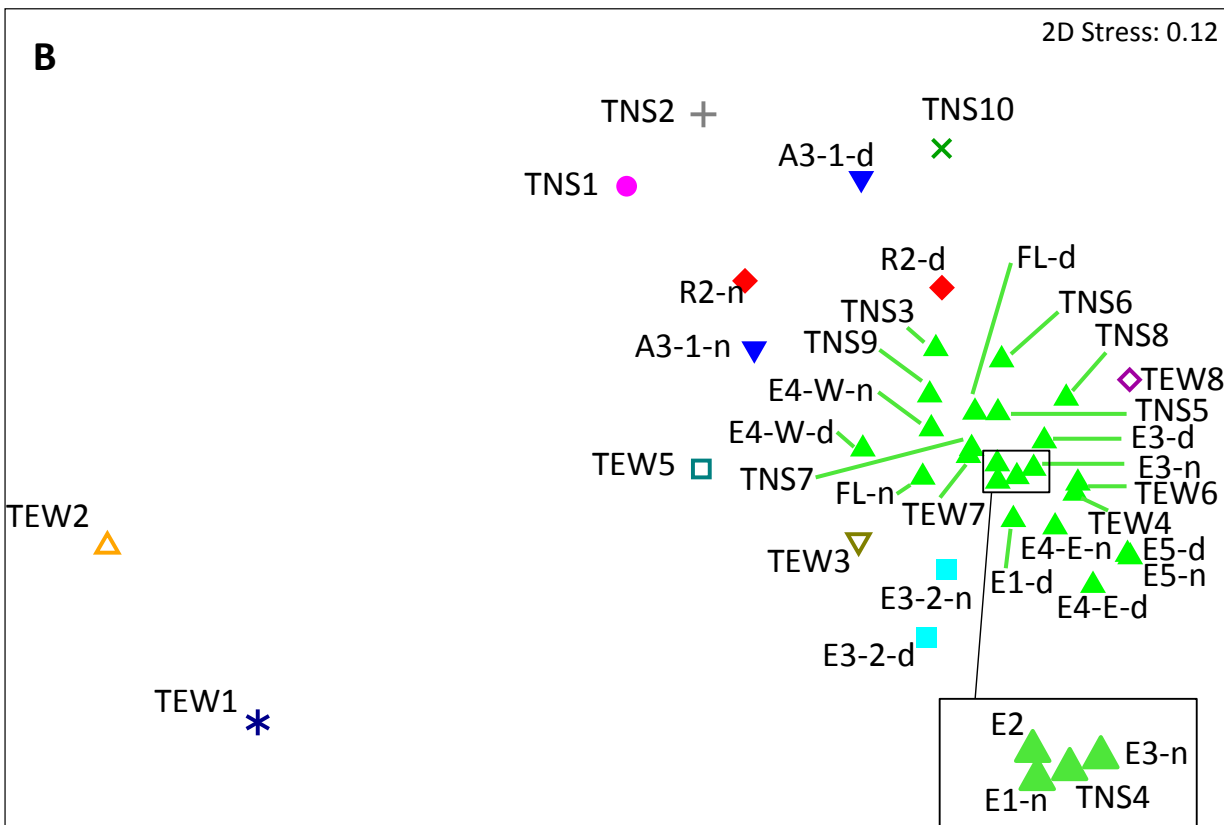
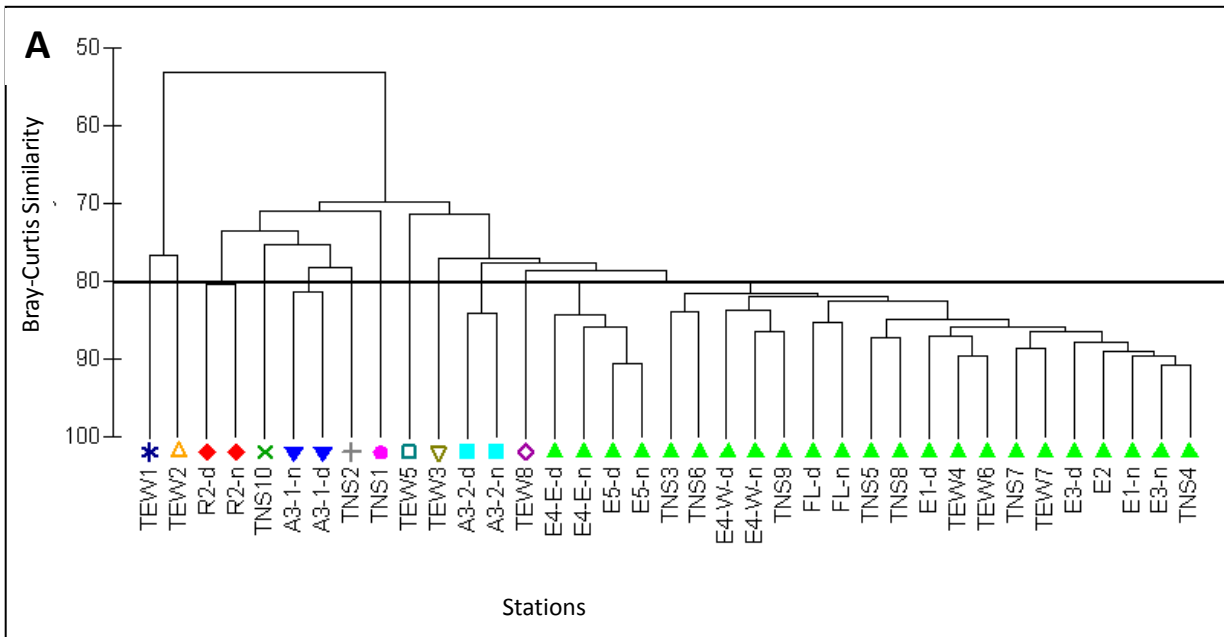
Figure 6 .



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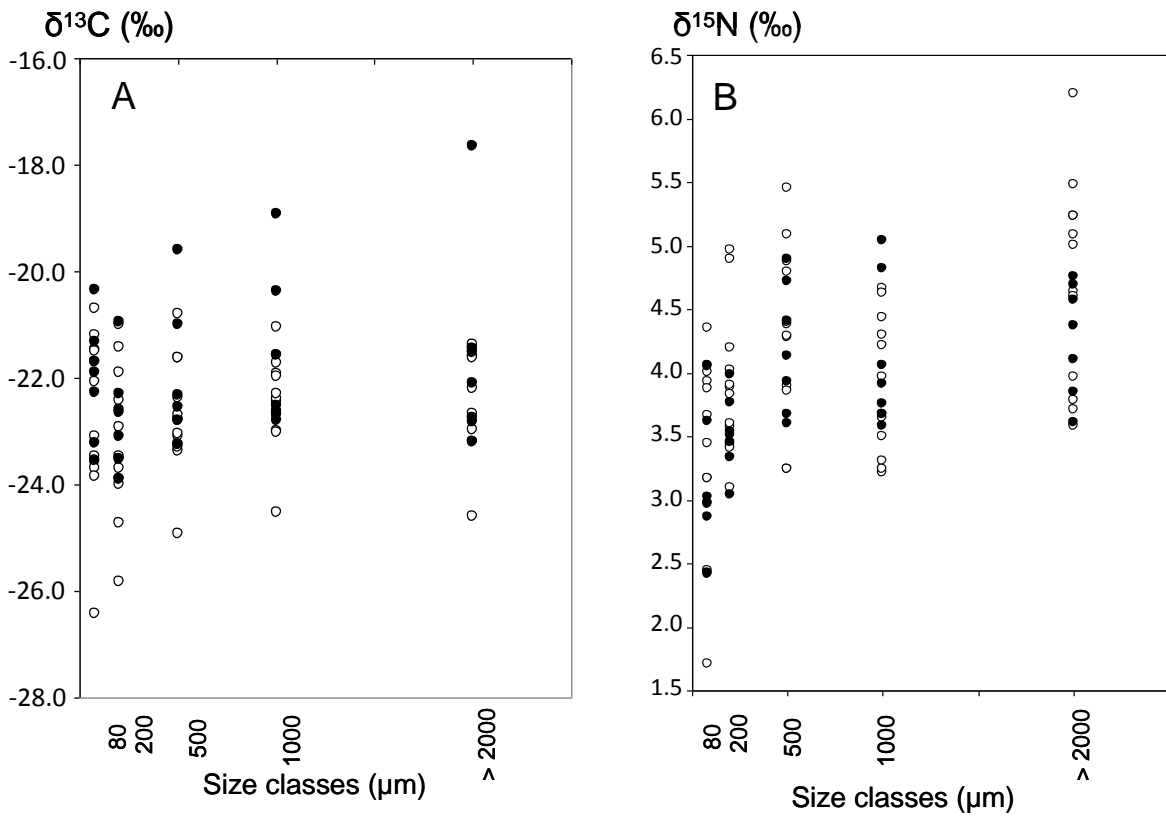
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**Figure 7.**



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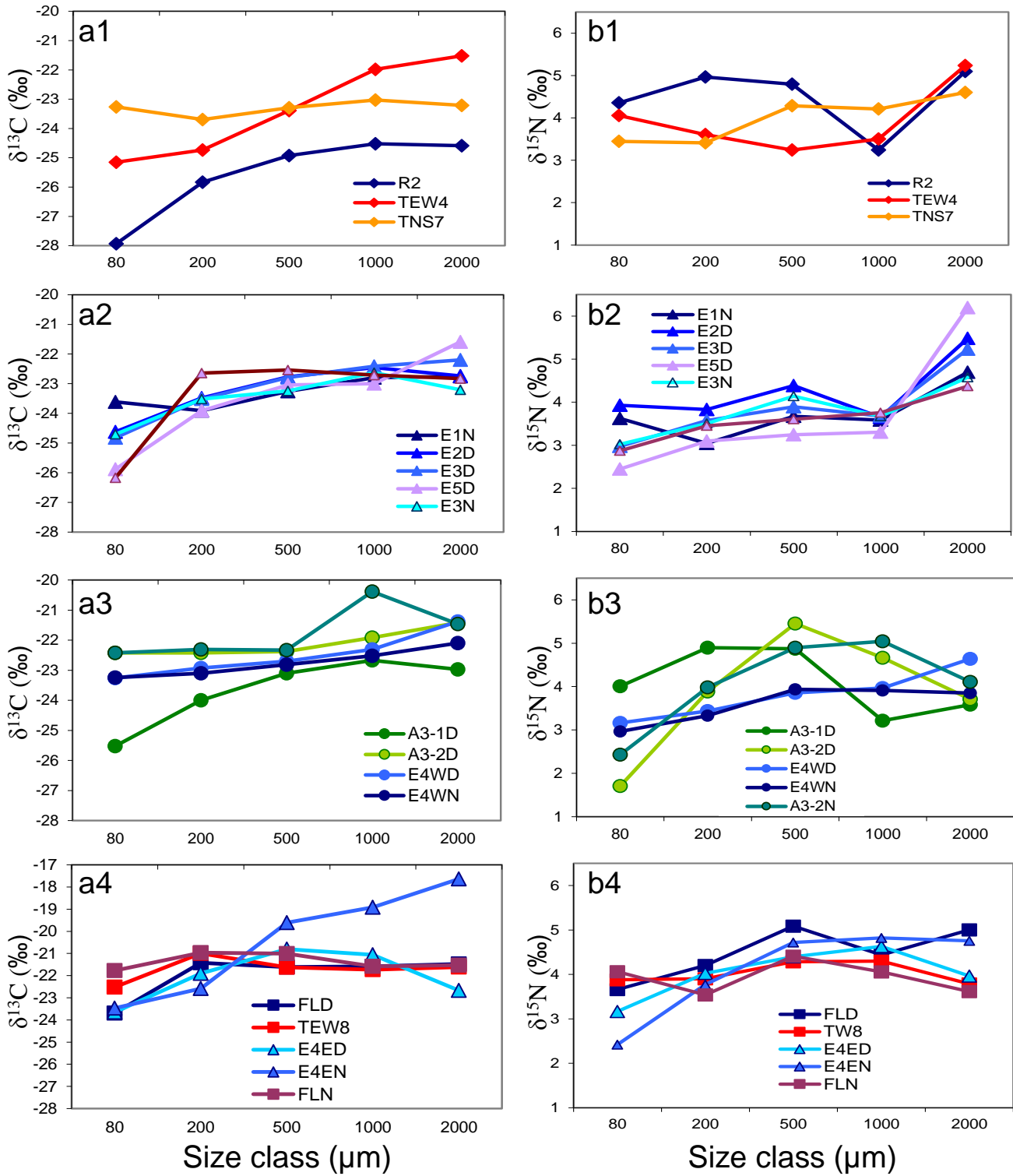
Figure 8



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2 **Figure 9**



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Figure 10

