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Zooplankton community structure, biomass and role in carbon fluxes during the second half of a phytoplankton bloom in the eastern sector of the Kerguelen Shelf (January–February 2005)

François Carlotti[a,b,*], Delphine Thibault-Botha[a,b], Antoine Nowaczyk[a,b], Dominique Lefèvre[c]

[a]*Laboratoire d'Océanographie et de Biogéochimie, Aix-Marseille Université, CNRS, LOB-UMR 6535, OSU/Centre d'Océanologie de Marseille, Campus de Luminy—Case 901, F-13288 Marseille Cedex 09, France*
[b]*CNRS (CNRS/INSU), UMR 6535, Campus de Luminy—Case 901, 163 Avenue de Luminy, F-13288 Marseille Cedex 09, France*
[c]*Laboratoire de Microbiologie, Géochimie et Ecologie Marines, Aix-Marseille Université, CNRS, LMGEM-UMR 6117, OSU/Centre d'Océanologie de Marseille, Campus de Luminy—Case 901, F-13288 Marseille Cedex 09, France*

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Abstract

During the KEOPS survey, zooplankton was sampled with vertical tows to estimate zooplankton stock and to study its composition and size structure both using traditional taxonomic identification and Optical Plankton Counter (OPC). Mesozooplankton OPC-biomass derived from OPC size spectra and integrated over 200 m was variable with average values about 10 g C m^{-2} along transects A and B and at the fixed station KERFIX, and only ~5 g C m^{-2} along transect C. Stations in the most oceanic area (A11, B11, and C11) presented biomass values 3 times lower than the mean value of their respective transects, highlighting a clear decrease of the biomass beyond the shelf. The mesozooplankton community was dominated by copepods, particularly by large- and medium-size calanoids and small Oithonidae. Large numbers of different copepodites stages and nauplii were found, as well as exuviae, indicating that individuals were in active growing phase over the whole area. Euphausiids, chaetognaths, appendicularians, amphipods, polychaetes, ostracods and salps were found as well.

Two reference stations, A3 located in the middle of the bloom on the shelf and C11 in the oceanic waters, were visited several times during the cruise. No particular temporal variations, neither in biomass nor in community structure, were observed, but differences in integrated biomass (average biomass at A3: 10.6 g C m^{-2}; at C11: 2.8 g C m^{-2}) between oceanic and shelf stations clearly show an enhanced secondary production on the shelf. Additional measurements at some stations were performed in order to quantify ingestion (gut contents) and respiration rates on key species and size groups. Gut pigment contents were higher during the first half of the survey at both stations, showing clear temporal changes probably linked to the prey field, with lower values always reported in the oceanic waters compared to the shelf.

Values of respiration and ingestion rates extrapolated from OPC size spectra using published allometric relationships are discussed.

Keywords: Zooplankton; Kerguelen Island; Heard Island; Biomass; Composition; Carbon budget

1. Introduction

The Southern Ocean is characterized by large areas of high surface-nutrient concentrations that are not linked to correspondingly high productivity as indicated by *in situ* and satellite-based chlorophyll measurements and primary productivity estimates, except in some shelf regions (Schlitzer, 2002). Such productive shelves can support

*Corresponding author at: Tel.: +33 491041644; fax: +33 491041643. Laboratoire d'Océanographie et de Biogéochimie, Aix-Marseille Université, CNRS, LOB-UMR 6535, OSU/Centre d'Océanologie de Marseille, Case 901, F-13288 Marseille Cedex 09, France.
E-mail address: francois.carlotti@univmed.fr (F. Carlotti).

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large stocks of mesozooplankton as shown around the South Georgia island (Ward et al., 1995; Atkinson et al., 1996), in the Prince Edward Archipelago (Froneman et al., 1999; Hunt and Pakhomov, 2003), in the Antarctic Peninsula (Hernández-León et al., 2000), in Terra Nova Bay (Fonda Umani et al., 2005), and around the Kerguelen Islands in the Indian sector of the Southern Ocean (Razouls et al., 1996, 1998; Mayzaud et al., 2002a, b). These regions are known to be breeding areas for many top predators (i.e. birds and seals), which reflect sufficient food availability at the levels of zooplankton and nekton (Pakhomov and McQuaid, 1996). Despite the potentially important role that these regions may play in the whole Southern Ocean ecosystem (Moore and Abbott, 2000), underlying mechanisms between physical features, such as fronts, eddies or internal waves and nutrients inputs, primary and secondary productions, are still poorly understood.

The interdisciplinary field experiment *KErguelen: compared study of the Ocean and the Plateau in Surface water* (KEOPS) program conducted during the late austral summer 2005 was designed to understand the mechanisms inducing the phytoplankton bloom and to quantify the carbon fixation and vertical fluxes over the area of the bloom on the Kerguelen Plateau, east of the Kerguelen Island—Heard Island line. The Kerguelen Islands are associated with eastwards-elevated chlorophyll concentrations linked to physical processes induced by the interplay between the eastward flow of the Antarctic Circumpolar Current (ACC) and the large topographic barrier of the shallow Kerguelen Plateau, which is oriented north-west/south-east along the 70°E meridian (Fig. 1). The recurrent south-east large bloom generally begins in November, peaks in January, and ends in late February (Blain et al., 2001, 2007; Schlitzer, 2002). In a previous study (Blain et al., 2001), a high chlorophyll plume observed north-east of the Kerguelen Island and north of the Polar Front has been correlated with both sufficient iron concentrations (dissolved Fe in the range 0.45–0.7 nM), and a more favorable light-mixing regime.

Several scientific programs have increased our understanding on the composition, structure and physiological activities of mesozooplankton and its impact on phytoplankton production particularly around the Kerguelen Island, at the field station KERFIX and on transect from Kerguelen Island to the ice edge on the Antarctic continent (Mayzaud and Razouls, 1992; Semelkina, 1993; Razouls et al., 1996, 1997, 1998; Errhif et al., 1997; Tirelli and Mayzaud, 1999; Blain et al., 2001; Mayzaud et al., 2002a, b). Zooplankton biomass on the south-eastern part of the Kerguelen Island has been documented once by Semelkina (1993). However, it is still unknown how strongly the zooplankton stock responds to this long-lasting phytoplankton bloom and whether it varies in space and time in relation to the phytoplankton and micro-zooplankton abundance and composition.

During the KEOPS survey, zooplankton were sampled in order (1) to identify whether differences in the standing stock and composition of mesozooplankton (using traditional taxonomic identification and Optical Plankton Counter) occurred between quite contrasted hydrological structures and (2) to characterize their dynamics at the end

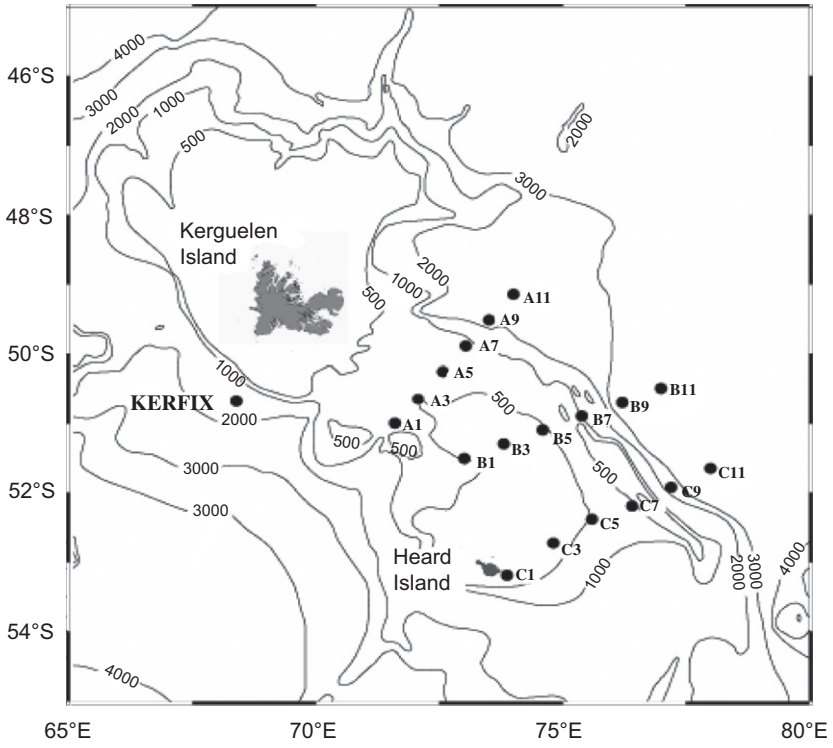

Fig. 1. Map of the studied area and locations of sampling stations during the KEOPS-cruise.

of a long-term natural iron-fertilized bloom. Additional physiological measurements were conducted at some stations to quantify respiration and ingestion rates on key species and size groups. Rates were then compared with size-dependent allometric relationships.

2. Material and methods

2.1. Study site and sampling strategy

The KEOPS study was conducted between January 19 and February 13, 2005 on board the R.V. *Marion Dufresne* and covered an area of 50,000 km^2 on the east–south-east area of the Kerguelen Islands. Cruise tracks showing the three main transects located over the mid-shelf to the oceanic waters and sampling sites are presented in Fig. 1. Details on the location of the sampling positions are presented elsewhere (see Table 1 in Armand et al., 2008).

The physical and chemical oceanography pertinent to the KEOPS study are presented in Park et al. (2008a, b), van Beek et al. (2008), Mongin et al. (2008), Mosseri et al. (2008), and Blain et al. (2007). Information on phytoplankton stock and production, stock and grazing of microzooplankton, and copepod grazing is presented in companion papers (Armand et al., 2008; Christaki et al., 2008; Sarthou et al., 2008). Complementary information on satellite-image-derived primary production has been supplied by Uitz et al. (submitted for publication).

2.2. Mesozooplankton sampling

Zooplankton vertical net tows were conducted at stations with odd numbers. Three stations (A3 and B5 in the core of the bloom, and C11 in high-nutrients low-chlorophyll—HNLC—waters) were visited several times during the cruise, allowing us to study temporal variations. Mesozooplankton were sampled using double Bongo nets fitted with 330-μm mesh sizes mounted with filtering cod ends. Hauls were done from 200 m to the surface at 1 m s^{-1}. A flow-meter was used to obtain accurate sampled volumes. The content of one of the two nets was preserved in buffered seawater–formalin solution (4%) for further laboratory study of zooplankton community structure and biomass. The material of the second net was placed in small containers and immediately deep-frozen (−80 °C) for further gut content analysis. At stations A3 and C11, part of the material was immediately diluted with filtered seawater for respiration-rate experiments (see the following text).

In addition, the abundance and vertical distribution of copepod nauplii were estimated at A3 (5 times) and C11 (once) using waters collected with the CTD/rosette at six depths (10, 20, 40, 60, 80 and 100 m). At each depth, 12 L of water was sieved through a 50-μm mesh. Samples were then preserved in 4% borax-buffered formalin seawater and counted once back in the laboratory in France.

2.3. Analysis of samples

Mesozooplankton community structure was described following two different approaches, the first was the traditional taxonomic determination using dissecting microscope, and the second was based on size spectrum analysis using a bench-top version of the Optical Plankton Counter Focal®OPC-1L (lab OPC).

Taxonomic determination was made at a limited number of key stations (A3, B5, C11 and KERFIX) using a LEICA MZ6 dissecting microscope and a Bogorov tray. Zooplankton were identified down to species level. For large calanoid copepod species, early (C1–C3) and late (C4 and C5) copepodite stages were counted separately.

Net tow samples from all stations were processed with a lab OPC. OPC has been recently used to study zooplankton community in various areas and has been validated by comparisons with traditional sampling methods (Huntley et al., 1995; Zhou and Huntley, 1997; Gallienne and Robins, 1998; Beaulieu et al., 1999; Grant et al., 2000; Woodd-Walker et al., 2000; Zhou and Tande, 2001; Edvardsen et al., 2002; Riandey et al., 2005; Sourisseau and Carlotti, 2006; Vanderploeg and Roman, 2006). Our lab OPC setup is similar to the one described by Beaulieu et al. (1999) and used in Riandey et al. (2005) and Sourisseau and Carlotti (2006). Organisms are gently introduced into the water circulation system. The cross-section of any particle is estimated (digital size) and is converted into equivalent spherical diameter (ESD) following a semi-empirical formula (Focal Technologies Inc., 1997). Any particle with an ESD larger than 250 μm is counted by the OPC. To avoid coincidence, we imposed a maximum count rate at 20 particles min^{-1} and a constant flow rate at 18 L min^{-1}. The shape of the size spectrum was obtained by counting at least 1000 particles (Sourisseau and Carlotti, 2006).

At most stations located on transects A and B, high densities of chains of diatoms (mainly *Thalassiossira antarctica*, see Armand et al., 2008) were also collected by the Bongo nets, which tended to clog the net. The presence of these diatoms led to a higher retention rate of small-size individuals. Therefore, before processing the samples through the OPC, samples had to be delicately cleared of large clump of diatom chains with fine forceps. Moreover, during the introduction of the sample into the glass tube of the water circulation system, we gently re-suspended the sample using a stainless steel grid (diameter 8 cm, mesh size 1 cm, open area ca. 70%, initially built for turbulent experiments, see Caparroy et al., 1998) that broke the agglomerates and detrital particles in smaller particles below the 250 μm ESD not detected by the lab OPC. For data treatment, particles counted within the eight first digits (below 287 μm) were not taken into account.

The biovolume of a particle of a given ESD was calculated by assuming each particle as a sphere. In order to estimate the total biomass of the particles measured by

the OPC, the total biovolume (BV, mm^3) was converted into biomass (W, mg DW) using the following relationship $\log(W) = 0.865 \log(BV) - 0.887$ (Riandey et al., 2005). Carbon content has been assumed to be 50% of body dry weight.

The abundance and biomass of each specific ESD were then grouped into four ESD size fractions (287–500, 500–1000, 1000–2000, and >2000 μm), and summed to deliver the total abundance and biomass per sample over the 200 upper m. Abundance and biomass values are normalized to the volume of water filtered *in situ*. In this article, OPC abundance and OPC biomass will correspond to the values derived from the lab OPC treatment.

ANOVA test (5% significance level) was used to test differences of abundances and biomass between stations or oceanic areas.

2.4. Copepod guts fluorescence method

Samples were quickly thawed, then sorted into three groups (small, large copepods and euphausiids) using a dissecting microscope under dim light and with cold-filtered seawater (at approximately 0–3 °C) and treated as described by Mackas and Bohrer (1976). Aliquots of 15 individuals of copepods larger than 3 mm, and aliquots of 50 individuals for smaller copepods, were picked and placed in glass tubes containing 10 mL of methanol in the cold and dark for extraction. Gut pigment analysis was done with a Turner Design fluorometer. Chlorophyll *a* and pheopigment concentration were measured according to the method of Yentsch and Menzel (1963) modified by Holm-Hansen et al. (1965). The gut pigment contents (ng Chl *a* eq ind^{-1}) were calculated according to Wang and Conover (1986), where ng chlorophyll *a* equivalents (ng Chl *a* eq) equal Chl *a* + pheopigment.

2.5. Individual respiration measured by coulometric total carbon dioxide technique

Respiration rates of key zooplanktonic species such as copepods, ctenophores, annelids, and euphausiids were measured during 24-h stations (A3 and C11). We used a coulometric total carbon dioxide technique to measure the CO_2 release (Mayzaud et al., 2005). Analysis of seawater TCO_2 throughout the cruises provided quality assessment of the precision and accuracy of the measurements.

The collected zooplankton was immediately placed in a large plastic cooler filled with surface seawater and kept at *in situ* temperature. Large individuals were rapidly sorted, and grouped on the basis of size and species or genera; each group was then placed in beakers filled with filtered seawater (0.45 μm) for less than 1 h. Individuals of a same species or genus were placed individually (for larger zooplankton organisms such as annelids, ctenophores and euphausiids) and by groups of 3–5 (for copepod species) in 125-mL flasks filled with filtered seawater saturated in oxygen. Animals were incubated in the dark at *in situ* temperature (~2–3 °C) for 15–20 h. Control bottles (0.45-μm-filtered seawater) without zooplankton were incubated under the same conditions. CO_2 production was computed by difference between start and end of the incubations, corrected for possible changes in control bottles.

2.6. Ingestion and respiration derived from global equations

In order to estimate the ingestion and respiration rates of the whole mesozooplankton, we applied two allometric relationships to the biomass size spectra delivered by the lab-OPC. First, Atkinson (1994) established a relationship between mass-specific ingestion (I, in μg C ind^{-1} day^{-1}) and individual body dry weight (DW, in μg) of grazers by pooling data from a large number of on board-incubation experiments: $\log I = 0.33(\pm 0.070) \log DW - 0.43$, where ingestion was mainly based on natural phytoplankton. Rather than using the whole dataset of Atkinson (1994), which gives ingestion rates with a range of one order of magnitude for any body dry weight, we propose a new relationship $\log(I) = 0.523 \log(DW) - 0.43$, which fits only the upper range of the mass-specific ingestion values of Atkinson (see his Fig. 4, 1994). This new relationship delivers a daily ingestion rate equal to 3% of the body carbon ingested per day by a copepod weighing 1 mg DW (i.e. copepod assemblages dominated by *Calanus propinquus*), comparable to the maximum value (3.3%) measured during grazing experiments run by Sarthou et al. (see their Table 2, 2008).

Similarly, a relationship established by Mayzaud et al. (2002a) between respiration rate (R, μl O_2 ind^{-1} day^{-1}) and body dry weight (DW, μg) of copepods from the Kerguelen area was used: $\log R = 0.78(\pm 0.018) \log DW + 1.28(\pm 0.016)$ ($R^2 = 0.988$). Respiration was converted to carbon assuming a RQ = 0.9 (Mayzaud et al., 2002a).

3. Results

3.1. Hydrology and trophic conditions

Different water masses were identified over the shelf, in the oceanic area, and at KERFIX (Park et al., 2008b). The upper 200 m of the water column consisted of Antarctic surface water with a wind-mixed layer (WML) ranging from 44 to 128 m in thickness, deepening from the shelf to oceanic waters. Over the whole area, the surface salinity varied very little, from 33.80 to 33.93 and decreased with depth by less than 0.5 within the upper 200 m. Surface temperature displayed, on the other hand, much stronger variation, with values between 1.74 and 1.98 °C at C11 and between 3.57 and 3.97 °C at A3, and decreased with depth, reaching a minimum value (−0.2 °C at C11 and 1 °C at A3) at 150–200 m depth, respectively (see Park et al., 2008b for more details).

Above the Kerguelen Shelf, A3 was located in the middle of the intense phytoplankton bloom (Blain et al., 2008).

Satellite images indicated that the bloom started 2 months before the KEOPS-cruise and lasted to the end of February. The mean chlorophyll concentration in the upper 200 m was, on an average, 3 times higher on the shelf than off shore. Surface phytoplankton biomass ranged from 0.26 to 2.78 μg Chl $a\,L^{-1}$ on the shelf, whereas in the HNLC region concentrations were overall very low (0.20–0.35 μg Chl $a\,L^{-1}$). The associated autotrophic (Armand et al., 2008), bacterial (Obernosterer et al., 2008) and microplanktonic (Christaki et al., 2008) communities revealed higher stocks and substantially higher biomass, and higher rates of production and respiration over the shelf than in the surrounding HNLC waters.The diatom community structure above the shelf site changed over time depending on the diatom responses to nutrient availability (Armand et al., 2008), maintaining the highest biomass (50–100 μg C L^{-1}), whereas in the offshore waters, out of the bloom region, the diatom community showed little changes over the 25-day period, with biomass lower than 25 μg C L^{-1}.

3.2. OPC abundance and OPC biomass distributions

Over the three transects (A, B and C), zooplankton OPC abundance (mean ± S.D.) were, respectively, 364.7 ± 265.2 × 10^3, 624.0 ± 327.0 × 10^3 and 276.1 ± 195.1 × 10^3 ind m^{-2} (Fig. 2). For the whole dataset, total zooplankton OPC abundance integrated over the top 200 m (Fig. 2) ranged between 58 × 10^3 ind m^{-2} (minimum observed at A11) and 1249 × 10^3 ind m^{-2} (maximum observed at B1). The OPC biomass varied from 3.44 g C m^{-2} (station A11) to 19.36 g C m^{-2} (station A9). Average biomass along the transects was 9.91 ± 5.98, 9.93 ± 5.78 and 5.7 ± 2.79 g C m^{-2}, respectively, for transects A, B and C. Biomass over the transect C appears to have been the lowest among the three transects, although the differences between the three transects were not statistically different (ANOVA, $p > 0.05$). Any spatial pattern was difficult to extract due to the variability of the biomass between and among transects, partly linked to diurnal variations (see Mayzaud et al., 2002b). Within each transect, the lowest biomass was observed at the most oceanic stations (A11, B11, and C11), with values 3 times lower than the mean biomass value of the transect, but no cross-shelf gradient was detected by ANOVA tests.

Two stations, A3 and C11, were visited several times during the cruise, allowing us to study temporal variations in the zooplankton community (Fig. 3). At A3, OPC abundance varied from 261 × 10^3 to 681 × 10^3 ind m^{-2} (mean ± S.D.: 492.1 ± 161.1 ind m^{-2}), with a corresponding mean value of 10.6 ± 3.6 g C m^{-2}, whereas in C11 OPC abundance varied from 84.2 × 10^3 to 184 × 10^3 ind m^{-2} (mean ± S.D.: 150.0 ± 63.9 ind m^{-2}), with a corresponding mean value of 2.8 ± 1.2 g C m^{-2}. The OPC abundance and OPC biomass values at each A3 and C11 stations showed no significant decrease during the cruise, but inter-site variations were significant (ANOVA, $p < 0.05$) for OPC biomass.

Zooplankton OPC abundance over the three transects was mainly dominated by the two smallest size fractions (285–500 and 500–1000 μm), representing over 80% of the total OPC abundance (Fig. 4), whereas the bulk of the OPC biomass was made of large individuals. The size fraction distribution along the three different transects

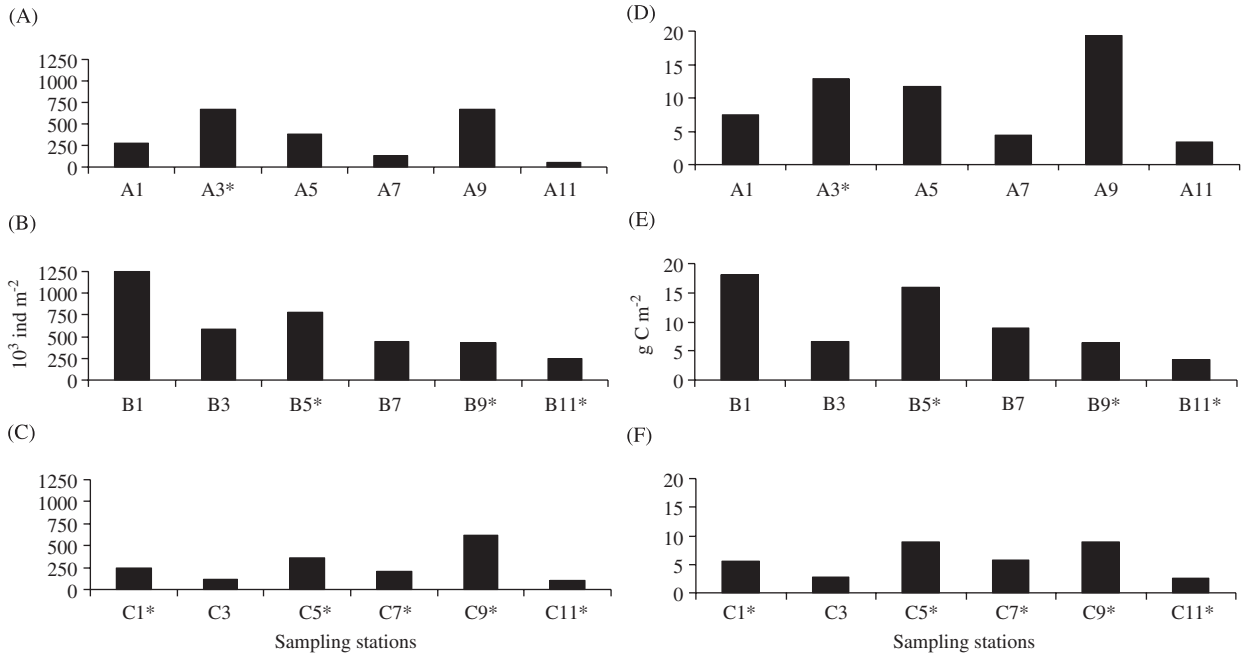

Fig. 2. Integrated 0–200 m OPC abundance (A–C) and OPC biomass (D–F) for the different stations over the three transects. Transect A from 20 to 23 January; transect B from 29 January to 2 February; transect C from 5 to 9 February. Asterisk (*) indicates dark-night sampling. Positions of all stations and bathymetry are presented in Fig. 1.

showed a relative homogeneity, except for the OPC biomass fraction >2000 μm along transect B, and the OPC abundance and OPC biomass fractions 285–500 μm for transect C.

No temporal changes in size structure could be detected at A3 and C11 between the different sampling dates (Fig. 5). Individuals >1 mm were slightly more abundant at A3 than at C11.

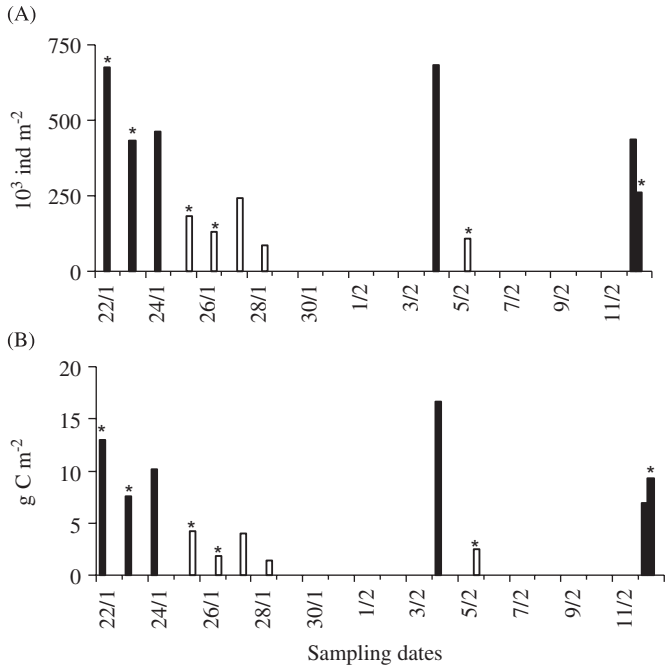

Fig. 3. Temporal variation of integrated 0–200 m OPC abundance (A) and OPC biomass (B) at A3 (black) and C11 (white). Asterisk (*) indicates dark-night sampling.

3.3. Taxonomic distribution

Total abundance estimated from microscopic counts was compared to the OPC abundance (Fig. 6). OPC counts appear slightly higher than microscopic counts, which might be explained by pieces of exuviae as well as aggregates of diatoms that were not differentiated from zooplankton organisms by OPC. However, the use of the lab OPC to estimate zooplanktonic abundance appeared valid, despite the high concentration of diatom chains in the samples (see Section 2).

The mesozooplankton abundance (Fig. 7) was dominated by copepods (>80%), especially by calanoid copepods of large size (*Calanus simillimus*, *C. propinquus*, *Metridia lucens*, *Paraeuchaeta* sp., *Pleuromama robusta* and *Rhincalanus gigas*) and medium size (late copepodite and adult stages of *Clausocalanus* spp. and *Microcalanus* spp.), and small copepods (Oithonidae and Oncaeidae). At A3, a large proportion of nauplii was found in the net samples linked to the presence of large quantities of chains of diatom. Undetermined copepodite forms were included under "other copepods". Other zooplankton taxa were represented by euphausiids, chaetognaths, appendicularians, amphipods, polychaetes, ostracods and salps. Non-copepod taxa represented around 4–8% of the overall total abundance. Pteropods quite abundant over the shelf (7–12% of the total abundance) were counted separately. Moreover, a large proportion of exuviae

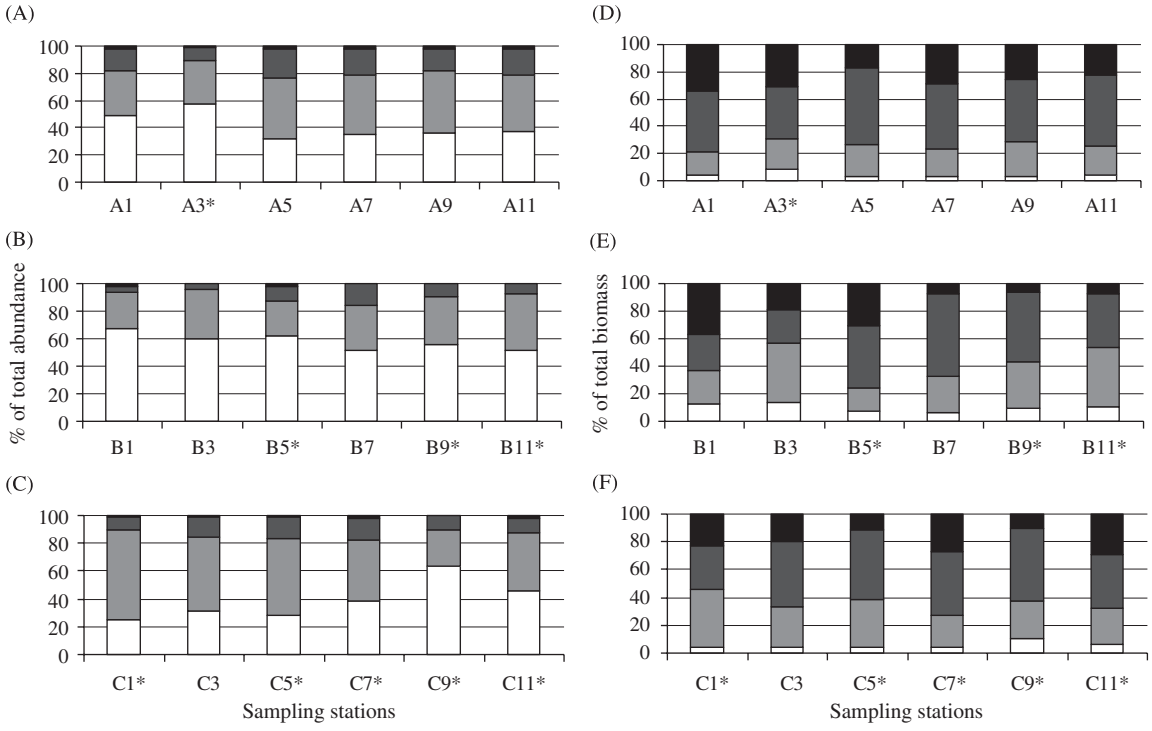

Fig. 4. Size fraction distribution of OPC abundance (A–C) and OPC biomass (D–F) for the four size fractions: <500 μm: white; 500–1000 μm: light gray; 1000–2000 μm: dark gray; >2000 μm: black. Asterisk (*) indicates dark-night sampling.

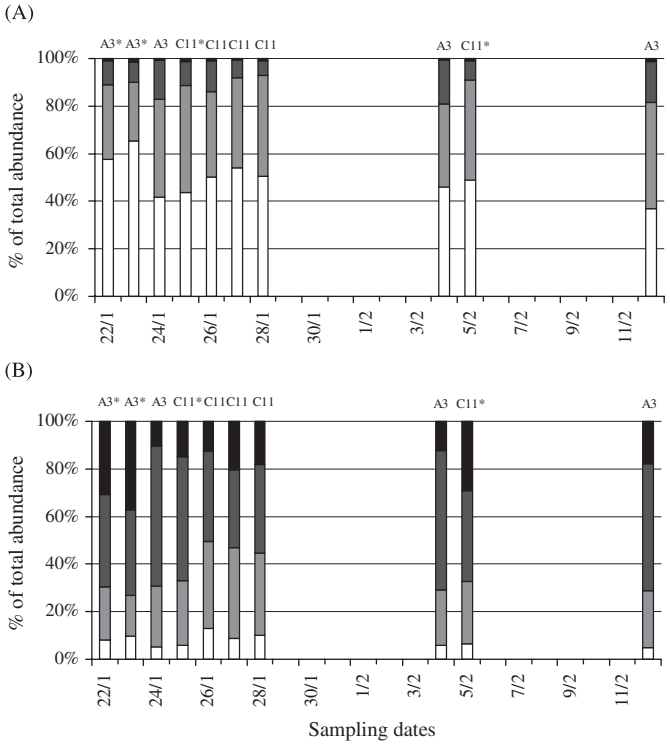

Fig. 5. Size fraction distribution of OPC abundance (A) and OPC biomass (B) at A3 and C11for the four size fractions: $<500\,\mu m$: white; 500–1000 μm: light gray; 1000–2000 μm: dark gray; $>2000\,\mu m$: black. Asterisk (*) indicates dark-night sampling.

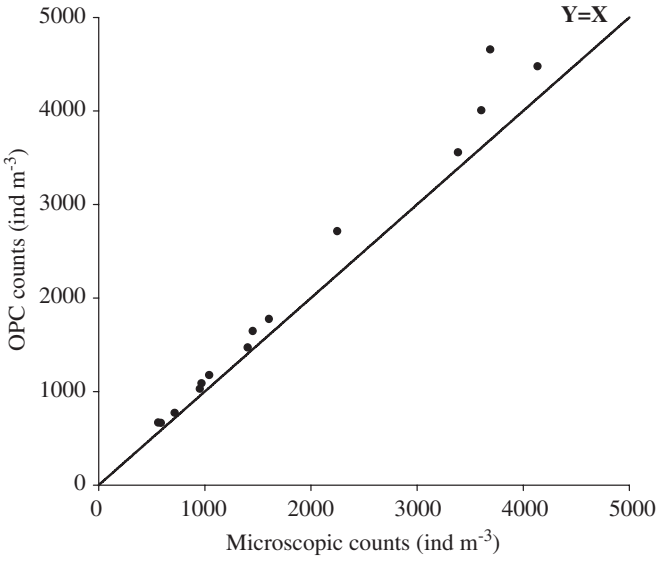

Fig. 6. Comparison between OPC and microscope counts for stations A3 (six samples), C11 (five samples), B5 (one sample) and KERFIX (two samples).

(>10%) was counted at C11 and at KERFIX, but represented only 1–2 % at A3 and B5.

Large calanoid copepods (Fig. 8) were mainly represented by young developmental stages, very few adults being collected over the entire period. Young copepodite stages of *R. gigas* were clearly the most dominant form

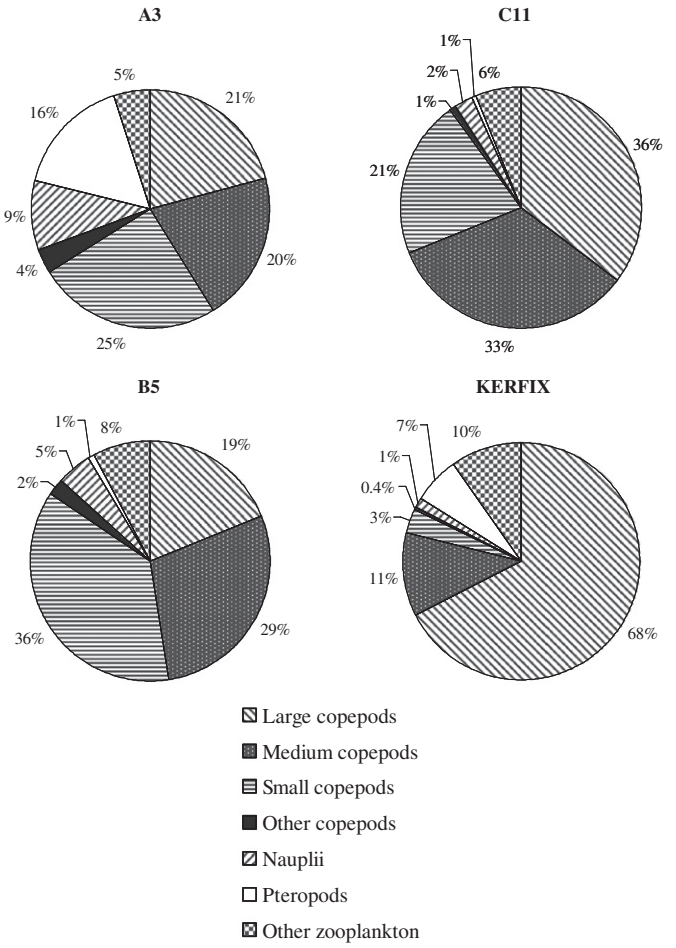

Fig. 7. Composition of the zooplankton community within the top 200 m at A3 (24 January), C11 (28 January), B5 (1 February), Kerfix (10 February). Large-size copepods are defined as all copepodites and adult stages of *Calanus simillimus*, *Calanus propinquus*, *Metridia lucens*, *Paraeuchaeta* sp., *Pleuromama robusta* and *Rhincalanus gigas*. Medium-size copepods are defined as late copepodite and adult stages of *Clausocalanus* spp. and *Microcalanus* spp. Small copepods are defined as adult stages of *Oithona similis*, *Oithona frigida* and *Oncea* sp. "Other copepods" and "Nauplii" represent undefined copepodite and nauplii stages. Other zooplankton organisms are defined as appendicularians, chaetognaths, euphausiids, polychaetes, amphipods, ostracods and radiolarians.

found for this species. For medium-sized copepods, copepodite stages C4 and C5 and adults were equally represented. *C. simillimus*, *C. propinquus*, *M. lucens*, and *Microcalanus* spp. had a higher proportion of adults at C11 than at A3.

The vertical distribution of nauplii density (Fig. 9) did not show any specific pattern within the top 80 m for the two stations A3 and C11, but density was 6 times lower at C11 ($\sim$10 nauplii L^{-1}) than at A3 (50–70 nauplii L^{-1}). The lowest densities were always reported below 100 m. Nauplii density did not display any temporal variations at A3 (Fig. 9A). Diel variation in the vertical distribution of the nauplii was studied twice at A3. A clear minimum was observed at 40 m for the two days studied (February 2 and February 12, 2005) during night samplings (Fig. 9B).

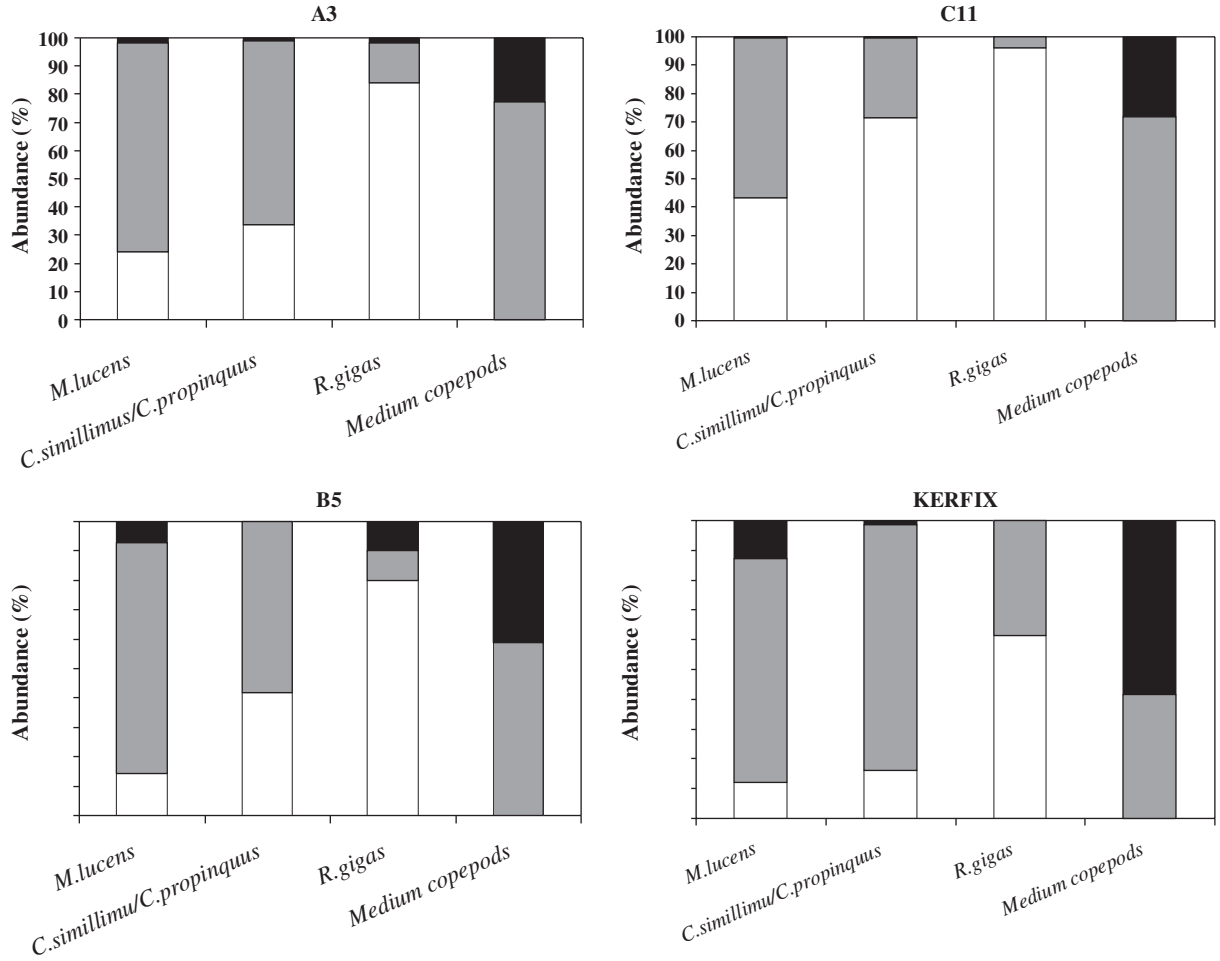

Fig. 8. Mean stage frequencies of early copepodite stages (C1–C3), in white bars, copepodite stages (C4 and C5), in gray bars, and adults, in black bars, in key copepod populations for different areas (see Fig. 1).

3.4. Metabolic rates

For both groups of copepods (small and large), gut pigment contents (Fig. 10) appeared to be highly variable. The highest values were found during the first half of the survey, with lower values reported in the HNLC waters than on the shelf. Then after 1st of February, phytoplankton appeared to represent only a minor component of the copepods diet at all stations. Our values indicate that the feeding on the phytoplankton component might be higher during the first half of the survey, and lower later in the season. Individual respiration rates are presented in Table 1.

Rates of ingestion and respiration (Fig. 11) were derived from allometric relationships (see material and methods). Calculation from OPC size spectra gave respiration rates ranging from 40 mg C m^{-2} d^{-1} at C11 to 560 mg C m^{-2} d^{-1} at B1. In general, the trend observed in the spatial variations of the respiration was directly related to the spatial distribution of total OPC biomass rather than to the size structure of the community itself. Specific respiration rate did not show any strong variation (between 2.67% and 3.48%), with a very low value measured at A11 (1.44%).

Estimated ingestion rates from our allometric relationship ranged from 140 mg C m^{-2} d^{-1} at offshore stations to 1895 mg C m^{-2} d^{-1} (shelf station B1). Specific ingestion rates were estimated between 4% and 12%.

4. Discussion

4.1. Zooplankton abundance, community structure and biomass

OPC systems, both laboratory and *in situ* versions, have been increasingly used since their development in the early 1990s (Vanderploeg and Roman, 2006), but only a few studies report their uses in Antarctic regions (Labat et al., 2002; Hernández-León and Montero, 2006). Nevertheless, our double approach confirmed the use of lab OPC to quickly examine Antarctic zooplankton samples. Mesozooplankton displayed high abundance and biomass during KEOPS, similar to those observed by Semelkina (1993) during the SKALP cruises conducted in the eastern region of the Kerguelen in February 1997 and 1998. The area (46–52°S, 64–73°E all round the Kerguelen Island from the shelf to oceanic waters with isobaths down to

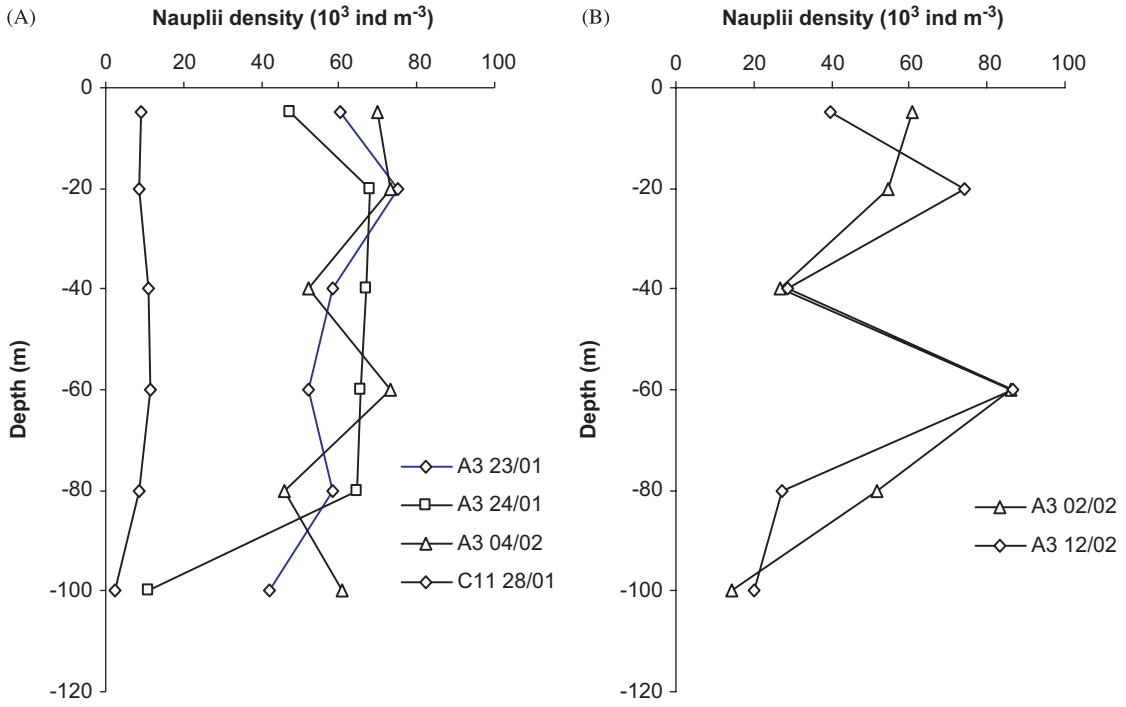

Fig. 9. Vertical distribution of nauplii densities at six stations within the top 100 m: (A) day sampling; (B) night sampling.

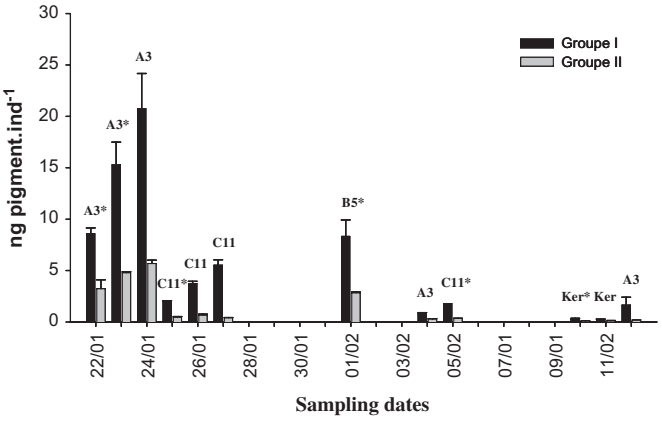

Fig. 10. Copepod gut contents for two groups of copepods. Groups 1 (black bars) and 2 (gray bars): cephalothoracic length, respectively, upper and lower than 3 mm. Asterisk (*) indicates dark-night sampling.

Table 1
Individual respiration rates of key zooplanktonic taxa during KEOPS

Taxa, species and developmental stages	Respiration rates (μg C ind^{-1} day^{-1})	No. of individuals	S.D.
R. gigas mainly C5	13.72	36	6.33
C4 and C5 of *C. propinquus* and *C. simillimus*	9.34	34	4.56
Ctenophores	53.89	4	20.01
Tomopteris sp.	819.00	4	154.60
Euphausiids	57.89–256.14	3	
Chaetognaths	79.65 and −103.50	2	

4000 m) and time frame (February, April, July–August 1997 and February 1998) sampled during those cruises were much wider than during KEOPS. Nevertheless, according to Semelkina (1993), the sampling period and region of KEOPS corresponded to the space and time window of the highest densities of mesozooplankton in the upper 200 m. Such high densities also were found during spring blooms at similar latitudes in the Antarctic Ocean, particularly in the vicinity of islands, both in the Indian (Errhif et al., 1997) and the Atlantic sectors (Ward et al., 1995; Fransz and Gonzalez, 1997).

The mesozooplankton community was dominated by copepods, particularly copepodite stages of large calanoid copepods, small copepods and nauplii. Semelkina (1993) found in February 1997 and 1998 during SKALP almost the same dominance of copepods (81% of the mesozooplankton biomass) and the same dominant taxa and species of zooplankton. High densities of copepod nauplii also were found both in the net samples and the bottle samples, confirming the possible clogging of the net by the diatoms chains; these nauplii are not usually efficiently retained by a 330-μm mesh size. These high abundances of copepod nauplii appeared to represent an important component of the microbial food web (Christaki et al., 2008). Exuviae also were found in large numbers both at C11 and KERFIX, and to a lesser extent at A3 and B5. Distributions of exuviae are highly dependent on the physical properties of the water column such as advection and mixing, and are also probably consumed by micro- and meso-zooplankton.

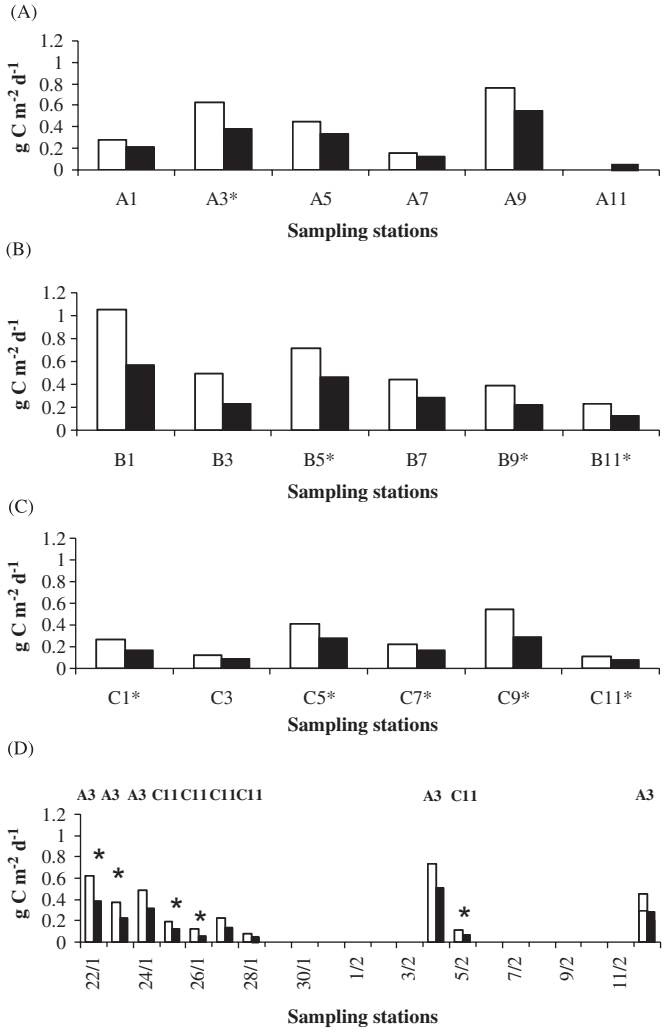

Fig. 11. Estimated integrated ingestion (white) and respiration rates (black) for the whole mesozooplankton biomass for all sampled stations. (A) Transect A from 20 to 23 January; (B) transect B from 29 January to 2 February; (C) transect C from 5 to 9 February; (D) Stations A3 and C11 for different visits (transect and time-series stations). Asterisk (*) indicates dark-night sampling.

Altogether, stage distribution of large copepods, densities of nauplii, and presence of exuviae show that growth and development rates of the organisms were particularly high on the shelf over the whole period of KEOPS, a situation found in other shelves in summertime (Shreeve and Ward, 1998; Shreeve et al., 2002).

Differences in integrated OPC biomass between oceanic and shelf stations have been reported for several regions (Ward and Shreeve, 1999), mainly due to enhanced primary production over the shelf. Lower average OPC biomass observed along transect C, which took place at the end of the survey, can be related to different factors (i.e. bloom phase, hydrodynamics). Potential effects of the advanced phase of the bloom were not supported by the successive samplings done at A3 and C11 (see Fig. 3), which showed no strong temporal variation in biomass. Hydrodynamic features observed along transect C are a stronger candidate (Park et al., 2008b). At C11, lower nauplii and copepodite densities reflected lower local egg production by females, and presence of juvenile stages of copepods also might be related to advection from the shelf rather than to local production.

OPC biomass observed in the south-east region of the Kerguelen Islands during our survey were similar to those measured by Semelkina (1993) in February 1987 and April 1987. She mentioned biomass up to 200 mg DW m^{-3} in the upper 100 m, mainly due to swarms of *C. simillimus*. Other published biomass values around Kerguelen were always lower, but sampling sites differed from those of KEOPS. During ANTARES 2 and 3 cruises along the 62°E (Mayzaud et al., 2002a, b), three stations sampled in the north of the permanent open ocean zone (POOZ) presented biomass ranging from 0.6 to 16.0 g DW m^{-2} in February–March 1994 with a dominance of young copepodite stages (ANTARES 2), and from 2 to 8 g DW m^{-2} in October–November 1995 with dominance of late copepodite and adult stages (ANTARES 3). Observations made during our survey are consistent with those made during ANTARES 2. Thus, it can be assumed that the mesozooplanktonic biomass and population structures during KEOPS at the end of the bloom corresponded to the usual second seasonal peak of biomass in summer related to the recruitment of the new generation (Hopkins, 1971) and exceed estimates made in earlier dates in the season and in areas outside of the bloom distribution.

Diel vertical migration probably had an effect on the size spectrum of abundance of zooplankton, but lack of wire time did not allow us to investigating further this component. However, almost all zooplankton taxa do perform vertical migrations that influence their vertical distribution in space and time (Ward et al., 1995).

4.2. *Mesozooplankton respiration and ingestion*

Respiration rates measured during the survey are in the higher range of published values for Antarctic zooplankton. Regarding copepods, Mayzaud et al. (2002a, b) obtained slightly lower values for the same area, but later in the season (September–October). Our values were similar or higher than measurements made by Schnack et al. (1985) in the Peninsula region and Drits et al. (1994) in the Weddell Sea. For the other zooplanktonic organisms, our data are consistent with published respiration rates (Ikeda and Fay, 1981; Ikeda and Mitchell, 1982; Alcaraz et al., 1998).

Based on our measurements of respiration rates and the high dominance of copepods in the region, the use of the allometric relationship between respiration rates and body weight of copepods established by Mayzaud et al. (2002a) delivers a reasonable estimate of the total community respiration. The integrated respiration rates of the whole mesozooplankton community during KEOPS were high compared to Mayzaud et al. (2002a) due to the high biomass of zooplankton found during KEOPS. However,

the specific respiration rates of the whole mesozooplankton community (~3.00% ± 0.36) is a standard value for this area (Mayzaud et al., 2002a).

The integrated ingestion rates of the whole zooplankton community calculated with our allometric relationship (see Section 2) applied to the OPC size spectra is around 3 times the respiration rate (Fig. 11). In comparable bloom conditions, Schnack et al. (1985) and Mayzaud et al. (2002b) measured ingestion rates 2–4 times higher than the respiration rates to cover for carbon requirement for growth or reproduction.

In its early phase, the highest values of measured gut contents are comparable to gut fullness reported for Antarctic copepods in other areas (Atkinson et al., 1992a, b; Drits et al., 1994; Tirelli and Mayzaud, 1999; Mayzaud et al., 2002a). Low gut content observed afterwards may be subject to different hypotheses. Changes in gut levels and percentage of individuals with full guts depend on the relative distribution of phytoplankton and grazers (Atkinson et al., 1992b). These low gut content values cannot be related to a reduced energy uptake by the mesozooplankton, due to the high respiration rates and the active growth and development phase during the whole survey, but rather to a shift of prey consumed from fresh phytoplankton to phyto-detritus or animal sources.

In regions where phytoplankton is low, many factors contribute to the functional response of copepods, omnivory being the most efficient feeding strategy (Gentleman et al., 2003). The various resources of mesozooplankton dominated by copepods are (1) phytoplankton both large cells, as diatoms, and small cells, (2) microzooplankton, mainly ciliates, (3) detritus, and (4) other zooplankton including cannibalism. Most of the dominant Antarctic copepods grow and reproduce whatever the phytoplankton concentration using other food resources such as microzooplankton (Atkinson, 1994, 1996; Mayzaud et al., 2002b) or small zooplankon, like nauplii and small copepodites (Metz and Schnack-Schiel, 1995; Atkinson, 1995) or on detritus (Michels and Schnack-Schiel, 2005).

In comparison with other estimates of grazing rates by copepods in Antarctica (Drits et al., 1994; Schnack et al., 1985; Mayzaud et al., 2002a; Schultes et al., 2006), the phytoplankton concentrations above the MLD (Uitz et al., submitted for publication) at A3 (1–2 μg Chl $a\,L^{-1}$) and at C11 (0.15–0.2 μg Chl $a\,L^{-1}$) are, respectively, sub-optimal and limiting for copepods. Sarthou et al. (2008), based on a limited number of experiments, estimated the copepod grazing to be 1–10% of the chlorophyll stocks. From our measurements of gut pigments contents, assuming a 30% loss of pigment into non-fluorescence substance (Mayzaud and Razouls, 1992), we estimate the daily impact of grazing of the two sizes of copepods on the phytoplankton stocks >10 μm. This impact at A3 decreased by a factor ~10 between the beginning and the end of the bloom, from 3.87 ± 2.86% to 0.42 ± 0.12% d^{-1} for large copepods and from 24.33 ± 14.31% to 0.20 ± 0.08% d^{-1} for the small copepods. Large and small copepods at C11 removed 1.98 ± 2.58% and 4.86 ± 3.29% d^{-1}, respectively. We calculated the daily ratio (% copepod body carbon per day) large and small copepods could cover from grazing on phytoplankton as >10 μm. Only small copepods at A3 during the first part of our survey could have thrived on phytoplankton with values (51.83 ± 14.11% body carbon d^{-1}) above the minimum of 20% body carbon d^{-1}, implying that food was not limited (Herman, 1983). At C11 and at A3 during the later stage of the bloom daily ratios, based only on phytoplankton food sources, were never met (2.22 ± 1.19% and 1.04 ± 0.46% body carbon d^{-1} for large copepods, respectively, and 5.23 ± 1.51% and 3.02 ± 1.08% body carbon d^{-1} for small copepods, respectively). In both areas, stocks of ciliates and HNF are probably controlled by mesozooplankton, but they represent a low contributor to the mesozooplankton ingestion at A3 at the beginning of the bloom, whereas they could be a sufficient food complement at A3 during the later stage of the bloom and at C11, when feeding on phytoplankton was low. Other potential food resources as detritus (i.e. phytodetritus, fecal pellets, dead bodies) and cannibalism could occur but cannot be estimated.

5. Conclusions

Recent iron-fertilization experiments launched from research vessels triggered very large blooms, covering several square miles, but the long-term impact of such artificial bloom on higher trophic levels could not be detected due to the length of the experiments (from a few days to over a month) in comparison to the time-scale from weeks to months needed for zooplankton community to develop (Rollwagen-Bollens and Landry, 2000; Zeldis, 2001; Tsuda et al., 2005, 2006). Obviously during KEOPS, throughout the second half of the natural long-term bloom (>3 months), the mesozooplankton populations were already well established. The zooplankton biomass did not increase, and species composition, dominated by copepods, did not change significantly. Such apparent absence of numerical response to iron-enriched bloom at high latitudes has been observed during SOIREE, SEEDS and SERIES (Zeldis, 2001; Tsuda et al., 2005, 2006). In the Southern Ocean, many zooplankton species are able to maintain high stocks of overwintering forms during winter time (Atkinson, 1998), which use the bloom to initiate new generations or to complete their life cycle. The high numbers of juvenile forms of copepods during KEOPS and the high respiration rates indicate active growth and development. More investigations are needed to study the mesozoopankton response in term of physiological and demographical rates to show how much the variability in intensity and duration of the recurrent bloom in Kerguelen could influence the persistence of these populations. Gut content observations show that the direct mesozooplankton grazing on phytoplankton probably played a minor role in the control of the primary production as shown in many studies in Antarctic waters (Hopkins, 1987; Atkinson

and Shreeve, 1995; Atkinson et al., 1996; Ward et al., 1995). However, its role as top predator of the planktonic system and particularly its control of the microzooplanton component should be investigated more thoroughly.

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References

Alcaraz, M., Saiz, E., Fernandez, J.A., Trepat, I., Figueiras, F., Calbet, A., Bautista, B., 1998. Antarctic zooplankton metabolism: carbon requirements and ammonium excretion of salps and crustacean zooplankton in the vicinity of the Bransfield strait during January 1994. Journal of Marine Systems 17, 347–359.

Armand, L., Cornet-Barthaux, V., Mosseri, J., Queguiner, B., 2008. Late summer diatom biomass and community structure on and around the naturally iron-fertilized Kerguelen Plateau in the Southern Ocean. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2007.12.031].

Atkinson, A., 1994. Diets and feeding selectivity among the epipelagic copepod community near South Georgia in summer. Polar Biology 14, 551–560.

Atkinson, A., 1995. Omnivory and feeding selectivity in five copepod species during spring in the Bellingshausen Sea, Antarctica. ICES Journal of Marine Science 52, 385–396.

Atkinson, A., 1996. Subantarctic copepods in an oceanic, low chlorophyll environment: ciliate predation, food selectivity and impact on prey populations. Marine Ecology Progress Series 130, 85–96.

Atkinson, A., 1998. Life cycle strategies of epipelagic copepods in the Southern Ocean. Journal of Marine Systems 15, 289–311.

Atkinson, A., Shreeve, R.S., 1995. Response of copepod community to a spring bloom in the Bellingshausen Sea. Deep-Sea Research I 42, 1291–1311.

Atkinson, A., Ward, P., Williams, R., Poulet, S.A., 1992a. Diel vertical migration and feeding of copepods at an oceanic site near South Georgia. Marine Biology 113, 583–593.

Atkinson, A., Ward, P., Williams, R., Poulet, S.A., 1992b. Feeding rates and diel vertical migration of copepods near South Georgia: comparison of shelf and oceanic sites. Marine Biology 114, 49–56.

Atkinson, A., Shreeve, R.S., Pakhomov, E.A., Priddle, J., Blight, S.P., Ward, P., 1996. Zooplankton response to a phytoplankton bloom near South Georgia, Antarctica. Marine Ecology Progress Series 144, 195–210.

Beaulieu, S.E., Mullin, M.M., Tang, V.T., Pyne, S.M., King, A.L., Twining, B.S., 1999. Using an optical plankton counter to determine the size distributions of preserved zooplankton samples. Journal of Plankton Research 21, 1939–1956.

Blain, S., Tréguer, P., Belviso, S., Bucciarelli, E., Denis, M., Desabre, S., Fiala, M., Martin-Jézéquel, V., Le Fèvre, J., Mayzaud, P., Marty, J.-C., Razouls, S., 2001. A biogeochemical study of the island mass effect in the context of the iron hypothesis: Kerguelen Islands, Southern Ocean. Deep-Sea Research I 48, 163–187.

Blain, S., Quéguiner, B., Armand, L., Belviso, S., Bombled, B., Bopp, L., Bowie, A., Brunet, C., Brussaard, C., Carlotti, F., Christaki, U., Corbière, A., Durand, I., Ebersbach, F., Fuda, J.-L., Garcia, N., Gerringa, L., Griffiths, B., Guigue, C., Guillerm, C., Jacquet, S., Jeandel, C., Laan, P., Lefèvre, D., Lomonaco, C., Malits, A., Mosseri, J., Obernosterer, I., Park, Y.-H., Picheral, M., Pondaven, P., Remeny, T., Sandroni, V., Sarthou, G., Savoye, N., Scouarnec, L., Souhaut, M., Thuiller, D., Timmermans, K., Trull, T., Uitz, J., van-Beek, P., Veldhuis, M., Vincent, D., Viollier, E., Vong, L., Wagener, T., 2007. Impacts of natural iron fertilisation on the Southern Ocean. Nature 446, 1070–1074.

Blain, S., Sarthou, G., Laan, P., 2008. Distribution of dissolved iron during the natural iron fertilisation experiment KEOPS (Kerguelen Plateau, Southern Ocean). Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2007.12.028].

Caparroy, P., Pérez, M.T., Carlotti, F., 1998. Feeding behaviour of *Centropages typicus* in calm and turbulent conditions. Marine Ecology Progress Series 113, 110–115.

Christaki, U., Obernosterer, I., Van Wambeke, F., Veldhuis, M.J.W., Garcia, N., Catala, P., 2008. Microbial food web structure in a naturally iron fertilized area in the Southern Ocean (Kerguelen Plateau). Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2007.12.009].

Drits, A.V., Pasternak, A.F., Kosobokova, K.N., 1994. Physiological characteristics of the Antarctic copepod *Calanoides acutus* during late summer in the Weddell Sea. Hydrobiologia 292/293, 201–207.

Edvardsen, A., Zhou, M., Tande, K.S., Zhu, Y., 2002. Zooplankton population dynamics: measuring in situ growth and mortality rates using an optical plankton counter. Marine Ecology Progress Series 227, 205–219.

Errhif, A., Razouls, C., Mayzaud, P., 1997. Composition and community structures of pelagic copepods in the Indian sector of the Antarctic Ocean during the end of the austral summer. Polar Biology 17, 418–430.

Focal Technologies Inc., 1997. Optical Plankton Counter User's Guide. Dartmouth, NS, Canada, 23pp.

Fonda Umani, S., Monti, M., Bergamasco, A., Cabrini, M., De Vittor, C., Burba, N., Del Negro, P., 2005. Plankton community structure and dynamics versus physical structure from Terra Nova Bay to Ross Ice Shelf (Antarctica). Journal of Marine Systems 55, 31–46.

Fransz, H.G., Gonzalez, S.R., 1997. Latitudinal metazoan plankton zones in the Antarctic Circumpolar Current along 6°W during austral spring 1992. Deep-Sea Research II 44, 395–414.

Froneman, P.W., Ansorge, I.J., Pakhomov, E.A., Lutjeharms, J.R.E., 1999. Plankton community structure in the physical environment surrounding the Prince Edward Islands (Southern Ocean). Polar Biology 22, 145–155.

Gallienne, C.P., Robins, D.B., 1998. Trans-oceanic characterization of zooplankton community size structure using an optical plankton counter. Fisheries Oceanography 7, 147–158.

Gentleman, W., Leising, A., Frost, B., Strom, S., Murray, J., 2003. Functional responses for zooplankton feeding on multiple resources: a review of assumptions and biological dynamics. Deep-Sea Research II 50, 2847–2875.

Grant, S., Ward, P., Murphy, E., Bone, D., Abbott, S., 2000. Field comparison of an LHPR net sampling system and an optical plankton counter (OPC) in the Southern Ocean. Journal of Plankton Research 22, 619–638.

Herman, A.W., 1983. Vertical distribution patterns of copepods, chlorophyll, and production in northeastern Baffin Bay. Limnology and Oceanography 28 (4), 709–719.

Hernández-León, S., Montero, I., 2006. Zooplankton biomass estimated from digitalized images in Antarctic waters: A calibration exercise. Journal of Geophysical Research 111, C05S09.

Hernández-León, S.C., Almedia, C., Portillo Hahnefeld, A., Gómez, M., Montero, I., 2000. Biomass and potential feeding, respiration and

growth of zooplankton in the Bransfield Strait (Antarctic Peninsula) during austral summer. Polar Biology 23, 679–690.
Holm-Hansen, O., Lorenzen., C., Holmes, R., Strickland, J., 1965. Fluorimetric determination of chlorophyll. Journal du Conseil/Conseil International pour l' Exploration de la Mer 30, 3–15.
Hopkins, T.L., 1971. Zooplankton standing crop in the Pacific sector of the Antarctic. In: Llano, G.W., Wallen, I.E. (Eds.), Biology of the Antarctic Seas, vol. 17. American Geophysical Union, Washington, DC, pp. 347–362.
Hopkins, T.L., 1987. Midwater food web in McMurdo Sound, Ross Sea, Antarctica. Marine Biology 96, 96–106.
Hunt, B.P.V., Pakhomov, E.A., 2003. Mesozooplankton interactions with the shelf around the sub-Antarctic Prince Edward Islands archipelago. Journal of Plankton Research 25, 885–904.
Huntley, M.E., Zhou, M., Nordhausen, W., 1995. Mesoscale distribution of zooplankton in the California Current in late spring, observed by optical plankton counter. Journal of Marine Systems 53, 647–674.
Ikeda, T., Fay, A.W., 1981. Metabolic activity of zooplankton of the Antarctic Ocean. Australian Journal of Marine and Freshwater Research 32, 921–930.
Ikeda, T., Mitchell, A.W., 1982. Oxygen uptake, ammonia excretion and phosphate excretion by krill and other Antarctic zooplankton in relation to their body size and chemical composition. Marine Biology 3, 283–298.
Labat, J.P., Mayzaud, P., Dallot, S., Errhif, A., Razouls, S., Sabini, S., 2002. Mesoscale distribution of zooplankton in the Sub-Antarctic Frontal system in the Indian part of the Southern Ocean: a comparison between optical plankton counter and net sampling. Deep-Sea Research I 49, 735–749.
Mackas, D., Bohrer, R., 1976. Fluorescence analysis of plankton gut contents and an investigation of die1 feeding patterns. Journal of Experimental Marine Biology and Ecology 25, 77–85.
Mayzaud, P., Razouls, S., 1992. Degradation of gut pigment during feeding by a subantarctic copepod: importance of feeding history and digestive acclimation. Limnology and Oceanography 37, 393–404.
Mayzaud, P., Razouls, S., Errhif, A., Tirelli, V., Labat, J.P., 2002a. Feeding, respiration and egg production rates of copepods during austral spring in the Indian sector of the Antarctic Ocean: role of the zooplankton community in carbon transformation. Deep-Sea Research I 49, 1027–1048.
Mayzaud, P., Tirelli, V., Errhif, A., Labat, J.P., Razouls, S., Perissinotto, R., 2002b. Carbon intake by zooplankton. Importance and role of zooplankton grazing in the Indian sector of the Southern Ocean. Deep-Sea Research II 49, 3169–3187.
Mayzaud, P., Boutoute, M., Gasparini, S., Mousseau, L., Lefevre, D., 2005. Respiration in marine zooplankton—the other side of the coin: CO_2 production. Limnology and Oceanography 50, 291–298.
Metz, C., Schnack-Schiel, S.B., 1995. Observations on carnivorous feeding in Antarctic calanoid copepods. Marine Ecology Progress Series 129 (1–3), 71–75.
Michels, J., Schnack-Schiel, S.B., 2005. Feeding in dominant Antarctic copepods—does the size of the mandibular gnathobases relate to diet? Marine Biology 146, 483–495.
Mongin, M., Molina, E., Trull, T., 2008. Seasonality and scale of the Kerguelen Plateau phytoplankton bloom: a remote sensing and modeling analysis of the influence of natural iron fertilization in the Southern Ocean. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2007.12.039].
Moore, J.K., Abbott, M.R., 2000. Phytoplankton chlorophyll distributions and primary production in the Southern Ocean. Journal of Geophysical Research 105, 28,709–28,722.
Mosseri, J., Queguiner, B., Armand, L., Cornet-Barthaux, V., 2008. Impact of iron on silicon utilization by diatoms in the Southern Ocean: a case of Si/N cycle decoupling in a naturally iron-enriched area. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2007.12.003].
Obernosterer, I., Christaki, U., Lefevre, D., Catala, P., Van Wambeke, F., Le Baron, P., 2008. Rapid bacterial mineralization of organic carbon produced during a phytoplankton bloom induced by natural iron fertilization in the Southern Ocean. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2007.12.005].
Pakhomov, E.A., McQuaid, C.D., 1996. Distribution of surface zooplankton and seabirds across the Southern Ocean. Polar Biology 16, 271–286.
Park, Y.H., Fuda, J.L., Durand, I., Naveira Garabato, A.C., 2008a. Internal tides and vertical mixing over the Kerguelen Plateau. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2007.12.027].
Park, Y.H., Roquet, F., Durand, I., Fuda, J.L., 2008b. Large scale circulation over and around the Northern Kerguelen Plateau. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2007.12.030].
Razouls, S., Koubbi, P., Mayzaud, P., 1996. Spatio-temporal distribution of mesozooplankton in a sub-Antarctic coastal basin of the Kerguelen Archipelago (southern Indian Ocean). Polar Biology 16, 581–587.
Razouls, S., de Bovée, F., Delille, D., Fiala, M., Mayzaud, P., 1997. Temporal variability of bacteria, phytoplankton and zooplankton assemblages of the sub-Antarctic Morbihan Bay (Kerguelen Archipelago). In: Battaglia, B., Valencia, J., Walton, D.W.H. (Eds.), Antarctic Communities: Species, Structure and Survival. Cambridge University Press, Cambridge, pp. 86–92.
Razouls, S., Du Réau, G., Guillot, P., Maison, J., Jeandel, C., 1998. Seasonal abundance of copepod assemblage and grazing pressure in the Kerguelen Island area (Southern Ocean). Journal of Plankton Research 20, 1599–1614.
Riandey, V., Champalbert, G., Carlotti, F., Taupier-Letage, I., Thibault-Botha, D., 2005. Zooplankton distribution related to the hydrodynamic features in the Algerian Basin (western Mediterranean Sea) in summer 1997. Deep-Sea Research I 52, 2029–2048.
Rollwagen-Bollens, G.C., Landry, M.R., 2000. Biological response to iron fertilization in the eastern equatorial Pacific (IronEx II). II. Mesozooplankton abundance, biomass, depth distribution and grazing. Marine Ecology Progress Series 201, 43–56.
Sarthou, G., Vincent, D., Christaki, U., Obernosterer, I., Timmermans, K.R., Brussaard, C.P.D., 2008. The fate of biogenic iron during a phytoplankton bloom induced by natural fertilization: impact of copepod grazing. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2007.12.033].
Schlitzer, R., 2002. Carbon export fluxes in the Southern Ocean: results from inverse modelling and comparison with satellite based estimates. Deep-Sea Research II 49, 1623–1644.
Schnack, S.B., Smetacek, V., Bodungen, B., Stegmann, P., 1985. Utilisation of phytoplankton by copepods in Antarctic water during spring. In: Gray, J., Christiansen, M.E. (Eds.), Marine Biology of Polar Region and Effects of Stress on Marine Organisms. Wiley, New York, pp. 65–81.
Schultes, S., Verity, P.G., Bathmann, U., 2006. Copepod grazing during an iron-induced diatom bloom in the Antarctic Circumpolar Current (EisenEx): I. Feeding patterns and grazing impact on prey populations. Journal of Experimental Marine Biology and Ecology 338 (1), 16–34.
Semelkina, A.N., 1993. Development of the zooplankton in the Kerguelen Island region in the years 1987–1988. In: Duhamel, G. (Ed.), Campagnes SKALP 1987 et 1988 aux îles Kerguelen à bord des navires 'SKIF' et 'KALPER'. Institut Français pour la recherche et la technologie polaires, Rapports des campagnes à la mer 93–01, pp. 90–103.
Shreeve, R.S., Ward, P., 1998. Moulting and growth of the early stages of two species of Antarctic calanoid copepod in relation to differences in food supply. Marine Ecology Progress Series 233, 169–183.
Shreeve, R.S., Ward, P., Whitehouse, M.J., 2002. Copepod growth and development around South Georgia: relationships with temperature, food and krill. Marine Ecology Progress Series 233, 169–183.
Sourisseau, M., Carlotti, F., 2006. Spatial distribution of zooplankton size spectra on the French continental shelf of the Bay of Biscay during spring 2000 and 2001. Journal of Geophysical Research 111, C05S09.
Tirelli, V., Mayzaud, P., 1999. Gut evacuation rates of Antarctic copepods during austral spring. Polar Biology 21, 197–200.
Tsuda, A., Saito, H., Nishioka, J., Ono, T., 2005. Mesozooplankton responses to iron-fertilization in the western subarctic Pacific (SEEDS2001). Progress in Oceanography 64 (2–4), 237–251.

Tsuda, A., Saito, H., Nishioka, J., Ono, T., Noiri, Y., Kudo, I., 2006. Mesozooplankton response to iron enrichment during the diatom bloom and bloom decline in SERIES (NE Pacific). Deep-Sea Research II 53, 2281–2296.

Uitz J., Claustre, H., Garcia, N., Griffiths, B.F., Ras, J., Sandroni, V. A phytoplankton class-specific primary production model applied to the Kerguelen Islands region (Southern Ocean). Deep-Sea Research I (in revision).

Van Beek, P., Bourquin, M., Reyss, J.L., Souhaut, M., Charette, M., Jeandel, C., 2008. Radium isotopes to investigate the water mass pathways on the Kerguelen Plateau (Southern Ocean). Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2007.12.025].

Vanderploeg, H.A., Roman, M.R., 2006. Introduction to special section on analysis of zooplankton distributions using the optical plankton counter. Journal of Geophysical Research 111, C05S09.

Wang, R., Conover, R.J., 1986. Dynamics of gut pigments in the copepod *Temora longicornis* (Muller) and the determination of *in situ* grazing rates. Limnology and Oceanography 31, 867–877.

Ward, P., Shreeve, R.S., 1999. The spring mesozooplankton community at South Georgia: a comparison of shelf and oceanic sites. Polar Biology 22, 289–301.

Ward, P., Atkinson, A., Murray, A.W.A., Wood, A.G.W., Williams, R., Poulet, S.A., 1995. The summer zooplankton community at South Georgia: biomass, vertical migration and grazing. Polar Biology 15, 195–208.

Woodd-Walker, R.S., Gallienne, C.P., Robins, D.B., 2000. A test for optical plankton counter (OPC) coincidence and a comparison of OPC derived and conventional measures of plankton abundance. Journal of Plankton Research 22, 473–483.

Yentsch, C.S., Menzel, D.W., 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep-Sea Research I 10, 221–231.

Zeldis, J., 2001. Mesozooplankton community composition, feeding, and export production during SOIREE. Deep-Sea Research II 48, 2615–2634.

Zhou, M., Huntley, M.E., 1997. Population dynamics theory of plankton based on biomass spectra. Marine Ecology Progress Series 159, 61–73.

Zhou, M., Tande, K. (Eds.), 2001. Global Ocean Ecosystem Dynamics, Optical Plankton Counter Workshop. GLOBEC Report No. 17, GLOBEC International Project Office, Plymouth, UK, 67pp.