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Seasonal changes in the vertical distribution and community structure of Antarctic macrozooplankton and micronekton

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ABSTRACT

The macrozooplankton and micronekton community of the Lazarev Sea (Southern Ocean) was investigated at 3 depth layers during austral summer, autumn and winter: (1) the surface layer (0–2 m); (2) the epipelagic layer (0–200 m); and (3) the deep layer (0–3000 m). Altogether, 132 species were identified. Species composition changed with depth from a euphausiid-dominated community in the surface layer, via a siphonophore-dominated community in the epipelagic layer, to a chaetognath-dominated community in the deep layer. The surface layer community predominantly changed along gradients of surface water temperature and sea ice parameters, whereas the epipelagic community mainly changed along hydrographical gradients. Although representing only 1% of the depth range of the epipelagic layer, mean per-area macrofauna densities in the surface layer ranged at 8% of corresponding epipelagic densities in summer, 6% in autumn, and 24% in winter. Seasonal shifts of these proportional densities in abundant species indicated different strategies in the use of the surface layer, including both hibernal downward and hibernal upward shift in the vertical distribution, as well as year-round surface layer use by Antarctic krill. These findings imply that the surface layer, especially when it is ice-covered, is an important functional node of the pelagic ecosystem that has been underestimated by conventional depth-integrated sampling in the past. The exposure of this key habitat to climate-driven forces most likely adds to the known susceptibility of Antarctic pelagic ecosystems to temperature rise and changing sea ice conditions.

1. Introduction

More than 90% of the Southern Ocean primary production occurs in pelagic offshore waters (Arrigo et al., 2008). The pelagic ecosystem of the Southern Ocean differs from most other pelagic systems on earth in the frequent dominance of a single micronektonic crustacean, Antarctic krill *Euphausia superba* (Knox, 2007). Due to its high abundance and economic importance, Antarctic krill has received disproportionally high attention compared to other species. Besides Antarctic krill, however, the Southern Ocean hosts a unique and diverse pelagic fauna that by itself contributes substantially to the carbon and energy budgets of its ecosystems (Collins and Rodhouse, 2006; Hunt et al., 2008; Kruse et al., 2010a).

The pelagic fauna of the Southern Ocean is characterised by a largely latitudinal zonation of communities (Hosie, 1994; Lutjeharms, 1990; Pakhomov et al., 2000). The most widely accepted biogeographical separation of the Southern Ocean distinguishes between a northerly Permanently Open Ocean Zone (POOZ), the Seasonal Ice Zone (SIZ), and a Coastal and Continental Shelf Zone (Tréguer and Jacques, 1992). The Antarctic SIZ is characterised by strong seasonal variability in temperature, light regime, and sea ice coverage (Hempel, 1985; Murphy et al., 2007). As a result, phytoplankton primary production is high during summer months, and drops to nearly zero in winter (Arrigo et al., 2008). Pelagic organisms respond to this strong pulse in productivity by adaptations in their life cycles,

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behaviour, horizontal and vertical distribution patterns (e.g. Atkinson, 1998).

For the understanding of ecosystem functioning in the Southern Ocean including carbon flux and carbon cycling, knowledge on seasonal changes in zooplankton communities in combination with species biology is vitally important (Cornejo-Donoso and Antezana, 2008). Knowledge about the seasonal variability in Antarctic pelagic communities, however, is still limited, mainly due to a lack of multi-seasonal studies in the same geographic area. As highlighted by Hunt et al. (2011), logistical difficulties under the prevailing extreme conditions continue to hinder the collection of data, especially in winter. Of the seasonal studies that have been conducted, the majority focused on just a few taxa, including Antarctic krill and large calanoid copepods. These studies considered the aspects of seasonal vertical distribution (Atkinson and Sinclair, 2000; Schnack-Schiel et al., 1998), life cycle (Atkinson, 1998; Nicol, 2006), and overwintering strategies (Daly, 2004; Frazer et al., 2002; Meyer et al., 2010). A review of the pertinent literature shows that the few available multi-seasonal macrozooplankton/micronekton community studies were mostly situated in shelf or shelf-break waters, and are thus not fully representative for the vast deep-sea basins dominating the Southern Ocean (e.g. Ashjian et al., 2004; Lancraft et al., 1989; Siegel and Piatkowski, 1990). Only Hosie (1994), Siegel and Harm (1996), and Fisher et al. (2004) analysed the macrofauna composition in deep sea areas of the Prydz Bay region (east Antarctica), the southern Bellingshausen Sea, and the north-western Weddell Sea, respectively.

A habitat largely neglected in the past is the surface layer, i.e. the upper few metres of the water column. Incidental reports from the Southern Ocean, dating from the early days of Antarctic research to modern-day observations, have emphasised the significance of the surface layer as a habitat often hosting increased abundances of life (Hardy and Gunther, 1935; Kaufmann et al., 1993; Krakatitsa et al., 1993; Pakhomov, 1993b). The surface layer has also been proposed as an important nursery habitat for Antarctic fishes (Hubold, 1985; White and Piatkowski, 1993). In most recent studies, however, the surface layer is integrated in a deeper epipelagic depth stratum, typically ranging from the surface to 50–300 m depth (e.g. Donnelly et al., 2006; Fisher et al., 2004; Hunt et al., 2007).

From late autumn until early summer, the surface layer of the Antarctic SIZ is covered by sea ice. During this period, the bulk of primary production occurs within sea ice rather than in the water column (Arrigo and Thomas, 2004; Lizotte, 2001; McMinn et al., 2010), making the ice–water interface layer a potentially important site of energy transmission between sea ice biota and the pelagic food web. Indeed, the ice-water interface layer has been reported to be at least a seasonal key habitat for Antarctic krill (Daly, 1990; Flores et al., 2012; Marschall, 1988), and some copepod species (Hoshiai et al., 1987; Schnack-Schiel et al., 2008). However, the significance of this habitat for other macrofauna species remains largely unknown. Many Antarctic top predators directly or indirectly depend on the surface layer community (Ainley et al., 1986). In sea ice situations, however, the paradox of high densities of endothermic top predators, combined with apparently low abundance of primary and secondary producers in the water column, strongly implies that the ice–water interface layer provides food for grazing plankton and nekton which in turn nourish higher trophic levels (van Franeker et al., 1997, 2001).

Our survey area in the Lazarev Sea extends between 6°W and 3°E, and from 60°S to over 70°S (Fig. 1). While the largest part of the investigated area is bathymetrically considered deep-sea, it also encompasses an isolated topographic feature, a sea mount named Maud Rise, which is centred at roughly 65°S, 3°E and rises by more than 3000 m from the surrounding deep-sea floor. The southern limit of the survey area was situated over the Antarctic continental slope. The Lazarev Sea is subject to pronounced seasonal variation. At the end of austral winter it is typically completely covered by sea ice, while at the end of austral summer it is entirely ice-free. In terms of general oceanography, the Lazarev Sea is governed by the southern limb of the Weddell Gyre, which transports water of more northerly, circumpolar origin in a south-westward direction. A second, westward setting current core is found above the continental shelf break, associated with the Antarctic Slope Front (Cisewski et al., 2011). Between 200 and 400 m depth, the southern limb of the Weddell Gyre incorporates Warm Deep Water (WDW, Carmack and Foster, 1975), also referred to as Upper Circumpolar Deep Water (UCDW, Orsi et al., 1993). Topographic interaction of the gyre flow with Maud Rise is considered as exerting an influence on the regional oceanographic conditions (Bersch et al., 1992; De Steur et al., 2007; Muench et al., 2001).

Several studies have focused on macrozooplankton and micronekton from the Lazarev Sea, partly using subsets of the data analysed in the present investigation. These studies, however, were either limited to one depth stratum (Flores et al., 2011; Hunt et al., 2011), or focused on few taxa (Flores et al., 2012; Kruse et al., 2010b; Meyer et al., 2010; Siegel, 2012). Earlier studies included only one season (Boysen-Ennen and Piatkowski, 1988; Efremenko, 1991; Pakhomov et al., 1994). With a multi-seasonal synthesis of data collected from 3 different depth strata, the present study set out to provide a synoptic investigation of the seasonal changes in the depth distribution of macrozooplankton and micronekton species and communities, and their relationship with the environment. We aimed to (1) conduct an inventory of the pelagic macrozooplankton and micronekton community in the Lazarev Sea from the surface to 3000 m depth; (2) investigate seasonal changes in the community composition and the distribution of dominant species within and between the surface (0–2 m) and the epipelagic (0–200 m) depth layers; and (3) analyse the relationship between the community structure and environmental drivers, including sea ice properties.

2. Material and methods

2.1. Sampling area

Data were collected during three expeditions of RV “*Polarstern*” in the Lazarev Sea in austral summer (ANT XXIV-2, 28 November 2007 to 4 February 2008), autumn (ANT XXI-4, 27 March to 6 May 2004), and winter (ANT XXIII-6, 17 June to 21 August 2006). The expeditions were part of a multi-year field experiment embedded in the largely German-funded *LA*zarev Sea *KRI*ll *S*tudy (LAKRIS) dedicated to the investigation of the distribution, population dynamics, and physiology of Antarctic krill *Euphausia superba*. The LAKRIS surveys sampled a regular station grid of 3–4 meridional transects with a spacing of 2–3° longitude and a latitudinal station spacing of 20–30 nm, ranging from 6°W to 3°E and from 60°S to the continental coast at approximately 71°S (Fig. 1). Here we present data collected in three different depth layers, which are referred to as the ‘surface layer’ (0–2 m), the ‘epipelagic layer’ (0–200 m) and the ‘deep layer’ (500–2500 m in summer and 0–3000 m in winter).

2.2. Hydrography and environmental data

Vertical profiles of temperature, salinity and density were derived from measurements made by lowering a CTD (conductivity, temperature, depth) probe to depths varying between 1000 m and the sea floor at LAKRIS grid stations (49 stations in autumn 2004, 59 in winter 2006 and 50 in summer 2007/2008). The CTD used was supplemented by an altimeter to measure the distance to the sea floor, and a transmissometer to measure the attenuation of

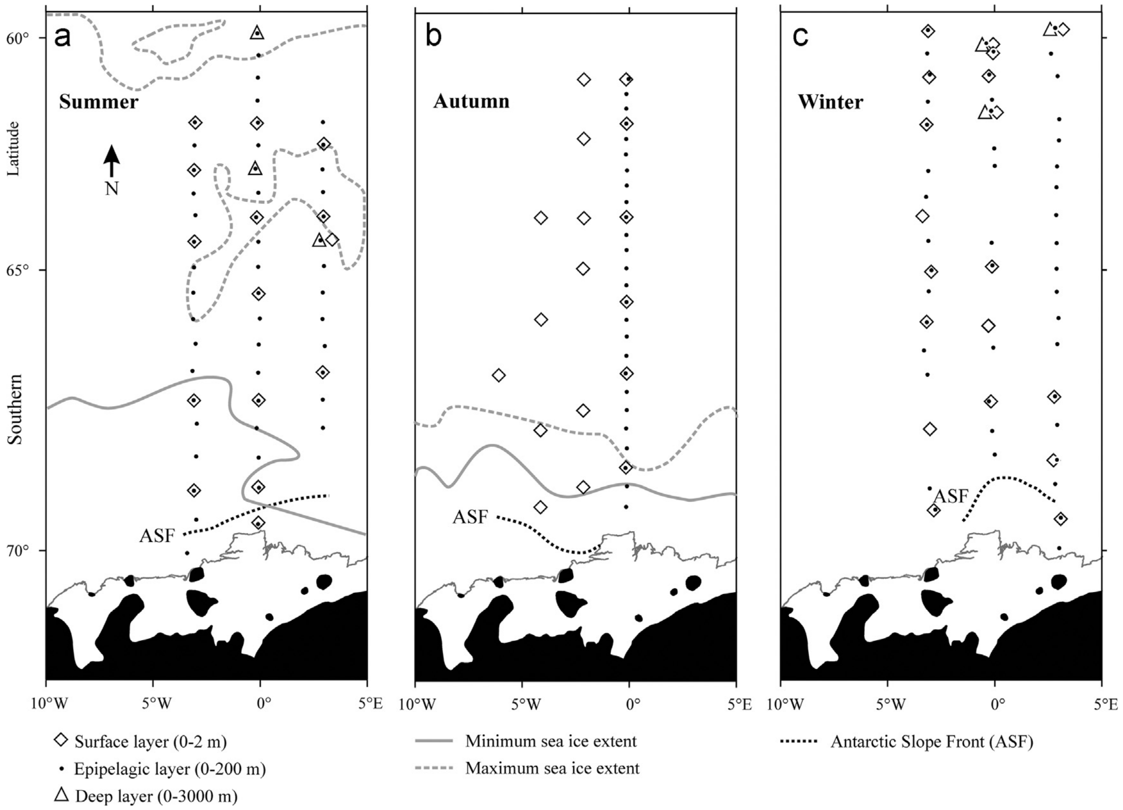

Fig. 1. Sampling locations on the LAKRIS grid and ice coverage in (a) summer (2007/2008), (b) autumn (2004), and (c) winter (2006). Minimum and maximum sea ice extents during the sampling period are indicated by approximate 15% ice cover derived from satellite data. The entire survey area was covered by pack-ice in winter.

light, which in the open ocean is linearly correlated with the concentration of particulate organic carbon (Gardner et al., 2006). A chlorophyll-sensitive fluorometer (Dr. Haardt BackScat) was used in winter and summer to estimate the chlorophyll *a* concentration [mg m^{-3}] in the upper 200 m of the water column. A difference criterion was applied to estimate the mixed layer depth (MLD) from the density stratification. The MLD was defined as the depth at which the calculated *in situ* density increased vertically by $\Delta\sigma_T = 0.02$ compared to the surface value (Cisewski et al., 2008, 2005). A detailed description of the hydrographical sampling procedure was provided by Hunt et al. (2011) and Pakhomov et al. (2011).

Solar radiation [W m^{-2}] during each haul was measured by the ship's meteorological system. Bottom depth [m] was estimated for each station position using modelled global bathymetry from a publicly available database (Smith and Sandwell, 1997; http://topex.ucsd.edu/marine_topo/mar_topo.html). Sea ice conditions were monitored by an observer on board while the ship was steaming between stations, according to the method described in van Franeker et al. (1997). For the purpose of this study, the percentage of the water surface covered by sea ice and mean floe size estimated between stations per 10 min steaming block were averaged over station positions. On each transect, the ice edge was considered as the latitude from whereon northwards ice coverage was below 5%. The latitudinal distance to the ice edge was then calculated for each station. This value was negative for sampling locations situated in ice-covered areas and positive for open water locations.

2.3. Surface layer sampling

Surface and Under Ice Trawls (SUIT; van Franeker et al., 2009) were used to sample macrozooplankton and nekton in the upper 2 m of the water column. The net systems consisted of a steel frame with an approximately 2×2 m^2 net opening with a 15 m long 7 mm half-mesh commercial shrimp net attached to it. Large floaters at the top of the frame kept the net at the surface. To enable sampling under undisturbed ice, an asymmetric bridle forced the net to shear at an angle of approximately 60° starboard from the ship's track at a cable length of 120 m. In autumn (2004), a circular plankton net (diameter 50 cm, 0.3 mm mesh) was mounted inside the shrimp net to sample mesozooplankton. In winter (2006) and summer (2007/2008), the rear 3 m of the net were lined with 0.3 mm plankton gauze.

An acoustic Doppler Current Profiler (ADCP) was used in summer and winter to estimate the amount of water entering the net, and to analyse its flow properties. The device, a Nortek EasyV river velocity monitor, operates with two 2 MHz measuring beams situated at an angle of 50° against each other. The ADCP is capable of measuring current speed at an accuracy of 1% of the measured value at three different positions horizontally across the net opening. The central measuring cell was used to estimate the effective water distance passed (eD) as the sum of the products of the duration [s] and the current speed [m s^{-1}] of each measuring interval (5–20 s).

For SUIT hauls conducted in autumn, eD was estimated a posteriori by means of a linear regression of ADCP-estimated eD versus the ship's track distance during trawling from the 2006 and 2007/2008 current speed measurements ($\mathrm{eD} = 0.8 \times \text{Ship track distance} + 148$ m; $R^2 = 0.88$; $p < 0.05$). The amount of filtered water [m^3] and the surface area sampled [m^2] were calculated for each haul by multiplying eD with the net's opening area and the opening width, respectively. Standard hauls lasted 25 min, with a minimum of 15 and a maximum of 49 min and an average towing speed of 1.5–2.5 knots (0.8–1.3 m s^{-1}). During each trawl, changes in ship speed, ice coverage [%], ice thickness [cm], and irregularities were recorded by an observer watching the net from the ship.

Of the 57 quantitative SUIT hauls south of 59°S considered in this study, 18 were conducted in summer, 17 in autumn, and 22 in winter. The majority of hauls were conducted at night (Table 1). The catch was sorted immediately after the retrieval of the net. Displacement volume and number of individuals were noted for each species. For the purpose of this study, zooplankton <0.5 cm was excluded from analysis in all nets (Flores et al., 2011).

2.4. Epipelagic sampling

Standardized double-oblique hauls between 200 m and the surface were conducted with a Rectangular Midwater Trawl (RMT) at all LAKRIS grid stations during the summer (2007/2008) and winter (2006) expeditions (48 and 50 stations, respectively), and at the 26 stations south of 59°S situated on the Greenwich meridian in autumn (2004). The sampling device consisted of an RMT 1 (mesh size = 0.33 mm) mounted above an RMT 8 with net openings of 1 and 8 m^2, respectively. The RMT 8 had a mesh size of 4.5 mm at the opening and a cod end mesh size of 0.85 mm. A calibrated mechanical impeller flow meter mounted outside the net opening allowed the volume of water passing through the net to be estimated. The mean trawling speed was 2.5 knots (1.3 m s^{-1}) (Table 1). For the purpose of this study, only RMT 8 samples were analysed. Immediately after catch retrieval, the volume of the RMT 8 sample was measured, and euphausiids were removed. The remaining sample was quantitatively preserved in a 4% hexamine-buffered formaldehyde and seawater solution. Macrozooplankton and nekton were later identified to the lowest possible taxon and counted. A detailed description of the RMT sampling procedure was provided in Flores et al. (2008) and Hunt et al. (2011).

2.5. Deep layer sampling

A multiple RMT (equipped with three RMT 8 and three RMT 1 nets) was deployed for stratified mesopelagic sampling in summer (2007/2008). The RMT 8 nets sampled with cod end-buckets of approximately 26 l volume. In winter (2006), the single RMT used for epipelagic sampling was used for 3 double oblique hauls between the surface and ~3000 m. The mean ship speed was 1.5 knots (0.77 ms^{-1}) during heaving of the nets (Table 1). We estimated the volume filtered by the trawl by multiplying the mouth area of the trawl by the distance crossed by the net in the water. This was calculated from the ship's speed and the period of trawling, after the trawl was opened in the water. Immediately after sampling, several individuals of each species were sorted, identified and preserved at $-80\,^{\circ}$C for further analysis. The remaining sample was preserved in 4% hexamine-buffered formaldehyde and seawater solution and subsequently analysed in the home laboratories.

2.6. Data analysis

Volumetric and areal densities [ind. 1000 m^{-3} and ind.m^{-2}, respectively] were calculated for each species and net haul. In the summer (2007/2008) stratified deep layer samples, densities were calculated for each depth stratum, as well as for the whole depth range (500–2500 m). To investigate seasonal patterns in the distribution of animals in the surface versus the epipelagic layer, proportional areal surface layer densities were expressed as percentages of areal epipelagic densities at corresponding sampling locations. Locations where only one of the two layers was sampled were excluded from the calculation of proportional surface layer densities.

For comparative community analysis, data were grouped by sampling season, and day versus night hauls. Winter samples from the deep layer were excluded from this analysis, because the large integrated depth range (0–3000 m) strongly limited the comparability of these samples with the summer samples from the deep layer, as well as with the epipelagic (0–200 m) and surface layer (0–2 m) samples. Initial data exploration showed that the distribution of animal densities was highly skewed towards low abundances. The significance of different overall densities between groupings was therefore assessed using the Kruskal–Wallis test. This non-parametric test is robust to non-normal distribution of the data. Because it can be applied to a large variety of distributions, it is well suited to yield comparable results in our multi-species dataset.

Hierarchical cluster analysis and non-metric multi-dimensional scaling (NMDS, Field et al., 1982; Kruskal, 1964) were used to investigate the community structure. Multivariate analyses were based on a Bray–Curtis dissimilarity matrix produced from the Wisconsin double-standardised abundance data after square-root transformation. Standardisation was computed separately for each sampling season and depth layer. In Wisconsin double standardisation, species are first standardised by maxima and then sites by site totals (Bray and Curtis, 1957; Oksanen et al., 2008). Analysis of similarity (ANOSIM, Clarke and Warwick, 2001) was used to test for significant differences in community composition of the *a priori* defined station groupings, for example by sampling season. Taxa not determined to species level that possibly represented more than one species were excluded from community analysis.

Table 1
Sampling schemes and gear characteristics of the sampling conducted in the surface layer (0–2 m) and the epipelagic layer (0–200 m) in summer (2007/2008), autumn (2004) and winter (2006), and in the deep layer in summer (500–2500 m) and winter (0–3000 m). *n* = Number of hauls; vol = average volume of water filtered per haul.

	Summer			Autumn		Winter		
	Surface layer	Epip. layer	Deep layer	Surface layer	Epip. layer	Surface layer	Epip. layer	Deep layer
Depth range [m]	0–2	0–200	500–2500[a]	0–2	0–200	0–2	0–200	0–3000
No of depth strata	1	1	3	1	1	1	1	1
Mouth opening [m^2]	4.5	8.0	8.0	5.1	8.0	5.1	8.0	8.0
Codend mesh size [mm]	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
Trawling speed [Kn]	1.5–2.5	2.5	1.5–2.0	1.5–2.5	2.5	1.5–2.5	2.5	1.5
Vol [m^3]	7750	20784	86333	13450	18291	8370	19864	246667
n (Day)	7	41	3	1	10	3	5	2
n (Night)	11	9	0	16	16	19	43	1
n (Sea ice)	12	29	1	4	4	22	48	3
n (Open water)	6	21	2	13	22	0	0	0
Total *n*	18	50	3	17	26	22	48	3

[a] Out of the 3 stations sampled, the depth range of 1 station was between 500 and 1900 m.

The correlation of the community structure of macrofauna captured in the surface and epipelagic layers with environmental variables was investigated with NMDS techniques. The distance between two samples in an NMDS plot is proportional to their dissimilarity in species composition. Thus in our data, the two sampling stations in an NMDS plot with the greatest distance from each other differ most in zooplankton species composition and density, and vice versa. NMDS ordination is often considered the method of choice to investigate community structure in ecological datasets, because it is well suited for non-normal or highly skewed data (e.g. Hosie, 1994; Rothenberger et al., 2009).

As a first step to investigate possible relationships of the zooplankton community structure with environmental parameters, we used the BIO-ENV procedure (Clarke and Ainsworth, 1993) to estimate the subset of environmental parameters that has the highest correlation between the dissimilarity matrices of the zooplankton samples with those of the environmental parameters in each sampling season. The following 13 environmental parameters were included in the analysis:

- bottom depth [m]
- mixed layer depth (MLD) [m];
- integrated water temperature (0 m – MLD) [°C];
- integrated water temperature (0–200 m) [°C];
- integrated salinity (0 m – MLD);
- integrated salinity (0–200 m);
- integrated attenuation (0 m – MLD);
- integrated attenuation (0–200 m);
- integrated chlorophyll *a* conc. (0–200 m; not in autumn 2004) [mg m^{-2}];
- solar radiation [W m^{-2}];
- proportional ice coverage [%];
- mean floe size [m]
- distance to ice edge [km]

In BIO-ENV, dissimilarity matrices are calculated for single variables, and each combination of normalised environmental parameters using Euclidian distances. Correlations between the environmental dissimilarity matrices and the biological dissimilarity matrix (in this case a Bray–Curtis dissimilarity matrix) are then calculated, and *p*-values calculated by permutation. The subset of environmental parameters yielding the highest correlation with the station dissimilarity matrix is then selected as the 'best' subset. This approach is most effective when pairwise relationships among environmental variables (if present) are linear, and skewedness of data is avoided (Clarke and Ainsworth, 1993). Therefore, the environmental dataset was assessed using pair plots (termed 'draftsman plot' by Clarke and Ainsworth, 1993). According to this assessment, radiation, chlorophyll *a* concentration, MLD, proportional ice coverage and mean floe size were fourth-root transformed in order to compensate for non-linear relationships and skewedness.

The emerging set of environmental parameters having the 'best' correlation with the observed community structure in each sampling season was then further investigated by analysing the correlation of the environmental variables with the NMDS ordination. Significant correlations were projected as vectors on the ordination to visualise their relationship with the sample ordination. The vectors point into the direction of the most rapid change in the environmental variable, and their length is proportional to the correlation between ordination and environmental variable. The significance of correlations was tested with a randomized permutation test using 10,000 permutations.

All statistical analyses were performed with the statistical programme R version 2.10.0, using additional packages 'car', 'labdsv', 'MASS', 'mgcv', and 'vegan' (http://www.r-project.org).

3. Results

3.1. Hydrography and ice coverage

The general hydrography of the area of investigation was described in Cisewski et al. (2011), Hunt et al. (2011), and Pakhomov et al. (2011). The circulation in the Lazarev Sea is dominated by the eastern Weddell Gyre. Since the axis of the Weddell Gyre is here located between 60°S and 62°S, the survey area covered mostly the southern, westward setting limb of the gyre, with which Warm Deep Water (WDW) of circumpolar origin enters the inner Weddell Sea. The bottom topography features a seamount, Maud Rise, centred at 3°E 65°S, which steers the major part of the inflowing WDW around its northern slope concentrated in a narrow jet. A few stations in the very south of the area of investigation were situated in the Coastal Current south of the Antarctic Slope Front (ASF) (Fig. 1), which constitutes the second most import route for the inflow into the Weddell Sea. Downstream of Maud Rise, roughly west of 0°E, the circulation is less well defined, and rather dominated by transient meso-scale eddies that are shed by the jet at the northern slope of the seamount, and then contribute to the mixing of water masses (Leach et al., 2011). The core of the WDW is found subsurface with maximum temperatures occasionally exceeding 1 °C in the depth range 200–300 m, overlain by Antarctic Surface Water colder than −1 °C. Because of the topographic steering and eddy mixing, the sea ice in the Maud Rise region is often thinner, and the seasonal ice coverage shorter than in the adjacent Weddell Gyre. The mixed layer depth within the survey area never exceeded 50 m in summer (2007/2008), whereas it ranged between 12 and 200 m in autumn (2004), and between 30 and 450 m in winter (2006).

A dynamic sea ice situation was characteristic in summer. Large parts of the survey area were ice-covered at the beginning of the sampling campaign in early December 2007. A polynia north of Maud Rise expanded during the investigation period, resulting in an intermediate situation with an open area between 63°S and 67°S. When the area was left in late January 2008, only a residual ice cover persisted south of 67°S (Fig. 1a). In autumn, significant amounts of sea ice only occurred south of 68°S (Fig. 1b). Most parts of the predominantly young ice cover in that season had formed only days to weeks before the sampling. In winter, a substantial pack-ice cover was present throughout the entire area of investigation (Fig.1c). The ice edge during this season was situated north of the sampling grid at approximately 57°S.

3.2. Species composition

We found 132 species from 8 phyla between the surface and 3000 m depth in the Lazarev Sea. Species richness increased with the depth range sampled, with lowest values in the surface layer (0–2 m) and highest values in the deep layer (500–2500 m in summer and 0–3000 m in winter) (Table 2). A complete account of the species encountered and their densities in the 3 depth layers is available in the online supplementary material (see appendix Table A1).

Among the 46 macrofauna species encountered in the surface layer, only 15 were common to all three sampling seasons. In spite of the assumed spatial overlap with the epipelagic layer, 11 species were only found in the surface layer, including 7 fishes. Species richness was highest in summer (34 species) compared to autumn (25 species) and winter (28 species) (Table 2). Among the

Table 2
Percentage of the overall mean density of species with an average density ≥ 1 ind. 1000 m^{-3} in summer (2007/2008), autumn (2004) and winter (2006). Summary rows show overall average densities of individuals and species richness. n=Number of hauls; –=not present.

	Summer			Autumn		Winter		
	Surface layer	Epip. layer	Mesop. layer	Surface layer	Epip. layer	Surface layer	Epip. layer	Mesop. layer
Depth range [m]	0–2	0–200	500–2500[a]	0–2	0–200	0–2	0–200	0–3000
n	18	50	3	17	26	22	48	3
Dimophyes arctica	–	4.1	0.3	–	0.0	–	0.0	0.3
Diphyes antarctica	0.0	19.5	0.7	0.1	33.0	0.9	35.1	3.9
Pyrostephos vanhoeffeni	–	1.8	–	–	0.0	–	1.9	–
Clio pyramidata	2.4	0.5	0.2	0.2	1.2	0.0	1.8	0.1
Clione limacina	0.1	0.3	–	0.0	0.1	0.2	0.3	0.1
Cyllopus lucasii	0.1	0.3	0.1	0.7	1.2	0.0	1.6	0.3
Eusirus laticarpus	0.6	0.0	–	–	–	0.0	–	–
Hyperiella dilatata	0.2	0.3	–	0.3	1.0	0.0	0.9	0.1
Primno macropa	0.1	0.1	0.9	0.0	1.3	0.0	2.4	0.3
Euphausia superba	71.5	8.3	0.8	97.6	29.2	98.5	33.2	1.2
Thysanoessa macrura	21.3	43.8	2.2	0.0	1.8	0.0	3.5	50.1
Eukrohnia bathypelagica	–	–	7.2	–	–	–	–	2.0
Eukrohnia hamata	0.0	7.6	30.4	0.6	9.3	0.1	2.4	12.5
Sagitta gazellae	3.1	8.1	11.9	0.2	10.6	0.1	6.5[b]	9.5
Ihlea racovitzai	0.0	0.8	0.1	0.0	1.5	0.0	4.4	0.3
Salpa thompsoni	0.0	0.1	–	0.0	2.1	0.0	0.2	0.0
Remaining species	0.6	4.3	34.5	0.3	7.7	0.2	12.3	8.6
Overall mean density [n 1000 m^{-3}]	521.9	67.9	9.1	350.3	59.7	1079.2	45.3	17.6
Overall mean density [n m^{-2}]	1.0	13.6	30.0	0.7	11.9	2.2	9.3	52.8
No. of species	34	52	68	25	43	28	56	83

[a] Out of the 3 stations sampled, the depth range of 1 station was between 500 and 1900 m.
[b] Sagitta spp.; mainly *S. gazellae*.

71 species sampled in the epipelagic layer (0–200 m), 32 occurred in all three sampling seasons, and 18 species were not encountered in the surface or deep layer. The overall species richness was similar in summer (52 species) and winter (56 species), and lowest in autumn (43 species) (Table 2). We found 68 species in the deep layer between 500 m and 2500 m depth in summer, and 83 species between 0 and 3000 m depth in winter (Table 2). Summer and winter samples combined, 50 species were exclusive to the deep layer.

Overall average volumetric macrofauna densities were consistently higher in the surface layer than in the epipelagic layer, and lowest in the deep layer (Table 2). In the surface layer, the highest average macrofauna density occurred in winter (1079 ind. 1000 m^{-3}). In summer, macrofauna density was about half that value (522 ind. 1000 m^{-3}). The lowest average density was encountered in autumn (350 ind. 1000 m^{-3}) (Table 2). The seasonal differences in average density largely reflected the variability in the density of Antarctic krill *Euphausia superba*, clearly the dominant species in all three seasons, accounting for 72% (in summer) to 99% (in winter) of the overall average density (Table 2).

In contrast with the surface layer, overall average densities in the epipelagic layer were lowest in winter (45 ind. 1000 m^{-3}), intermediate in autumn (60 ind. 1000 m^{-3}) and highest in summer (68 ind. 1000 m^{-3}) (Table 2). The siphonophore *Diphyes antarctica* dominated the species composition in autumn and winter, closely followed by Antarctic krill (Table 2). In summer, the most abundant species were *Thysanoessa macrura* (44%), followed by *D. antarctica* (20%) and Antarctic krill (8%) (Table 2).

In the deep layer, the community was dominated by chaetognaths in summer, collectively accounting for 66% of the average macrofauna density (Table 2). In winter, deep layer sampling was conducted from 3000 m to the surface, and epipelagic species therefore contributed to the sampled community. In terms of relative average density, *T. macrura* (50%) was clearly the most abundant species, followed by *Eukrohnia hamata* (13%) and *Sagitta gazellae* (10%).

3.3. Community structure

Fig. 2 shows a cluster dendrogram visualising the community structure of all samples taken in the surface layer (0–2 m), epipelagic layer (0–200 m) and deep layer (summer samples: 500–2500 m). The community composition differed markedly among the depth layers (ANOSIM $R=0.76$; $p=0.001$), and with one exception the cluster analysis grouped samples in distinct clusters for each depth stratum (Fig. 2). The community composition in the surface layer was also notably different among seasons (ANOSIM $R=0.72$; $p=0.001$). This effect was most clearly reflected in the cluster analysis by a separation of 16 of the 18 summer samples at a dissimilarity of about 80%. The autumn and winter communities were less distinct from each other, but with few exceptions grouped apart at a dissimilarity of about 72% (Fig. 2). In the epipelagic layer, the seasonal difference in community structure was still significant, but less pronounced (ANOSIM $R=0.54$; $p=0.001$). In the cluster analysis, samples clustered generally apart from each other according to sampling season (Fig. 2). In summer samples from the deep layer, the dissimilarity in species composition between different depth strata was significantly greater than within each depth stratum (ANOSIM $R=0.80$; $p=0.01$).

The relationship of the community composition with the variability of environmental conditions throughout the extensive area covered by sampling locations of the surface layer and the epipelagic layer was investigated with a two-step NMDS-based analysis using the BIO-ENV method (Clarke and Ainsworth, 1993), and linear relationships between environmental gradients and the NMDS ordination of samples. Due to the seasonal structure of the species composition, we conducted this analysis separately for each season, thereby accounting for the possibility that the community composition responded to different environmental parameters in each sampling season. In the surface layer, samples from ice-covered stations clustered generally apart from open water samples in summer and autumn (Fig. 3a and b). No open

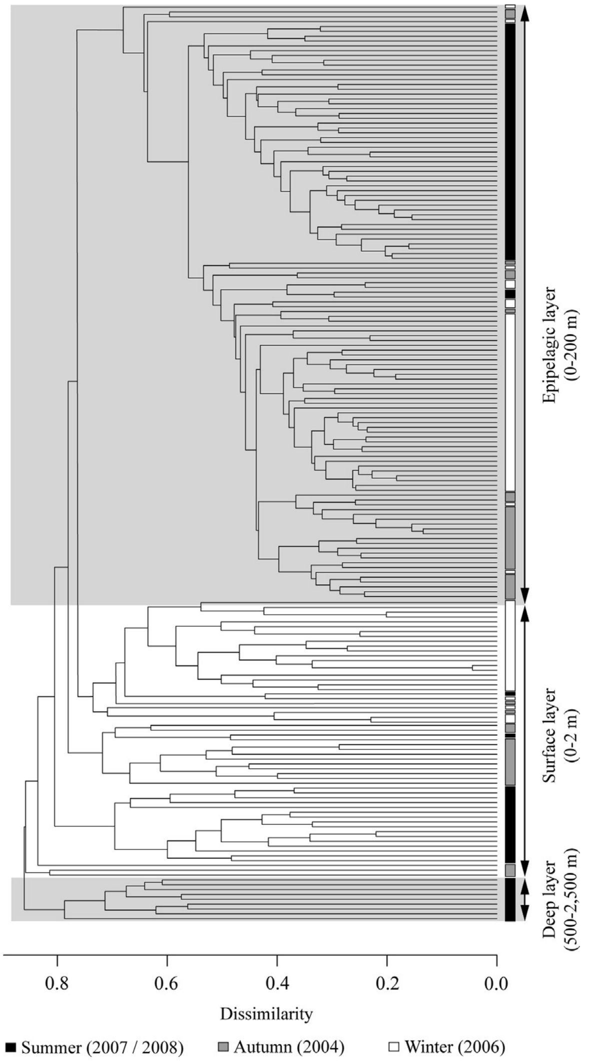

Fig. 2. Cluster dendrogram of the species composition of all samples taken in the surface layer (0–2 m), the epipelagic layer (0–200 m), and the deep layer (summer samples: 500–2500 m). The dendrogram was based on a Bray–Curtis dissimilarity matrix and constructed using average linkage. Samples were marked according to sampling season. Samples from different depth layers were contrasted from each other by grey/white shading.

water stations were sampled in winter. During summer, the community composition correlated best with a set of 5 environmental parameters (BIO-ENV correlation: 0.61, $p=0.001$; Table 3). The graphical representation of significant linear correlations indicated that the species composition changed mainly with increasing bottom depth, increasing mixed layer temperature, and decreasing floe size. The community composition also correlated with a second gradient of increasing radiation (Fig. 3a). In autumn, the surface layer community composition correlated best with a set of 3 environmental parameters (BIO-ENV correlation: 0.51, $p=0.001$; Table 3). Species composition changed mainly with increasing mixed layer temperature and decreasing floe size (Fig. 3b). In winter, the surface layer community composition correlated best with the 2 parameters bottom depth and distance to ice edge (BIO-ENV correlation: 0.46, $p=0.001$; Table 3). Change in community structure was significantly correlated with decreasing southward distance from the ice edge (Fig. 3c).

In the epipelagic layer, a clear grouping of samples according to the presence of sea ice was not apparent (Fig. 3d and e). During summer, the community composition correlated best with a set of 8 environmental parameters (BIO-ENV correlation: 0.47, $p=0.001$; Table 4). Species composition mainly changed with increasing bottom depth, integrated mixed layer attenuation, integrated attenuation of the 0–200 m depth layer, northward distance from the ice edge, and with decreasing floe size and surface salinity (Fig. 3d). In autumn, the community of the epipelagic layer correlated best with the 2 environmental parameters radiation and distance to ice edge (BIO-ENV correlation: 0.47, $p=0.001$; Fig. 3e; Table 4). In winter, the community of the epipelagic layer correlated best with a set of 5 environmental parameters (BIO-ENV correlation: 0.46, $p=0.001$; Table 4). The orientation of significant linear vectors in the NMDS plot indicated interaction along gradients of decreasing southward distance from the ice edge with increasing integrated attenuation in the 0–200 m depth layer, and integrated salinity of the 0–200 m layer (Fig. 3f).

3.4. Seasonal and diel variability of species in the surface versus the epipelagic layer

Seasonal patterns in the densities of macrofauna species in the surface layer (0–2 m) relative to epipelagic layer (0–200 m) densities were investigated by expressing areal surface layer densities (expressed as ind. m^{-2}) as percentages of areal epipelagic densities at corresponding sampling locations. Here, we present data for 8 of the 16 dominant species listed in Table 2, in which the median areal density exceeded 0.001 ind. m^{-2} in at least one depth layer and season (Fig. 4).

In 4 species, the proportional surface layer density was significantly higher in summer than in autumn and winter (Kruskal–Wallis test, $p<0.05$; Fig. 4b, e, f, and h). Among them, median proportional surface layer densities reached up to 18% of corresponding epipelagic layer densities in *Clio pyramidata*, and 205% in Antarctic krill *E. superba* (Fig. 4b and e). Median proportional densities of Antarctic krill were 21% in autumn and 9% in winter. The median proportional density of *S. gazellae* was low during autumn and winter, but reached 4% during summer. *T. macrura* was absent in autumn and winter samples from the surface layer, and proportional median densities were ~1% during summer (Fig. 4f). *Cyllopus lucasii* was the only species with proportional surface layer densities that were significantly higher in autumn than in summer and winter (Kruskal–Wallis test, $p<0.05$; Fig. 4d).

In 3 species, the proportional surface layer density was significantly higher in winter than in autumn and summer (Kruskal–Wallis test, $p<0.001$; Fig. 4a, c, and g). The lowest proportional winter densities were recorded in *D. antarctica*, which was not found in the surface layer during summer and autumn. In *Clione limacina*, median proportional surface layer densities reached as much as 16% of the corresponding epipelagic densities (Fig. 4c). Proportional densities of *E. hamata* were close to zero during summer and autumn, and had a median of 1% during winter (Fig. 4g).

In the surface layer, only a few stations were sampled during daytime in each of the three sampling seasons, impeding a statistical comparison of daytime versus night-time densities of animals. For summer and winter, comparisons of day versus night hauls at identical sampling sites for the most abundant species were shown in Flores et al. (2011).

For the 14 dominant species from the epipelagic layer shown in Table 2, we tested the null hypothesis that median densities were equal during the day and night using separate Kruskal–Wallis tests for each season (Table 5). Significantly elevated night-time densities were apparent from 6 out of the dominant species tested, accounting for 1.7% of the overall mean density in summer, 34.0% in autumn, and 38.3% in winter (Tables 2 and 5). Among them, this diel pattern was significant throughout all three seasons only in *C. lucasii*. The most pronounced diel pattern occurred in *C. pyramidata* in summer. Night-time densities of the pteropod were seven-fold higher compared to daytime values during this season, but no significant diel pattern was apparent in autumn and

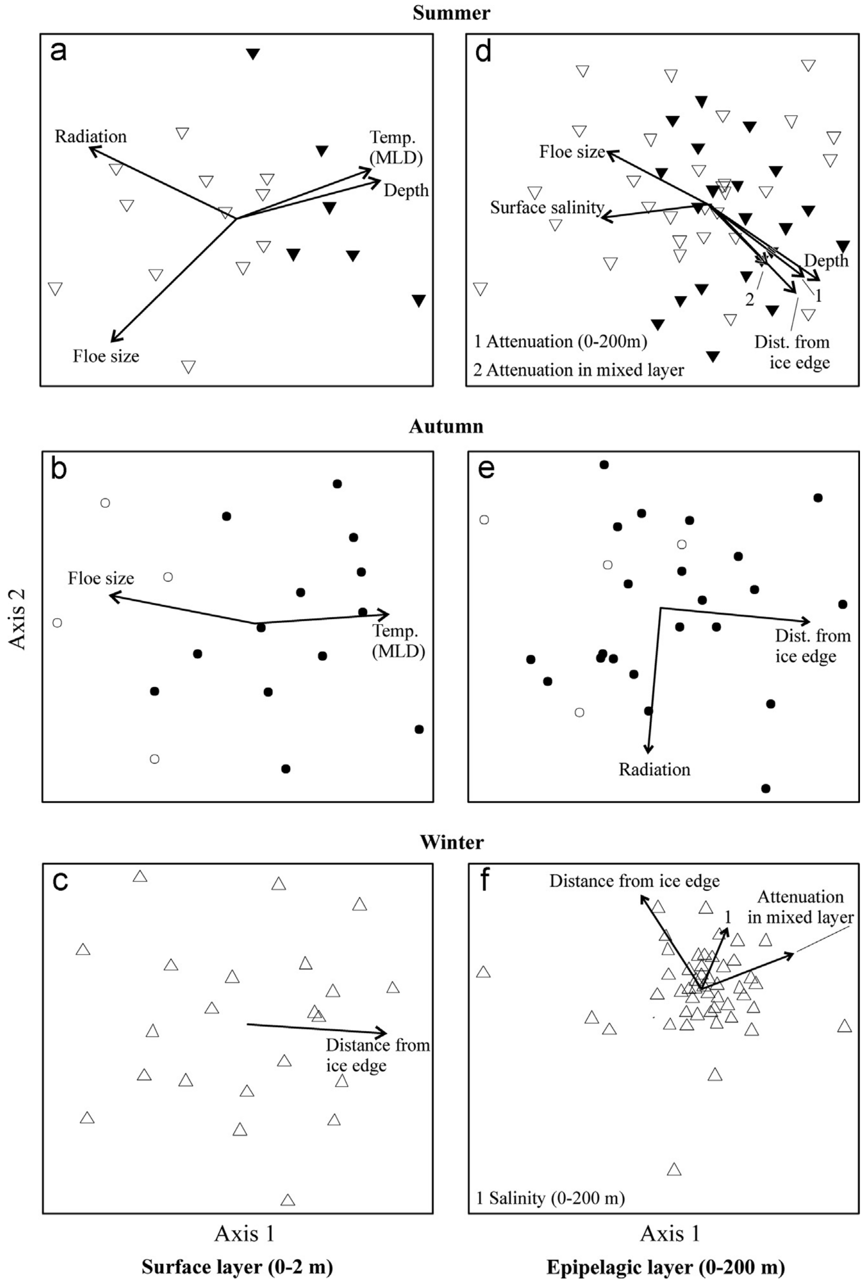

Fig. 3. Vectors of significant linear correlation of environmental parameters with NMDS ordination of samples in (a–c) the surface layer (0–2 m) and (d–f) the epipelagic layer (0–200 m) in (a and d) summer, (b and e) autumn and (c and f) winter. Gradients of environmental parameters with significant linear correlations with the NMDS ordination ($p < 0.05$) were indicated by vectors pointing into the direction of increasing values. Sampling locations in the NMDS ordinations were marked according to the sampling season and ice coverage (▿/▾ = summer; ○/● = autumn; Δ = winter; white symbols = ice-covered; black symbols = open water).

winter. In Antarctic krill, a significant diel pattern was evident in autumn and winter. Significant diel patterns were also found in *T. macrura* (winter), the salps *Ihlea racovitzai* (summer, autumn) and *Salpa thompsoni*, which was only present in sufficient numbers for statistical comparison in autumn (Table 5).

4. Discussion

4.1. Species composition

Considering all seasons combined, we found a minimum of 132 macrozooplankton and micronekton species between the surface and 3000 m depth in the Lazarev Sea. The majority of the species sampled in our study were found in the deep layer, at depths scarcely sampled by previous surveys. The meso- and bathypelagic community of the deep layer had the lowest sampling effort, both in terms of sample size and total amount of waters filtered. The diversity of this realm was therefore likely substantially underestimated. In the frequently sampled epipelagic layer, the 43–56 species per season identified in our study were at the high end of the range previously reported for macrozooplankton/micronekton in Antarctic off-shelf waters between 0 and 300 m depth in the wider Weddell Sea (Boysen-Ennen and Piatkowski, 1988; Fisher et al., 2004; Siegel et al., 1992), as well as in other parts of the Southern Ocean (Hunt et al., 2007; Lancraft et al., 2004; Siegel and Harm, 1996).

The higher species richness in the epipelagic layer (0–200 m) compared to the surface layer (0–2 m) may confirm the expectation that differences in species composition were mainly caused by

Table 3
Surface layer (0–2 m). Summary statistics of environmental parameters that best correlated with differences in species composition among sampling localities in summer (2007/2008), autumn (2004) and winter (2006). MLD = mixed layer depth; axis 1, 2 = NMDS ordination axes.

Season	Parameter	Linear correlation			
		r (axis 1)	*r* (axis 2)	R^2	*p*
Summer	Depth	−0.966	0.258	0.406	0.020
	Radiation	0.899	0.437	0.492	0.007
	Temperature (integr., 0 m – MLD)	0.938	0.346	0.379	0.026
	Floe size	−0.713	−0.701	0.570	0.002
	Distance from ice edge	0.780	0.626	0.306	0.068
Autumn	Temperature (integr., 0 m – MLD)	0.998	0.068	0.493	0.006
	Temperature (integr., 0–200 m)	0.658	0.753	0.001	0.991
	Floe size	−0.982	0.187	0.602	< 0.001
Winter	Depth	0.949	0.314	0.248	0.063
	Distance from ice edge	0.997	−0.071	0.490	0.002

Table 4
Epipelagic layer (0–200 m). Summary statistics of environmental parameters that best correlated with differences in species composition among sampling localities in summer (2007/2008), autumn (2004) and winter (2006). MLD = mixed layer depth; axis 1, 2 = NMDS ordination axes.

Season	Parameter	Linear correlation			
		r (axis 1)	*r* (axis 2)	R^2	*p*
Summer	Depth	0.707	−0.707	0.214	0.003
	Salinity (surface)	−0.992	−0.122	0.348	< 0.001
	Attenuation (integr., 0 m – MLD)	0.798	−0.602	0.439	< 0.001
	Temperature (integr., 0–200 m)	0.941	0.339	0.068	0.189
	Attenuation (integr., 0–200 m)	0.828	−0.560	0.550	< 0.001
	Chlorophyll (integr., 0–200 m)	0.205	−0.979	0.090	0.103
	Floe size	−0.884	0.467	0.392	< 0.001
	Distance from ice edge	0.696	−0.718	0.383	< 0.001
Autumn	Radiation	−0.087	−0.996	0.585	0.006
	Distance from ice edge	0.996	−0.923	0.615	< 0.001
Winter	Temperature (surface)	0.968	0.252	0.062	0.231
	MLD	−0.032	−0.999	0.150	0.052
	Salinity (integr., 0–200 m)	0.416	0.909	0.165	0.030
	Attenuation (integr., 0–200 m)	0.935	0.355	0.339	0.003
	Distance from ice edge	−0.541	0.841	0.437	< 0.001

a higher sampling effort in the epipelagic layer, or by species avoiding the surface layer, such as *Dimophyes arctica* and *Pyrostephos vanhoeffeni* (Table 2). More remarkable than the absence of species from the surface layer, however, was the exclusive presence of 11 species in the 0–2 m depth stratum. Seven of these species were larval or juvenile fishes, and 2 were juvenile squids (see appendix Table A1), supporting the contention that the Antarctic surface and under-ice habitat serves as a nursery habitat for juvenile nekton (Collins and Rodhouse, 2006; Hubold, 1985; Krakatitsa et al., 1993; White and Piatkowski, 1993). All species unique to the surface layer were sampled either in summer or in winter. During these seasons, all surface layer samples were matched by corresponding epipelagic samples, excluding the possibility that the presence of these species in the surface layer was due to different spatial coverage in the sampling of the two depth layers (Fig. 1). More likely, the exclusive presence of species in the surface layer indicates that the surface layer community was underrepresented in epipelagic samples. This may apply particularly to ice-associated species, because the RMT does not sample the ice–water interface layer. Among these 11 species, however, only *Eusirus* spp. have been reported to be associated with sea ice (Arndt and Swadling, 2006). Also in ice-free water, under-representation of the surface community can occur, because the RMT samples the upper 10–15 m in the wake of the ship, where surface water is displaced by the forward moving vessel and propeller mixing. In contrast, the SUIT samples the surface layer away from the ship in comparatively undisturbed water (Flores et al., 2012). To date, no obligate neuston species have been described south of the Antarctic Polar Front. Krakatitsa et al. (1993) did not find a unique surface dwelling zooplankton community in the ice-free Prydz Bay region during summer, and documented a less diverse assemblage in the top 1 m water layer compared to the epipelagic layer. This preliminary study also clearly identified surface micro-layers (in the range of 20–40 cm) to be microhabitats for juvenile and larval stages of both ‘warmer’ and ‘colder’ water species, such as *Salpa thompsoni* and Antarctic krill (Krakatitsa et al., 1993).

4.2. Community structure

In the Southern Ocean, meso-scale zooplankton species composition is determined by the distribution of water masses, ocean currents and sea ice (Hosie, 1994; Hunt et al., 2007; Pakhomov, 1989, 1993a; Pakhomov et al., 2000). With the exception of the Antarctic Slope Front, beyond which little sampling was conducted, our study area did not cross major oceanographic fronts (Fig. 1). Accordingly, the community structure was relatively uniform within each depth layer and season (Figs. 2 and 3). When depth layers and seasons were compared with each other,

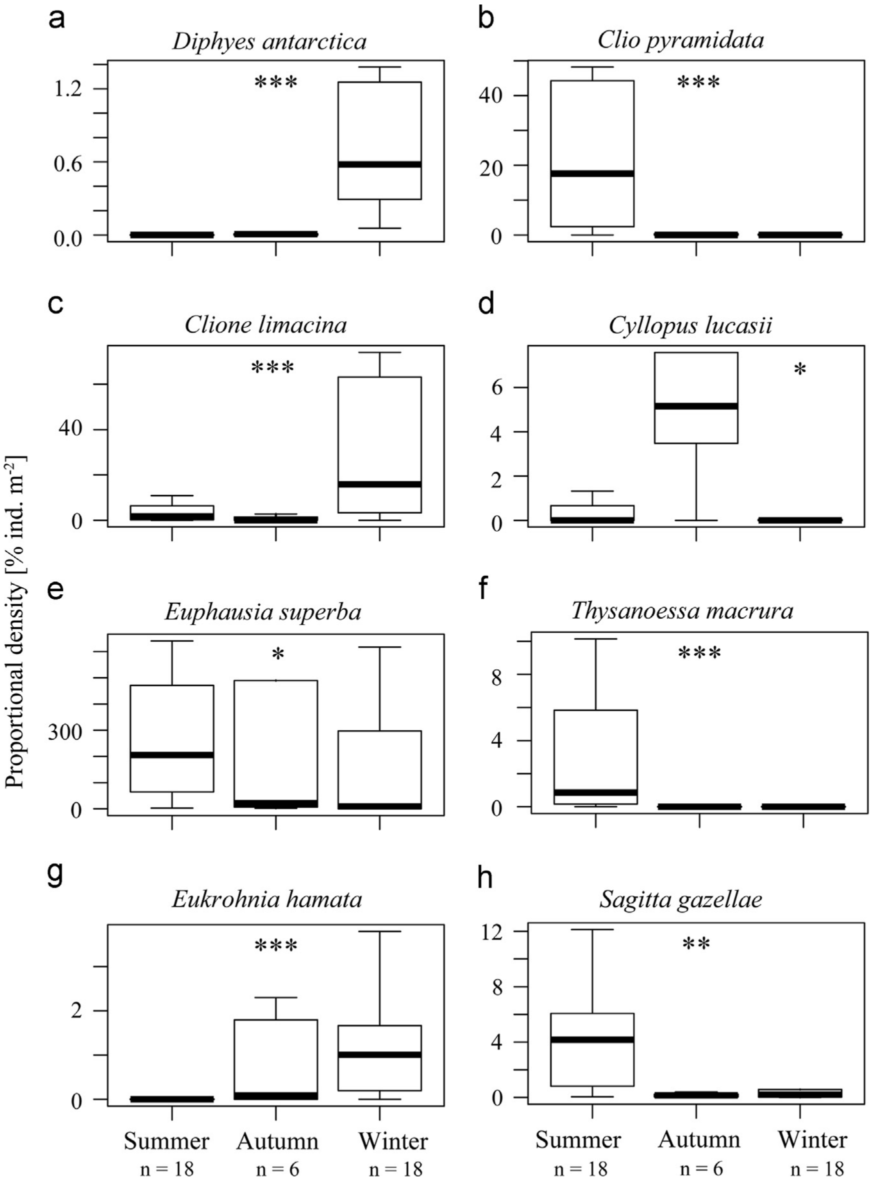

Fig. 4. Seasonal comparison of proportional densities of 8 abundant species in the surface layer (0–2 m) relative to the epipelagic layer (0–200 m). The horizontal bars in the box plots indicate median proportional densities. The upper and lower edges of the 'box' (the 'hinges') denote the approximate 1st and 3rd quartiles, respectively. The vertical error bars extend to the lowest and highest data value inside a range of 1.5 times the inter-quartile range, respectively (R-Development-Core-Team, 2008). Extreme values were not shown. Kruskal–Wallis significance of differences in proportional density among seasons: $^{*}p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

however, significant differences were apparent. Besides predictable differences in community composition between the surface (0–2 m) and epipelagic layers (0–200 m) versus the deep layer (500–2500 m in summer), there was a remarkable dissimilarity of the surface layer community from the presumably overlapping epipelagic community in each season (Fig. 2). This difference in community structure can in large parts be attributed to an overwhelming dominance of euphausiids in the surface layer, most likely caused by a close association of Antarctic krill with the underside of sea ice (Flores et al., 2012; Marschall, 1988; Siegel et al., 1990). Besides Antarctic krill, several other species are positively or negatively associated with sea ice, which thus acts as a key factor in structuring the surface layer community in the Lazarev Sea (Flores et al., 2011).

Similar to the present study, a distinct seasonal change in the community structure of zooplankton has been reported from similar latitudes south of Australia (Hunt and Hosie, 2006), and off the Antarctic Peninsula (Siegel and Piatkowski, 1990). Comparison of our 2007/2008 summer data from the epipelagic layer with data collected in summer 2005/2006 showed that the relative contribution of euphausiid and chaetognath species was very similar in both summers, and differed from autumn and winter. Cluster analysis of the epipelagic macrozooplankton/micronekton community confirmed highly similar assemblages in both summers (Hunt et al., 2011). It is therefore likely that the variability in the community structure between summer (2007/2008), autumn (2004) and winter (2006) reflects seasonal rather than inter-annual variability. Because the data considered here were not collected in consecutive seasons, however, inter-annual variability cannot be entirely excluded as a contributor to the observed seasonal differences in community structure.

Change in community structure in relation to the environment was rather gradual than abrupt, probably due to the lack of significant biogeographic barriers in the survey area. Both in the surface layer and the epipelagic layer, there was an overarching quasi-latitudinal transition from a neritic community in the southern, mostly ice-covered part of the survey area, towards an oceanic community in northern, ice-free waters. This coincided with a significant linear

Table 5
Diel comparison of the median densities of abundant species (n 1000 m^{-3}) in the epipelagic layer (0–200 m) in summer (2007/2008), autumn (2004) and winter (2006). Statistically significant (Kruskal–Wallis test $p < 0.05$) differences between daytime and night-time densities were highlighted in **bold** print.

Species	Summer		Autumn		Winter	
	Night	Day	Night	Day	Night	Day
Dimophyes arctica	1.30	2.24	0.00	0.00	0.00	0.00
Diphyes antarctica	13.51	12.02	16.37	16.01	14.32	17.53
Pyrostephos vanhoeffeni	0.00	0.39	0.00	0.00	0.00	0.32
Clio pyramidata	**1.16**	**0.16**	0.41	0.71	0.50	1.37
Clione limacina	0.16	0.13	0.05	0.00	0.07	0.10
Cyllopus lucasii	**0.33**	**0.15**	**0.68**	**0.17**	**0.57**	**0.06**
Hyperiella dilatata	0.19	0.15	0.44	0.66	0.32	0.46
Primno macropa	0.00	0.05	0.28	1.07	0.88	0.63
Euphausia superba	1.35	0.67	**7.65**	**0.00**	**2.18**	**0.13**
Thysanoessa macrura	10.03	10.80	0.76	0.11	**0.85**	**0.42**
Eukrohnia hamata	2.47	2.98	5.75	4.39	0.74	0.61
Sagitta gazellae	2.57	4.07	4.27	4.77	2.72	1.73
Ihlea racovitzai	**0.61**	**0.06**	**1.00**	**0.00**	1.85	1.22
Salpa thompsoni	0.00	0.00	**0.93**	**0.00**	0.00	0.00

[a] Sagitta spp.; mainly *S. gazellae*.

correlation of the distance from the ice edge with the NMDS ordination of the community structure in 4 of the 6 datasets (Tables 3 and 4). A similar, but more distinct latitudinal zonation of macrozooplankton communities was described by Hosie (1994) and Pakhomov (1993a) in the Prydz Bay Region. This quasi-latitudinal pattern, however, was related to different environmental drivers in the 2 depth layers. In the surface layer, the community structure changed largely along a gradient ranging from large floe size and low mixed layer temperatures (ice-covered) to small floe sizes and high mixed layer temperatures (~open water) in summer and autumn (Fig. 3a and b; Table 3). In winter, ranges in both ice coverage and floe size were probably too small to detect a significant correlation with the community structure, because the entire survey area was covered with pack-ice. A significant relationship of solar radiation with the community ordination in summer was probably caused by strong diel variability of a few abundant species in the surface layer, such as *Thysanoessa macrura* and *Clio pyramidata* (Flores et al., 2011, 2012). In autumn and winter, the influence of light intensity on community composition was unlikely to be detected based on the few stations sampled during weak daylight (Table 1).

In the epipelagic layer, change in community structure was rather associated with gradients of temperature, salinity and integrated attenuation in the upper 200 m in summer and winter (Fig. 3d and f; Table 4). Because attenuation is related to the concentration of particulate organic carbon in oceanic waters (Gardner et al., 2006), this parameter can be considered as indicative of biological productivity. Solar radiation was significantly related to community ordination in autumn. During this season, Antarctic krill and 3 other abundant species exhibited pronounced diel variability in the epipelagic layer (Table 5). In summer, the abundance of the few diel migratory species was too low to significantly impact on community structure (Table 5). In winter, only 5 out of 48 stations were sampled during weak daylight (Table 1), probably limiting a significant correlation of the short radiation gradient with community ordination.

With regard to the descriptive nature of the BIO-ENV and MDS procedures, correlations of environmental parameters with the community structure and their associations with species' density vectors should neither be interpreted as causal, nor as exclusive (Clarke and Ainsworth, 1993). Nonetheless, our results from the epipelagic layer agree with numerous studies in the Southern Ocean sampling a similar depth range in finding that zooplankton community structure was predominantly driven by hydrography and pelagic productivity (e.g. Chiba et al., 2001; Hosie, 1994; Pinkerton et al., 2010). In the surface layer, these water column characteristics were apparently less important. Instead, the community structure rather responded to sea ice properties and surface temperature (Tables 3 and 4; Fig. 3a–c).

4.3. *Significance of the surface layer habitat*

Per-area macrofauna densities in the surface layer (0–2 m) ranged from 8% of the overall areal epipelagic (0–200 m) macrofauna density in summer, to 6% in autumn, and 24% in winter, despite representing only 1% of the epipelagic depth range (Table 2). Acoustic backscatter data showed that zooplankton aggregated at discrete horizontal depth horizons rather than being randomly dispersed in the water column (Brierley et al., 1998; Cisewski et al., 2010). Considering that, without a statistical preference for any specific depth layer, mean areal surface densities would range at ~1% of mean depth-integrated epipelagic densities, the observed values indicate a pronounced concentration of animals in the surface layer. A significant concentration of animals in the surface layer was also reported by Krakatitsa et al. (1993), who conducted the only available study in the Antarctic using dedicated surface layer sampling, and found that proportional 1 m surface layer zooplankton biomass was nearly double that of the 0–200 m biomass.

The observed differences in species density between depth layers, however, may reflect differences in net avoidance, or in size selectivity of the different sampling gear used. In the surface layer, net avoidance due to better visibility of the sampling gear can be considered low, because most hauls were conducted at night. No significant differences were detected between the size distributions of Antarctic krill caught by the SUIT versus the RMT in any of the 3 sampling seasons, indicating that the size composition of the catch, and hence size-dependent escape ability, was not an important factor (Flores et al., 2012). If anything, the observed elevated densities in the surface layer were rather under-estimates relative to the epipelagic layer, because the SUIT had a smaller net opening than the RMT.

The observed differences in species composition and macrofauna density between depth layers may further be subject to bias caused by diel vertical migration (DVM) in seasons where the depth layers differed from each other in the proportion of daytime versus night-time sampling. In autumn and winter, samples from both depth layers largely reflect differences in the nocturnal density of species, because the vast majority of hauls were conducted at night. During summer, the epipelagic layer had a higher proportion of daytime hauls than the surface layer (Table 1). There were significant diel patterns in the density of 3 species from the epipelagic layer in summer, but these patterns accounted for less than 2% of the overall density (Tables 2 and 5). This indicated that the impact of diel differences in the sampling scheme during summer was probably negligible, and did not affect comparisons of overall zooplankton densities and community structure between depth layers and seasons.

The observed differences in community structure between the surface layer and the epipelagic layer may in part be attributed to seasonal changes in the depth distribution of abundant species. Our analysis of 8 abundant macrozooplankton species showed that the use of the surface layer could vary considerably between species, but also seasonally within species. This variability largely reflected the seasonal variability of the upper limit of their DVM. Cisewski et al. (2010) described 2 modes of DVM based on acoustic backscattering recorded by 3 moorings in the Lazarev Sea: (1) shallow DVM between the upper 50 m during the night and slightly deeper than 200 m during the day, and (2) deep DVM between the upper 50 m at night and well below 350 m at day. These acoustically tracked DVM patterns persisted during the months February to October, i.e. from late summer through autumn and winter until the next summer season. A similar seasonal change in DVM amplitude was also recorded for Antarctic krill in the Lazarev Sea (Siegel, 2012). Cisewski et al. (2010) assumed that in summer DVM ceased largely, because the bulk of backscattering zooplankton remained in the upper 50 m throughout the day/night cycle. Considerable diel differences in the density of many abundant zooplankton species in the surface layer, however, indicated a decrease in amplitude rather than a pause of DVM during summer (Flores et al., 2011, 2012). Such changes in the upper metres of the water column could not be detected by Cisewski et al. (2010), because they did not sample above 20 m water depth. Similar limitations apply to other studies using acoustic sensors (Brierley et al., 2002, 1998; Zhou et al., 1994), as well as net-based investigations integrating the upper 50–300 m in a single density figure (Boysen-Ennen and Piatkowski, 1988; Fisher et al., 2004; Lancraft et al., 2004; Siegel, 2012). Within the range of uncertainty that is associated with the limitations of the acoustic method in resolving the near-surface layer and in discriminating species, the results of this study are however consistent with the DVM annual time series of Cisewski et al. (2010). Taking DVM into account, our results provide evidence for 3 strategies of seasonal use of the surface layer:

(1) *Summer use.* Proportional surface layer densities of *Clio pyramidata*, *Thysanoessa macrura* and *Sagitta gazellae* were close to zero during autumn and winter and $\geq 1\%$ of corresponding epipelagic densities in summer, indicating that they used the surface layer almost exclusively during the productive summer months. During summertime, shallow ice melt blooms are common while the pack-ice is breaking up, providing high concentrations of phytoplankton near the surface, a crucial food source for *C. pyramidata* and *T. macrura* (Pakhomov and Froneman, 2004; Hunt et al., 2008). Conversely, *S. gazellae* was probably attracted by copepods, euphausiid larvae and other grazers in surface waters (Froneman and Pakhomov, 1998; Froneman et al., 1998; Oresland, 1990). Pronounced diel variability in the surface layer during summertime has been reported for both *C. pyramidata* and *S. gazellae* from the Lazarev Sea (Flores et al., 2011). In *C. pyramidata*, corresponding strong diel variability in the epipelagic layer indicated a deep mode of DVM (Table 5). Due to this pronounced DVM, a large part of the unexpectedly high proportional surface layer density of *C. pyramidata* in summer can be attributed to a relative under-representation of night-time sampling in the epipelagic layer (Table 1). Surface layer densities of *C. pyramidata*, however, were still significantly higher in summer than in autumn and winter (Kruskal–Wallis test, $p < 0.001$), indicating that the general pattern of elevated surface layer use in summer was not simply an artefact of this sampling bias in the epipelagic layer (see appendix Table A1). In *S. gazellae* and *T. macrura*, a shallow mode of DVM was apparent from pronounced diel variability in the surface layer in combination with weak diel variability in the epipelagic layer during summer (Table 5; Flores et al., 2011, 2012). The surface layer use of *T. macrura* was clearly restricted to the summer. In winter, *T. macrura* shifted its vertical distribution centre below 200 m depth, as indicated by high densities in the 0–3000 m depth stratum versus low densities in the epipelagic, and zero densities in the surface layer (see appendix Table A 1). Absence from the surface layer combined with strong diel variability in the epipelagic layer indicated a deep mode of DVM during the dark period of the year. This picture is in agreement with a recent detailed analysis of the seasonal vertical distribution of *T. macrura* (Haraldsson and Siegel, in press).

(2) *Winter use.* Seasonally elevated summer surface layer densities of abundant species, such as Antarctic krill and *T. macrura*, agree well with the widely accepted paradigm that zooplankton is generally distributed higher in the water column in summer and shifts to greater depth in winter in Polar Regions (Cisewski et al., 2010; Lancraft et al., 1991). This perception, however, was challenged by *Diphyes antarctica*, *C. limacina*, and *Eukrohnia hamata.* These abundant species reached significantly higher proportional surface layer densities in winter than in summer and autumn, indicating that they used the surface layer predominantly during winter (Fig. 4a, c, and g). *D. antarctica* showed no evidence of DVM in any season, but merely shifted its vertical distribution towards the surface in winter. Pronounced diel variability of C. *limacina* and *E. hamata* in the surface layer combined with the absence of diel variability in the epipelagic layer indicated a shallow mode of DVM during winter. There was no indication of DVM in these species during summer and autumn (Table 5; Flores et al., 2011). Remarkably, all 3 species using the surface layer in winter were predators. *E. hamata* is feeding in winter, with copepods representing its major prey (Kruse et al., 2010b; Oresland, 1995). Observations in Gerlache Strait, Antarctic Peninsula indicate that this chaetognath together with other carnivorous zooplankton species may have a high predation impact in winter (Oresland, 1995). Sea ice-associated copepods and other prey may have attracted *E. hamata* to the surface in winter. The importance of the ice–water interface has been highlighted for certain copepods (Hoshiai et al., 1987; Schnack-Schiel et al., 2008; Tanimura et al., 2008) and Antarctic krill larvae (Daly, 2004; Meyer et al., 2009). In *C. limacina*, areal surface layer densities reached almost 20% of corresponding epipelagic densities, indicating that the under-ice habitat may be of key importance for this carnivorous pteropod during winter. *C. limacina*'s attraction to the under-ice habitat may reflect the behaviour of its presumed sole prey species *Limacina helicina*. This filter-feeding pteropod may rely on detritus sinking from the sea ice during winter (Flores et al., 2011; Gannefors et al., 2005; Kobayashi, 1974). A similar mode of life during winter may be assumed for the filter-feeding siphonophore *D. antarctica*.

(3) *Year-round use.* In Antarctic krill, considerably higher than expected proportional surface layer densities in all 3 seasons indicated a pronounced use of the surface layer virtually year-round. Especially during summer, the median proportional density of Antarctic krill in the surface layer reached over 200% of corresponding epipelagic densities. This extra-ordinarily high proportional surface layer density was unlikely to be confounded by the different diel sampling regime of the surface versus the epipelagic layer, because during summertime there is no evidence of DVM in Antarctic krill at high latitudes (Table 5; Siegel, 2005, 2012). Even a tentative correction of the almost two-fold higher night-time than daytime median densities in the epipelagic layer would result in summer surface layer densities still about 2 orders of magnitude higher than expected from random depth distribution (Fig. 4e; Table 5). The attraction of Antarctic krill to the surface layer probably reflects their association with the underside of sea ice. The association of Antarctic krill with sea ice was addressed in more detail in a dedicated study by Flores et al. (2012), using a subset of the data presented here. The authors concluded that Antarctic krill were attracted to the underside of sea ice by ice algae and phytoplankton blooms in a shallow mixed layer, when present. In autumn and winter, a deep mode of DVM was apparent from significant diel differences in Antarctic krill density of the epipelagic layer (Table 5). Our results agree generally with commonly accepted paradigms of seasonal DVM patterns in Antarctic krill (Siegel, 2005, 2012; Taki et al., 2005). The data shown here extend the accepted model of hibernal DVM by highlighting that nocturnal upward migration encompasses the surface layer even in winter (Flores et al., 2012).

The results of this study indicate that besides Antarctic krill, various other species concentrate in the surface layer during different times of the year. During summer, such preference for the surface layer is probably related to enhanced productivity in the upper metres that follows the vernal stratification of the water column. In winter, when the surface is covered by sea ice, ice algae are often the only dependable source of production, attracting pelagic life to the surface (Brierley and Thomas, 2002). During all seasons investigated, volumetric macrofauna surface layer densities up to an order of magnitude above epipelagic densities emphasise the attractiveness of the surface layer as a foraging ground of higher predators (Table 2). The upper surface layer is especially attractive to even deep-diving air breathing predators, because they need less energy performing shallow dives, and because krill as by far the most abundant prey species at the surface, constitutes an abundant and energetically rewarding prey species.

5. Conclusions

With a multi-seasonal inventory of the macrozooplankton/micronekton community from the surface to 3000 m depth, our results indicate that even in the relatively homogeneous deep-sea environment of the Lazarev Sea, the pelagic community can be as diverse as in hydrographically more complex environments, such as the Weddell-Scotia Confluence Zone, or on the Antarctic shelf. A well-defined vertical community structure was indicated by distinct faunal compositions with various unique species in each of the 3 depth layers investigated. The surface layer community, often neglected or integrated in epipelagic sampling without differentiation, was surprisingly diverse and differed from the epipelagic community in composition, structure and enhanced macrozooplankton density. Although the degree of overlap between the surface and epipelagic layers remains unknown, the considerable differences in species composition, community structure and species densities between them indicate that our perception of epipelagic communities derived from depth-integrated sampling with stern-towed nets may have been biased towards the deeper-dwelling parts of the community in the past, leading to a potential under-estimate of macrofauna diversity and abundance, particularly when sea ice is present.

Seasonal changes in the community structure of the 3 depth layers could in large parts be related to changes in the upper vertical distribution limit of abundant species. There was, however, no overall common pattern in the seasonal depth distribution of the investigated species. An upward shift of the upper distribution limit of zooplankton in spring and a downward shift in winter are likely to largely reflect the seasonal cycle of food availability near the surface. This common perception, however, was challenged by high winter zooplankton densities in the surface layer due to high densities of Antarctic krill and several other species in the ice-water interface layer. This concentration of organisms under the ice suggests a vivid interaction of Antarctic macrozooplankton and micronekton with sea ice and ice-associated biota.

In several species, unexpectedly high proportional surface layer densities relative to epipelagic values imply that the surface layer plays a critical role in the ecosystem functioning of the Antarctic seasonal sea ice zone that has not been detected by conventional standardised sampling schemes for the epipelagic realm. Especially when ice-covered, the surface layer may be underestimated as a functional node of the food web, providing resources for numerous zooplankton and micronekton species, and the predators depending on them. This habitat is extremely dynamic due to seasonal fluctuations, but is also highly susceptible to longer term environmental forcing, such as global warming, acidification and UV radiation.

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Appendix A. Supplementary matreial

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr.2013.11.001.

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