Macrozooplankton and micronekton in the surface layer and under sea ice

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INTRODUCTION

The seasonal sea-ice zone of the Southern Ocean is well known for its rich wildlife. In summer, high densities of warm blooded top predators (birds, seals, whales) concentrate at the ice edge and often increase towards the inner pack-ice, indicating considerable primary and secondary production in these areas (Van Franeker et al. 1997). Water column primary production, however, is low in ice-covered waters. In recent years, ice algae have gained increasing attention as a major source of production in the sea-ice system. However, the physical and biochemical complexity of the ice environment has posed difficulties to an accurate determination of ice algal productivity so far. Another way to shed light on the energy flow in the sea-ice system is to follow the food chains from higher trophic levels downwards (van Franeker et al., this volume). In order to explain feeding and prey distribution of the higher level predators in the ice-covered ocean, a good understanding of the ice-associated species community is essential.

The structure and capacity of the sea-ice system are not yet clearly understood. Sea-ice seems to be an important factor in the ecology of larval and adult krill *Euphausia superba* (Loeb et al. 1997, Atkinson et al. 2004). Repeated reports of dense aggregations of krill directly under ice stress the importance of this habitat for the euphausiid (e.g. Brierly et al. 2002). To date, little is known to which extent krill, fish, squid or other macrofauna can be found under the sea-ice. At IMARES Texel, the need to investigate the under-ice habitat in more detail led to the development of a special under-ice trawl (SUIT = Surface and Under Ice Trawl).

Due to the dynamic nature of the subsurface environment, a close interaction with the water column system can be expected. Therefore it is essential to view the data collected from the surface layer in the context of physical, chemical and biological data from the entire water column down to the sea floor. The summer expedition ANT XXIV-2 provided an excellent opportunity to collect a wide range of data in a concerted manner, forming the basis for an integrated analysis.

MATERIALS & METHODS

Trawling of SUIT was attempted 19 times on the regular RMT station grid and twice at one station in the Antarctic Circumpolar Current between December 5th, 2007 and January 22nd, 2008 (Figure 1).

The net system consisted of a steel frame with a 2.1 x 2.1 m net opening and a 15 m long 7 mm half-mesh commercial shrimp net attached to it. The rear two meters of the net were lined with 0.3 mm mesh plankton gaze. Large floaters at the top the frame kept the net at the surface. Wheels on top of the frame allowed the net to 'roll' along the underside of ice floes. To enable sampling under undisturbed ice, an asymmetric sprout let the net shear starboard from the ship's track at a cable length of 120 m.

An acoustic Doppler current profiler was used as an acoustic flow meter (AFM). The device operated with two 2 MHz measuring beams situated at an angle of 50° against each other. The AFM was capable to measure current speed at three different positions horizontally across the net opening. They were set to 60, 90 and 120 cm distance from the frame's port side during most operations. Analysis of the obtained real-time current speed data allowed the identification of the effective towing time, which was defined as the time during which the current was constantly directed into the net. The amount of water filtered [m^3] was calculated as the product of effective towing time [s], average towing speed [$m\ s^{-1}$] and net opening area ($2.1^2 = 4.41\ m^2$).

Fishing was done during dark hours in 18 of the 21 completed hauls, when most plankton and nekton species were expected to approach the surface. Daytime hauls were generally excluded from analysis, except for day-night comparisons which were performed at three stations. Towing speed was 1.5 – 2 kn. Standard hauls lasted between 15 and 30 minutes towing time. During each trawl, irregularities, changes in ship speed, ice coverage [%] and ice thickness [cm] were recorded.

Animals ≥ 0.5 cm were separated to species level where possible. Displacement volume [ml] and number of individuals of each species were noted. The fractions were frozen separately for further analysis at -80°C. Taxonomic samples and the remaining small zooplankton were preserved on 4% hexamine-buffered formaldehyde-seawater solution.

When catches were larger than 2000 ml, they were subsampled with a plankton splitter to obtain representative subsamples for length-frequency analysis of Antarctic krill *Euphausia superba* and *Thysanoessa macrura*. The remaining sample was analysed quantitatively according to the procedure outlined above. In catches > 5000 ml, a subsample of ca. 2000 ml was treated as above, and the remainder was frozen immediately at -20°C.

The length of euphausiids and large amphipods were measured directly after capture. When working procedure and sample size impeded immediate measurement, they were fixed in formaldehyde solution for 48 to 96 hours before measurement. Euphausiids were grouped into males, females, juveniles and gravid females. *E. superba* and amphipod length measurements were done according to the 'Discovery' method (front edge of eye to tip of telson). All other euphausiids were measured from the tip of the rostrum to the tip of the telson.

The density of animals [ind. m^{-2}] was calculated as the number of individuals per m^2 trawled surface. Wet mass density per station [$g\ m^{-2}$] was calculated in a similar way, assuming 1 ml = 1 g.

Coelenterates were excluded from abundance and biomass calculations because these fragile animals were susceptible to disruption when the net collected ice.

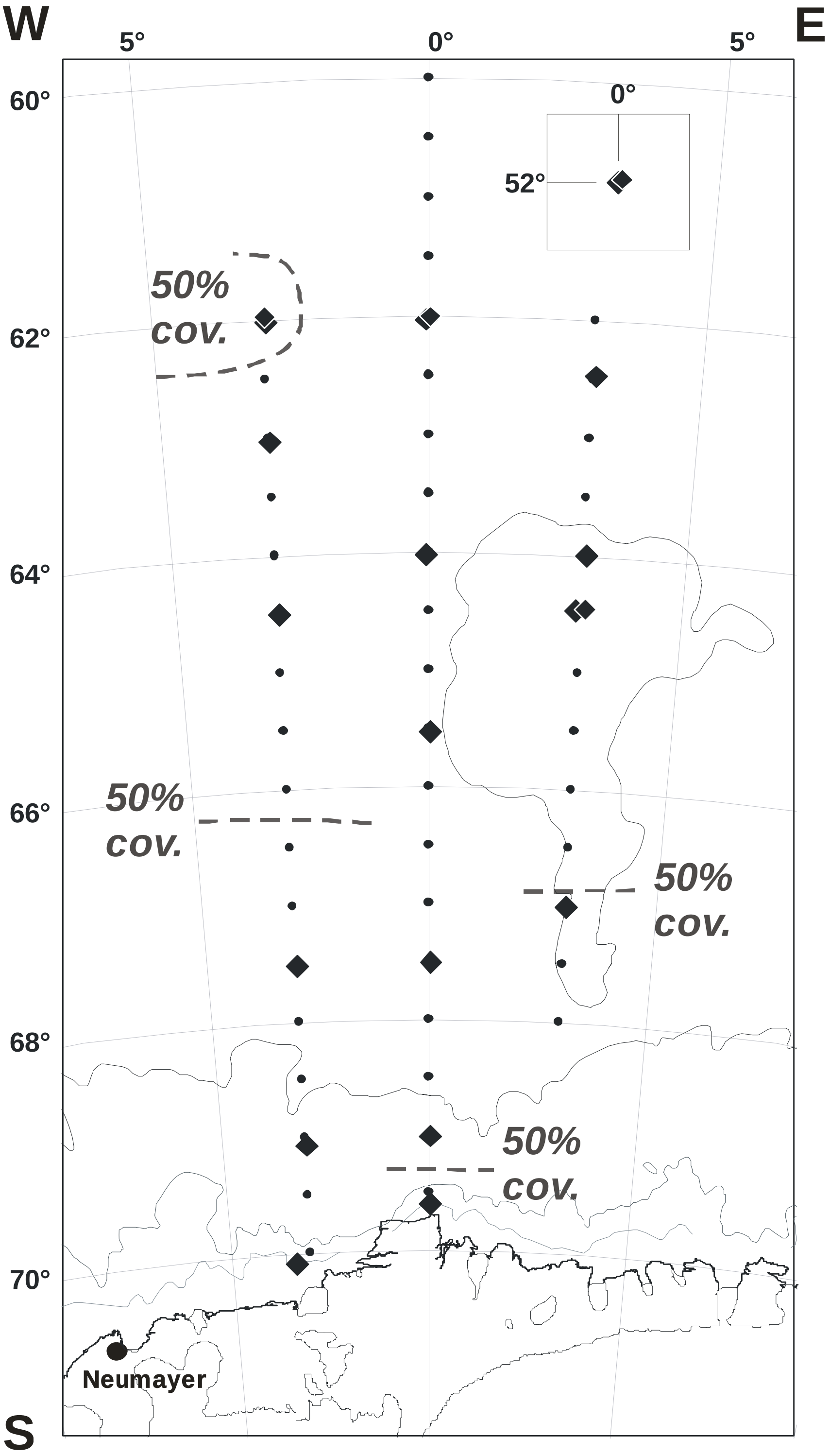

Figure 1. RMT station grid (●) of ANT XXIV-2. SUIT stations (♦) were conducted south of 62°S. An additional repeated station conducted at at 52°S 0°. Dashed line (- - -) denotes 50% ice coverage. Note that the Prime Meridian was sampled with a delay of two weeks after the 3°W and 3°E transect. By that time, the ice had retreated considerably southwards.

RESULTS

Species composition

Macrozooplankton / micronekton species represented a wide range of taxa, adding up to at least 40 species. The species encountered most often were Antarctic krill *Euphausia superba*, *Thysanoessa macrura*, the arrow worm *Sagitta gazellae*, the pteropod *Clio pyramidata* and the amphipod *Eusirus laticarpus*. Various species of larval and juvenile fish and squid were collected from the surface layer, among which the squid *Kondakovia longimana* and juvenile fish *Notolepis coatsi*.

Station 17 (Antarctic Circumpolar Current)

Station 17 was sampled in two consecutive nights, allowing to assess the variability of SUIT catches at one location. This station was situated at 52°S 0°, far away from the northern border of the RMT sampling grid (60°S). Species composition therefore differed from the stations sampled further south (Table 1, Figure 2), most evidently indicated by the presence of the subantarctic euphausiid *Euphausia frigida*. A comparison of the two hauls conducted at this location shows that the seven most abundant species were present at both occasions, dominated by *E. frigida* and *Salpa thompsoni* (Figure 2). Both hauls differed in the composition of less abundant species, for example squid and fish larvae (Figure 2).

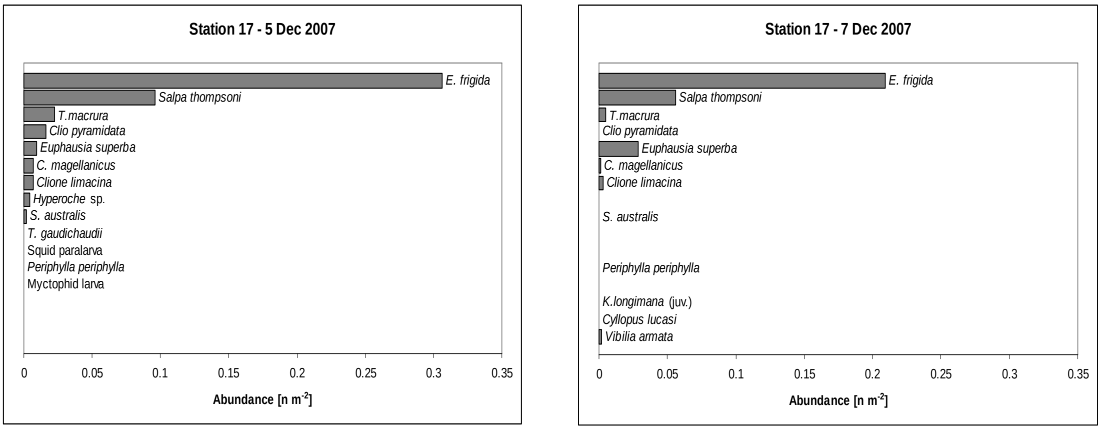

Figure 2. Comparison of abundance and species composition at two repetitive hauls at the same location (Station 17, 52°S 0°). Species were ordered by abundance at the first haul.

Table 1. List of macrozooplankton species (≥ 5 mm) sampled with SUIT. Number of individuals caught (N) and the number of stations where each species occurred are provided. Species marked with an asterisk (*) exclusively occurred at station 1z (Circumpolar current)

Taxon	N	No of stations
Cnidaria		
*Periphylla periphylla**	2	2
Unid. Siphonophore	1	1
Ctenophora		
Beroe cucumis	26	6
B. forskalii	75	6
Beroe sp.	1	1
Callianira antarctica	82	11
Unid. ctenophore	9	3
Mollusca		
Clio pyramidata	1,843	17
C. piatkowskii	3	2
Clione limacina	137	15
Spongiobranchaea australis	7	3
Undid. pteropod	8	2
Kondakovia longimana (juv.)*	1	1
Unid. squid larva	7	5
Annelida (Polychaeta)		
Tomopteris carpenteri	69	11
T. septentrionalis	2	2
Vanadis antarctica	1	1
Arthropoda (Crustacea)		
Eusirus microps	31	9
E. laticarpus	480	17
Eusirus sp.	13	2
*Vibilia armata**	6	1
Cyllopus lucasi	62	6
*C. magellanicus**	22	2
Hyperia macrocephala	7	5
Hyperoche medusarum	21	8
Primno macropa	60	10
*Themisto gaudichaudii**	1	1
Euphausia superba	58,886	21
*E. frigida**	1,460	2
E. frigida furcilia*	114	1
E. crystallorophias	61	2
Thysanoessa macrura	15,529	18
T. macrura furcilia	24	3
Unid. furcilia larva	7	2
Decapod larva	10	4
Chaetognatha		
Sagitta gazellae	2,360	18
Chordata		
Salpa thompsoni	427	3
Ihlea racovitzai	9	2
Unid. salp	2	1
Notolepis coatsi (juv.)	5	3
Myctophid larva*	1	1
Artedidraco sp. larva	1	1
Channichthyid larva	1	1
Dissostichus sp. larva	1	1
Trematomus loennbergii larva	2	2
Unid. Nototheniid larva	2	1

RMT sampling grid: Distribution, abundance and wet mass

Bulk zooplankton wet mass (coelenterates excluded) was largely dominated by krill, averaging at 0.233 g m^{-2} and ranging between 0.003 and 1.792 g m^{-2} (Figure 3). The most frequent and most abundant species *E. superba* was present at every station sampled with SUIT. Abundances were generally elevated in the area south of 67°S on the 3°W and 0° transects. Clearly the highest abundances were encountered on the 3°E transect, with the maximum abundance of 12 individuals per m^2 over the southern slope of Maud Rise (Figure 4a). In contrast, only few krill were caught at the two stations west of Maud Rise. *T. macrura* occurred less frequently, but abundances were generally in the range of *E. superba* when they were present, showing no distinct geographical pattern (Figure 4b). The third most abundant species, *Sagitta gazellae*, was more abundant in the part of the sampling area north of 64°S than to the south (Figure 4c). A similar distribution pattern was apparent from *Clio pyramidata*.

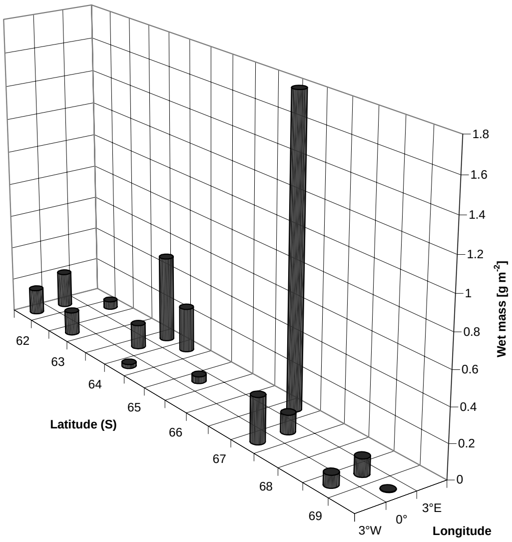

Figure 3. Distribution of bulk zooplankton wet mass (coelenterates excluded).

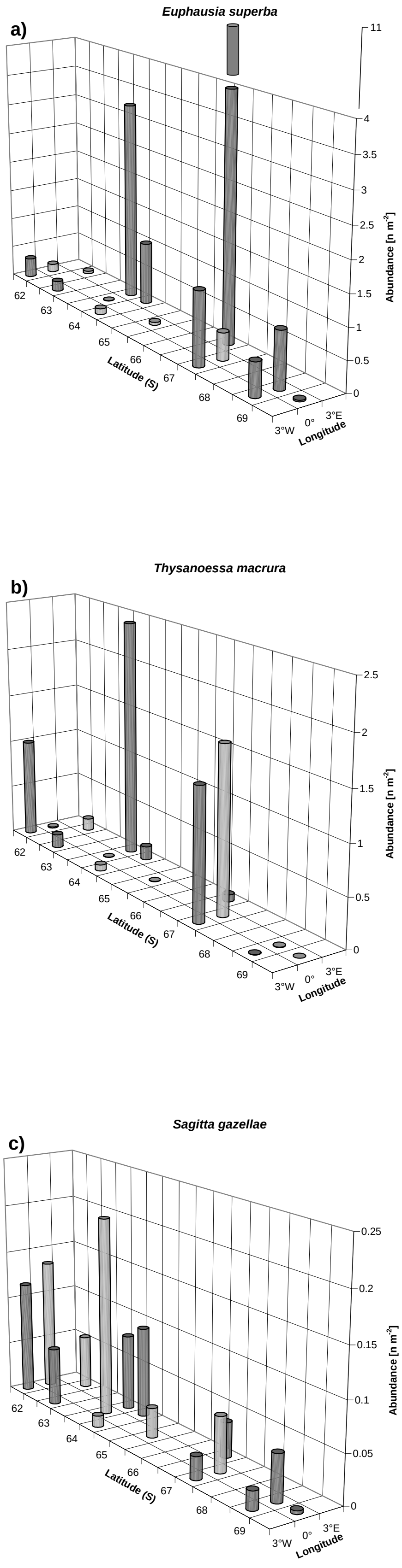

Figure 4. Abundance distribution of *Euphausia superba* (a), *Thysanoessa macrura* (b) and *Sagitta gazellae* (c).

Association with sea ice

A difference was apparent between stations sampled in open water and those were the SUIT was towed along the underside of ice floes. Antarctic krill for example was more abundant under ice floes than in the surface layer of the open ocean, whereas the abundance of *T. macrura* did not differ between open water and ice stations (Figure 5a). The amphipod *Eusirus laticarpus* was almost exclusively encountered under sea ice. In *Clio pyramidata*, a trend towards higher abundances in open water was apparent, whereas the abundance of *Sagitta gazellae*, similar to *T. macrura*, was comparable both under sea ice and in open water (Figure 5b).

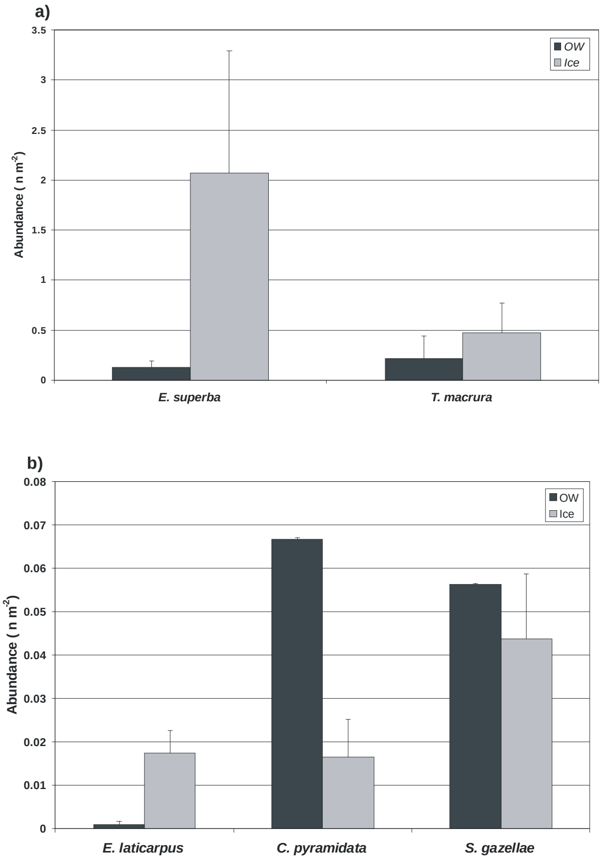

Figure 5. Comparison of stations sampled under sea ice and in open water (OW): Average abundances of *Euphausia superba* and *Thysanoessa macrura* (a), *Eusirus laticarpus*, *Clio pyramidata* and *Sagitta gazellae* (b). Error bars denote 75% confidence intervals.

Day-Night comparison

On three occasions, day and night trawls were performed at the same location. At all three stations, catches differed remarkably depending on the time of day, both in quality and quantity. *E. superba* was abundant in the SUIT catches both at night and at day. Yet, abundances were highest at day at all three stations (Figure 6a). The abundance of *E. laticarpus* showed no dependence of the time of day (Figure 6b). *S. gazellae* exemplifies the group of species which were clearly more abundant in the surface layer during the dark hours and almost absent at daytime (Figure 6c). This group includes also *T. macrura* and and *C. pyramidata*.

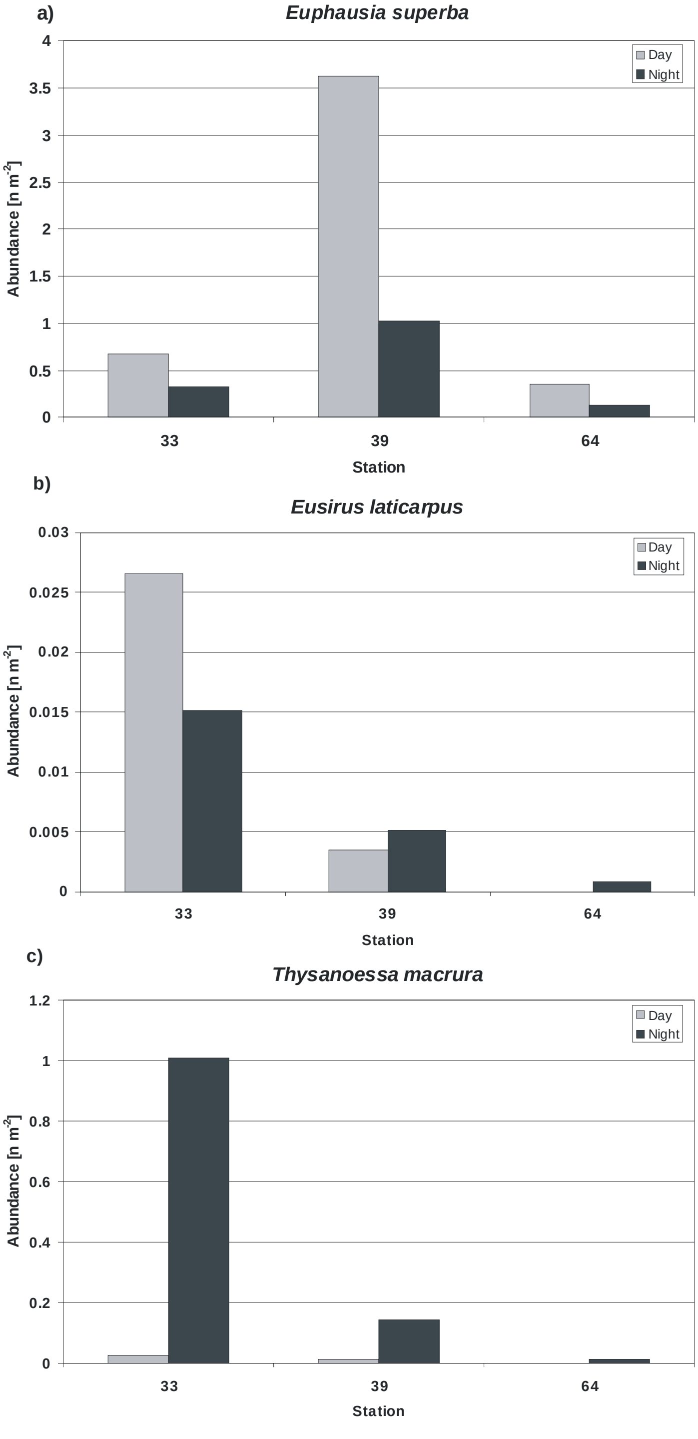

Figure 6. Day-night comparison of abundant zooplankton species at three stations.

Euphausiid length distribution

The size of *E. superba* ranged between 10 and 52 mm. The length-frequency distribution showed two modes at 18 and 30 mm. The lower mode was entirely composed of juveniles which dominated the sampled population. The mode at 30 mm was equally composed of males and females. Larger animals had only a minor contribution to the size composition of Antarctic krill.

In *T. macrura*, only data from samples taken on the 3°W and the 3°E meridian could be analysed during the expedition. The size of *T. macrura* ranged from 8 to 30 mm. The sampled population was dominated by sexually differentiated animals. The Size distribution peaked at 16 mm length, with minor modes at 12 and 20 mm (only females).

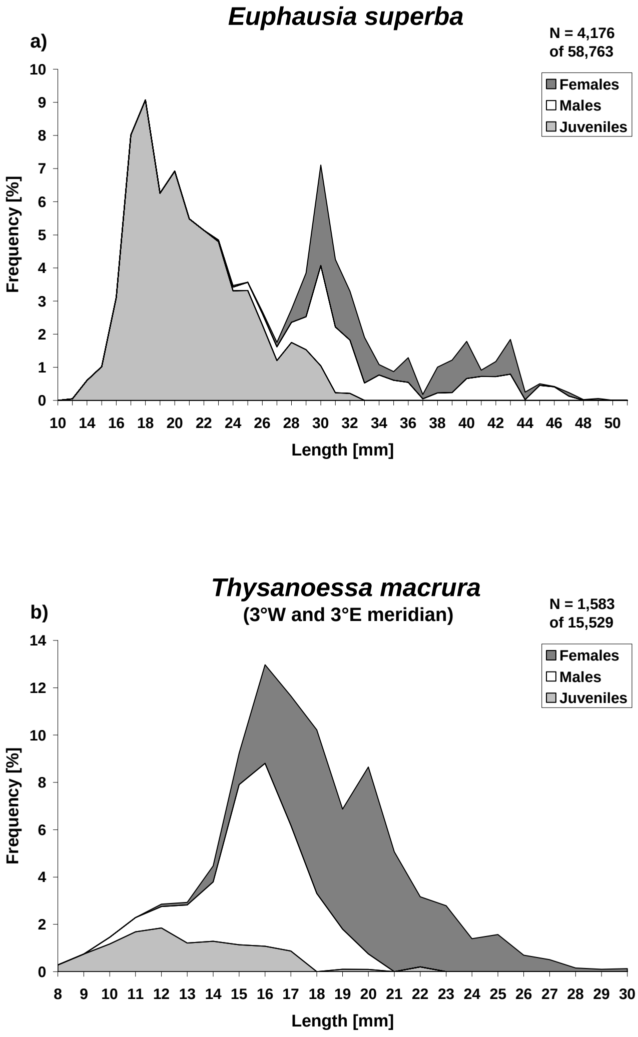

Figure 7. Length-frequency distribution of post-larval *Euphausia superba* (a) and *Thysanoessa macrura* (b). For *T. macrura*, samples taken on the 0° meridian were not analysed for this report.

DISCUSSION

The data collected on the Antarctic summer expedition ANT XXIV-2 illustrate the significance of the surface layer to a wide range of macrozooplankton and micronekton species. The presence of sea ice apparently had a strong influence on the composition of the near-surface community. In spite of the differences in species composition, the surface layer was rich in macrozooplankton / micronekton, both under ice floes and in open water. Some species were concentrated under the ice, such as *Euphausia superba* and *Eusirus laticarpus*, indicating that ice plays a major role for these species as a habitat and foraging ground.

E. superba was clearly more abundant under ice than in the surface layer of the open ocean, especially if one takes into account that the large confidence interval shown in figure 5a was mainly influenced by the extra-ordinary large catch at St. 44 (67°S / 3°E; Figure 4a). The notion that krill often aggregated in thin layers not only under ice, but also at the surface in open water is further supported by the observation of surface swarms (van Franeker et al., this volume). A concentration of krill under sea ice might partly explain the high abundance of Antarctic krill encountered by the SUIT in the surface / under ice layer compared to water column abundances sampled by the RMT in the area south of 62°S (Siegel et al., this volume).

In contrast to *E. superba*, the abundance of *Thysanoessa macrura* showed no difference between stations sampled under ice floes and those fished in open water (Figure 5a). They were more efficiently caught by the RMT, indicating a more dispersed distribution over a wide depth range (Siegel et al., this volume). In spite of the differences in euphausiid abundances, SUIT and RMT catches were related to each other, as exemplified by the significant positive relationships between SUIT bulk wet mass and RMT abundances of *E. superba* and *T. macrura*, respectively (Figure 8 b,c).

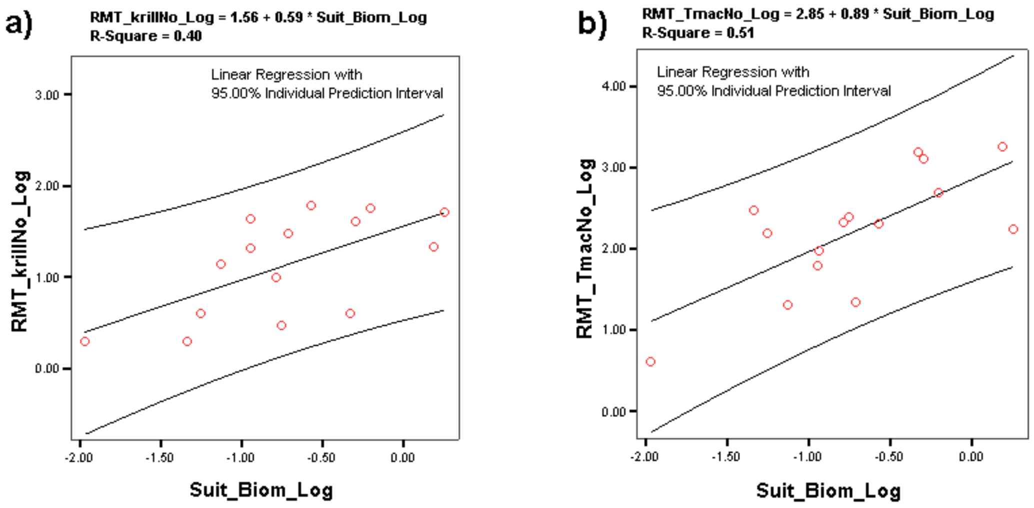

Figure 8. Linear regressions of log-transformed SUIT wet mass versus log-transformed numbers of *E. superba* (b: *P* = 0.01) and *T. macrura* (c: *P* = 0.03) caught by RMT

The observed geographical distribution patterns must be carefully considered in the light of the two-weeks time lag between the 3°E transect and the 0° transect, which introduced an unknown seasonal component. The separation of various environmental factors according to their influence on the observed distribution patterns is difficult, and the results should thus not be interpreted in terms of mono-causal relationships. Next to sea ice and temporal developments, hydrography is an important factor influencing the distribution of species in the area of investigation. For example, the elevated abundances of *Clio pyramidata* and *Sagitta gazellae* in the northern part of the area of investigation coincided with water masses of the northern (eastward-flowing) limb of the Weddel Gyre and at the same time with the area largely devoid of sea ice. The hydrographical peculiarities of Maud Rise further complicated the situation (Strass et al., this volume). This survey's highest krill abundances both by RMT and SUIT sampling on the southern slope of Maud Rise, as well as the extremely low krill abundances encountered to the west of Maud Rise might have been related to the seamount's specific current patterns.

A pronounced diel pattern was apparent in the presence of *T. macrura*, *C. pyramidata* and *S. gazellae* in the surface layer. At the three day/night comparison stations sampled, these species were almost absent from SUIT catches during daylight hours, whereas at night they were abundant (Figure 6c). Most often, such diel migration behaviour is explained as the avoidance of visual predators. Yet, at least in the two species carrying almost no pigmentation, *T. macrura* and *S. gazellae*, avoidance of harmful UV radiation could be an alternative explanation.

In contrast, *E. superba* even showed a tendency to higher abundances at day (Figure 6a). Apparently, the benefit of grazing under the ice and in the phytoplankton-rich surface layer in open water was higher than the danger imposed by predation during summer. Interestingly, the opposite behaviour was observed in winter 2006, when krill only was abundant under the ice at night (Flores et al., in press). No diel pattern was observed in *Eusirus laticarpus*, indicating that the amphipod continuously stays in the ice habitat (Figure 6b).
Initial comparisons of the abundances of surface / under ice macrozooplankton and the food requirements of the top predator community showed no simple overall correlation (van Franeker et al. this volume). Further integrated analysis of all potentially relevant biological and physical datasets is warranted to increase our understanding of the functioning of the high-Antarctic ecosystem.

Acknowledgements

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