Fresh from the fridge: Top predators' food sources under the pack-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) at the ice edge persist and sometimes even increase towards the inner pack-ice, indicating considerable primary and secondary production in these areas (Van Franeker et al. 1997). But water column primary production 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. In this top-down approach, the distribution of the prey of birds and mammals is the next logical step after quantifying the occurrence of top predators (van Franeker et al., this volume).

Flying birds, and on many occasions also penguins, seals and whales, often rely on prey they find in the upper few meters of the water column. In order to explain feeding and prey distribution of these abundant 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 during winter.

At IMARES Texel, the need to investigate the ice-associated community in more detail led to the development of a special under-ice trawl (SUIT = Surface and Under Ice Trawl). After a first LAKRIS campaign with SUIT in austral autumn 2004, the winter expedition 2006 provided the rare opportunity to sample under Antarctic pack-ice during the dark period of the year.

MATERIALS & METHODS

Trawling of SUIT was attempted 29 times on the regular CCAMLR grid and at one station at the northern ice edge between June 30th and August 14th, 2006.

The net system consisted of a steel frame with a 2.25 x 2.25 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 at the surface. To enable sampling under undisturbed ice, an asymmetric sprout let the net shear at an angle of ca. 30° starboard from the ship's track at a cable length of 120 m. Wheels on top of the frame allowed the net to 'roll' along the underside of ice floes. A flashlight was attached to the frame in order to reduce escaping of animals by shock-blinding them.

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 80, 110 and 130 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 ($2.25^2 = 5{,}06\ m^2$). A mechanical impeller flow meter (Hydrobios) was mounted additionally for comparison with conventional flow meter data.

Fishing was done during complete darkness in 22 of the 30 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 25 and 30 minutes towing time, with the exception of the ice edge station, where towing time was 49 minutes. During each trawl, irregularities, changes in ship speed, ice coverage [%] and ice thickness [cm] were constantly recorded.

Animals ≥ 0.5 cm were separated to species level where possible. Displacement volume 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. 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 -30°C.

The total length (TL, front edge of eye - tip of telson) of krill 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. Krill were grouped into males, females / juveniles and gravid females. The standard length (SL, tip of snout - beginning of tail fin) was used in size measurements of fish and fish larvae. Cephalopod size was expressed as TL and mantle length (ML).

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

RESULTS

Net performance

Of the 30 hauls, 22 could be completed successfully. Due to storm and ice damage, only three southerly stations on the 3°E transect could be completed. The other two transects (0° and 3°W) could be covered over the entire latitudinal range.

Current speed of water entering the net opening showed a consistant pattern in each successful haul. During deployment and heaving, current speed was low. In these periods, high signal amplitudes indicated disturbance. As soon as the net reached its dedicated position, current speed and amplitudes stabilized. Typically, current speed in the net was slightly lower than the ship's speed. The real-time data collection also allowed identifying periods of poor towing performance and other irregularities which helped to draw conclusions on the overall quality of each tow (Figure 1).

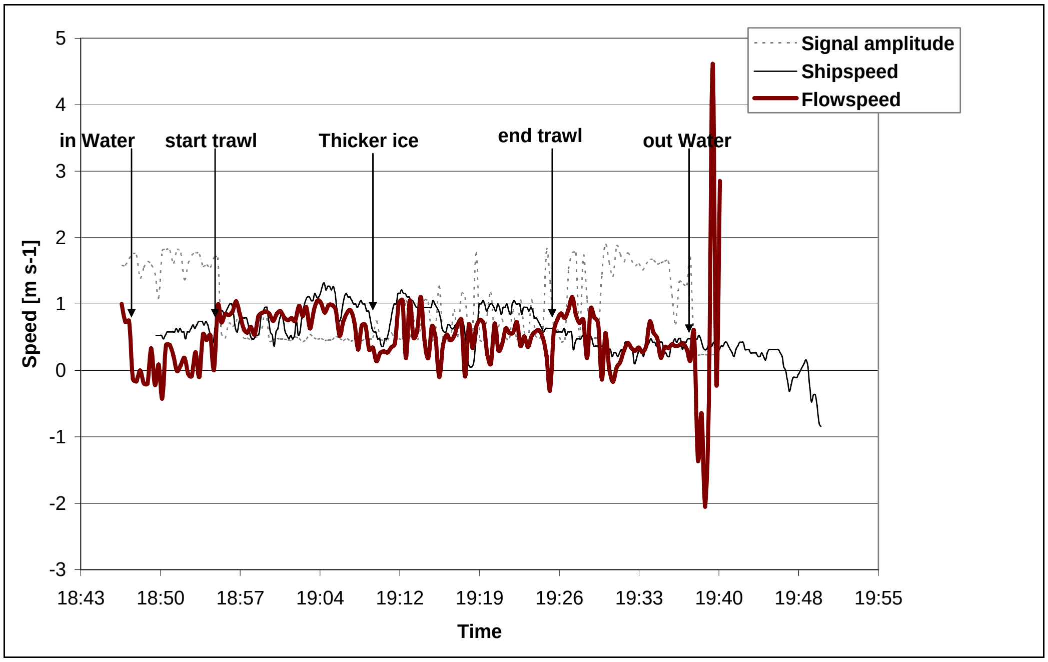

Figure 1. Example of real-time current speed measurements in SUIT frame opening. Specific events during trawling indicated in graph.

Species composition

Zooplankton and nekton species represented a wide range of taxa. They covered a size spectrum from < 5 to > 400 mm in total length. The species encountered most often were *E. superba*, the siphonophore *Diphyes antarctica* and the pteropod *Clione* sp. The amphipod *Eusirus microps* was found on 9 stations. Individuals from this species covered a wide size range. Larval *Trematomus loennbergi* and larvae of at least one other nototheniid species (cf. *Pagothenia borchgrevinki*) were also caught under the pack-ice. Among the nekton caught under ice were two species of theutoid squid, *Electrona antarctica* and a nototheniid fish (Table 1).

Table 1. List of makrozooplankton and nekton species and euphausiid larvae collected during ANT XXIII-6 and number of hauls where they occurred

Taxon	No of hauls	Size range [mm]*
Calycopsis borchgrevinki	6	
Siphonophora (cf. *Diphyes antarctica*)	24	
Ctenophora indet.	9	
Clio pyramidata	6	
Clione sp.	23	
Spongiobranchaea australis	4	
Theutoidea indet.	1	ca. 200
Theutoidea indet. (cf. *Kondacovia longimana*)	1	420
Tomopteridae indet.	4	
Vanadis antarctica	3	
Eusirus microps	9	6-40
Eusirus sp.	4	
Hyperiidae indet.	6	
Hyperia macrocephala	2	
Hyperiella dilatata	2	
Hyperoche sp.	*2*	
Cyllopus lucasi	7	
Primno macropa	5	
Euphausia superba	23	18-51
E. superba furcilia larvae	13**	
Thysanoessa macrura furcilia larvae	1**	
Sagitta gazellae	16	
Salpidae indet.	4	
Electrona antarctica	1	
Nototheniidae indet.	1	136
Pisces indet. larvae	1	37
Nototheniidae indet. larvae	2	50
Trematomus loennbergi larvae	4	27-41

*TL; SL for fish. **Furciliae only partly identified

While krill was caught at most stations, it was abundant only in the northern part of the 3°W-transect. At those stations, it dominated all other zooplankton species by several orders of magnitude, reaching densities of up to 31 ind. m^{-2}. A difference between the two fully covered transects (0° and 3°W) was evident also in the other species. When krill was excluded, *Clione* sp. dominated the species community throughout the latter transect, whereas their density was low on the other, except for the two northernmost stations (Figure 2a, b). A latitudinal pattern was apparent for several species like krill larvae (furciliae), *E. microps* and larval *T. loennbergi*, which were caught mainly in the southern part of the survey area.

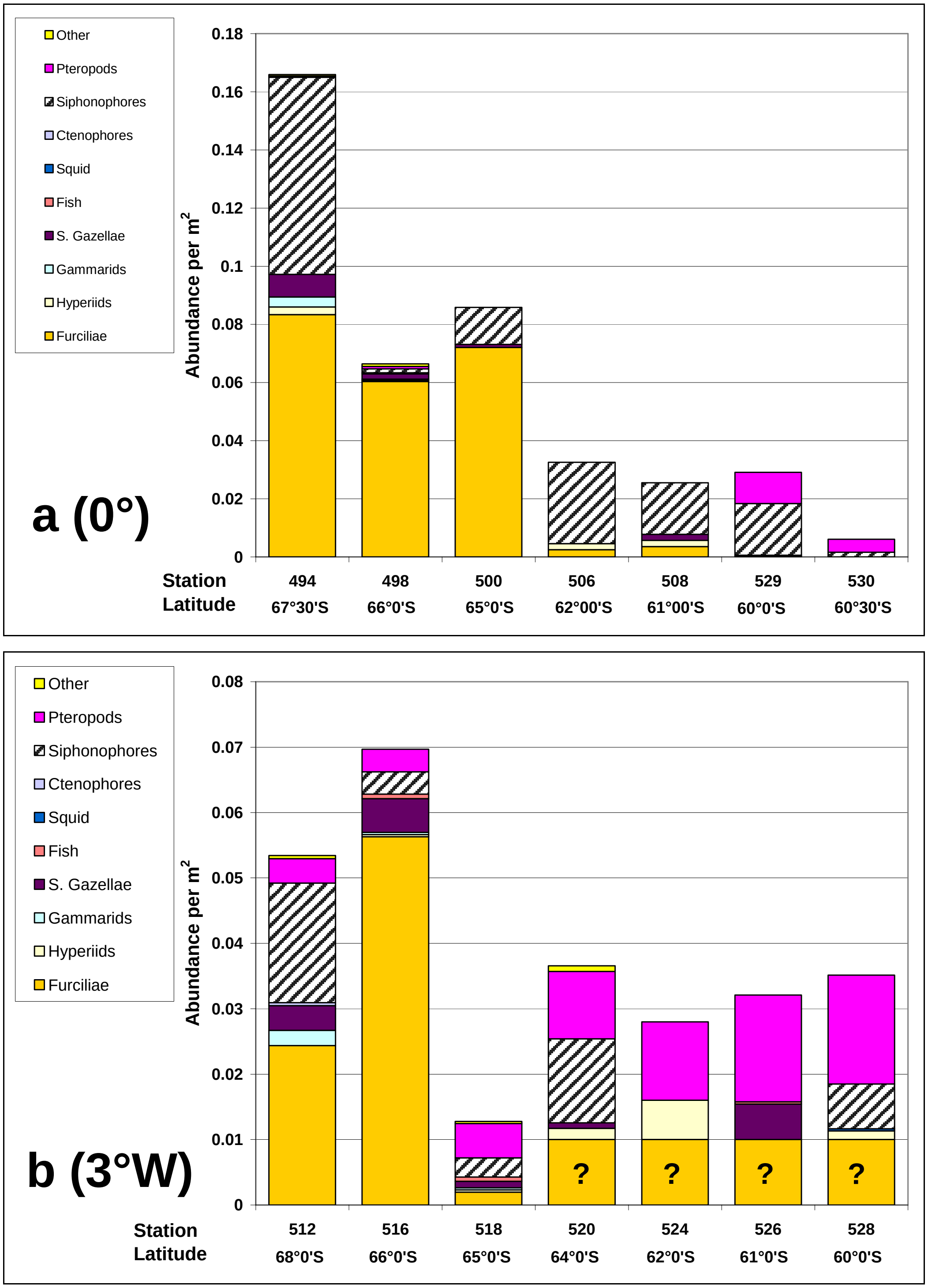

Figure 2. Abundance distribution of species on the 0° (**a**) and 3°W transects (**b**). Note that furciliae were not quantified from station 520 onwards.

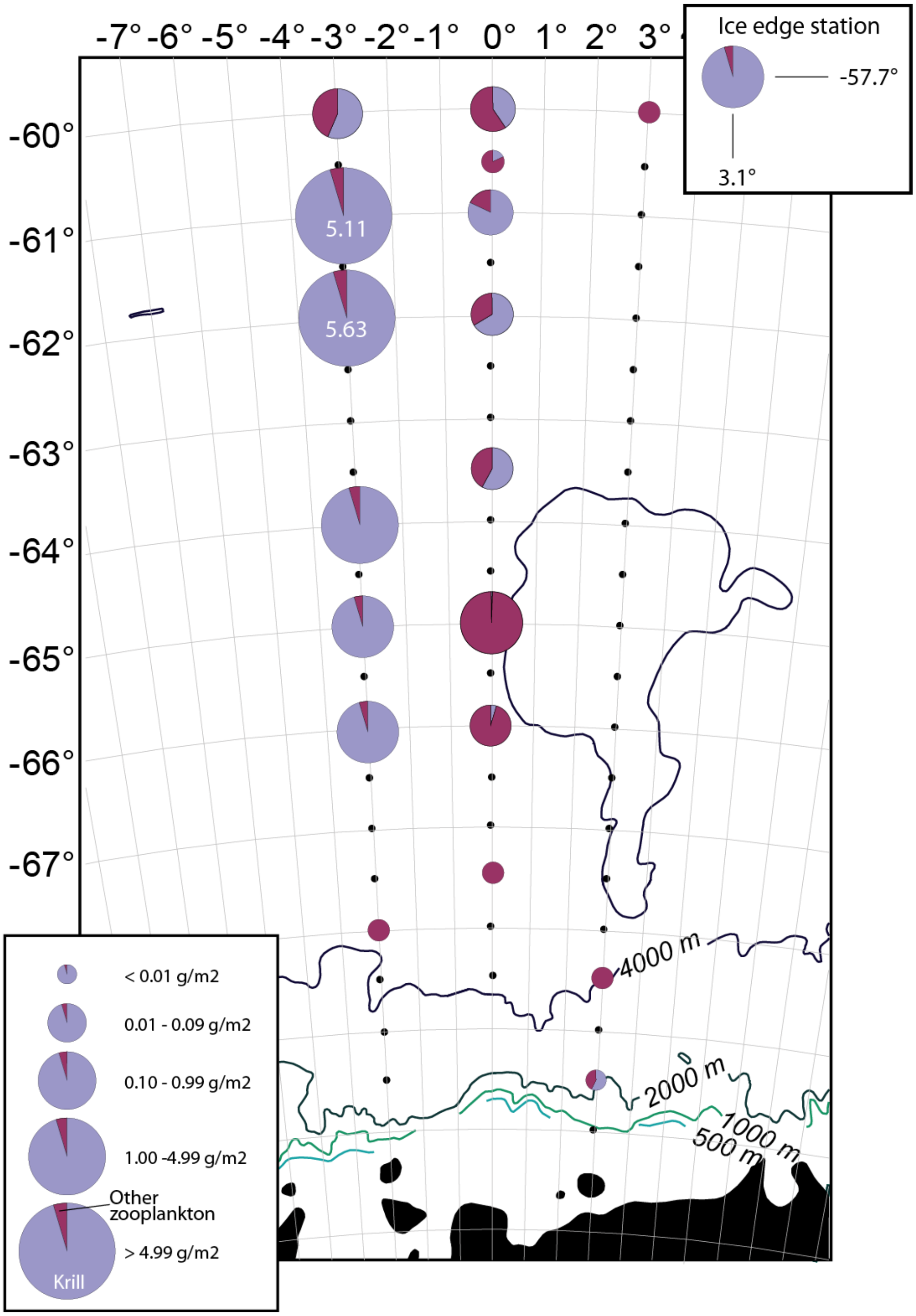

Figure 3. Biomass distribution of surface zooplankton and nekton in the area of investigation.

Biomass distribution

On the westernmost transect, catches were dominated by large amounts of krill on 5 of the 7 stations, peaking at more than 5 g m^{-2} on the 61°S and 62°S stations. In contrast, biomass density of krill was moderate compared to other zooplankton and nekton on the prime meridian and eastern transect, where biomass density under the ice was below 0.1 g m^{-2} at most stations. It was below 0.01 g m^{-2} at the four stations south of 67°S. *E. superba* also dominated the biomass composition at the ice edge station, where total biomass density (0.8 g m^{-2}) was comparable to the 3°W transect (Figure 3).

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. Among them, station 498 (66°S 0°) differed from the other two in yielding a low amount of krill, both at day (0.006 m^{-2}) and night (0.001 m^{-2}; Figure 4).

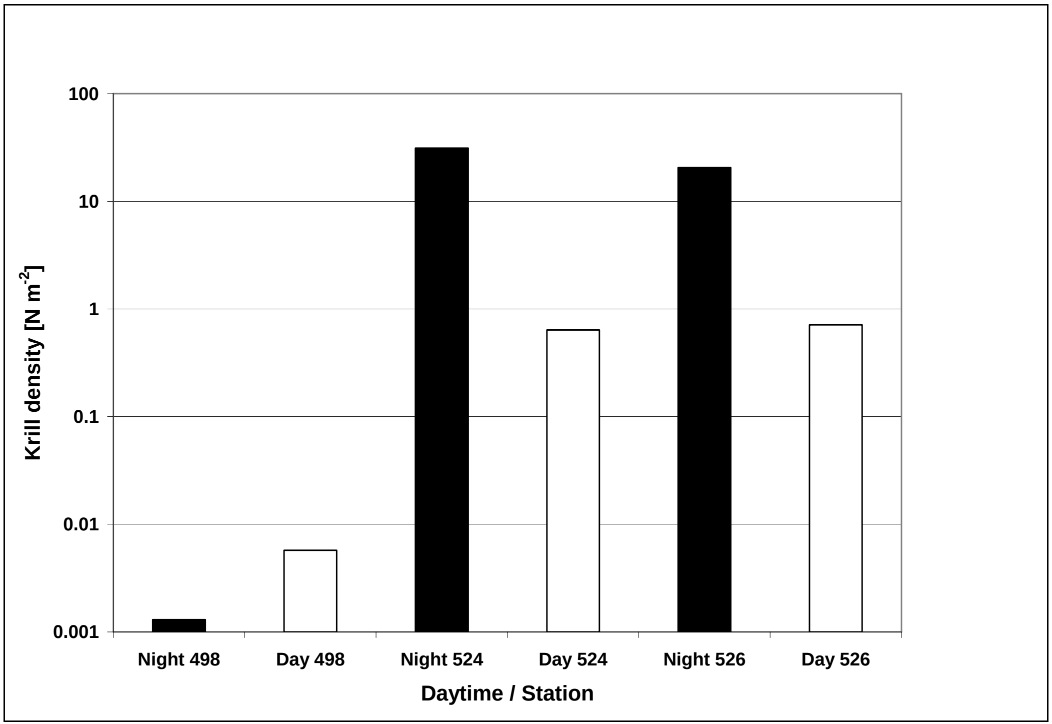

Figure 4. Day-night comparison of krill density. Note logarithmic scale of y axis.

The catch was dominated by furcilia larvae which occurred in similar amounts at both times. The density of siphonophores (mainly *D. antarctica*), which were the second most abundant group at day, was significantly lower during the night. The opposite pattern was apparent for *Clione* sp., which was absent from the daytime catch (Figure 5a). The other two stations, 524 (62°S 3°W) and 526 (61°S 3°W), were clearly dominated by juvenile and adult krill. In both of them, krill catches at night were two orders of magnitude higher than at day (Figure 4). Among other zooplankton, a pattern similar to Station 498 was apparent for siphonophores (mainly *D. antarctica*) and pteropods (mainly *Clione* sp.; Figure 5b). Ctenophores, which were caught at Station 498 at nighttime but could not be quantified due to disruption, only occurred at day at station 524 and 526.

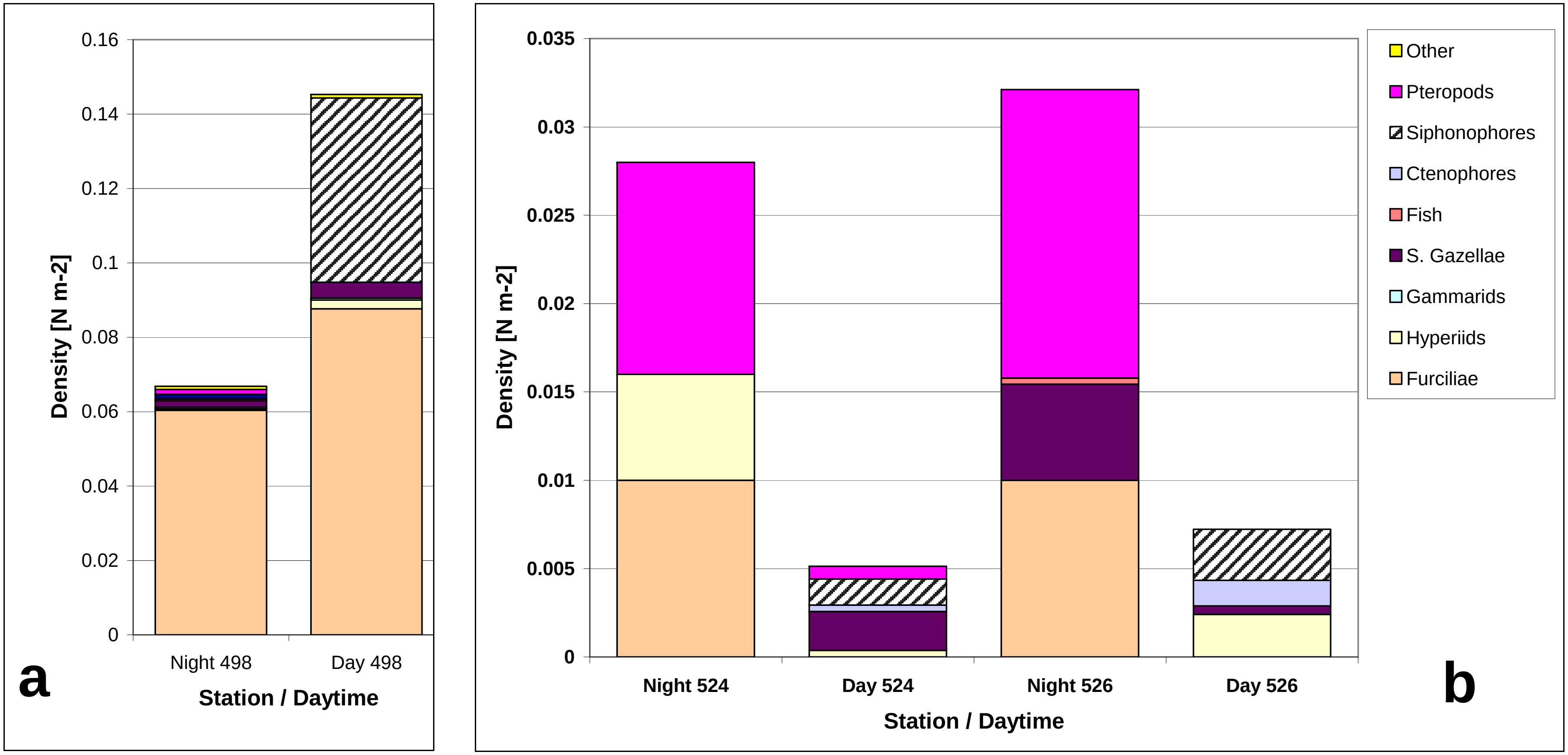

Figure 5. Day-night comparison of species composition when krill is excluded. Note the different scale of figure **5a** (station 498) and **6b** (stations 524 and 526).

Krill length distribution

The size of adult and juvenile krill ranged from 18 to 51 mm in females / juveniles and 23 to 48 mm in males. Major peaks were at 33 and 28 mm in both sexes, indicating that most animals were probably 1-2 years old (Figure 6).

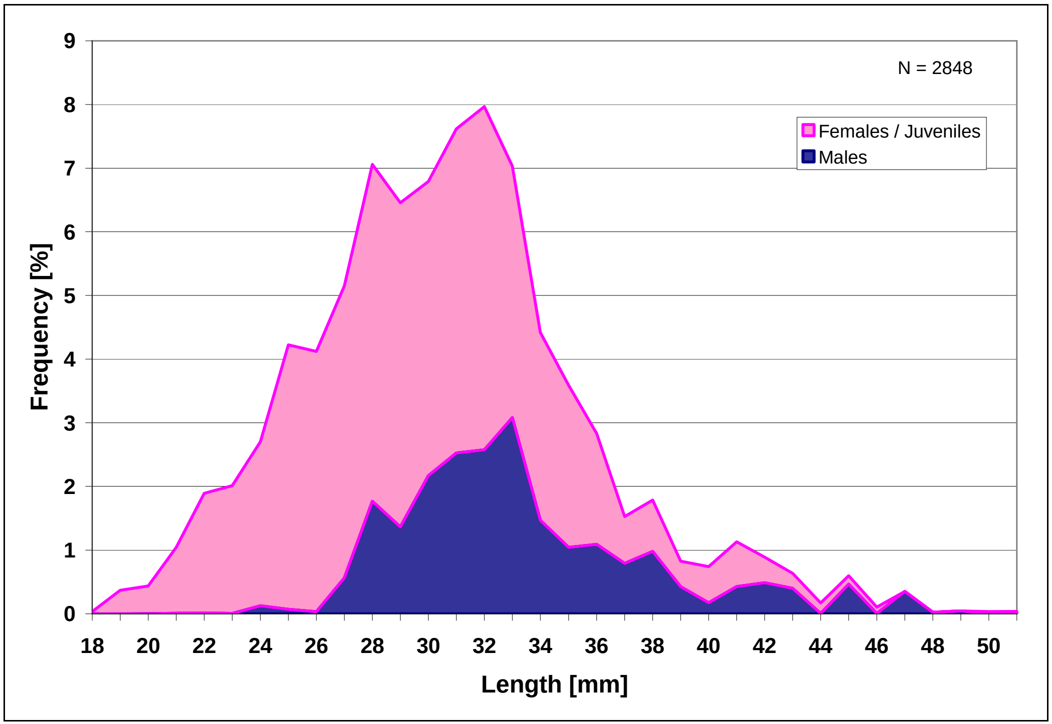

Figure 6. Length-frequency distribution of post-larval krill.

DISCUSSION

Net performance

In spite of severe storm rampage and several damages caused by heavy ice in the beginning of the sampling period, more than 73 % of the SUIT deployments could be completed successfully. Across all successful stations, a stable pattern in water flow indicated that the orientation of the opening as well as the net’s speed were steady and predictable during the effective towing time. During deployment and heaving, turbulences were indicated by reduced inward current speeds and high signal amplitudes which were probably caused by air bubbles mixed into the water. These turbulences most likely occurred because the net opening was not oriented in flow with the movement of the net. Therefore, we regard catchability to be low outside the effective towing period.

While density estimates based on SUIT trawling are most likely realistic for most species of macrozooplankton including krill (Flores et al. 2005), smaller species (e.g. furciliae) were probably underestimated because of the relatively large mesh size in the frontal part of the net. Conversely, fast swimming species like adult fish and squid were perhaps not sampled quantitatively due to their ability to escape the net.

Species composition and distribution patterns

The results of the under-ice trawls illustrate that a considerable variety of macrofauna can be found in close proximity to sea-ice in winter. For most of the planktonic species, it cannot be determined if they represented parts of pelagic populations randomly dispersed to the surface layer, or if they actively seeked the ice environment. Some species were more evidently associated with the sea-ice undersurface, like furcilia larvae of krill which were observed to aggregate in crevices and caves during this expedition (Freier et al., this volume). Furciliae are probably a valuable prey for predators like *S. gazellae*, ctenophores, larger crustaceans, fish and squid. The repeated occurrence of *E. microps* in SUIT catches and its consistent size range add evidence to the hypothesis of a sympagic or pelago-sympagic mode of life of this species (Krapp et al., in press). The encounter of a juvenile nototheniid and two species of squid indicates that large nekton species also make use of the ice habitat to an extent which is possibly underestimated by SUIT sampling, as discussed above.

Except for the northernmost stations, the 3°W transect differed significantly from the 0° transect in species composition and biomass. Hydrographical features, like advection from other water masses, seem the most likely explanation of the observed pattern. The role of hydrography in the distribution pattern of under-ice zooplankton and nekton will be investigated in detail as soon as detailed hydrographical data become available.

Krill and sea ice

The importance of sea-ice for krill larvae is widely acknowledged (e.g. Daly 2004). High densities of krill furciliae caught directly under ice in the southern part of the area investigated and observations of divers during this expedition confirm this view.

Our results provide quantitative evidence that juvenile and adult krill can be found in dense aggregations under ice during winter, supporting the hypothesis that *E. superba* uses the sea ice as a foraging ground during the dark season (e.g. Sprong & Schalk 1992). Day-night comparisons indicate that the use of the ice habitat followed a diel pattern. This perception was supported by aggregations of acoustic targets moving from mesopelagic depths to the surface at dusk and back down at dawn during this expedition (U. Bathmann, pers. comm.). At stations where high amounts of krill were caught under the ice, standard RMT catches were low, indicating that the vast majority of the migrating krill did not stay in the water column, but resided directly under the ice. However, due to the limited sampling depth of the standard RMT (200 m), it cannot be excluded that a part of the krill population remained at greater depth.

Top predator – prey correlation

For a preliminary comparison of SUIT-based distribution of surface zooplankton / nekton and top predator densities see van Franeker et al., this volume. Sampling the under-ice environment with SUIT proved to be valuable to illustrate that many prey species of common Antarctic top predators can be found in close association with sea-ice. However, it turned out to be difficult to relate the distribution of predators and their potential prey quantitatively. These difficulties were probably caused by a combination of low prey density under ice at most stations and the top predator community being dominated by animals (seals, whales) which can also rely on deeper-dwelling prey, e.g. mesopelagic fish (Van de Putte et al., this volume). The ice edge station could exemplify that concentrations of surface-feeding petrels can be correlated with appropriate amounts of prey in the surface layer of ice-covered waters.

Acknowledgements

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