Large and small-scale distribution of krill *(Euphausia superba)* **between South Georgia and Bouvet Island in the Southern Ocean**

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Preface

This thesis was written at the department of Biology at the University of Oslo in the period 2008-2009. It is written with guidance by my main supervisor Professor Stein Kaartvedt, and co-supervisor Thor Klevjer.

I would first like to thank Stein Kaartvedt for a good and constructive feedback throughout the work with my thesis. He has been available for questions when I needed it, especially in the finishing part of the process.

Secondly, Thor Klevjer has been a priceless ally working with Sonar 5, the computer software used to interpret the acoustic data from the survey. Always available for questions and feedback. Also an appreciation for the time taking care of, and joining us on the AKES 1 survey down in Antarctica.

I thank cruise leader Svein Iversen for good leadership, and the Institute of Marine Research (IMR), for our possibility to join this survey with the research Wessel G.O.Sars down to Antarctic waters. I will also thank the crew and the scientists onboard for the experience of my lifetime down in Antarctica.

A special thanks goes to Einar Loshamn for good companionship on the Antarctic cruise and for encouragement on late working days at Blindern, and for proofreading my thesis in the end of the process. A thanks to Eirik Kristianslund for feedback and proofreading and to my parents for proofreading and support. Thanks to all students at Blindern for the best 5 years of my life, and to all happy faces I meet every week at "the office" nr 4131, at level 4 in the biology building, - Nico, Arian, Bjørnar, André, Harald, Silje and all the other girls. The last thanks goes to my girlfriend Mari Olerud for good understanding, support and encouragement throughout the process. You are incredible!

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Abstract

The abundance and distribution of Antarctic krill is poorly known for some parts of the Southern Ocean. Recent, and anticipated enhanced interest in krill fisheries highlights the need for precise and reliable data to secure the population through international agreements.

The acoustic survey AKES 1 (Acoustic Krill Estimation Survey) made by IMR (Institute for Marine Research, Norway) was conducted in the Southern Ocean between South Georgia and Bouvet Island, during January and February 2008, as a part of the International Polar Year 2007/2008. Waters around South Georgia, the Open Sea region between South Georgia and Bouvet, and the area close to Bouvet Island were investigated. There is limited knowledge on krill distribution in the two last areas.

The abundance of the Antarctic krill, *Euphausia superba*, was studied using a 38 kHz and 120 kHz Simrad EK60 echo sounder, and by sampling with a "krill trawl". Acoustic characteristics of krill, together with trawl catches were used to identify the acoustic targets. Antarctic krill was the prevailing organism in the water column. Sampling of environmental data comprised continuous measurements of surface temperature, salinity and fluorescence along the cruise track, as well as vertical profiles (CTD) at selected stations.

The acoustic logging was made continuously throughout the entire survey. In the subsequent analysis, data for the depth interval 0-200m were allocated to three regions; South Georgia, Open Sea and Bouvet Island. Krill abundance, vertical and horizontal distribution, school structures and variations between night and day were analyzed.

Krill aggregations had larger size and density close to South Georgia and Bouvet Island, compared with the Open Sea. At South Georgia aggregations were over all larger than in the two other areas, and this was the region with the highest krill abundance per surface area. The largest single aggregations of krill were found at Bouvet Island, though few in numbers. The Open Sea area hold few and small aggregations compared to the volume sampled, even in cold waters south of the Polar Front. The krill were more or less absent close to, and north of the Polar Front.

The higher abundance of krill close to the two islands coincided with intermediate chlorophyll a levels (chl a), known to be one of the factors contributing to preferable krill habitats.

Krill occurred in the densest aggregations and displayed the most marked Diel Vertical Migrations (DVM) in waters around South Georgia, which I ascribe to the highest predation pressure from land-based predators in the region.

At South Georgia the Antarctic krill aggregated in a dense belt close to the surface (though sometimes with a vertical extension of 60-70 m) during night and became assemblaged into even denser swarms of varying size at 50-100m during day.

In the Open Sea south of the Polar Front, krill often occurred in a continuous low-density belt in the upper 60m of the water column during night. At daytime krill formed small aggregations with a peak around 40-60m depth, with densities higher than what could be found in the diffuse belt at night.

At Bouvet Island krill aggregated close to the surface in dense compact swarms during night and at daytime krill formed both small swarms with a low density and some large aggregations between 20-80m depth.

Our findings on regional differences in DVM are not known from previous studies. Predation pressure, together with growth potential and food concentrations (chl a), seem to be the three factors with the largest influences on krill distribution in this study.

Introduction

The Southern Ocean accounts for 20% of the world's oceans, and it plays a very important role both biologically and in controlling the climate in the world (Sarmiento et al. 1998; Boyd 2002)

Antarctic krill, *Euphausia superba*, occupy a key role in the Antarctic ecosystem. They are a major prey source for mammals and seabirds, a dominant grazer on larger phytoplankton, and producers of fast sinking fecal pellets that contribute to the carbon flux (Ducklow *et al.* 2007). Being the major link in a short food chain between primary production and vertebrate predators it serves as an essential part for the functioning of the Southern Ocean food web (Murphy *et al.* 2007). Krill is omnivorous, and in addition to the main contribution from diatoms in the diet, krill can also feed on micro- and mesozooplankton in the pelagic realm and on benthic organisms in shelf areas (Ligowski 2000; Daly 2004; Murphy *et al.* 2007). In sea ice covered regions, feeding on ice algae appears to be important during winter (Ligowski 2000; Murphy *et al.* 2007).

Krill are rich in omega-3 oils, contain strong anti-oxidants and desirable pigments, and has served as a food source for aquaculture since the 1960s. There is an increasing demand for krill protein, and the pigment carotene from the krill exoskeleton in aquaculture industry. Furthermore, new methods for processing krill and extraction of substances for pharmaceutical- and human health and lifestyle products expectedly will increase the demand for krill, with consequent increased fishing pressure. The recent interest in krill fishing highlights the need for precise and reliable data to secure the population, and a sustainable ecosystem, through international agreements.

As a Norwegian contribution to improve the knowledge of krill in the Southern Ocean, the Institute of Marine Research (IMR), together with several other Norwegian organizations, conducted a survey to the Southern Oceans during January and February 2008. This survey was one of the Norwegian scientific efforts related to the "International Polar Year (IPY) – 2007-2008" which is an "international program of coordinated, interdisciplinary scientific research and observations in the earth's polar regions" (http://www.ipy.org/). The aim of the survey was to increase our knowledge of Antarctic ecosystems, focusing mainly on krill biomass estimation of the Antarctic krill stock in these areas. Data collected on this survey makes up the basis for this thesis.

E. superba have a circumpolar distribution, but 70% of the population is believed to lie within the "Atlantic sector" between longitudes 0° and 90°W (Atkinson *et al.* 2008). Here krill are abundant both over the continental shelf and in the off-shelf ocean (Atkinson *et al.* 2008). Most research in this sector is conducted close to the Scotia Sea and South Georgia. Studies here have shown that in the winter, mortality and dispersal leads to a decline in krill abundance in the northern regions, while in the summer, a large amount of krill occurs in these waters (Atkinson *et al.* 2004). A modern concept quotes that *E. superba* in the Southern Ocean is largely inhabiting waters above the shelf edges and their vicinity, i.e. in areas were we find the highest densities of krill (Trathan *et al.* 2003; Reid *et al.* 2004; Nicol 2006; Atkinson *et al.* 2008). However, due to the larger areas of open sea, recent analysis show that a majority of *E. superba* is found in the open sea, with an estimate of 87 % of the total krill stock living over waters at more than 2000m depth (Atkinson *et al.* 2008).

Many marine organisms commonly display diel vertical migration, and some studies suggest that this is evident for the Antarctic krill as well (Brierley *et al.* 2006). Avoidance of visual predators in the deep during the day and foraging in food rich, often warmer waters close to the surface at night, is normally seen as the ultimate cause for such vertical migrations (Zaret & Suffern 1976; Giske *et al.* 1998). In the Southern Ocean, the upper 200m of the water column is largely unstratified, so little energetic advantage would therefore be gained from vertical migration. Avoidance from predation is left as the most reasonable explanation for this migration pattern (Robison 2003; Collins & Rodhouse 2006).

In response to predation pressure and differences in food concentrations, krill swarms are formed and shaped (Hofmann *et al.* 2004). In areas with increased predation pressure krill migrate down in the water column at day to reduce predation risk and this is known for South Georgia (Brierley *et al.* 2006) . However, of the many studies done on Antarctic krill, few have identified any consistent simple relationships between environmental properties and krill distribution (Siegel 2005).

At South Georgia, good krill habitats, high renewal rates and an intense predation pressure from breeding colonies of mainly fur seals and penguins, creates an environment with a high predation to krill abundance ratio, yet with krill abundance being maintained at a high level. Here first-year krill are rarely found, and because of this krill are not supposed to reproduce successfully at this locality (Nicol 2006). Reproduction of *E.*

superba is thereby low, and the recruitment of krill at South Georgia is believed to come from the input through the Weddel Sea Current (WSC) and the Antarctic Costal Current (ACC) (Atkinson *et al.* 2008). The high predatory demand for krill is within 200-250 km of the island (Murphy *et al.* 2007) and within this area, vertical migration is extensive (Brierley *et al.* 2006). An intense predation pressure is also believed to co-occur with high krill concentrations evident for other islands in the area (Atkinson *et al.* 2001). Areas far out to sea have a lower predation pressure from land-based predators possibly resulting in different distributional and behavioral patterns. A study by Everson et al. (1996) states that *E. superba* is not only distributed at the shelf break near South Georgia, but widely distributed in schools through out the region, with no clear link to bathymetry or hydrography. However, the open sea areas covered by our survey have until now been little studied, and little is known about krill in these regions.

Though research has been limited, distribution in the open sea is believed to relate to coldwater masses, and areas with intermediate food concentrations as preferred habitats for krill (Atkinson *et al.* 2008). In the open sea growth rates are lower than close to the islands and over shelves. The ocean provides a refuge for krill from shelf and land-based predators. At Bouvet Island, conditions for krill are believed to resemble other islands in Southern Ocean (Atkinson *et al.* 2001), but little is known about this remote island.

In this study, acoustic methods were used to sample data. This is a common approach used to study krill in the Southern Ocean. We use hull-mounted echo sounders at frequencies of 38 kHz and 120 kHz. The krill estimates are based on approved methods used by and for the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). The acoustic measurements were supplemented with other environmental data such as salinity, temperature and fluorescence (chl a). Trawling was also conducted for identification of krill swarms, other acoustic structures, and samples of krill for various studies, which are not further referred to here.

The primary aims of this study were to assess the large-scale vertical and horizontal distribution of Antarctic krill between South Georgia Island and the Bouvet Island. And further look at the different areas and analyze them at a small scale, with focus on vertical distribution between night and day. Based on what is found in the literature, some predictions and hypothesis were put forward:

Hypotheses

1. Densities of krill decrease with an increase in distance from land. In areas close to islands, shelves and shelf breaks abundance will be high.
2. Water masses with increased temperatures are negatively correlated with krill abundance.
3. Areas with increased to intermediate chl a levels, together with cold water masses will have increased abundance of krill.
4. Predation pressure increases with decreased distance to land and an increased number of breeding colonies near by for land breeding predators (Given that hypothesis 5 and 6 is supported)
5. An increase in predation pressure will give extensive migration patterns between night and day for the Antarctic krill
6. Increased predation pressure will lead to larger and denser swarm structure for Antarctic krill.

From this follows that we expected to find large quantities of krill, distributed on-shelf, off-shelf and on the shelves edges, in proximity to South Georgia Island. Based on the fact that a large amount of the total stock of *E. superba* occurs in the Open Sea, and that the predation pressure here are reduced due to decreased impact from land-based predators, I expected to a find low densities, but a considerable total amount of *E. superba* distributed along the survey track in this area, possibly with a different school structure and diel vertical migration patterns than for the near-land part of the population. I expected that krill distribution at Bouvet Island to some extent resembled South Georgia Island due to the effect of the shelf, proven as good krill habitats with an increased abundance, and the presence of land-based predators that might affect vertical migration and swarm structure. However, since the effect from a small Island like Bouvet combined with a lower land-based predation pressure, may be insignificant on krill distributional patterns, I also expected similarities between the Open Seas and Bouvet.

Materials and methods

The survey

The survey track between South Georgia and the Bouvet Island is used as a baseline for my thesis. From this track I have sorted the data into three zones; South Georgia (January 18th - 23rd); the Open Sea (January 24th to February 1st); and Bouvet Island (February 2nd - 06th). The grouping into these zones is based on the assumption that the krill have different behavior close to islands and shelves compared to open water areas and consequently related to where we were close to the island and on to shelf areas (see Table 1).

The AKES 1 survey was conducted with the research ship F/F G.O. Sars from January 02nd to February 14th, 2008. The aim of the survey was mainly to assess the krill distribution in these three areas and to find better target strength (TS) values of krill for use in acoustic abundance estimates. The survey followed a pre-set cruise track (Fig. 1), with predestined sampling stations including; a Conductivity, Temperature and Density profiler (CTD), trawling and TS-probing, using a submersible unit with echo sounders. The vessel departed from Montevideo, Uruguay, on the first transport stretch towards South Georgia, following the coast southward along Argentina, passing the Falkland Islands. The survey continued to South Georgia Island, where the echo sounders were calibrated during 3-4 days in the calm and sheltered Strømnes bay, with subsequent sampling in South Georgian waters. The survey thereafter continued south of the polar front from the shelf close to South Georgia towards east, then turned north, crossing the polar front to sample 1-3 stations, before re-entering polar waters where the remaining stations were sampled. The southern most station was at 59.5° S. The last sampling stations were on the shelf around the Bouvet Island. The survey ended up in Cape Town, South Africa.

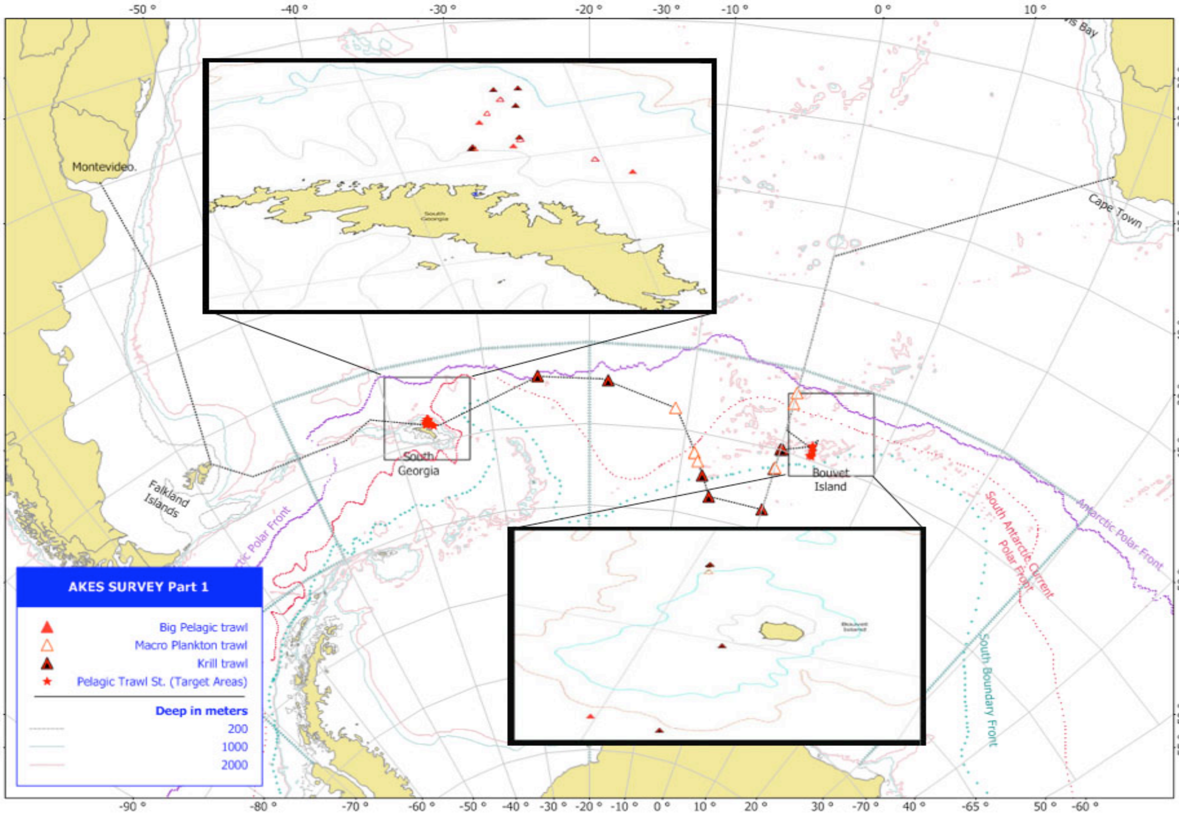

Fig. 1 - Map of Pelagic-, plankton- and krill trawl stations taken along the AKES 1 survey, and zooming in on South Georgia and Bouvet Island (Iversen 2008)

Shelf areas and Open water

The shelf areas sampled during this cruise span water depths from 180 to 750m (Table 1). Table 1 summarizes the positions and times of studies of the respective areas.

Table 1 - Detected bottom during the survey split up in dates

January 18th – 23rd South Georgia	-54,1601677° N/S, -36,6888351° E/W to -53,387001° N/S, -30,8516598° E/W	Shelf areas – shelf between 50 – 750m. Shelf depth was most of the time between 200-350m
January 24th to February 1st Open Sea	-53,3826675° N/S, -30,8366699° E/W to -55,0422592° N/S, -0,0001302° E/W	no shelf
February 2nd – 3rd Bouvet Island	-54,9256668° N/S, 0,3838379° E/W to -51,9235001° N/S, -0,0700033° E/W	Shelf areas – shelf down to 700m
February 4th – 6th		no shelf

Acoustics

Simrad EK60 echo sounders were operated continuously along the cruise track. Records were made at the frequencies 12 kHz, 38 kHz, 75 kHz, 120 kHz, 200 kHz, and 333 kHz deployed in a drop keel, but only data from 38 kHz and 120 kHz are analyzed in this thesis.

Short About Acoustics

An echo sounder (transducer) sends out sound pulses (pings) in the water column, either from a hull mounted position on a ship or attached to a mooring, looking up or down in the water column. The pings are reflected back at different intensities when they hit objects of different properties in the water. An objects ability to reflect sound is given by its backscattering area (σ), viewed upon as an objects acoustic signature or size. The backscattering area generally increases with size, but is also altered by tilt angel of the object in the water, the density, and the sound reflecting properties of the object (swim bladder, shell etc.). An organisms backscatter is measured as TS (40 log R), which is a decibel-value directly connected to σ, were TS = 10 log ($\sigma/4\pi$). S_v is the value for the acoustic backscatter pr unit volume (20 log R) and is a proxy for biomass, expressed in decibels (dB). S_v increases with TS and number of targets. S_v =TS + 10 log ρ (ρ = individuals/m^3)."

Acoustic characteristics

Different organisms can to some extent be identified based on their echo signature (e.g. by behavior like schooling) and by comparing records at different acoustic frequencies. For zooplankton most of the groups are too small to be detected at 38 kHz, but assemblages of krill (euphausiids) will be detected. For the survey area, Antarctic krill is believed to form mostly mono-specific aggregations (Miller & Hampton 1989b). This behavior makes krill well visible on 38 kHz. Earlier studies have developed methods for discriminating Antarctic krill scattering from that of other animals, mainly based on differences in scattering at different acoustic frequencies, between 38 kHz and 120 kHz (Madureira *et al.* 1993; Mitson *et al.* 1996; Watkins & Brierley 2002; Azzali *et al.* 2004; Demer 2004; Lawson *et al.* 2008b). A species "fingerprint" based on the difference between frequencies can be used as a map to find or locate different organisms in echo-datasets.

Echo data and Logging

The Simrad EK60 echo sounders onboard G. O. Sars have split beam transducers and were mounted on a drop keel. This keel is about 7-8m below sea level, and the first 10m below the echo sounder is not sampled. This gives a “deadzone” of almost 20m, giving a “blank” in the data for the upper 20m of the water column. At night krill often form near-surface swarms (Lawson *et al.* 2008a), and visual spotting of such swarms is difficult. Lack of data for the upper 20m will therefore likely underestimate biomass in acoustic assessments. The echo sounders logged continuously during the cruise. Results for the first part of the cruise (03-13/01/08: steaming from Montevideo – South Georgia and 14-17/01/08: calibration of the echo sounders in Strømnes Bay, South Georgia) are excluded from further analyses. Echo data from the start of the krill survey at the shelf around South Georgia (18/01/08) until 2 days after we left the Bouvet Island (06/02/08) were stored on the ships server. These echo data were logged relative to distance sailed (GPS coordinates) and analyzed in this study. Data from 22/01/08 and 05/02/08 were excluded due to data trouble and a hurricane.

Other data collection and sampling

Trawling was performed to identify acoustic structures and to get samples for analyses. Krill and macro zooplankton were collected using a krill trawl with a “Multi Plankton Sampler (MPS)” cod end. The Krill trawl net is 45m long with a mouth opening area of 6x6m. It is constructed with two net layers, an inner one made of 3 mm squared mesh size from the opening to the cod-end and an outer supporting layer of coarser mesh. The trawl is towed after the boat at a speed of 2-3 knots The MPS has 5 nets with a mesh size of 3mm, and it is opened and closed sequentially on command from the ship. At the “deep stations” the deepest net started fishing at 750 m. Once on deck, samples were sorted according to taxa. For large catches a subsample was taken. Krill were sorted into different species and for *E. superba*, length, sex and stage distribution were assessed for a minimum of 300 individuals if enough krill were caught. Krill were fixed on formalin and ethanol.

CTD and thermosalinograph

CTD casts were taken at specified stations along the cruise track. The CTD was equipped with temperature and conductivity sensors and a Chelsea Aquatracker III fluorometer together with a SeaBird oxygen sensor (SBE43). Temperature, salinity and fluorescence were recorded continuously along the complete track of the cruise using a ship-mounted thermosalinograph (SBE21) with water intake about 6m below the sea surface and a temperature sensor mounted close to the intake. The fluorometers were calibrated, and values are given in µg chla/l

Day and night data

The cruise lasted for 6 weeks, with the krill survey part spanning 20 days (January 18th to February 6th). The krill survey covered a wide geographic range (-54,1601677° N/S, -36,6888351° E/W at South Georgia to -51,9235001° N/S, -0,0700033° E/W for the Bouvet Island area) giving sunrise and sunset variations of 2-3 h. Data for sunset and sunrise were downloaded from the U.S. Department of Commerce, National Oceanic & Atmospheric Administration, NOAA Research (http://www.srrb.noaa.gov/). In the transfer zone between night and day, a buffer zone of +- 1 hour from both sunrise and sunset was set. This eliminates two hours of data around sunset and sunrise to facilitate observations of trends in the data material. Data were split into day and night.

Post processing of the acoustic data

Post-processing of acoustic data was done using the software Sonar 5 Pro (Balk & Lindem). The echo data were analyzed and judged for the appearance and behavioral trends of krill from South Georgia to the Bouvet Islands. Data affected by sampling procedures and bad weather were excluded, resulting in some days with limited data. All acoustic data, both 38 kHz and 120 kHz, were processed for bottom detection down to 200 m, a process automated in Sonar 5 (-50 dB threshold, range 200 m). Data were split into appropriate data size for integration: into depth intervals, and distance frames. Distance frames were set to 1 nautical mile (nm), and the water column (200 m) was spilt into 5-meter depth intervals, starting from 10m below the drop keel and down (190 m, 38 sub layers). This procedure allocated acoustic backscatter according to a grid as outlined in Fig 2. Data were imported to Microsoft Excel and S_V data from all 38-sub layers were sorted into 1 nautical mile intervals. Krill data were extracted from the data sets based on a method used on earlier surveys, where a difference in S_v - value between 120 kHz and 38 kHz, of between 2 to 16 dB is proven to be a good acoustic signature for Antarctic krill (Madureira *et al.* 1993; Mitson *et al.* 1996; Watkins & Brierley 2002; Azzali *et al.* 2004; Demer 2004; Lawson *et al.* 2008b). Krill abundance was estimated based on the extracted krill data. In conversion of total backscatter into numbers of krill, I used – 75 dB as TS at 120 kHz, and -83 dB for 38 kHz (Brierley *et al.* 2006; Lawson *et al.* 2008b). The TS of -75 dB was converted to its linear form ($10^{TS/10}$) to give sigmakrill, as were extracted krill data ($S_v$tot) ($10^{SvTot/10}$). The equation: linear $S_v$tot / sigmakrill, gave an estimate of density of krill pr m^3 within each 1 nm interval.

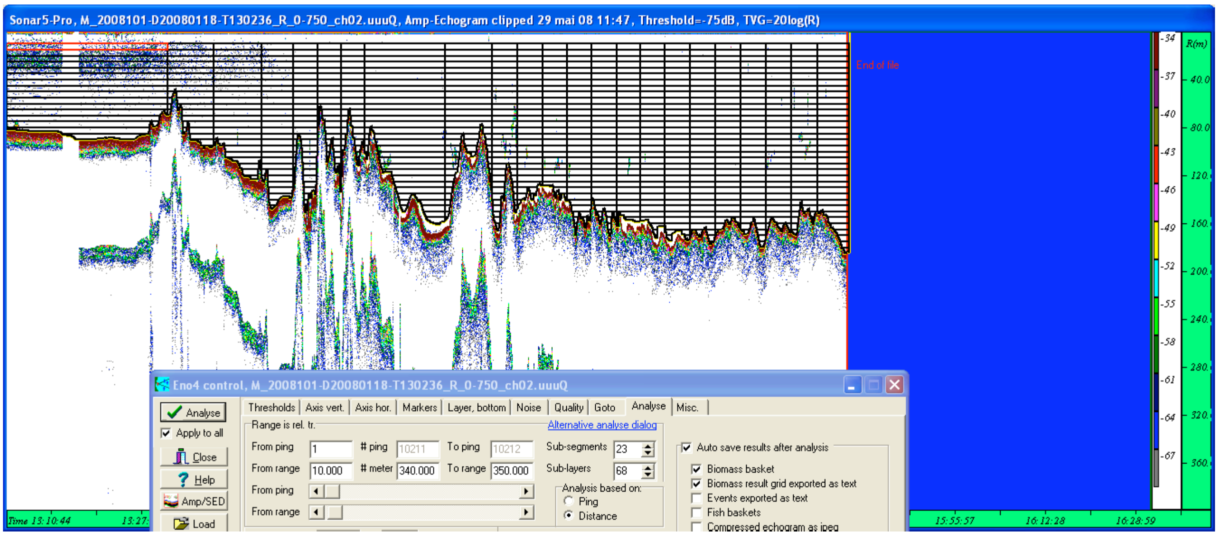

Fig. 2 - Grid system after integration (January 18th) in the software Sonar 5. Each grid represents one interval (1nm long and 5m deep)

Results

Hydrography

Salinity and fluorescence values

Salinity levels were relatively constant within the krill survey area, with an increase in the southernmost part, south of the Southern boundary of the Antarctic Circumpolar Current (ACC). When entering the Antarctic Polar Front (PF), salinity levels (Fig. 3) decreased from 34.0-34.1 ‰ to 33.8-33.9 ‰ south of the front, reaching 33.7 ‰ when arriving at South Georgia. Close to the South Boundary of ACC salinity increased to 33.9-34.0 ‰. On the north side of the Southern Front of the ACC, levels decreased again to values down towards 33.7-33.8 ‰. At the Southern most part of the survey, we crossed the Southern Boundary of ACC and salinity increased to 34.0-34.2 ‰, again to drop as the survey went north, crossing the Southern Boundary of ACC one last time approaching Bouvet Island.

Fluorescence (chl a) was generally higher in warmer waters (Fig. 3) than in areas with cold waters, but the levels peaked close to or between the different fronts, indicating more phytoplankton in areas with an influx of nutrients in the frontal regions. Fluorescence increased across the Antarctic Polar Front south of the Falkland Islands, and increased again between the Antarctic Polar Front and the Southern Front of ACC when we were approaching South Georgia. An increase in fluorescence could bee seen in the area were we touched the Antarctic Polar Front at our northern most point of the survey, when inside Polar waters. At both South Georgia and Bouvet Island fluorescence values in the surface waters were low (~ 0.05-0.2 [μg chla/l]). Inside polar waters, towards 60° S, fluorescence were very low (0.00-0.20 [μg chla/l])

Temperature

In the Drake Passage, at the start of the survey, the temperatures (at **6m depth**) ranged from 8-9 °C close to the Falkland Islands and decreased to 5-6 °C towards South Georgia (Fig. 3). Crossing the main front of the Antarctic Polar Front (red), temperatures decreased to ~ 3-4 °C. Temperatures decreased to ~ 1°C after crossing the Southern Front of ACC (blue). At South Georgia temperatures varied between approximately 0 and 3 °C.

After leaving South Georgia and proceeding westwards into the Open Ocean, the survey went northwest crossing the mean positions of the fronts South Boundary of ACC (green). The northern most point touched the edge of the PF, recording three pulses of warmer waters reaching 5-6 °C. From this point the survey headed south to the southern most point on the survey (59.5° S) crossing the two fronts once more, encountering the coldest waters of the survey (-1 to 1°C). From this point the survey turned north again along 0° E/W meridian towards the Bouvet Island and crossed the South Boundary of ACC reaching warmer water masses.

From South Georgia to Bouvet Island, fluorescence, salinity and temperature varied and the effect on the distribution of krill abundance will be further addressed in the discussion.

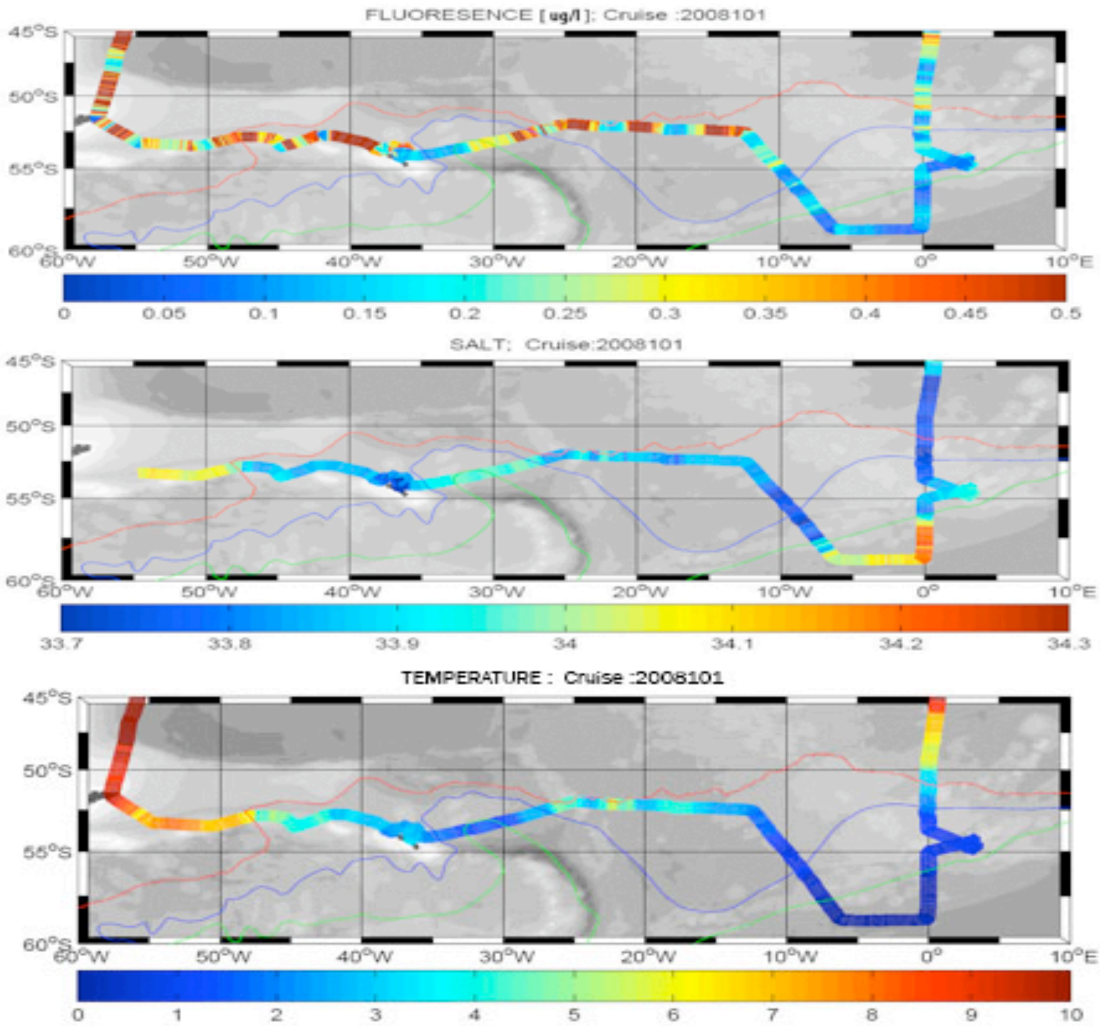

Fig. 3 – Fluorescence [µg chla/l], Salinity and temperature at 6m-depth along the cruise track. Bottom depth in grey shades, dark deep and lighter shallower. Mean positions of the fronts, South Boundary of ACC (green), Southern Front of ACC (blue), and Antarctic Polar Front (red), indicated with thin lines (Iversen 2008).

CTD

During the cruise 50 CTD casts were taken, 14 of these replicates for water sampling, leaving a total of 36 CTD´s for further use. Four of these are shown below (Fig. 4), taken to represent waters at South Georgia, close to PF, close to the coldest point of the survey the Open Sea and at Bouvet

CTD station 10 on January 20th (Fig. 4) was close to South Georgia and south of the PF. Here surface temperature was just above 2.5°C, with a narrow temperature minimum of 0.5°C at 120-130 m, temperature increasing again to ~1.5-2°C at 200–500 m. Salinity increased from just above 33.8‰ in the surface to ~34.2‰ at 200 m. Fluorescence levels had a shallow maximum of ~0.5-0.6 µg chla/l at 30-60m. Levels decrease to 0.1-0.0 µg chla/l from 70m and down to 500m.

After leaving South Georgia we encountered warmer waters at CTD station 18 (January 26th), located at the PF. Here surface temp was 4.2°C, decreasing to 1.8°C at 140-200m, and stabilize between 1.5-2.2°C down to 500m. Salinity increased from just above 33.8‰ in the surface to ~34.1‰ at 200 m. Fluorescence levels had a shallow maximum of ~1.0-1.2 µg chla/l at 50-70m. Levels decrease to 0.1-0.0 µg chla/l from 100m and down to 500m.

From this point on we headed southeast and encountered colder waters, reaching one of the coldest station (CTD station 24, January 29th) on the cruise. The surface temperature here was close to 0.5°C and there was a narrow temperature minimum of -0.4°C at 100m stabilizing at ~1.3-1.4°C towards the deep. Salinity increased from 33.8‰ in the surface to ~34.4‰ at 200m. In the upper 100m salinity had the same value. Fluorescence levels where more or less even at ~0.05-0.1 µg chla/l in the upper 130m.

After this cold station temperature gradually increased, but remained low (close to 0.5°C) up towards CTD station 39 located at Bouvet Island (February 03rd). Here surface temperature was ~0.7-0.8°C, and there was a shallow temperature minimum at 100m of ~0.2°C. Temperature stabilized at 1.5°C towards 500m. Salinity increased from 33.9‰ in the surface to ~34.5‰ at 200m. Fluorescence levels where more or less even at ~0.1-0.3 µg chla/l in the upper 120m. Levels where 0.0 µg chla/l from 120m and down to 500 m. On all stations inside and south of the PF, there was a shallow temperature minimum, formed by a layer of water from last winter's cooling, called Winter Cooled Water (Iversen *et al.* 2008). This shallow temperature minimum below a broad temperature maximum in the vertical is present on all of the vertical profiles shown in Fig. 4. Down to this shallow temperature minimum, salinity values where more or less similar between all areas. Fluorescence levels in the upper 100m where higher at South Georgia and the Open Sea at PF, than what was seen for Open Sea south of PF and Bouvet Island. Still fluorescence was higher at Bouvet (0.1-0.3 µg chla/l) than at Open Sea (~0.1 µg chla/l).

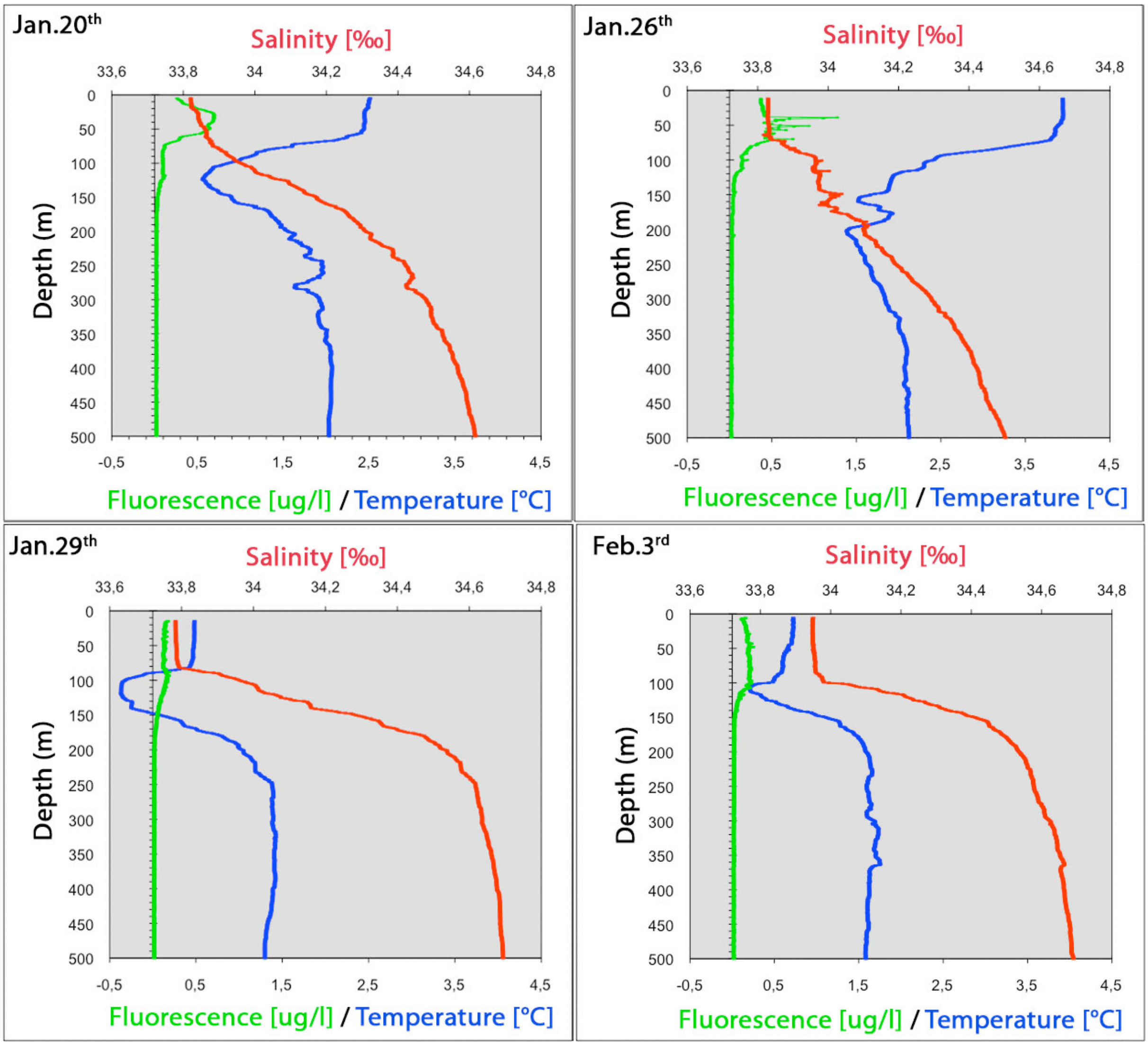

Fig. 4 - Selected vertical CTD profiles of potential temperature (blue), salinity (red) and fluorescence (green). Stations 10 (South Georgia, January 20th), 18 (Open Sea close to PF, January 26th), 24 (Open Sea, coldest area, January 29th) and 39 (Bouvet Island, February 3rd)(Iversen 2008).

Catches of macrozooplankton

A complete dataset on trawl catches from the AKES 1 survey is so far lacking as these results are still being processed at IMR in Bergen. However, a rough assessment can be made based on observations during the survey. Three zooplankton species appeared in high numbers in the trawl catches. The Antarctic krill, *E. superba* dominated in all three areas. The two other zooplankton species, the salp - *Salpa thompsoni* and the amphipod - *Themisto gaudichaudii*, varied in abundance with regard to east-west distribution. At South Georgia, *S. thompsoni* was low in abundance, but dense registrations of the amphipod *T. gaudichaudii* were observed, forming diffuse acoustic scattering layers in the water column. *T. gaudichudii* seemed to outnumber *E. superba* outside the krill swarms. At South Georgia some of the trawls contained large numbers of these amphipods but almost always together with Antarctic krill, and the Antarctic krill appeared occasionally in very large quantities in the trawls. Other euphausiid species were *E. triacantha* and *E. frigida*, which were the most abundant krill species besides *E. superba* in the South Georgia region. Open Sea trawl catches mostly comprised Antarctic krill of length 40 – 50 mm and a low abundance of salps, but no amphipods of the species *T. gaudichudii*. In the Bouvet region salps dominated, while amphipods where not seen. The highest quantities of salps were observed from the surface layers down to 120m and in Fig. 11 they can bee seen as diffuse acoustic scattering layers around 100m depth. Some of the trawl catches at Bouvet Island where very large, containing almost only salps, and hardly any krill, consequently there is no doubt that salps were abundant.

Krill distribution along the transect South Georgia - Bouvet Island

Horizontal distribution

Figure 5, 6 and 7 shows the horizontal distribution of krill abundance around South Georgia, the Open Sea and Bouvet. The Y-axis shows density of krill (krill pr m^3) pr 1 nautical mile (nm) intervals. The x-axis displays time elapsed during the survey (each bar in figure 5-7 = data from 1 nm). Boat speed during the survey was ~10 knots. The abundance and distributional patterns of Antarctic krill differed between the three zones. At South Georgia (Fig. 5) the densities of Antarctic krill were estimated at 5-15 krill pr m^3, with densities occasionally reaching over 30 krill pr m^3 in the water column implying dense aggregations in these areas. The acoustics and the sampling showed that krill are spread throughout the entire area. In the Open Sea (Fig. 6.) densities were lower, 2-5 krill pr m^3 in most intervals containing krill, reaching up to 10 krill pr m^3 in some areas. In the open ocean krill seemed to be clustered into two areas, with a zone almost void of krill in the middle of the area (further outlined below). At Bouvet Island (Fig. 7) densities were around 5 krill pr m^3, but it seems that a majority of the krill in the area was clustered into some large aggregations – giving in some cases densities up to 40 krill pr m^3, ~ 0,04 krill pr liter of water. Note that these values represent average in 1 nautical mile intervals, and densities within swarms in the surveyed area can be much higher (> 30000 krill pr m^3).

At South Georgia, the medium to large sized swarms had densities estimated at ~1200 to 32.000 krill pr m^3 and a size of 5-20m in diameter, while estimates for the Open Sea swarms were densities of ~30 to 1600 krill pr m^3 with a size of 5-10m in diameter. At Bouvet the small swarms had lower densities, often clustered into belts, of ~5 to 35 krill pr m^3, while the large swarms had a density of ~150 to 4.000 krill pr m^3 reaching up to 60 x >100m in size. When comparing the three zones, both true swarm densities and abundance of krill pr nm intervals, there seems to be a trend towards high-density distributions of krill occurring close to the Islands (Fig. 5 and 7).

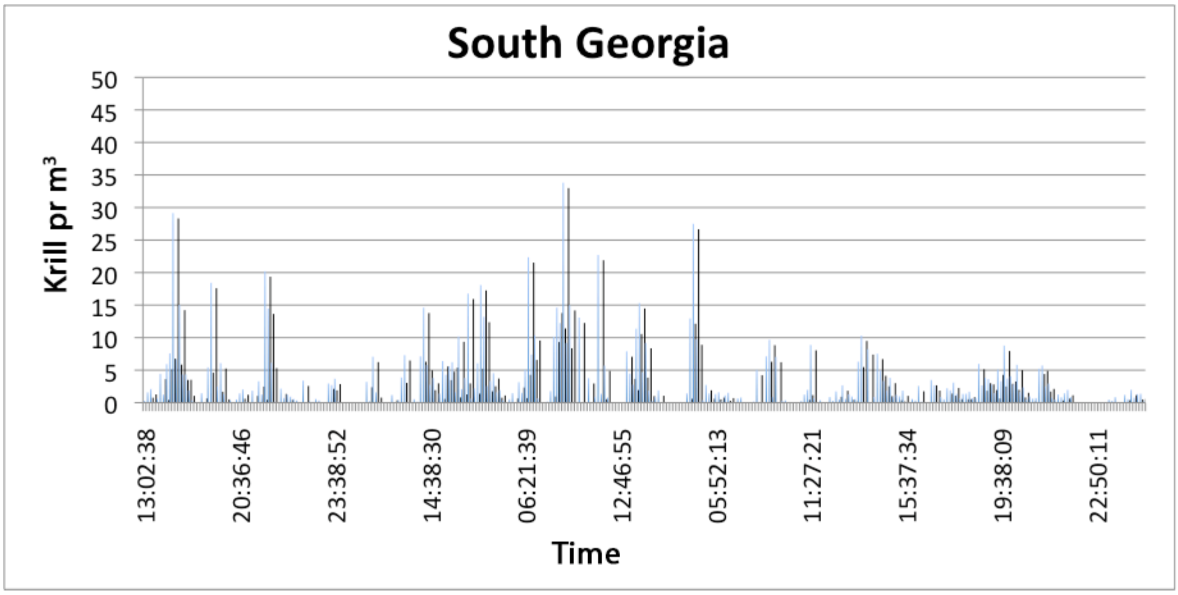

Fig. 5 - Distribution of krill abundance around South Georgia Island. Y-axis showing krill pr m^3 pr 1 nautical mile interval, the x-axis showing time elapsed during the survey at South Georgia (one bar = data from 1 nm – each datapoint represents densities in a 1 nm segment) Boat speed ~10 knots.

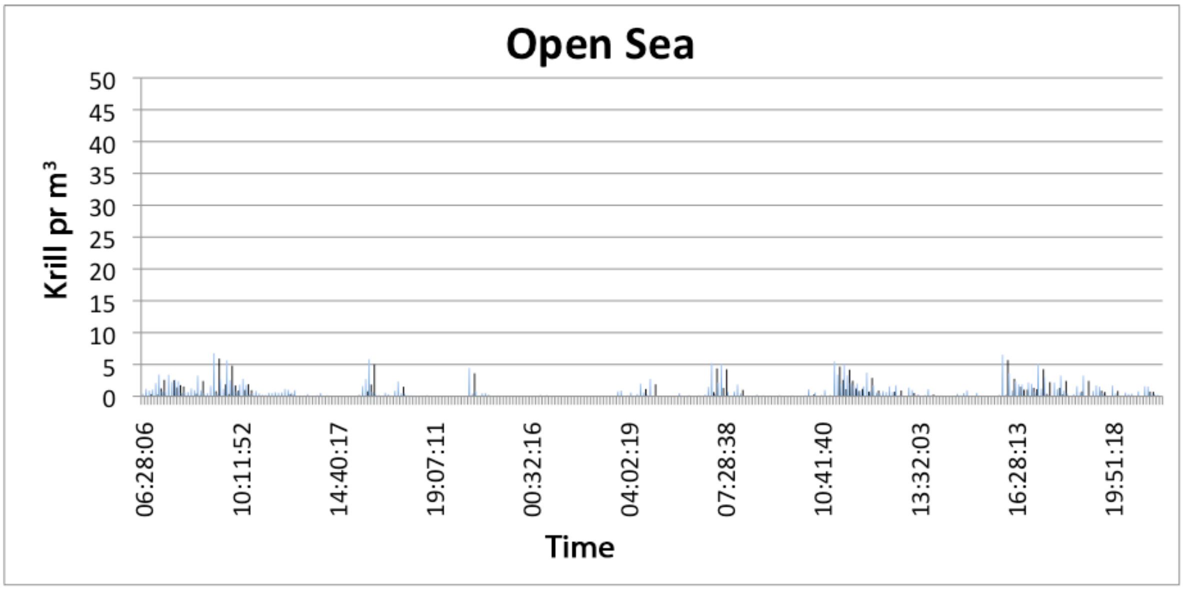

Fig. 6 – An excerpt of the distribution of krill abundance in the Open Sea, density scale same as in Fig. 5. Y-axis showing krill pr m^3 pr 1 nautical mile interval, the x-axis showing time elapsed during the survey at South Georgia (one bar = data from 1 nm – each datapoint represents densities in a 1 nm segment). Boat speed ~10 knots.

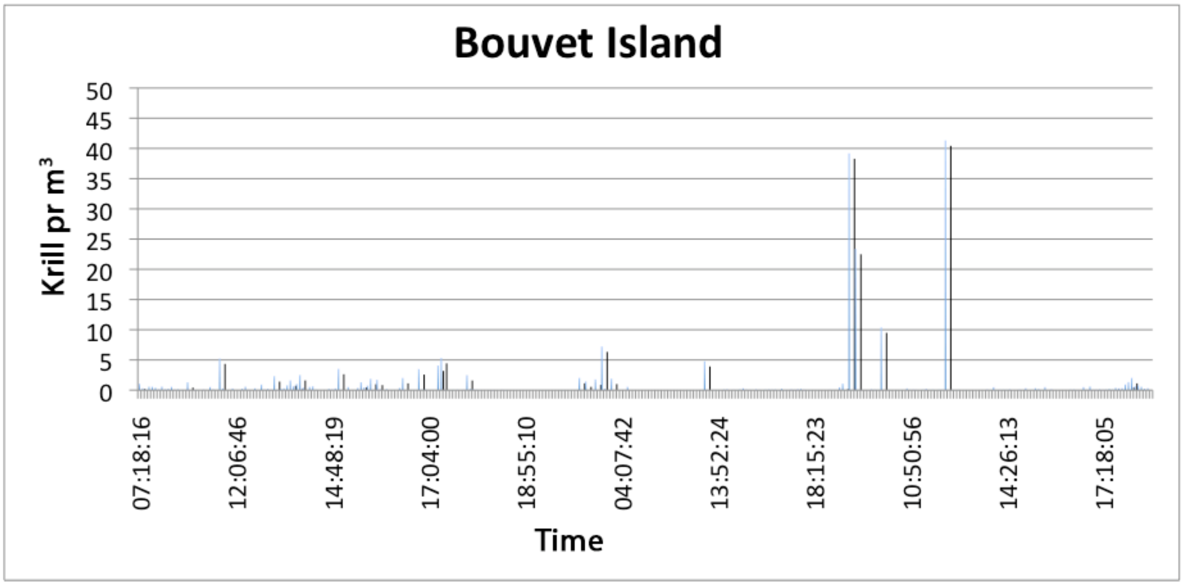

Fig. 7 - Distribution of krill abundance around Bouvet Island. Y-axis showing krill pr m^3 pr 1 nautical mile interval, the x-axis showing time elapsed during the survey at South Georgia (one bar = data from 1 nm – each datapoint represents densities in a 1 nm segment). Boat speed ~10 knots.

Fig. 8 shows percentage of krill aggregations allocated to 14 different density groups (krill pr m^3), pr nm sampled within the three areas. Percentage distribution is used, to get comparable data between the three areas, due to the larger area sampled for the Open Sea zone. The distance differs; 316 nm were sampled around South Georgia, 1449 nm in the

Open Sea and 393 nm for the Bouvet Island area. As results are based on acoustic integration over 1 nm segments, these results represent the cross product of actual physical densities found within swarms and the sizes of the swarms, and are a measure of biomass within the 1 nm segments.

For the three different areas, South Georgia and the Bouvet Island have a larger range in the density for krill aggregations, as they in contrast to the open ocean also include very dense or larger aggregations. Fig. 8 shows that the krill aggregations with the highest densities appear close to the islands. The Open Sea and the Bouvet Island also resemble each other in the distribution of krill densities, in contrast to South Georgia who has a low number of small density intervals, and a high degree of larger aggregations (high densities).

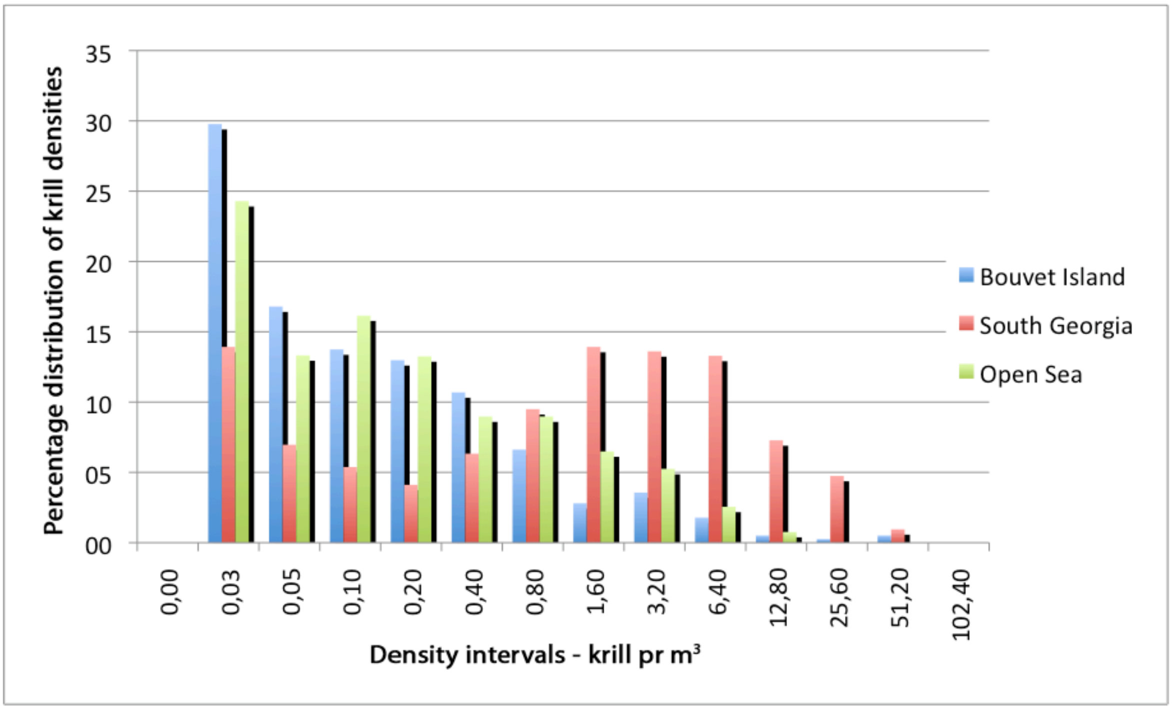

Fig. 8 - Histogram of krill biomass densities along the transect between South Georgia and Bouvet Island. Y-axis showing the percentage distribution of krill densities found within the three areas against the x-axis showing the density intervals (krill pr m^3).

Running a Kolmogorov-Smirnov test (Table 2) unveils that the krill biomass distribution from these areas is significantly different from each other. South Georgia and the Open Sea are highly significantly different from each other, South Georgia and Bouvet Island are significantly different from each other and the Bouvet Island and Open Sea are significantly different from each other (Table 2). This confirms the patterns from the graphs above, showing that at South Georgia, the number of intervals with a high density of krill is significantly higher than the majority of intervals with a low density of krill found at Bouvet and Open Sea. The same is evident between Bouvet and Open Sea (though with a slightly lower significance value), related to the absence of high-density intervals in the Open Sea, in contrast to the Bouvet shelf.

Table 2 - Two-sample Kolmogorov-Smirnov test for South Georgia vs. Open Sea and Bouvet Island vs. Open Sea.

South Georgia vs. Open Sea	**South Georgia vs. Bouvet Island**	**Bouvet Island vs. Open Sea**
data: sg$sg and os$os D = 0.4117, p<<0.0001 alternative hypothesis: two-sided	data: sg$sg and bi$bi D = 0.4849, p<<0.0001 alternative hypothesis: two-sided	data: bi$bi and os$os D = 0.0937, p-value = 0.008769 alternative hypothesis: two-sided

Large-scale trends along the transect from South Georgia to Bouvet Island

In the figures 9-11, echograms with krill aggregates are used to visualize the main differences between the three zones. At South Georgia there is a high degree of medium to large sized krill aggregations, both dense and large ones. The schools in Fig. 9 have S_V-values between 31-44 dB, sampled from the centre of the aggregations, with a diameter in the swarms between 5-20m. These swarms are of medium – large size compared to the ones in the Open sea area, and of high density. The high density swarms found at South Georgia at this locality (31-44 dB), corresponds to estimated krill densities of ~1200 to 32.000 krill pr m^3. At South Georgia the amphipod *T. gaudichaudi* is present and layers of these are often seen in proximity to the krill aggregations.

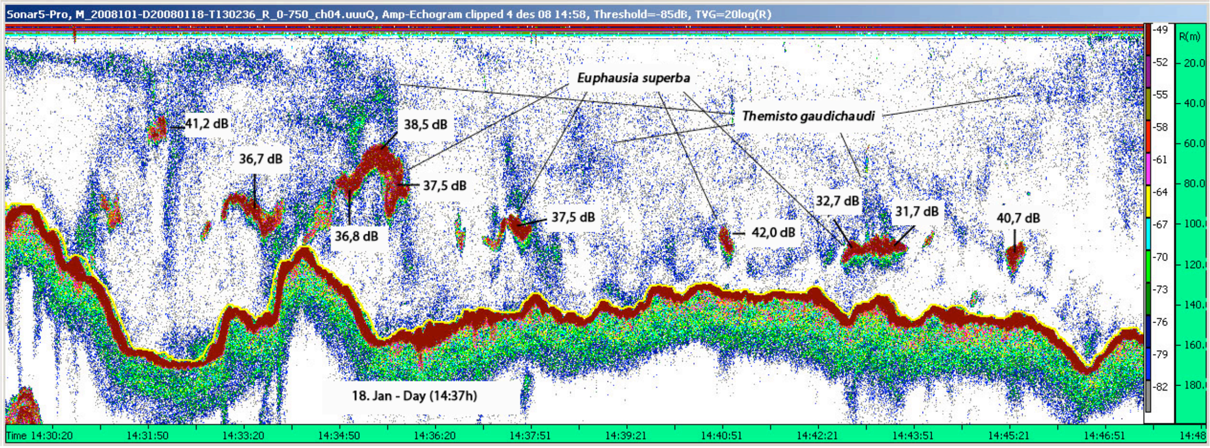

Fig. 9 – Date: January 18th (14:30-14:42h), South Georgia shelf. Krill aggregations (red) marked with dB values together with likely records of amphipods (*T. gaudichaudi*). Bottom displayed as a continuous red line. R = range from transducer, a deviation of 15-20m from true depth.

In the Open Sea (Fig. 10), aggregations are scarce, and the swarms found are smaller (5-10m in diameter) and not so dense as the ones at South Georgia with lower S_v-values of 43-60 dB in centre. These dB value (43-60 dB) correspond to estimated krill densities of ~30 to 1.600 krill pr m-3.

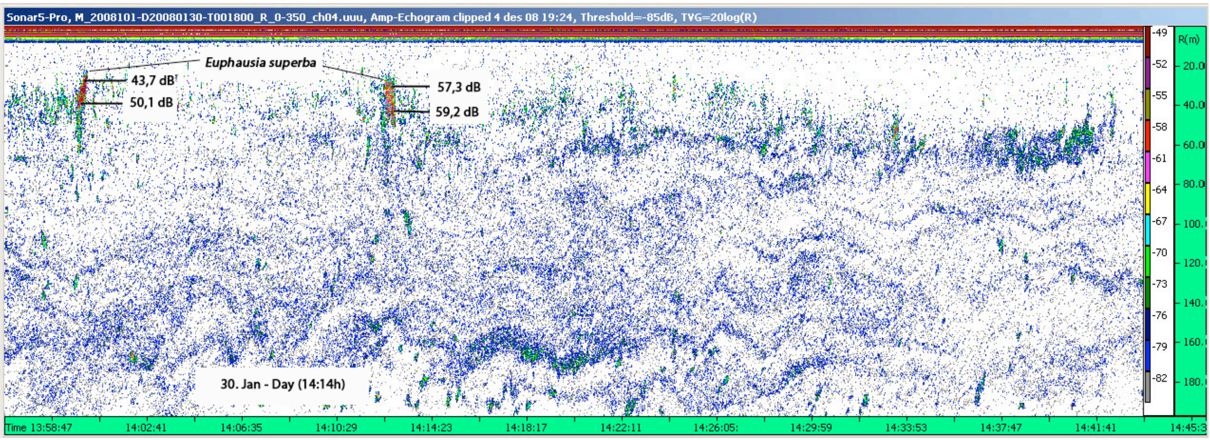

Fig. 10 - Date: January 30th (13:58-14:45h), Open Sea in Cold waters. Krill aggregations (red) marked with dB values. R = range from transducer, a deviation of 15-20m from true depth.

At Bouvet, some large and dense aggregations were present (Fig. 11), together with swarms small in size and not as dense as the largest swarms. The swarms in Fig. 11 are two of the largest swarms we sampled in this area with S_v-values between 39-53 db in the center of the aggregations and a height in the water column of more than 60m with a width of 5-15m. These dB values (39-53 dB) found within the swarms in the Open Sea at this locality, corresponds to estimated krill densities of ~150 to 4.000 krill pr m-3. Due to the large swarm size (60 x 15m) and the density (~4000 krill pr m-3), a large amount of krill biomass are found within these swarms. The small swarms found in this area had dB values of 60-67, corresponding to ~5 to 35 krill pr m-3. The layers of organisms, which co-occur with most of the krill aggregations at Bouvet, are believed to be salps, of the species *Salpa thompsoni*.

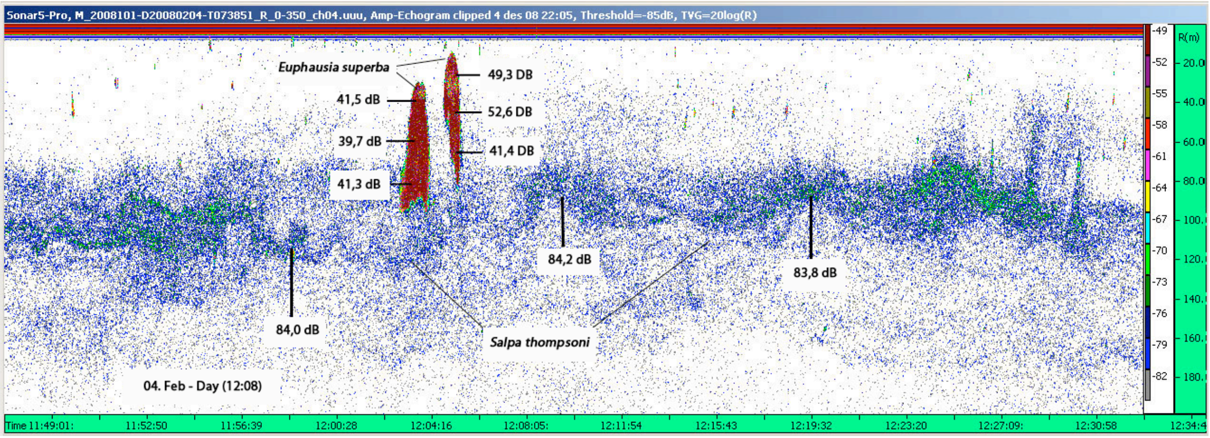

Fig. 11. – Date: February 4th (11:49-12:34h), Bouvet Island shelf. Krill aggregations (red) together with likely records of salps (*Salpa thomsoni*), seen as the layer at ~100m depth. R = range from transducer, a deviation of 15-20m from true depth.

Horizontal distribution within the Open Sea

From January 23rd – 26th G. O. Sars left South Georgian waters and the survey proceeded northeast and crossed the Southern Front of ACC and came into the polar front. Temperatures were higher than for the other parts of the Open Sea zone, reaching 5-6°C. Abundance of Antarctic krill was lower than inside the polar front (Fig 12), except from relatively high counts of low-density assemblages in the area north of the polar front. It may be questioned whether these low-density acoustic records are Antarctic krill at all, as we have no trawl catches to back up the acoustic identification in these areas.

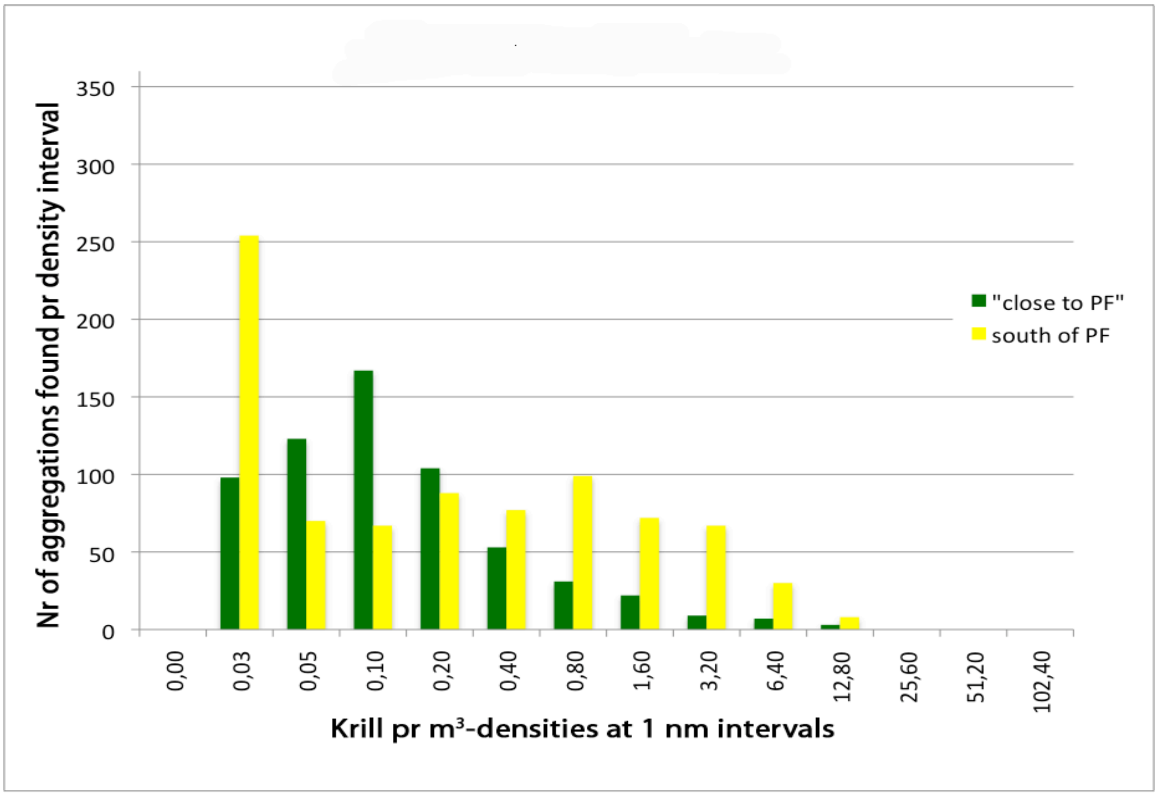

Fig. 12 - Histogram of the distribution of different sized krill aggregations in the Open Sea area – close to PF vs. south of PF.

In the period we were inside warmer waters January 23rd – 26th, densities of krill decreased to a low level, clearly distinguishable from the cold waters. Fig. 13 shows the decrease in number of krill aggregation observed acoustically in warmer waters. Fig. 14 shows the increased in number of small krill aggregation observed upon returning to cold waters.

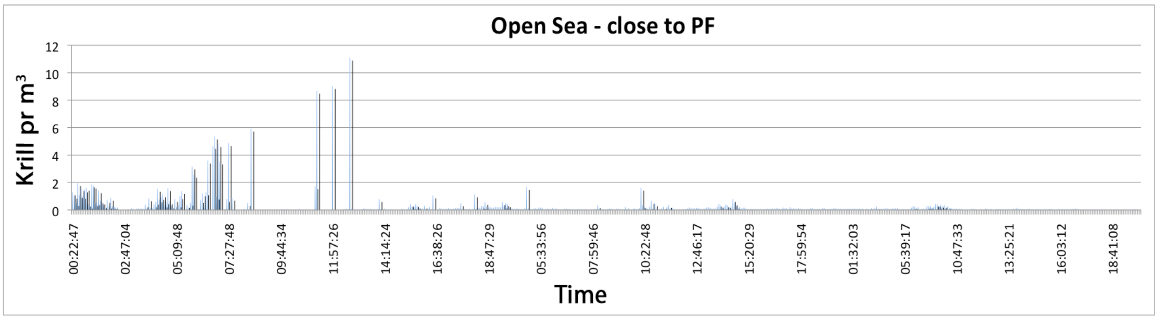

Fig. 13 - Horizontal distribution of krill (January 23rd – 26th). Densities decreased to a low level when close to PF (one column = data from 1 nm).

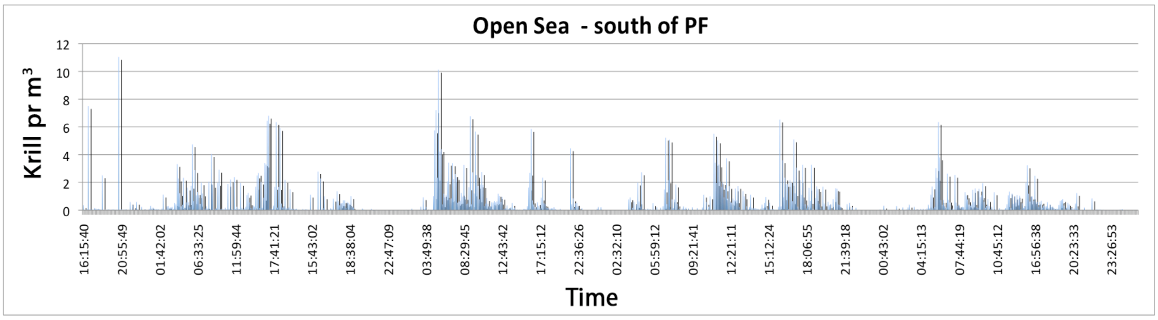

Fig. 14 - Horizontal distribution of krill (January 27th – February 1st). Higher krill abundance values where found south of PF (one column = data from 1 nm).

Running a Kolmogorov-Smirnov test (Table 3) shows that the datasets containing krill density estimates from these areas are significantly different from each other. The area close to and south of PF is significantly different from each other with a $p << 0.0001$.

Table 3 - Two-sample Kolmogorov-Smirnov test for north of PF vs. south of PF

North of PF vs. south of PF
data: north$north and south$south - D = 0.2291, p-value <<0.0001 alternative hypothesis: two-sided

Vertical distribution of krill – Diel Vertical Migration (DVM)

The vertical distribution of krill and their diel vertical migration patterns differed between South Georgia, the Open Sea and the Bouvet Island (Fig. 12). In all regions, krill was basically found in the upper ~100m at day (Fig 12), yet krill around South Georgia appeared to have a bi-modal distribution, with one peak in the upper 20-30m and a smaller peak at 110-115m. For the Open Sea and Bouvet, krill occurred in the upper 20-100m at day; with peak concentrations around 40-50m. Below 100m, records drop towards zero. During night, krill at South Georgia migrated up to the upper 20-50m, with highest concentrations at 20-30m (Fig 12), leaving little krill in waters below 70m. Night-values increased 6 fold compared to day-values close to the surface. However, the distribution was bimodal, with a secondary peak at ~50m. Also at Bouvet, krill migrated towards the surface at night, mainly being distributed in the upper 30m. In contrast, for the Open Sea, night and day distribution appeared equal, with nocturnal krill concentrations in the upper 70m and a peak at ~50m.

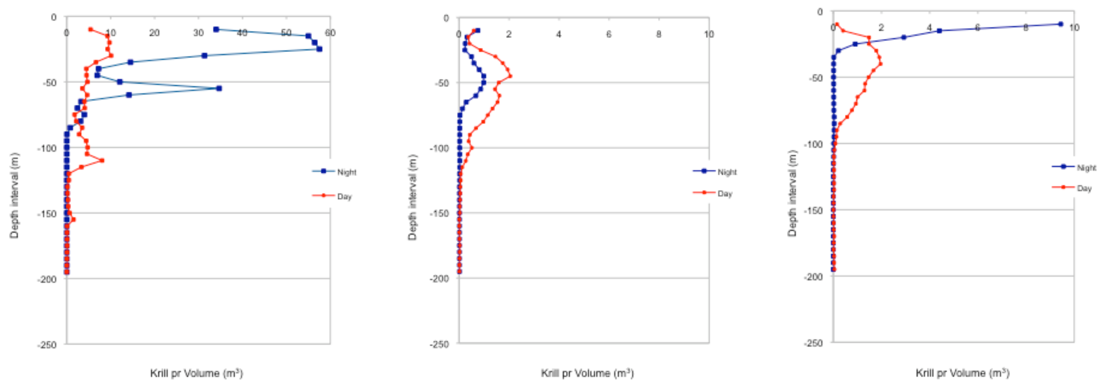

Fig. 15 - Vertical distribution of krill. Mean krill pr volume (m^3) distribution in the water column during night (blue) and day (red) at South Georgia, Open Sea and Bouvet Island. Data are based on total acoustic estimates of krill in the water column. <u>The scale is different for South Georgia than for Open Sea and Bouvet Island due to a magnitude of difference in values between these areas</u>. R = range from transducer, a deviation of 15-20m from true depth.

Small-scale trends, night and day - South Georgia, Open Sea and Bouvet Island

In addition to different abundance, vertical distribution and DVM patterns, also swarm structures varied between the South Georgia area, Open Sea and in the Bouvet Island area. Figure 16-18 below show the distinct features most dominant within each area. Around South Georgia (Fig. 16) at night (1 hour after sunset to 1 hour before sunrise), high abundance of krill tends to occur in extended layers in the upper 80m increasing towards the surface. During day, krill concentrate into smaller, but denser swarms (S_v-values of 29-34 dB in Fig. 16) and spread through the water down to 100-120m, some aggregations even deeper.

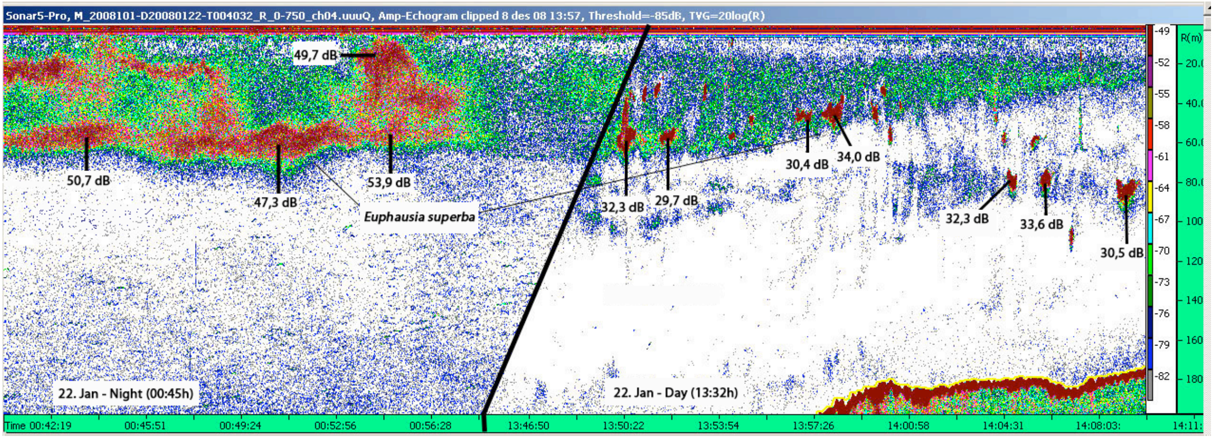

Fig. 16 - Night (left) (00:42-00:56h) and day (13:46-14:11h) distribution of krill aggregations and other organisms in the South Georgia zone January 22nd. R = range from transducer, a deviation of 15-20m from true depth. Black line marks the change between night and day.

At night in the Open Sea zone (Fig. 17) krill occurs in the upper 60m, often in a continuous low density belt (S_v-values of 72-80 dB) as seen here. Krill are distributed evenly in a large part of the sampled water column. At daytime (right side of Fig. 17) krill form small swarms with densities higher than at night (S_v-values of 47-67 dB for the presented examples), and abundance peaks around 40-60m.

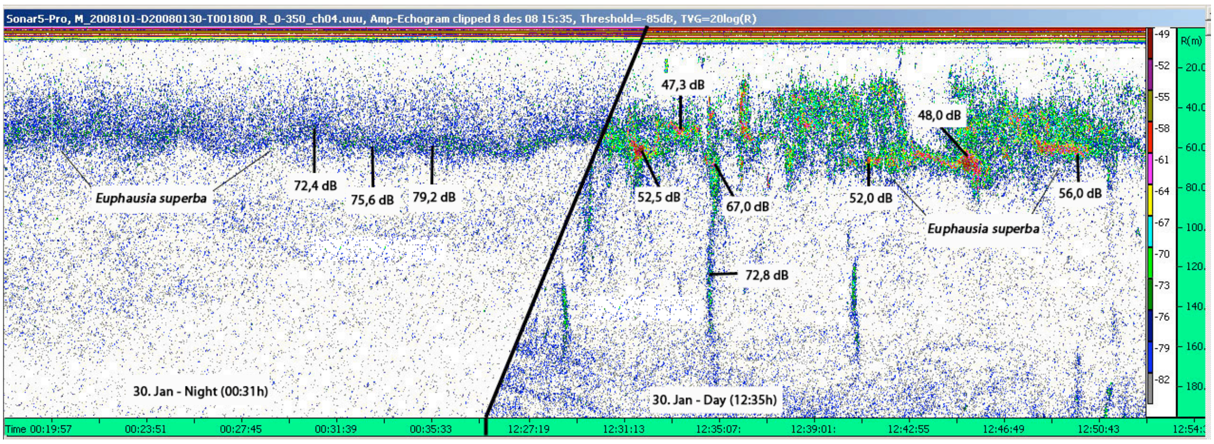

Fig. 17 - Night (left) (00:19-00:35h) and day (12:27-12:54h) distribution of krill aggregations and other organisms in the Open Sea zone on the south side of the Polar Front January 30th. R = range from transducer, a deviation of 15-20m from true depth. Black line marks the change between night and day.

At Bouvet Island (Fig.18) krill aggregations are mostly small, but some large aggregations occur. At night krill aggregates close to the surface (upper 30m) in large dense swarms (60 x >100m) with S_v-values of 42-56 dB (left side of Fig. 18). At daytime krill form both small swarms with a low density (S_v-values of 65-69 dB) and a few large ones in the upper 80m (S_v-values of 39-53 dB), with some of them reaching 60-80m in height (right side of Fig.18).

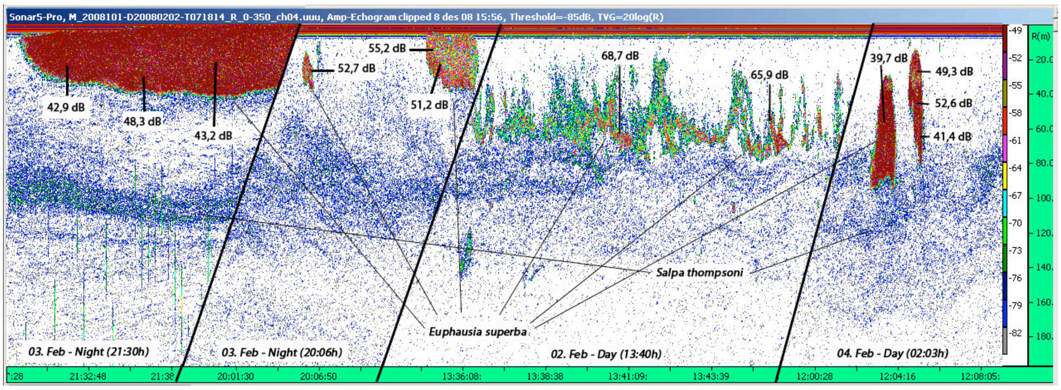

Fig. 18 - Night (2 to the left) (20:01-21:38h) and day (12:00-13:45h) distribution of krill aggregations and other organisms at the Bouvet Island zone. February 2nd – 4th. R = range from transducer, a deviation of 15-20m from true depth. Black line marks the change between night and day.

There are no systematic relationships between abundance estimates for day and night among the three zones (Table 4). For the South Georgia area values are approximately double at night, while in the Open Sea values are double during daytime. At Bouvet Island there is no difference in abundance estimates day and night.

Table 4 - Mean abundance of krill present in the water column (200m) at South Georgia, the Open Sea and Bouvet Island during day and night.

Mean krill abundance (krill pr m^3)

	Day	Night
South Georgia	**3,17**	**8,89**
Open Sea	**0,59**	**0,21**
Bouvet Island	**0,51**	**0,48**

Discussion

Acoustic data made up the baseline for this investigation of horizontal and vertical distribution of the Antarctic krill, *E. superba*. Detailed trawl catch data are not included in this thesis, due to the timing for processing such data. Nevertheless the relevant species compositions in these waters are basically easy to assess based on the acoustics data. At South Georgia, *E. superba* were present in large quantities in trawl catches, together with the amphipod *T. gaudichudii. E. superba* are known to form dense swarms, and are most often easily distinguished from other zooplankton. Amphipods may form dense aggregations, (Atkinson *et al.* 1999) and if they do, some of the data on the abundance and distribution on *E. superba* may be influenced by the appearance of amphipods in these waters. This would not affect the conclusions that krill abundance was higher in the South Georgia area compared to the Open Seas and Bouvet Island, and that *E. superba* is very abundant along the coastline of South Georgia Island. Further *E. superba* was present along the whole survey, and across all catches the most dominant species. At Bouvet *E. superba* was present in many small and a few very large aggregations, with the salp, *S. thompsonii* being the other common macroplankton species. Salps are known to form aggregations with lower TS than krill (David *et al.* 2001; Woodd-Walker *et al.* 2003) and are not believed to interfere with my krill abundance and distribution measurements.

Large-scale distribution of krill

Krill abundance was found to be high close to South Georgia and Bouvet Island and low out in the Open Sea. In this region there was no clear relation between water bottom depth and krill distribution (1500-5000m). The same was evident within the areas around the two islands, where no direct link was seen between abundance of krill in relation to variations in bottom depth between 50-750m.

At South Georgia Island I found that krill abundance was high on-shelf, on the shelf break and off-shelf. The krill was patchily distributed and no clear relations to topography were seen between these three areas. According to the literature, the most reliable place to find *E. superba* is at the shelf break on the north side of the Island

(Pakhomov *et al.* 1997; Priddle *et al.* 1997). However, Everson et al. (1996) stated that *E. superba* were widely distributed in schools through out the region. Other studies state that krill abundance at South Georgia Island is greatest on the shelf, where there generally is relatively low chl a concentrations and low temperatures (Priddle *et al.* 2003; Shreeve *et al.* 2005; Ward *et al.* 2005; Murphy *et al.* 2007). My results are best in accordance with the conclusions by Everson et al. (1996) of patchily distributed krill throughout the South Georgian waters.

The abundance of krill around South Georgia Island was higher than for the two other areas investigated. This is in accordance with earlier studies, showing that the concentrations of Antarctic krill around South Georgia is higher than surrounding areas (Marr 1962). *E. superba* tend to occur close to the Antarctic continent (approx. 75° to 65° S), but in the Scotia Sea and close to South Georgia, its distribution extends all the way north to 53° S. South Georgia is close to the northern limit for the distribution of the Antarctic krill (Marr 1962) while *E. superba* thrives close to the seasonal ice zone. This makes South Georgia an atypical habitat, having hardly any pack ice during the year (Atkinson *et al.* 2001).

Several explanations for the high krill abundance around South Georgia have been discussed in literature. This "hot spot" has been explained by advection Marr (1962) due to patterns of the surface currents in general, and outflows from the Weddel Sea together with ACC and the Weddel Sea Current (WSC). Recent studies (Murphy *et al.* 2007; Thorpe *et al.* 2007) further indicate that merging of surface waters in the Scotia Sea is an important factor for the large-scale distribution of *E. superba*, supplying plankton from around the Southern Ocean. Close to the Falkland Islands and southwest of South Georgia, coldwater masses from the Southern Ocean are pushed north to lower latitudes by the effect of the Scotia Arc on the Antarctic Circumpolar Current (ACC). These cold currents carry with them krill to South Georgia and the surrounding areas during spring and summer, so that about half of the overall krill population is believed to occur close to South Georgia and the Scotia Sea (Atkinson *et al.* 2004; Murphy *et al.* 2007). Other studies have suggested that small-scale circulation patterns in local areas like the shelf slope, together with active horizontal and vertical migration by krill, may be a better explanation for the high abundance and distribution patterns seen for krill, than what can be explained by supply from ACC and WSC (Ichii *et al.* 1998; Lascara *et al.* 1999; Nicol *et al.* 2000).

In the Open Sea area, I found lower abundances of krill and that krill was quite evenly distributed over large areas. However, in total, a considerable amount of krill occurs in this region since the area sampled was much larger than the area sampled near the two islands. The oceanic large-scale distribution of krill close to the polar front in this area is poorly known from earlier studies, but my results roughly accord with findings of Atkinson et al. (2008). By combining all available data from all net sampling stations south of the polar front in the Southern Ocean, Atkinson et al. (2008) found that the mean krill density over shelf-slope areas with a depth of less than 2000m was only 1.65 times higher that of deep ocean. This is further confirmed by acoustic data (Reid *et al.* 2004). At a circumpolar scale, the habitat of deep oceans are a 10-fold larger than the near shore habitats, so that in spite of a decreasing krill density from the coast to offshore – most of the Antarctic krill population are oceanic, with at recent estimate of 87 % of the total krill population living over waters of more than 2000m depth (Atkinson *et al.* 2008). Consequently the bulk of the *E. superba* biomass occurs in the Open Sea.

At Bouvet Island, my results showed relatively low krill abundance, but with a few high density records in the proximity of the shelf and the shelf edge. The total abundance of krill to area sampled, was lower at Bouvet than in the area for South Georgia, but the abundance was higher than the densities pr nautical miles sampled out at sea. Shelf areas may be preferred habitats for krill due to increased levels of nutrients from upwelling at the shelf break or vertical mixing at the shelf, and supply from land may also increase iron fertilization, thereby enhancing phytoplankton growth (de Baar *et al.* 1995; Smetacek *et al.* 2004; Atkinson *et al.* 2008). Enhanced abundance of krill close to both South Georgia and Bouvet, underlines an "island effect" in the distribution of krill. This matches hypothesis "1" for this study. ("Densities of krill decrease with an increase in distance from land. In areas close to islands, shelves and shelf breaks abundance will be high").

Distribution in relation to water masses (temperature, salinity and fluorescence)

Antarctic krill are found in cold waters (< 6 to 8°C) within the Southern Ocean and was present in all areas covered by this survey, though in very low numbers northeast of South Georgia, where intrusion of warm waters occurred close to, and at the Polar Front. In the other parts of the survey, water temperature was not seen as a limiting factor for the distribution/presence of krill. The relation of krill distribution to fluorescence (chl a) suggested a relation between intermediate chl a levels and krill abundance close to the two islands, though this may be due to other factors as well. No link was seen between krill distribution and salinity.

Temperature

The Southern Ocean is surrounded by fronts that separate it from warmer water masses. The main front is called the Polar Front (PF) (see Fig. 1). South of the polar front, within the circumpolar current, summer surface temperatures are relatively consistent, and the temperatures reported for these areas correlate fairly well with the measurements on our survey, approximately 4-5 °C in the northern part, and 0 to -1 °C just south of the Southern Boundary of ACC (Sievers & Nowlin 1984; Whitworth & Nowlin 1987; Moore *et al.* 1999; Brandon 2004). Subsequent to crossing ACC, environmental conditions are relatively consistent (Murphy *et al.* 2007).

Along the survey, temperatures were relatively constant, and where influxes of warm waters mix with the cold-water masses northeast of South Georgia. Here the high temperature seemed to be a limiting factor for the krill, with only small, and often no acoustic registrations. Trawl catches from this area gave some particularly deep catches of krill (750-500m). This suggests that krill may occur close to and past the PF, otherwise known as the northern limit for *E. superba* (Naumov & Chekunova 1980; Atkinson *et al.* 2008), by inhabiting cold water at depths. Both in the surface waters and the vertical temperature registrations, temperature seemed too high for the krill to thrive, and krill were not observed here apart for a few, large individuals, as previously reported from the northern areas in the Scotia Sea were *E. superba* survives close to or on their northern temperature limit (Murphy *et al.* 2007).

Increased temperatures were evident for the area close to PF where krill abundance was low. This underlines the polar front and the high temperature as a limiting factor for the distribution of krill, in accordance with hypothesis “2” for this study (“Water masses with increased temperatures are negatively correlated with krill abundance”).

Fluorescence and salinity

In the Southern Ocean the distribution of *E. superba* is highly uneven compared to other Antarctic zooplankton (e.g. amphipods and copepods), and 70% of the total krill stock lies within the Atlantic sector between longitudes 0° and 90°W (Atkinson *et al.* 2008), where this survey was conducted. In the same area mesozooplankton reach a maximum near the Polar Front were chl a levels increase. On our survey, fluorescence levels increased close to the polar front, between cold and warm water masses, without a corresponding increase in abundance of krill. The section with low krill abundance close to the polar front did not correspond to increased or lowered salinity or fluorescence levels. In the other parts of the survey with cold water masses, salinity levels were constant and fluorescence levels low to intermediate close to the two islands.

There is some previous evidence that krill is most abundant where the highest production of plankton is found (Atkinson *et al.* 2004), though the relation between krill abundance and productivity in the Southern Ocean is not straightforward (Constable *et al.* 2003). In the study done by Atkinson et al. (2008) they tested the relationship between density of krill to both food and water depth. They found no significant effect of water depth after including the effect of food. This suggests that the krill’s relationship to food is stronger than the relation to water depth.

Along our survey track, fluorescence levels in the surface waters were generally low at 0.05-0.2 [µg chla/l] and the highest fluorescence of levels up to 0.5 [µg chla/l] occurred in the Open Sea; areas that had the lowest abundance of krill. A possible explanation for somewhat higher fluorescence in Open Sea may be decreased grazing in this area.

The vertical profiles showed increased fluorescence levels close to 50m depth for South Georgia (0.5-0.6 µg chla/l) and the Open Sea area close to the polar front (<1.5 µg chla/l), while south of the polar front fluorescence levels were even around 0.1 µg chla/l in the upper 130m of the water column. At Bouvet, some increase in the fluorescence levels compared to Open Sea area was recorded, with even fluorescence levels of 0.1-0.3 µg chla/l in the upper 120m. In all vertical graphs a decrease in fluorescence values were seen in the uppermost meters towards the surface. The shallow part of fluorescence measurements (10-20m) is known to be of variable accuracy, due to the interfering effect from increased light exposure. Fluorescence values may often be overestimated in near-surface waters; while values during this survey tended to decrease close to the surface (upper 10-20m), suggesting a lower near-surface abundance of phytoplankton.

The highest fluorescence values occurred in the area close to the polar front, concurrent with intrusions of warmer waters with temperatures approaching the upper limit for Antarctic krill. This temperature increase can be a possible cause that no effect of increased food concentration on krill abundance was seen. Out in the Open Sea, no obvious positive correlation was seen between the highest levels of fluorescence and the abundance of Antarctic krill.

The areas with the highest krill abundance at South Georgia Island and Bouvet Island had intermediate to low fluorescence values in the surface layers of 0.05 to 0.2 [µg chla/l], with vertical fluorescence maxima of 0.5-0.6 µg chla/l and 0.1-0.3 µg chla/l at ~50m respectively. These values concords with what have been reported to be normal for krill habitats, as the literature states that krill occupy regions with moderate food concentrations (0.5 to 1.0 mg chl a m^{-3}) (Atkinson *et al.* 2008) (i.e. 0.5-1 µg chla/l). Yet cold and highly productive waters of the Antarctic continental shelf offer the highest growth potential for krill (Atkinson *et al.* 2008). Intermediate chl a levels and cold water masses together with an increased abundance of krill, where evident for South Georgia Island and partly Bouvet Island. This accords to hypothesis “3” in this study (“Areas with increased to intermediate chl a levels, together with cold water masses will have increased abundance of krill”).

Predation pressure

Krill abundance peaked close to the two islands. Krill-eating land-based predators has established breeding colonies on both islands. Here predation pressure and the resulting effect on krill are believed to be extensive. Out at sea the impact from land-based predators is reduced due to large distances from breeding colonies. However, some predators like whales and sea birds are still found, and during summer many predators forage over large distances, and these trips can last from a few days to months (Croxall *et al.* 1984; Croxall *et al.* 1985).

Of the many studies done on Antarctic krill, few have identified simple and consistent straight relationships between environmental properties and krill distribution (Siegel 2005).

> Many explanations for the circumpolar distribution of krill have been proposed, including sea ice (Mackintosh 1973; Brierley *et al.* 2002), gyres (Marr 1962; Pakhomov 2000; Nicol 2006), fronts (Witek *et al.* 1988; Spiridonov 1996; Tynan 1998), shelf edges (Siegel 2005; Nicol 2006) and high food concentrations (Constable *et al.* 2003; Atkinson *et al.* 2004). However, none of these fully accounts for the distribution patterns, as exceptions apply to each. One common factor, however, is that all are bottom–up interpretations, which relate krill to areas of enhanced food. (Atkinson *et al.*2008:7)

In the Southern Ocean literature, few krill studies have addressed the trade-off between finding food and avoiding predation. Mortality is one of the most important factors forming and affecting krill population dynamics (Pakhomov 2000; Murphy & Reid 2001), with more than 100 million tonnes of krill removed every year by predators (Miller & Hampton 1989a; Mori & Butterworth 2006). This important top-down controlling factor would vary geographically. Murphy et al. (2007) assessed the krill centered food web in the Southern Ocean. They found a spatially heterogeneous demand for krill within our surveyed area, with intense hotspots where high concentrations of krill and predation pressure co-occur (Murphy & Reid 2001) as seen in the South Georgia area.

Predators include several species and among them the most dominate krill foragers; macaroni penguins (Eudyptes chrsolophus Forster) and fur seals (Arctocephalus gazella). These two species are responsible for > 75% of krill eaten by land based predators at South Georgia Island (Atkinson *et al.* 2001), and these two species are also found at the small land-breeding colony at Bouvet Island. Fur seals forage out over the shelf and in off-shelf regions were krill is supplied by advection, while macaroni penguins forage on the shelf (Boyd *et al.* 2002; Boyd 2002; Staniland & Pond 2004). Other land-based predators, such as sea birds, also consume krill. An example is the Black-browed albatrosses (Diomedea melanophris Temminick), which travel large distances to forage at the shelf or out at sea (>1000 km) (Croxall *et al.* 1997). On the

South Georgian shelf, also ice fish (nothotheneide) feed on krill. They are found at the shelf edges and towards land, known to stay close to the seabed at daytime and migrate up towards the surface during night were it feeds on its preferred diet, *E. superba* (Everson *et al.* 1999).

At Bouvet Island studies of krill and predators are few, but similar islands have been investigated. A study made by Atkinson et al. (2001) states that at smaller scales, like on Bird Island, localized predation could be intense from e.g. Macaroni penguins. This pressure is especially high on larger krill sizes (Reid & Arnould 1996; Atkinson *et al.* 2001). Such predation pressure may also be evident on Bouvet Island where a small seal- and penguin colony are present.

Vertical distribution patterns, Day vs. night – Diel Vertical Migration

Diel Vertical Migration (DVM) of plankton is normally ascribed to avoidance from visually searching predators during day, and foraging in the surface layers at night (Robison 2003; Collins & Rodhouse 2006). Due to the high predation pressure at South Georgia we hypothesized marked vertical migration of krill in this region, while we hypothesized the least tendency for migration in the Open Sea. And these patterns became evident in our investigation. In the waters of the South Georgia Island, a massive migration of krill was seen between night and day, clustering into dense belts in the surface at night. In the waters of Bouvet Island, krill carried out a similar diel vertical migration as near South Georgia, aggregating close to the surface at night. In contrast, hardly any change in vertical distribution between day and night was observed in the Open Sea.

In accordance with my results, Brierley et al. (2006) found that during a 26 day period there was a clear daily cyclicity in the vertical distribution of krill near South Georgia, and most echograms at dusk and dawn had signs of vertical migration. Density was low during nighttime, and generally higher at daytime. This was believed to be in part due to krill migration into the upper "dead zone" at dusk, and down away from the surface at dawn. The upper "dead zone" is believed to camouflage some degree of biomass when conducting acoustic surveys. The loss of krill observed in the water column during day, to the "deadzone" during night, was not evident in my results for

South Georgia, with a change from 3.17 to 8.89 krill pr m^3 between day and night respectively. This may relate to the vertical distribution of algae, as the vertical distribution of fluorescence showed a marked subsurface peak at South Georgia.

In all regions investigated, krill was basically found in the upper ~100m at daytime. At South Georgia there was a bi-modal pattern with the majority of krill seen at 110-115 m, largely in according with studies by Taki et al. (2005) and Brierley et al. (2006) finding that depths around 100m is the midpoint for the distribution of krill aggregations at South Georgia in daylight. The other peak at South Georgia during day was found at 20-30m depth. This bi-modal pattern was from a mean across all day-data sampled for the area, and looking at Fig. 14, one can see that the krill was scattered into many small dense aggregations throughout the water column.

During day at the Open Sea, krill abundance maximum was situated at 50m (see Fig. 17) compared to 30-40m for Bouvet (see Fig. 18). For both areas, this layer is made up of many small aggregations/dense belts. At Bouvet also a few very large and dense aggregations were found in the upper 100m at day, being over 60 to 80m in height. Another difference is that no krill was observed near the surface at Bouvet, while some records were made of near-surface krill in the Open Sea, potentially related to low predation risk, so that some krill would risk to stay up in the surface to feed in daylight.

In the Southern Ocean, the water column is largely unstratified, so little energetic advantage would be gained from vertical migration (Robison 2003; Collins & Rodhouse 2006). There was a shallow temperature minimum at 100-140m for all areas, formed by a layer of water from last winter's cooling, called Winter Cooled Water (Iversen *et al.* 2008). This temperature minimum followed by a broad temperature maximum above in the vertical is present on all of the vertical profiles, though close to the polar front temperature in the surface was high reaching ~4 C. Most of the abundance of krill found above the shallow temperature minimum at 100-140m. Primary production was only found in this upper unstratified zone, corresponding to the distribution of krill. Out at sea were the variations in vertical levels of fluorescence was low, migration was at a minimum. At South Georgia, fluorescence levels were high at 30 to 50m and seem to be a driving force for the migration of krill up to these depths at night from a daytime depth of 100m.

In summary, it seems that the areas close to Islands have the most extensive migration pattern, seemingly correlated with a high predation pressure. These finding supports my “4” and “5” hypothesis stating that: “ Predation pressure increases with decreased distance to land and an increased number of breeding colonies near by for land breeding predators (Given that hypothesis 5 and 6 is supported)” and “An increase in predation pressure will give extensive migration patterns between night and day for the Antarctic krill”.

Krill swarm structure

The densities within the aggregations differed between the three areas, with the largest and densest aggregations during daytime at South Georgia Island and Bouvet Island, the latter region being characterized by many small dense aggregations and a few large ones. The Open Sea area had small aggregations with a low density and the krill being more scattered into diffuse scattering layers than aggregated into swarms.

The schooling behavior of krill may be related to predation pressure, and Antarctic krill may form dense and large aggregations as a defense mechanism (Nicol & Foster 2003). Also availability of food may play a role (Hofmann *et al.* 2004). The occurrence of medium to large sized aggregations at South Georgia (and to some extent also near Bouvet) can be correlated with the high number of breeding colonies and the high predation pressure, but the intermediate chl a levels close to the islands may contribute to the increased number and sizes of krill aggregations close to the two islands surveyed in this study.

The findings on school structures more or less confirm my hypothesis “6” which state that: ”Increased predation pressure will lead to larger and denser swarm structure for Antarctic krill”.

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