Spatial patterns in the vertical structure of euphausiids in Gullmarsfjord, Sweden: identifying influences on bilayer formation and distribution

GERAINT A. TARLING[1*], FINLO R. COTTIER[2], INIGO EVERSON[3]

[1]British Antarctic Survey, Natural Environment Research Council, High Cross, Cambridge, UK.
[2] Scottish Association for Marine Science, Scottish Marine Institute, Oban, Argyll, UK.
[3] Environmental Science Research Centre, Anglia Ruskin University, Cambridge, UK.

*Corresponding author: Geraint A. Tarling, British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Rd, Cambridge, CB3 0ET, UK.
E-mail: gant@bas.ac.uk

Running head: Euphausiid bilayers in Gullmarsfjord

Abstract

The formation of two vertically discrete layers (bilayers) at nighttime is a commonly observed phenomenon in zooplankton and is regularly found in Gullmarsfjord, a fjord with a 50 m sill depth, deep basin and a 3 layered water column. In an acoustic and net sampling survey in September 2003, nighttime euphausiid layers occurred at 15 m and 45 m, with the deeper layer containing relatively higher concentrations of adult Northern krill (*Meganyctiphanes norvegica*). The main nighttime predatory threat came from the upward migration of demersal fish, which reached the deeper but not shallower euphausiid layer. Shoreward advection of coastal waters across the sill creates a layer of resuspended organic matter between 40 and 50 m. The deeper bilayer was located at those depths, particularly at the mouth of the fjord where this organic matter was most concentrated. Krill in the lower bilayer experienced waters that were 4°C cooler than in the upper bilayer, which can decrease the cost of respiration by around 20%. Accompanying studies have shown significantly higher growth rates in krill consuming sedimentary organic material and benthic filamentous algae. When combined with the present study, it appears that energetic benefit and predatory threat were greatest in the deeper rather than the shallower bilayer in Gullmarsfjord. This is the reverse of most other euphausiid habitats, where the highest risk and reward is in the upper bilayer, illustrating that euphausiids adapt their stereotypic vertical migration pattern to local environmental conditions.

Key words: DVM, Northern krill, acoustics, predation, feeding, respiration

Introduction

The vertical distribution of pelagic organisms can be considered a trade-off between food intake and mortality risk (Clark & Levy 1988) to which diel vertical migration, the ascent to the surface at night and descent during the day, is believed to provide an optimal solution across a wide variety of environments (Russell, 1927, Cushing 1951). However, there are a number of factors that modify this behavioural pattern. For instance, the presence of pelagic fish in surface waters may induce relatively deep distributions of their prey even at night (Bollens & Frost 1991, Frost & Bollens 1992, Loose & Dawidowicz 1994, Onsrud and Kaartvedt 1998). Nocturnal upward migrations may likewise be interrupted where suitable feeding conditions are encountered (Sameoto 1980, Dagg et al. 1997). There may be metabolic benefits to reducing the time spent in warmer surface layers where the costs of respiration are higher (McLaren 1963). Furthermore, environmental conditions in certain depth strata may otherwise be intolerable, such as high temperatures at the surface (Andersen & Sardou 1992) or anoxic layers at depth (Spicer & Strömberg 2002).

Euphausiids (otherwise called ‘krill’) are prolific vertical migrators (Mauchline & Fisher 1969; Kaartvedt 2010) and this behaviour has been shown to be strongly influenced by their feeding habits (Ponomareva 1971; Hu 1978; Willason & Cox, 1987). Most euphausiids are believed to be omnivorous and it has been posited for some time that these animals can only meet their metabolic requirements through migration (Ohman 1984; McClatchie 1985; Price et al. 1988). Feeding behaviour does not appear to be stereotypic across all individuals within krill populations and there can be considerable inter-individual variability in diet, even within enclosed sites such as Gullmarsfjord, Sweden (Schmidt 2010 Pond et al. 2012). In a study of Northern krill *Meganyctiphanes norvegica* (M. Sars, 1857) in Gullmarsfjord, Pond et al.

(2012) related differences in diet to rates of instantaneous growth and found that individuals consuming certain food items had significantly higher growth rates. In particular, highest growth rates were seen in those individuals containing markers for filamentous algae and terrestrial carbon sources. Neither the algae nor terrestrial sediment are commonly found in the surface layers of the water column, implying that they must have been consumed either in the deeper parts of the water column or in the vicinity of the sea-bed interface. In an accompanying study, Schmidt (2010) found filamentous algae occurred in *M. norvegica* stomachs mainly during nighttime, when the population was closer to the surface. These studies illustrate that there is additional complexity to the diel vertical migration pattern of this species in Gullmarsfjord that has a significant influence on individual performance.

Gullmarsfjord is 28 km long and has an effective sill depth of 43 m and a maximum depth of ~120 m at about 10 km from the fjord entrance (Arneborg & Liljebladh 2001; Liljebladh & Thomasson 2001). The density structure is dominated by the coastal stratification which varies due to the freshwater fluxes from the Baltic. It is typically described by three layers comprising (i) warm and relatively fresh (salinity (S)=24-27), homogeneous surface water from the Kattegat, (ii) colder and more saline (S=32-33) intermediate water from the Skagerrak, and (iii) stagnant basin water which is colder and more saline winter Skagerrak water (Arneborg et al. 2004). The surface and intermediate waters are separated by a strong pycnocline at depths varying from 5-20 m (Arneborg & Liljebladh 2001), corresponding to the S=28 isohaline (Arneborg et al. 2004) and the intermediate and basin waters are separated by a weaker pycnocline at ~50 m (Arneborg & Liljebladh 2001). Observations of suspended sediment showed greatest concentrations closest to the seabed with a mid-water maximum in concentration identified below the halocline at approximately sill depth. Arneborg et al.

(2004) considered that this layer comprised either falling organic matter or inflow of turbid waters from outside the fjord.

A previous study on the vertical distribution of the euphausiids *M. norvegica* and *Thysanoessa raschii* (M. Sars, 1864) in Gullmarsfjord was carried out by Bergström & Strömberg (1997) who found a two layered distribution during the night-time, the upper euphausiid layer within the warm relatively fresh surface layer (~20 m) and lower euphausiid layer at the ~50 m pycnocline. It was proposed that the pattern resulted from *T. raschii* migrating through the thermocline and *M. norvegica* remaining below it because of their differing physiological capabilities. However, this has been questioned by further studies in which *M. norvegica* has been shown to be capable of tolerating surface conditions in this fjord (Kaartvedt 2002). In this study, we re-examine the factors contributing to this night-time bilayered distribution of euphausiids in Gullmarsfjord, with a particular focus on the horizontal as well as the vertical structure of the bilayers. The survey was carried out in the autumn, which is a post-bloom period when the diet of *M. norvegica* is particularly diverse (Schmidt 2010).

Identifying euphausiids amongst other types of potential acoustic scatterers is complex and, in this study, a post-processing technique is applied that exploits the difference in signal strength between 120 kHz and 38 kHz (ΔS_v). The technique has been applied widely to surveys of Antarctic krill *Euphausia superba* (Dana, 1850) in the Southern Ocean (Madureira et al. 1993a, b; Woodd-Walker et al. 2003. Hewitt et al. (2004) and Everson et al. (2007) refined the ΔS_v technique for examining *M. norvegica* abundance and distribution. The present study also considers the distribution of euphausiid predators through the application of single target analysis to the same acoustic traces (Soule et al. 1995, 1996, 1997; Ona & Barange 1999). In light of accompanying studies on the euphausiid community in this fjord

(Everson et al. 2007; Schmidt 2010; Pond et al. 2012), our specific aim in the present study was to determine whether spatial patterns in the nighttime bilayered structure were consistent with the exploitation of alternative deep food sources. Furthermore, we examined how this structure related to the abiotic influences such as temperature and salinity as well as biotic factors such as predation.

Methods

Survey design

The aim of the survey design was to produce a series of acoustic transects running both along and across the depth contours of the fjord. The chosen design was a zig-zag pattern of eight transects composed of four transects oriented approximately north/south and four east/west (Fig. 1). Transects 1,3,5 and 7 constituted the east/west series and 2,4,6 and 8 the north/south series on each survey. Two surveys were made on each voyage, one in the outbound direction (from transect 1 to 8) and the other in the inbound direction (from transect 8 to 1). A total of 4 voyages were made between 8th and 11th September 2003, 2 in the daytime and 2 at night (Table 1). This made a total of 8 surveys, each with 8 transects over the course of 3 days. CTDs and net samples were taken at the mid-point of each voyage after completion of the outbound survey and before the start of the inbound survey.

Environmental data

A G. O. Mark IIIc CTD recorder was used to obtain profiles of conductivity and temperature at a single site at 58˚ 19.2' N 11˚ 32.7' E, the deepest part of the fjord. Oxygen saturation and Chl-a profiles were obtained from measurements made as part of the ongoing monitoring programme of the fjord by Kristineberg Marine Research Station using the same CTD plus water bottle rosette device as above. For oxygen, it was necessary to combine two profiles from different locations in the fjord to make up a complete profile of the water column. Measurements of the upper water column (0 to 60 m) were made in the inner Gullmarn (58° 24' N, 11° 38' E) while the deeper water column (60 to 117 m) was measured at Alsbäck (58° 19' N, 11° 33' E). Both measurements were taken on 3rd September. Chl-a measurements were taken on 3rd September between the surface and 30 m at Alsbäck and between the surface and 50 m at the mouth of the fjord (58° 17’ N, 11° 29’ E). Water samples for Chl-a measurements were taken between 5 and 10 m depth intervals.

Net sampling

Oblique net samples were taken with an Isaacs Kidd Midwater Trawl (IKMT) with a one square metre mouth opening and a mesh size of 1. 5mm. The net was equipped with a “Scanmar” trawl sensor, to determine net-depth in real time and a calibrated flow-meter, to measure volume sampled. All net hauls were carried out near to the centre of the deepest part of the fjord and close to the centre of the acoustic survey area (58˚ 19.0’ N, 11˚ 32.5’ E, Fig. 1). Two hauls were taken on each voyage. One of these hauls went from the surface to within 10 m of the seabed (water depth was around 120 m at the sampling site), the other haul went from the surface to 50 m.

All species of euphausiids as well as the calanoid copepod *Pareuchaeta norvegica* (Boeck, 1872) were enumerated from each catch, with the maturity of each *Meganyctiphanes. norvegica* specimen (i.e. adult or juvenile) also being noted. Random sub-samples of specimens from each catch were measured to determine length-frequency distributions. For euphausiids, total length was measured from the front of the eye to the tip of the telson, to the nearest mm. The length of the cephalothorax was measured to the nearest mm for *P. norvegica*.

The cohort structure within length frequency data was analysed using MIX 3.1a (Icthus Data Systems, Hamilton, Ontario, Canada. Computer program.). The data was applied without constraints being placed on fitting the means, standard deviations and proportions to the length frequency data. A quasi Newton algorithm was used for the fitting procedures. The routines were applied separately to the dominant macrozooplankton components in net catches: *P. norvegica*, *Thysanoessa* spp, juvenile *M. norvegica*, adult *M. norvegica*.

Acoustic hardware and signal processing

A Simrad EK60 scientific echosounder operating at 38 kHz and 120 kHz was used for the acoustic measurements. This had been installed and maintained on the R/V *Arne Tiselius* according to the manufacturer's specification at the bottom of the ship's hull, at a depth of 3.7 m. below the waterline. The echosounder was interfaced to a GPS to provide accurate information on vessel position and speed throughout the study. Calibration of the echosounder was carried out according to the SIMRAD calibration protocol on 3rd September 2003 (see Everson et al. 2007). Raw data were logged onto a PC and backup files made after each voyage.

Post-processing of acoustic data

Overview: The raw-data generated by the Simrad Echosounders was analysed by Echoview (Sonardata, www.sonardata.com, version 3.45.58.3520, accessed 30 June 2013). The software enables acoustic data to be manipulated and exported in forms that allow further statistical analyses to be performed. The key to this process is the ability to divide up the data into various horizontal and vertical sections to allow spatial comparisons of backscattering strength between regions.

Comparison of scattering strengths of the 38 kHz and 120 kHz sounders enables the contributions to acoustic backscatter made by different size classes of organisms to be assessed separately. Specifically, the Echoview software enables acoustic records to be masked such that only the components with certain levels of difference between scattering strength on the two sounders, $\Delta S_{v120\text{-}38}$, remain visible for subsequent integration. Two groups of $\Delta S_{v120\text{-}38}$ were used: 12 to 20 dB for detecting smaller organisms such as juvenile

Meganyctiphanes norvegica, *Thysanoessa* spp. and *Pareuchaeta norvergica*, and 6 to 12 dB for medium-sized organisms such as adult *M. norvegica*.

Identification and enumeration of the number of single targets was used as a means of assessing the number of large fish within a region. The identification procedure was performed through the application of algorithms designed to differentiate between the signals from individual as opposed to multiple targets. A more detailed description of each of the analytical steps is given below. Further details of the masking and resampling procedures are given in Everson et al. (2007).

ΔS_v analysis

Division and resampling: The raw data was divided into transects (1 to 8) and then sub-divided into 0.1 nautical mile (nm) horizontal sections. For some analyses, each transect was alternatively sub-divided into 5 m vertical bins. The uppermost 5 m and lowermost 1 m were excluded from the analysis to avoid bad data generated from turbulence and incorrect bottom-detection respectively. Resampling was done on the basis of pings, with each resampled cell consisting of the mean of 2 pings.

Masking: The $\Delta S_{v120\text{-}38}$ was calculated for each cell in the dataset. The values were used to create two masks. One mask excluded all values except those within a $\Delta S_{v120\text{-}38}$ range of 12 to 20 dB, the other, 6 to 12 dB. Both masks were applied to the 120 kHz data sets only.

Thresholding: In an associated study, Everson et al. (2007) determined dB threshold levels that produced consistent results in terms of calculating the numerical density of adult *Meganyctiphanes norvegica*. Accordingly, a threshold was set at –77 dB for the data that remained visible after applying the 6 to 12 dB ΔS_v mask. This threshold level is approximately equivalent to 1 adult *M. norvegica* m^{-3} (Foote et al. 1990, Everson et al. 2007). A lower threshold of –90 dB was set for data remaining after application of the 12 to 20 dB

ΔS_v mask, given that this mask was aimed at revealing smaller individuals with lower acoustic target strengths.

Integration: The 120 kHz acoustic dataset was used to perform any integration analyses. In particular, to analyse vertical distribution patterns, each transect was divided into 5 m depth bins and then grouped according to whether it was sampled during daytime or night-time. The mean and SD of each depth bin was subsequently determined for both the day and the night datasets (S_v values were converted into the linear domain before the descriptive statistics were calculated).

Single target analysis

A single target is an acoustic echo that is attributed to a single backscattering target detected within an acoustic beam. The difficulty with analyses of this sort is in determining whether an echo is received from just a single target or a number of targets in close proximity. Algorithms developed by Soule et al. (1995, 1996, 1997) and Ona and Barange (1999) discriminate between these two possibilities and have been integrated into Echoview software for this purpose. The software applies the algorithms to the data on a ping-by-ping basis, firstly removing data for which no targets need to be determined (i.e. data above and below the exclusions lines) before carrying out 2 main procedures: (i) identifying all the TS peaks that may indicate single targets, (ii) rejecting any peaks that indicate that there are overlapping pulses (ie. from more than 1 target). The identification and rejection procedures are based on a number of parameters, which are listed along with the values used in Table 2. These parameter values are particularly suited to identifying individual large fish that are dispersed rather than aggregated. In the present study, the procedures were applied to the 38 kHz data set. Identified targets were exported for further statistical analysis on vertical and horizontal distributional trends.

Results

Environmental data

Temperature and salinity profiles were characteristic of many fjordic environments in this region (Fig. 2). The upper 20 m contained brackish water, indicating the influence of Baltic Sea water. The intermediate layers down to the sill depth of 50 m contained water with lower salinity than the water in the deep basin of the fjord, probably derived from the mixing of Baltic, Skagerrak and North Sea water and was uniformly 17.0 ˚C until 30 m, where there was strong thermocline down to 60 m. Between 60 m and the bottom, typical temperatures were around 6.3˚C and salinities, 34.2, most likely originating from the Skaggerak. Levels of Chl-a (Fig. 3) indicate that there was still a relatively high level of primary productivity ongoing at this time of year, with surface concentrations of around 1 µg l^{-1} and a subsurface maximum, located at 20 m, of 3 µg l^{-1}. There was little difference in the Chl-a profiles between the fjord mouth and the inner fjord.

Comparing the two salinity profiles obtained at the start (8th Sept 2003, 1100) and towards the end (10th Sept 2003, 2300) in Fig. 2 shows that there was no renewal of the deep, basin water during the survey period. Past studies have shown that this deep water is renewed most often at yearly intervals (Svansson 1984) although exceptions have occurred. The observed low level of oxygen saturation (27%) suggests that the deep water had not been renewed for many months (Fig. 3). Above 60m, salinity increased during the survey period, with the greatest increases occurring in the halocline region (S = 28 – 32) separating the upper and intermediate layers. The bottom of this halocline (indicated by horizontal lines) ascended by ~5 m during the survey. The lower halocline remains relatively static at a depth of ~ 55 m. There was relatively little change in the salinity of the surface water.

Net samples

All net catches were dominated by *Meganyctiphanes norvegica* juveniles (Fig. 4), which reached concentrations of more than 5 ind m^{-3} above 50 m during the night time. The majority of juveniles were located below 50 m during the daytime. The estimated concentration of adult *M. norvegica* during the night-time was approximately 1 ind m^{-3}, and these were more evenly spread than the juveniles through the water column given that their concentrations were similar in the 0 to 50 m and 0 to 100 m nets. Adults were only caught in the deeper haul during the day, indicating that all individuals migrated vertically to deeper water after dawn. The euphausiid *Thysanoessa* spp. and the calanoid copepod *Pareuchaeta norvegica* were caught at similar concentrations to adult *M. norvegica* and were also absent from the upper water column during the day. *Nyctiphanes couchii* (Bell, 1853) was present in the catches but only in small numbers.

The adult population of *M. norvegica* comprised two size classes, one with a modal peak of around 34 mm, the other, 39 mm (Fig. 5, Table 3). The body lengths of juvenile Northern krill were less than half those of the adults, with a single modal peak at 14 mm. *Thysanoessa* spp. were slightly smaller again, with an average body length of 10 mm. The cephalothorax length of *Pareuchaeta norvegica* specimens ranged between 6 and 10 mm.

ΔS_v analysis

General patterns: A deep scattering layer between 80 m and 100 m was apparent during the daytime (Fig. 6). The level of backscatter in these layers became particularly strong towards the edges of the fjord (i.e. close to the apparent sharp peaks in bathymetry along the survey track). There was very little scatter in the upper water column at this time. Much of the deep scattering layers had dispersed during the night-time and there was an increase in scattering in the surface layers (Fig. 6).

Vertical distribution: There was a clear vertical migration from deeper layers in the daytime to upper layers in both the 12 to 20 dB and the 6 to 12 dB ΔS_v ranges (Fig. 7). The peak layer of backscatter during the daytime was at 90 m while, at night, it separated into two peaks at 15 m and 45 m. The relative strength of these two peaks was significantly different between the two ΔS_v ranges (Chi-squared 24.39, v=1, P<0.001), with the strongest peak in the 12 to 20 dB ΔS_v range being at 15 m, while that in the 6 to 12 dB ΔS_v range was at 45 m. Given that *M. norvegica* adults are likely to be the main contributor to S_v in the 6 to 12 dB ΔS_v range, this suggests that they were more likely to be present in the deeper of the two upper scattering layers than juvenile *M. norvegica*, *Thysanoessa* spp. and *P. norvegica*.

Single target analysis

The single target search algorithm had a lower threshold of –50 dB. We found that peak TS value of targets was just above this value, at –46 dB. 90% of the single targets had a TS value of between –48 dB and –34dB, while the remaining 10% had stronger TS values (<-34 dB). Single targets showed a pattern of residing deep during the day and migrating to upper layers during night-time (Fig. 8). The most common daytime depth was 110 m while the majority moved to a depth of 40-50 m at night. Particularly notable during the night-time was the development of a bimodal distribution, with a mean of 38% (SD 28%) of targets migrating upwards, the rest remaining at 110 m. The majority of upward migrators resided between 40 and 50 m with only a mean of 11% (SD 20%) of scatterers going above 30 m at this time.

Vertical distribution patterns along the fjord axis

Fig. 9 combines the results of the 6 -12 dB $\Delta S_{v120\text{-}38}$ analysis (distinguishing adult Northern krill) with the single target analysis (distinguishing fish) for each of the 8 transects taken along the fjord axis during the 2 night-time surveys. It shows that the night-time vertical distribution of both the ‘krill-like’ scatterers and the ‘fish-like’ targets altered depending on their location in the fjord. In terms of the krill-like scatterers, there was a distinct bilayer distribution pattern in the majority of transects, with the depth of layers relatively invariant between transects, the upper layer located around 15 m and the lower layer around 45 m. However, the relative scattering strengths of these layers did alter between transects. Close to the sill (transects 1, 2 and 3), the scattering strength of the lower layer was 2-4 dB greater than the upper layer (-69.8 to -70.6 dB lower layer, -72.9 to -74.8 dB upper layer). At the mid-point in the fjord axis (transects 4, 5 and 6), the scattering strength of both layers was relatively similar (-71.6 to -75.5 dB lower layer, -73.7 to -74.9 dB upper layer). Towards the head of the fjord (transects 7 and 8), only the upper layer was readily apparent (-72.6 to -74.3 dB) with the lower layer being barely distinguishable above background levels (-79 dB).

In terms of fish-like targets, an average of 72% (SD 28%) remained at 70 m or deeper during the night-time, with there being no particular spatial trend as to where the highest and lowest proportions occurred. Of those targets that had migrated upwards, the strongest concentrations were seen at the same depth as the lower ΔS_v scattering layer, at around 40 to 50 m. These depths accounted for an average of 58% (SD 34%) of all targets above 70 m. An average of 26% (SD 34%) of fish-targets above 70 m were located in the upper ΔS_v scattering layer.

With respect to the overlap between the fish-like and krill-like targets, between 26% and 28% of the biomass of these two groups co-occurred in the 40-50 m depth layer in transects 1 and 2, close to the mouth of the fjord. This overlap declined further in to the fjord, with between 10 and 15% co-occurring in the 40-50 m depth layer in transects 3, 4 and 5, dropping further to 8% at the head of the fjord (transect 8). Overall, the greatest overlap in krill- and fish-like targets was seen towards the mouth of the fjord, where the deep krill layer was most prominent.

Discussion

Our surveys provide a spatially resolved description of the day and night vertical distributions of acoustic scattering layers and single targets over a large area of Gullmarsfjord. Through applying dB difference techniques to the acoustic data, we were able to partition acoustic scattering into smaller and larger zooplankton categories, with the assumption that the former mainly consisted of juvenile *Meganyctiphanes norvegica* and some *Thysanoessa* spp. and the latter, adult *M. norvegica*. The surveys ascertained that both the small and large categories occupied two upper depth layers during night-time, one at around 15 m and the other around 45 m. The smaller zooplankton category was generally more concentrated in the upper scattering layer while the larger zooplankton category was more concentrated in the deeper scattering layer. The deeper scattering layer was most prominent towards the sill end of the fjord and became almost indistinguishable towards the head of the fjord. The upper scattering layer remained present throughout the length of the fjord. During daytime, both the smaller and larger zooplankton categories resided in one layer, between 80 and 100 m. The depth of fish, determined through single target analysis, was mainly around 110 m during the day. By night, only around half of the fish were found above 70 m, of which most were concentrated between 40 and 50 m. Very few fish were found above 30 m during night and none during the day.

Species contribution to acoustics patterns

Two pieces of evidence point to *Meganyctiphanes norvegica* being the principal contributor to the scattering observed in the 12 to 20 dB and 6 to 12 dB ΔS_v ranges. Firstly, this species was the most abundant macrozooplankton in net catches. Secondly, the vertical distribution of the 12 to 20 dB and 6 to 12 dB ΔS_v ranges showed a close resemblance to those described for this species by other net catches and acoustic studies in this region. For instance, Liljebladh & Thomasson (2001) found *M. norvegica* in this fjord occupied layers between 70 m and 90 m during the day and 10 m to 30 m at night, during the period August and October 1997. Spicer et al. (1999) found a similar daytime distribution.

We used acoustic information to distinguish between different size classes of euphausiid, principally adult *M. norvegica*, with a size range of 30 mm to 45 mm total body length, and juveniles, which ranged from 10 mm to 20 mm total body length. To distinguish adult *M. norvegica*, we masked out all data apart from that within a $\Delta S_{v120\text{-}38\ \mathrm{kHz}}$ range of 6 to 12 dB. Empirical experiments by Foote et al. (1990) on Antarctic krill between 30 mm and 39 mm found TS values of –85.1 dB at 38 kHz and –76.1 dB at 120 kHz, giving a difference of 9 dB between the two frequencies. Our application of ±3dB to this value allows for the range in TS values reported by Foote et al. (1990) of around 6 dB. Such variance is probably a product of changing orientation (Everson 1982). The 6 to 12 dB ΔS_v applied here is narrower than the 2 to 12 dB ΔS_v range used in acoustic studies of Antarctic krill (Watkins and Brierley 2002). Everson et al. (2007) found that the wider ΔS_v range was more likely to produce erroneous results when applied to *M. norvegica*. This may be a result of the smaller maximum size of *M. norvegica* (50 mm) compared with 65 mm for Antarctic krill (Mauchline 1977) and also planktivorous fish falling within the 2 to 12 dB ΔS_v range (Martin Collins, personal communication).

A $\Delta S_{v120\text{-}38\ \mathrm{kHz}}$ range of 12 to 20 dB was used to identify juvenile *M. norvergica* and *Thysanoessa* spp. There has been little work on the target strength of juvenile euphausiids. One of the few estimates available is from stochastic distorted-wave Born approximation (SDWBA) models (Demer & Conti 2003, 2004) that, although focussing on adult krill, allow extrapolation to smaller sizes. Nevertheless, some caution is required in extrapolating these models too far outside the adult Antarctic krill size range for which they were originally parameterised. In Demer & Conti (2004), an extrapolation to a minimum size of 20 mm total length was carried out, for which the predicted difference in TS between 38 kHz and 120 kHz was around 14 dB. Our ΔS_v range of 12 to 20 dB allowed for the fact that many juvenile *M. norvegica* in the present study had a total length of 15 mm or shorter. Further development of target strength models focussing on smaller krill would benefit this area of research and allow appropriate ΔS_v ranges to be further refined.

The focus of the present study was to carry out spatially comprehensive acoustics transects to compliment previous work that had mainly used nets to describe distribution patterns (Bergström & Strömberg 1997; Thomasson et al. 2003). Our net catches were principally to provide qualitative information as to which species were likely to be the main contributors to the observed acoustic scattering patterns. In an accompanying study, Everson et al. (2007) considered methodological aspects of estimating Northern krill biomass with acoustics. They found estimates of adult Northern krill densities in nets and acoustic data in the present survey to be overlapping, mainly within the range of 0.5 to 1 ind m^{-3}. Therefore, although net catches were limited in their scope, they did not appear to suffer from avoidance to any great degree.

Our identification of fish was based on acoustic characteristics alone, since carrying out accompanying fish-trawling operations was not possible. A threshold of –50 dB at 38 kHz was set to ensure that smaller targets like krill (with TS of –85 dB at 38 kHz) were not included in our single target analysis. The peak TS of single targets in this study was –46 dB, and maximum TS, approximately –28dB. Assuming these targets are gadoid fish, their equivalent length (L, cm) can be estimated from the following equation, derived by Foote (1987):

$$TS = 20 \log L - 67.4$$

Accordingly, targets with a TS of –46 dB would be around 10 cm long while those with a TS of –28 dB could be up to 1 m in length.

The size and the behaviour of these targets are characteristic of benthopelagic fish species such as Norway pout *Trisopterus esmarkii* (Nilsson, 1855) and cod *Gadus morhua* Linnaeus, 1758. Both species are a common component of benthic trawls carried out in the adjacent Skagerrak (Poulsen 1968; Albert 1994). Furthermore, like the acoustic patterns, they have been found to leave their daytime habitat in the epibenthic zone to migrate vertically into the mid to upper layers at night (dos Santos & Falk-Petersen 1985; Kaartvedt et al. 1996; Torgersen et al. 1997; Onsrud et al. 2004). *Meganyctiphanes norvegica* are a common constituent of the diet of Norway pout and cod, with the gut contents of some individuals showing exclusive consumption of krill (Pearcy et al. 1979; Asthorsson & Palsson 1987; Onsrud et al. 2004).

Factors influencing the nighttime bilayered structure

Our observation that the euphausiid community divided into 2 vertical layers at night-time has been reported widely in krill distributions and a variety of factors have been proposed to drive such patterns (Pearre 2003). We will consider in turn some of the major factors likely to influence vertical distribution patterns observed in the present study.

I) Pycnocline as a physical barrier

The temperature and salinity profiles from the CTD data show that the hydrography of Gulmarsfjorden during the period of the study conformed to the well-described three layer structure. Temperatures in the surface brackish layer (salinity of 24) and intermediate layer down to 30 m (salinity between 25 and 32) were uniformly 17°C, after which there was a strong thermocline down to 60 m. Therefore, compared to the upper bilayer, which was located in waters that were 17°C, the prevailing temperature in the lower bilayer was 5°C cooler, at 12°C, while salinity differed by ~6 units between the 2 layers (26.5 and 32.3 for upper and lower bilayers respectively).

A previous study on the vertical distribution of euphausiids in Gullmarsfjord was carried out by Bergström & Strömberg (1997) who found a two layered distribution during the night-time, the upper euphausiid layer within the warm relatively fresh surface layer (~20 m) and lower euphausiid layer at the ~50 m pycnocline. The euphausiid species *Thysanoessa raschii* (M. Sars, 1864) was more common in the upper layer while *Meganyctiphanes norvegica* dominated the lower layer. It was posited that *M. norvegica* was less physiologically capable than *T. raschii* of tolerating the upper layer temperatures (above 15°C). Nevertheless, such an interpretation does not fit with other available evidence on the capabilities of *M. norvegica,* since it has a very broad geographic distribution and lives in habitats spanning wide temperature ranges (Tarling et al. 2010). In the Ligurian Sea (Mediterranean), the species regularly migrates into waters above 22°C (Tarling et al. 1999) while, even within temperate regions, it has been reported that it ascends into temperatures near 20°C at night (Kaartvedt et al., 2002). Furthermore, it is not always true that *T. raschii* is associated with warmer waters than co-occurring *M. norvegica* since, in the Gulf of St Lawrence, *T. raschii* was more commonly found in the colder strata of the water column (Plourde et al. 2013). Therefore, although temperature plays a significant role in the physiology of these species (see below) it is unlikely to act as a physical barrier that separates their specific vertical migration patterns (Kaartvedt 2010).

A steep salinity gradient to a minimum of 24 occurred above 15 m. Forward & Fyhn (1983) found the lower lethal limit of *M. norvegica* to occur at 20-24 salinity units. Buchholz et al. (1995) studied DVM in *M. norvegica* in the nearby Kattegat and considered the surface brackish layer to be of little importance in determining the pattern of migration. Harvey et al. (2009) considered the vertical migration of both *M. norvegica* and *T. raschii* in the St Lawrence estuary and Gulf of St Lawrence and found that both species were capable of migrating into the low salinity surface layers, although there was a tendency for *M. norvegica* to be located a little deeper than *T. raschii* at some, but not all, times of year. The bilayer structure in the present study is located well below the steep salinity gradients in the surface water and we conclude that it was not an important influence on the pattern of vertical distribution of these two species.

II) Metabolic advantages of different bilayers

The clear relationship between respiration rate and temperature in marine zooplankton (Ikeda 1985) suggests an adaptive value in moving up and down between vertical temperature gradients in order to gain maximum metabolic advantage. The different temperatures experienced in the two bilayers is likely to have an influence on respiration rate and overall energy expenditure. Saborowski et al. (2000, 2002) found that Northern krill from the Kattegat, the Clyde Sea, and the Ligurian Sea all exhibited approximately the same level of oxygen consumption (30–35 µmol O2 g^{-1} dry wt h^{-1}) when incubated at the ambient temperatures found in their respective environments (9°C, 5°C, and 12°C) indicating that krill adjust their overall metabolic rates to the prevailing thermal conditions. Nevertheless, when moved rapidly between temperatures (within the range 4 to 16°C), oxygen consumption increased exponentially with increasing experimental temperature with rates rising to 89.9 35 µmol O2 g^{-1} dry wt h^{-1}.

Assuming that the physiological capabilities of Northern krill in Gullmarsfjord are the same as those in the nearby Kattegat, individuals occupying the lower bilayer (12°C) would have a respiration rate of 50 µmol O2 g^{-1} dry wt h^{-1}, whereas those in the upper bilayer (16°C) would reach a rate of 70 µmol O2 g^{-1} dry wt h^{-1}. Accordingly, there would be a 20% saving in metabolic rate through occupying the lower bilayer during the nighttime phase. Nevertheless, overall energetic balance by these individuals will only be achieved if a suitable food source is also found.

III) Vertical and spatial distribution of food

The Chl-a maximum at the time of sampling occurred at around 20 m which coincides with the vertical location of the upper bilayer across a wide area of the fjord. However, at least in transects towards the mouth of the fjord, the strongest levels of backscatter (equating to the greatest euphausiid biomass) was located in the lower bilayer. Further away from the fjord mouth, this lower layer became weaker and the majority of euphausiids occurred in the upper bilayer. The distribution pattern suggests that there is an alternative deep food source in the vicinity of the fjord mouth that is exploited by the euphausiids occurring there.

Previous surveys have shown that there is often an inflow of new Skagerrak water across the sill and into the intermediate layer of Gullmarsfjord (Arneborg et al. 2004), which was probably the case during the period of the present surveys given that the upper halocline ascended by 5 m between the 8th and 10th September. Furthermore, given the observations of Arnerborg et al. (2004), it is very likely that such an inflow will be accompanied by an influx of biogenic material, derived from the coastal waters or resuspended from the sill, into the intermediate water layer. An exchange of intermediate water will generally propagate to the head of the fjord but the biogenic material brought into the fjord will tend to settle out at the base of the intermediate layer at ~45 m, with a greater concentration found towards the sill. This will give rise to bilayers of varying biogenic character. Organic matter produced in the surface water of the fjord will tend to settle onto the top of the upper halocline at ~20 m, while that advected into the sill in the inflowing coastal waters will tend to settle out closest to the sill at ~45 m. Both of these regions will provide a food-rich layer for feeding, though the quantity of material in the lower layer will decay with distance from the sill, by virtue of the fact that it is an advected source rather than a locally produced source.

Gut content analysis on adult *M. norvegica* captured during the present sampling campaigns show a varied diet, including small and large diatoms, copepods, tintinnids, pollen, lithogenic particles and filamentous algae (Schmidt 2010). Through comparative analysis of the gut contents of individuals caught during the night and day, Schmidt (2010) was able to identify when particular food items were most likely to have been eaten. Large copepods such as *Calanus* and *Metridia* were eaten mainly during the day. Dinoflagellates, younger stages of *Calanus* and filamentous algae were consumed both day and night and tintinnids, pollen and lithogenic particles were only eaten during the night. Given that feeding continues both day and night, it is apparent that adult *M. norvegica* are not completely reliant on feeding in the surface layers in order to meet their food intake requirements. The fact that phytoplankton, tintinnids and lithogenic particles were eaten is an indication that at least some individuals visited the upper bilayer during the nighttime. Food items such as filamentous algae, which were mainly consumed at night, were likely to have been eaten in the lower bilayer since this is an item that has probably entered as part of the suspended sedimentary flux at sill depth. Although it is possible that this material was consumed at the seafloor, the observed acoustic patterns indicate that euphausiid scattering layer did not go within 30 m of the seabed during its deepest phase during the day, making benthic feeding unlikely in the majority of individuals. Filamentous algae was most likely consumed when it was suspended after being washed in from the sill.

Fatty acid biomarker analysis carried out by Pond et al. (2012) found that adult *M. norvegica* that had consumed greater amounts of filamentous algae exhibited the highest growth rates. No such pattern was found in juvenile *M. norvegica*. This finding is consistent with the fact that juveniles were more likely to be found in the upper bilayer and adults in the lower bilayer where the filamentous algae and organic sediment was most likely to occur. Furthermore, our observation that the strength of acoustic scattering in the lower bilayer was highest at the sill and decreased into the fjord further supports the interpretation that sedimented organic material advected from the sill is a major food source on which these organisms concentrate their nighttime distribution. The fact that the marker for filamentous algae correlates to higher growth does not necessarily indicate that it is the consumption of the algae alone that is responsible for increased growth. For instance, the algae may co-occur with other energy-rich items for which fatty acid markers were not readily distinguished. Alternatively, krill eating these algae occupy deeper, colder waters and so have a metabolic advantage over those feeding in the upper bilayer (see above).

IV) Risk of predation

A particularly interesting aspect of the survey was the comparison of the night-time depth distribution of benthopelagic fish compared to that of the euphausiids. In particular, towards the mouth of the fjord, it was apparent that those fish that did make upward migrations were mainly concentrated at the depths of the lower bilayer. From the euphausiid perspective, therefore, although occupying the lower bilayer depth appears to be most profitable in terms of the potential for growth, it also presents the greatest risk of predation.

In considering patterns of vertical migration and the exchange of individuals between bilayers, Ohman (1990) proposed that sinking was mainly a means by which to avoid predation. However, whether it is a result of an entrained behaviour or an immediate response to the perception of predatory threat has remained difficult to determine in the marine environment. De Robertis et al. (2003) found that the presence of a fish at distances of 20–300 cm did not affect the swimming speed or turning of the euphausiids, suggesting that they did not respond to the presence of a potential predator at these distances. Similarly, in a study of a sea-bed environment in the Faroe-Shetland Channel, Hirai & Jones (2012) found no correlation between sites of higher or reduced predation pressure and the concentration of Northern krill. Therefore, in the present study, it is likely that the krill occupying this lower bilayer do not perceive or respond to the higher predation risk they encountered, and selected their environment mainly on the detection of food resources.

From the perspective of the planktivorous fish, it is evident firstly that only around 40% appear to be in the water column as opposed to the epibenthic layer at any one time during the night, while by day, they all are concentrated towards the bottom. The pattern may be the result of upward forays made by different individuals at different times through the night or, alternatively, by individuals migrating every 2nd or 3rd night. Secondly, of those individuals that did make an upward migration, the upper migration limit was at the lower rather than upper bilayer. This patterm may be the result of a combination of factors. Firstly, the fact that older, larger, more lipid-rich euphausiids are located in the lower bilayer makes this a more profitable food patch on which to focus foraging efforts. This is similar to Wishner et al. (1995), who reported that whales were most likely to be found around copepod aggregations containing older life stages. Secondly, such planktivores will themselves have predators searching by sight (Kaartvedt et al. 2005). Therefore, the risk of upward migrations from the epibenthic layer is minimised by only performing them at night, limiting the number of forays made and only venturing to mid rather than upper water column depths.

Based on the evidence presented in this study, the interaction between fish predators and euphausiid prey can be summarised as follows (Fig. 10). During the daytime, the euphausiids and fish aggregate in the deeper layers, the euphausiids occupying depth strata above that of the fish. During the nighttime, the euphausiids migrate upwards and form bilayers at 15 m and 45 m. Euphausiids at the 15 m depth bilayer feed on phytoplankton at the Chl-a maximum while those in the 45 m depth bilayer feed on organic sediment advected from the sill, with the upper bilayer being mainly smaller euphausiids (juvenile *M. norvegica* and and *Thysanoessa* spp.) and the lower layer adult *M. norvegica*. Nevertheless, the fact that bilayers were evident in both ΔS_v classes means that there is a flux of individuals between bilayers. Only part of the fish population migrates upwards during the night, with the majority of those occurring at the same depth as the lower bilayer (40 to 50 m).

The choice of depth by the euphausiids is similarly a trade-off between feeding in the most profitable food patches and minimising the risk of predation. Encountering the resource-rich lower bilayer probably halted the upward migration of euphausiids during dusk. Gibbons et al. (1991), for instance, found that *Euphausia lucens* Hansen, 1905 slowed their upward migration through layers of potential food as a strategy to remain for longer periods within 'preferred' vertical strata. A similar pattern was observed by Youngbluth (1976) in *Euphausia pacifica* Hansen, 1911 in the California Current.

Concluding remarks

Variance in the diel vertical migration behaviour in *Meganyctiphanes norvegica* has been widely document (Kaartvedt 2010). Balino & Aksnes (1993), for instance, found that *M. norvegica* ascended to the surface at one location but remained below 40 m at another location within the same fjord. However, few studies have demonstrated the consequences of such variability on life-cycle parameters such as growth. This study, combined with the accompanying observations reported by Schmidt (2010) and Pond et al. (2012), describe not only variability in DVM patterns over small spatial scales and between different life-stages, but also how this pattern relates both to the feeding and predation environments. In turn, it reveals a situation that is the reverse of the standard explanation for the formation of bilayers in vertical distribution, in that the most rewarding and risky environments were in the lower rather than upper bilayer. It is a demonstration of the plastic response to the risk reward environment that has been predicted by a number of models examining the factors controlling diel vertical migration behaviour (Clark & Levy 1988; Mangel & Clark 1988; Ohman 1990; Fiksen & Giske 1995; Fiksen & Carlotti 1998).

Acknowledgements

We thank Bo Bergström, Mike Thorndyke, scientists and staff of Kristineberg Marine Research Station for hosting and supporting the fieldwork at Gullmarsfjord. Matilda Haraldsson and the master and crew of MV "Arne Teselius" ably assisted our work. Odd Lindahl helped us access the time-series of physical data on Gullmarsfjorden collated by Kristineberg Marine Research Station (http://www.smhi.se). Peter Fretwell of MAGIC at British Antarctic Survey provided the bathymetric map figure. Malin Daase of the Norwegian Polar Institute, Tromsø, drafted the schematic figure of euphausiid behaviour. The Royal Swedish Academy of Sciences is thanked for their invitation to GT and IE to undertake the research. The project was supported by a grant from the European Commission 6th Framework Programme on "Research Technological Development and Demonstration: Access to Research Infrastructure programme". GT carried out this work as part of the ECOSYSTEMS programme at the British Antarctic Survey.

References

Albert OT. 1994. Biology and ecology of Norway pout (*Trisopterus esmarki* Nilsson, 1855) in the Norwegian Deep. Ices Journal of Marine Science 51:46-61.

Andersen V, Sardou J. 1992. The diel migrations and vertical distributions of zooplankton and micronekton in the Northwestern Mediterranean Sea 1. Euphausiids, mysids, decapods and fishes. Journal of Plankton Research 14:1129-54.

Arneborg L, Erlandsson CP, Liljebladh B, Stigebrandt A. 2004. The rate of inflow and mixing during deep-water renewal in a sill fjord. Limnology and Oceanography 49:768-77.

Arneborg L, Liljebladh B. 2001. The internal seiches in Gullmar Fjord. Part I: Dynamics. Journal of Physical Oceanography 31:2549-66.

Astthorsson OS, Palsson OK. 1987. Predation on euphausiids by cod, *Gadus morhua*, in winter in Icelandic subartic waters. Marine Biology 96:327-34.

Balino BM, Aksnes DL. 1993. Winter distribution and migration of the sound scattering layers, zooplankton and micronekton in Masfjorden, western Norway. Marine Ecology Progress Series 102:35-50.

Bergström B, Strömberg J-O. 1997. Behavioral differences in relation to pycnoclines during vertical migration of the euphausiids *Meganyctiphanes norvegica* (M.Sars) and *Thysanoessa raschii* (M.Sars). Journal of Plankton Research 19:255-61.

Bollens SM, Frost BW. 1991. Diel vertical migration in zooplankton - rapid individual response to predators. Journal of Plankton Research 13:1359-65.

Buchholz F, Buchholz C, Reppin J, Fischer J. 1995. Diel vertical migrations of *Meganyctiphanes norvegica* in the Kattegat - comparison of net catches and measurements with acoustic Doppler current profilers. Helgolander Meeresuntersuchungen 49:849-66.

Clark CW, Levy DA. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. American Naturalist 131:271-90.

Cushing DH. 1951. The vertical migration of planktonic crustacea. Biological Reviews 26:158-92.

Dagg MJ, Frost BW, Newton JA. 1997. Vertical migration and feeding behavior of *Calanus pacificus* females during a phytoplankton bloom in Dabob Bay, U.S. Limnology and Oceanography 42:974-80.

De Robertis A, Schell C, Jaffe JS. 2003. Acoustic observations of the swimming behavior of the euphausiid *Euphausia pacifica* Hansen. Ices Journal of Marine Science 60:885-98.

Demer DA, Conti SG. 2003. Validation of the stochastic distorted-wave Born approximation model with broad bandwidth total target strength measurements of Antarctic krill. Ices Journal of Marine Science 60:625-35.

Demer DA, Conti SG. 2004. Erratum: Validation of the stochastic distorted-wave Born approximation model with broad bandwidth total target strength measurements of Antarctic krill (Vol 60, pg 625, 2003). Ices Journal of Marine Science 61:155-156

Dos Santos J, Falk-Petersen S. 1989. Feeding ecology of cod *Gadus morhua* L. in Balsfjord and Ullsfjord Northern Norway 1982-1983. Journal du Conseil International pour l'Exploration de la Mer 45:190-9.

Everson I. 1982. Diurnal variations in mean volume backscattering strength of an Antarctic krill (*Euphausia superba*) patch. Journal of Plankton Research 4:155-6.2

Everson I, Tarling GA, Bergström B. 2007. Improving acoustic estimates of krill: experience from repeat sampling of northern krill (*Meganyctiphanes norvegica*) in Gullmarsfjord, Sweden. Ices Journal of Marine Science 64:39-48.

Fiksen O, Carlotti F. 1998. A model of optimal life history and diel vertical migration in *Calanus finmarchicus*. Sarsia 83:129-47.

Fiksen O, Giske J. 1995. Vertical distribution and population dynamics of copepods by dynamic optimization. Ices Journal of Marine Science 52:483-503.

Foote KG. 1987. Fish target strengths for use in echo integrator surveys. Journal of Acoustic Society of America 82:981-7.

Foote KG, Everson I, Watkins JL, Bone DG. 1990. Target strength of Antarctic krill (*Euphausia superba*) at 38 and 120 kHz. Journal of Acoustic Society of America 87:16-24.

Forward RB, Fyhn HJ. 1983. Osmotic regulation of the krill *Meganyctiphanes norvegica*. Comparative Biochemistry and Physiology 74A:301-5.

Frost BW, Bollens SM. 1992. Variability of diel vertical migration in the marine planktonic copepod *Pseudocalanus newmani* in relation to its predators. Canadian Journal of Fisheries and Aquatic Sciences 49:1137-41.

Gibbons MJ, Barange M, Pillar SC. 1991. Vertical migration and feeding of *Euphausia lucens* (Euphausiacea) in the Southern Benguela. Journal of Plankton Research 13:473-86.

Harvey M, Galbraith PS, Descroix A. 2009. Vertical distribution and diel migration of macrozooplankton in the St. Lawrence marine system (Canada) in relation with the cold intermediate layer thermal properties. Progress in Oceanography 80:1-21.

Hewitt RP, Kim S, Naganobu M, Gutierrez M, Kang D, Takao Y, Quinones J, Lee YH, Shin HC, Kawaguchi S, Emery JH, Demer DA, Loeb VJ. 2004. Variation in the biomass density and demography of Antarctic krill in the vicinity of the South Shetland Islands during the 1999/2000 austral summer. Deep-Sea Research Pt II 51:1411-19.

Hirai J, Jones DOB. 2012. The temporal and spatial distribution of krill (*Meganyctiphanes norvegica*) at the deep seabed of the Faroe-Shetland Channel, UK: A potential mechanism for rapid carbon flux to deep sea communities. Marine Biology Research

8:48-60.

Hu VJH. 1978. Relationships between vertical migration and diet in four species of euphausiids. Limnology and Oceanography 23:296-306.

Ikeda T. 1985. Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. Marine Biology 85:1-11.

Kaartvedt S. 2010. Diel vertical migration behaviour of Northern krill (*Meganyctiphanes norvegica* Sars). In: Tarling GA, editor. Advances in Marine Biology,. San Diego: Elsevier Academic Press Inc,. Vol 57 p 255-75.

Kaartvedt S, Larsen T, Hjelmseth K, Onsrud MSR. 2002. Is the omnivorous krill Meganyctiphanes norvegica primarily a selectively feeding carnivore? Marine Ecology Progress Series 228:193-204.

Kaartvedt S, Melle W, Knutsen T, Skjoldal HR. 1996. Vertical distribution of fish and krill beneath water of varying optical properties. Marine Ecology Progress Series 136:51-8.

Kaartvedt S, Rostad A, Fiksen O, Melle W, Torgersen T, Tiseth-Breien M, Klevjer TA. 2005. Piscovorous fish patrol krill swarms. Marine Ecology Progress Series 299:1-5.

Liljebladh B, Thomasson MA. 2001. Krill behaviour as recorded by acoustic doppler current profilers in the Gullmarsfjord. Journal of Marine Systems 27:301-13.

Loose CJ, Dawidowicz P. 1994. Trade-offs in diel vertical migration by zooplankton - the costs of predator avoidance. Ecology 75:2255-63.

Madureira LSP, Everson I, Murphy EJ. 1993a. Interpretation of acoustic data at two frequencies to discriminate between Antarctic krill (*Euphausia superba)* and other scatterers. Journal of Plankton Research 15:787-802.

Madureira LSP, Ward P, Atkinson A. 1993b. Differences in backscattering strength determined at 120 and 38 kHz for three species of Antarctic macroplankton. Marine

Ecology Progress Series 93:17-24.

Mangel M, Clark CW. 1988. Dynamic modelling in Behavioral Ecology. Princeton, New Jersey: Princeton University Press. 308 pages.

Mauchline J. 1977. Growth and moulting of crustacea, especially euphausiids In: Andersen NR, Zahuranec BJ, editors. Oceanic Sound Scattering and Prediction. New York: Plenum Press. p 401-22,

Mauchline J, Fisher LR. 1969. The biology of euphausiids. Advances in Marine Biology. 7: 1-454.

McClatchie S. 1985. Feeding behavior in *Meganyctiphanes norvegica* (M.Sars) (Crustacea : Euphausiacea). Journal of Experimental Marine Biology and Ecology 86:271-84.

McLaren IA. 1963. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. Journal of Fisheries Research Board of Canada 20:685-727.

Ohman MD. 1984. Omnivory by *Euphausia pacifica*: the role of copepod prey. Marine Ecology Progress Series 19:125-31.

Ohman MD. 1990. The demographic benefits of diel vertical migration by zooplankton. Ecological Monographs 60:257-81.

Ona E, Barange M. 1999. Single target recognition. ICES Cooperative Research Reports 235:28-43.

Onsrud MSR, Kaartvedt S. 1998. Diel vertical migration of the krill *Meganyctiphanes norvegica* in relation to physical environment, food and predators. Marine Ecology Progress Series 171:209-19.

Onsrud MSR, Kaartvedt S, Rostad A, Klevjer TA. 2004. Vertical distribution and feeding patterns in fish foraging on the krill *Meganyctiphanes norvegica*. Ices Journal of Marine Science 61:1278-90.

Pearcy WG, Hopkins CCE, Gronvik S, Evans RA. 1979. Feeding habits of cod, capelin and herring in Balsfjorden, northern Norway, July-August 1978: the importance of euphausiids. Sarsia 67:269-77.

Pearre S. 2003. Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. Biological Reviews 78:1-79.

Plourde S, McQuinn IH, Maps F, St-Pierre J-F, Lavoie D ,Joly P. 2013. Daytime depth and thermal habitat of two sympatric krill species in response to surface salinity variability in the Gulf of St Lawrence, eastern Canada. Ices Journal of Marine Science. Doi :10.1093/icesjms/fst023(10 pages).

Pond DW, Tarling GA, Schmidt K, Everson I. 2012. Diet and growth rates of *Meganyctiphanes norvegica* in autumn. Marine Biology Research 8:615-23.

Ponomareva LA. 1971. Circadian migrations and feeding rhythm of some Indian ocean euphausiid species. Oceanology 11:226-31.

Poulsen E. 1968. Norway pout: stock movements in the Skagerrak and the north-eastern North Sea. Rapports et Procès-Verbaux des Réunions / Conseil International pour l'Exploration de la Mer 158:80-5.

Price HJ, K. R. Boyd, C. M. Boyd. 1988. Omnivorous feeding behaviour of the Antarctic krill *Euphausia superba*. Marine Biology 97:67-77.

Russell FS. 1927. The vertical distribution of plankton in the sea. Biological Reviews 2:213-61.

Saborowski R, Buchholz F. 2002. Metabolic properties of Northern krill, *Meganyctiphanes norvegica*, from different climatic zones. II. Enzyme characteristics and activities. Marine Biology 140:557-65.

Saborowski R, Salomon M, Buchholz F. 2000. The physiological response of krill *(Meganyctiphanes norvegica)* to temperature gradients in the Kattegat. Hydrobiologia 426:157-60.

Sameoto DD. 1980. Relationships between stomach contents and vertical migration in *Meganyctiphanes norvegica*, *Thysanoessa raschii* and *T.inermis* (Crustacea Euphausiacea). Journal of Plankton Research 2:129-43.

Schmidt K. 2010. Food and feeding in Northern krill (*Meganyctiphanes norvegica* Sars). In: Tarling GA, editor. Advances in Marine Biology. San Diego: Elsevier Academic Press Inc., Vol 57, p 127-171,

Soule M, Barange M, Hampton I. 1995. Evidence of bias in estimates of target strength obtained with a split-beam echosounder. Ices Journal of Marine Science 52:139-44.

Soule M, Barange M, Hampton I. 1996. Potential improvements to current methods of recognizing single targets with a split-beam echosounder. Ices Journal of Marine Science 53:237-43.

Soule M, Barange M, Solli H, Hampton I. 1997. Performance of a new phase algorithm for discriminating between single and overlapping echoes in a split-beam echosounder. Ices Journal of Marine Science 54:934-8.

Spicer JI, Strömberg JO. 2002. Diel vertical migration and the haemocyanin of krill *Meganyctiphanes norvegica*. Marine Ecology Progress Series 238:153-62.

Spicer JI, Thomasson MA, Stromberg JO. 1999. Possessing a poor anaerobic capacity does not prevent the diel vertical migration of Nordic krill *Meganyctiphanes norvegica* into hypoxic waters. Marine Ecology Progress Series:181-7.

Svansson A. 1984. Hydrography of the Gullmar fjord. Fisheries Board of Sweden, Institute for Hydrographic Research 23: 1-91.

Tarling GA, Buchholz F, Matthews JBL. 1999. The effect of a lunar eclipse on the vertical migration behaviour of Meganyctiphanes norvegica (Crustacea : Euphausiacea) in the Ligurian Sea. Journal of Plankton Research 21:1475-88.

Tarling GA, Ensor NS, Fregin T, Goodall-Copestake WP, Fretwell P. 2010. An introduction to the biology of Northern krill (*Meganyctiphanes norvegica* Sars). In: Tarling GA, editor. Advances in Marine Biology, San Diego: Elsevier Academic Press Inc.,Vol 57 p 1-40.

Thomasson MA, Johnson ML, Stromberg JO, Gaten E. 2003. Swimming capacity and pleopod beat rate as a function of sex, size and moult stage in Northern krill *Meganyctiphanes norvegica*. Marine Ecology Progress Series 250:205-13.

Torgersen T, Kaartvedt S, Melle W, Knutsen T. 1997. Large scale distribution of acoustical scattering layers at the Norwegian continental shelf and the eastern Norwegian Sea. Sarsia 82:87-96.

Watkins JL, Brierley AS. 2002. Verification of the acoustic techniques used to identify Antarctic krill. Ices Journal of Marine Science 59:1326-36.

Willason SW, Cox JL. 1987. Diel feeding, laminarinase activity and phytoplankton consumption by euphausiids. Biological Oceanography 4:1-24.

Wishner KF, Schoenherr JR, Beardsley R, Chen CS. 1995. Abundance, distribution and population structure of the copepod *Calanus finmarchicus* in a springtime Right Whale feeding area in the southwestern Gulf of Maine. Continental Shelf Research 15:475-507.

Woodd-Walker RS, Watkins JL, Brierley AS. 2003. Identification of Southern Ocean acoustic targets using aggregation backscatter and shape characteristics. Ices Journal of Marine Science 60:641-9.

Youngbluth MJ.1976. Vertical distribution and diel migration of euphausiids in central region of California Current. Fishery Bulletin 74:925-36.

	Day			Night		
Transect	Start	End	Duration (min)	Start	End	Duration (min)
Series	8 Sep					
Outbound	07:28:01	08:28:24	60:23	19:17:30	20:19:10	61:40
Inbound	13:32:00	14:37:00	65:00	23:02:00	00:06:00	64:00
	10 Sep					
Outbound	07:31:30	08:38:15	66:45	19:31:11	20:39:28	68:17
Inbound	12:01:00	13:05:49	64:49	23:37:32	00:52:00	74:28

Table 1: The timings of the 8 surveys carried out between 8th and 11h September 2003. All times are in Universal Time Coordinated (UTC). Local celestial times are ahead of UTC by 46 minutes.

Single Target Parameter	Value
TS threshold (dB)	-50
Pulse length determination level (milliseconds)	6
Minimum normalized pulse length (milliseconds)	0.8
Maximum normalized pulse length (milliseconds)	1.5
Maximum beam compensation (dB)	6
Maximum SD of minor-axis angles (°)	0.6
Maximum SD of major-axis angles (°)	0.6
Beam compensation model	Simrad LOBE

Table 2: Parameters and their values used in single target identification analysis. The analysis uses the target strength (TS) and angular position within the split beam to determine the likelihood of an echo being from a single target.

Species	Mean total body length (mm)	SD (mm)	Proportion
Euchaeta norvegica	8.13	1.23	NA
Thysanoessa spp.	9.59	1.11	NA
Juvenile *Meganyctiphanes norvegica*	13.24	1.76	NA
Adult *M.* norvegica (Cohort 1)	33.69	1.05	0.29
Adult *M. norvegica* (Cohort 2)	38.25	1.55	0.71

Table 3: Mean total body lengths and SD of the dominant macrozooplankton species present in net samples taken in Gullmarsfjorden on 8th and 10th September 2003. Only one cohort was present in the populations of *Euchaeta norvegica*, *Thysanoessa* spp. and juvenile *Meganyctiphanes norvegica.* Two cohorts were identified in adult *M. norvegica*, which were split according to the proportions given in the final column.

Figures

Fig 1: Gullmarsfjord showing the acoustic transect path and the location of the CTD/net sampling station.

Fig 2: Temperature and salinity profiles in Gullmarsfjord (58° 19.2'N 11° 32.7'E) taken at 11:00 on 8th September 2003 (thick line) and at 23:00 on 10th September (thin line). Horizontal line indicates the depth of the halocline on 8th Sept. (thick line) and 10th Sept. (thin line)

Fig 3: Chl-a and O_2 profiles in Gulmarsfjord on 3rd September 2003. Chl-a measurements were taken close to the CTD/net sampling station at Alsbäck (58° 19'N 11° 33'E, 0 to 30 m) and also at the mouth of fjord (58° 17'N 11° 29'E, 0 to 50 m). O_2 measurements between 0 and 60 m were made at inner Gullmarn (58° 24'N 11° 38'E), and between 60 and 117 m at Alsbäck.

Fig 4: Concentration (ind m^{-3}) of the main macrozooplankton components in oblique IKMT net catches taken day and night on 8th and 10th September 2003 at 58° 19.0' N, 11° 32.5' E. *M. n. (ad)* – adult *Meganyctiphanes norvegica*; *M. n. (juv)* – juvenile *M. norvegica*; *T.* spp – *Thysanoessa* spp; *P. n. – Pareuchaeta norvegica*

Fig 5: Length-frequency of *Meganyctiphanes norvegica* adults (*M. n. (ad)*), juvenile *M. norvegica* (*M. n. (juv)*), *Thysanoessa* spp. (*T.* spp) and *Euchaeta norvegica* (*P. n.*)

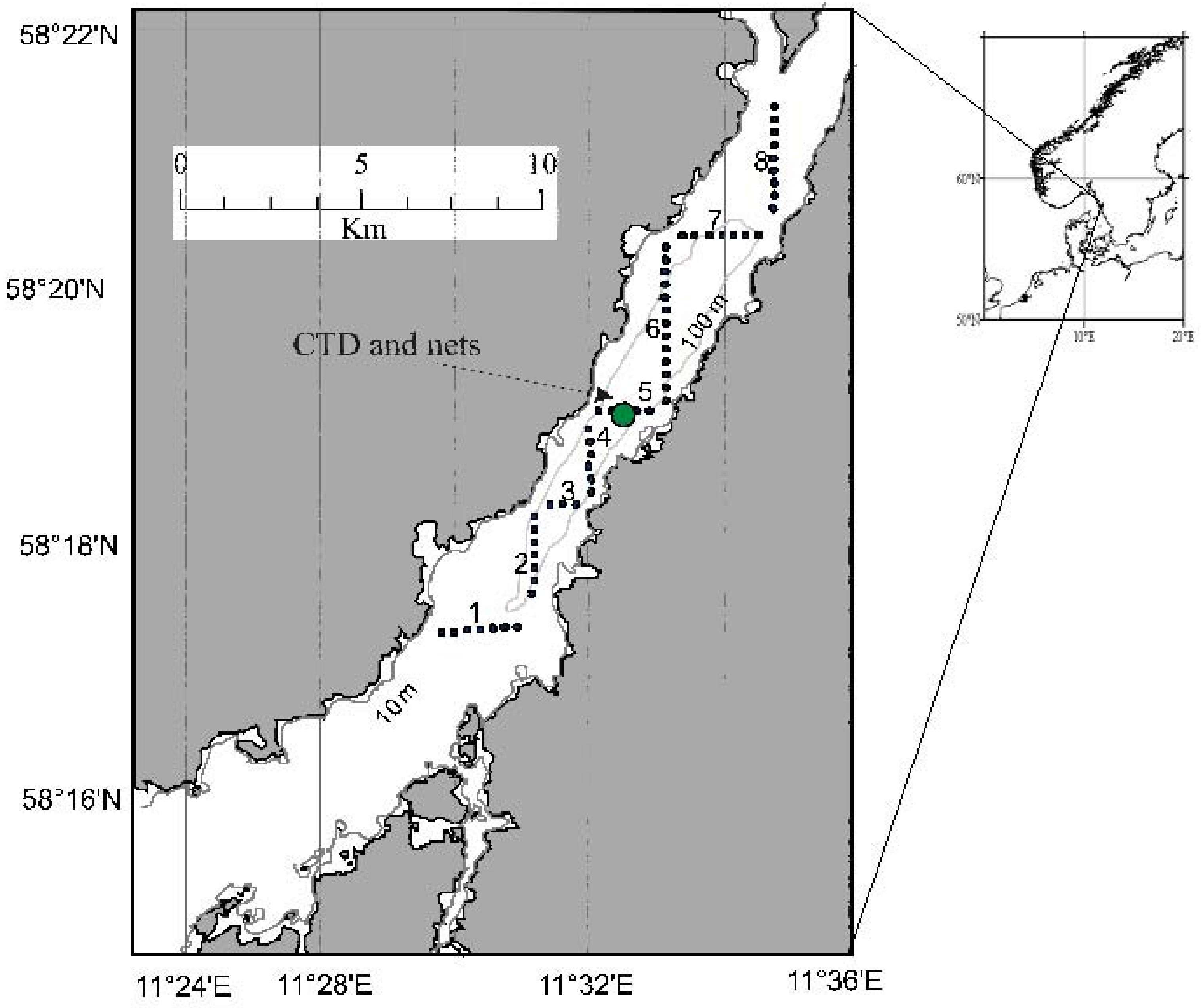
Fig 6: Backscatter (S_v, dB) extracted from the 120 kHz acoustic data collected during the outward daytime and nightime surveys on 8th September 2003. The divisions in the profiles demark the extent of the 8 transects, as show on Fig. 1. The steep changes in topography at the ends of each transect reflect the shallowing at the edges of the fjord. A threshold of –77 dB was applied.

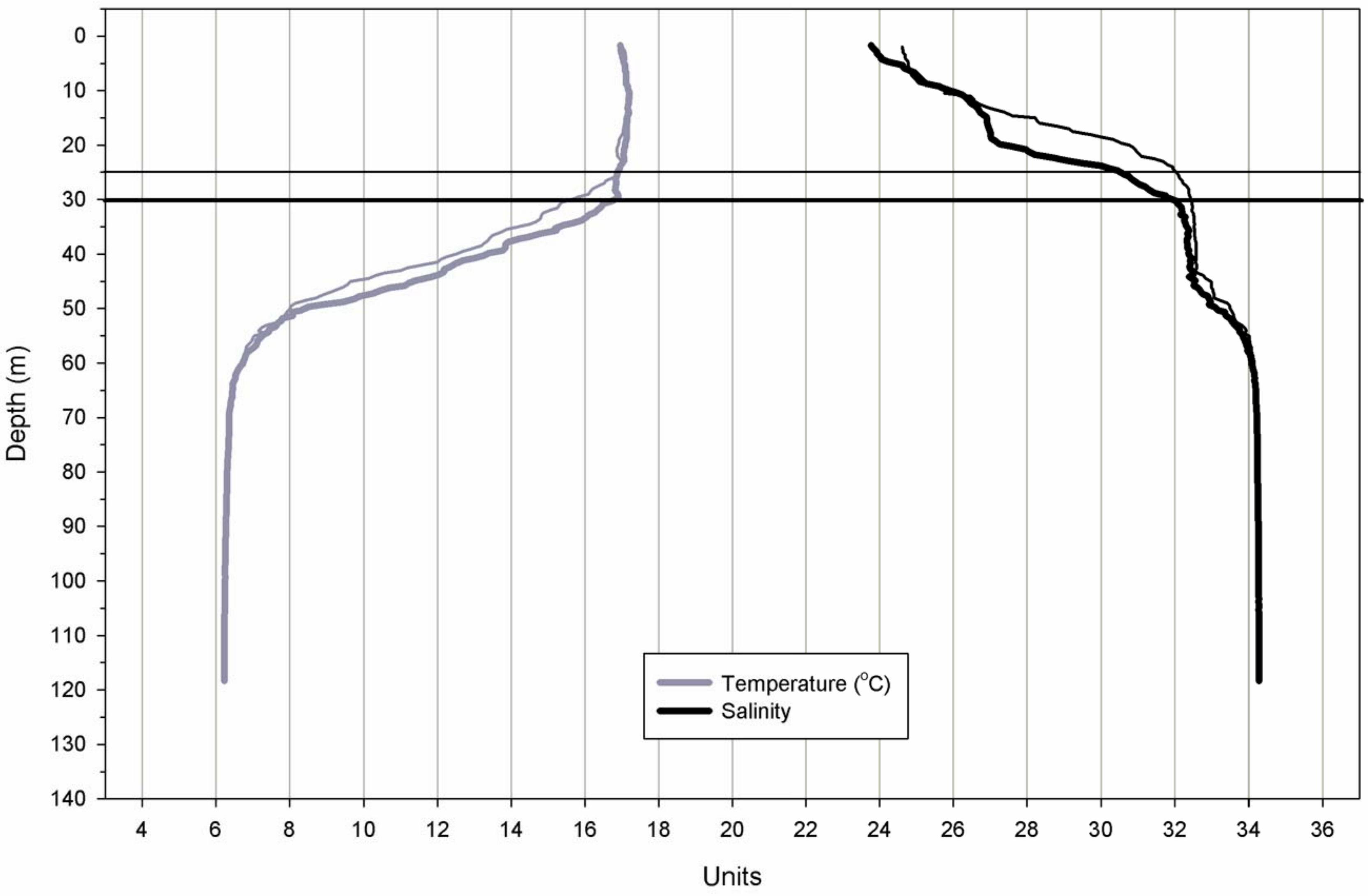
Fig 7: Vertical profiles of mean S_v (dB) of the two ΔSv 120 – 38 kHz components (upper: a ΔSv of 12-20 dB for which larval *Meganyctiphanes norvegica* and small euphausiids were the most likely scatterers; lower: a ΔSv of 6-12 dB for which adult *M. norvegica* were the most likely scatterers) extracted from the daytime and night time 120 kHz acoustic data. Each horizontal bar represents the mean of four surveys, the error bars, 1 SD. All averaging was done in the linear domain before converting to Sv

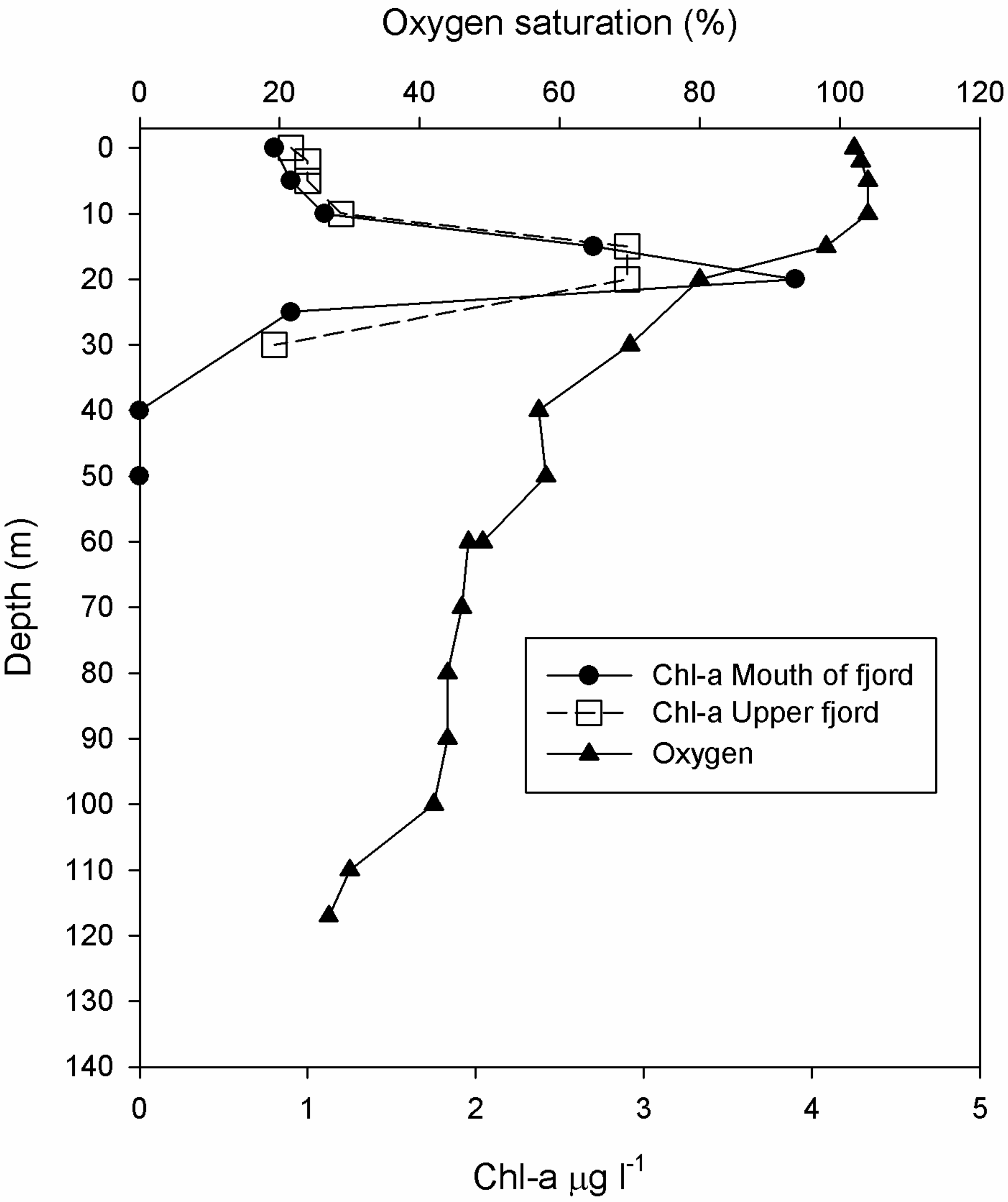
Fig 8: The vertical distribution of single targets during day and night. Data from 8th and 10th September surveys were combined

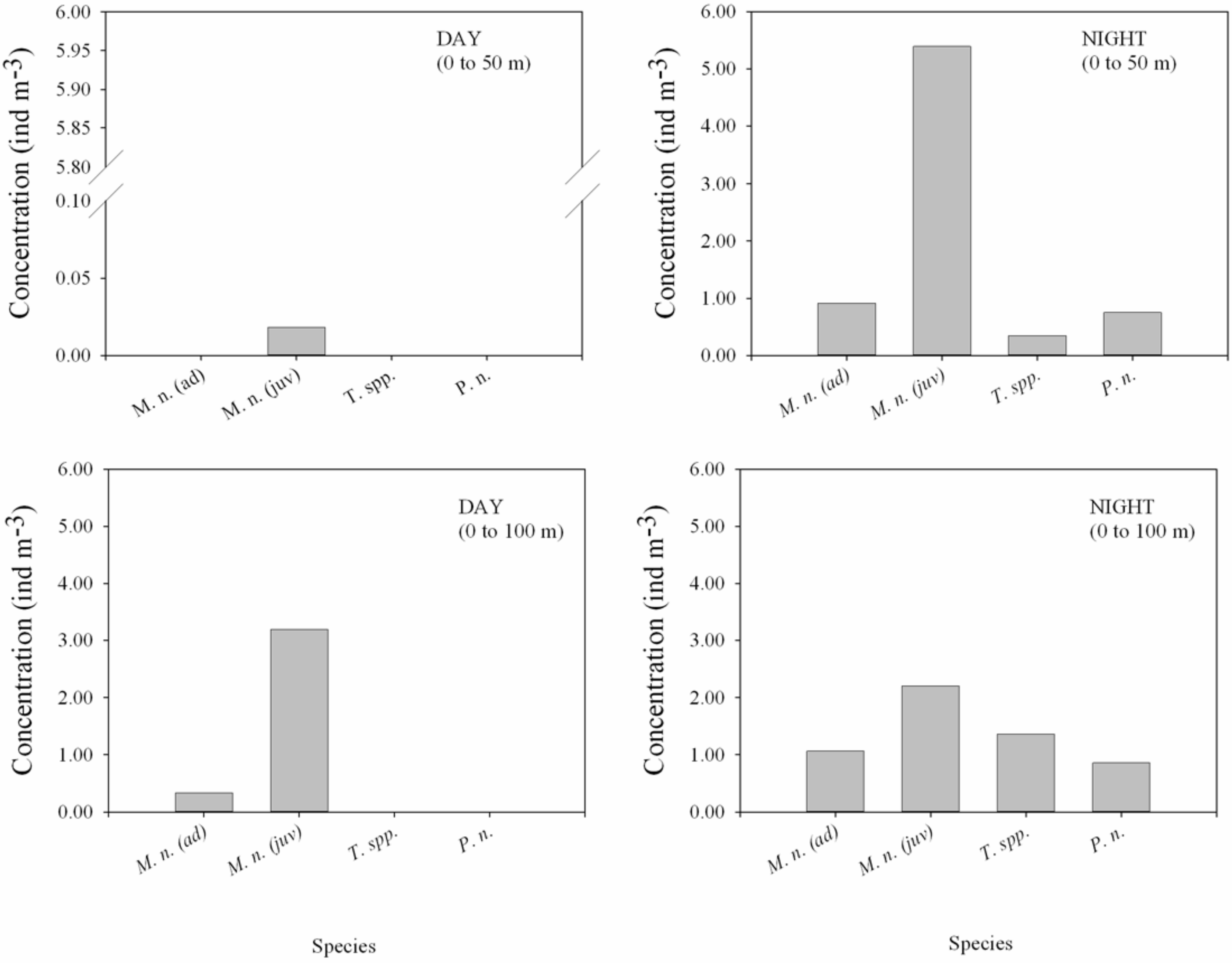
Fig 9: A comparison of the night time depth distribution of S_v (ΔSv of 6-12 dB; lines) and single targets (bars) in each of the 8 transects carried out on 8th and 10th September 2003. The solid line represents the mean S_v of the 2 outward and 2 inward night time surveys, the dashed lines, the minimum and maximum S_v observed over the 4 surveys. The bars represent the sum of all single targets identified during the 4 surveys.

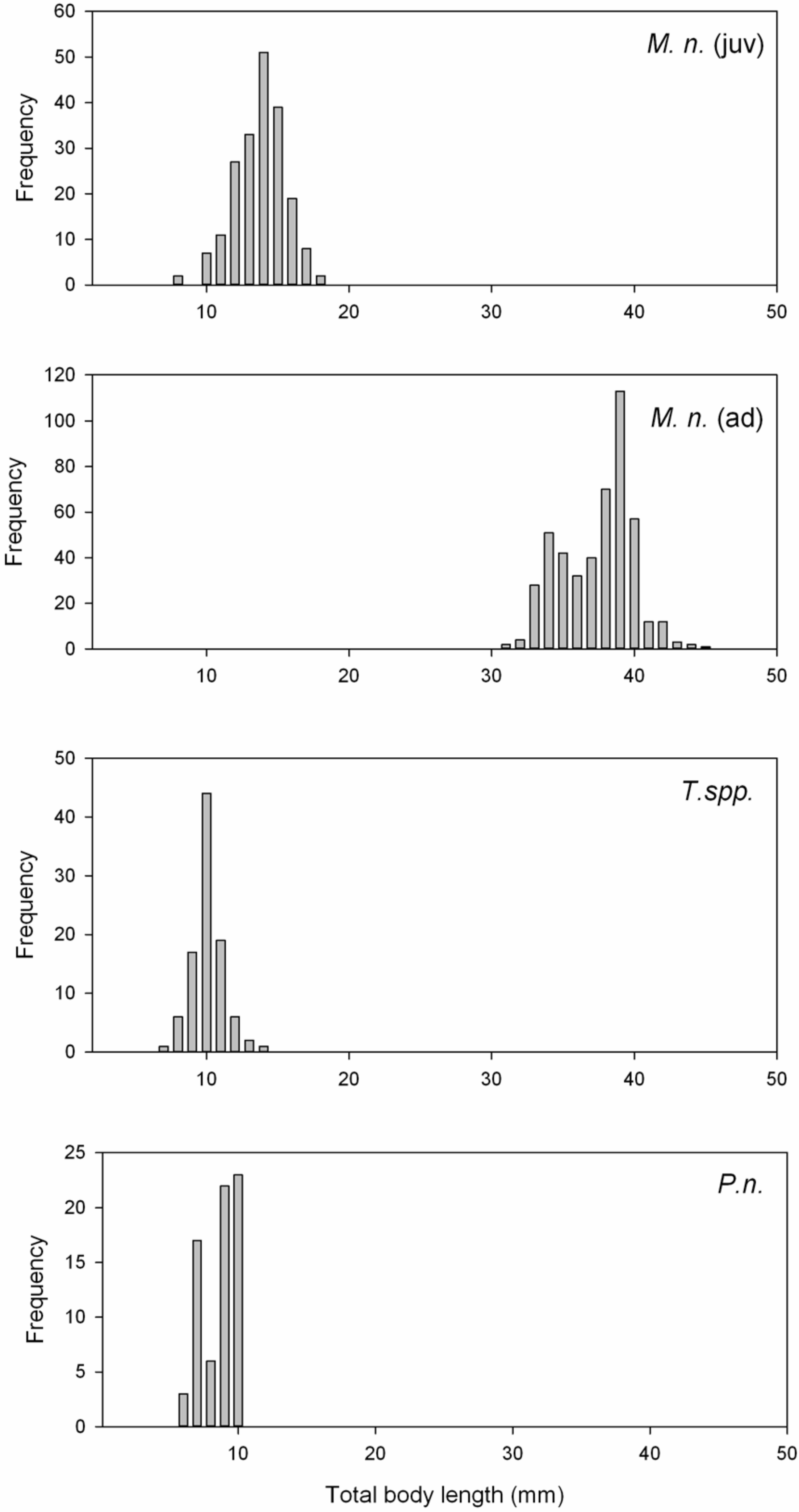
Fig 10: A schematic representation of spatial dynamics of krill and planktivorous fish in Gullmarsfjord during the survey period. Towards the sill mouth, krill migrate to either ~15 m (Chl-a maximum) or ~45 m (resuspended sediment layer). Towards the inner part of the fjord, krill mainly reside at ~15 m Krill feeding in the lower layer have a higher body condition and growth rate. However, this is a riskier layer to occupy given the higher concentration of fish there.

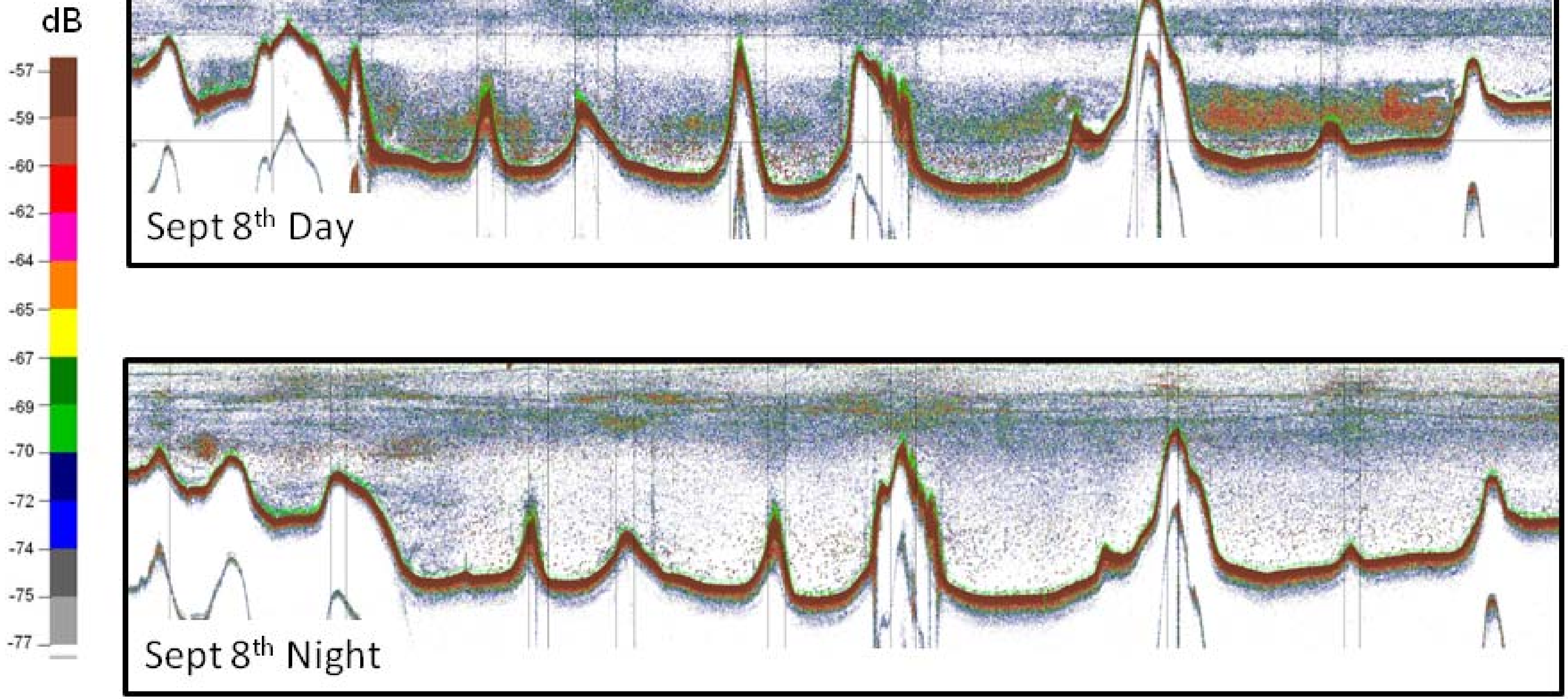

58°22'N
58°20'N
58°18'N
58°16'N
11°24'E
11°28'E
11°32'E
11°36'E
0
5
10
Km
CTD and nets
1
2
3
4
5
6
7
8
10 m
100 m
60°N
50°N
10°E
20°E


Depth (m)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
Units
Temperature (^{o}C)
Salinity

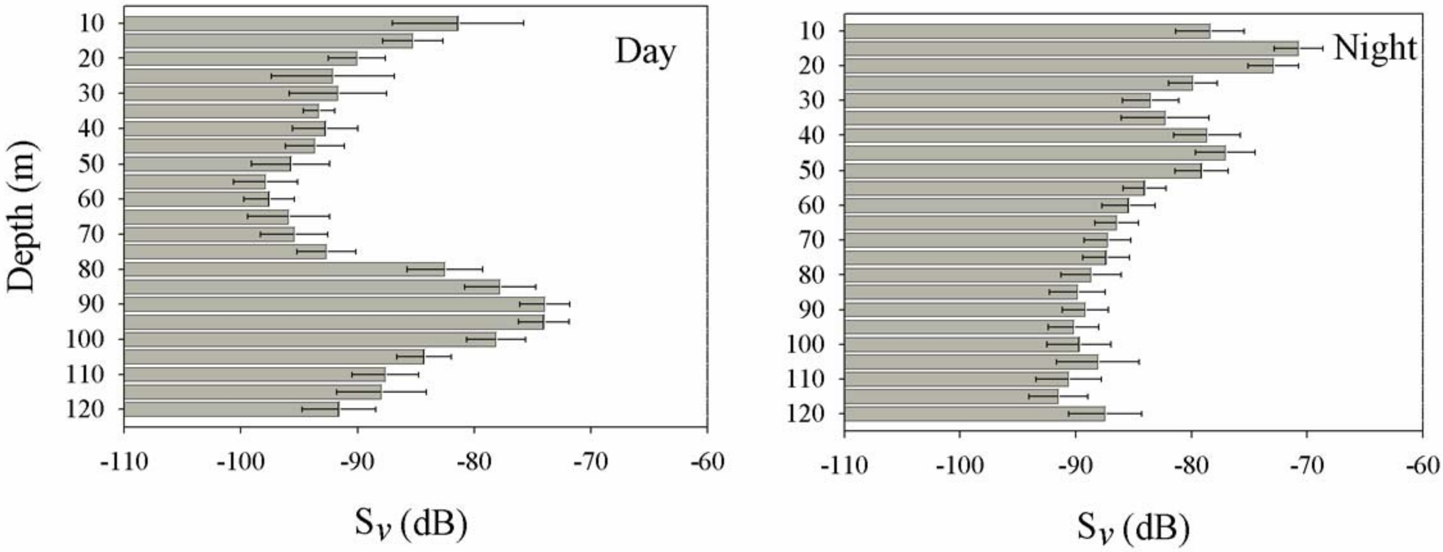

Oxygen saturation (%)
0
20
40
60
80
100
120
Depth (m)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
0
1
2
3
4
5
Chl-a μg l^{-1}
Chl-a Mouth of fjord
Chl-a Upper fjord
Oxygen


DAY
(0 to 50 m)
Concentration (ind m^{-3})
6.00
5.95
5.90
5.85
5.80
0.10
0.05
0.00
M. n. (ad)
M. n. (juv)
T. spp.
P. n.
NIGHT
(0 to 50 m)
Concentration (ind m^{-3})
6.00
5.00
4.00
3.00
2.00
1.00
0.00
M. n. (ad)
M. n. (juv)
T. spp.
P. n.
DAY
(0 to 100 m)
Concentration (ind m^{-3})
6.00
5.00
4.00
3.00
2.00
1.00
0.00
M. n. (ad)
M. n. (juv)
T. spp.
P. n.
Species
NIGHT
(0 to 100 m)
Concentration (ind m^{-3})
6.00
5.00
4.00
3.00
2.00
1.00
0.00
M. n. (ad)
M. n. (juv)
T. spp.
P. n.
Species

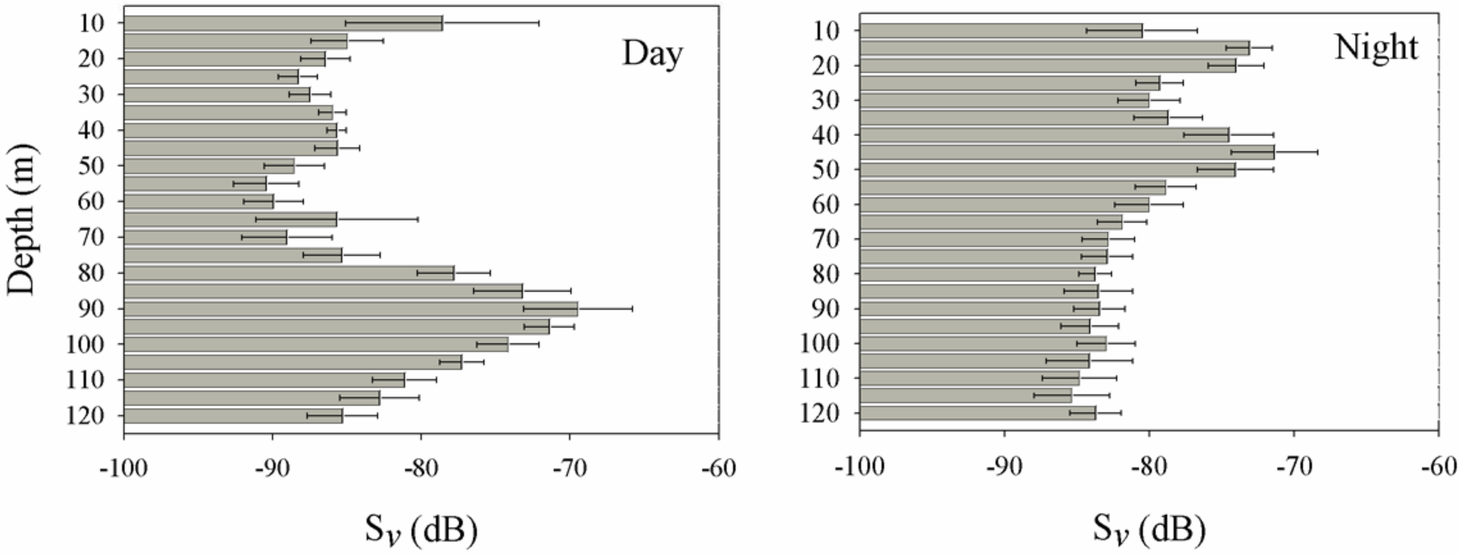

M. n. (juv)
Frequency
0
10
20
30
40
50
60
10
20
30
40
50
M. n. (ad)
Frequency
0
20
40
60
80
100
120
10
20
30
40
50
T.spp.
Frequency
0
10
20
30
40
50
10
20
30
40
50
P.n.
Frequency
0
5
10
15
20
25
10
20
30
40
50
Total body length (mm)

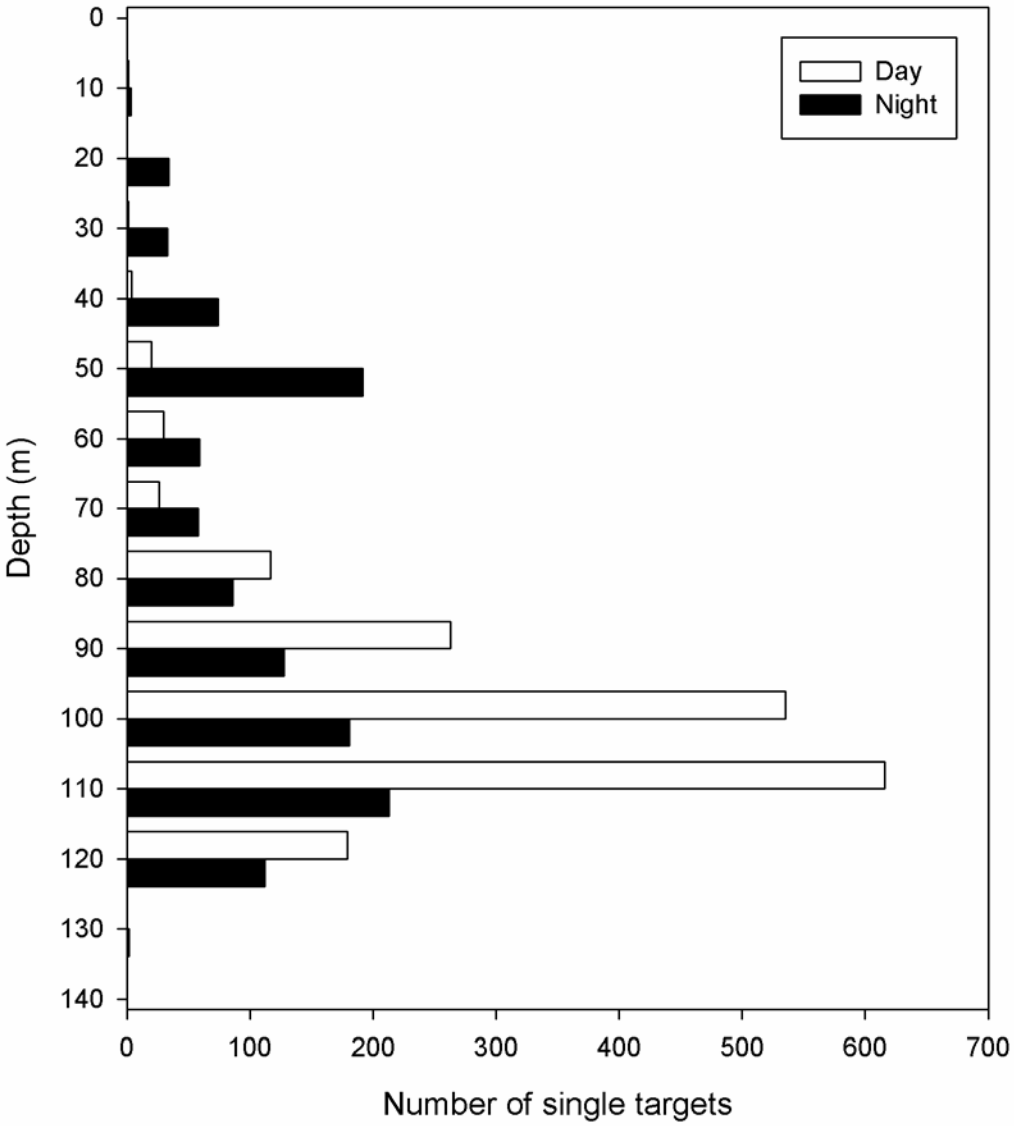

dB
-57
-59
-60
-62
-64
-65
-67
-69
-70
-72
-74
-75
-77
Sept 8th Day
Sept 8th Night

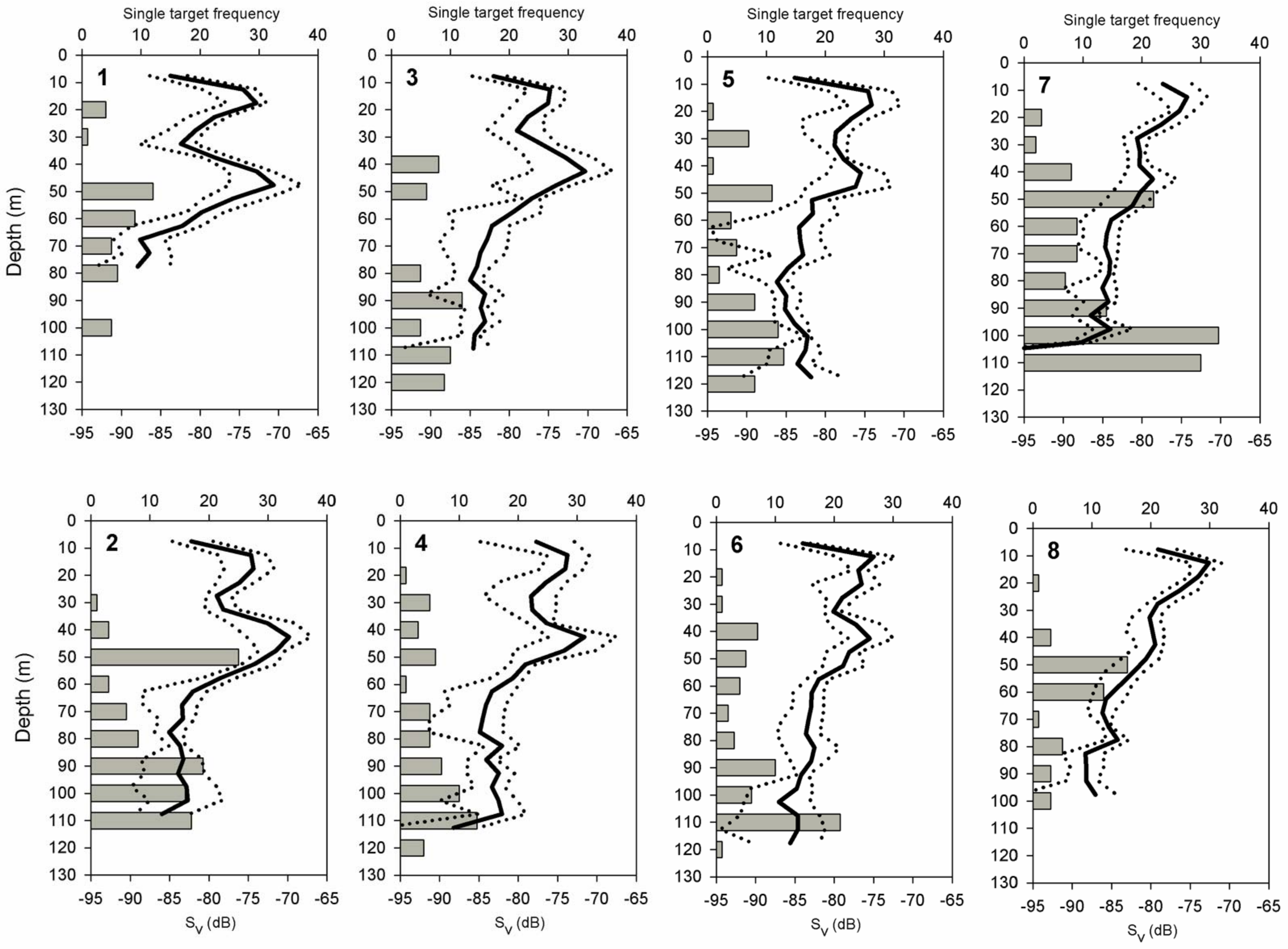
M. norvegica larvae and small euphausiids (12 to 20 dB $\Delta S_{v\ 120\text{-}38\ kHz}$)

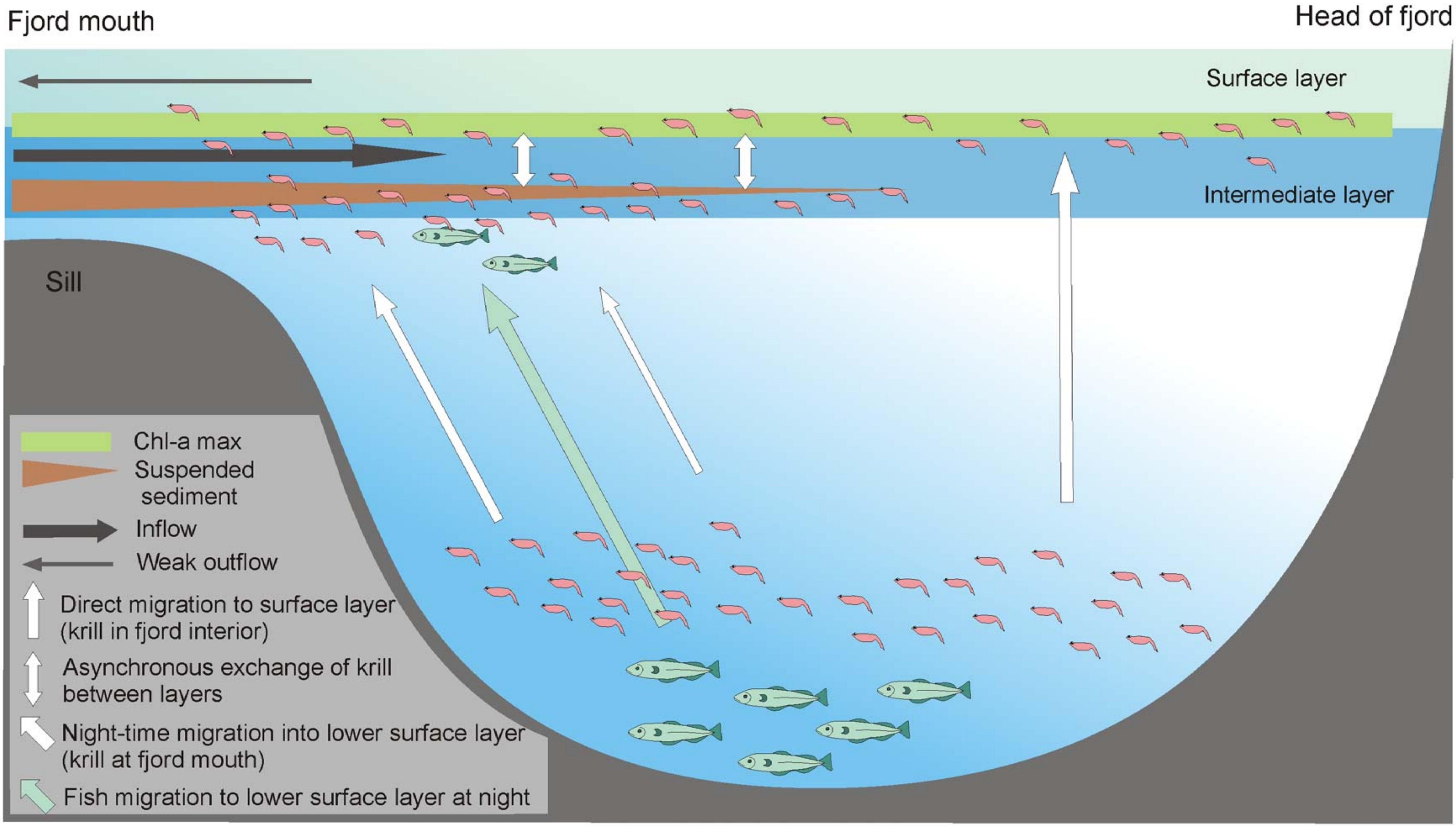


M. norvegica adults (6 to 12 dB $\Delta S_{v\ 120\text{-}38\ kHz}$)




Day
Night
Depth (m)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
0
100
200
300
400
500
600
700
Number of single targets


Single target frequency
0
10
20
30
40
Depth (m)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
-95
-90
-85
-80
-75
-70
-65
S_V (dB)
1
2
3
4
5
6
7
8


Fjord mouth
Head of fjord
Surface layer
Intermediate layer
Sill
Chl-a max
Suspended sediment
Inflow
Weak outflow
Direct migration to surface layer (krill in fjord interior)
Asynchronous exchange of krill between layers
Night-time migration into lower surface layer (krill at fjord mouth)
Fish migration to lower surface layer at night