

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

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Running head: Euphausiid bilayers in Gullmarsfjord

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23

22 **Abstract**

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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

33 bilayer experienced waters that were 4°C cooler than in the upper bilayer, which can decrease  
34 the cost of respiration by around 20%. Accompanying studies have shown significantly  
35 higher growth rates in krill consuming sedimentary organic material and benthic filamentous  
36 algae. When combined with the present study, it appears that energetic benefit and predatory  
37 threat were greatest in the deeper rather than the shallower bilayer in Gullmarsfjord. This is  
38 the reverse of most other euphausiid habitats, where the highest risk and reward is in the  
39 upper bilayer, illustrating that euphausiids adapt their stereotypic vertical migration pattern to  
40 local environmental conditions.

41

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

## 43 **Introduction**

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

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58 Euphausiids (otherwise called 'krill') are prolific vertical migrators (Mauchline & Fisher  
59 1969; Kaartvedt 2010) and this behaviour has been shown to be strongly influenced by their  
60 feeding habits (Ponomareva 1971; Hu 1978; Willason & Cox, 1987). Most euphausiids are  
61 believed to be omnivorous and it has been posited for some time that these animals can only  
62 meet their metabolic requirements through migration (Ohman 1984; McClatchie 1985; Price  
63 et al. 1988). Feeding behaviour does not appear to be stereotypic across all individuals within  
64 krill populations and there can be considerable inter-individual variability in diet, even within  
65 enclosed sites such as Gullmarsfjord, Sweden (Schmidt 2010 Pond et al. 2012). In a study of  
66 Northern krill *Meganyctiphanes norvegica* (M. Sars, 1857) in Gullmarsfjord, Pond et al.

67 (2012) related differences in diet to rates of instantaneous growth and found that individuals  
68 consuming certain food items had significantly higher growth rates. In particular, highest  
69 growth rates were seen in those individuals containing markers for filamentous algae and  
70 terrestrial carbon sources. Neither the algae nor terrestrial sediment are commonly found in  
71 the surface layers of the water column, implying that they must have been consumed either in  
72 the deeper parts of the water column or in the vicinity of the sea-bed interface. In an  
73 accompanying study, Schmidt (2010) found filamentous algae occurred in *M. norvegica*  
74 stomachs mainly during nighttime, when the population was closer to the surface. These  
75 studies illustrate that there is additional complexity to the diel vertical migration pattern of  
76 this species in Gullmarsfjord that has a significant influence on individual performance.

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78 Gullmarsfjord is 28 km long and has an effective sill depth of 43 m and a maximum depth of  
79 ~120 m at about 10 km from the fjord entrance (Arneborg & Liljebladh 2001; Liljebladh &  
80 Thomasson 2001). The density structure is dominated by the coastal stratification which  
81 varies due to the freshwater fluxes from the Baltic. It is typically described by three layers  
82 comprising (i) warm and relatively fresh (salinity (S)=24-27), homogeneous surface water  
83 from the Kattegat, (ii) colder and more saline (S=32-33) intermediate water from the  
84 Skagerrak, and (iii) stagnant basin water which is colder and more saline winter Skagerrak  
85 water (Arneborg et al. 2004). The surface and intermediate waters are separated by a strong  
86 pycnocline at depths varying from 5-20 m (Arneborg & Liljebladh 2001), corresponding to  
87 the S=28 isohaline (Arneborg et al. 2004) and the intermediate and basin waters are separated  
88 by a weaker pycnocline at ~50 m (Arneborg & Liljebladh 2001). Observations of suspended  
89 sediment showed greatest concentrations closest to the seabed with a mid-water maximum in  
90 concentration identified below the halocline at approximately sill depth. Arneborg et al.

91 (2004) considered that this layer comprised either falling organic matter or inflow of turbid  
92 waters from outside the fjord.

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

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

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

120 **Methods**

121

122 *Survey design*

123 The aim of the survey design was to produce a series of acoustic transects running both along  
124 and across the depth contours of the fjord. The chosen design was a zig-zag pattern of eight  
125 transects composed of four transects oriented approximately north/south and four east/west  
126 (Fig. 1). Transects 1,3,5 and 7 constituted the east/west series and 2,4,6 and 8 the north/south  
127 series on each survey. Two surveys were made on each voyage, one in the outbound direction  
128 (from transect 1 to 8) and the other in the inbound direction (from transect 8 to 1). A total of  
129 4 voyages were made between 8<sup>th</sup> and 11<sup>th</sup> September 2003, 2 in the daytime and 2 at night  
130 (Table 1). This made a total of 8 surveys, each with 8 transects over the course of 3 days.  
131 CTDs and net samples were taken at the mid-point of each voyage after completion of the  
132 outbound survey and before the start of the inbound survey.

133 *Environmental data*

134 A G. O. Mark IIIc CTD recorder was used to obtain profiles of conductivity and temperature  
135 at a single site at 58° 19.2' N 11° 32.7' E, the deepest part of the fjord. Oxygen saturation  
136 and Chl-a profiles were obtained from measurements made as part of the ongoing monitoring  
137 programme of the fjord by Kristineberg Marine Research Station using the same CTD plus  
138 water bottle rosette device as above. For oxygen, it was necessary to combine two profiles  
139 from different locations in the fjord to make up a complete profile of the water column.  
140 Measurements of the upper water column (0 to 60 m) were made in the inner Gullmarn (58°  
141 24' N, 11° 38' E) while the deeper water column (60 to 117 m) was measured at Alsbäck  
142 (58° 19' N, 11° 33' E). Both measurements were taken on 3rd September. Chl-a  
143 measurements were taken on 3rd September between the surface and 30 m at Alsbäck and

144 between the surface and 50 m at the mouth of the fjord (58° 17' N, 11° 29' E). Water samples  
145 for Chl-a measurements were taken between 5 and 10 m depth intervals.

146

#### 147 *Net sampling*

148 Oblique net samples were taken with an Isaacs Kidd Midwater Trawl (IKMT) with a one  
149 square metre mouth opening and a mesh size of 1.5 mm. The net was equipped with a  
150 “Scanmar” trawl sensor, to determine net-depth in real time and a calibrated flow-meter, to  
151 measure volume sampled. All net hauls were carried out near to the centre of the deepest part  
152 of the fjord and close to the centre of the acoustic survey area (58° 19.0' N, 11° 32.5' E, Fig.  
153 1). Two hauls were taken on each voyage. One of these hauls went from the surface to within  
154 10 m of the seabed (water depth was around 120 m at the sampling site), the other haul went  
155 from the surface to 50 m.

156 All species of euphausiids as well as the calanoid copepod *Pareuchaeta norvegica* (Boeck,  
157 1872) were enumerated from each catch, with the maturity of each *Meganyctiphanes*.  
158 *norvegica* specimen (i.e. adult or juvenile) also being noted. Random sub-samples of  
159 specimens from each catch were measured to determine length-frequency distributions. For  
160 euphausiids, total length was measured from the front of the eye to the tip of the telson, to the  
161 nearest mm. The length of the cephalothorax was measured to the nearest mm for *P.*  
162 *norvegica*.

163 The cohort structure within length frequency data was analysed using MIX 3.1a (Icthus Data  
164 Systems, Hamilton, Ontario, Canada. Computer program. ). The data was applied without  
165 constraints being placed on fitting the means, standard deviations and proportions to the  
166 length frequency data. A quasi Newton algorithm was used for the fitting procedures. The

167 routines were applied separately to the dominant macrozooplankton components in net  
168 catches: *P. norvegica*, *Thysanoessa* spp, juvenile *M. norvegica*, adult *M. norvegica*.

### 169 *Acoustic hardware and signal processing*

170 A Simrad EK60 scientific echosounder operating at 38 kHz and 120 kHz was used for the  
171 acoustic measurements. This had been installed and maintained on the R/V *Arne Tiselius*  
172 according to the manufacturer's specification at the bottom of the ship's hull, at a depth of 3.7  
173 m. below the waterline. The echosounder was interfaced to a GPS to provide accurate  
174 information on vessel position and speed throughout the study. Calibration of the  
175 echosounder was carried out according to the SIMRAD calibration protocol on 3<sup>rd</sup> September  
176 2003 (see Everson et al. 2007). Raw data were logged onto a PC and backup files made after  
177 each voyage.

### 178 *Post-processing of acoustic data*

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

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

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

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

#### 199 $\Delta S_v$ analysis

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

206 *Masking*: The  $\Delta S_{v120-38}$  was calculated for each cell in the dataset. The values were used to  
207 create two masks. One mask excluded all values except those within a  $\Delta S_{v120-38}$  range of 12 to  
208 20 dB, the other, 6 to 12 dB. Both masks were applied to the 120 kHz data sets only.

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

215  $\Delta S_v$  mask, given that this mask was aimed at revealing smaller individuals with lower  
216 acoustic target strengths.

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

### 223 *Single target analysis*

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

239 **Results**

240

241 *Environmental data*

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

253 Comparing the two salinity profiles obtained at the start (8<sup>th</sup> Sept 2003, 1100) and towards  
254 the end (10<sup>th</sup> Sept 2003, 2300) in Fig. 2 shows that there was no renewal of the deep, basin  
255 water during the survey period. Past studies have shown that this deep water is renewed most  
256 often at yearly intervals (Svansson 1984) although exceptions have occurred. The observed  
257 low level of oxygen saturation (27%) suggests that the deep water had not been renewed for  
258 many months (Fig. 3). Above 60m, salinity increased during the survey period, with the  
259 greatest increases occurring in the halocline region (S = 28 – 32) separating the upper and  
260 intermediate layers. The bottom of this halocline (indicated by horizontal lines) ascended by  
261 ~5 m during the survey. The lower halocline remains relatively static at a depth of ~ 55 m.  
262 There was relatively little change in the salinity of the surface water.

263 *Net samples*

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

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

280 *ΔS<sub>v</sub> analysis*

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

287 *Vertical distribution:* There was a clear vertical migration from deeper layers in the daytime  
288 to upper layers in both the 12 to 20 dB and the 6 to 12 dB  $\Delta S_v$  ranges (Fig. 7). The peak layer  
289 of backscatter during the daytime was at 90 m while, at night, it separated into two peaks at  
290 15 m and 45 m. The relative strength of these two peaks was significantly different between  
291 the two  $\Delta S_v$  ranges (Chi-squared 24.39,  $\nu=1$ ,  $P<0.001$ ), with the strongest peak in the 12 to 20  
292 dB  $\Delta S_v$  range being at 15 m, while that in the 6 to 12 dB  $\Delta S_v$  range was at 45 m. Given that  
293 *M. norvegica* adults are likely to be the main contributor to  $S_v$  in the 6 to 12 dB  $\Delta S_v$  range,  
294 this suggests that they were more likely to be present in the deeper of the two upper scattering  
295 layers than juvenile *M. norvegica*, *Thysanoessa* spp. and *P. norvegica*.

#### 296 *Single target analysis*

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

#### 306 *Vertical distribution patterns along the fjord axis*

307 Fig. 9 combines the results of the 6 -12 dB  $\Delta S_{v120-38}$  analysis (distinguishing adult Northern  
308 krill) with the single target analysis (distinguishing fish) for each of the 8 transects taken  
309 along the fjord axis during the 2 night-time surveys. It shows that the night-time vertical  
310 distribution of both the 'krill-like' scatterers and the 'fish-like' targets altered depending on  
311 their location in the fjord. In terms of the krill-like scatterers, there was a distinct bilayer

312 distribution pattern in the majority of transects, with the depth of layers relatively invariant  
313 between transects, the upper layer located around 15 m and the lower layer around 45 m.  
314 However, the relative scattering strengths of these layers did alter between transects. Close to  
315 the sill (transects 1, 2 and 3), the scattering strength of the lower layer was 2-4 dB greater  
316 than the upper layer (-69.8 to -70.6 dB lower layer, -72.9 to -74.8 dB upper layer). At the  
317 mid-point in the fjord axis (transects 4, 5 and 6), the scattering strength of both layers was  
318 relatively similar (-71.6 to -75.5 dB lower layer, -73.7 to -74.9 dB upper layer). Towards the  
319 head of the fjord (transects 7 and 8), only the upper layer was readily apparent (-72.6 to -74.3  
320 dB) with the lower layer being barely distinguishable above background levels (-79 dB).

321 In terms of fish-like targets, an average of 72% (SD 28%) remained at 70 m or deeper during  
322 the night-time, with there being no particular spatial trend as to where the highest and lowest  
323 proportions occurred. Of those targets that had migrated upwards, the strongest  
324 concentrations were seen at the same depth as the lower  $\Delta S_v$  scattering layer, at around 40 to  
325 50 m. These depths accounted for an average of 58% (SD 34%) of all targets above 70 m. An  
326 average of 26% (SD 34%) of fish-targets above 70 m were located in the upper  $\Delta S_v$  scattering  
327 layer.

328 With respect to the overlap between the fish-like and krill-like targets, between 26% and 28%  
329 of the biomass of these two groups co-occurred in the 40-50 m depth layer in transects 1 and  
330 2, close to the mouth of the fjord. This overlap declined further in to the fjord, with between  
331 10 and 15% co-occurring in the 40-50 m depth layer in transects 3, 4 and 5, dropping further  
332 to 8% at the head of the fjord (transect 8). Overall, the greatest overlap in krill- and fish-like  
333 targets was seen towards the mouth of the fjord, where the deep krill layer was most  
334 prominent.

335

## 336 **Discussion**

337

338 Our surveys provide a spatially resolved description of the day and night vertical distributions  
339 of acoustic scattering layers and single targets over a large area of Gullmarsfjord. Through  
340 applying dB difference techniques to the acoustic data, we were able to partition acoustic  
341 scattering into smaller and larger zooplankton categories, with the assumption that the former  
342 mainly consisted of juvenile *Meganyctiphanes norvegica* and some *Thysanoessa* spp. and the  
343 latter, adult *M. norvegica*. The surveys ascertained that both the small and large categories  
344 occupied two upper depth layers during night-time, one at around 15 m and the other around  
345 45 m. The smaller zooplankton category was generally more concentrated in the upper  
346 scattering layer while the larger zooplankton category was more concentrated in the deeper  
347 scattering layer. The deeper scattering layer was most prominent towards the sill end of the  
348 fjord and became almost indistinguishable towards the head of the fjord. The upper scattering  
349 layer remained present throughout the length of the fjord. During daytime, both the smaller  
350 and larger zooplankton categories resided in one layer, between 80 and 100 m. The depth of  
351 fish, determined through single target analysis, was mainly around 110 m during the day. By  
352 night, only around half of the fish were found above 70 m, of which most were concentrated  
353 between 40 and 50 m. Very few fish were found above 30 m during night and none during  
354 the day.

### 355 *Species contribution to acoustics patterns*

356 Two pieces of evidence point to *Meganyctiphanes norvegica* being the principal contributor  
357 to the scattering observed in the 12 to 20 dB and 6 to 12 dB  $\Delta S_v$  ranges. Firstly, this species  
358 was the most abundant macrozooplankton in net catches. Secondly, the vertical distribution  
359 of the 12 to 20 dB and 6 to 12 dB  $\Delta S_v$  ranges showed a close resemblance to those described  
360 for this species by other net catches and acoustic studies in this region. For instance,

361 Liljebladh & Thomasson (2001) found *M. norvegica* in this fjord occupied layers between 70  
362 m and 90 m during the day and 10 m to 30 m at night, during the period August and October  
363 1997. Spicer et al. (1999) found a similar daytime distribution.

364 We used acoustic information to distinguish between different size classes of euphausiid,  
365 principally adult *M. norvegica*, with a size range of 30 mm to 45 mm total body length, and  
366 juveniles, which ranged from 10 mm to 20 mm total body length. To distinguish adult *M.*  
367 *norvegica*, we masked out all data apart from that within a  $\Delta S_{v120-38 \text{ kHz}}$  range of 6 to 12 dB.  
368 Empirical experiments by Foote et al. (1990) on Antarctic krill between 30 mm and 39 mm  
369 found TS values of  $-85.1 \text{ dB}$  at 38 kHz and  $-76.1 \text{ dB}$  at 120 kHz, giving a difference of 9 dB  
370 between the two frequencies. Our application of  $\pm 3 \text{ dB}$  to this value allows for the range in  
371 TS values reported by Foote et al. (1990) of around 6 dB. Such variance is probably a product  
372 of changing orientation (Everson 1982). The 6 to 12 dB  $\Delta S_v$  applied here is narrower than the  
373 2 to 12 dB  $\Delta S_v$  range used in acoustic studies of Antarctic krill (Watkins and Brierley 2002).  
374 Everson et al. (2007) found that the wider  $\Delta S_v$  range was more likely to produce erroneous  
375 results when applied to *M. norvegica*. This may be a result of the smaller maximum size of  
376 *M. norvegica* (50 mm) compared with 65 mm for Antarctic krill (Mauchline 1977) and also  
377 planktivorous fish falling within the 2 to 12 dB  $\Delta S_v$  range (Martin Collins, personal  
378 communication).

379 A  $\Delta S_{v120-38 \text{ kHz}}$  range of 12 to 20 dB was used to identify juvenile *M. norvegica* and  
380 *Thysanoessa* spp. There has been little work on the target strength of juvenile euphausiids.  
381 One of the few estimates available is from stochastic distorted-wave Born approximation  
382 (SDWBA) models (Demer & Conti 2003, 2004) that, although focussing on adult krill, allow  
383 extrapolation to smaller sizes. Nevertheless, some caution is required in extrapolating these  
384 models too far outside the adult Antarctic krill size range for which they were originally

385 parameterised. In Demer & Conti (2004), an extrapolation to a minimum size of 20 mm total  
386 length was carried out, for which the predicted difference in TS between 38 kHz and 120 kHz  
387 was around 14 dB. Our  $\Delta S_v$  range of 12 to 20 dB allowed for the fact that many juvenile *M.*  
388 *norvegica* in the present study had a total length of 15 mm or shorter. Further development of  
389 target strength models focussing on smaller krill would benefit this area of research and allow  
390 appropriate  $\Delta S_v$  ranges to be further refined.

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

401 Our identification of fish was based on acoustic characteristics alone, since carrying out  
402 accompanying fish-trawling operations was not possible. A threshold of -50 dB at 38 kHz  
403 was set to ensure that smaller targets like krill (with TS of -85 dB at 38 kHz) were not  
404 included in our single target analysis. The peak TS of single targets in this study was -46 dB,  
405 and maximum TS, approximately -28dB. Assuming these targets are gadoid fish, their  
406 equivalent length (L, cm) can be estimated from the following equation, derived by Foote  
407 (1987):

408

409  $TS = 20 \log L - 67.4$

410

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

413 The size and the behaviour of these targets are characteristic of benthopelagic fish species  
414 such as Norway pout *Trisopterus esmarkii* (Nilsson, 1855) and cod *Gadus morhua* Linnaeus,  
415 1758. Both species are a common component of benthic trawls carried out in the adjacent  
416 Skagerrak (Poulsen 1968; Albert 1994). Furthermore, like the acoustic patterns, they have  
417 been found to leave their daytime habitat in the epibenthic zone to migrate vertically into the  
418 mid to upper layers at night (dos Santos & Falk-Petersen 1985; Kaartvedt et al. 1996;  
419 Torgersen et al. 1997; Onsrud et al. 2004). *Meganyctiphanes norvegica* are a common  
420 constituent of the diet of Norway pout and cod, with the gut contents of some individuals  
421 showing exclusive consumption of krill (Pearcy et al. 1979; Asthorsson & Palsson 1987;  
422 Onsrud et al. 2004).

#### 423 *Factors influencing the nighttime bilayered structure*

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

#### 428 I) Pycnocline as a physical barrier

429 The temperature and salinity profiles from the CTD data show that the hydrography of  
430 Gulmarsfjorden during the period of the study conformed to the well-described three layer  
431 structure. Temperatures in the surface brackish layer (salinity of 24) and intermediate layer

432 down to 30 m (salinity between 25 and 32) were uniformly 17°C, after which there was a  
433 strong thermocline down to 60 m. Therefore, compared to the upper bilayer, which was  
434 located in waters that were 17°C, the prevailing temperature in the lower bilayer was 5°C  
435 cooler, at 12°C, while salinity differed by ~6 units between the 2 layers (26.5 and 32.3 for  
436 upper and lower bilayers respectively).

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

455 A steep salinity gradient to a minimum of 24 occurred above 15 m. Forward & Fyhn (1983)  
456 found the lower lethal limit of *M. norvegica* to occur at 20-24 salinity units. Buchholz et al.  
457 (1995) studied DVM in *M. norvegica* in the nearby Kattegat and considered the surface  
458 brackish layer to be of little importance in determining the pattern of migration. Harvey et al.  
459 (2009) considered the vertical migration of both *M. norvegica* and *T. raschii* in the St  
460 Lawrence estuary and Gulf of St Lawrence and found that both species were capable of  
461 migrating into the low salinity surface layers, although there was a tendency for *M. norvegica*  
462 to be located a little deeper than *T. raschii* at some, but not all, times of year. The bilayer  
463 structure in the present study is located well below the steep salinity gradients in the surface  
464 water and we conclude that it was not an important influence on the pattern of vertical  
465 distribution of these two species.

## 466 II) Metabolic advantages of different bilayers

467 The clear relationship between respiration rate and temperature in marine zooplankton (Ikeda  
468 1985) suggests an adaptive value in moving up and down between vertical temperature  
469 gradients in order to gain maximum metabolic advantage. The different temperatures  
470 experienced in the two bilayers is likely to have an influence on respiration rate and overall  
471 energy expenditure. Saborowski et al. (2000, 2002) found that Northern krill from the  
472 Kattegat, the Clyde Sea, and the Ligurian Sea all exhibited approximately the same level of  
473 oxygen consumption ( $30\text{--}35 \mu\text{mol O}_2 \text{ g}^{-1} \text{ dry wt h}^{-1}$ ) when incubated at the ambient  
474 temperatures found in their respective environments ( $9^\circ\text{C}$ ,  $5^\circ\text{C}$ , and  $12^\circ\text{C}$ ) indicating that krill  
475 adjust their overall metabolic rates to the prevailing thermal conditions. Nevertheless, when  
476 moved rapidly between temperatures (within the range  $4$  to  $16^\circ\text{C}$ ), oxygen consumption  
477 increased exponentially with increasing experimental temperature with rates rising to  $89.9 \text{ } 35$   
478  $\mu\text{mol O}_2 \text{ g}^{-1} \text{ dry wt h}^{-1}$ .

479

480 Assuming that the physiological capabilities of Northern krill in Gullmarsfjord are the same  
481 as those in the nearby Kattegat, individuals occupying the lower bilayer (12°C) would have a  
482 respiration rate of  $50 \mu\text{mol O}_2 \text{ g}^{-1} \text{ dry wt h}^{-1}$ , whereas those in the upper bilayer (16°C)  
483 would reach a rate of  $70 \mu\text{mol O}_2 \text{ g}^{-1} \text{ dry wt h}^{-1}$ . Accordingly, there would be a 20% saving  
484 in metabolic rate through occupying the lower bilayer during the nighttime phase.  
485 Nevertheless, overall energetic balance by these individuals will only be achieved if a  
486 suitable food source is also found.

487

### 488 III) Vertical and spatial distribution of food

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

496 Previous surveys have shown that there is often an inflow of new Skagerrak water across the  
497 sill and into the intermediate layer of Gullmarsfjord (Arneborg et al. 2004), which was  
498 probably the case during the period of the present surveys given that the upper halocline  
499 ascended by 5 m between the 8<sup>th</sup> and 10<sup>th</sup> September. Furthermore, given the observations of  
500 Arnerborg et al. (2004), it is very likely that such an inflow will be accompanied by an influx  
501 of biogenic material, derived from the coastal waters or resuspended from the sill, into the  
502 intermediate water layer. An exchange of intermediate water will generally propagate to the

503 head of the fjord but the biogenic material brought into the fjord will tend to settle out at the  
504 base of the intermediate layer at ~45 m, with a greater concentration found towards the sill.  
505 This will give rise to bilayers of varying biogenic character. Organic matter produced in the  
506 surface water of the fjord will tend to settle onto the top of the upper halocline at ~20 m,  
507 while that advected into the sill in the inflowing coastal waters will tend to settle out closest  
508 to the sill at ~45 m. Both of these regions will provide a food-rich layer for feeding, though  
509 the quantity of material in the lower layer will decay with distance from the sill, by virtue of  
510 the fact that it is an advected source rather than a locally produced source.

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

527 its deepest phase during the day, making benthic feeding unlikely in the majority of  
528 individuals. Filamentous algae was most likely consumed when it was suspended after being  
529 washed in from the sill.

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

#### 544 IV) Risk of predation

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

551 In considering patterns of vertical migration and the exchange of individuals between  
552 bilayers, Ohman (1990) proposed that sinking was mainly a means by which to avoid  
553 predation. However, whether it is a result of an entrained behaviour or an immediate response  
554 to the perception of predatory threat has remained difficult to determine in the marine  
555 environment. De Robertis et al. (2003) found that the presence of a fish at distances of 20–  
556 300 cm did not affect the swimming speed or turning of the euphausiids, suggesting that they  
557 did not respond to the presence of a potential predator at these distances. Similarly, in a study  
558 of a sea-bed environment in the Faroe-Shetland Channel, Hirai & Jones (2012) found no  
559 correlation between sites of higher or reduced predation pressure and the concentration of  
560 Northern krill. Therefore, in the present study, it is likely that the krill occupying this lower  
561 bilayer do not perceive or respond to the higher predation risk they encountered, and selected  
562 their environment mainly on the detection of food resources.

563 From the perspective of the planktivorous fish, it is evident firstly that only around 40%  
564 appear to be in the water column as opposed to the epibenthic layer at any one time during  
565 the night, while by day, they all are concentrated towards the bottom. The pattern may be the  
566 result of upward forays made by different individuals at different times through the night or,  
567 alternatively, by individuals migrating every 2<sup>nd</sup> or 3<sup>rd</sup> night. Secondly, of those individuals  
568 that did make an upward migration, the upper migration limit was at the lower rather than  
569 upper bilayer. This pattern may be the result of a combination of factors. Firstly, the fact that  
570 older, larger, more lipid-rich euphausiids are located in the lower bilayer makes this a more  
571 profitable food patch on which to focus foraging efforts. This is similar to Wishner et al.  
572 (1995), who reported that whales were most likely to be found around copepod aggregations  
573 containing older life stages. Secondly, such planktivores will themselves have predators  
574 searching by sight (Kaartvedt et al. 2005). Therefore, the risk of upward migrations from the

575 epibenthic layer is minimised by only performing them at night, limiting the number of  
576 forays made and only venturing to mid rather than upper water column depths.

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

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

#### 595 *Concluding remarks*

596 Variance in the diel vertical migration behaviour in *Meganyctiphanes norvegica* has been  
597 widely document (Kaartvedt 2010). Balino & Aksnes (1993), for instance, found that *M.*  
598 *norvegica* ascended to the surface at one location but remained below 40 m at another

599 location within the same fjord. However, few studies have demonstrated the consequences of  
600 such variability on life-cycle parameters such as growth. This study, combined with the  
601 accompanying observations reported by Schmidt (2010) and Pond et al. (2012), describe not  
602 only variability in DVM patterns over small spatial scales and between different life-stages,  
603 but also how this pattern relates both to the feeding and predation environments. In turn, it  
604 reveals a situation that is the reverse of the standard explanation for the formation of bilayers  
605 in vertical distribution, in that the most rewarding and risky environments were in the lower  
606 rather than upper bilayer. It is a demonstration of the plastic response to the risk reward  
607 environment that has been predicted by a number of models examining the factors controlling  
608 diel vertical migration behaviour (Clark & Levy 1988; Mangel & Clark 1988; Ohman 1990;  
609 Fiksen & Giske 1995; Fiksen & Carlotti 1998).

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623

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	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

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823

824

825 Table 1: The timings of the 8 surveys carried out between 8<sup>th</sup> and 11<sup>h</sup> September 2003. All  
826 times are in Universal Time Coordinated (UTC). Local celestial times are ahead of UTC by  
827 46 minutes.

828

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

830

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

834

835

836

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

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837

838

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

844

845

## 846 **Figures**

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

849 Fig 2: Temperature and salinity profiles in Gullmarsfjord ( $58^{\circ} 19.2'N$   $11^{\circ} 32.7'E$ ) taken at  
850 11:00 on 8<sup>th</sup> September 2003 (thick line) and at 23:00 on 10<sup>th</sup> September (thin line).  
851 Horizontal line indicates the depth of the halocline on 8<sup>th</sup> Sept. (thick line) and 10<sup>th</sup> Sept. (thin  
852 line)

853 Fig 3: Chl-a and O<sub>2</sub> profiles in Gulmarsfjord on 3<sup>rd</sup> September 2003. Chl-a measurements  
854 were taken close to the CTD/net sampling station at Alsbäck ( $58^{\circ} 19'N$   $11^{\circ} 33'E$ , 0 to 30 m)  
855 and also at the mouth of fjord ( $58^{\circ} 17'N$   $11^{\circ} 29'E$ , 0 to 50 m). O<sub>2</sub> measurements between 0  
856 and 60 m were made at inner Gullmarn ( $58^{\circ} 24'N$   $11^{\circ} 38'E$ ), and between 60 and 117 m at  
857 Alsbäck.

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

862  
863 Fig 5: Length-frequency of *Meganyctiphanes norvegica* adults (*M. n. (ad)*), juvenile *M.*  
864 *norvegica* (*M. n. (juv)*), *Thysanoessa spp.* (*T. spp*) and *Euchaeta norvegica* (*P. n.*)

865  
866 Fig 6: Backscatter ( $S_v$ , dB) extracted from the 120 kHz acoustic data collected during the  
867 outward daytime and nighttime surveys on 8<sup>th</sup> September 2003. The divisions in the profiles  
868 demark the extent of the 8 transects, as show on Fig. 1. The steep changes in topography at

869 the ends of each transect reflect the shallowing at the edges of the fjord. A threshold of  $-77$   
870 dB was applied.

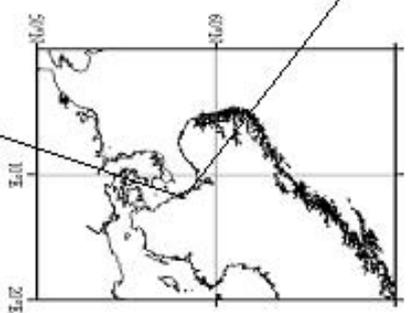
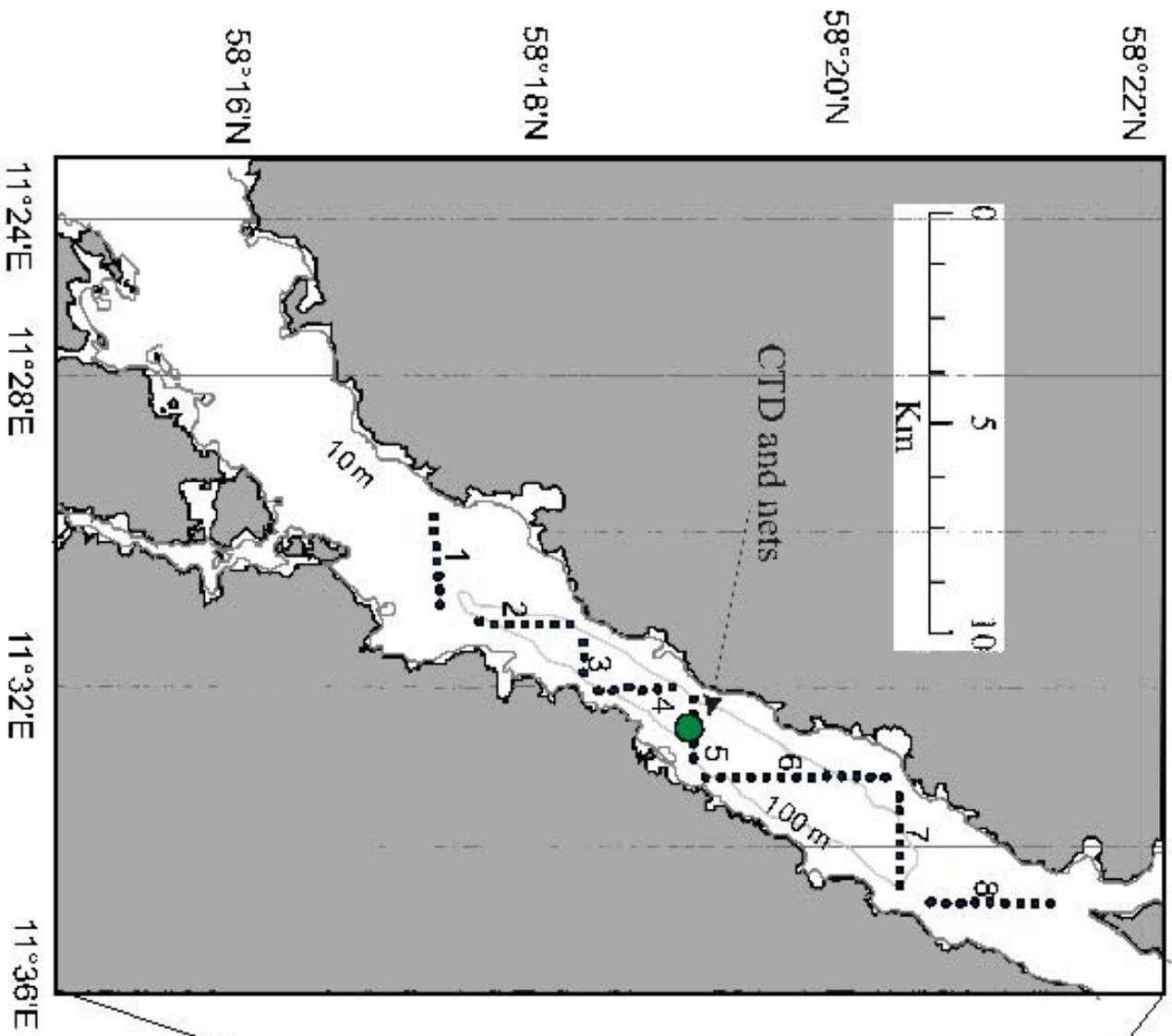
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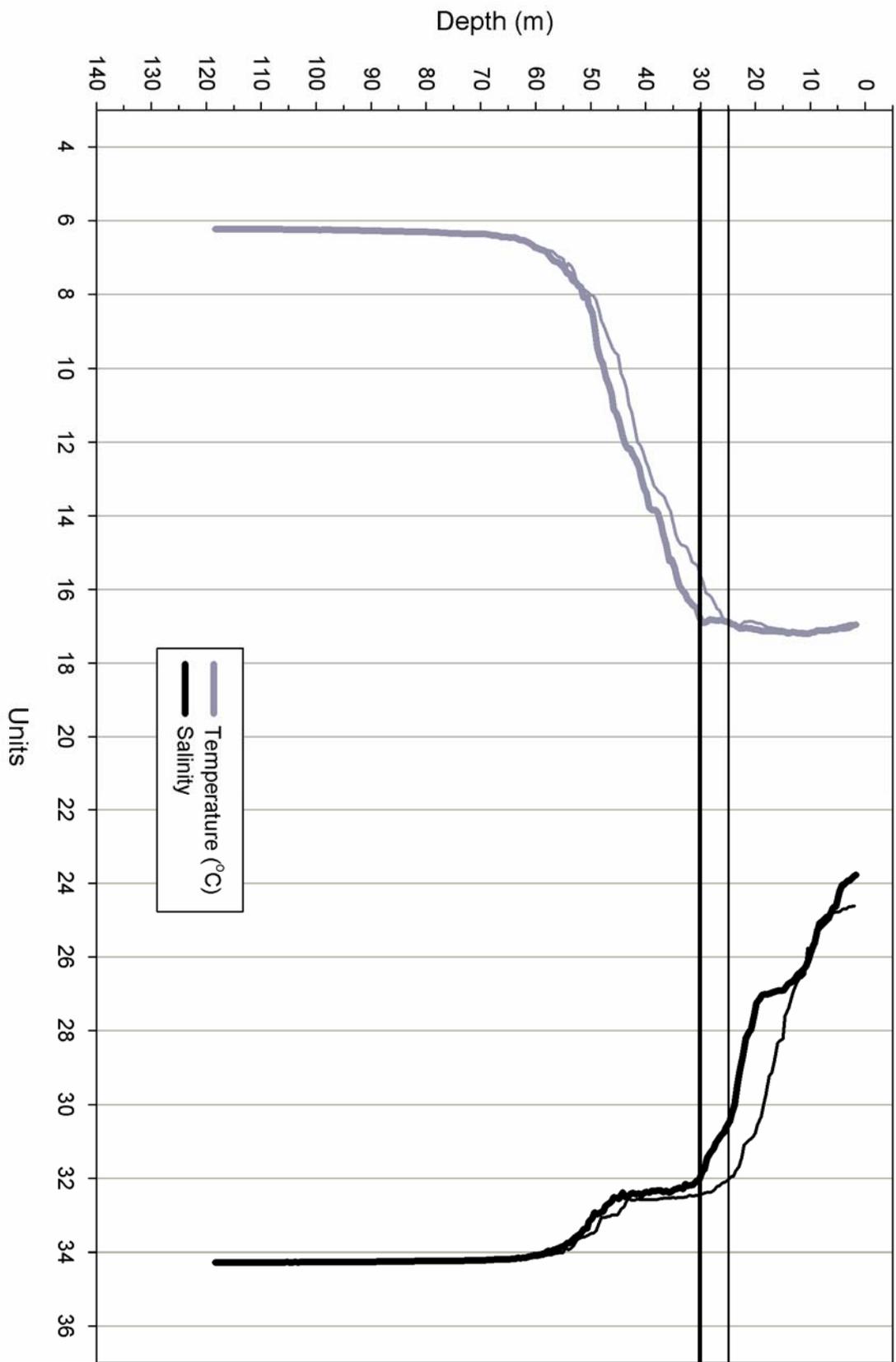
872 Fig 7: Vertical profiles of mean  $S_v$  (dB) of the two  $\Delta S_v$  120 – 38 kHz components (upper: a  
873  $\Delta S_v$  of 12-20 dB for which larval *Meganyctiphanes norvegica* and small euphausiids were  
874 the most likely scatterers; lower: a  $\Delta S_v$  of 6-12 dB for which adult *M.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

878 Fig 8: The vertical distribution of single targets during day and night. Data from 8<sup>th</sup>  
879 and 10<sup>th</sup> September surveys were combined

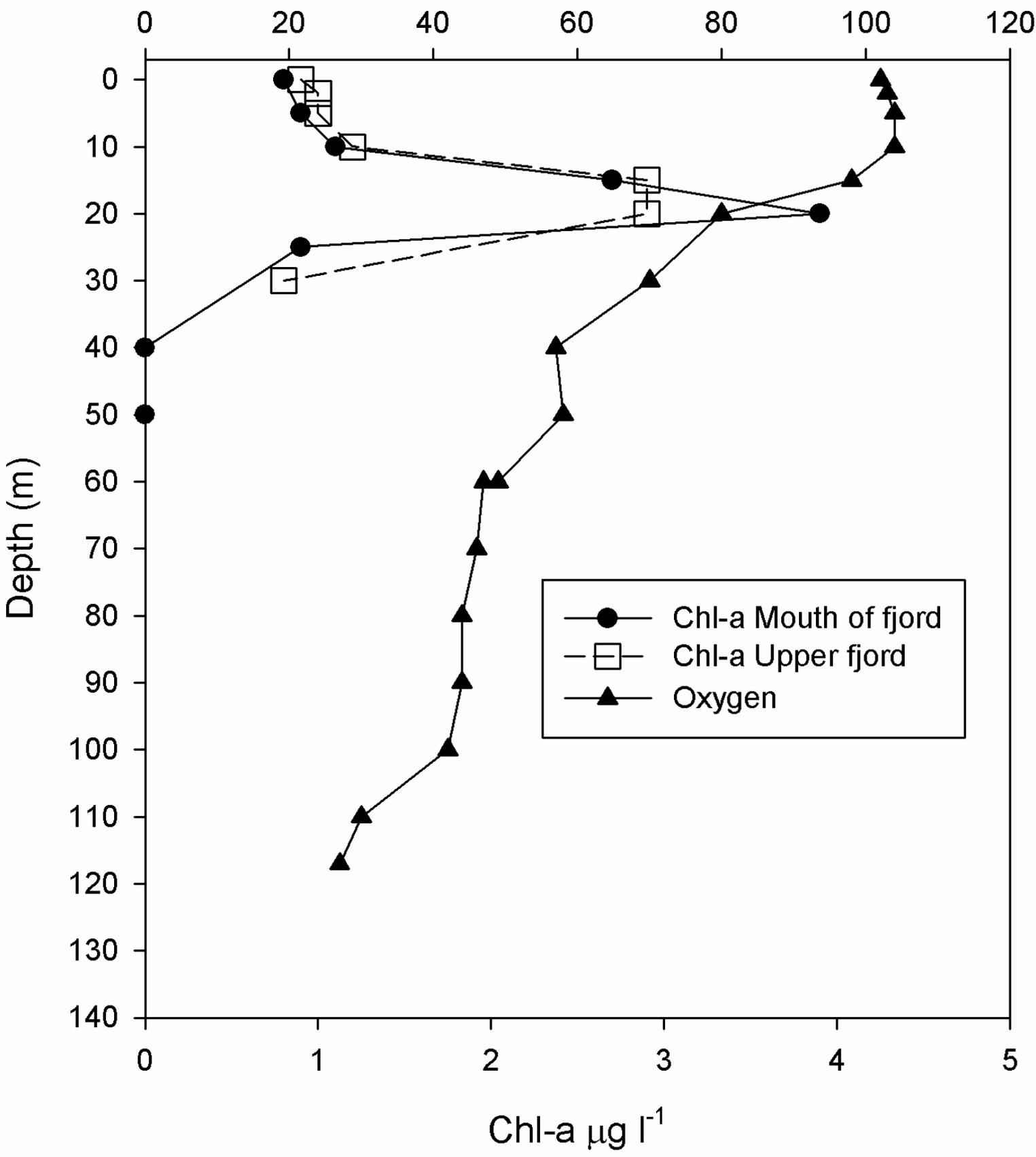
880 Fig 9: A comparison of the night time depth distribution of  $S_v$  ( $\Delta S_v$  of 6-12 dB; lines) and  
881 single targets (bars) in each of the 8 transects carried out on 8<sup>th</sup> and 10<sup>th</sup> September 2003. The  
882 solid line represents the mean  $S_v$  of the 2 outward and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

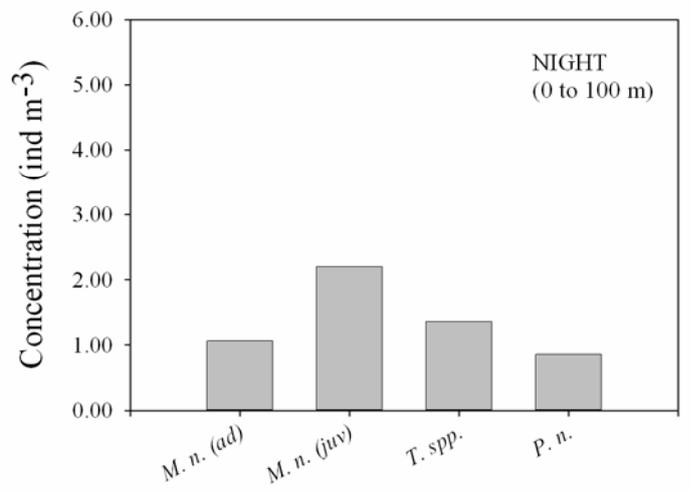
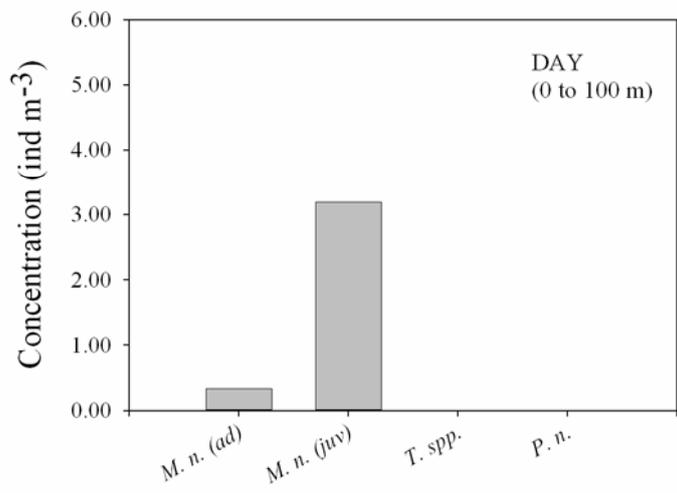
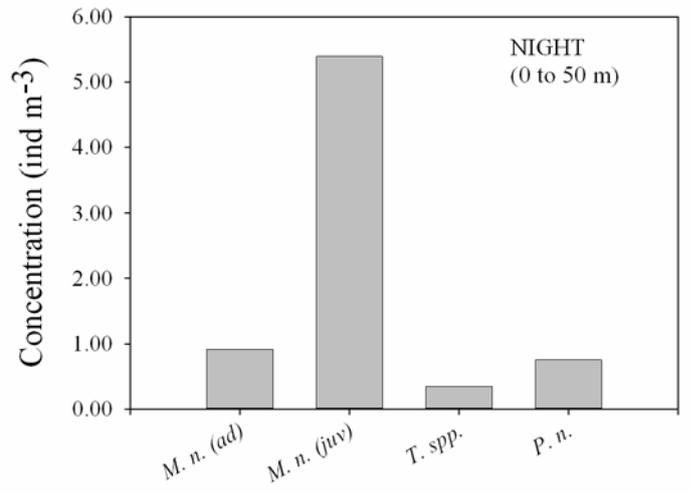
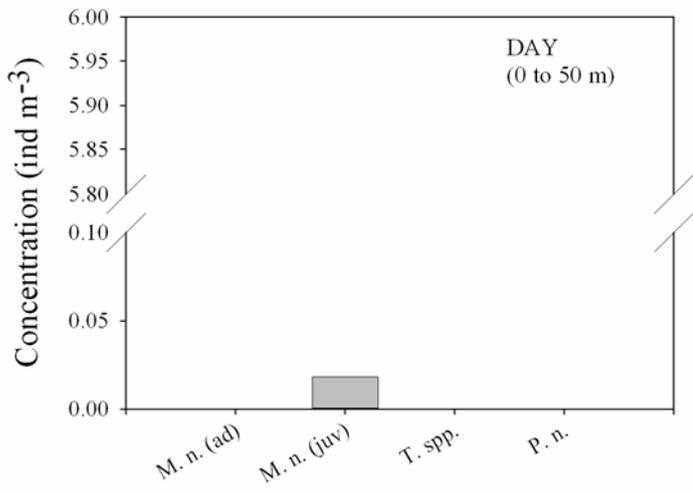
885 Fig 10: A schematic representation of spatial dynamics of krill and planktivorous fish  
886 in Gullmarsfjord during the survey period. Towards the sill mouth, krill migrate to either  $\sim 15$   
887 m (Chl-a maximum) or  $\sim 45$  m (resuspended sediment layer). Towards the inner part of the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





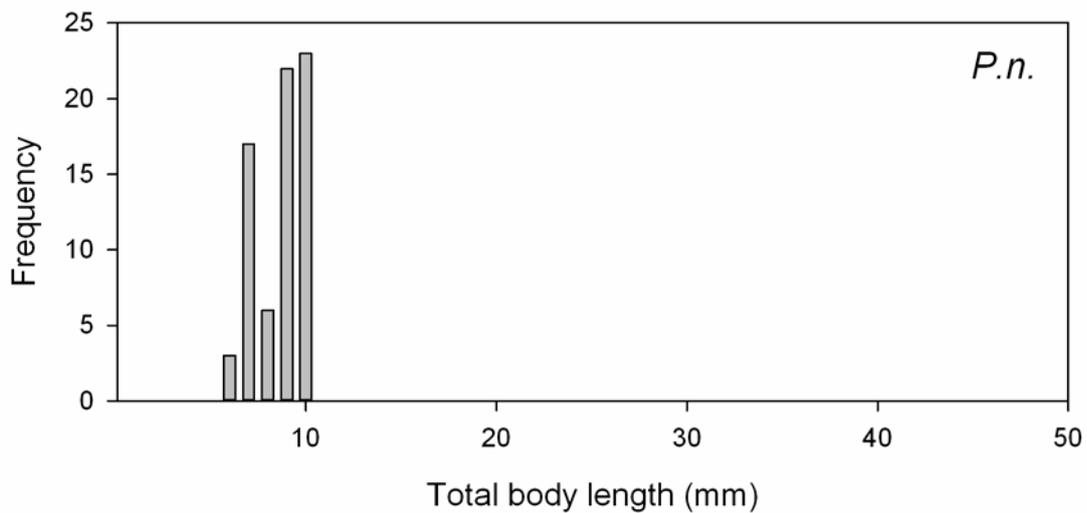
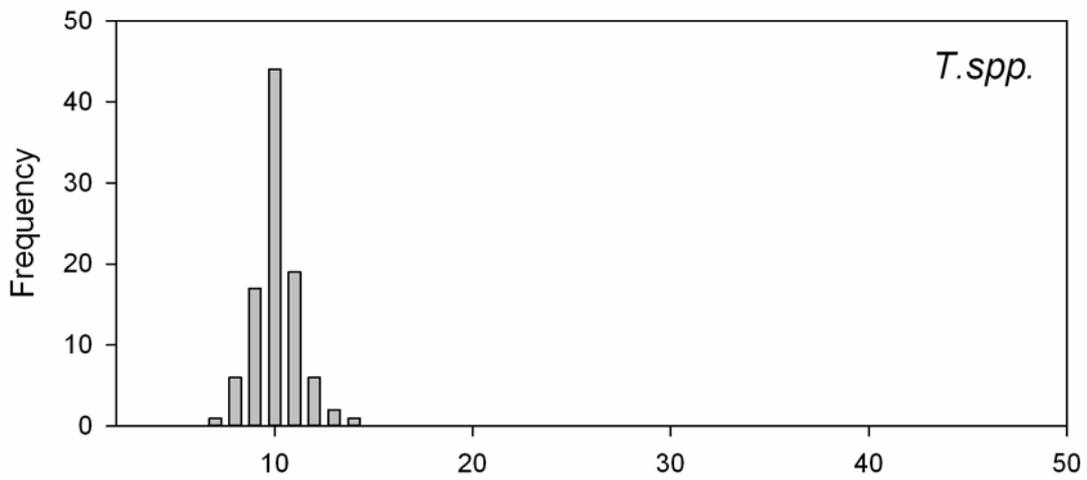
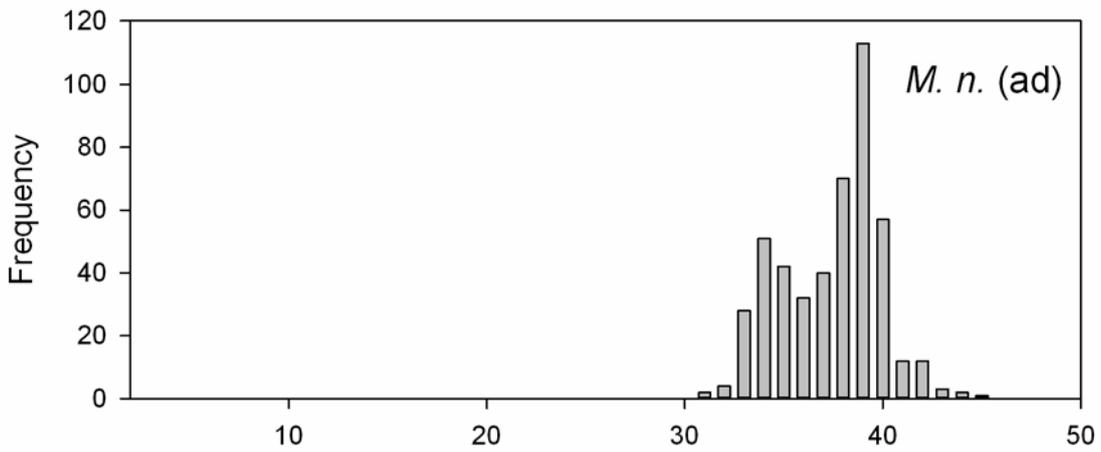
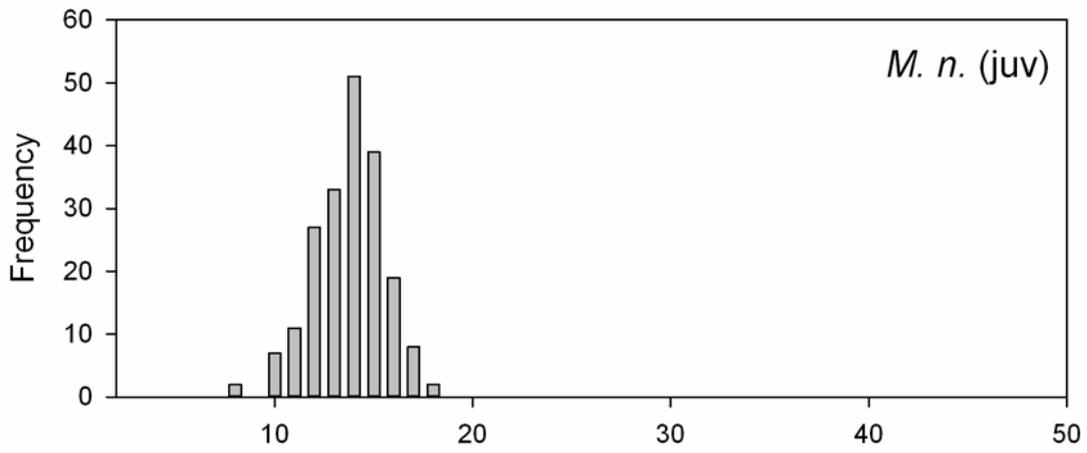
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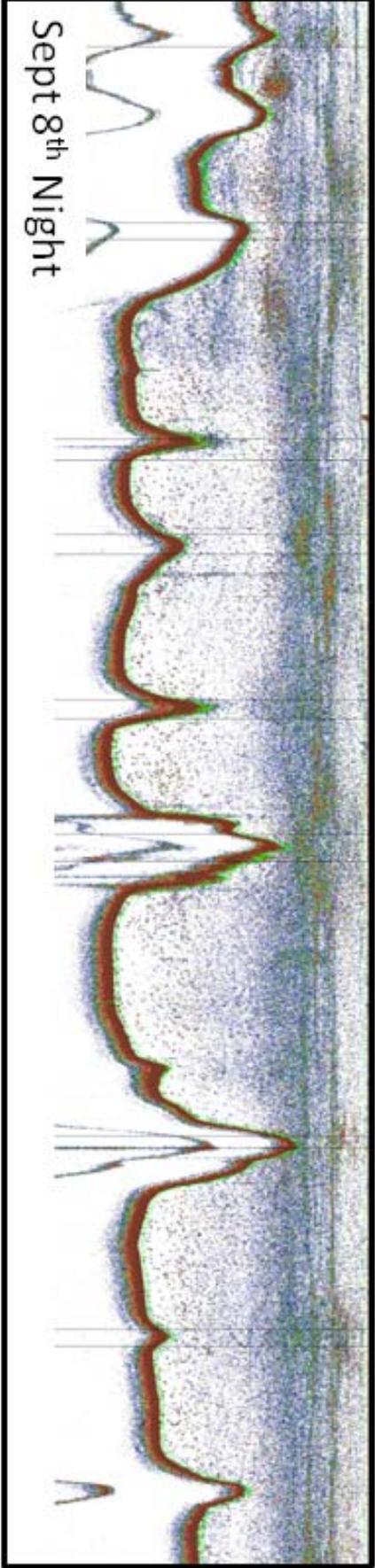
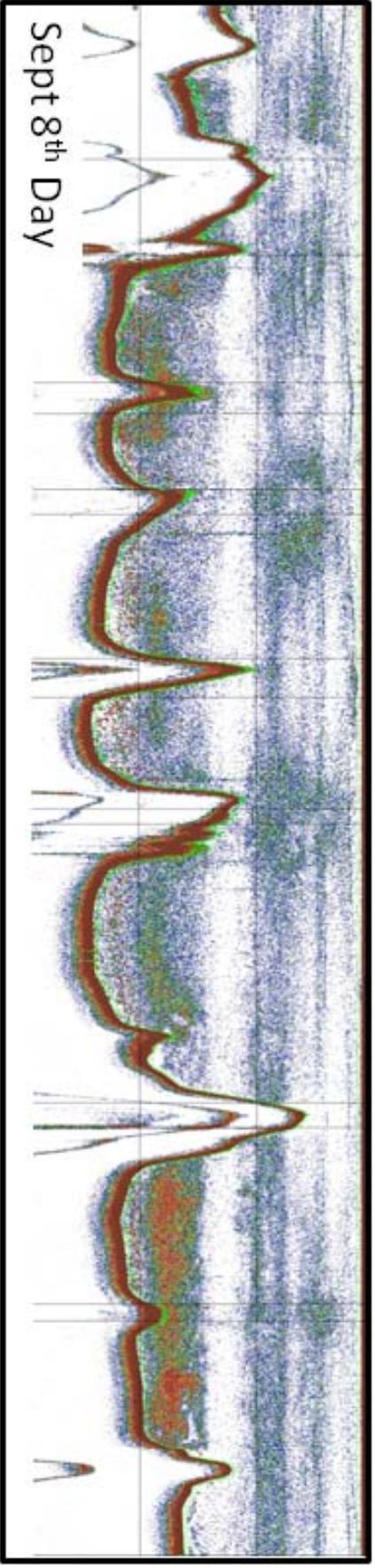
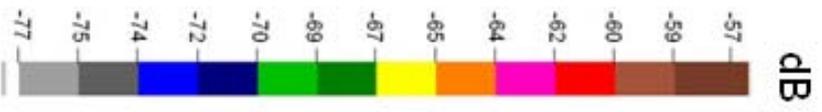




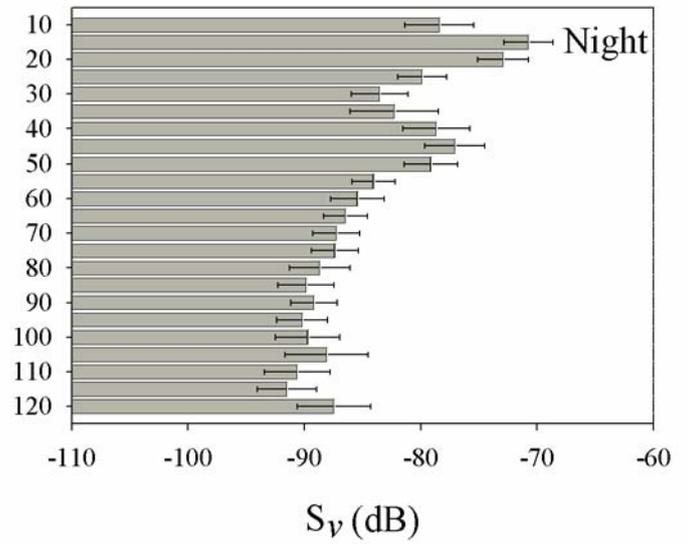
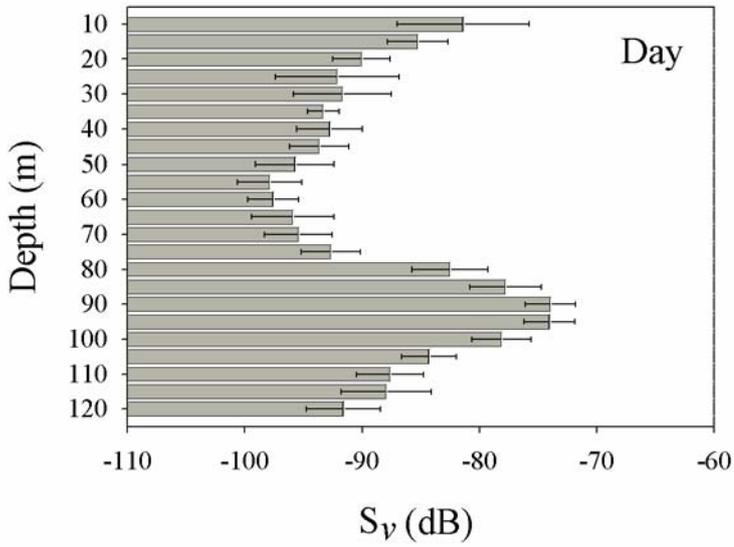
Species

Species

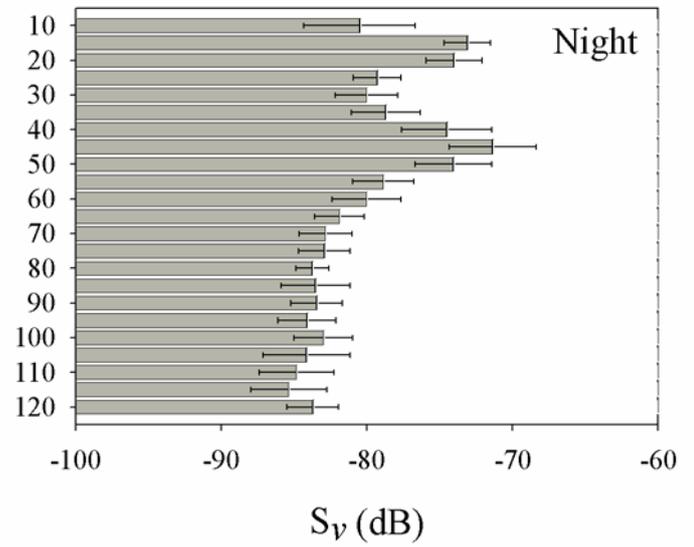
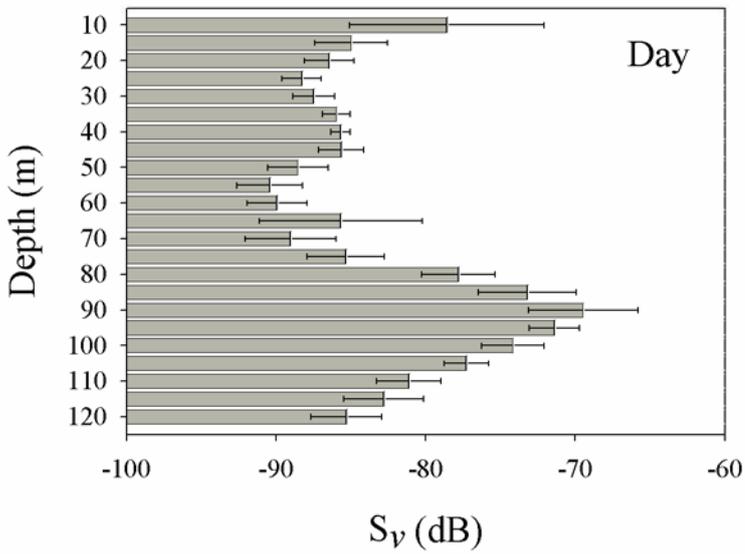


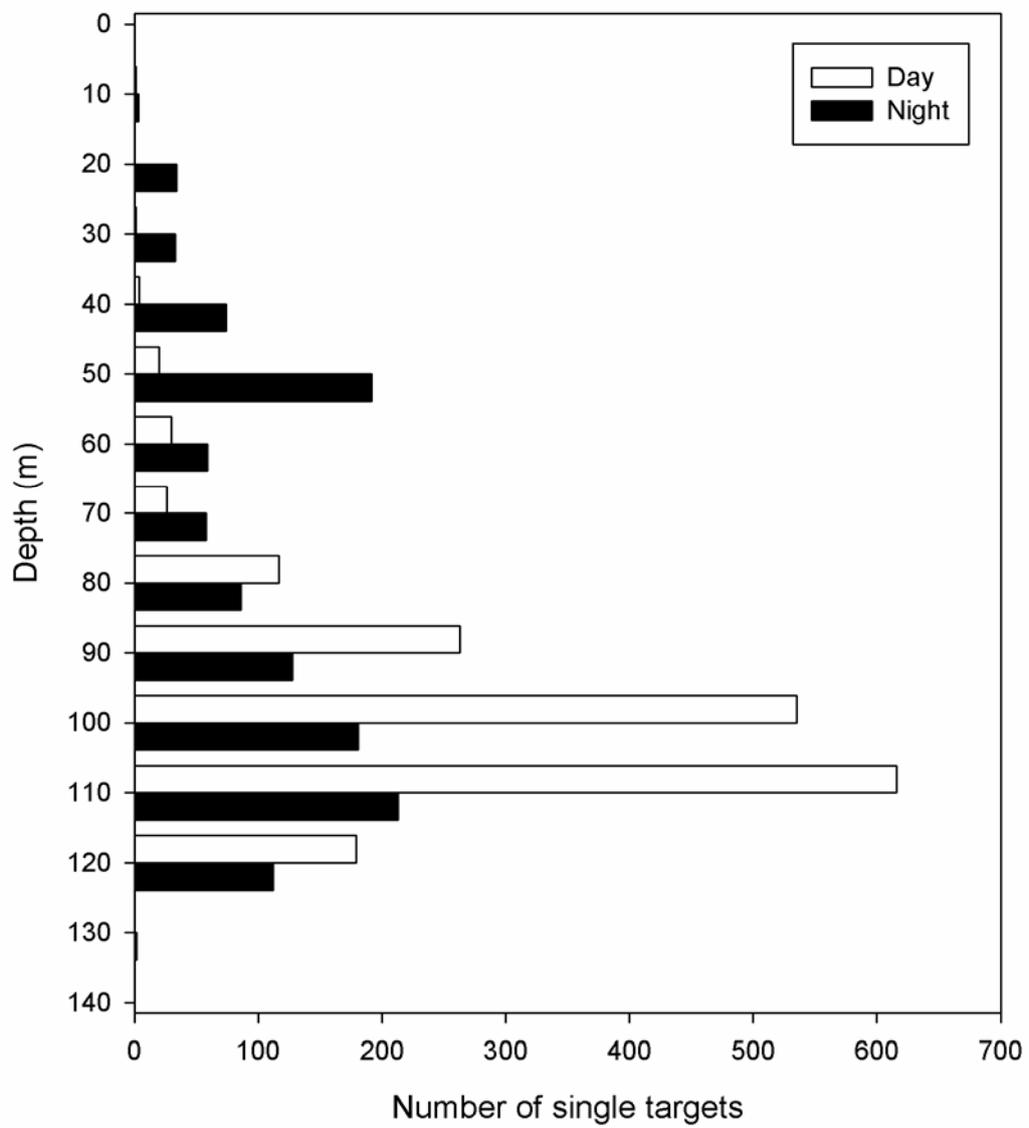


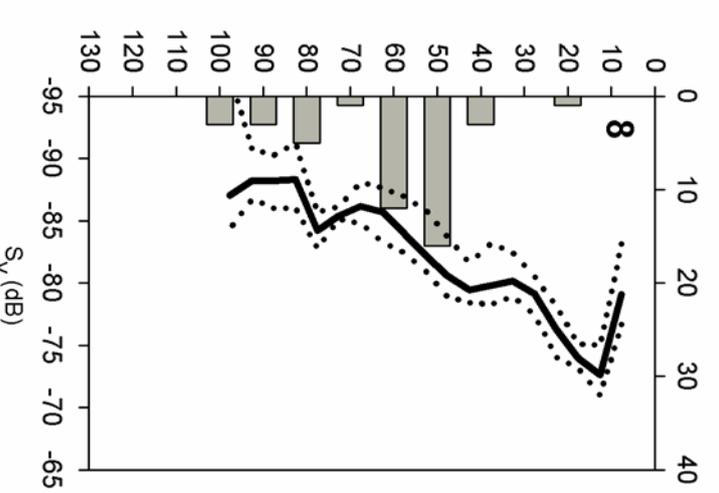
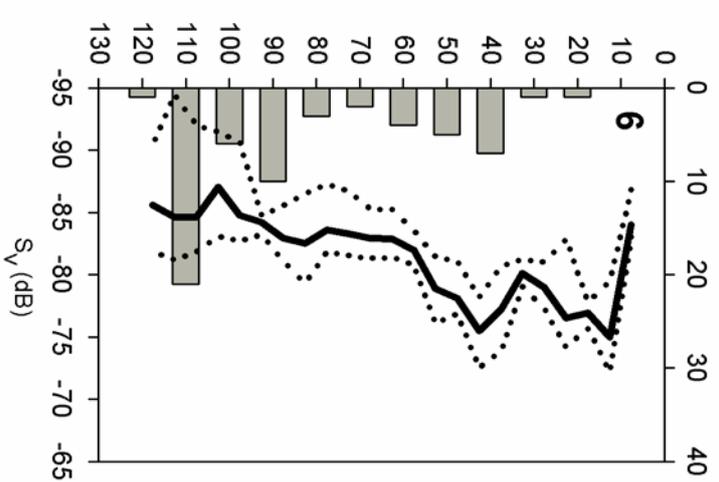
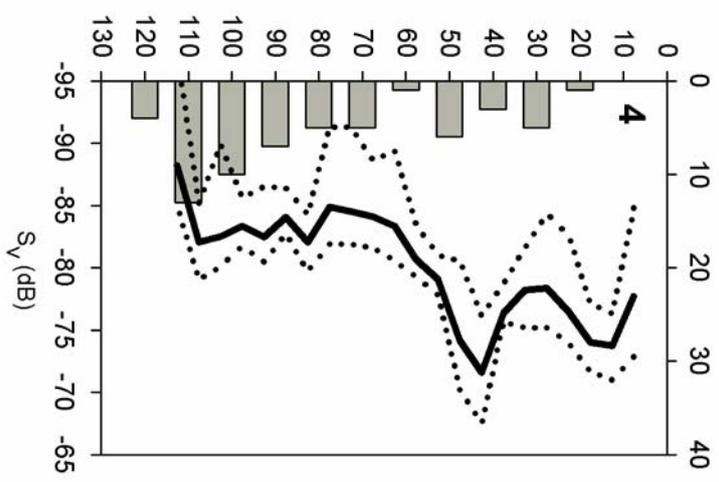
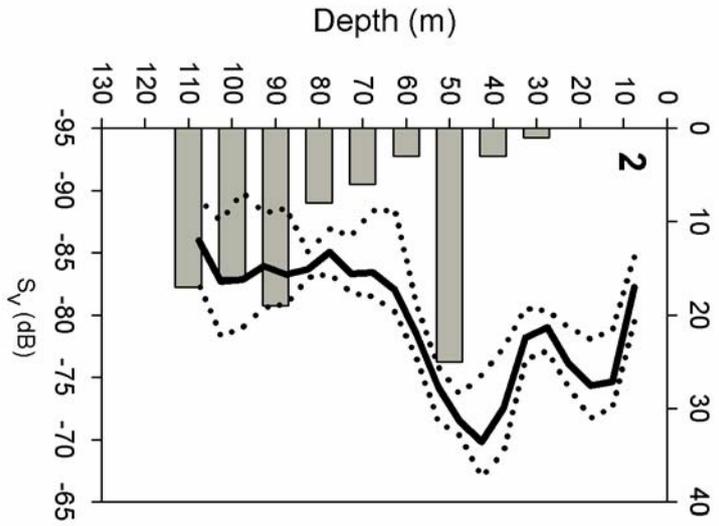
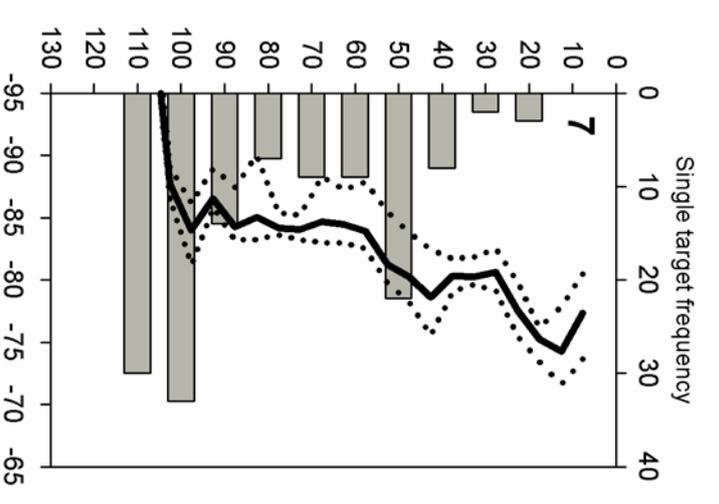
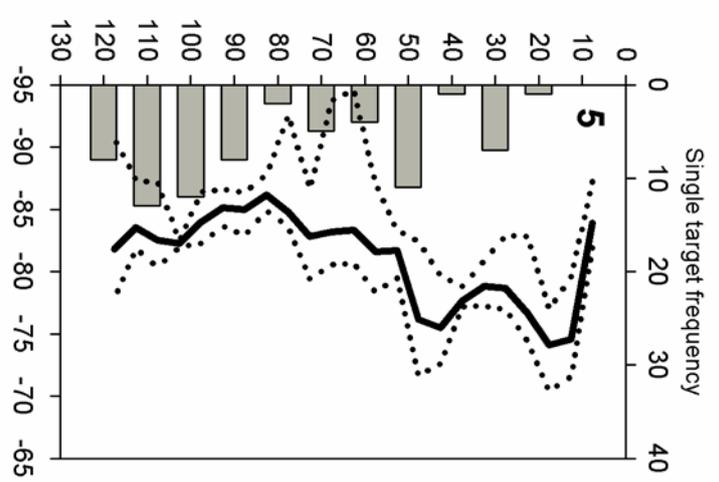
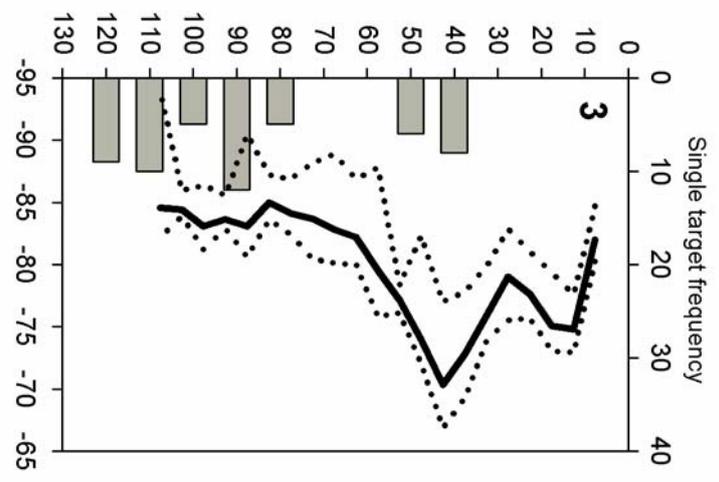
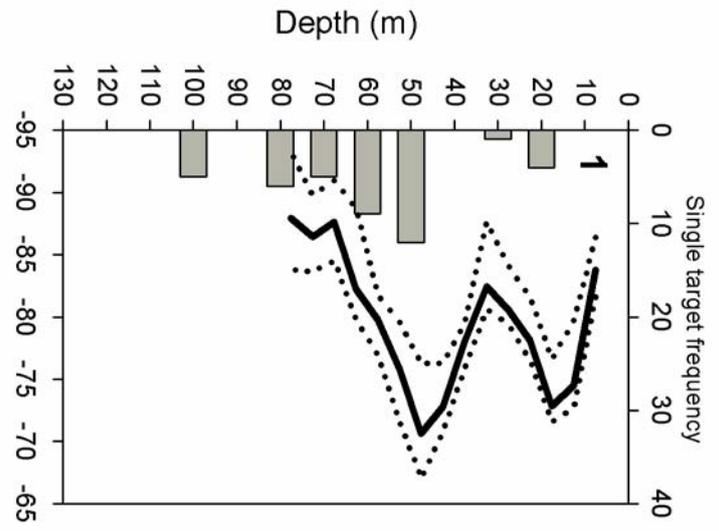
*M. norvegica* larvae and small euphausiids (12 to 20 dB  $\Delta S_V$  120-38 kHz)



*M. norvegica* adults (6 to 12 dB  $\Delta S_V$  120-38 kHz)

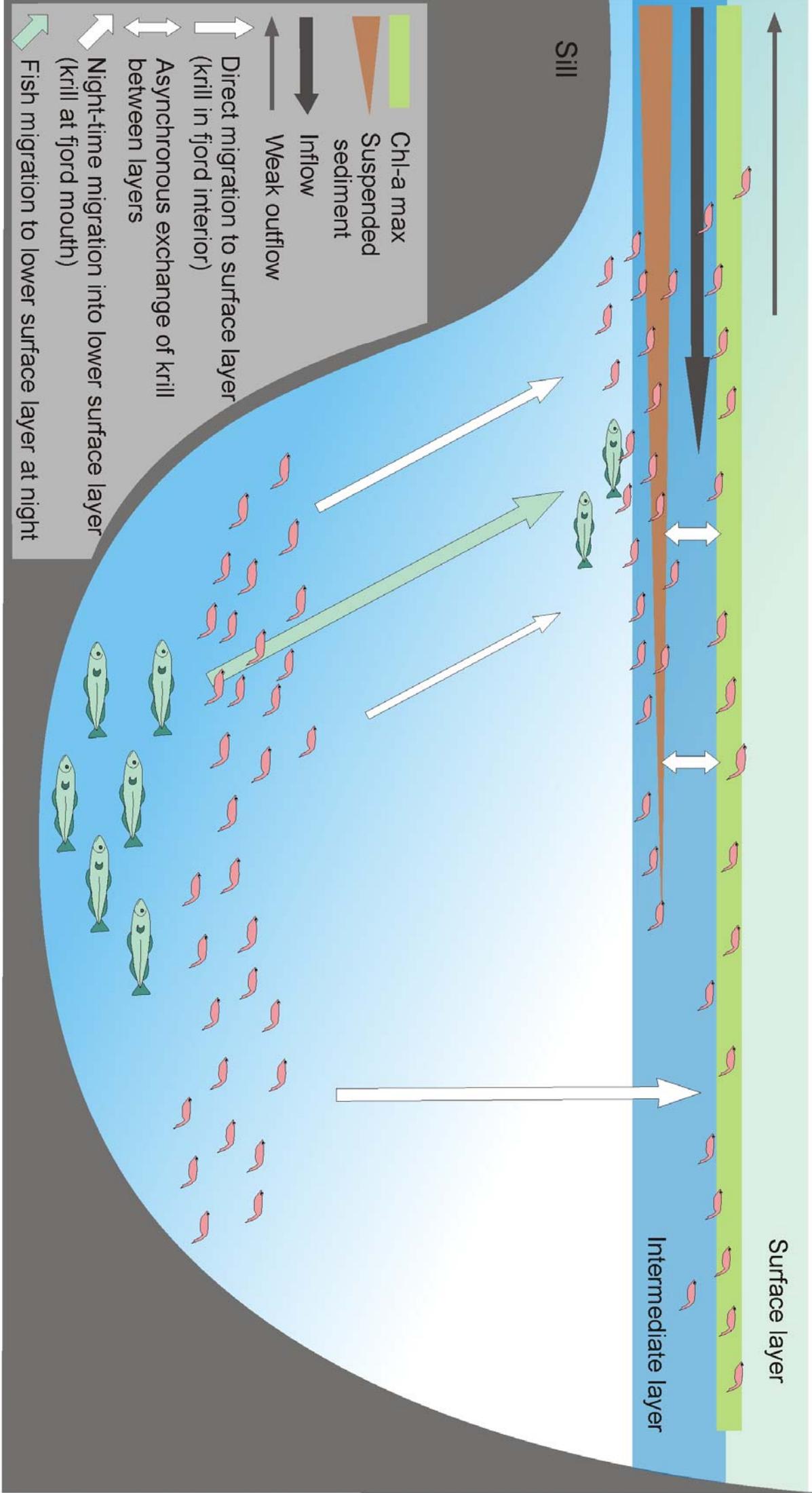






Fjord mouth

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