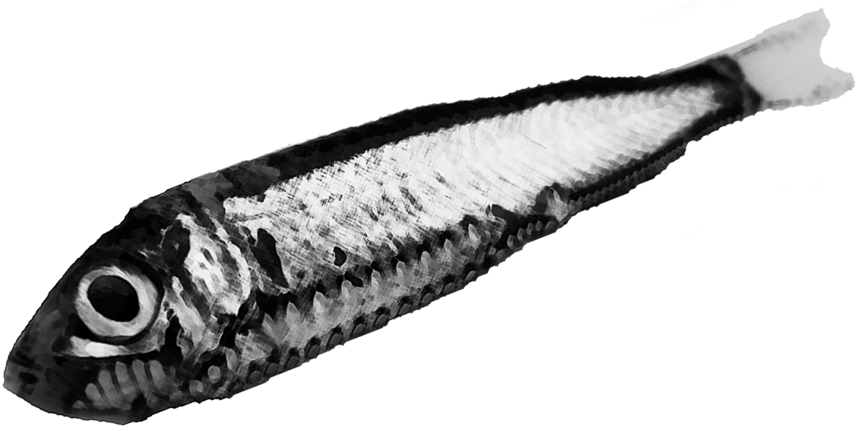
Diel vertical migration and feeding pattern of *M. muelleri* in Masfjorden in late autumn



By

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Abstract

The purpose of this study was to investigate diel vertical migration, feeding pattern and diet composition of mesopelagic fish *Maurolicus muelleri* in Masfjorden in late autumn and compare these with the previous studies. Sound scattering layers (SSLs) were obtained from an acoustic echo sounder device placed at the bottom which may give a better resolution and precision on the SSLs detection. The fish samples were taken by a pelagic midwater trawl equipped with 3 nets that can open and close while in the water at the different depths which may give better accuracy of the fish catches at each depth. The stomach content of pearlsides collected from different SSLs at different times of the day was analysed. *M. muelleri* comprised two SSLs located at approximately 25 to 200 m. The fish performed dusk and dawn feedings and the fish in the shallow layer more pronounced diel vertical migration than the fish below. Some large fish with lower condition factor also performed diel vertical migration in order to feed at dusk and dawn. The degree of stomach fullness and digestion varied through day and night. There was a size dependent trend in stomach fullness of *M. muelleri* as small fish had higher degree of stomach fullness than the large fish. Copepods were found to dominate zooplankton community in this study, and also comprised the main prey items of *M. muelleri*. The diel vertical migration and feeding pattern of the fish could be explained in relation to light regime, fish size, stomach dynamic, zooplankton distribution, environmental parameters and fish condition factor. The findings are in accordance with previous studies on *M. muelleri.*

Key word: feeding pattern, pelagic fish, *Maurolicus muelleri*

Content

Introduction

The mesopelagic fish, *Maurolicus muelleri* (Gmelin, 1789) commonly called Müller's pearlside, is found along the continental shelf in the Atlantic, Pacific, and Indian Oceans as well as in deep fiords, with very low abundance in offshore and Arctic and sub-Arctic waters (Salvanes and Kristofersen, 2001). In Norwegian waters, *M. muelleri* is a dominating species of the micronekton community and commonly found in the ocean and in the fjords (Kaartvedt et al., 1988). It is also found to dominate the biomass in Masfjorden (Kaartvedt et al., 1988) and have the highest trawl catch in Masfjorden and Sørfjorden (Bagøien et al., 2001). *M. muelleri* reaches a size of 5 - 7 cm and lives for 4-5 years (Falk-Petersen et al., 1986). In Masfjorden *M. muelleri* matures as one year old with size at maturity of 31 mm (Goodson et al., 1995). The species plays an important role in the food trophic interactions between deep waters and the epipelagic zone. It feeds on zooplankton and represents an important prey source for large predators, such as blue whiting *Micromesistius poutassou* and saithe *Pollachius virens* (Giske et al., 1990; Bjelland, 1995) and it also transfers energy through the ecosystem as it composed of high content of lipid and wax ester (Gjøsæter and Kawaguchi, 1980; Falk-Petersen et al., 1986). It has been an important model organism in studies of behavior and life history (Strand et al., 2002).

The life history, vertical distribution and feeding pattern of *M. muelleri* on the Norwegian west coast have been the subject for many studies over the last two decades (Giske et al., 1990; Giske and Aksnes, 1992; Baliño and Aksnes, 1993; Rasmussen, 1993; Rasmussen and Giske, 1994; Rosland and Giske, 1994; Bjelland, 1995; Goodson et al., 1995; Kaartvedt at al., 1996; Kaartvedt at al., 1998; Kristoffersen and Salvanes, 1998; Skagseth, 1999). In most waters *M. muelleri* occurred in sound scattering layers (SSLs) and performed diel vertical migration. Two sound scattering layers (SSLs) were observed in the upper 250 m along a cross-shelf transect from oceanic waters through a front on the shelf during spring (Kaartvedt et al., 1996), and in Norwegian fjords during winter (Giske et al., 1990; Baliño and Aksnes, 1993; Skagseth, 1999) and during spring (Bjelland, 1995; Goodson et al., 1995; Skagseth, 1999). In summer, *M. muelleri* comprised a sound scattering layer in fjordic and oceanic environment in the upper 250 m (Rasmussen and Giske, 1993; Kristoffersen and Salvanes, 1998). In Storfjorden, western Norway, *M.*

muelleri was found schooling in summer as a procedure to extend the feeding time or as a protection against predators (Kaartvedt, 1998).

Sound scattering layers of *M. mueleri* were separated in term of size distribution. The upper layer was composed of juvenile fish and the lower layer of adult fish (> 40 mm) (Bagøien et al., 2001; Baliño and Aksnes, 1993). Bjelland (1995) studied the life-history strategies of two fjord populations of *M. muelleri* in spring and reported a clear distinction of length frequency distribution of *M. muelleri* in Herdlafjorden in two sublayers composed of 26 mm fish in upper layer and 39 mm fish in lower layer in day time, which was contradictory to the study by Goodson et al. (1995) who found clear size separation between SSLs in Herdlefjorden in winter and distinct size coincide between upper and lower layers in Spring. During night the length frequency distributions were unimodal both in Masfjorden and Herdlafjorden. The length frequency distribution pattern of *M. muelleri* in winter was similar to that reported by Goodson et al. (1995). The small fish (22-34 mm) dominated the upper layer while the lower layer contained the larger ones (36-57 mm). Rasmussen and Giske (1993) found the bimodal length frequency distribution of *M. muelleri* in Masfjorden with peaks of about 29 and 42 mm indicated the two year classes (1 and 2 year) dominated in summer. Goodson et al. (1995) found a significant different in the length weight relationships of *M. muelleri* in Masfjorden between seasons and age groups. The length weight relationships of the same year class *M. muelleri* differed significantly between Masfjorden and Herdlafjorden and within each fjord in spring and the fish condition factors appear to differ extensively with area and time (Bjelland, 1995).

M. muelleri performed diel vertical migration as reported by Rasmussen and Giske (1994), Bjelland (1995), Goodson et al. (1995) and Skagseth (1999). The upper layer of juvenile pearlside fish carried out diel vertical migration, ascending to near the surface at dusk, then descending to between 20-70 m (midnight descending), just to rise again to the surface at dawn before returning to stay at daytime depth at approximately 100 m (during winter and spring). In contrast the deeper layer composed of adult fish stayed at depths between 150-250 m during both day and night time (Kaartvedt et al., 1988; Gjøsæter and Kawaguchi, 1980; Giske et al., 1990; Baliño and Aksnes, 1993; Bjelland, 1995; Goodsen et al., 1995; Skagseth, 1999; Bagøien et al., 2001). In summer *M. muelleri* in Masfjorden was located in one layer and vertical distribution was related to changes of surface light (Rasmussen and Giske, 1994). Goodson et al. (1995) reported an increasing vertical migration of adult fish from winter to spring and summer season as a shift in motivation from predator avoidance towards growth to support gonad development and reproduction.

Feeding patterns and main preys of *M. muelleri* were different between fish size and seasons. Giske et al. (1990) and Baliño and Aksnes (1993) found that *M. muelleri* in Masfjorden was a day time feeder in winter. The stomach fullness increased from afternoon through night and almost emptied before sunrise. The main prey of both juvenile and adult fish was copepods. Contradictory to the study of Bagøien et al. (2001) who found that juvenile fish in Masfjorden performed night time feeding while the matured fish performed day time feeding in winter. They also found that copepods were the main prey of *M. muelleri* in winter. There was a diel variation in stomach fullness and degree of digestion of *M. muelleri* in Masfjorden during spring and summer. From the study by Bjelland (1995), the stomach fullness of *M. muelleri* differed between length groups. Small fish had mostly half full or full stomach and large fish had mostly haft full or empty stomach. Main preys were *Coscinodiscus* spp. and copepod in Masfjorden and cirriped nauplii and copepod in Herdlafjorden. Degree of stomach fullness and digestion varied through day and night in both fjords. Rasmussen and Giske (1994) studied life-history parameters and the vertical distribution of *Maurolicus muelleri* in Masfjorden in summer. They reported that the stomach fullness decreased during day and increased at night, while the number of empty stomach increased with fish size. The main preys found in most stomach were cladocerans, veliger bivalvia and copepods. Fish performed night time feeding in order to keep low risk of mortality and high rate of feeding. Feeding strategy differs with season and area (Bjelland, 1995) and the different in main prey is an effect of seasonal differences in zooplankton abundance (Skagseth, 1999)

This study investigates field data on *M. muelleri* and environmental variables collected from Masfjorden in November 2007. The aim of the study is to investigate the diel vertical migration patterns, feeding patterns and diet composition of the fish from different SSLs and how these processes relate to fish length, fish weight, environmental variables and time of the diel cycle. The acoustic data were obtained from the device placed at the bottom which may give a better resolution and precision on the sound scattering layer (SSL) detection. The fish samples were taken by a pelagic midwater trawl equipped with 3 nets that can open and close while in the water at the different depths which may give better accuracy of the fish catches at each depth.

Material and methods

Location

The study was carried out in Masfjorden, on the west coast of Norway north of Bergen (60º 50’ N, 5º 30’ E) between the 1st and 4th of November 2007 onboard the RV Håkon Mosby. The fjord is approximately 20 km long and on average 1 km wide, and has a sill depth of 75 m and a maximum depth of 494 m (Figure 1).

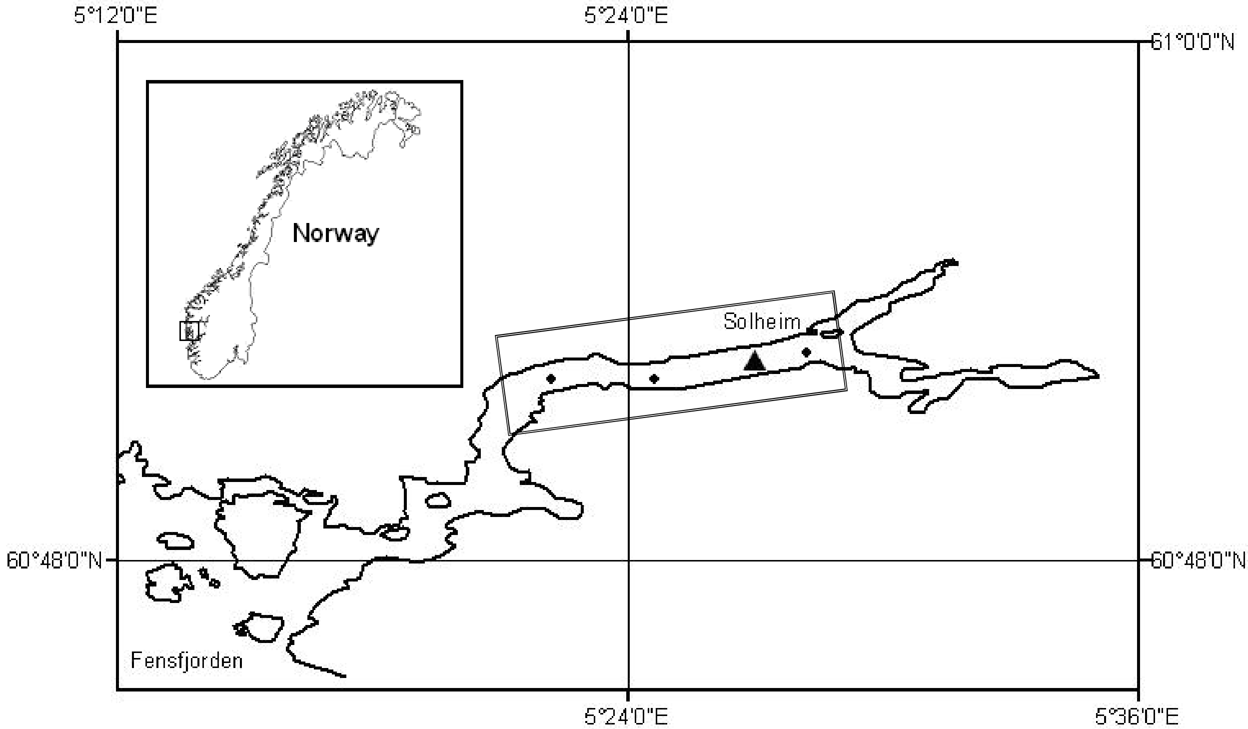


Figure 1 Location of Masfjorden. Diamonds indicate positions of environmental stations, the triangle the location of an echo sounder, while the rectangle the area where trawling was done.

Sampling

The vertical position of sound scattering layers (SSL) was continuously monitored using an upward facing 38 kHz (SIMRAD) split beam echo sounder placed on the fjord bottom at approximately 390 m. The echo sounder was connected to a laptop on land via a cable, real time data was stored on the laptop, and obtained daily echogram was post processed with MATLAB. The sound scattering layers were identified and the species composition determined by trawling, using a pelagic Harstad trawl, equipped with a multisampler and 3 remotely controllable cod ends (Figure 2).

Figure 2 A pelagic midwater trawl with a multisampler attached

A total of five hauls were carried out during day time and 11 hauls during night time (Table 1). The duration of each trawl was between 5-10 minutes at approximately 3 knots trawling speed. Fish from each haul was counted and weighted during the cruise. The entire trawl catch was weighted and sorted if the total catch was small, but if the catch was big a sub-sample of approximately 100 fish were sampled by random from the trawl catch. This explains the difference in the number of fish of each station. Fish in the sub-samples were sampled randomly and were kept for later stomach analysis in the laboratory.

Table 1 Station, trawl number, date, time and sampling depth of fish in Masfjorden

Station	Trawl number	Date	Time (GMT)	Depth (m)
1	158	2 Nov 2007	00:28-00:39	40
	159	2 Nov 2007	00:39-00:49	40
	160	2 Nov 2007	00:49-00:59	40
2	162	2 Nov 2007	02:05-02:15	70
	163	2 Nov 2007	02:15-02:26	70
3	164	2 Nov 2007	03:19-03:29	140
	165	2 Nov 2007	03:32-03:42	140
	166	2 Nov 2007	03:42-03:53	140
4	167	2 Nov 2007	10:39-10:50	70
	168	2 Nov 2007	10:50-11:01	70
5	170	2 Nov 2007	12:13-12:24	150
	171	2 Nov 2007	12:24-12:35	150
6	174	2 Nov 2007	14:05-14:15	270
7	185	3 Nov 2007	03:36-03:46	40
	186	4 Nov 2007	03:47-03:57	40
	191	4 Nov 2007	04:22-04:32	40

Oxygen, temperature and salinity with depth in Masfjorden were obtained by SEABIRD 911 CTD.

Zooplankton sampling and analysis

Zooplankton was collected from different depth ranges between 0-450 m using a multinet (Hydro-Bios, Kiel) (Table 2). The multinet has a 0.5 m x 0.5 m opening with five nets (mesh size 180 µm) which can be closed at desired depths. Each sample was divided into two sub-samples, one of which was frozen for ash free dry weight (AFDW) determination at a later stage and the other preserved in 4% neutralised formaldehyde solution for zooplankton composition identification. During the AFDW analysis, samples were dried at 60 ºC for 24 hours, weight, burnt at 490 ºC for 3 hours, and weight again. The AFDW is obtained by calculating the weight lost after burning. The samples preserved in alcohol were diluted with water to 250 ml volume. Thereafter 6 of 5 ml sub-samples were taken with a plunger sampling pipette (Hydro-Bios) for analysis under a light/stereo microscope. The individual items in each sub-sample were sorted by groups and counted. Random length (mm) measurements of copepods for each sub-sample were conducted using a light/stereo microscope equipped with a micrometer eye-piece. The body length of copepod was measured from the beginning of cephalotorax to the end of the caudal rami without measuring the caudal setae.

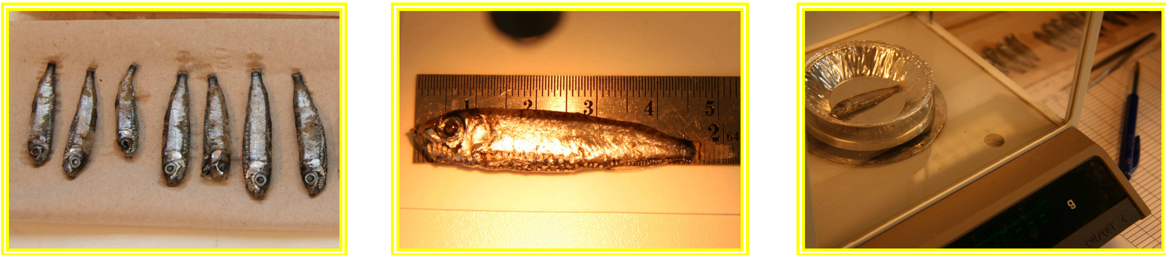
Table 2 Station, date, time and sampling depth of zooplankton in Masfjorden

Station	Date	Time (GMT)	Depth range (m)
1	1 Nov 2007	19:30	50-450
2	1 Nov 2007	22:30	100-450
3	3 Nov 2007	9:40	50-450
4	4 Nov 2007	02:00	50-450

Length, weight and stomach content of *M. muelleri*

In most cases 40 fish were randomly taken from each trawl and length (mm), weight (mg) and stomach content were measured and determined in the laboratory. The standard length (snout tip to caudal peduncle) was measured to the nearest mm, and weight to nearest mg wet weight. The fish were thawed and excess moisture was removed with absorbent paper before weighting. The stomach was removed and the content was mounted on the glass slides and then inspected under a stereo or light microscopes (N = 491). Unidentifiable objects were photographed and assessed later.

The degree of stomach fullness was measured on a scale of 0-1 (Bjelland, 1995), where 0 = empty, 0.25 = some content, 0.5 = half stomach, 0.75 = more than half and 1 = full stomach. Individual food items were identified to group level and count. The degree of digestion was measured on a scale of 0-1, where 0 = fresh, 0.25 = digest start, 0.5 = partly digest, 0.75 = unidentified and 1 = digested. Earlier a length-weight relationship was established by linear regression on ln-transformed length and weight data. A chow-test was used to compare the length-weight relationships of fish from different depths.



a b C

Figure 3 Method applied to measure length and weight data from each trawl: exceed moisture absorbent (a), length determination (b), and weight determination (c)

Results

The environment

Oxygen, temperature and salinity profiles were fairly constant below sill depth (100 m), but varied with depth between the surface and sill depth (approximately 70-80 m) (Figure 4). The highest dissolved oxygen, temperature and the lowest salinity were found in the surface layer. Here the maximum dissolved oxygen was 5.5 mg/L, declining gradually to 150 m depth where after it remained just below 4 mg/L. The maximum temperature (12 ºC) was recorded at the surface and declined to 8.5 ºC at 75 m depth. The minimum salinity (32 psu) was observed at the surface and increased to 35 psu at 75 m depth.

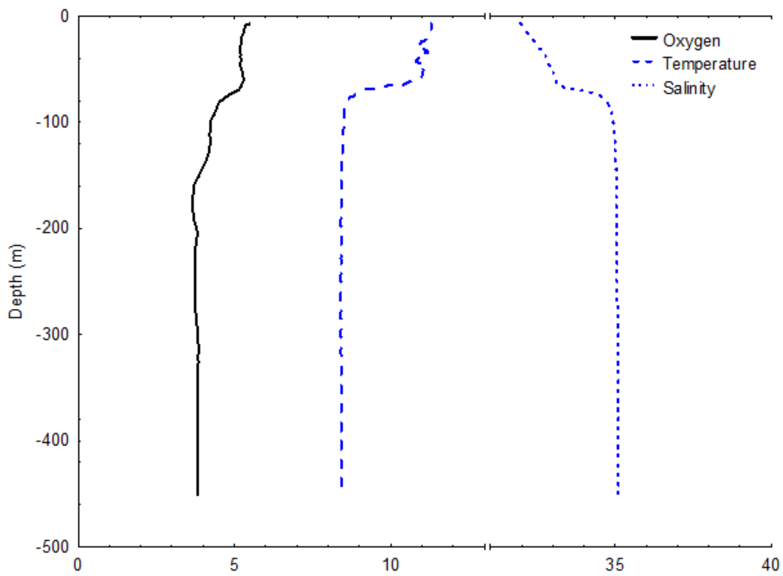


Figure 4 Vertical profiles of oxygen, temperature and salinity in Masfjorden

Zooplankton

Biomass, abundance, composition and distribution

The overall zooplankton biomass from all 4 stations varied between 8.19 and 17.23 mg AFDW/m^3. The lowest was recorded at 50-100 m depth at station 4 while the highest value was recorded at 400-450 m depth at station 3. The total zooplankton abundance varied between 91 and 638 individuals m^{-3}. Lowest abundance was recorded at 200-250 m depth at station 1 while highest abundance was recorded in the surface layer (0-100 m) of station 2 (Appendix 3).

The vertical distribution of zooplankton biomass during daytime (station 3 at 0940 hrs) and nighttime (station 1 at 1930 hrs and 4 at 0200 hrs) in Masfjorden is shown in Figure 5. The distribution of plankton biomass varies marginally throughout the water column, at least in the upper 250 m. The numerical abundance of zooplankton was distributed throughout the water column and high abundance in the upper layer (0-50 m) both in day and night. The abundances decreased with depth until about 150-200 m during day time and at 250-300 m during night time at which abundances increased again. The lowest abundances were observed at 100-150 m depth in day time and at 200-250 m depth at night. There was a higher abundance at the surface at night than at day.

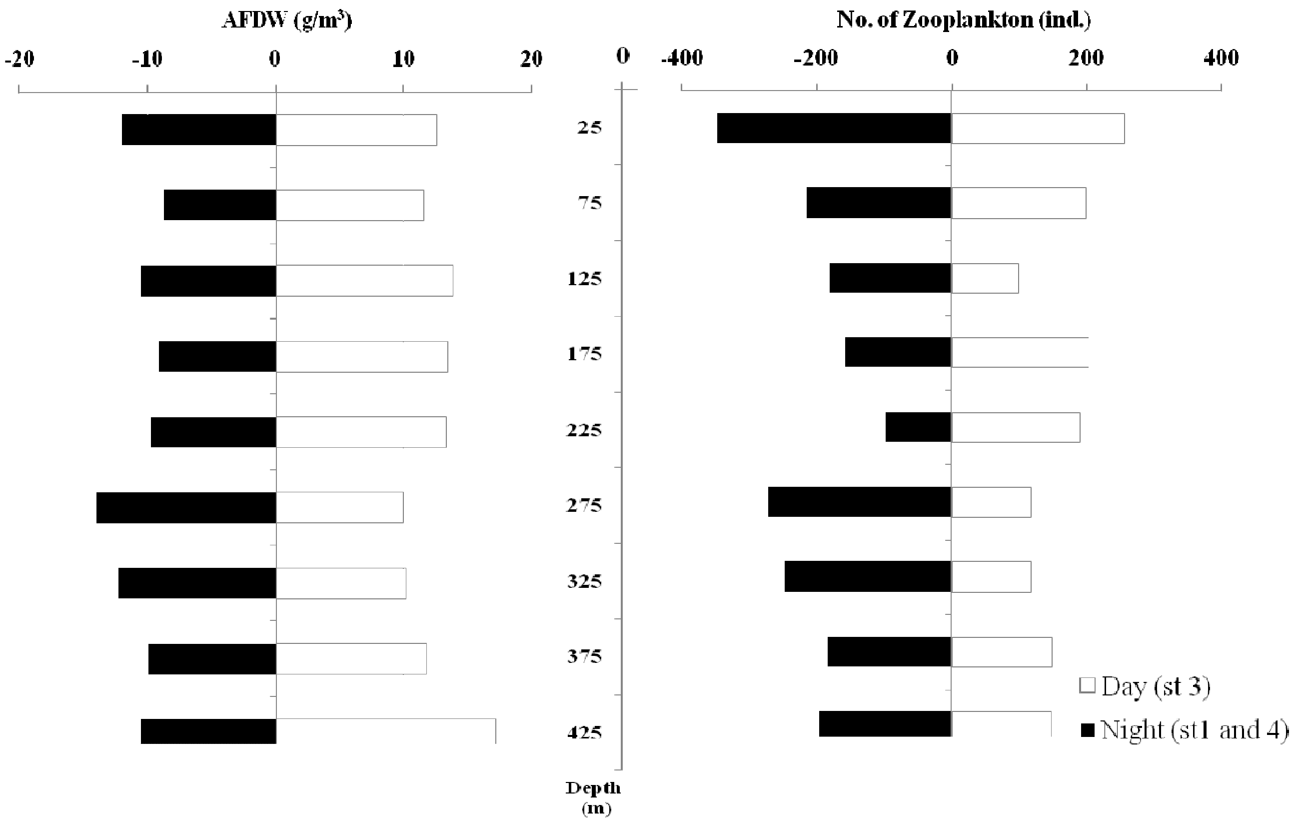


Figure 5 Vertical distribution of zooplankton biomass (mg AFDW m^{-3}) (left) and number of individuals (right) in Masfjorden during daytime (station 3 at 0940 hrs) and nighttime (station 1 at 1930 hrs and 4 at 0200 hrs)

Copepods dominated the zooplankton community numerically, contributing more than 90% of the total zooplankton in Masfjorden (Figure 6). Other identified zooplankton included cnidarais, ostracods, amphopods, chaetognaths, polychaete, polychaete larvae, copeopod nuplii, cyphonautes larvae, heliozoas, eggs and resting eggs. Other less abundant zooplankton occurred in low numbers and showed very scattered distributions throughout the water column.

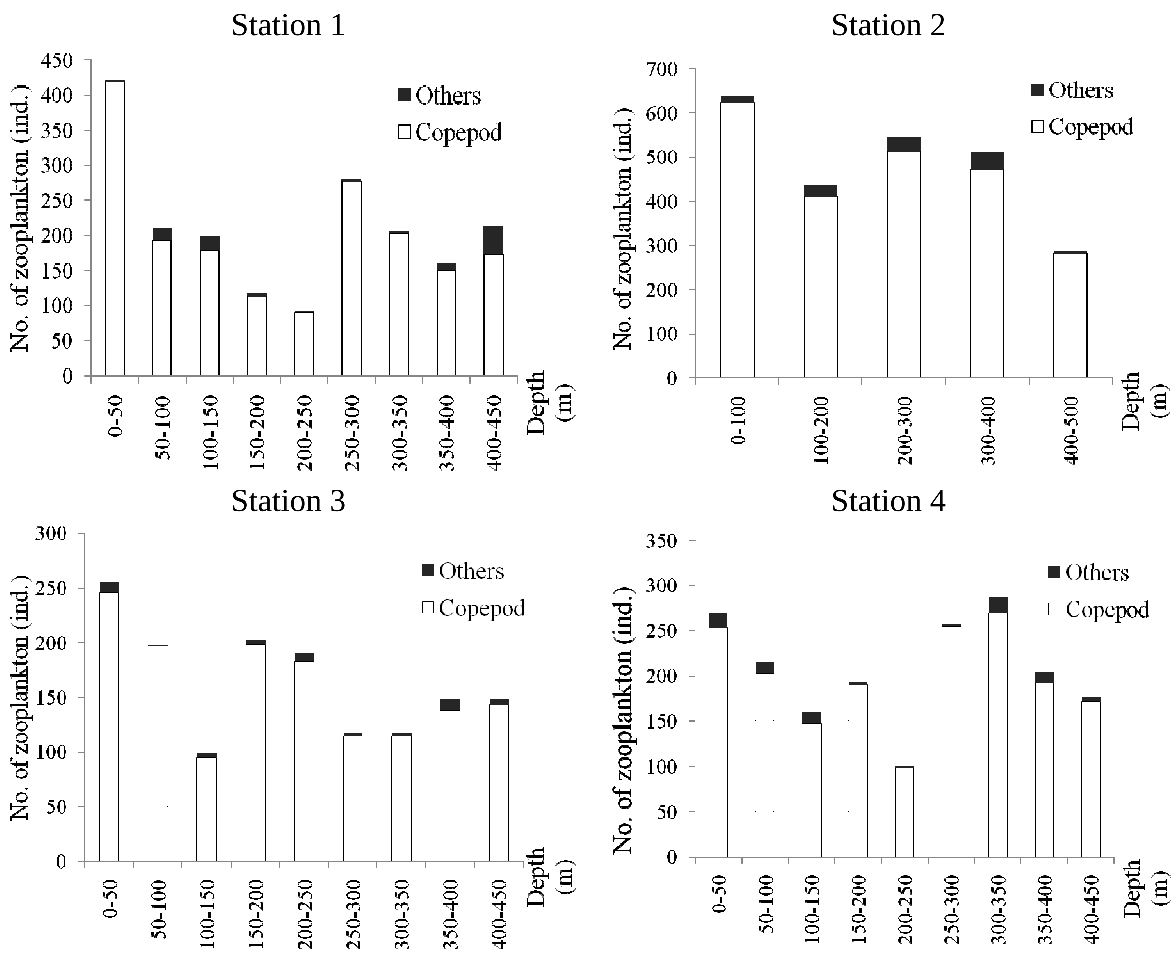


Figure 6 Zooplankton composition of each station at different depth intervals. The category “others” include cnidarais, ostracods, amphopods, chaetognaths, polychaete, polychaete larvae, copeopod nuplii, cyphonautes larvae, heliozoas, eggs and resting eggs.

Copepod size distribution in each station and depth

The size of copepods was ranged from 0.275 mm to 3.600 mm. The smallest copepods were found at station 1 (350-400 m) and the largest copepods were found in station 2 (300-450 m). Mean sizes of copepod at different depth interval are shown in Figure 7. The body size of copepods varied indistinctly with depth.

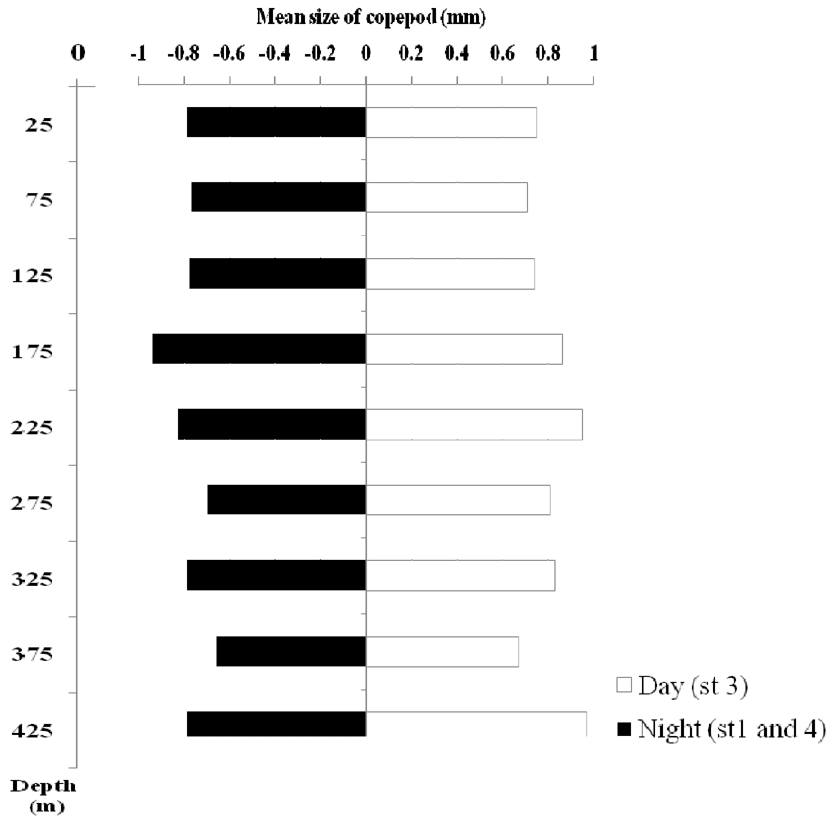


Figure 7 Average body length (mm) distribution of copepod at different depth intervals in Masfjorden during daytime (station 3 at 0940 hrs) and nighttime (station 1 at 1930 hrs and 4 at 0200 hrs). The length was measured from the beginning of cephalotorax to the end of the caudal rami without measuring the caudal setae.

Vertical distribution of *M. muelleri*

Echogram

The vertical distribution of the Sound Scattering Layers (SSLs) in Masfjorden is shown in Figure 8. Two distinct SSLs were visible in the upper 200 m during day and night. The 7 stations (16 trawls) were taken in the different layers, both in the dense layers and below the dense layers. The shallow layer reached the surface around 0500 hrs (GMT) and stayed near the surface for one hour and a half, then descended to about 60-75 m and stayed at this depth during day time. The layer performed another ascend at 1500 hrs, reached the surface at 1600 hrs, stayed there for two hours before descending to 25-50 m at night. The fish in the dense layer were commonly found at depths between 125-200 m. Some large fish migrated up from the deeper layer to feed at the surface at dusk, performed a descent during night, ascended again to feed at the surface at dawn, before returning back to stay in the deeper layer (125-200 m) during day time.

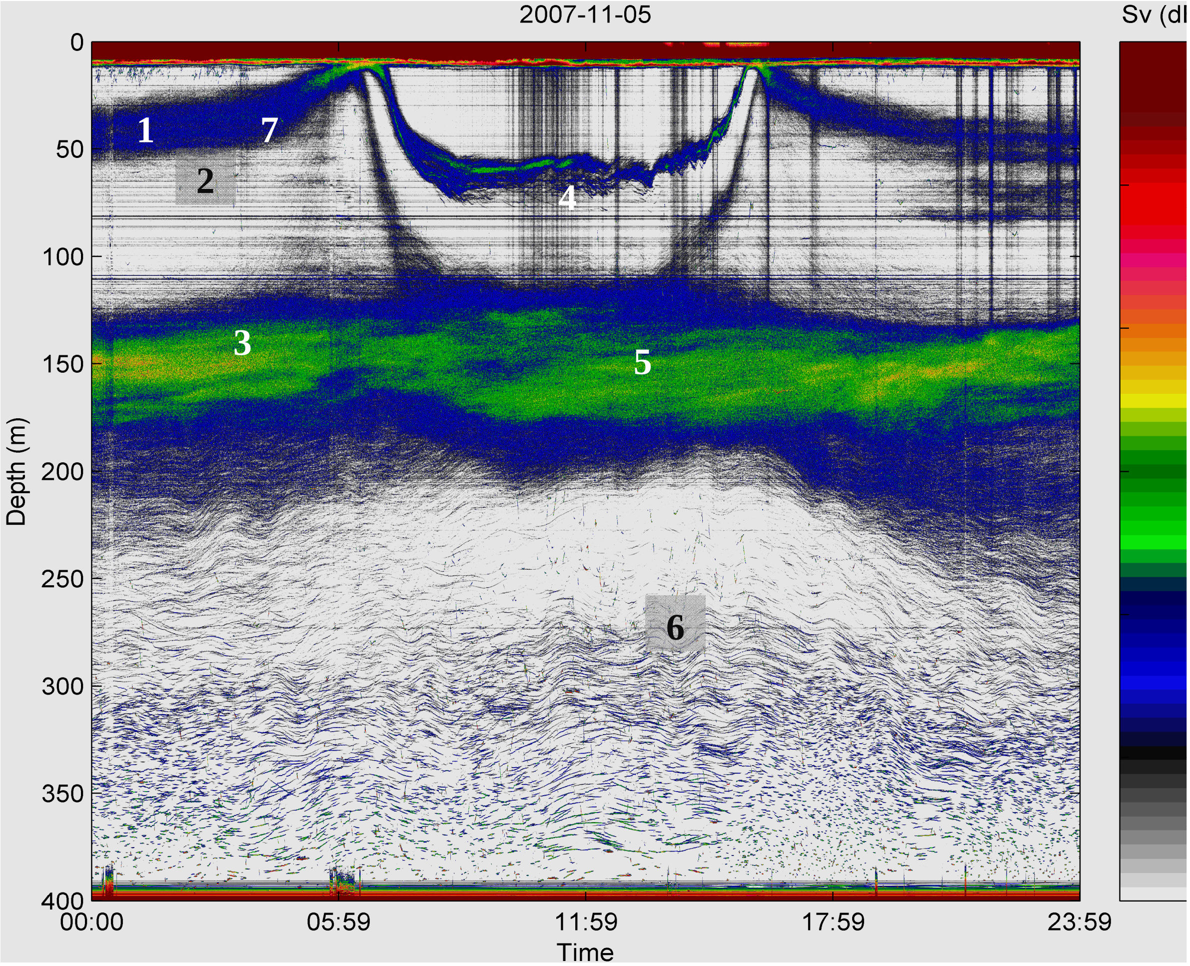


Figure 8 Vertical distribution of SSLs containing mostly *M. muelleri* in Masfjorden in early November. Time is given in GMT.

Fish length frequency distribution of M. muelleri with depth and time

Length frequency distributions of *M. muelleri* in Masfjorden are shown in Figure 9. The overall length frequency distribution was bimodal. The length of first group which contained the small fish ranged from 19 mm to 30 mm, while the second group contained fish greater than 30 mm. The length distributions from stations 2, 3, 5 and 6 were unimodal while stations 1, 4 and 7 had a bimodal length frequency distribution. During night the upper layer (station 1, 2 and 7) was dominated by large fish with a small proportion of small fish, although distributions from these stations varied. During day the upper layer (station 4) contained mostly small fish. The lower layer (station 3, 5 and 6) was dominated by large fish both during day and night.

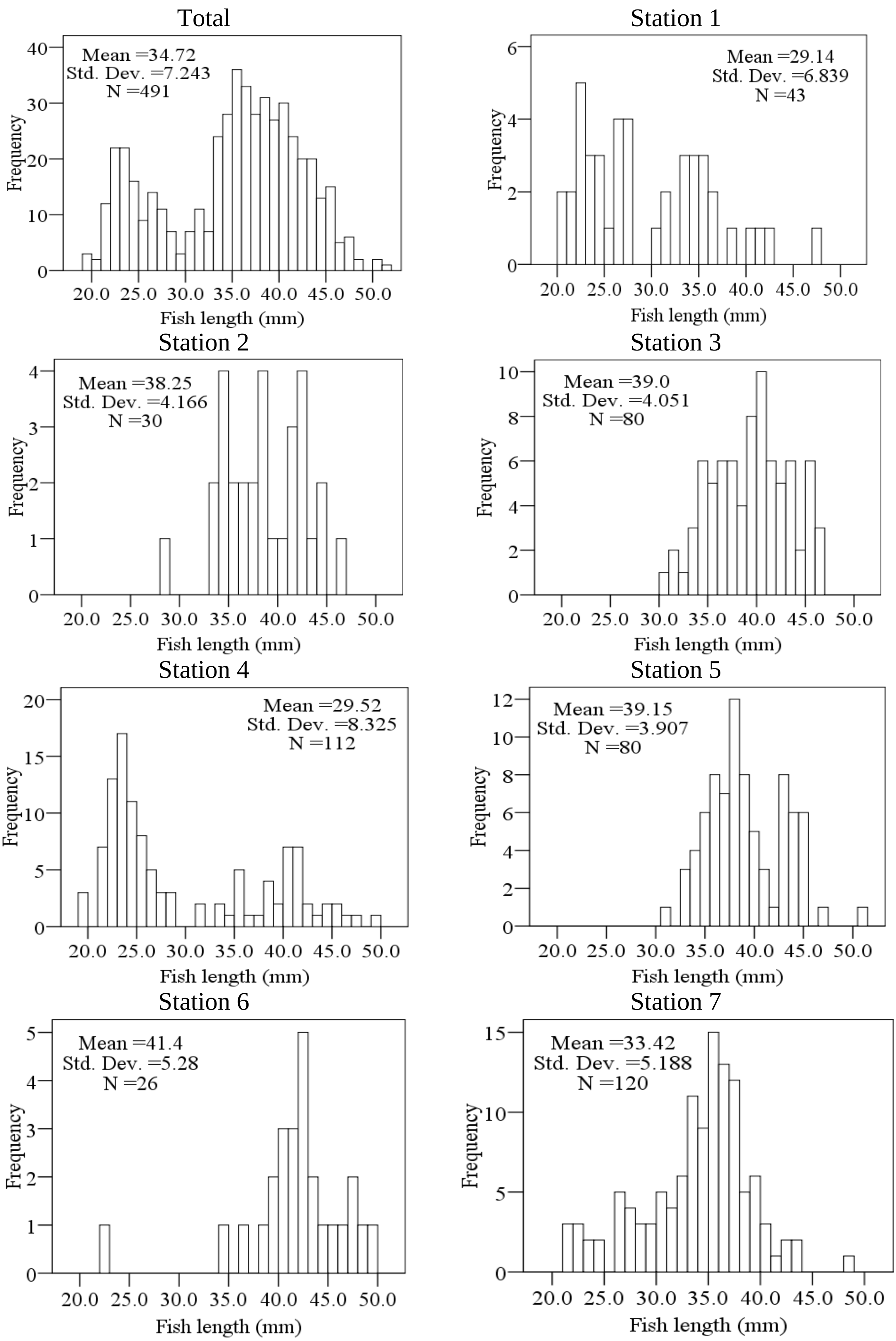


Figure 9 Length frequency distribution of *M. muelleri* of each station in Masfjorden. St 1 at 40 m (0028-0059 hrs), St 2 at 70 m (0205-0226 hrs), St 3 at 140 m (0319-0353 hrs), St 4 at 70 m (1039-1101 hrs), St 5 at 150 m (1213-1235 hrs), St 6 at 270 m (1405-1415 hrs) and St 7 at 40 m (0336-0432 hrs).

The fish size distribution with depth was bimodal in the upper layer (station 1, 2, 4 and 7) and ranged from 19 to 50 mm with an average length of 31 mm. The fish size in the lower layer (station 3 and 5) ranged from 30 to 51 mm with an average length of 39 mm (Figure 10).

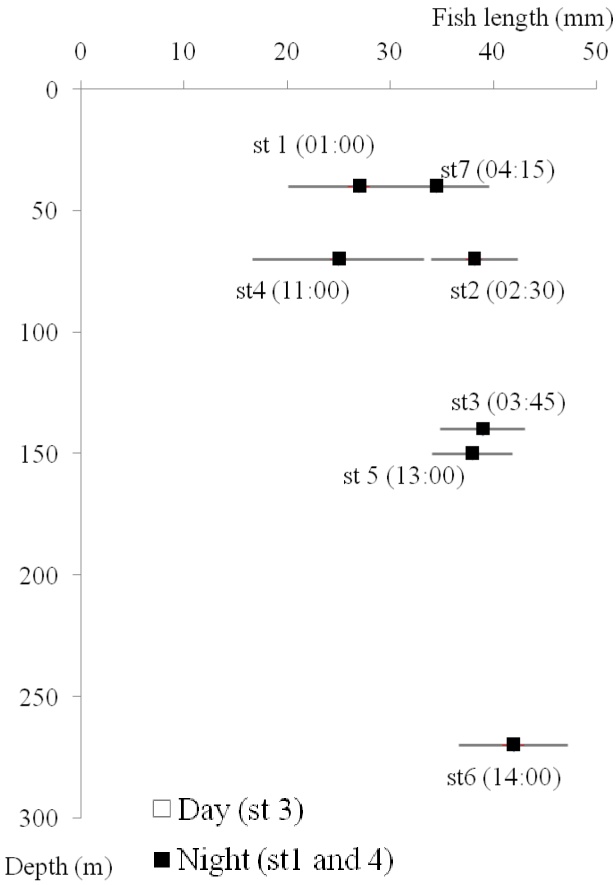


Figure 10 Length distribution by depth of *M. muelleri* in Masfjorden. The bars represent standard deviation and the numbers in brackets show the trawling times (GMT).

Length-weight of *M. muelleri*

The length and weight relationship of *M. muelleri* in Masfjorden is shown in Figure 11. Least squares regression of W (g) on L (mm) was derived after ln transformation of the two variables (ln w= ln q + bln l). The wet weight ranged from 61 mg to 1548 mg, with 20 (4.1%) of individuals being more than 1000 mg. Wet weight (W, mg) can be calculated from length (L, mm) by

$$W = 0.004282578L^{3.244152} \quad (1)$$

$$(N= 491, r^2 = 0.983, 19 \leq L \leq 51)$$

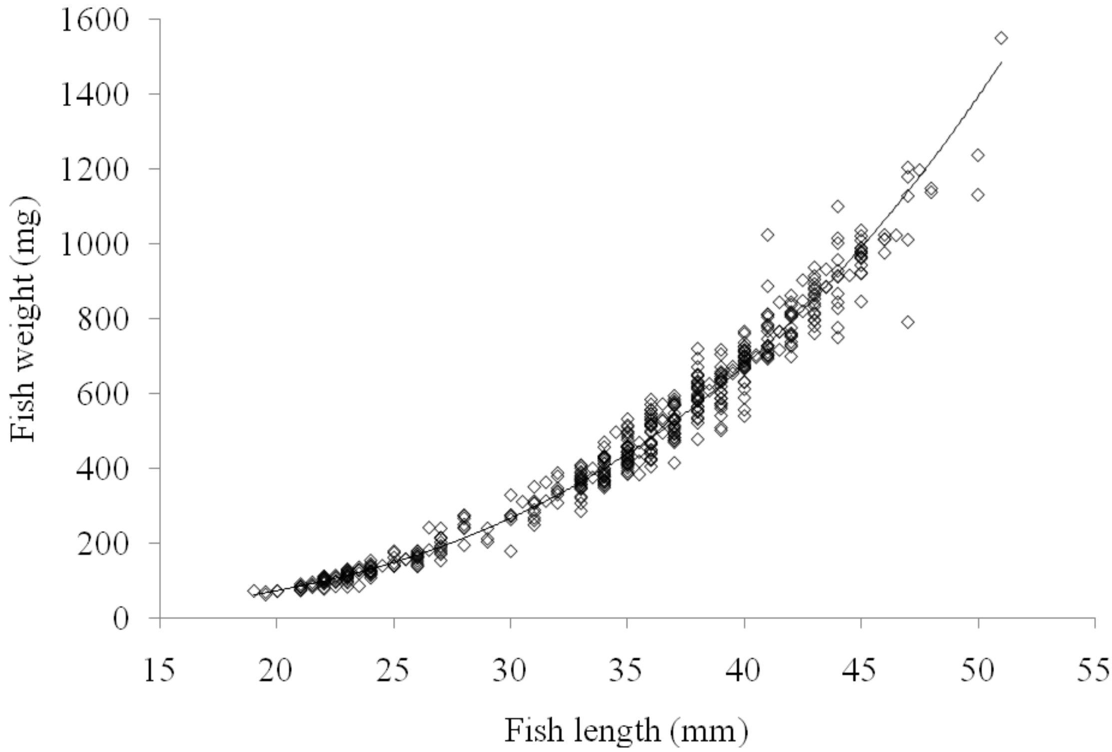


Figure 11 Length and weight of measured *M. muelleri* in Masfjorden. Relationship between length and weight is given by equation 1. The equation was found by linear regression on ln transformed data.

Regression lines between length and weight of large fish (34.5-51 mm) from the upper and lower SSLs are given in Figure 12. Fish in the upper SSL were from station 1, 2, 4 and 7 and the fish in the lower SSL were from station 3, 5 and 6. The length-weight relationships of two layers are given by the equations below. For more detail see Appendix 6 and 7.

Upper layer $$W = 0.00858L^{3.051751} \qquad (2)$$
$$(N= 131,\ r^2 = 0.903,\ 34.5 \le L \le 50)$$

Lower layer $$W = 0.016774L^{2.881919} \qquad (3)$$
$$(N= 127,\ r^2 = 0.903,\ 35 \le L \le 51)$$

Large fish from the upper layer had slightly lower weights than the fish from lower layer. A Chow-test revealed that the length-weight relationships of large fish between layers were significantly different (p-value < 0.01). For more detail see Appendix 8.

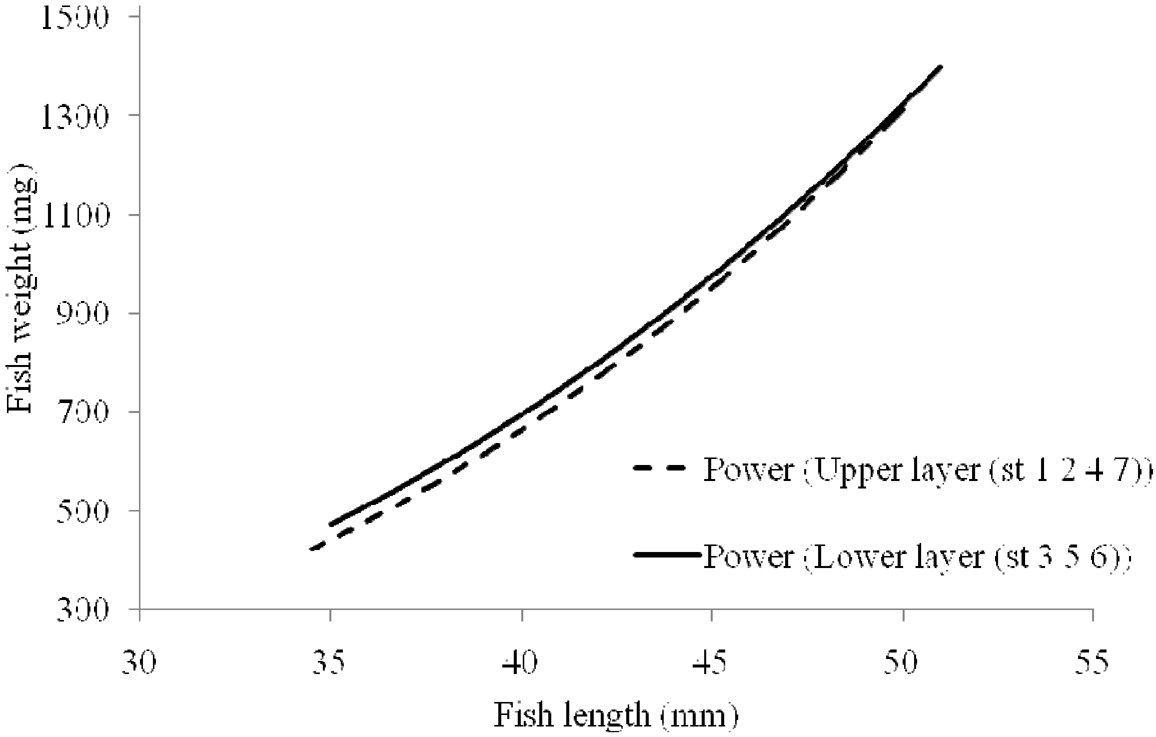
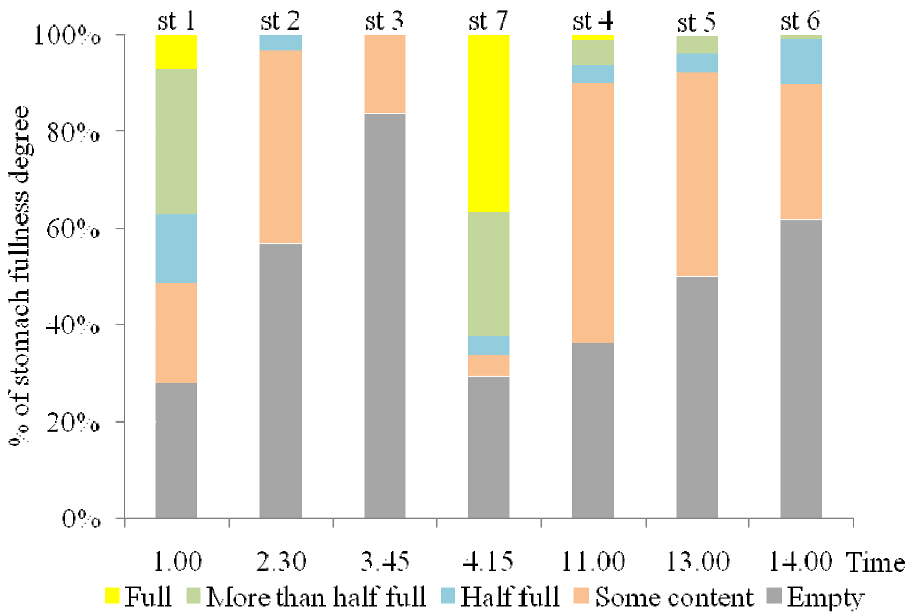


Figure 12 Regression lines of wet weight as function of length of large *M. muelleri* in the upper and lower layer. Relationships between length and weight of the upper and lower layer are given by equation 2 and 3, respectively. The equations were found by linear regression on ln transformed data.

Feeding and stomach content of *M. muelleri*

The degree of stomach fullness and digestion for *M. muelleri* from 7 pelagic stations (16 trawls) are given in Figure 13. Most of the fish in each station had empty stomachs, except the fish from station 1 (0100 hr), station 4 (1100 hr) and station 7 (0415 hr) where the stomachs were mainly defined as more than half full, with some content, and full respectively. Station 3 (0345 hr) had the highest percentage of fish with empty stomachs (83.8 %) and most fish (36.6 %) from station 7 (0415 hr) had full stomach. For the degree of digestion, the fish with food in the stomach mostly had the digestion stage as 'partly digest'. Most fish from station 3 (0345 hr) and station 4 (1100 hr) had the digestion stage as unidentified and digestion started, respectively.



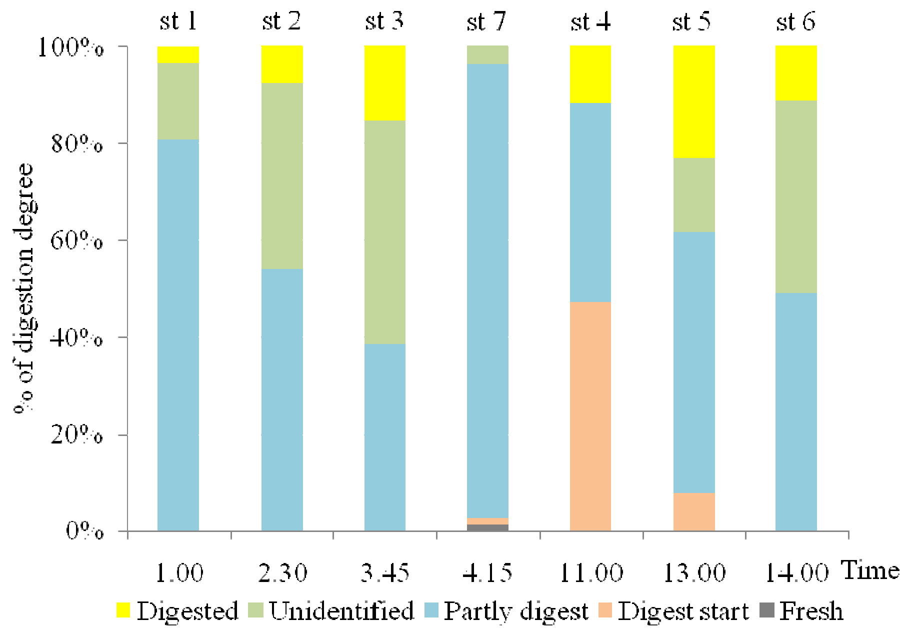


Figure 13 Degree of stomach fullness and digestion expressed as percentage (100% refers to full stomach and fully digested stomach content)

The diel variations of average stomach fullness and digestion degrees are shown in Figure 14. The degree of stomach fullness and digestion varied with daytime. The average stomach fullness declined from less than half full at 0100 hr to the lowest at 0345 hr. The fish had the average stomach fullness increasing again at 0415 hr to the highest at 1100 hr, and decrease from 1300 hr to about some content at 1400 hr. The average degree of digestion increased from partly digest at 0100 hr to about unidentified at 0345 hr, then, declined from 0415 hr to the lowest (less than partly digest) at 1300 hr before increased again to more than partly digest at 1400 hr. The highest stomach fullness was found in the fish from 1100 hr trawl (70 m depth) which mostly contained small fish. The lowest was observed for large fish from 0345 hr trawl at 140 m depth. At the lowest degree of stomach fullness, the degree of digestion was the highest (almost unidentified). The lowest degree of digestion (less than partly digest) was found for fish caught during the 1300 hr trawl.

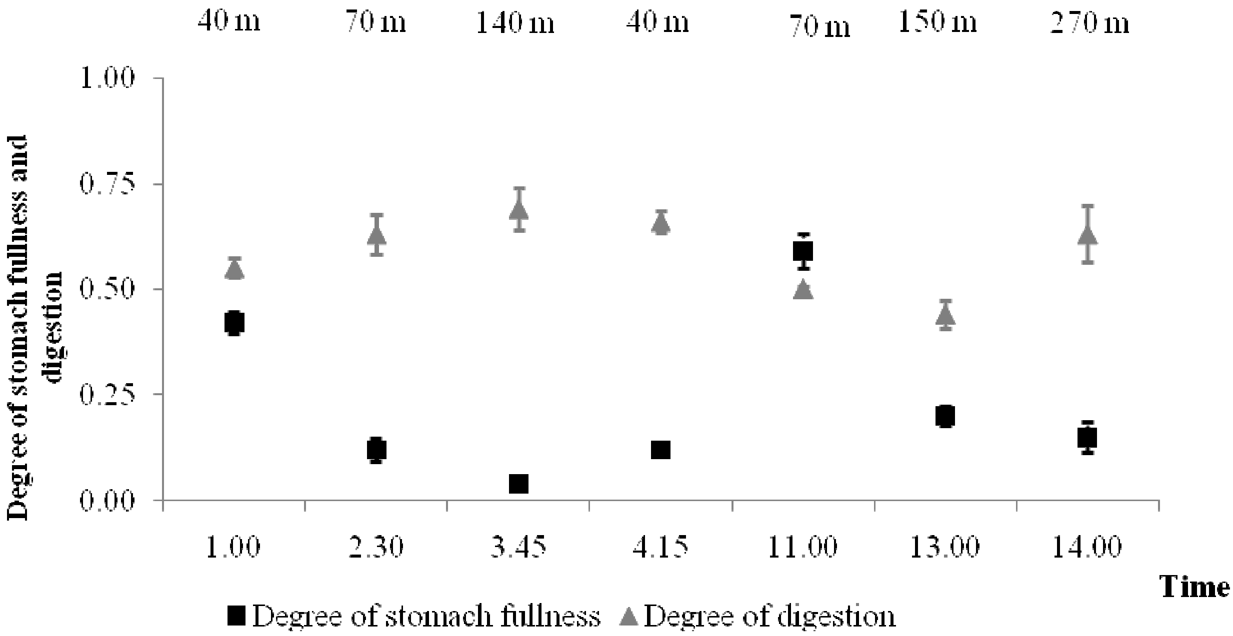


Figure 14 Diel variation of average degree of stomach fullness and digestion of *M. Muelleri*. The bars represent standard deviation. Time is in GMT.

Stomach fullness of *M. muelleri* was dependent of length as shown in Figure 15. The fraction of more than half full and full stomachs decreased with increasing size. The fish between 19 mm to 28 mm had mainly half full and full stomachs, while the large fish (29-51 mm) mainly had empty stomachs and with some content.

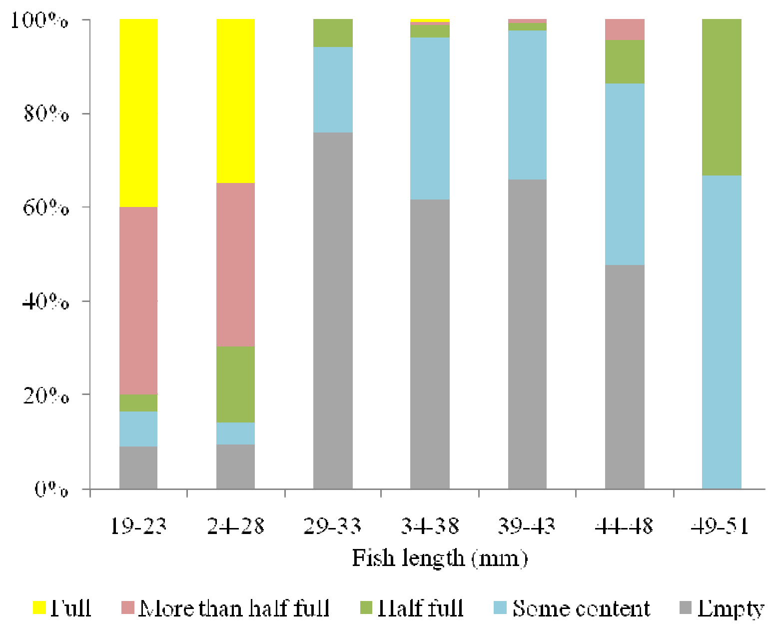


Figure 15 Stomach fullness of *M. muelleri* in different length groups (mm)

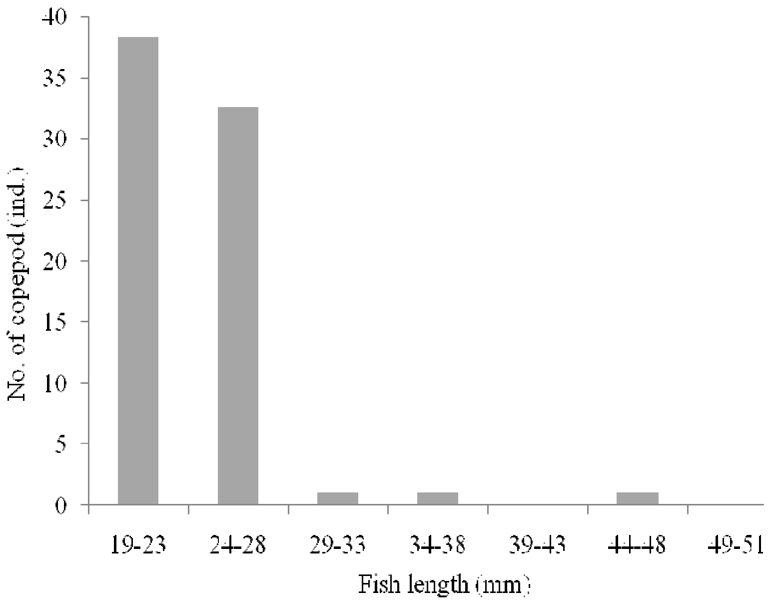


Figure 16 Mean number of copepod (ind.) in different length groups *M. muelleri*

The most numerous food items in the fish stomach were copepod in all length groups. The stomach of small fish (19-28 mm) contained mostly copepods while the large fish had very few occurrence of copepod (Figure 16). Others food items (euphausids, amphipods and egg shells) were less frequency found - two stomachs with euphausids, one stomach with amphipods and nine stomachs with egg shells (N=491).

Discussion

In the present study diel vertical migration and feeding pattern of *M. muelleri* in Masfjorden was investigated. The acoustic data was obtained from the echo sounder placed at the fjord bottom and thus had the benefit of recoding data without receiving noise from the ship. This may give a better resolution of the sound scattering layer (SSL). Fish samples were taken in or near the SSLs using a pelagic Harstad trawl, equipped with 3 nets that could be opened and closed remotely. This gives better accuracy of the fish catches at each depth since fish are not captured while the trawl moves down and up from the target depth. The selection of depths is important when sampling with a trawl and the chosen trawling depths in this study were corresponded with observed acoustic target depths. Fish sub-samples were selected randomly for the stomach analysis. The sex classification of fish was skipped in this study as most of the fish was found to be female probably due to the fish preservation method that affects the gonad to be unidentified. Partly digested preys were difficult to examine with the present method and leads to underestimate of number of food items in each stomach. The zooplankton sampling method has several limitations such as limited horizontal coverage, localised sampling will not pick up horizontal patchiness and fine scale vertical distributions are not picked up if sampling depth interval is large. The individual zooplankton in each sub-sample was sorted to groups only. Diel vertical distribution of the SSLs is closely related to changes in surface radiation (Rasmussen and Giske, 1994), but there was no light intensity measurement in the present study.

In the present study *M. muelleri* in Masfjorden in late autumn comprised two sound scattering layers (SSLs) located at approximately 25 to 200 m. The fish in the upper layer had stronger dusk and dawn migration than the fish below. The migratory depth of fish in upper layer was at approximately 25 to 75 m. This preferred depth range could be related to freshwater influence (low salinity) and higher turbidity in the water above sill depth. As suggested by Rosland and Giske (2004) these conditions could benefit a planktivorous predator, like *M. muelleri*, with a short visual prey detection distance compared to a piscivorous predator with a relatively longer visual prey detection distance. This preferred depth also could be related to the high temperature above sill depth as the fish can increase the metabolic conversion rate and thereby increasing the growth (Rosland, 1993). The diel vertical migration in this study resembled the winter distribution of *M. muelleri* in

Masfjorden reported by Giske et al. (1990), Baliño and Aksnes (1993) and Skagseth (1999). Studies in spring also found *M. muelleri* in Masfjorden in two SSLs in which the upper layer performed diel vertical migration (Bjelland, 1995; Goodson et al. 1995; Skagseth, 1999). Kaartvedt et al. (1996) found two SSLs along the cross-shelf transect from Norwegian oceanic waters and through a front on the shelf in spring. This diel vertical migration of one SSL was also found in summer in fjordic and oceanic environment in the upper 250 m (Rasmussen and Giske, 1993; Kristoffersen and Salvanes, 1998). The different in diel vertical migration between seasons of *M. muelleri* can be explained by the sensitivity of fish to the fluctuating light (Kaartvedt et al., 1996), the change of surface radiation between seasons (Rasmussen and Giske, 1994), high concentration of food and visibility near the surface (Giske and Aksnes, 1992; Rosland and Giske, 1994). Another important factor is the ontogenetic shift in juvenile fish that enter adult stage during spring which influence the motivation for diel vertical migration and the gradual merging of the two layers throughout the spring (Goodson et al., 1995).

M. muelleri in this study primarily performed dusk and dawn feedings. This is most likely a trade-off between catching food and avoiding predators. Feeding in late autumn is limited in time due to short days and low light intensities. The only option for feeding in late autumn in order to maintain growth and reduce the mortality risk is to feed when there is optimal light for visual predation on zooplankton and minimizing the visibility toward predators at dawn and dusk. This finding corresponds with study of Rasmussen and Giske (1994) who found this fish preformed nighttime feeding in summer in Masfjorden probably because the fish wanted to keep low mortality risk and high feeding rate. In some other areas, *M. muelleri* also fed at the similar period of time of all year in continental slope waters of eastern Tasmania in Australia (Young and Blaber, 1986) and in the northern Red Sea in March 1981 (Dalpadado and Gjøsæter, 1987). After dawn feeding, fish with some stomach content in the upper layer occupied the depth at about 20 m lower than during the night in order to reduce the predator risk in daytime. The decrease of stomach fullness degree after dawn feeding indicates the strong encounter-limitation on feeding during daytime and leads to a high feeding at dusk as explained by Rosland and Giske (1994). Most of adult fish remains constantly between 125-200 m depth both during day and night with mostly empty stomach over late autumn. This has implications on their overwintering mortality as well as their post winter spawning success. Rosland and Giske (1994) explained that at this depth the feeding and mortality rates vary according to surface light intensity, the feeding rate is limited by visual prey encounter rate and thus stomach fullness degree is constantly low.

Some large fish from lower SSL also performed diel vertical migration to feed at dusk and dawn when most of them remained at 125-200 m depth. This can be explained by the condition (weight/length relation of the fish) since the large migratory fish had a lower condition factor than the non-migration fish. This large fish may feed to grow, maintain the condition factor, develop gonads and thus increase fecundity. Age and size of the fishes also seem to influence the priority for feeding and predator avoidance, and may reflect short term (starvation) and long term (fecundity) trade-offs. The roaming of large fish between SSLs can also be explained by Rasmussen and Giske (1994) and Rosland and Giske (1997) who found that the migration of mature fish from the lower layer to feed due to the different of motivation for feeding and different of preferred depths. This is supported by Skagseth (1999) who found that the motivation of fish change continuously as fish grows. The fish may be attracted to strategies of feeding to grow, minimizing mortality from predators and to survive overwintering at the same time.

Degree of stomach fullness and digestion varied through day and night. The degree of digestion also indicated time of feeding. The fish in late autumn seemed to have high feeding rate at dawn and dusk which confirm the dynamic model for vertical distribution of different age groups of the mesopelagic fish Müller's pearlside (*Maurolicus muelleri*) studied by Rosland (1994). This is due to empty stomach during night and day without feeding or with very low feeding rate as there is no sufficient light for visual feeding during nighttime in late autumn. During daytime when the light intensity is very high the fish had limited feeding due to digestive process, prey encounter rate and predator encounter rate (Rosland, 1994). There was a size dependent trend in stomach fullness of *M. muelleri* in the present study. Small fish had higher degree of stomach fullness than the large fish. Studies of Rasmussen and Giske (1994) in summer and Bjelland (1995) in spring in Masfjorden revealed that juvenile *M. muelleri* had a higher degree of stomach fullness than the adult fish when Skagseth (1999) found no clear size-dependent trend in stomach fullness in Masfjorden during spring. The fraction of empty stomachs in the current study increased with size. The difference in feeding rate between length groups seems to be related to the purposes of feeding. This supported by Goodson et al. (1995) who found small fish in Herdlefjorden during winter to spring fed to grow in order to become mature and to keep the generation time low. Large fish with low feeding rate in Masfjorden in winter focused to survive to the next spawning period (Giske and Aksnes, 1992). Adult fish had low feeding rate due to the limitation of visual prey encounter rate (Rosland and Giske, 1994). Giske et al. (1990) also observed that juvenile *M. muelleri* emphasize on feeding more than the adult fish.

M. muelleri fed on zooplankton at dusk and dawn, when light intensities are sufficient enough for visual feeding on plankton, but low for predators. The main prey of *M. muelleri* was copepod in all length groups as copepods were also the dominant group of zooplankton in this study. The juvenile stomachs contained most of copepods during day and night as they occupied the shallow depth with high abundance of zooplankton. The adult fish with very low number of copepod in their stomach occupied the depths at approximately 125 to 200 m during daytime and extend to about 250 m depth during night time. This distribution of both juvenile and adult fish corresponded with zooplankton distribution and they seemed to follow to feed zooplankton at different depths. The adult fish seemed to feed by chance at the depth with insufficient light and low zooplankton abundance during daytime and nighttime. Copepods found to be a dominant prey for *M. muelleri* in many studies (Giske et al., 1990; Baliño and Aksnes, 1993; Skagseth, 1999; Bagøien et al., 2001). In summer in Masfjorden this fish fed on Cladocerans ranked by number and on copepod by biomass (Rasmussen and Giske, 1994). Bjelland (1995) reported copepods and *Coscinodiscus* spp. to be main prey in Masfjorden and and cirriped nauplii and copepod in Herdlafjorden in spring. In other areas, *M. muelleri* fed primarily on euphausids and secondarily on copepods all year round in eastern Tasmania, Australia (Young and Blaber, 1986). Copepods were also the dominant diet of this fish in the Red Sea in summer (Dalpadado and Gjøsæter, 1987). The variation of prey availability was probably related to seasonal abundances, current system, fjord topography and biological interactions as suggested by Kaartvedt et al. (1988). *M. muelleri* was also found to have a flexible feeding when the availability of different prey types occurs (Young and Blaber, 1986).

Conclusion

M. muelleri in Masfjorden in late autumn comprised two sound scattering layers of two length groups, small fish in the upper layer and large fish in lower layer. The fish in the shallow layer performed stronger diel vertical migration than the fish below and fed intensively on zooplankton at dusk and dawn. The diel vertical migration and feeding pattern of the fish seem to be a response to environment factors (shifting light regime, zooplankton distribution, temperature, water turbidity) and the state if the fish (size, stomach fullness and weight/length ratio). These findings are in accordance with previous studies and support the idea that diel vertical migrations of *M. muelleri* are driven by a combination of environment conditions, ontogenetic factors and instant changes in physiological condition.

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Appendix

Appendix 1 Average number of individuals caught per hour (ind/hr)

Depth range	Day	Night
25-50	-	665
50-100	3,694	93
100-150	39,938	-
150-200	-	15,560
200-250	-	-
>250	112	52

Appendix 2 Average percentage of pearlside in catches (in number)

Depth range	Day	Night
25-50		38
50-100	100	15
100-150	100	0
150-200	0	78
200-250	0	0
>250	11	4

Appendix 3 Total number of zooplankton, other zooplankton, mean length and number measured of copepods

Station	Time	Depth (m)	AFDW (mg/m^3)	Zooplankton ($ind./m^3$)	Others (ind/m^3)	Length (mm)	LengthSD (mm)	No. measured (ind.)
1	19:30	50	8.97	422	3	0.81	0.48	150
		100	9.34	210	17	0.73	0.26	77
		150	10.66	200	20	0.77	0.34	68
		200	9.52	118	5	0.82	0.65	40
		250	10.06	91	1	0.87	0.66	28
		300	13.55	281	4	0.70	0.28	101
		350	8.77	206	3	0.81	0.54	94
		400	9.11	161	10	0.56	0.40	53
		450	9.79	213	40	0.74	0.47	53
2	22:30	100	11.56	638	15	0.79	0.29	239
		200	9.57	437	25	0.82	0.56	140
		300	10.28	546	32	0.76	0.48	177
		400	12.34	512	40	0.70	0.42	162
		450	14.31	290	6	0.74	0.49	91
3	9:40	50	12.60	255	10	0.74	0.20	82
		100	11.65	198	1	0.71	0.20	64
		150	13.85	99	4	0.74	0.28	34
		200	13.50	202	4	0.86	0.53	85
		250	13.38	190	8	0.95	0.70	59
		300	9.96	118	3	0.81	0.46	40
		350	10.16	118	4	0.83	0.59	35
		400	11.78	149	11	0.68	0.12	41
		450	17.23	148	6	0.97	0.74	42
4	02:00	50	14.94	270	16	0.78	0.26	86
		100	8.19	216	13	0.83	0.35	63
		150	10.43	160	12	0.79	0.36	53
		200	8.75	193	3	1.02	0.73	62
		250	9.48	100	2	0.81	0.47	32
		300	14.37	258	3	0.69	0.27	88
		350	15.71	287	18	0.77	0.52	96
		400	10.91	204	12	0.75	0.44	69
		450	11.32	177	5	0.84	0.58	56

Appendix 4 Zooplankton composition (ind./m^3)

Station	Depth	Copepod	Ostracod	Amphipod	Chaetognaths	Cnidaria	Polychaete	Polychaete larvae	copepod nauplii	cyphonautes larvea	resting egg	Heliozoa	Egg
1	50-0	419.4	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	1.3
1	100-50	193.1	0.0	0.0	1.1	0.0	0.2	0.0	16.0	0.0	0.0	0.0	0.0
1	150-100	179.4	0.0	0.0	0.2	0.0	0.0	10.7	0.0	9.3	0.0	0.0	0.0
1	200-150	113.3	1.3	0.0	0.5	0.0	0.0	1.3	0.0	1.3	0.0	0.0	0.0
1	250-200	90.1	0.0	0.0	0.5	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1	300-250	276.5	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1	350-300	202.7	0.0	0.0	0.6	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0
1	400-350	150.4	8	0	0.48	0	0	1.6	0	0	0	0	0.0
1	450-400	173.1	5.3	0.0	1.0	0.0	0.0	0.0	5.3	0.0	1.3	26.7	0.0
2	100-0	622.7	5.3	1.3	0.6	1.3	0.0	0.0	5.3	0.0	0.0	1.3	0.0
2	200-100	411.7	1.3	0.2	0.5	1.4	0.2	1.3	0.0	20.0	0.0	0.0	0.5
2	300-200	514.1	4.0	0.0	1.0	0.0	0.2	0.0	0.0	2.7	0.0	24.0	0.2
2	400-300	472.0	16.0	0.0	2.4	1.1	0.0	1.3	4.0	2.7	0.0	12.0	0.0
2	460-400	283.5	4.0	0.0	1.1	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.2
3	50-0	245.9	1.3	0.0	0.2	0.0	0.0	1.3	4.0	2.7	0.0	0.0	0.0
3	100-50	197.1	0.0	0.0	0.5	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
3	150-100	94.7	1.3	0.0	0.3	0.0	0.0	0.0	1.3	1.3	0.0	0.0	0.0
3	200-150	198.7	1.3	0.0	0.6	0.3	0.0	0.0	0.0	1.3	0.0	0.0	0.0
3	250-200	182.1	4.0	0.3	0.5	0.5	0.0	0.0	0.0	1.3	0.0	1.3	0.0
3	300-250	114.7	1.3	0.0	0.3	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.2
3	350-300	114.1	2.7	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.2	0.2
3	400-350	137.9	5.3	0.0	1.1	0.2	0.0	0.0	1.3	0.0	0.0	0.2	2.7
3	450-400	142.9	4.0	0.0	0.0	0.2	0.0	0.0	1.3	0.0	0.0	0.0	0.0
4	50-0	253.9	1.3	0.0	8.0	0.0	0.0	0.0	4.0	2.7	0.0	0.0	0.0
4	100-50	202.7	2.7	0.0	0.6	0.0	0.2	0.0	4.0	5.3	0.0	0.0	0.0
4	150-100	147.7	0.0	0.0	0.0	0.0	0.0	2.7	1.3	8.0	0.0	0.0	0.0
4	200-150	190.7	1.3	0.0	0.8	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4	250-200	98.1	1.3	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4	300-250	254.9	1.3	0.0	0.2	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0
4	350-300	269.3	10.7	0.0	1.3	0.2	0.0	0.0	2.7	1.3	0.0	1.3	0.2
4	400-350	192.3	8.0	0.0	1.1	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0
4	450-400	172.0	2.7	0.2	0.5	0.3	0.0	0.0	0.0	0.0	0.0	0.0	1.3

Appendix 5 Regression analysis of length-weight relationship of overall *M. muelleri*

Regression Statistics	
Multiple R	0.991385
R Square	0.982843
Adjusted R Square	0.982808
Standard Error	0.097329
Observations	491

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	265.3663238	265.3663238	28013.26	0
Residual	489	4.632239009	0.009472881		
Total	490	269.9985628			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*	*Lower 95.0%*	*Upper 95.0%*
Intercept	-5.4532	0.068426877	-79.69385392	2.7E-282	-5.58765	-5.31875	-5.58765	-5.31875
Variable	3.244152	0.019382929	167.3716331	0	3.206068	3.282237	3.206068	3.282237

Appendix 6 Regression analysis of length-weight relationship of large *M. muelleri* in the upper SSL

Regression Statistics	
Multiple R	0.950775
R Square	0.903972
Adjusted R Square	0.903229
Standard Error	0.083558
Observations	131

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	8.478632	8.478632	1214.361	1.71E-67
Residual	129	0.900674	0.006982		
Total	130	9.379306			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*	*Lower 95.0%*	*Upper 95.0%*
Intercept	-4.75829	0.320021	-14.8687	9.51E-30	-5.39146	-4.12512	-5/39146	-4.12512
Variable	3.051751	0.087574	34.84769	1.71E-67	2.878484	3.225018	2.878383	3.225018

Appendix 7 Regression analysis of length-weight relationship of large *M. muelleri* in the lower SSL

Regression Statistics	
Multiple R	0.950725
R Square	0.903877
Adjusted R Square	0.903108
Standard Error	0.081808
Observations	127

ANOVA

	Df	*SS*	*MS*	*F*	*Significance F*
Regression	1	7.866497	7.866497	1175.421	2E-65
Residual	125	0.836562	0.006692		
Total	126	8.703059			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*	*Lower 95.0%*	*Upper 95.0%*
Intercept	-4.08792	0.311012	-13.1439	2.56E-25	-4.70345	-3.47239	-4.70345	-3.47239
Variable	2.881919	0.084059	34.28441	2E-65	2.715556	3.048283	2.715556	3.048283

Appendix 8 Chow-tests of length-weight relation of large *M. muelleri* between layers

Test of between –subject effects

Dependent Variable: W

Source	Type III Sum of squares	df	Mean Square	F	Sig.
Corrected Model	9271053.903a	2	4635526.951	1291.578	.000
Intercept	3722769.140	1	3722769.140	1037.260	.000
L	8297242.468	1	8297242.468	2311.827	.000
Group*L	44069.722	1	44069.722	12.279	.001
Error	915205.558	255	3589.041		
Total	128997719	258			
Corrected total	10186259.5	257			

a. R squared = 0.910 (adjusted R squared = 0.909)

Appendix 9 Average of degree of stomach fullness and digestion of *M. muelleri*

Station	Time	Depth (m)	Degree of stomach fullness		Degree of digestion	
			Average	SD	Average	SD
1	01:00	40	0.42	0.34	0.55	0.12
2	02:30	70	0.12	0.14	0.63	0.17
3	03:45	140	0.04	0.09	0.69	0.18
4	11:00	70	0.59	0.42	0.50	0.8
5	13:00	150	0.20	0.21	0.44	0.24
6	14:00	270	0.15	0.19	0.63	0.24
7	04:15	40	0.12	0.17	0.66	0.17