VERTICAL DISTRIBUTION AND TROPHIC INTERACTIONS OF ZOOPLANKTON AND FISH IN MASFJORDEN, NORWAY

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The distribution, biomass, and predator-prey relationships of the pelagic assemblage in Masfjorden, western Norway, was studied in January 1989. The pelagic biomass was dominated by particulate organic matter. Biomasses of copepods, macroplankton, and mesopelagic fishes were of the same order of magnitude, while the biomass of larger pelagic fishes were one order less. Predator-prey relationships seemed most important at intermediate and higher trophic levels. Two sound-scattering layers, consisting of adult *Maurolicus muelleri* (lower layer) and juvenile *M. muelleri* (upper layer) performed instantaneous light-dependent vertical migration. Vertical distributions are explained in terms of balancing food demands against predation risk.

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INTRODUCTION

Although vertical distribution and vertical migration are among the most studied topics in aquatic biology, only a few studies have focused on the distribution of a marine community (ANONYMOUS 1974, 1975; HOPKINS & al. 1978, 1989; VINOGRADOV & TSEITLIN 1983; ROE & al. 1984). Here we describe the pelagic ecosystem in Masfjorden, western Norway, with herbivorous and carnivorous zooplankton, mesopelagic planktivorous fishes, and piscivore toppredators.

Previous cruises to the fjord (unpubl.) have revealed distinct sound-scattering layers (SSLs) which often show marked vertical migrations. The species composition of the SSLs in Masfjorden have until now not been identified due to improper sampling gear, and the factors determining the vertical distributions are not known.

The two principal goals of this investigation were therefore (1) to determine the contents of the sound-scattering layers and (2) to estimate the biomasses, describe the vertical distributions, and identify the main predator-prey relationships of the pelagic assemblage in winter.

THE FJORD

Masfjorden (Fig. 1) is 20 km long and 0.5–1.5 km wide, with a sill depth of 75 m and maximum depth of 494 m. The main fjord (25 km^2) is divided into three basins with maximum depths of 300 (Stn A), 494 (Stn B), and 200 m (Stn D). Descriptions of the pelagic environment are given by KAARTVEDT & al. (1988), AKSNES & al. (1989), and KAARTVEDT (1989).

MATERIAL AND METHODS

Distribution and biomass

Samples were collected during a cruise with R/V *Håkon Mosby* 6–12 January 1989. The main investigation was carried out in the deep B basin, and some studies were performed at the innermost Stn D.

Salinity and temperature profiles were measured with a Neil Brown CTD Mark III. Underwater light was measured five times in the upper 30–70 m by a 4π QSP-160 quantum sensor. Surface light was registered by a 2π LI-185 photometer continuously from 0800 to 1600 h local time throughout three days.

Samples of particulate organic carbon (POC) and nitrogen (PON) were obtained by a rosette Niskin water sampler. 1–1.5 litres were filtered from each sampling depth (Table 1). Concentrations of POC and PON were determined with a Carlo Erba Strumentatione 1106 CHN-analyzer, and the respective C : N ratio calculated.

Locations of two SSLs were obtained from printouts from a 120 kHz Simrad echo sounder. First, lines were drawn by hand along the top and the bottom of the SSL records obtained 8 January. Then the boundary depths of the SSLs were found at approximately 8 min intervals and the respective light intensities were calculated using surface light from the same minute and light extinction coefficients determined from the under-water light intensity measurements.

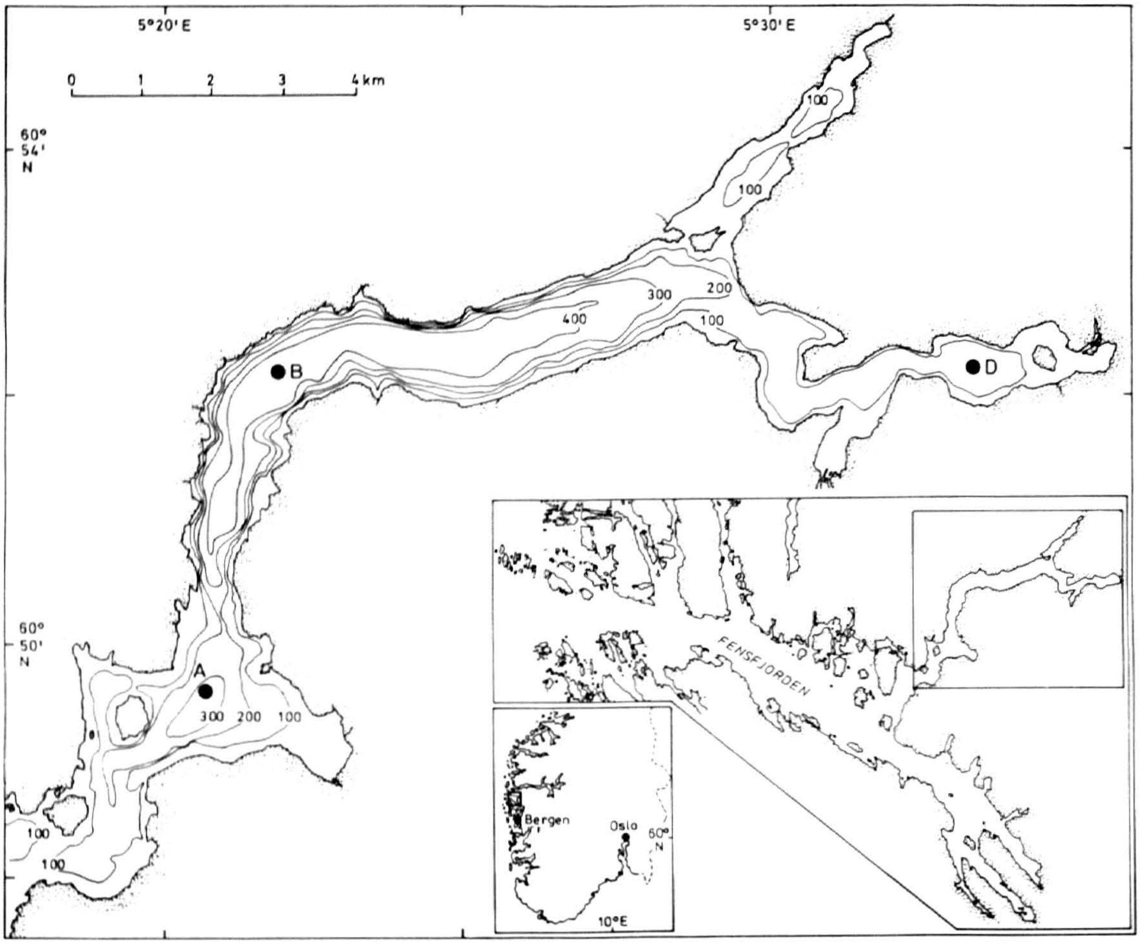

Fig. 1. Map of Masfjorden. Locations of sampling stations is indicated.

For simplicity, we classify the pelagic animals into four categories. Animals smaller than krill are called 'zooplankton' while krill and prawns are called 'macroplankton'. 'Mesopelagic fishes' refer to *Benthosema glaciale* (REINHARDT) and *Maurolicus muelleri* (GMELIN), while larger fishes are called 'large fishes'. Biomass conversions between ash free dry weight (AFDW), dry weight (DW), and wet weight (WW) are done according to OMORI (1969) and PARSONS & al. (1977). For zooplankton a DW : AFDW of 2 and a WW : DW of 7 is assumed. For macroplankton and fishes a WW : DW ratio of 5 and 10 % ash content of DW is used.

Table 1. Sampling design.

Device	Station	Sampling depths (m) or periodicity
38 and 120 kHz sounder		continually
120 kHz integrator	B	0–160 during Harstad trawling in lower SSL
Neil Brown CTD	B	0–480
QSP 160 quantum sensor	B,D	Each m until Iz < 10^{-3} μE m^{-2} s^{-1}
LI 185 photometer		continually during daylight
Buster ROV	B,D	0–200 at daytime (B) and dusk (D)
Niskin water sampler	B	10, 30, 50, 70, 90, 125, 175, 250, 350
Juday net	B	0–50, 50–100, 100–150, 150–200, 200–300, 300–400, 400–480, 0–480
MOCNESS trawl	B	0–20, 20–40, 40–60, 60–100, 100–150, 150–200, 200–300, 300–400
MOCNESS trawl	D	0–20, 20–40, 40–60, 60–80, 80–100, 100–120, 120–140, 140–160
IKMT	B	0–100 at night, in SSLs during day
Harstad trawl	B	mainly 0–250, 1 in lower SSL

To get information on the fine-scale distribution of plankton and mesopelagic fishes, underwater video recording was made down to 200 m with a Buster Remotely Operated Vehicle (ROV). Macroplankton, mesopelagic fishes, siphonophores, and chaetognaths were counted in each depth layer, and smaller 'particles' were counted from four frozen images from each 20 m. The recordings were done using continuous artificial light, and the range of the camera was probably not much affected by changes in natural light. Absolute quantification is impossible since we do not know the range of the camera, or whether animals were attracted by, insensitive to or frightened by the light and the ROV, but the video gave qualitative information of finer scale vertical distribution. While flashlight probably would have disturbed the distributions and densities less, continuous light was used to detect sharp vertical gradients.

Zooplankton sampling was only performed at night. Zooplankton was caught with a double Juday net (diameter = 1 m, mesh size = 180 μm, vertical hauling speed = 0.5 m s^{-1}) and with a 1 m^2 Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS; WIEBE & al. 1985; mesh size = 330 μm, vertical hauling speed = 0.25 m s^{-1}, horizontal speed = 1 m $^{-1}$). Table 1 gives sampling intervals. One Juday-net sample was preserved in 4 % buffered formaldehyde for identification (copepods were identified to genus) and enumeration, the other was frozen for later determination of AFDW. Mesopelagic fishes, pelagic prawns, and euphausiids from the MOCNESS samples were identified and counted on board. The residual MOCNESS samples were fractionated by sieve into two zooplankton size classes: < 2 mm and > 2 mm. The largest size class was frozen for later AFDW determination. The smallest size class was split with a Folsom splitter to determine the distributions of the taxa and biomass as for the Juday series.

Macroplankton and mesopelagic fishes were also sampled by a 10 m^2 Isaacs–Kidd Midwater Trawl (IKMT) (ANONYMOUS 1981). Five hauls were taken between 100-0 m at night and four hauls were taken in the SSLs at day. The depth was controlled during sampling by a Simrad trawl eye. Otherwise, the sampling procedure followed KAARTVEDT & al. (1988). To get estimates of biomasses in the entire water column, original estimates of night hauls were first corrected for gear performance compared to a smaller IKMT as in KAARTVEDT & al. (1988). Then the estimates were corrected for the fraction of each population known from MOCNESS night samples to stay below the range of the IKMT-hauls.

A midwater trawl ('Harstad-trawl') was used to catch large pelagic fishes for identification and stomach analyses, and also to sample the lower SSL (Table 1). The opening of the trawl is 20 x 20 m during trawling at 1.5 m $^{-1}$ at 0–50 m depth, and the opening area decreases slightly with increasing depth (NEDREAAS & SMEDSTAD 1987). Maximum and minimum stretched mesh size of the trawl is 100 and 30 mm, while the stretched mesh size of the cod end is 8 mm. The cod end is 15 m long, and its opening during trawling varies between 1.5 x 1.5 m^2 and 3.1 x 3.1 m^2. This trawl also caught mesopelagic fishes and prawns. Due to a general selective sampling by trawling, all estimates of prawns and mesopelagic fishes based on the Harstad trawl are underestimates. All krill passed through except in the cod end. Fishing during shooting and hauling of the trawl is included in the volume calculations, which leads to underestimation of the real densities. The Harstad trawl was towed at speeds of 1.5 and 2.5 m s^{-1} and the depth was controlled during trawling by a Simrad trawl eye.

An estimate of the biomass of macroplankton and mesopelagic fishes was made, based on the Harstad trawl catch and simultaneous 120 kHz echo integration in the upper 160 m. The trawl fished horizontally in the lower SSL except during shooting and hauling. Comparison of trawl catches and echo integration depends on equal sampling efficiency of all particles giving echo and no echo from unsampled particles:

(1) $BF = CT \cdot (DF/DL) \cdot (VF/VT)$

where BF is estimated biomass (WW) in upper 160 m of sound reflecting animals, DF and DL are mean deflection in 0-160 m and in lower SSL, respectively, CT is catch in the trawl and VF and VT are basin volume 0-160 m and trawled volume, respectively. The time-varied gain (TVG) depth limit of the 120 kHz echo sounder is 120 m, but reliable quantitative data of relative densities can be obtained down to 200 m (FALK-PETERSEN & HOPKINS 1981).

Abundance estimates of large fishes were obtained by counting typically dome-shaped echogram registrations of individual fishes when analyzing the echograms of a 38 kHz Simrad echo sounder. The sounder was used with a 20 Log R TVG compensation. The depth (z) of each individual fish recording was also noted. The counts were arranged for each 50 m depth interval. The upper 0–50 m were not included in the estimates since large errors occur at shallow depth (ONA 1987). Calculation of fish densities and biomasses were performed according to ONA (1987): an area-dependent fish density (r) was estimated and transformed to biomass values using volume data for each depth stratum and the distance sailed by the ship during echo registrations. The formulas were modified to express all results in metric units:

(2) $r = N/A$

where N is the number of fish counts in a stratum and A is the effective sampling area of the sounder beam. A can be found as a function of the maximum detection angle θ_{max}:

(3) $A = z \cdot 2\tan(\theta_{max}) \cdot d$

where z is the mean depth of the stratum and d is the distance sailed during echo registrations. A regression relating θ_{max} to depth is given by ONA (1987) for similar instrumentation and for fish sizes comparable to the ones in the trawl catches from Masfjorden.

Stomach analyses

Stomach analyses of the euphausiid *Meganyctiphanes norvegica* (M. SARS) was performed on specimens taken from IKMT night samples (2100, 0200, and 0500 h). The stomachs of 12 individuals were dissected from each sample. Six individuals were of similar size, with carapace lengths of 4.5–5 mm, six were spread along the size range available in the sample. The degree of fullness of the stomachs was judged according to an 1–4 scale (full, at least half full, containing some food, and empty). C : N analyses of the stomach-content were performed in order to compare with the values of the water column. The C and N values of the stomach contents were obtained by subtraction of values calculated from a size-dependent regression of the C and N content of the stomach walls.

Stomach-content analyses of adult *M. muelleri* and *B. glaciale* were performed on specimens from Harstad trawl catches taken at 1400, 1700, 2200, and 0400 h. The con-

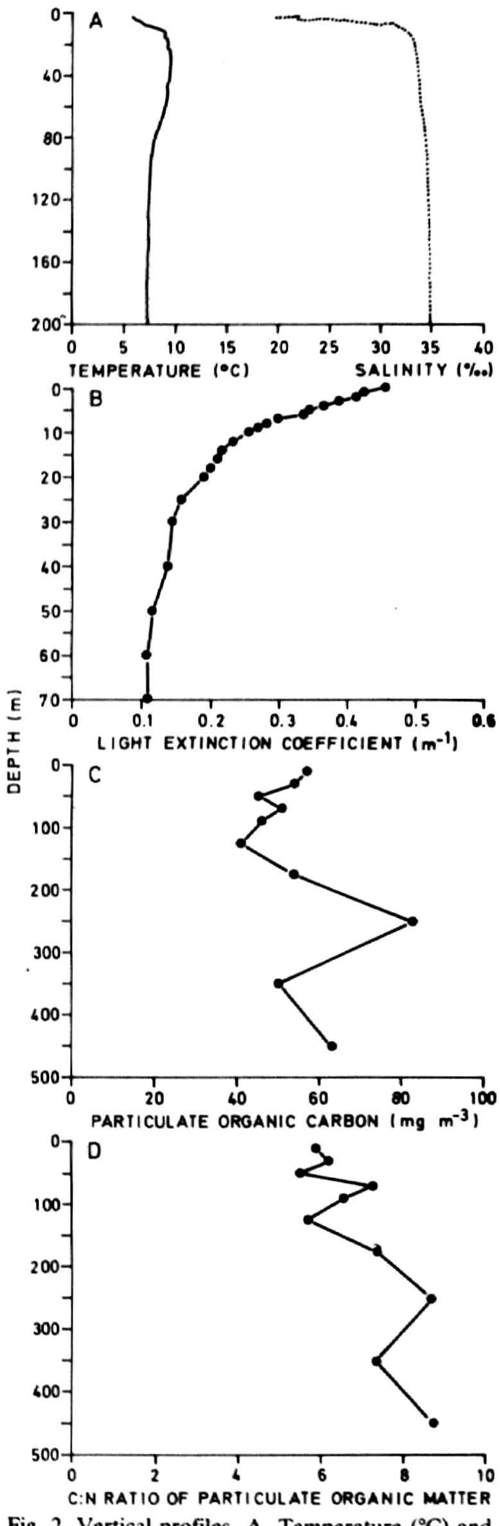

Fig. 2. Vertical profiles. A. Temperature (°C) and salinity (‰ S). B. Light extinction coefficient (m^{-1}). C. Particulate organic carbon POC (mg carbon m^{-3}). D. C : N ratio of POC and PON.

tent of 20–30 stomachs of each species were identified, and classified as fresh, decomposed, or unidentified. All items were counted and grouped to lowest possible taxon.

Degree of stomach fullness of large fishes from Harstad trawl catches was classified as empty, a little content, half full, full, extended or turned. Individual food items were identified to the lowest taxon possible and grouped according to size and degree of digestion (fresh, digestion started, all species identifiable, half digested, almost digested, fully digested). Excess moisture was absorbed by absorbant tissue, each group was weighted to the nearest milligram and the individuals counted.

RESULTS

Distributions

Physical and chemical properties

Fig. 2A shows salinity and temperature profiles from Stn B. There was a temperature maximum at 35 m (9.7° C). Below 150 m the temperature was 7.3° C. Maximum surface light intensities were 60–70 μE m^{-2} s^{-1} Fig. 2B gives vertical light extinction coefficients.

POC and PON

POC concentrations varied between between 40 and 60 mg m^{-3}, except the maximum registration at 250 m (Fig. 2C). The C : N ratio (Fig. 2D) varied with depth, showing an overall increase from a minimum of 5.5 at 50 m depth to a maximum of 8.8 at 450 m.

Zooplankton

Fig. 3A gives particle counts (still-photos) in the upper 200 m at Stn D (daytime) and at Stn B (dusk). Particles far away from and too close to the camera lens were difficult to identify. The shapes and movements of the more visible particles suggested that they were copepods. At Stn B there was a local particle maximum at 100 m depth, and another at 180–200 m. The particles above 50 m seemed to be smaller than the deeper particles. Densities were generally lower at Stn D. Except for the maximum about 100 m, there was little vertical variation in particle content at this station.

Vertical distribution of zooplankton from Juday and MOCNESS night samples are given in Fig. 4 and in Table 2. A peak in both numerical abundance and biomass was found between 150 and 200 m C > 300 ind m^{-3}). Above 100 m there were approximately 70 ind m^{-3} (from Juday), and below 200 m the densities declined gradually. A minimum was indicated between 100 and 150 m.

The body sizes of zooplankton organisms varied with depth (Fig. 5). In the upper 100 m small copepods like *Oithona* spp. and *Microcalanus* spp. were numerically dominant (Table 2). The largest densities of CV *Calanus finmarchicus* (Gunnerus) were

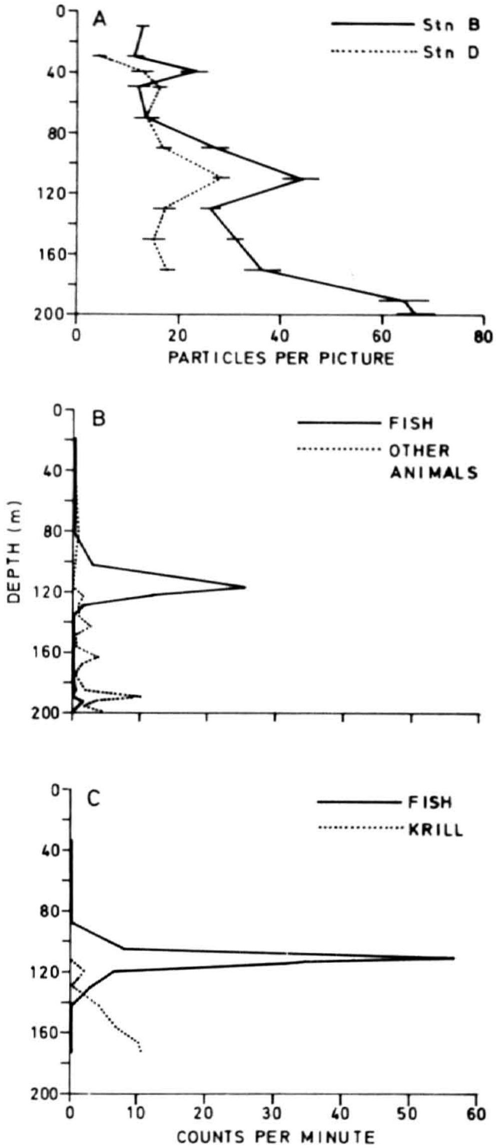

Fig. 3. Observations from the ROV. A. Particle counts (mainly copepods) in Stns B and D. B. Counts of mesopelagic fishes and other animals from Stn B. C. Counts of mesopelagic fishes and krill in Stn D.

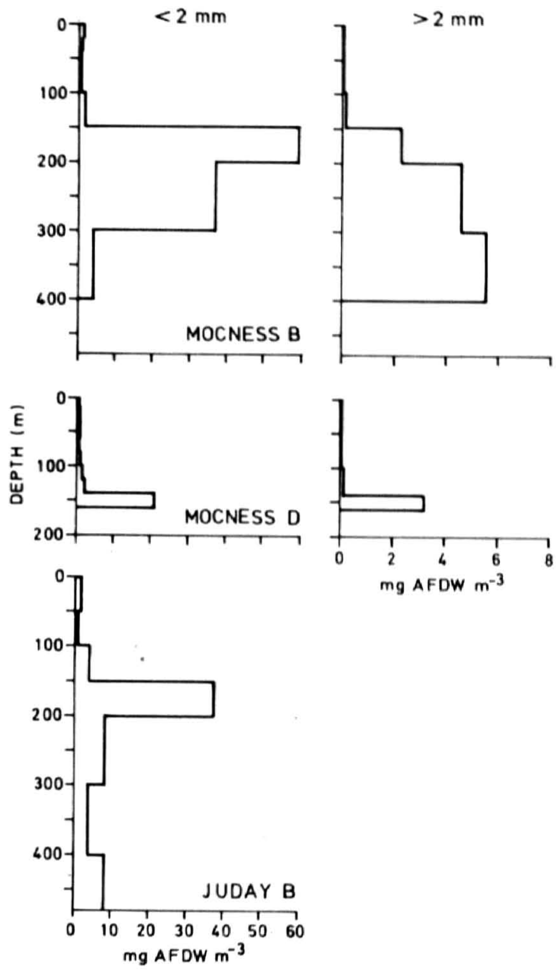

Fig. 4. Vertical profiles of zooplankton. Biomass (mg AFDW m^{-3}) of animals smaller than 2 mm (at left) and larger than 2 mm (at right). MOCNESS trawl in Stn B (upper row) and Stn D (middle), and Juday-net hauls in Stn B (lower row).

found in the 150–200 m (but also 200–300 m) layer, while the biomass of the largest zooplankters (> 2 mm, Fig. 4) had its maximum in the deepest sample. The largest zooplankters at Stn D were only found in the deepest strata sampled (140–160 m). The layer below 150 m had the maximum total density and biomass of total zooplankton regardless of station and sampling gear.

Macroplankton and mesopelagic fishes

The 120 kHz echogram showed two distinct sound-scattering layers both day and night (Fig. 6). Midday depths were 50–100 m for the 'upper SSL' and 100–150 m for the 'lower SSL'. The upper SSL moved to the surface at dusk and from the surface at dawn, but was located at 30–60 m during the night. The lower SSL stayed in the same depth both during the day and the night. The vertical extension of the layers at daytime was approximately 20–50 m, and their boundaries sometimes overlapped. The light intensities in the centers of the layers differed by a factor of 200 at daytime (Fig. 7). During day, both layers moved vertically in response to short-time fluctuations in surface light.

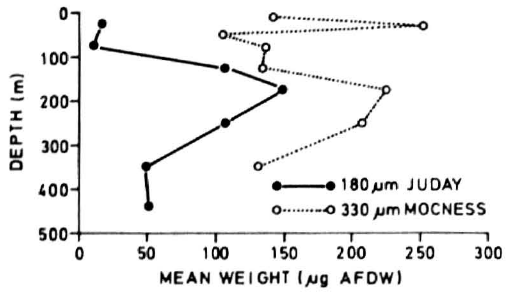

Fig. 5. Mean individual weight (µg AFDW) of zooplankton. Vertical profile of the size class less than 2 mm from MOCNESS trawl and Juday net.

A layer (100–125 m) of mesopelagic fishes was recognized by the ROV (Fig. 3B) at the depth of the lower SSL at Stn B at dusk. All fishes that came close to the camera seemed to be of the same size. The upper SSL could not be visually discriminated from the pelagic assemblages above and below. Similarly, at Stn D (at daytime 1430 h) a layer of mesopelagic fish was observed at 100–135 m (Fig. 3C), and the upper SSL was not detected. Among the 'other animals' in Fig. 3B, each group had distinct depth distributions. Siphonophores were seen between 70 and 150 m, large crustaceans below 150 m, chaetognaths at 189–190 m and medusae or pteropods (identification from video difficult) below 190 m. (According to Fig. 4, most of the large zooplankters at Stn B were located below 200 m and out of the range of the video. These distinct layers are therefore in the upper range of their vertical distributions.) At Stn D, only mesopelagic fishes and krill were identified (Fig. 3C), the latter in very high densities close to the bottom.

An IKMT catch from the upper SSL (0–27 m) taken in the morning consisted of 43 % (by number) juvenile *M. muelleri* and 57 % (predominantly juvenile) *M. norvegica*. (Table 3). At midday, the IKMT only caught juvenile *M. muelleri* in the upper SSL (65–92 m). An IKMT towed through the entire lower SSL (116–162 m) contained all five species of macroplankton and mesopelagic fishes, while the catch from the center of the lower SSL (125–140 m) contained little but siphonophores. A Harstad trawl catch from the lower SSL (125–150 m) at midday consisted of 420 kg (> 99 %) *M. muelleri* adults.

The night time vertical distributions of the mesopelagic fishes *M. muelleri* and *B. glaciale*, the prawns *Pasiphaea multidentata* ESMARK and *Sergestes arcticus* KRØYER, and the krill *M. norvegica* at Stn B and Stn D from MOCNESS are given in Fig. 8. *P. multidentata* and *S. arcticus* were not captured at the shallowest Stn D, while the smallest species,

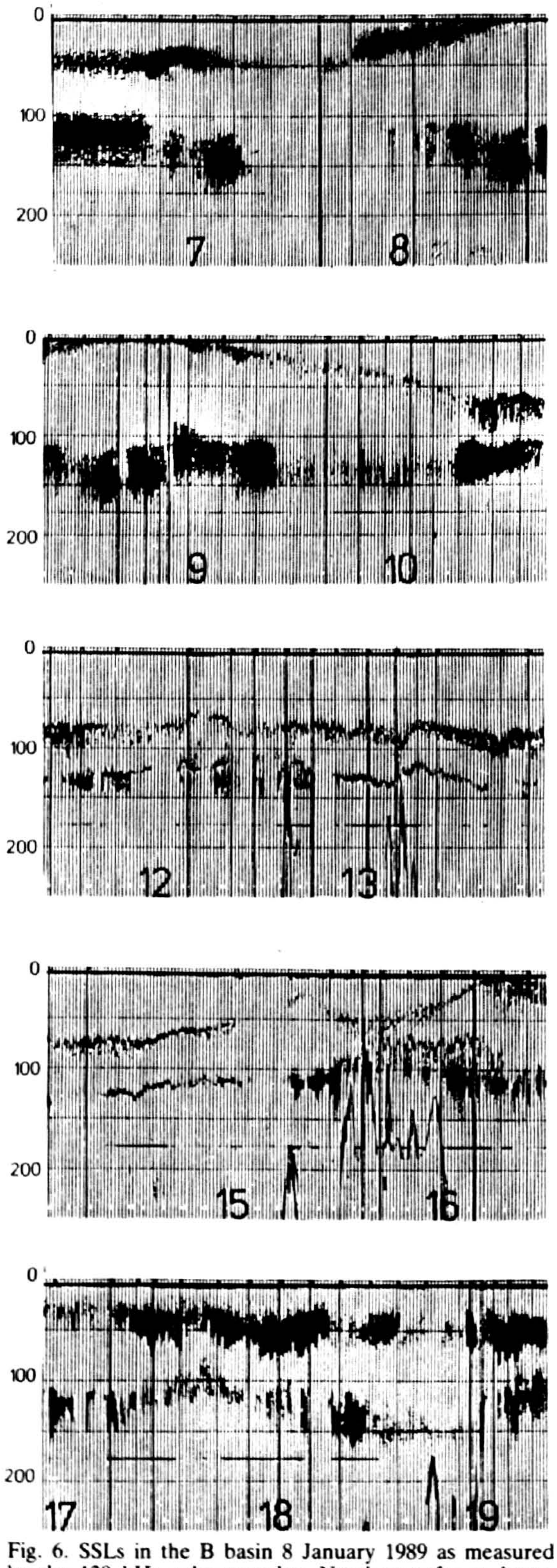

Fig. 6. SSLs in the B basin 8 January 1989 as measured by the 120 kHz echo sounder. Numbers refer to hour.

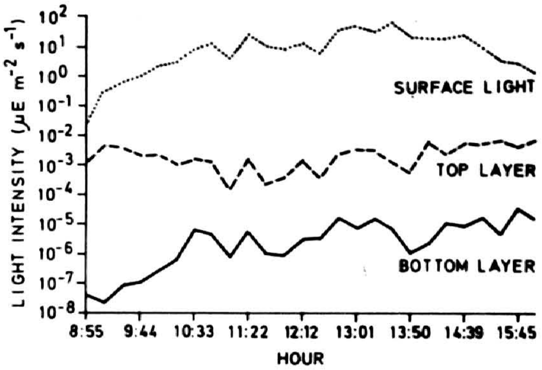

Fig. 7. Light intensities at surface and in centre of SSLs 8 January 1989, calculated from distribution of SSLs (Fig. 6).

M. norvegica, was found in large densities at this station. The night time distribution of juvenile *M. muelleri* (40–60 m) coincided with the extension of the upper SSL (Fig. 6). *M. norvegica* had their maximum densities above the upper SSL.

Large fishes

Table 4 gives the vertical distribution of large fishes in the B basin at 2000 h. The table is constructed from echograms (eqs 2–3). Densities were higher than average between 150 and 350 m, with maximum densities in the 250–300 m interval.

Biomass

Table 5 gives biomass figures of POC, zooplankton, macroplankton, mesopelagic fishes, and large fishes in the B basin. Biomass of POC (from Fig. 2C) of the B basin was estimated to 213.1 tonne carbon. Total zooplankton biomass was estimated to 29.5 tonne AFDW from Juday hauls and 59.0 tonne AFDW of the 2 mm fraction from the MOCNESS trawls. The differences between the estimates are mainly due to lower catches of *C. finmarchicus* by the Juday net (Table 2). The biomass of the size fraction 2 mm from MOCNESS in the B basin is estimated to 7.0 tonne AFDW.

Simultaneous trawling and echo integration in the lower SSL (125–150 m) gave a catch of 420 kg WW, consisting almost entirely of adult *M. muelleri*. From total catch of adult *M. muelleri*, volume of the layer ($2.8 \cdot 10^8 m^3$) and trawled volume ($1.5 \cdot 10^6$ m^3), the biomass of adult *M. muelleri* in

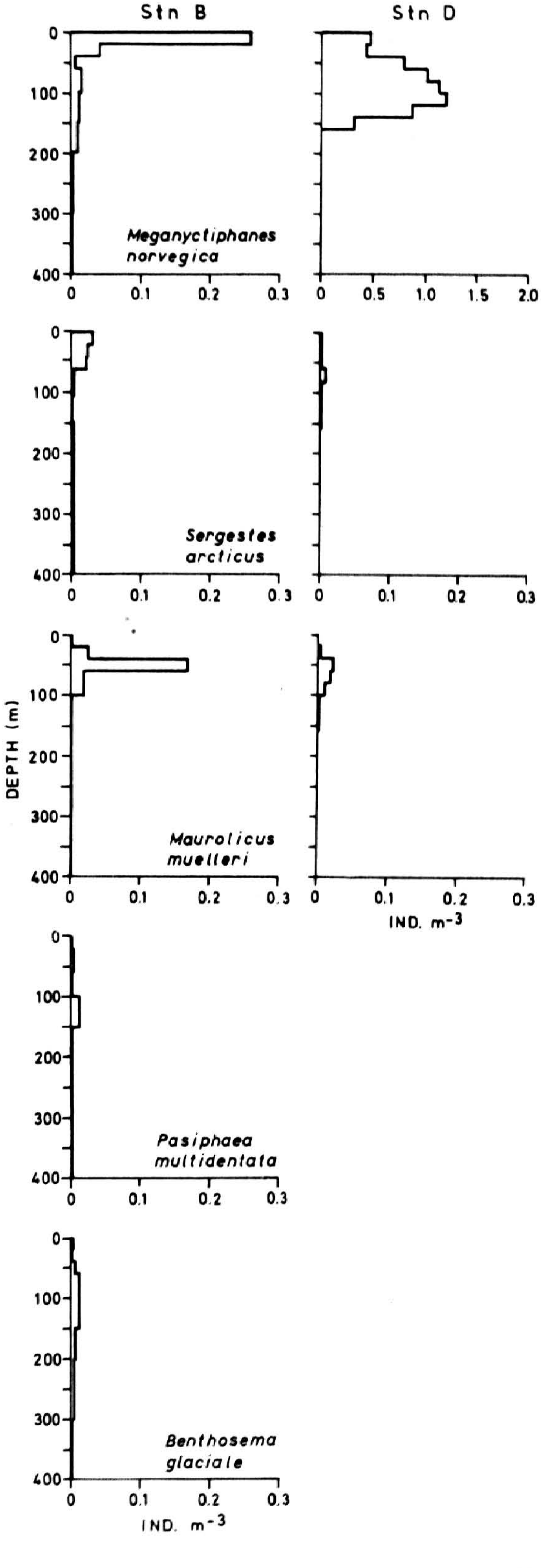

Fig. 8. Night time vertical distribution of macroplankton and mesopelagic fishes. Average densities (ind m^{-3}) from MOCNESS catches. Catches from B basin in left column and catches from D basin at right.

Table 2. Vertical distribution of zooplankton (ind · m^{-3}) from Juday net and MOCNESS trawl. The 0–400 m and 0–160 m columns in the MOCNESS series and the first of the 0–480 m column of the Juday series are the calculated averages of the individual hauls, while the second 0–480 m (Juday) column is the integrated haul.

Juday net in station B:									
Top of layer (m)	0	50	100	150	200	300	400	0	0
Bottom of layer (m)	50	100	150	200	300	400	480	480	480
Total individuals	77.4	72.5	38.4	252.7	77.6	80.9	73.5	90.4	91.2
Copepods	74.5	71.6	37.5	250.8	75.1	73.5	67.6	87.7	87.5
Calanus finmarchicus	2.1	1.0	7.7	209.5	36.5	4.3	3.2	32.7	32.0
Microcalanus	8.4	6.3	1.9	5.0	10.6	28.1	25.1	14.5	14.5
Metridia	1.5	1.1	0.7	5.0	4.6	1.9	0.9	2.0	2.4
Oithona	58.6	62.1	26.8	30.3	21.8	33.5	31.6	35.7	35.3
Acartia	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1
Copepod nauplii	2.4	0.5	0.2	0.0	0.5	1.7	3.0	0.7	1.3
Other copepods	1.0	0.6	0.4	1.0	1.1	4.0	3.9	2.1	2.0
Non-copepods	2.9	0.9	0.8	1.9	2.5	7.4	6.0	2.8	3.7
MOCNESS in station B:									
Top of layer (m)	0	20	40	60	100	150	200	300	0
Bottom of layer (m)	20	40	60	100	150	200	300	400	400
Total individuals	1.9	6.1	6.1	6.5	13.4	296.8	151.9	24.5	84.7
Copepods	11.4	5.7	5.7	6.2	12.6	294.7	149.3	22.1	83.0
Calanus finmarchicus	15.8	1.0	1.2	1.3	7.8	288.3	138.3	14.8	75.8
Microcalanus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metridia	2.7	2.0	1.3	0.6	1.3	5.2	10.4	5.8	5.2
Oithona	0.1	0.8	1.3	3.6	2.7	1.0	0.2	0.0	1.0
Acartia	2.0	0.6	0.1	0.0	0.0	0.0	0.0	0.0	0.1
Copepod nauplii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Other copepods	0.8	1.4	1.8	0.7	0.8	0.1	0.4	1.3	0.8
Non-copepods	0.4	0.4	0.4	0.3	0.8	2.0	2.6	2.4	1.7
MOCNESS in station D:									
Top of layer (m)	0	20	40	60	80	100	120	140	0
Bottom of layer (m)	20	40	60	80	100	120	140	160	160
Total individuals	23.6	14.8	7.9	8.1	10.8	21.8	19.1	173.9	35.0
Copepods	23.4	14.6	7.7	7.9	10.4	21.4	18.8	173.7	34.7
Calanus finmarchicus	5.3	2.4	1.5	0.9	1.7	10.5	5.3	149.3	22.1
Microcalanus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Metridia	1.9	0.5	0.8	0.8	1.1	7.5	10.9	23.6	5.9
Oithona	1.1	3.8	4.5	5.2	7.3	3.2	2.1	0.5	3.4
Acartia	14.7	7.1	0.4	0.3	0.1	0.0	0.0	0.0	2.8
Copepod nauplii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other copepods	0.5	0.9	0.6	0.7	0.3	0.2	0.4	0.3	0.5
Non-copepods	0.2	0.2	0.2	0.2	0.3	0.4	0.3	0.3	0.3

the lower SSL was at least 78 tonne WW in the B basin. Based on mean weight of *M. muelleri* from this Harstad trawl catch (0.90 g WW), this corresponds to 87 million (0.3 m^{-3}) *M. muelleri* in the lower SSL in the B basin.

The mean deflection to the 120 kHz echo integrator was 18.5 mm in the whole column 6–160 m and 30.5 mm in the lower SSL. Thus, the total biomass of macroplankton and mesopelagic fishes in the upper 160 m of the B basin at daytime is estimated to 322 tonne WW (eq. 1).

Table 3 gives results of the IKMT hauls in the 0–100 m layer at night. The adjusted estimate for macroplankton and *B. glaciale* in the B basin totals 363 mill. individuals. Since only juvenile *M. muelleri* were caught by the MOCNESS, and the lower SSL consisted of adults, the adjustment for fraction of MOCNESS sample caught below 100 m is not done for *M. muelleri*. Total density of *M. muelleri*, as the sum of IKMT catches in the upper 100 m and numbers in the lower SSL is estimated to 105 mill. individuals. The biomass estimate is 454 tonne WW for the macroplankton and *B. glaciale*, and a combined estimate of *M. muelleri* from IKMT and echo integration / trawling totals 93 tonne WW for *M. muelleri* in the upper 160 m in the B basin.

Table 3. IKMT catches. A. Results from IKMT night hauls. Density, mean weight, and biomass of macroplankton and mesopelagic fishes in the B basin. See text for explanation of the calculation procedure. B. IKMT catches from SSLs. Densities (numbers in 1000 m^3), mean weights (g WW), and biomasses (mg WW m^{-3}) of macroplankton and mesopelagic fishes.

A	Numbers in 1000 m^3 (IKMT)	Fraction of MOCNESS below 100 m	Total number (in millions) 0–100 m	0–400 m	Mean weight g WW	Total biomass (tonne WW) 0–100 m	0–400 m
P. multidentata	1.53	0.91	9.8	111.4	3.16	30.95	351.73
S. arcticus	4.44	0.21	8.9	11.2	0.92	8.21	10.34
B. glaciale	0.94	0.74	2.6	10.0	2.81	7.18	28.03
M. muelleri	15.91		18.8		0.81	15.21	
M. norvegica	40.44	0.16	193.8	230.7	0.28	54.27	64.60
Total	63.25		233.9	363.2		115.81	454.70

B					
	Time of day (h)	0830	0930	1100	1200
	Depth interval (m)	0–27	116–162	65–92	125–140
	Sound-scattering layer	upper	lower	upper	lower
P. multidentata	density	0	0.29	0	0
	biomass		0.10		
	ind.weight		0.36		
S. arcticus	density	0	2.93	0	0
	biomass		1.43		
	ind.weight		0.49		
B. glaciale	density	0	0.75	0	0
	biomass		0.89		
	ind.weight		1.19		
M. muelleri	density	16.28	1.34	3.01	0.16
	biomass	1.86	1.03	0.31	0.07
	ind.weight	0.11	0.77	0.10	0.45
M.norvegica	density	21.63	11.99	0	0.32
	biomass	1.91	2.28		0.02
	ind.weight	0.09	0.19		0.08
Siphonophora	biomass	0	0	0	0.25

Table 4. Distribution of larger fish in the B basin, according to registrations of individual fish with a 38 kHz echo sounder (eqs 2–3).

Layer (m)	Counts on paper	Number of fish	Tonnes WW	Density 10^{-6} m^{-3}
50–100	17	1490	1.07	2.48
100–150	48	2670	1.92	4.68
150–200	140	4590	3.30	10.48
200–250	197	5130	3.69	12.07
250–300	383	8730	6.27	22.27
300–350	262	3900	2.80	13.36
350–400	131	1600	1.15	6.69
400–450	95	590	0.43	5.84
450–495	33	120	0.09	2.78

Numbers and biomasses of large fishes in the B basin from counts on the echogram are summarized in Table 4. An estimate of 28 800 fishes and 20.7 tonne WW may be obtained for the 50–495 m interval.

Table 5. Biomass estimates for the B basin. Abbreviations for sampling methods: C = counts on 38 kHz echogram paper, E + T = 120 kHz echo integration and Harstad trawl, I + M = IKMT (except *M. muelleri*) adjusted for gear performances and MOCNESS catches, J = double Juday net, M = 1 m^2 MOCNESS, N = Niskin water bottles.

Category	Depth interv.	Sampling method	Tonne AFDW	Tonne WW
POC	0–480	N	[1]213.1	
Zooplankton	0–480	J	29.5	413
Zooplankton < 2 mm	0–400	M	59.0	887
Zooplankton > 2 mm	0–400	M	7.0	105
Macroplankton and fish	0–160	E+T	58.0	322
Macroplankton and *B. glaciale*	0–400	I+M	81.7	454
M. muelleri in lower SSL	125–150	E+T	14.0	78
Large fishes	50–495	C	3.7	21

[1] POC is measured in tonne carbon.

Table 6. Stomach content of adult *Maurolicus muelleri* and *Benthosema glaciale* from pelagic Harstad trawl catches. Number of stomachs sorted according to stomach content.

Sampling hour	1400	1700	2230	0400
M. muelleri				
Empty stomach	12	15	15	20
Fresh copepods	14	1	0	0
Fresh cop. and other	2	1	0	0
Fish eggs	2	2	1	0
Fresh other	0	0	0	0
Unident. or decomposed	1	2	6	2
Examined stomachs	31	21	22	22
B. glaciale				
Empty stomach		7	11	14
Fresh copepods		9	0	1
Fresh cop. and other		1	0	0
Fish eggs		0	0	1
Fresh other		0	1	0
Unident. or decomposed		4	10	10
Examined stomachs	0	21	22	26

Table 7. Stomach fullness of large fishes caught in the Harstad trawl. Abbreviations for species names: PV = *Pollachius virens*, MP = *Micromesistius poutassou*, SA = *Squalus acanthias*, CL = *Cyclopterus lumpus*, and AS = *Argentina silus*. Individuals with distended or turned stomachs excluded.

Species Number of ind.	PV 6	MP 45	SA 2	CL 4	AS 1
Empty stomach	0	20	2	4	1
Some content	3	13	0	0	0
Half full	1	8	0	0	0
Full	2	4	0	0	0

Stomach analysis and diel feeding patterns

The degree of fullness of krill stomachs showed a clear decrease through the night: all individuals captured at 2100 h had full stomachs, while more than 40 % of the stomachs from 0500 h were empty. The 0200 h values were intermediate. The colour of the stomach contents were often brown-green or white-green, but analyses under dissecting microscope could not reveal the proper identity of the finely chewed particles. No size-dependent trend concerning kind of food in the stomachs could be detected. Material originating from crustaceans were observed in only one stomach. The C : N values of krill stomachs were within the range of the measurements in the water column.

The main food items of mesopelagic fishes were copepods (*C. finmarchicus* and *Pseudocalanus* cf. *elongatus* were identified) (Table 6). Most fishes with fresh stomach content had only eaten copepods, but fragments of one prawn, one krill, and one *M. muelleri* (20–25 mm, based on eye size) were found in 3 of the 69 *B. glaciale* stomachs examined. Based on our stomach analyses, we assume a stomach capacity of at least 15, 20, and 25 copepods for juvenile *M. muelleri*, adult *M. muelleri* and adult *B. glaciale* respectively. The time series of stomach composition of mesopelagic fishes (Table 6) show that the fraction of fresh food and identifiable items decreased from the afternoon through the night, while the fraction of empty stomachs increased. Before sunrise almost all stomachs of both fish species were empty, indicating daytime feeding.

Table 8. Stomach content of *Micromesistius poutassou* and *Pollachius virens* from Harstad trawl catches. Number of prey in each length group. Decomposed, uncountable items are excluded.

M. poutassou Species/length	Total	1–2	Prey length (cm) 2–3	3–4	4–5	5–6	6–7	Un- known
M. muelleri	115	0	11	67	29	6	0	2
M. muelleri?	10	0	0	0	0	0	0	10
B. glaciale	6	0	0	0	3	1	1	1
M. norvegica	18	2	5	1	0	0	0	10
P. multidentata	3	0	0	0	0	1	0	2
S. arcticus	2	0	0	0	1	0	0	1
Crustacea	1	0	0	0	0	0	0	1
Total prey items	155	2	16	68	33	8	1	27
P. virens **Species/length**	**Total**	**1–2**	**Prey length (cm)** **2–3**	**3–4**	**4–5**	**5–6**	**6–7**	**Un-** **known**
M. muelleri	91	0	2	44	28	3	0	14
M. muelleri?	2	0	0	0	0	0	0	2
B. glaciale	20	0	7	5	2	3	3	0
M. norvegica	6	5	1	0	0	0	0	0
P. multidentata	1	0	0	0	0	0	0	1
S. arcticus	2	0	0	1	1	0	0	0
Crustacea	0	0	0	0	0	0	0	0
Total prey items	122	5	10	50	31	6	3	17

Sixty four large fishes were caught during the 10 pelagic Harstad trawl catches (Table 7): 50 blue whitings *Micromesistius poutassou* (RISSO), 7 saithes *Pollachius virens* (L.), 4 lumpsuckers *Cyclopterus lumpus* (L.), 2 spurdogs *Squalus acanthias* L., and one silver smelt *Argentina silus* (ASCANIUS). Of these fishes, 30 of the *M. poutassou* and all *P. virens* had prey in their stomachs, the other 22 stomachs were empty. All recognizable food items found in stomachs of blue whiting and saithe are given in Table 8. *M. muelleri* was dominant in stomachs of both *P. virens* (76 % by number) and *M. poutassou* (81 % by number). By including *B. glaciale* and *M. norvegica*, 96–98 % of the items are accounted for. By number, 69 % of all *M. muelleri* found in stomachs of *M. poutassou* and 50 % of all found in *P. virens* were juveniles. The 30 *M. poutassou* and the 7 *P. virens* had an average stomach content of 5.2 and 17.4 items, respectively, or 11.4 and 8.9 items per kilo predator. On average, large fishes had a stomach content of 2.8 items or 3.8 items per kilo predator.

DISCUSSION

Identification of sound-scattering layers

During day, the two SSLs responded simultaneously to changes in surface light. The lower SSL showed a small dusk ascent and dawn descent, but remained at 100–150 m depth. The upper SSL ascended to surface at dusk followed by night-time sinking to 30–60 m depth, ascended again to surface at dawn and thereafter returned to a day-time depth of 50–100 m. Both layers performed short-time migrations during day to compensate for changes in light intensity. This upper SSL thus behaved as the krill layer described by HOPKINS & al. (1978). Both layers were distinct at night, although more dispersed than during day. They were most concentrated during the dusk and dawn migrations.

An early morning IKMT sample from the upper SSL in surface water consisted of *Meganyctiphanes norvegica* and *Maurolicus muelleri*, while only juvenile *M. muelleri* were captured during the day. At night, the upper SSL coincided with the distribution of juvenile *M. muelleri* from MOCNESS, but not with the distribution of *M. norvegica*. *M. norvegica* descends from surface waters at night to depths below 150 m during daytime (see later). Thus it seems that the upper SSL consisted of juvenile *M. muelleri*, and that *M. norvegica* was caught by the IKMT as they migrated downwards through the layer. Both from the trawl sampling and video recording in the lower SSL it seem that this layer consisted of adult *M. muelleri*.

The SSLs in Masfjorden differ from the situation in fjords in northern Norway, where one layer has been found, consisting of euphausiids (FALK- PETERSEN & HOPKINS 1981) or euphausiids in association with calanoid copepods and chaetognaths (HOPKINS & al. 1978). They report that fishes (gadoids) were rare in the SSL. In Masfjorden, neither layer was connected with high concentrations of zooplankton (Fig. 4 and Table 2).

The situation in Masfjorden also differs from coastal waters off Norway and in the North Sea, where co-occurrence of *M. norvegica* and *M. muelleri* in a scattering layer is a common observation (HAMRE & NAKKEN 1970, 1971; JAKUPSSTOVU 1974; GJØSÆTER 1986; BERGSTAD 1989). BERGSTAD (1989) found a layer of these two species at 100–200 m in the Norwegian Deep, overlying a layer of blue whiting *Micromesistius poutassou*. This species was also caught in Masfjorden, but according to counts on echogram printouts, it did not aggregate to a particular sound-scattering layer. The density maximum of large fishes was found below the lower SSL.

Sergestes arcticus, *Pasiphaea multidentata*, and *Benthosema glaciale* were caught both by the IKMT and by the Harstad trawl. However, these species were not common in catches from the SSLs. The mesh size of the cod end of the Harstad trawl (8 mm), allowed capture of *M. norvegica* and juvenile *M. muelleri* in low numbers. Their absence from the catches, thus, indicate that they were absent from the lower SSL. The extended vertical distribution of *B. glaciale* is consistent with the observations of KAARTVEDT & al. (1988) in Masfjorden. Elsewhere, *B. glaciale* contributes to mesopelagic SSLs. GJØSÆTER (1986) found *B. glaciale* together with *M. muelleri* in a SSL west of the British Isles and in the Norwegian Deep. DALPADADO & GJØSÆTER (1987) found a layer of *B. pterotum* (ALCOCK) at 350–450 m at daytime in the Red Sea, while a layer of *M. muelleri* often was observed between 50 and 200 m. However, adult *B. glaciale* has a fat-filled swim-bladder (ZAHURANEC & PUGH 1971; GJØSÆTER 1986), and contributes therefore little to the scatter. A deep layer of adult *B. glaciale* would therefore perhaps not be detected by the echo sounder.

Trophic relationships

The brown-green colour of the *M. norvegica* stomach content and its C : N ratio indicate that particulate organic matter (POM) was a major food source. This is in accordance with FISHER & GOLDIE (1959) who found that detritus as well as microalgae and particles of terrestrial origin were major food items of *M. norvegica* in Loch Fyne, Scotland. Our observations are also compatible with BERKES (1976), who found copepods to play a minor role in January. Decreasing stomach content during night was also found by SAMEOTO (1980), for *M. norvegica* feeding on copepods.

According to ROE (1984) both *S. arcticus* and *P. multidentata* are carnivores, and copepods are their main prey.

Copepods are generally important in the diet of *B. glaciale* and *M. muelleri* (SAMYSHEV & SCHETINKIN 1971; GJØSÆTER 1973, 1981a; KINSER 1977, 1982; WÖRNER 1979; KAWAGUCHI & MAUCHLINE 1982; ROE & BADCOCK 1984; DALPADADO & GJØSÆTER 1987; SAMEOTO 1988). Compared with other Norwegian investigations (GJØSÆTER 1973, 1981a) feeding on euphausiids was low in Masfjorden, although *M. norvegica* was abundant in the plankton. Our investigation indicate that the mesopelagic fishes were feeding during the day. WÖRNER (1979) reports in an intensive time series of stomach composition of *B. glaciale*, that stomach fullness was low in the late day and afternoon, and was highest during night (2200 h – 0300 h). GJØSÆTER (1973) inferred maximum feeding of Norwegian *B. glaciale* in the evening, and KINSER (1977, 1982), ROE & BADCOCK (1984), and SAMEOTO (1988) report both day and night feeding for *B. glaciale*. The literature is more sparse regarding *M. muelleri*. SAMYSHEV & SCHETINKIN (1971) found no diel feeding pattern for *M. muelleri*. They had however no late night samples, and both the index of stomach filling and per cent non-empty stomachs were decreasing from afternoon to the evening. The lack of, or low importance of, night feeding in this investigation is noteworthy with respect to the long night (17–18 hours of darkness).

Relative to our abundance estimates of potential prey in Masfjorden, *M. muelleri* is over-represented in the stomachs of large fishes. According to BERGSTAD (1989), *M. norvegica* is the main prey for blue whiting in the Norwegian Deep, although *M. muelleri* is present in the same SSL. GORDON (1977) found that *M. poutassou* from Scottish inshore waters mainly fed on *M. norvegica* and *Pasiphaea* spp., and BAILEY (1982) stated that euphausiids and other pelagic plankton appear to be principal food for blue whiting. An over-representation of *M. muelleri* may be expected from the trawling procedure, but still *M. muelleri* seem to be a selected prey for the large fishes. This is consistent with GJØSÆTER (1981a,b), who calculated annual mortality rates of adult *M. muelleri* in western Norwegian fjords to be 2–3 times higher than mortality rates of adult *B. glaciale* in the same fjords. By assuming a food intake rate of 1 % of predator body weight per day (HAWKINS & al. 1985; MEHL 1989), the estimated 20.7 tonne of large fishes would eat 207 kg WW. By further assuming *M. muelleri* to be the only prey, of which 60 % are juveniles (Table 8), 300 000 juvenile and 200 000 adult *M. muelleri* would be eaten per day. This corresponds to a predation rate of 1.6 % and 0.22 % per day for juvenile and adult *M. muelleri*, respectively.

Densities and biomasses

Biomass of POC was an order of magnitude higher than that of zooplankton. Zooplankton biomass were of the same order of magnitude as the biomass of its predators (macroplankton and mesopelagic fishes), while the biomass of the pelagic top-predators was an order of magnitude less. The pelagic habitat in Masfjorden is however not a closed ecosystem, advective transport across the sill may be more important than local production for the zooplankton biomass (AKSNES & al. 1989). The depth distribution of planktonic animals in January 1989 indicate however that only *M. norvegica* and the smaller copepods could be transported over the sill (75 m). Trophic interactions in the fjord may therefore be important at higher trophic levels.

KAARTVEDT & al. (1988) estimated the densities of macroplankton and mesopelagic fishes in the total fjord volume in winter 1986 to 13 million *B. glaciale*, 8 million *M. muelleri*, 7 million *P. multidentata*, 8 million *S. arcticus*, and 545 million *M. norvegica*. Most *M. muelleri* and almost all *B. glaciale* and *S. arcticus* were caught in the B basin, while only 30 % of *P. multidentata*, and 40 % of *M. norvegica* were found in the B basin. Their estimates from winter 1986 of *B. glaciale*, *S. arcticus*, and *M. norvegica* are therefore of the same order as ours from 1989. However, for *P. multidentata* and probably *M. muelleri* their estimates are only a fraction of ours. The reason for these deviations are probably methodological. For *M. muelleri* our estimate is based on echo integration and trawl catches, the latter sampling fast fishes better than the IKMT.

The estimates of the fish biomass obtained by registrations of individual fishes on an echogram can be compared to actual catches obtained in the trawl (6.4 fishes per trawl on average). Assuming a trawl opening area of 400 m^2 and a 30 min haul at 1.5 ms^{-1} in the 250–0 m layer, with uniform sampling at all strata, an expected catch of 8.3 fishes is obtained. In spite of the many existing sources of errors in these estimations, the difference between the actual and expected catch is small.

Distributions

Zooplankton

Body sizes of zooplankton increased with depth. The size fraction > 2 mm was predominantly located below the smaller animals, and within the fraction < 2 mm there was also a tendency of increasing size with depth, although larger individuals also were found in surface waters.

If zooplankton was distributed so as to maximize food intake, and if POM was a major food source in January, the largest desities of zooplankters should be found around 250 m. If zooplankton was distributed as to minimize predation from mesopelagic fishes, it should be located below 300 m at daytime. This depth was however the centre for carnivorous zooplankton, such as chaetognaths and siphonophores. At daytime, the water masses above the upper SSL (the upper 50 m) seem to have been a habitat free from planktivores. However, at dusk and dawn and at night, this area was inhabited by *M. norvegica* and juvenile *M. muelleri*.

Zooplankton must therefore trade-off several selective forces: (1) the visual predation from mesopelagic fishes, (2) the nocturnal feeding of macroplankton in the upper layers, (3) the non-visual predation from deep living carnivorous zooplankton, (4) the deep distribution of food, and (5) the cost of migrations. The bulk of the zooplankton biomass was found at depths where fish predation was rather low, the biomass of predacious zooplankton was low, and POM concentrations were rather high. Some of these selective pressures may be eliminated by hibernation. This is shown for fjord populations of copepods by HIRCHE (1983), BÅMSTEDT & ERVIK (1984), and BÅMSTEDT & TANDE (1988). Own unpublished data from Masfjorden January 1988 indicate that deep-living *C. finmarchicus* was hibernating while animals closer to the surface were active.

If larger zooplankton (> 2 mm) was distributed as to maximize food intake of smaller zooplankton, they should concentrate in the 150–200 m layer. If they were to reduce predation from macroplankton and visually feeding mesopelagic fishes, they should stay as deep as possible. Larger zooplankton seems to balance these opposing forces by staying in a sub-optimal feeding habitat below 200 m.

Macroplankton

M. norvegica was caught in surface waters by the MOCNESS at night, in the upper SSL in the morning, but was not caught during the day. KAARTVEDT & al. (1988) found few specimens of *M. norvegica* in the upper 100 m during the day, and a possible maximum at 200–300 m depth. The classical interpretation of the vertical migration pattern of plankton is deep distribution during day to avoid visual predation and ascent to food-rich habitat at night. During night, *M. norvegica* seems to have moved away from its food. However, if *M. norvegica* is a visual feeder, i.e. its feeding rate is lower in darkness than in light, staying above the highest concentration of POM may allow higher feeding than in the actual layer. The depth of maximum feeding will then depend on its visual capacity, light extinction, and food concentration. Crepuscular vertical migration increases the time of the visual feeding period (CLARK & LEVY 1988) of a January day in Masfjorden from 6 to 7 hours.

It is difficult to establish the vertical distribution of the prawns *P. multidentata* and *S. arcticus* from this investigation. In a more thorough investigation January 1988 (BALIÑO 1990), these species were only found in the deepest MOCNESS sample (300–400 m) at daytime, while they were spread out in the whole water column at night. KAARTVEDT & al. (1988), using IKMT, also found maximum daytime densities in their deepest samples (220–370 m). They found, however, rather high densities of *S. arcticus* above 200 m. During night, both species were dispersed in the water column.

Mesopelagic fishes

Three patterns of vertical distribution were observed for mesopelagic fishes. Juvenile *M. muelleri* was found in a vertically migrating SSL while adult *M. muelleri* stayed in a deeper SSL with less extensive dusk and dawn migration. *B. glaciale* was spread out in the water column, with a large part of the population below the lower SSL. The day-time distributions may be explained in terms of balancing predation risk and food demands: visually feeding fishes feed at low rates in deeper, darker water, but are also less visible for a visual feeding piscivore. With similar risks of predation, juveniles may stay higher in the water column than the adults, and *M. muelleri* may stay higher than the larger *B. glaciale*. The smallest and least visible fish stayed in the most illuminated water mass, and the largest and most visible fish stayed deepest. For all visual feeders, dusk and dawn migrations increase the length of the feeding period (CLARK & LEVY 1988).

The night-time distribution of juvenile *M. muelleri* coincided with the vertical temperature maximum. WURTZBAUGH & NEVERMAN (1988) explained a similar behaviour of juvenile sculpin as a way of maximizing growth during a short night. This does not hold for *M. muelleri* in Masfjorden: without food intake during the night, and with all food eva-

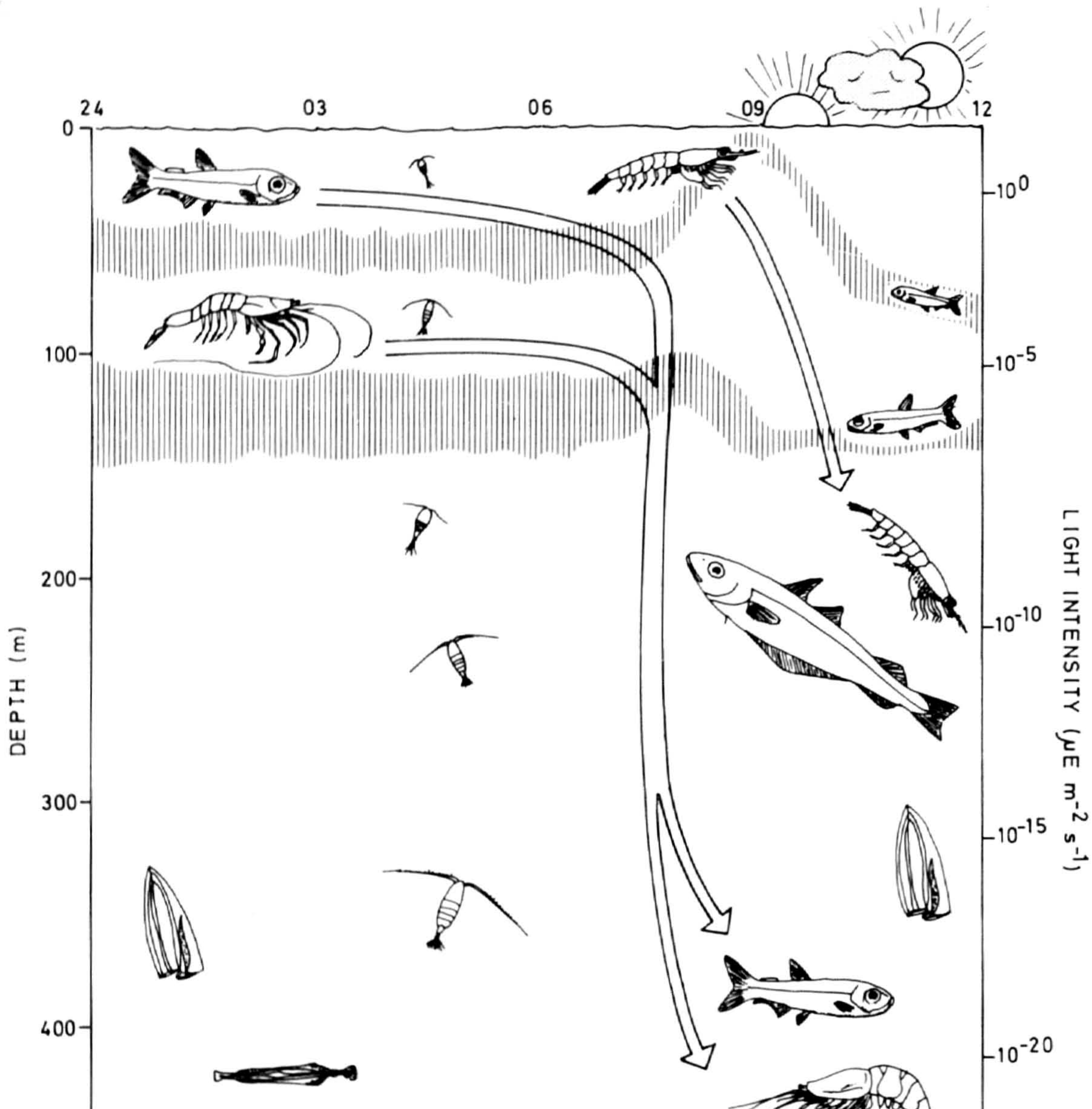

Fig. 9. Schematic presentation of vertical distributions from mid-night to mid-day in Masfjorden in winter. Light intensity refers to mid-day situations in January 1989. The sound-scattering layers consist of small (upper layer) and large (lower layer) *Maurolicus. muelleri*, while euphausiids, prawns, and *Benthosema glaciale* migrate through the layers. Large pelagic fishes stay mainly below the lower SSL and feed on *M. muelleri*. Zooplankton size increases with depth.

cuated after 17 hours of darkness irrespective of 7.5 or 9° C, there is only a net respiratory cost of staying in warmer water. Assuming a respiratory Q_{10} of 3.2° C (GISKE & al. 1989), the increased respiration at 9° C relative to 7.5° C is 19 %. The diel increase in respiratory cost of staying 15 hours in warmer water is 12 %. Assuming a maximum respiratory rate of 0.006 day^{-1} (GISKE & al. 1989), the cost of 15 hours in 9° and 7.5° is 1.07 % and 0.89 % of body weight, respectively. A juvenile *M.*

muelleri of 0.1 g WW can balance this increased cost by eating one small copepod more. By staying near the surface, these fishes may respond to low levels of surface light, thus allowing for a prolonged feeding period.

Large fishes

Large fishes stayed mainly below the lower SSL. The same behaviour has been reported by FALK-PETERSEN & HOPKINS (1981) for gadoids in fjords of northern Norway, and by HAMRE & NAKKEN (1970), BLINDHEIM & al. (1971), and BERGSTAD (1989) for *M. poutassou* preying in a SSL containing *M. muelleri* and *M. norvegica* in the northeastern Atlantic and in the North Sea.

Horizontal distributions

Stn D is shallower, more directly influenced by freshwater run-off and located closer to the head of the fjord than Stn B. The distribution of *C. finmarchicus* and the largest size-fraction of zooplankton indicate that such animals might have been constrained by the lack of a suitable depth in the inner basin. *Acartia* spp. was the only numerically important species-group with higher densities at Stn D than at Stn B; it was the most common taxon in surface waters at Stn D, but was scarce at Stn B.

The densities of *M. norvegica* were an order of magnitude higher at Stn D than at Stn B, as also reported by KAARTVEDT & al. (1988). They ascribed the horizontal distribution of krill to advective processes. *C. finmarchicus* is also passively advected, but its vertical distribution reduces the continuous renewal through the shallow channel (190 m deep) to the inner basin.

Absence of *S. arcticus* and *P. multidentata* at Stn D was also observed by KAARTVEDT & al. (1988). This may be an effect of lack of a deep day-time habitat, which implies lack of shelter from carnivores at day-time. These species seem generally to occur at depths deeper than 300–400 m at day-time (MATTHEWS & PINNOI 1973; FASHAM & FOXTON 1979; HARGREAVES 1984; ROE 1984). KAARTVEDT & al. (1988) found highest numbers of *P. multidentata* at Stn A, which is shallower than 300 m. However, the larger, and thus more visible individuals were only found in the deeper basin.

CONCLUSIONS

Based on biomass estimates, predator-prey relationships seem to be important at all trophic levels from zooplankton to large fishes in Masfjorden in winter. Food demand and risk of predation mortality may therefore be important structural forces for vertical distributions. Fig. 9 summarizes the main components in the pelagic assemblage, and their vertical distributions. Zooplankton size and density increase with depth, the most visible forms only found in deep waters. During night, macroplankton and mesopelagic fishes are dispersed in the water column. At the first increase in light intensity in the morning, the upper SSL of juvenile *Maurolicus muelleri* migrate to the surface to maximize their feeding period. Larger pearlsides, being more visible, stay in a deeper SSL. Both SSLs respond to changes in light intensities during day, in order to balance vision versus visibility. At dawn, the euphausiid *Meganyctiphanes norvegica* descends from surface waters to midwater depths. The larger mesopelagic fish *Benthosema glaciale* and the pelagic prawns *Sergestes arcticus* and *Pasiphaea multidentata* migrate in the morning to even darker water. Large pelagic fishes are found in the entire water column, with highest densities below the lower SSL, feeding mainly on *M. muelleri*.

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