

Diel vertical migrations of *Meganyctiphanes norvegica* in the Kattegat: Comparison of net catches and measurements with Acoustic Doppler Current Profilers

F. Buchholz¹, C. Buchholz¹, J. Reppin² & J. Fischer²

¹*Biologische Anstalt Helgoland (Meeresstation); D-27483 Helgoland, Germany*

²*Institut für Meereskunde, Abtlg. Reg. Ozeanographie; D-24105 Kiel, Germany*

ABSTRACT: Diel vertical migration of a stable and well-defined population of Nordic krill, *Meganyctiphanes norvegica* (Crustacea, Euphausiacea) was investigated during eight days in August 1989, in the Läsö-Deep, East of the Danish island Läsö. Net catches with a multi-net (MOCNESS) and measurements with a moored and a shipboard Acoustic Doppler Current Profiler (ADCP) were compared. Backscattered energy as a measure for biomass gave good correlations to the dry weight of *M. norvegica* and smaller zooplankton from net catches. Diel migratory patterns matched well, as determined, parallel with both methods. Migratory vertical velocity was determined with ADCP at 2–3 cm sec⁻¹. The potential for the use of ADCPs for biological investigation is discussed. Vertical migration was dependent on environmental parameters. The krill did not cross a temperature barrier of 14°C, although rich food sources were situated beyond it. Differences in salinity did not play a role. Currents were involved in plankton distribution. Light was an important Zeitgeber (synchronizer) and determined the density of the krill aggregations. Feeding behaviour did not interfere with the light-induced migratory pattern of Nordic krill at the Läsö-Deep.

INTRODUCTION

Vertical migration is typical in almost all zooplankton and other pelagic taxonomic groups. To date, however, there is still much confusion about the cause and effect of governing abiotic and biotic factors (Haney, 1988). There is little doubt that light plays the major role as an important Zeitgeber. Seasonal, as well as vertical, changes in temperature and salinity are also involved. The search for food, predator-avoidance and metabolic advantages are interlinked with endogeneous rhythmic cycles of activity (reviews by Hutchison, 1967; Longhurst, 1976, Forward, 1988; Haney, 1988).

Most likely, experimental difficulties are the cause for analytical problems in field studies of vertical migration. Patchiness is typical for zooplankton behaviour. Accordingly, it is problematic to follow distinct populations over longer times, and therefore most studies either concentrate on analysis over a few days or on singular but regular sampling, e.g. on an annual monthly regime. However, recent development of multi-opening and closing nets and sonar devices considerably facilitate field studies, particularly when concentrating on multifactorial analysis of vertical migration.

Our study was a continuation of a long-term investigation on a seasonally and geographically stable population of the Northern krill, *Meganyctiphanes norvegica*, in

the Scandinavian Kattegat (Boysen & Buchholz, 1984; Buchholz & Prado-Fiedler, 1987; Buchholz & Boysen, 1988). It is regularly found at the so-called Läsö-Deep which is part of the Kattegat Channel east of the island Läsö (Ulrich, 1983). Here, the krill is known to migrate regularly between the bottom of the Läsö-Deep of 143 m, and the surface layers. Besides krill, copepods dominate in the water-column. Accordingly, it is a simple system to analyse. The stability of the population was advantageous for our intensive study of eight days, analysing vertical migration in relation to light, salinity, temperature, currents, and other zooplankton.

A central aim was to employ Acoustic Doppler Current Profilers (ADCP), one vessel-mounted and the other deployed centrally in the Alkor-Deep. These sonar devices measure the horizontal and vertical velocity of moving particles in the water-column. If these particles (in the case of zooplankton), move by themselves, errors in velocity measurements of currents result in oceanographic investigations (Schott & Johns, 1987). Therefore, calibration is needed to differentiate between migratory and current speeds determined in the vertical. A great potential for biological applications lies in the ability of the ADCP to collect data on the biomass of zooplankton calculated from the backscattered signal strength (Flagg & Smith, 1989; Plueddeman & Pinkel, 1989; Roe & Griffiths, 1993). Our study was aimed at directly combining the oceanographic and biological approaches, using a larger data set on vertical migration of a well-defined zooplankton population. We used a multi-opening and closing net (MOCNESS: Wiebe et al., 1976) to document the abundance of zooplankton and its movements patterns, five times in 24 hours. Calibration and differentiation of migration and current velocities and the capability of the ADCP to measure biomass, is the subject of a diploma thesis (Reppin, 1990). Here we compare abundance and distributional pattern of *M. norvegica* and accompanying zooplankton as determined parallel with ADCP and net catches in relation to environmental factors.

MATERIAL AND METHODS

The Läsö-Deep, called "Alkor-Tiefe" (Fig. 1), is situated approx. 12 nm east of the Danish island Läsö as part of the Kattegat Channel. Its maximum depth is 143 m, the surrounding sea bottom being between 40 and 70 m deep. The dimensions of the Deep are ca 3×1 km. The topography of the area is described in detail by Ulrich (1983).

Sampling was carried out from RV "Poseidon" between 5th and 12th August, 1989, Cruise No. 161/1.

Hydrographic parameters, salinity and temperature were determined daily at 7:00 and 17:00 h GMT from 0 to 95 m, using a CTD-sonde (ME-Meerestechnik). Global radiation was measured continuously by the ship's meteorological system. Sunrise on 9th August 1989 was 03:33, and sunset at 19:17 UTC. Currents throughout the water-column were monitored continuously by the deployed ADCP, and evaluated as stick-plots.

A self-contained (SC-)ADCP was moored at the area of maximum depth of the Läsö-Deep at 134 m (Fig. 1; $11^{\circ}25.10'E$; $57^{\circ}16.55'N$). The transducer was 4 m from the sea-bottom, pointing upwards. Vertical resolution of measurements was 4.4 ± 0.05 m, which corresponded to one vertical depth cell or "bin". Due to surface-reflection, the last 7.8 m from the surface could not be evaluated. Four sonar impulse-beams of 4° width were emitted at an angle of 20° from the vertical, at 153.6 kHz. Measurement ensembles of 400

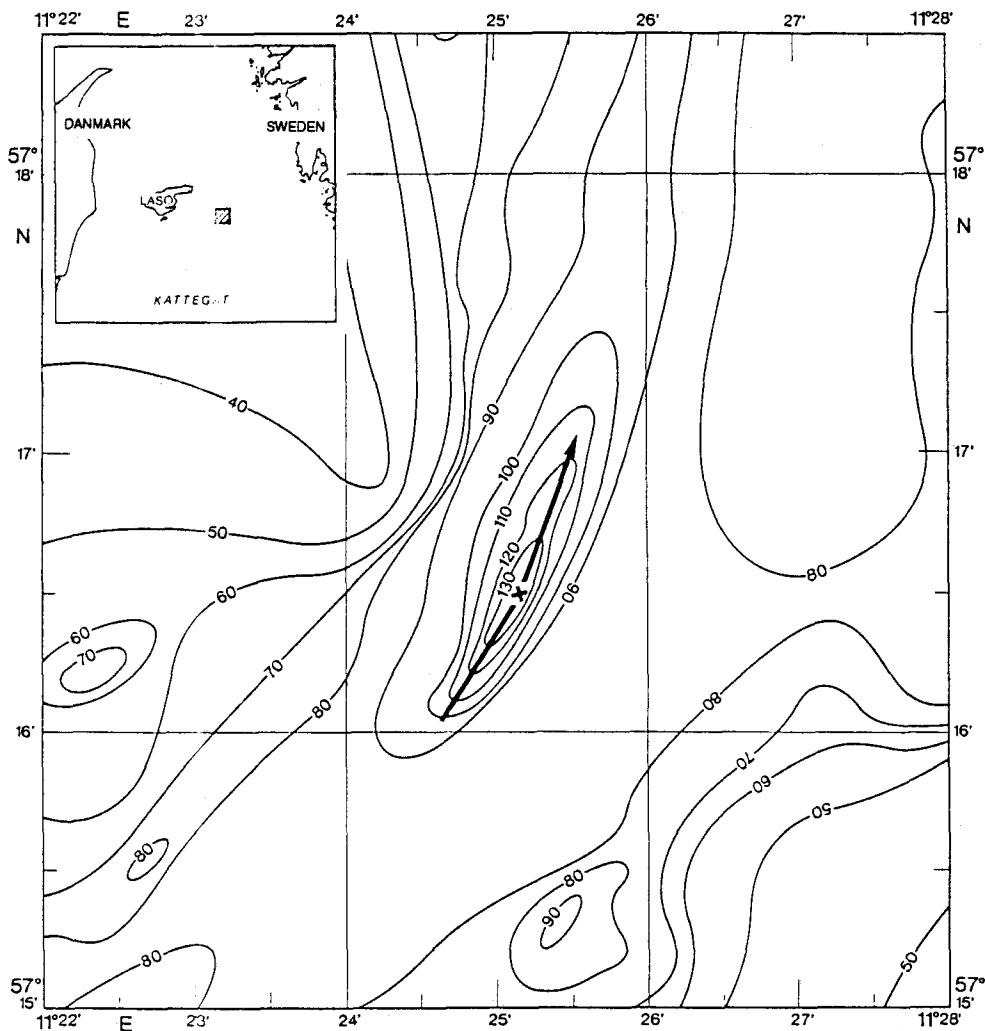


Fig. 1. Topography of the Läsö-Deep

pulses over 200 sec were averaged every 30 min. Measurements of vertical and horizontal velocity, error-velocity and amplitude of echo were evaluated. Calibrating the backscatter strength with biomass from net catches allowed estimates of plankton abundance with high resolution in time and space (for details see Reppin, 1990). For the biomass data used here (Fig. 6), the logarithm of the dry weight of zooplankton was regressed with backscatter strength [dB m^{-3}]. Parameters of regression were: $r = 0.60$; bias = -3.47 ± 0.77 ; slope = 0.105 ± 0.016 ; $n = 76$.

A vessel-mounted (VM-)ADCP emitted sonar-pulses at 153.6 kHz towards the sea-bottom. About 220 pulses over 360 sec were averaged every 5 min. Due to bottom-reflection, the last 15% of the water-column could not be evaluated. The VM-ADCP was

only operated at times of net-hauls between the measurements of the moored ADCP. On 8th August, from 19:25 to 19:43, a high resolution section was run across the Läsö-Deep, where sonar impulses were averaged every 30 sec, instead of 5 min. There was no parallel net-haul. ADCPs were from RD Instruments, San Diego, USA.

Zooplankton were caught with a MOCNESS (Multi Opening and Closing Net with Environmental Sensing System: Wiebe et al., 1976). Net opening was 1 m², mesh size 300 µm, of 9 single nets. The haul-track followed the length of the Läsö-Deep from S to N (Fig. 1). The net was first lowered to 120 m. Controlled by ship-board echo-sounder, a safe minimum distance from the bottom of 20 m was maintained. Subsequently, at 3.0 knots, the net was hauled up – continuously, at 0.5 m/sec. At 15 m depth-intervals, the subsequent net was opened, which automatically closed the previous one. Depth of the net, in situ temperature and cumulative volume filtered for the open net, were displayed and recorded. Volumes filtered per net were 120 m³ on average (range: 45–230). Haul times (5–12 August, 1989) were 11:30, 17:30, 20:30, 02:30, and 06:00 GMT.

The sample from the first net was discarded because it was open when the net was lowered. The samples of the remaining 8 nets were passed through a sieve of 5 mm mesh in order to obtain two fractions, one containing the large zooplankton, which consisted almost exclusively of *M. norvegica* (Coelenterata were discarded). Length/frequency distributions on ca. 200 specimens were collected daily. These showed little variation during the experiment. A sharp maximum of second-year krill dominated the distributions (mean length: 32.80 ± 0.05 mm, n = 1200). Small fish (occasionally caught in the nets above 30 m), were juvenile whittings, *Merlangius merlangius*, and were discarded. The fraction of small zooplankton was dominated by copepods, and also contained small amounts of smaller euphausiid species, *Thysanoessa raschii* and *T. inermis* of less than 20 mm length, and some euphausiid larvae less than 10 mm length. On board, the volumes of the large and small fraction were determined separately as displacement volumes in seawater in graded glass-cylinders of appropriate size. Subsequently, the samples were dried with tissue and frozen. Dry weights were determined after lyophilization for 24 h to constant weight (Heraeus-Christ freeze-dryer). The accuracy of the procedures was checked on increasing amounts of both zooplankton fractions.

On 11th August, at 22:14 GMT, an additional net haul was undertaken, concentrating on the discontinuity layer of salinity and temperature, which invariably occurred between 15 and 45 m. Here, the relevant 8 nets were opened in 5 m-steps from 55 to 15 m.

On 12th August, at 11:30 GMT, the MOCNESS was towed at a constant depth of 105 m over the central area of the Läsö-Deep, with nets opened at constant time-intervals, in order to study the horizontal distribution of the deep zooplankton during daytime.

The distribution of copepod species was investigated in relation to water layers. The diurnal cycle between 11:30 on 6. 8. 1989 to 11:30 on 7. 8. 1989 was chosen as an example. Furthermore, the stomach content of *M. norvegica* was analysed for the same period. 20 specimens from each net were investigated. The stomach content was carefully emptied on to a microscope-slide and fixed and stained with a solution of Polyvinyl-Lactophenol and Orange G or A, according to Dr. Renate Haass (pers. comm.). Whole or parts of all species of copepods found in the water-column could be identified in krill stomachs and were registered. Unidentifiable remains of copepods which were most frequently found, were also noted.

RESULTS

The hydrographical data showed the typical triple-layered water-column (Fig. 2) which is found all year in the Läsö-Deep (Buchholz & Boysen, 1988). During the time of the experiment, the following parameters were almost constant. A 10–15 m thick surface layer with lowest salinity of 26 ppt and highest temperature of 16.5 °C was followed by a mixed layer down to 55 m, where salinity increases continuously to 33 ppt, accompanied by a steep temperature gradient decreasing to 9 °C from 30 to 50 m. Below 50 m, salinity and temperature were constantly near 35 ppt and 9 °C. The water masses above the thermocline originated from Baltic outflow or were mixed, whereas below it, North Sea water dominated.

The current measurements (Fig. 3) reached maximal horizontal values of 35 cm sec⁻¹. Weak semi-diurnal tidal currents alternated in the direction of the N/S-orientation of the Deep, and were superimposed in the deeper layers by a constant inflow from the North Sea. In 20 to 42 m depth, the alternating tidal currents were also superimposed by a

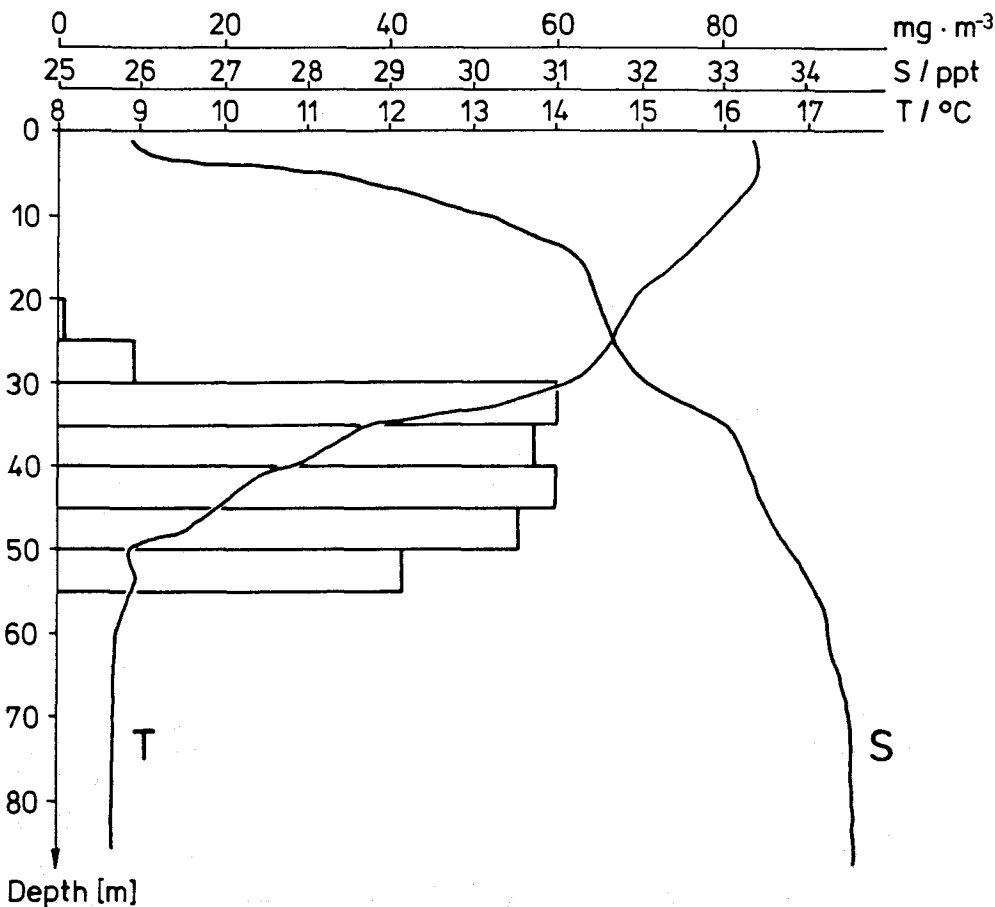


Fig. 2. Vertical section of hydrography and net haul (bars) in the vicinity of the discontinuity layer

southward inflow from the North Sea which changed to a northward outflow from the Baltic during the second half of the experiment. This change was not as clear at 40 m. Occasional reversal of the shallow currents appeared to be wind-driven.

Both the apparent hydrographic stratification and the course of currents indicated a boundary of water masses at an approximate depth of 40 m.

The global radiation alternated in the normal daily cycle (Fig. 7a), but showed different heights of maxima, due to changing cloud-cover. Moonlight did not play a substantial role because the phase was shortly after new moon at the beginning of the experiment.

The zooplankton data of eight days were averaged for each haul time (Table 1). At 11:30 GMT euphausiids were at a dense maximum at 100 m (Fig. 4). Apparently already before sunset, a sharp upward movement to a maximum at 50 m at 20:30 occurred. Between 17:30 and 20:30 GMT, the speed of migration between maximum densities of animals was 10 m h^{-1} , or approx. 0.3 cm sec^{-1} . Between 20:30 and 02:30 most animals were at a depth of 50 m, but seemed to disperse throughout the water-column. At 23:30, the highest animals were at 20 m, but even in the deep area, substantial amounts of euphausiids were caught. The density of animals diminished between 11:30 and 02:30, from a sharp maximum between 90–105 m of 290 mg m^{-3} , to between 8–51 mg m^{-3} at depths of between 15 and 115 m (Table 1, Fig. 4). Three hours before sunrise, descent began, and a dense aggregation was already seen at 100 m at 06:00, approximately one hour after sunrise. Between 02:30 and 06:00 downward migration was at a velocity of 0.4 cm sec^{-1} . The maximum range of migration was from the sea bottom to approximately 20 m, but the highest densities were found to alternate between 100 and 50 m.

During the day, when euphausiids were deep, the maximum density was close to the centre of the Läsö-Deep, and concentration diminished towards the sides (Fig. 5).

A closer look at the situation in the vicinity of the discontinuity layer at 22:00 (Fig. 2) revealed that a substantial portion of euphausiids ascended to 30 m, where a temperature close to 14°C prevails. Only a few animals were found higher. Accordingly, during vertical migration, euphausiids encountered a maximum difference in temperature of 5°C (9–14) and in salinity of 5 ppt (30–35).

The small zooplankton, mainly copepods, did not migrate intensively (Fig. 4, values averaged from 7 days). Highest concentrations were invariably between the surface and 40 m. At 23:30 a small maximum was found near the surface and a downward dent in isopleths appeared at 02:30. A relatively high concentration was also apparent at 11:30 at 80 m, which dispersed during the night, diminishing by a factor of 2.7 ($27\text{--}10 \text{ mg m}^{-3}$). Generally, maximum concentrations of small zooplankton were lower by one order of magnitude than that of krill. Copepods appeared in two layers, one above and the other below the thermocline. This appeared to be reflected in the distribution of species (Table 2).

A discrepancy in biomass values appeared when values integrated over the whole water-column were considered (Table 1, last row). Here, the maximum value in euphausiids diminished from 558 mg m^{-3} at 17:30, to a minimum of 126 mg m^{-3} at 02:30. In contrast, integrated biomass in the small zooplankton varied little: between 104 and 128 mg m^{-3} .

From the Doppler shifts measured by ADCP, the vertical migration velocities were calculated. Values of the time series over 7 days were averaged. Maxima were at 2.5 cm

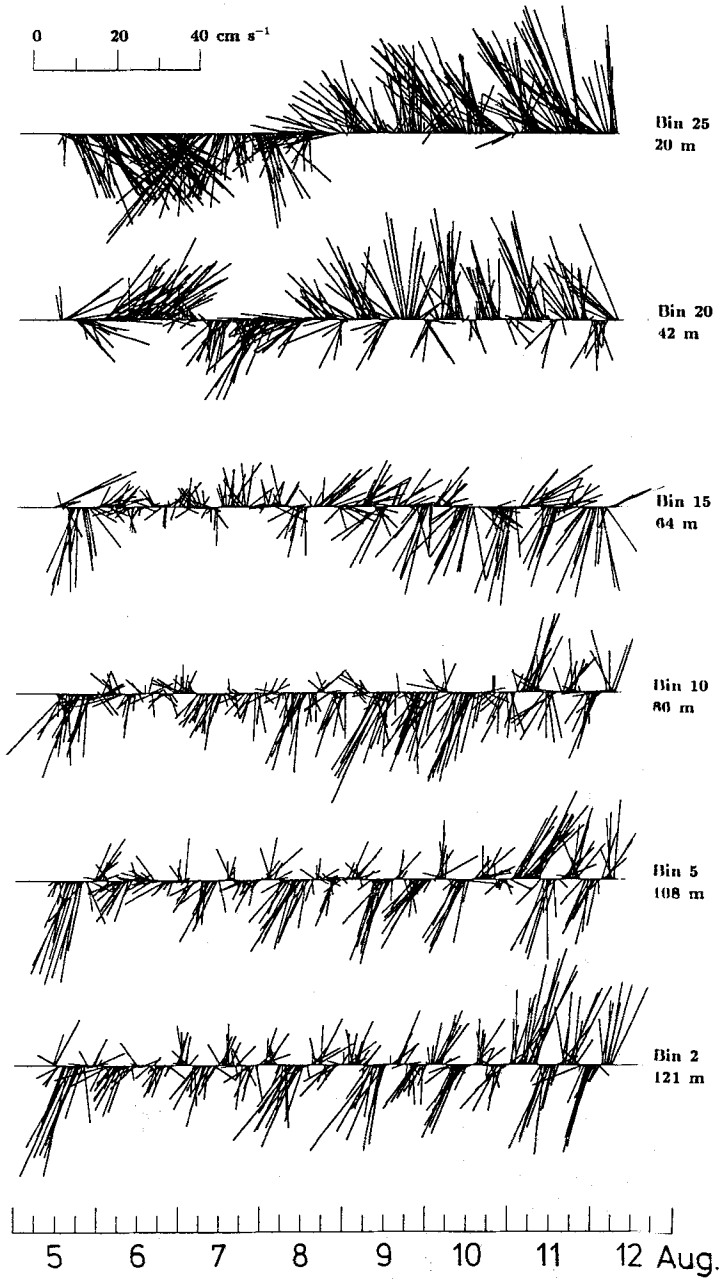


Fig. 3. Stick-plot of horizontal current velocities at different depths

Table 1. Average biomass of large (lg) and small (sm) plankton fraction in MOCNESS-samples as dry-weights in mg/m^{-3}

Time of catch Depth m	11:30		17:30		20:30		23:30		02:30		06:00	
	lg mg/m^{-3}	sm mg/m^{-3}	lg mg/m^{-3}	sm mg/m^{-3}	lg mg/m^{-3}	sm mg/m^{-3}	lg mg/m^{-3}	sm mg/m^{-3}	lg mg/m^{-3}	sm mg/m^{-3}	lg	sm
115-105	128	10	114	8	34	5	51	5	10	8	46	8
105-90	290	13	213	11	31	6	51	6	10	8	139	13
90-75	48	27	231	19	38	10	36	10	22	8	80	19
75-60	0	8	7	15	27	7	46	8	38	8	4	15
60-45	0	6	0	7	45	4	43	4	46	12	0	4
45-30	0	18	0	10	34	11	44	9	0	22	0	7
30-15	0	16	0	19	1	25	8	20	0	19	0	15
15-00	0	26	0	39	0	36	0	49	0	24	0	31
integrated	466	124	558	128	210	104	279	107	126	109	269	112

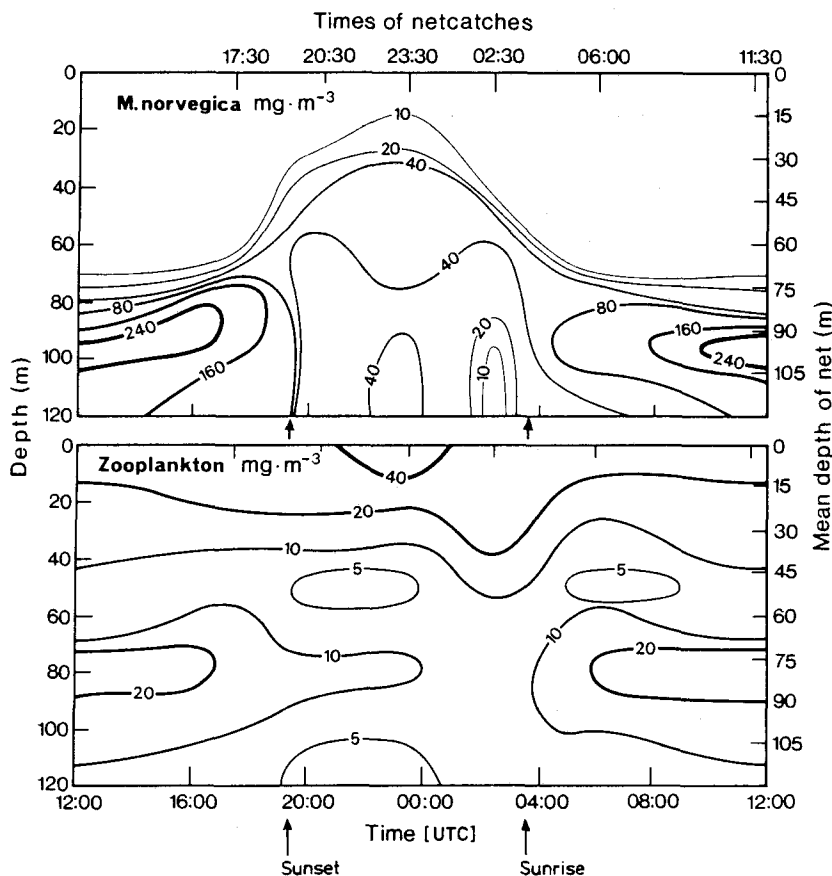


Fig. 4. a: Diel average distribution and abundance of *M. norvegica* in the Läsö-Deep (net catches)
 b: Diel average distribution and abundance of small zooplankton in the Läsö-Deep (net catches)

sec^{-1} upward but less downward (approx. 1 cm sec^{-1}), in relation to the diel cycle. Measured maximal values were significantly greater than the error for the ADCP-measurements of 0.71 cm sec^{-1} (Reppin, 1990).

The measurements of the relative backscatter intensity of the SC-ADCP as well as the VM-ADCP resulted in good correlation with the dry-weight of zooplankton. Generally, the comparison of ADCP-measurements and net catches gave reliable data to determine biomass. A more thorough evaluation of the data on biomass determination is in Reppin (1990).

Biomass values were calculated as relative backscatter cross-section in $\text{m}^2 \text{ m}^{-3}$. The data were averaged over the 7 days of the experiment. A clear diel pattern emerged (Fig. 6; data of SC-ADCP shown). A horizontal band of maximal signal intensity was found at 95 m from 12:00 until ca. 19:00, shortly before sunset. Subsequently, isopleths turned sharply upward until, at 20:30, they were again horizontally orientated at 45 m until 03:30, when a steep downward gradient followed, until a band of horizontal isopleths at

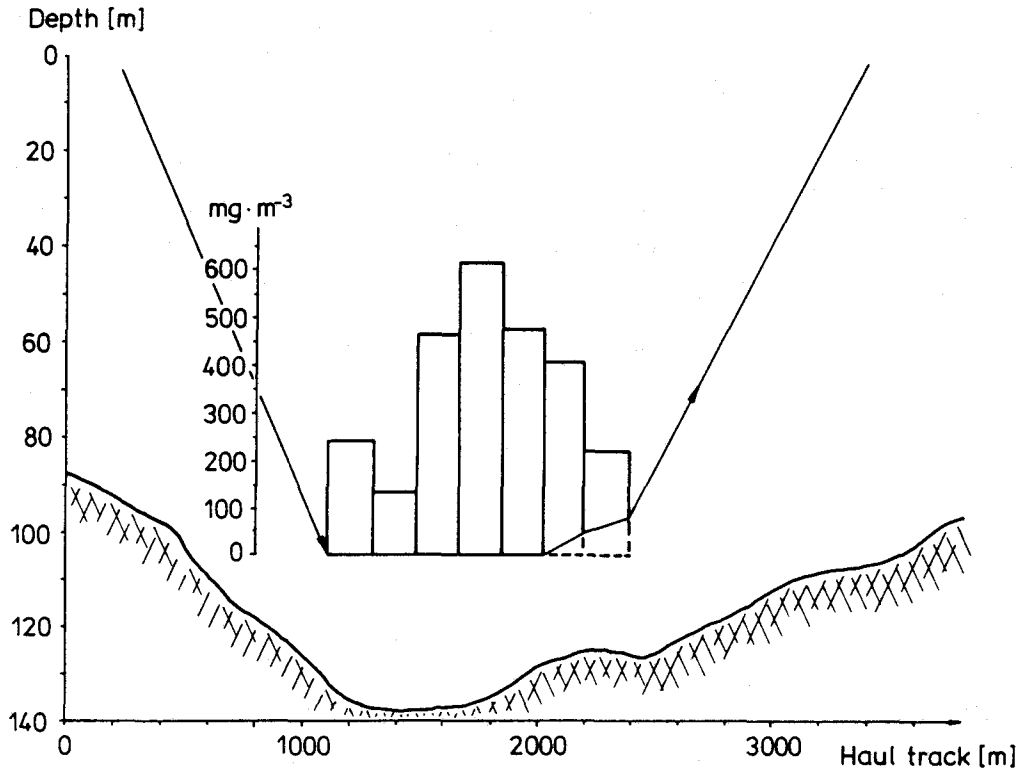


Fig. 5. Daytime horizontal net haul

95 m prevailed again from 05:00 to 12:00. Maximal values of $200 \text{ m}^2 \text{ m}^{-3}$ did not vary considerably during these times and depths. From the surface to 42 m, isopleths stayed horizontal at low intensity from 12:00 to 20:00, and from 04:00 to 12:00, bordered by steep or even vertical gradients of intensity, particularly between 03:00 and 04:00. Biomass was up to $600 \text{ m}^2 \text{ m}^{-3}$ in the surface layer above 42 m.

Table 2. Species composition of copepods at the Läsö-Deep

Depth	Species
0–60 m	<i>Centropages typicus</i> <i>Temora longicornis</i> <i>Calanus finnmarchicus</i>
60–75 m	Transition-zone with different species dominating
75–120 m	<i>C. finnmarchicus</i>

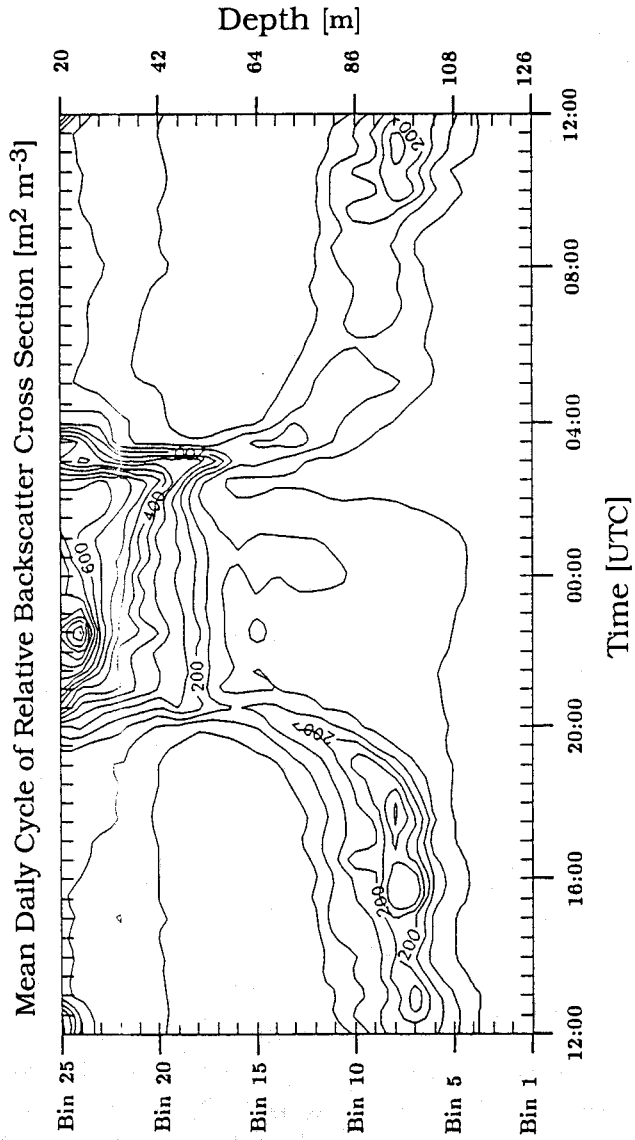


Fig. 6. Diel average relative backscatter cross-section calibrated for biomass of zooplankton in $m^2 m^{-3}$

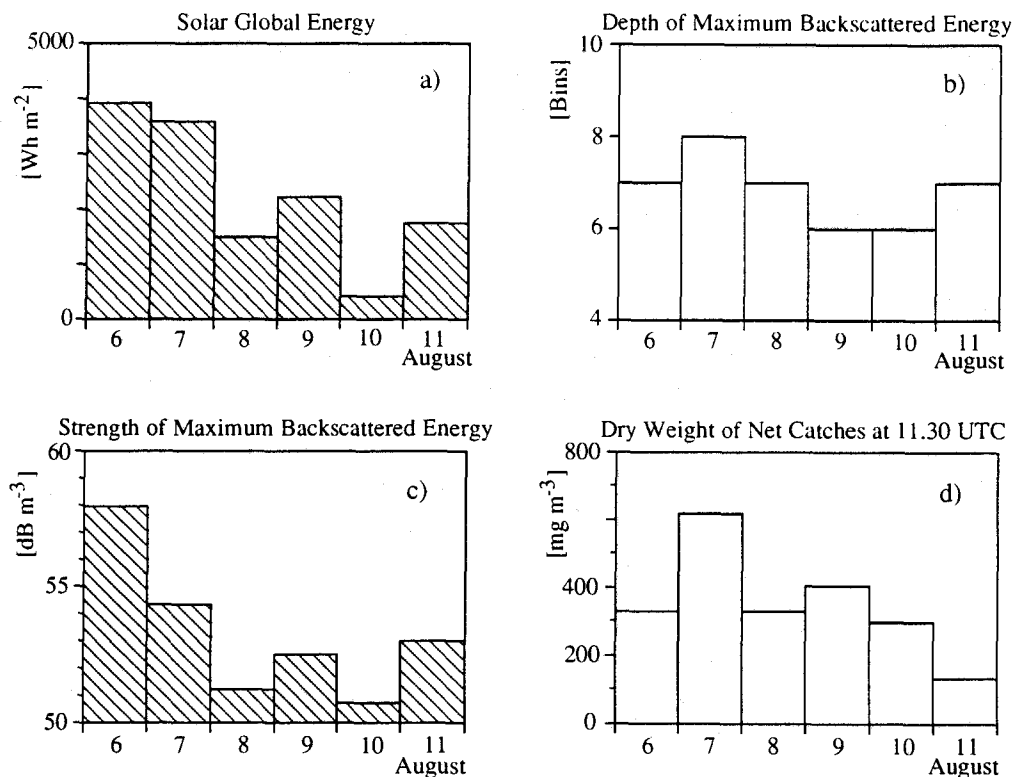


Fig. 7. a: Integrated irradiation energies; b: depth of maximum backscattered energy; c: strength of maximum backscattered energy; d: averaged dry weight of net catches at 11:30 UTC

An interdependence between irradiation energy and the intensity of maximal backscatter was noted (Fig. 7). Total radiation energy was integrated for each day, resulting in considerable differences (Fig. 7a). The depth of the maximum backscatter, averaged between 11:00 and 16:30, varied only by 2 bin-lengths, i.e. 8.8 m (Fig. 7b). However, the intensity of maximal backscatter was clearly parallel to the time-course of radiation energy (Fig. 7c). The dry weights averaged daily from net catches at 11:30 did not reflect this pattern (Fig. 7d).

From the mean echo amplitude during a high resolution section across the Läsö-Deep, the relative backscatter cross-sectional area was calculated. The high echo integration rate of 30 sec showed a clear picture of the distribution of scattering particles across the Deep (Fig. 8). The spatial resolution corresponded to an average of 50 m. A sharp maximum of backscatter was noted at bin 16 and 17 (i.e. 64–72 m) which was horizontally oriented towards the south side of the Deep. No parallel net haul was run – but seen in relation to the above distributional data this maximum most probably corresponded to the ascending krill during that time.

The distribution of copepods differed considerably in relation to the three hydrographical layers already described (Table 2). *Centropages typicus* clearly dominated the surface layer. Here, small numbers of *Acartia clausi* and *Anomalocera petersoni*

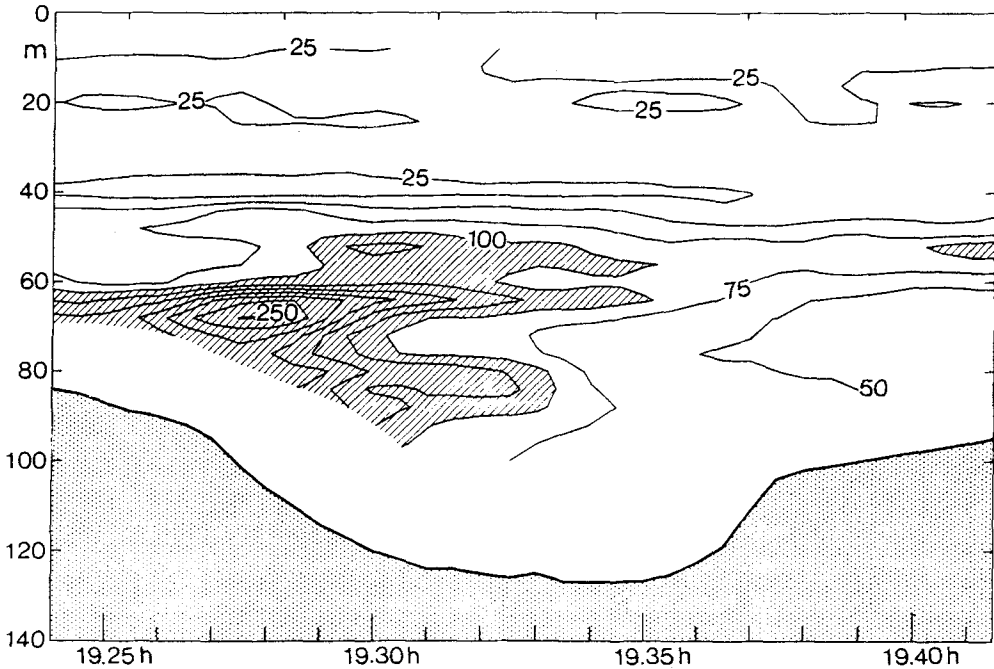


Fig. 8. High resolution section with VM-ADCP across the centre of the Läsö-Deep between 19:24–19:42 on Aug. 8th 1989 (given as decimal time on the abscissa). Isoleths show biomass in mg m^{-3}

appeared additionally with *Temora longicornis* and *Calanus helgolandicus*. Between 30 and 75 m, the species composition varied, with *T. longicornis* or *C. helgolandicus* as dominating species. Below 90 m, only *C. helgolandicus* was found (Fig. 9). The stomach contents of the krill clearly reflected the species composition of copepods in the triple-layered water-column. However, unidentifiable fragments predominated. These, and parts of *T. longicornis* which were ingested in considerable amounts, are shown quantitatively in Fig. 9 (bars). The main period of feeding was between 20:30 and 23:30 in the middle layer between 45 and 75 m. Stomach content at 02:30 indicated mainly digested fragments. During these times and at these depths, relatively small numbers of copepods were found in the water-column (Fig. 9 and Fig. 4). Krill at 90 m also fed between 20:30 and 23:30. Some occasional feeding was also observed at 11:30, when the krill was deep. In this case, only *C. helgolandicus* was ingested.

DISCUSSION

Distribution and abundance of *M. norvegica* and accompanying zooplankton, as exemplified by the net catches, was strongly influenced by abiotic parameters. The highest concentration of copepods was between the surface and the approximate lower limit of the discontinuity layer at approx. 40 m, which also appeared to be the lower distributional limit of this upper layer of copepods. A second layer was found during

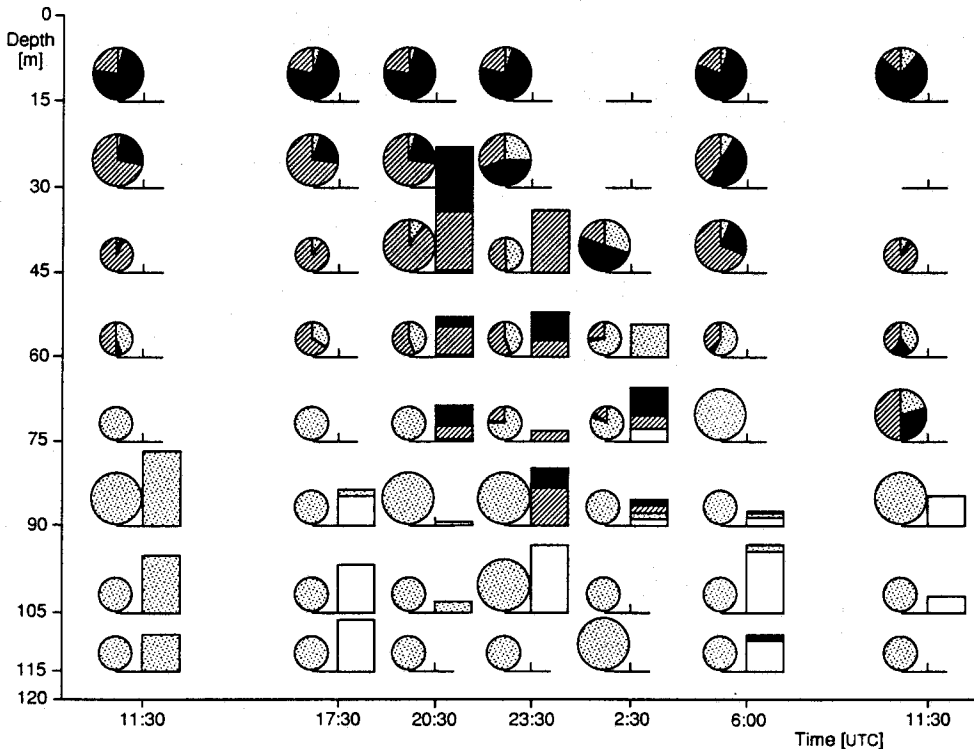


Fig. 9. Distribution and species composition of copepods in the water-column (circles) and stomach contents of *Meganyctiphanes norvegica* (bars, $n = 20$) on the 6th and 8th of August, 1989 (averaged). Large circles: $10\text{--}50 \text{ mg} \times \text{m}^{-3}$; small circles $<10 \text{ mg} \times \text{m}^{-3}$. Stippled: *Calanus helgolandicus*, hatched: *Temora longicornis*, black: *Centropages typicus*, white: unidentified

daytime just above the rim of the Läsö-Deep. The vertical distribution of copepod species were different (see below).

In contrast to the small zooplankton, *M. norvegica* intensively migrated, vertically, in a clear pattern, and seemed to be also influenced by abiotic factors. Krill migrated well into the trough of the Läsö-Deep, where highest concentrations were found during daytime. Isoleths indicate that a certain proportion also nears the bottom. However, observations (Culik & Buchholz, unpubl.) using a remote controlled video-submersible showed that krill stayed clear of the bottom. This was consistent with observations of Sameoto (1980a) in the Gulf of St. Lawrence. In the present study, the upper migration limit appeared to be the discontinuity layer at approximately 20–40 m. With higher resolution (Fig. 2) it was observed that the upward movement was stopped short by a temperature effect. 14°C seemed to be the upper tolerance limit. Unpublished laboratory observations coincide with this, because Kattegat krill showed high mortality at 15°C , whereas they did survive below this temperature for longer times. However, Simard et al. (1986) observed *M. norvegica* to cross the thermocline in the River of St. Lawrence. But highest temperatures at the surface were only 12°C , and at the level of the shallow

thermocline, 6°C. We found the upper temperature limit of *M. norvegica* to occur at 14–15°C. This is remarkable in the case of the Läsö-Deep population, because this temperature limit excluded the krill from the rich supply of copepods as food organisms near the surface. This also applies to phytoplankton. *M. norvegica* is omnivorous (Sameoto, 1980a; Klages, 1983). Usually, during August, chlorophyll levels at the Läsö-Deep are low, at less than 2 µg l, and phytoplankton blooms at other times increased in concentrations only at a depth of between 5 and 20 m (Klages, 1983, and unpubl. obs.).

The ambient differences in salinity appeared to be unimportant with respect to plankton migration, because a steep gradient to a minimum of 26 ppt only occurred above 15 m, which krill did not reach (Fig. 2). This was also in accordance with laboratory data of Forward & Fyhn (1983), who found the lower lethal limit of *M. norvegica* to occur at 20–24 ppt, which is lower than the ambient salinities of the present study.

The currents in the different water masses (Fig. 2) were probably responsible for establishing or at least stabilizing the said temperature limit. Maximal current values were in the same order of magnitude as the possible continuous swimming-speed of *M. norvegica* of approx. 10–15 cm sec⁻¹ (Kils, 1981, and pers. comm.). This obviously was enough for krill to be able to regularly reconcentrate in the Läsö-Deep against currents during daytime. However, a shift of the krill to the south side of the Läsö-Deep indicated that the krill was, to some extent, transported with the current. A possible more thorough evaluation of krill movements in relation to currents is beyond the scope of this paper.

A strong influence of light on the distribution of krill and as a Zeitgeber (synchronizer) steering migratory activity could be demonstrated. However, light-dependent distributional patterns were not possible to dissolve by net catches in this case, but were visible in ADCP-analysis. The daily depth of maximum backscatter did not vary much, but the backscatter intensity showed a parallel pattern to the irradiance of sunlight (Fig. 7). This indicated that euphausiids were more dispersed during days with less irradiation, caused by cloud-cover, and concentrate during bright days in more distinct bands. The concentration of these bands, as indicated by back-scatter intensity, was directly dependent on irradiation intensity. Such a light-induced concentration effect was also reported by Roe (1983), for euphausiids in the NE-Atlantic. In contrast, Roe's and the present data suggest that krill did not orient itself with respect to "isolumes" (Boden & Campa, 1967), i.e. in certain depth zones in relation to the underwater light intensity. Future ADCP-measurements in conjunction with direct light measurements would promise a convenient way to analyse such an interdependence in more detail.

Net catches indicated that at dusk, krill in the Läsö-Deep moved sharply upward, and at 80 m copepods began to disperse. Close to midnight, krill reached its highest levels, stopped by the temperature limit, and some copepods in the upper layer concentrated at the surface. 2 hours before sunrise krill were already migrating downwards again. A conspicuous dent in isopleths of copepods indicated quick descent. The early initiation of descent and relatively high swimming velocities (ADCP-values) were a further indication of light as the governing factor of vertical migration. Before dawn, animals were high up in the water-column and encountered increasing light intensities earlier than diminishing irradiance at dusk, hence higher swimming-speeds ensued.

The ADCP-data on migratory-speeds could be determined with great accuracy and continuously, and thus probably with less error in comparison to the net catches at 3-h intervals. This might have been the reason for the high swimming-speeds determined by

ADCP, which were one order of magnitude higher than those calculated from net catches. Likewise, the assessment of diel distributional patterns of zooplankton appeared more reliable with ADCP, in quantitative terms. However, large and small zooplankton – in this case mainly *M. norvegica* and copepods – could not be differentiated by the sonar alone. Nevertheless, the qualitative pattern of diel migratory behaviour was in close accordance, as documented by net catches and ADCP (Fig. 4 and Fig. 6).

Quantitative comparison of net catches and ADCP-data agreed to some extent, but also differed considerably. Discrepant quantitative values appeared to be due to possible errors in net sampling and to interference of animals other than zooplankton in ADCP-measurements. Net-avoidance in krill was to be expected, probably as an unknown but constant factor, and was therefore neglected in the quantifications. A major quantitative difference was found during night-time. Here, krill concentrations as integrated over the whole water-column diminished considerably in net catches (Table 1) but not in ADCP-data (Fig. 6). This could have been generally due to better resolution of the stationary ADCP which was deployed at the centre of the Läsö-Deep. The path of the MOCNESS, being hauled obliquely, usually went from one rim of the Deep to the other (Fig. 1). The second net, opened, ran over the centre of the Deep, whereas the nets opened later were already outside the centre, and thus only met the fringes of the krill-patch. The relatively constant biomass data determined by SC-ADCP indicate that the krill-swarm is able to orient itself with respect to the Deep and is not carried far out of it. This is in contrast to the smaller zooplankton. Here, the integrated biomass values determined by net catches were constant over the measuring period (Table 1), irrespective of the path of the MOCNESS. Accordingly, the small zooplankton was predominantly advected horizontally and evenly by the prevailing currents. An advantage of the ADCP over the MOCNESS in quantitative terms, is the larger cross-section of measurement. At a depth of 45 m, the stationary ADCP measured a horizontal distance of several metres, due to the beam angle of 40°, whereas the net opening was only 1 m².

Another quantitative discrepancy between net and ADCP-analysis was in zooplankton concentration above the thermocline during night-time. Here, the overall structure of isopleths was comparable, but density measured by ADCP was the highest. This was not found in net catches. A possible source of sonar reflection might have been small whittings, which were also caught occasionally in this layer – but not quantitatively, due to net-avoidance. Fish in this layer also appeared on the ship's fish-sonar (Krupp-Atlas, 33 kHz) or were observed at the surface, from the ship. These fish might have been actively feeding on dense copepod patches, and probably considerably increased the biomass values measured by ADCP.

Most surprising was that aggregations of krill and copepods never clearly overlapped. The daytime deep layers did not coincide, and when krill was found at the highest levels during night-time, copepods were only present at low densities. The surface layer rich in copepods could not be reached by the krill at all. However, krill fed unselectively on those copepod species which were in the relevant layers of the water-column, corresponding to reports by Sameoto (1980b), Simard et al. (1986), and Simard & Mackas (1989). The highest feeding activity was during night-time, when most of *M. norvegica* were high in the water-column. Some occasional feeding was also observed during the day, in the deep (see also Sameoto, 1980b). Apparently, vertical migration of krill at the Läsö-Deep was governed by the light regime and was little, if at all, dependent on the

density of food organisms. Accordingly, light was the determining factor of vertical migration. The pattern of migration was apparently not influenced by the search for food, although feeding activity was also of a cyclical nature.

During the experiment, VM-ADCP measurements were constantly displayed as on-screen data. The ADCP turned out to be a valuable tool to locate zooplankton in real-time analysis. Furthermore, the high-resolution section by VM-ADCP gave a good impression of krill-distribution. Such profiles could also be evaluated already, on board, and compared to net catches. ADCPs are widespread now, e.g. all larger German research vessels are so equipped. Accordingly, studies of zooplankton abundance and distribution could be easily evaluated, e.g. in conjunction with the current-data gained at the same time, or additional light-intensity measurements. Furthermore, the exact location of zooplankton patches would facilitate directed net sampling to study physiological cycles, e.g. of enzyme or metabolic activities (in prep.).

A great potential of ADCPs lies in long-term moorings. Here, zooplankton dynamics can be studied under seasonal aspects. Particularly interesting, measurements are still possible in high latitude areas, when the sea is covered by ice. Data from several annual deep-sea deployments of ADCPs in the Greenland Sea showed vertical migration patterns of zooplankton. An interdependence of the depth distribution and the seasonal light-cycle was demonstrated (Fischer & Visbeck, 1993). Nevertheless, it must be noted that (as shown here) quantitative biomass analysis must always be combined with at least occasional net catches to identify migrating species and calibrate the backscatter intensities. Potentially, ADCPs are also valuable in studying annual cycles in Antarctic krill, *Euphausia superba*. Net sampling in Antarctic waters is problematic due to long periods of ice cover. In general, the major advantages of ADCP in biological applications are long-term measurements and the possibility of real-time analysis on board, in conjunction with determination of other abiotic and biotic parameters, as was shown here, with *M. norvegica* in the Läsö-Deep as an example.

Acknowledgements. We thank Prof. Dr. F. Schott for support and encouragement. The contribution of the shipboard team, particularly Dipl.-Biol. K. Wieland are gratefully acknowledged. U. Papenburg fought a successful battle with a stubborn net-release mechanism. Cpt. M. Groß and his crew contributed much enthusiasm and expert navigational skills. We thank Dr. Renate Haass for advice, and Dipl.-Biol. S. Kosfeld for practical help in identifying copepod species in samples from net catches and krill stomachs.

LITERATURE CITED

- Boden, B. P. & Kampa, E. M., 1967. The influence of natural light on the vertical migrations of an animal community in the sea. – Symp. zool. Soc. Lond. 19, 15–26.
- Boysen, E. & Buchholz, F., 1984. *Meganyctiphanes norvegica* in the Kattegat: studies on the annual development of a pelagic population. – Mar. Biol. 79, 195–207.
- Buchholz, F. & Boysen-Ennen, E., 1988. *Meganyctiphanes norvegica* in the Kattegat: studies on the horizontal distribution in relation to hydrography and zooplankton. – Ophelia 29, 71–82.
- Buchholz, F. & Prado-Fiedler, R., 1987. Studies on the seasonal biochemistry of the Northern krill *Meganyctiphanes norvegica* in the Kattegat. – Helgoländer Meeresunters. 41, 1–9.
- Fischer, J. & Visbeck, M., 1993. Seasonal variation of the daily zooplankton migration in the Greenland Sea. – Deep-Sea Res. 40, 1547–1557.
- Flagg, C. N. & Smith, S. L., 1989. On the use of the Acoustic Doppler Current Profiler to measure zooplankton abundance. – Deep-Sea Res. 36, 455–474.

- Forward, R. B., 1988. Diel and vertical migration: Zooplankton photobiology and behavior. – *Oceanogr. mar. Biol.* 26, 361–393.
- Forward, R. B. & Fyhn, H. J., 1983. Osmotic regulation of the krill *Meganyctiphanes norvegica*. – *Comp. Biochem. Physiol.* 74A, 301–305.
- Haney, J. F., 1988. Diel patterns of zooplankton behavior. – *Bull. mar. Sci.* 43, 538–603.
- Hutchinson, G. E., 1967. A treatise on limnology. Wiley, New York, 2, 725–809.
- Kils, U., 1981. Size dissociation in krill swarms. – *Kieler Meeresforsch. (Sonderh.)* 5, 262–263.
- Klages, N., 1983. Der nordische Krill *Meganyctiphanes norvegica* (M. Sars). Diss., Univ. Kiel, 104 pp.
- Longhurst, A. R., 1976. Vertical migration. In: *The ecology of the seas*. Ed. by D. H. Cushing & J. J. Walsh. Blackwell, Oxford, 116–137.
- Plueddemann, A. J. & Pintel, R., 1989. Characterization of the patterns of diel migration using a Doppler sonar. – *Deep-Sea Res.* 36, 509–530.
- Reppin, J., 1990. Analyse von Rückstreumplitude und Dopplergeschwindigkeit von ADCPs im Vergleich mit Zooplanktonvorkommen. Dipl.Arb., Kiel, 80 pp.
- Roe, H. S. J., 1983. Vertical distributions of euphausiids and fish in relation to light intensity in the northeastern Atlantic. – *Mar. Biol.* 77, 287–298.
- Roe, H. S. J. & Griffiths, G., 1993. Biological information from an Acoustic Doppler Current Profiler. – *Mar. Biol.* 115, 339–346.
- Sameoto, D. D., 1980a. Relationships between stomach contents and vertical migration in *Meganyctiphanes norvegica*, *Thysanoessa raschii* and *T. inermis* (Crustacea Euphausiacea). – *J. Plankton Res.* 2, 129–143.
- Sameoto, D. D., 1980b. Quantitative measurements of Euphausiids using a 120-kHz sounder and their in-situ orientation. – *Can. J. Fish. aquat. Sci.* 37, 693–702.
- Schott, F. & Johns, W., 1987. Half-year-long measurements with a buoy-mounted Acoustic Doppler Current Profiler in the Somali current. – *J. geophys. Res.* 92, 5169–5176.
- Simard, Y. & Mackas, D. L., 1989. Mesoscale aggregations of euphausiid sound scattering layers on the continental shelf of Vancouver Island. – *Can. J. Fish. aquat. Sci.* 46, 1238–1249.
- Simard, Y., Lacroix, G. & Legendre, L., 1986. Diel vertical migration and nocturnal feeding of a dense coastal krill scattering layer (*Thysanoëssa raschii* and *Meganyctiphanes norvegica*) in stratified surface waters. – *Mar. Biol.* 91, 93–105.
- Ulrich, J., 1983. Zur Bathymetrie und Topographie der nördlichen Kattegat-Rinne. – *Meeresforsch.* 30, 61–68.
- Wiebe, P. H., Burt, K. H., Boyd, S. H. & Morton, A. W., 1976. A multiple opening/closing net and environmental sensing system for sampling zooplankton. – *J. mar. Res.* 34, 313–326.