

Diel, seasonal and ontogenetic variations in the vertical distributions of four marine copepods

T. Falkenhaus^{1,*}, K. S. Tande^{1,2}, T. Semenova²

¹Norwegian College of Fishery Science, University of Tromsø, N-9037 Tromsø, Norway

²Institute of Oceanology, Russian Academy of Sciences, Krasikova St. 23, Moscow 117218, Russia

ABSTRACT: Diel and seasonal variations in the vertical distributions of *Calanus finmarchicus*, *Metridia longa*, *M. lucens* and *Chiridius armatus* in Malangen, northern Norway, were determined from February until December 1992. The vertical behaviour differed among the species and among the different stages of a single species. The vertical distribution of *C. finmarchicus* was dominated by seasonal rather than diel vertical migration, and this species was found in surface waters during the spring phytoplankton bloom (March to May), and at the bottom of the fjord in the fall and winter. *Metridia* spp. were generally consistent diel vertical migrators. However, *M. longa* usually stayed deeper and had a larger migration amplitude than *M. lucens*. *M. longa* was more deeply distributed in the winter than during the summer, while *M. lucens* showed no such seasonal trend. The vertical behaviour of *C. armatus* was related to the seasonal change in day length, and diel vertical migration was strong in periods of large day/night contrast (spring and autumn), but ceased during the periods of midnight sun and winter darkness. During the summer *C. armatus* stayed deep both day and night. Diel vertical behaviour in young stages of all 4 species was weak or undetectable by the sampling method used. Younger stages of *C. finmarchicus* and *Metridia* spp. remained higher in the water column, while the opposite was observed in *C. armatus*. While seasonal variations in vertical behaviour are related to variations in food and light conditions, inter- and intraspecific differences may be due to life history, diet and susceptibility to predation.

KEY WORDS: Zooplankton · Copepods · Vertical distribution · Vertical migration · Fjords · Northern Norway

INTRODUCTION

The water column of the ocean provides a diverse habitat gradient in which light, temperature, food and predation risk all change with depth (e.g. Banse 1964, Mullin 1979). Thus, the vertical distribution of zooplankton may be regarded as a process of habitat selection, in which the organism must trade off various selective forces (Giske et al. 1990): (1) visual predation from fish, (2) non-visual predation from carnivorous zooplankton, (3) the vertical distribution of food, and (4) the cost of migration. The outcome of this trade-off is influenced by environmental factors such as light (Russel 1927, Cushing 1951, Ringelberg 1991), abundance of food (Pearre 1973, Huntley & Brooks 1982), predator abundance (Bollens & Frost 1989, Lampert

1989, Ohman 1990) and hydrography (Banse 1964, Pearre 1979). Furthermore, inter- and intraspecific differences in the response to these environmental factors are due to differences in fecundity (Gabriel & Thomas 1988), size (Landry 1978, Sullivan 1980, Yen 1985), behaviour (Gerritsen & Strickler 1977, Zaret 1980, Greene 1988, Ramcharan & Sprules 1991) and pigmentation (Kerfoot 1985). Temporal variations in environmental factors combined with species-specific responses to these changes enhance diel and seasonal variations in the vertical distribution of zooplankton organisms. The vertical distribution and migration of zooplankton has been studied since the early years of plankton research (Russel 1927, Cushing 1951, Banse 1964) and the literature on the vertical distributions and migration of copepods is extremely large. However, most studies have been limited seasonally, or focused primarily on the adult females.

*E-mail: tonef@nfh.uit.no

This paper presents monthly data on the vertical distribution of *Calanus finmarchicus* (Gunnerus), *Metridia longa* (Lubbock), *M. lucens* and *Chiridius armatus* in a north Norwegian fjord. These species are among the dominant species in the fjords and coastal areas of northern Norway (Falkenhaug et al. 1997) and differ in body size, pigmentation, trophic position and life history. At high latitudes, several environmental factors change dramatically with the season: the day length (sun above horizon) varies from 24 h in the summer to 0 h during winter. The length of the primary production period is restricted to a few months in the spring (Eilertsen et al. 1981), and the hydrography in coastal waters undergoes strong seasonal variations. Accordingly, this study covers different seasons, species and developmental stages, providing a wide variety of biotic and abiotic conditions which are expected to affect the vertical distributions of copepods. With predation being invoked as the primary selective force behind diel vertical migration (DVM), the following specific predictions can be made: (1) copepods should have a deeper night-distribution during summer, (2) DVM decreases during periods of small diel changes in light and (3) the intensity of DVM increases with susceptibility to predation.

MATERIALS AND METHODS

The study was carried out in Malangen (69° 30' N, 18° 21' E) in the vicinity of Tromsø, northern Norway (Fig. 1). The fjord is separated from the ocean in the north by a 200 m deep sill, and is divided into 2 basins with maximum depths of 250 and 400 m. Between the 2 basins lies a shallower area with a sill depth of 160 m. The fjord is highly influenced by the coastal waters along the coast, resulting in high temperatures (6 to 7°C) and salinities (34 to 34.5‰) in the deeper layers all year (Falkenhaug et al. 1995, 1997). Stratification of the water column during spring and summer is due to freshwater run-off from the river Målselv at the fjord head (Falkenhaug et al. 1995). A more detailed description of the fjord is provided by Falkenhaug et al. (1995). The light climate in the Malangen area changes dramatically during the year (Fig. 2), varying from winter darkness (28 November until 14 January) to midnight sun (19 May until 26 July). Between these periods, the day length changes from 0 to 24 h in the course of 4 mo.

Ten cruises were made between February 21 and December 16, 1992, with RV 'Johan Ruud'. Zooplankton sampling was performed during the day (10:00 to 14:00 h

local time) and at night (22:00 to 02:00 h local time) with a 1 m² MOCNESS (Wiebe et al. 1985; mesh size = 180 µm, vertical hauling speed = 0.16 m s⁻¹, horizontal speed = 0.6 m s⁻¹). The following discrete depth strata were sampled: 0–20, 20–50, 50–100, 100–150, 150–200, 200–250, and 250–360 m. Hydrographical data were obtained using a Neil Brown CTD profiler and chlorophyll fluorescence was measured with a BackScat Fluorometer Model 1121 MP/Chla mounted on a Multiparameter CTD Probe OTS 1500 (ME Meerestechnik-Elektronik GmbH).

Zooplankton samples were split with a Motoda splitter device (Motoda 1959). One half of the sample was preserved in 4% buffered formalin-seawater solution for identification and enumeration of copepods, while the other half was frozen for later determination of ash free dry weight (AFDW). Data on zooplankton biomass are presented elsewhere (Falkenhaug et al. 1995, Falkenhaug 1996). In the

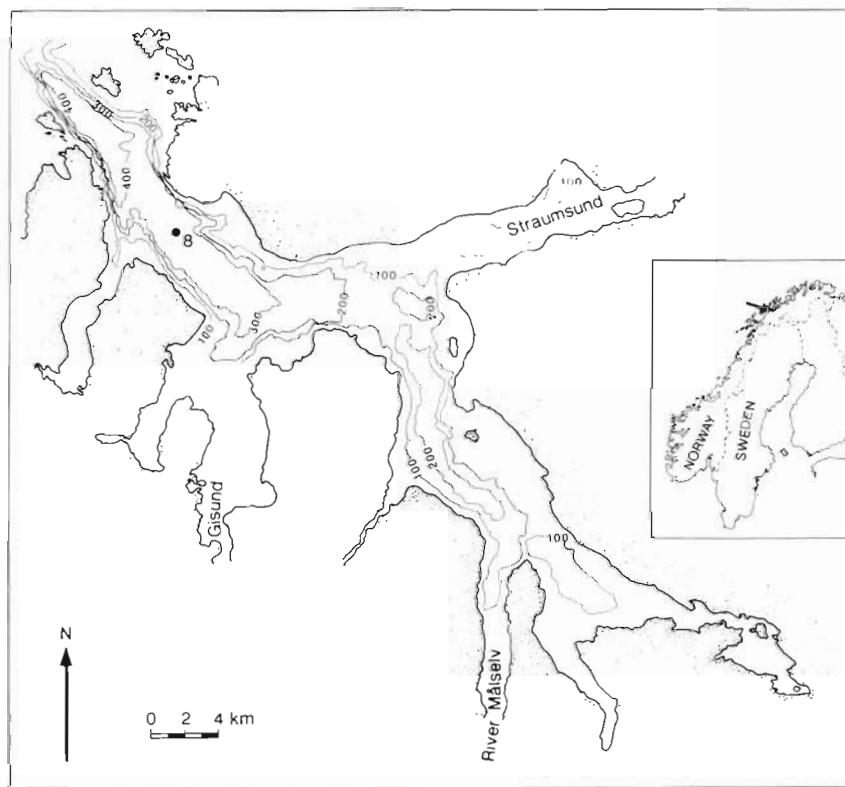


Fig. 1 Malangen fjord, Norway, with sampling station (8) and 100 m depth curves

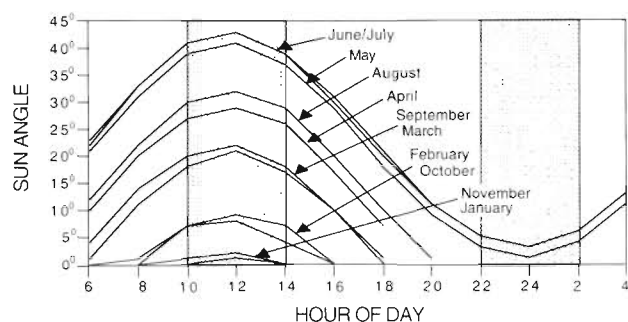


Fig. 2. Elevation of the sun in Tromsø on each sampling date. Shaded areas indicate time of sampling

laboratory, mesozooplankton were identified and counted under a binocular microscope on subsamples no less than 1/100 of the total sample.

We used 2 separate indices of DVM as employed by Bollens & Frost (1989): (1) the weighted mean depth (WMD) was determined for each daytime and night-time vertical series of samples as

$$\text{WMD} = (\sum n_i d_i) / \sum n_i$$

where n_i is abundance (no. m^{-3}) at depth d_i , taken to be the midpoint of each stratum. Migration amplitude was defined as the difference between night WMD and day WMD. (2) The strength of migration behaviour, or the proportion of individuals migrating across a given depth during a diel cycle (V), was calculated as the difference between the proportion of the population above a given reference depth at night and the proportion above that same depth during the day. The maximum depth and amplitude of migration varies seasonally. Thus separate reference depths were calculated for each vertical profile as the midpoint between day WMD and night WMD. The V parameter varies between 1 and -1, with positive values indicating normal DVM and negative values indicating reverse DVM. Each station was sampled only once during the day and once at night. Differences in WMD and the V parameter thus could not be tested statistically, but were assumed to indicate seasonal and ontogenetic variations in the vertical behav-

iour of the 4 copepod species studied. In addition, the magnitudes of migrations may have been underestimated, as the samples were not necessarily obtained when the copepod populations were at their minimum or maximum depth distributions. Day and night WMDs should therefore be regarded as approximations.

RESULTS

Hydrography and fluorescence

The water column was fairly homogeneous during winter (33 to 34.9‰), and stratification, due to fresh water run-off, started in April/May and lasted until August/September (Fig. 3). The halocline oscillated around 10 m during summer, and the greatest stability occurred in June-July. The spring phytoplankton bloom in Malangen in 1992 started in late March/early April, and reached a peak in late April (Fig. 3). After a summer minimum from mid-May until June, a secondary but smaller bloom was found in early July to late August. Chlorophyll values returned to pre-spring bloom levels from mid-October, reaching a minimum in December.

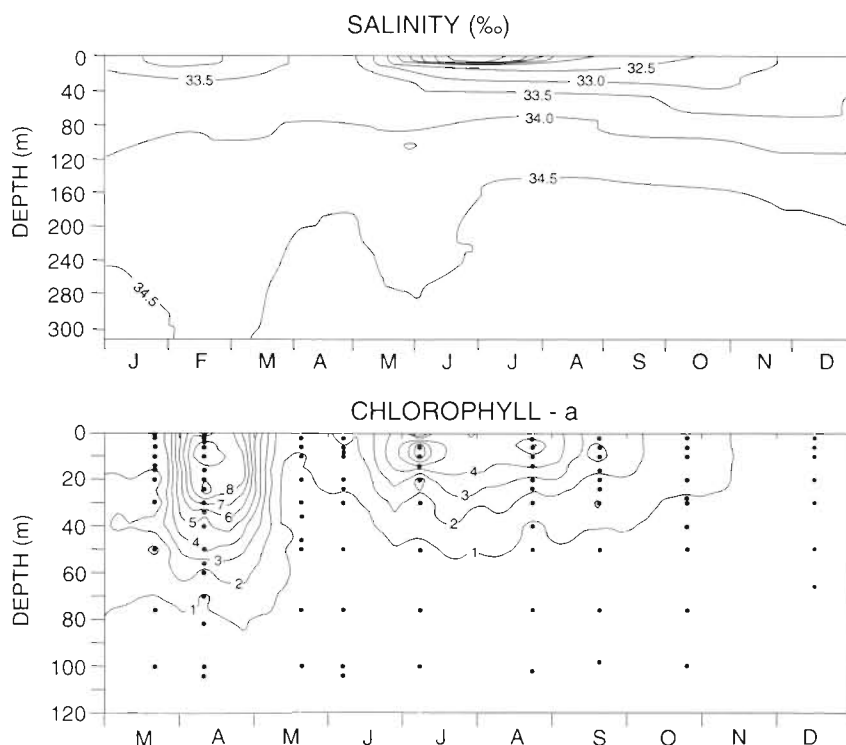


Fig. 3. Salinity and *in situ* fluorescence ($\mu\text{g chl } a \text{ equivalents l}^{-1}$) at sampling station, Malangen, 1992

Calanus finmarchicus

Calanus finmarchicus stages CI–CIII appeared in the top 50 m in April, with younger stages found slightly higher than the next older stage (Fig. 4a). The depth distribution was usually unimodal, with small migration amplitudes and little indication of any migration on the scales sampled. *C. finmarchicus* CIV–CV underwent a seasonal migration, in which most of the population stayed below 150 m during the autumn and winter months (July to February) and returned to the surface in February/March (Fig. 4b). Stages CIV–CV were often bimodally distributed with small differences between day and night distributions. However, unimodal distributions for all stages were observed in April (above 250 m) and in winter, October/December (below 150 m). Stages IV–V were found in the surface during both day and night in the spring (February to May), but tended to avoid the top 20 m during the day from June onwards. *C. finmarchicus* adult females were found in the upper 100 m, in spring (February to April) and fall (September to December). During the summer (May to August) the copepods were bimodally distributed. *C. finmarchicus* adult males had a broad vertical distribution in February/March, which gradually became shallower and more concentrated later in the season.

The strength of diel vertical migration (V) in *Calanus finmarchicus* was usually slight (<0.5) and showed no seasonal trend (Table 1). The highest values were found in stage CV and adult females. Migration of *C. finmarchicus* males was usually weak, and with low amplitudes. It should be noted that the negative values on some of the dates are due to missing surface data (July) or to low numbers of individuals in the samples.

Metridia spp.

Metridia spp. stages I–III (Fig. 5a) were found in the top 150 m during the spring (February/March) and fall (August to December). During the summer, the copepods had a broader vertical distribution and were

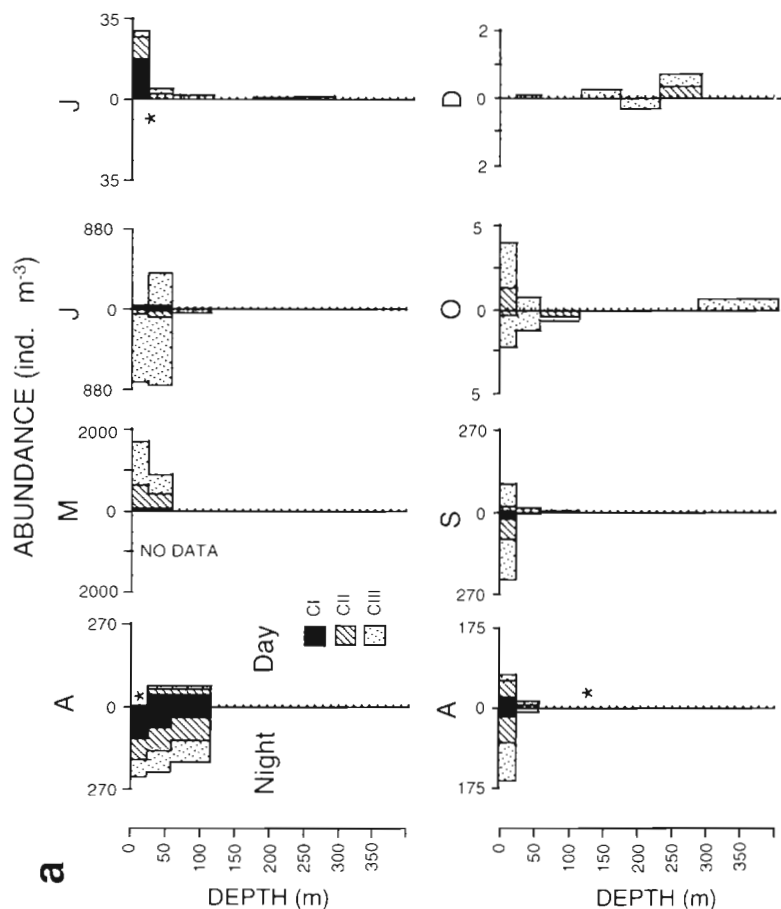


Fig. 4. Vertical distribution of *Calanus finmarchicus*. (a) Stages CI–CIII at night and during the day from April to December 1992. (b) Stages CIV–CV, and CVI females (F) and males (M) at night (black) and during the day (white) from February to December 1992. Note different scales on abscissa. * Data missing

found at depths down to 350 m. Stages I–II avoided the upper 20 m during the day from March to September, but stayed in the surface layer both day and night in February and in October/December. Migration strengths of *Metridia* spp. stages I–III were usually low and variable, but the higher values were found during summer (April to July; Table 1).

Metridia longa stages IV–V always avoided the top 20 m during day, and stage V performed diel vertical migrations during summer (June to September; Fig. 5b). The abundances of CIV–CV were low in February and March, so the migration strength observed on these dates may not be real. High values were found in summer, increasing to 0.6 in September (Table 1). The daytime depth of CV rose from 100–250 m in May to 150–250 m in June/July and 250–350 m in August. Most of the stage V population was below 150 m in October/December. *M. longa* adult females remained below 150 m in February/March and October/December (Fig. 5b). Females had a broader distribution in March to June, with a proportion of the population in the surface layers at night. As with *M. longa* stage V, especially strong migrations were observed in adult females in September (Fig. 5b,

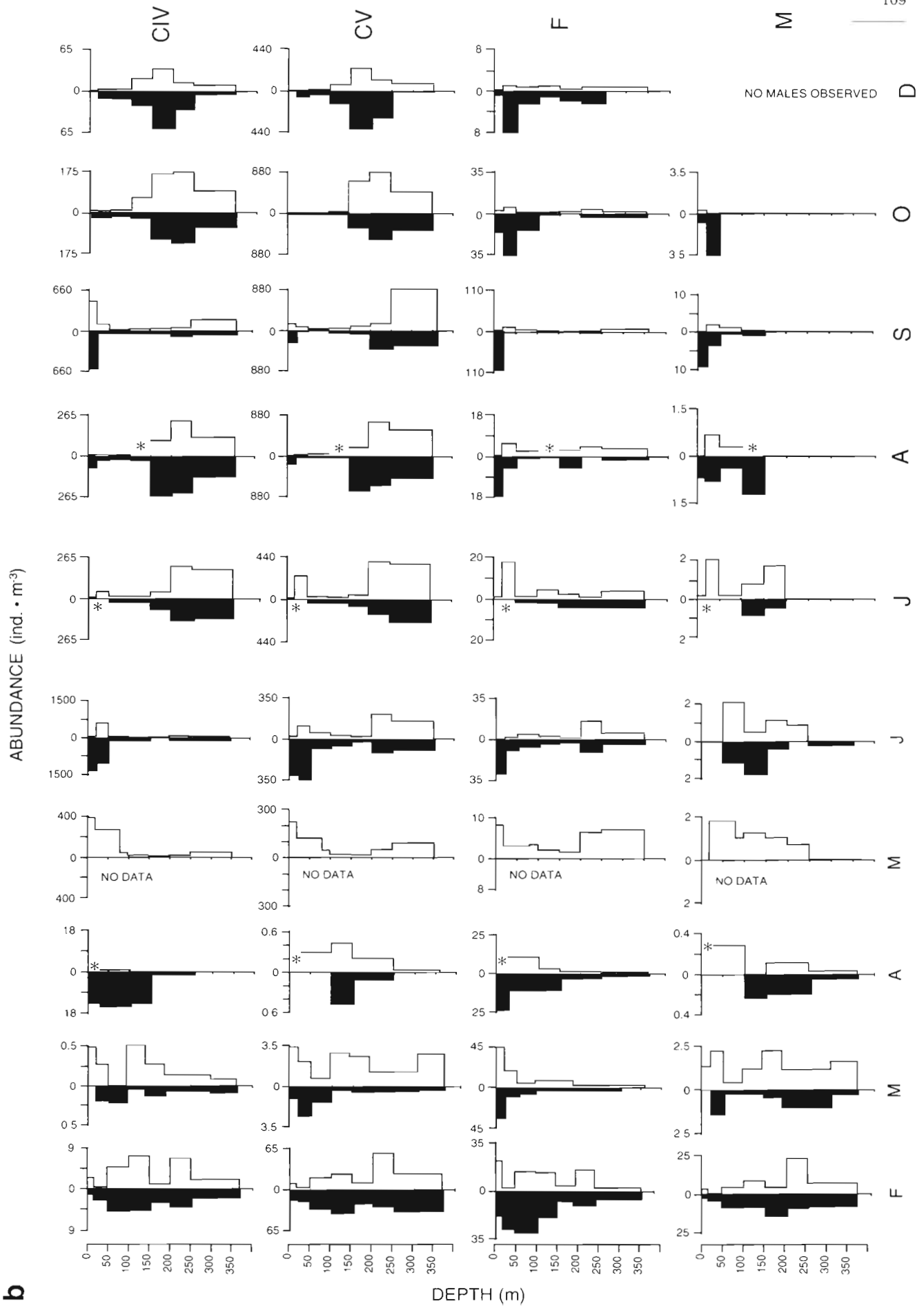


Table 1). At this date, stages IV–VI were almost absent from the daytime samples, but high abundances were found in the upper 20 m at night. There was no apparent difference in the depth distribution of adult males and adult females.

Metridia lucens IV–V were more shallowly distributed than *M. longa* and were found in the top 200 m, except from July when the copepod had a broader vertical distribution (Fig. 5c). Stages IV–V always avoided the top 20 m at day and usually performed diel vertical migration between the surface and 150–200 m. The migration strength of stage V reached its highest values (0.4 to 0.5) during the summer (July to September; Table 1). *M. lucens* adult females were distributed in the top 250 m, being more shallow in April than in other months. Adult females always avoided the top 20 m at day and performed diel vertical migrations on all sampling dates. Migration in *M. lucens* adult females was usually stronger than for stages IV and V, and varied between 0.07 and 0.76, the highest value being obtained in September (Table 1).

Chiridius armatus

Chiridius armatus stages I–III avoided the surface 20 m both day and night, except in February when stages I–III were found in the surface layer at night (Fig. 6a). Migration strengths of stages I–III were variable, but high values were found in February and August to December (Table 1). In summer (June/July) the copepods stayed at greater depths both day and night. Stages I–III usually stayed below 150 m in the day and below 50 m during night. Night distributions of stage I were slightly deeper than stage II, which in turn were deeper than stage III. *C. armatus* stage IV were usually distributed below 150 m during day and migrated to the surface at night (Fig. 6b). However, the copepod avoided the top 20 m both day and night in June to August and October. Migration strengths were high all year, with maximum values in February (Table 1). *C. armatus* stage V and adult females and

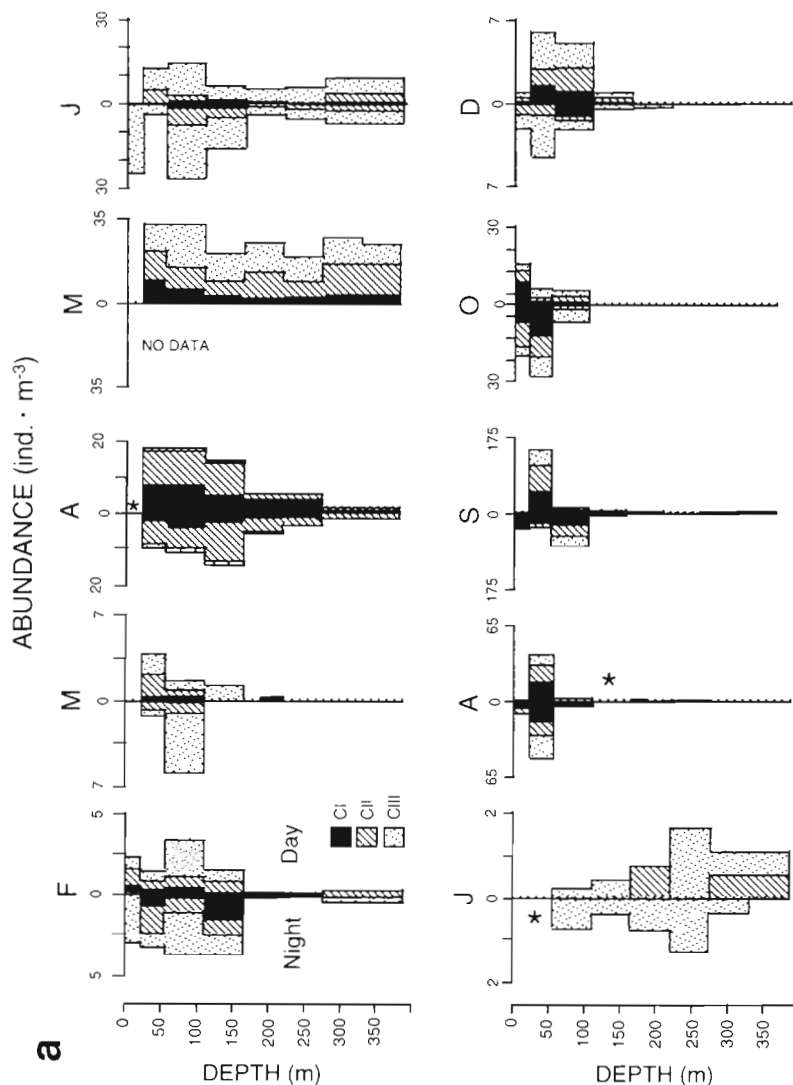
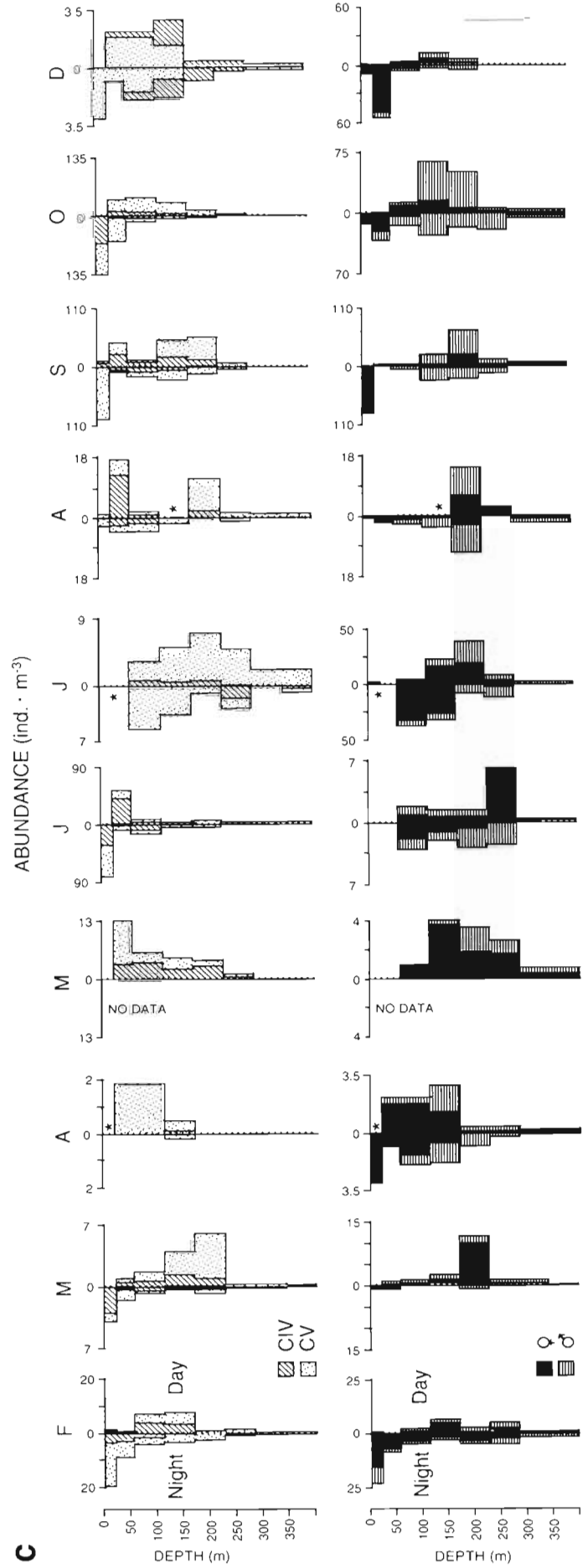
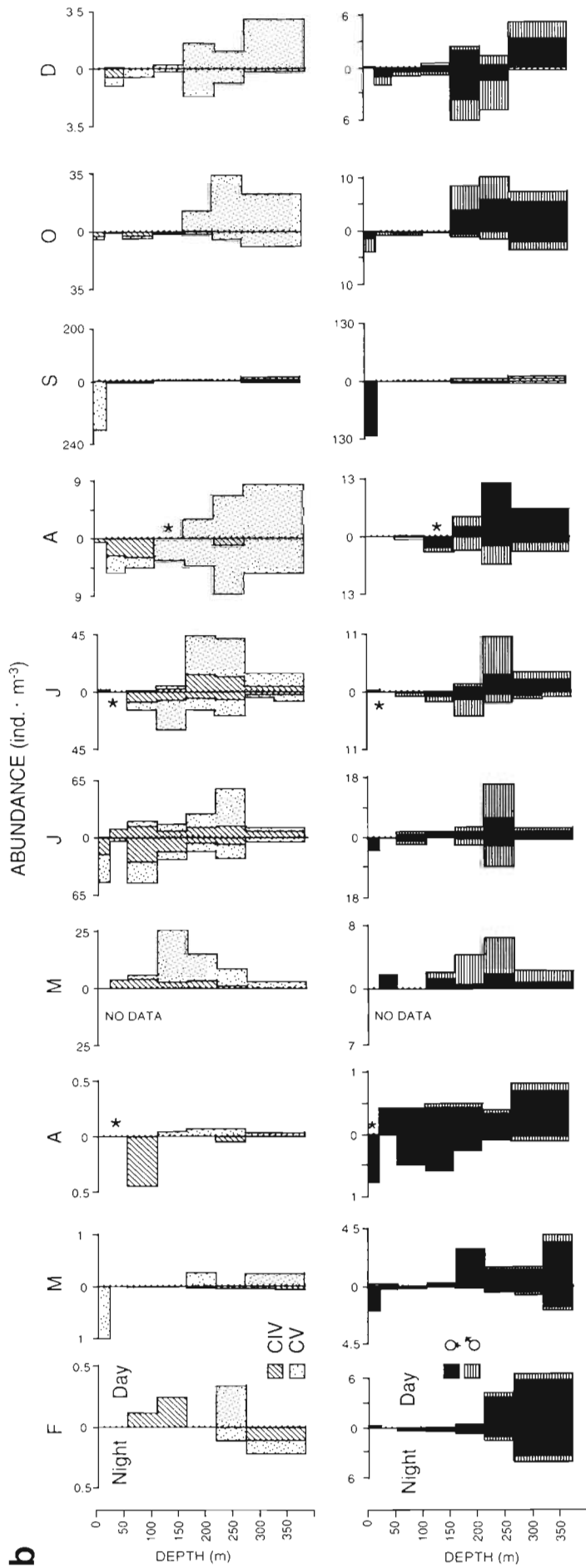


Fig. 5. *Metridia* spp. Vertical distribution at night and during the day from February to December 1992. (a) *Metridia* spp. stages CI–CIII. (b) *Metridia longa* stages CIV–CV, and CVI females (♀) and males (♂). (c) *Metridia lucens* stages CIV–CV, and CVI females (♀) and males (♂). Note different scales on abscissa. *Data missing

males performed strong vertical migration in February to April and August to December (Fig. 6b). Migration strengths in these periods were high, reaching values close to 1.0 (Table 1), indicating that 100% of the population crossed the reference depth during the diel cycle. *C. armatus* stage V and adult females were found near the surface 20 m at night in February and March, but avoided the surface from April to December. During the summer, migration ceased (Table 1) and stages IV–VI stayed below 150 m both day and night.

Interspecific comparisons

The vertical behaviour of all stages of the 4 species is illustrated as day and night WMD on all the dates sampled (Figs. 7 & 8). Younger copepodid stages of *Calanus finmarchicus* and *Metridia* spp. were generally



more shallowly distributed than older stages. However, in *Chiridius armatus* the situation was the opposite: younger stages were found deeper than older stages. There was a trend to older copepodid stages of all 4 species showing larger migration amplitudes than the younger ones. However, males usually had low migration amplitudes, with the exception of *C. armatus* males, where high migration amplitudes were observed.

Calanus finmarchicus stages I–III were generally more shallowly distributed than *Chiridius armatus* stages I–III, while *Metridia* spp. stages I–III were intermediate in depth (Fig. 7). *C. finmarchicus* stages IV–V had similar WMD to *Metridia longa* stages IV–V, except from the spring/summer period, when *C. finmarchicus* were shallower. *M. lucens* IV–V were usually shallower than both *C. finmarchicus* and *M. longa* IV–V. *C. armatus* IV–V had the deepest day WMDs of the copepods studied, while their night WMDs were similar to *M. longa*. *C. finmarchicus* adult females had similar WMDs to those of *M. lucens* adult females, remaining shallower than both *M. longa* and *C. armatus* females. *C. finmarchicus* stages I–III stayed in the surface 50 m during the whole season. *Metridia* spp. and *C. armatus* stages I–III had deeper WMDs during the summer months than in winter. *C. finmarchicus* stages IV–V and adult females all showed a lessening of the day and night WMD in April, followed by a deepening in June/July. This seasonal trend was also seen in *M. longa* and *M. lucens* stage V and adult females, where the WMDs became more shallow in April/May, and deepened again in the late summer.

Chiridius armatus stages IV–VI had almost constant day WMDs for all stages on all dates (Fig. 8). However, a slight reduction in the daytime WMD was observed in April/May. The night WMDs of *C. armatus* varied during the season, being shallow in February, deepening in April to July, and becoming more shallow again in September/October. *Calanus finmarchicus* males showed no clear DVM, and were found deeper than adult females in early spring. As the migration amplitude of females increased later in the season, males stayed both day and night at the night WMD of females, which gradually became more shallow during the season. *Metridia longa* and *M. lucens* adult males

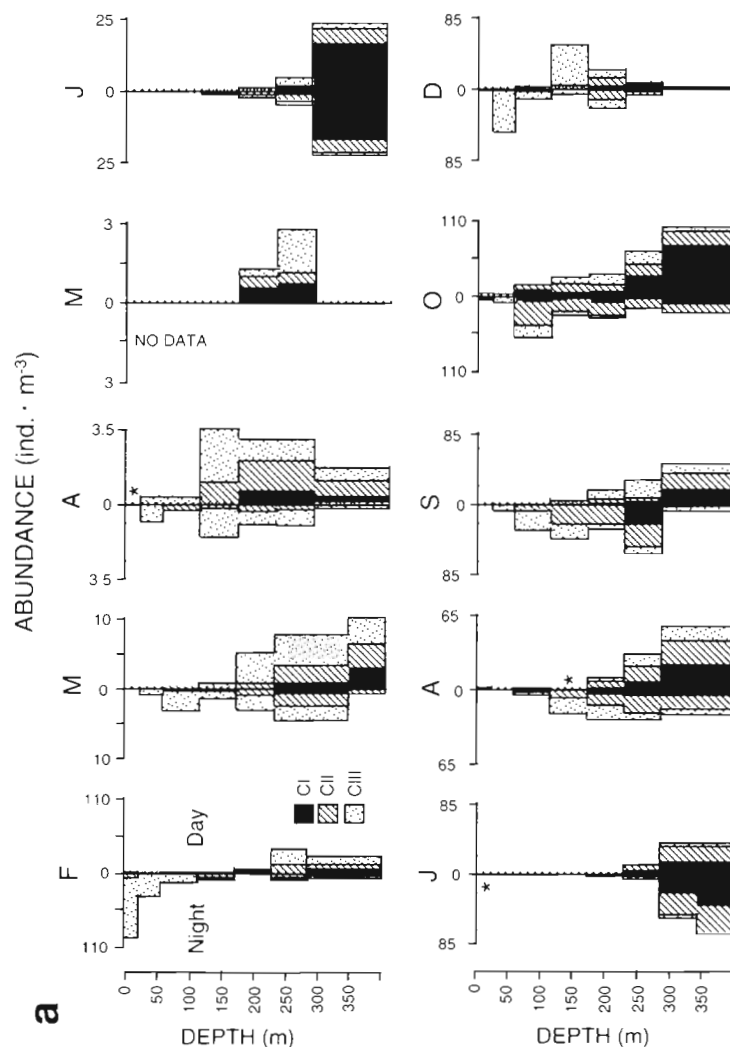


Fig. 6. *Chiridius armatus*. Vertical distribution from February to December 1992. (a) Stages CI–CIII at night and during the day (b) Stages CIV–CV, and CVI females (F) and males (M) at night (black) and during the day (white). Note different scales on abscissa. *Data missing

were usually slightly deeper than their females, especially during night. *C. armatus* males showed similar vertical distribution and migration patterns to those of their females.

DISCUSSION

The avoidance of visual predators, such as planktivorous fish, is considered to be an important ultimate reason for DVM (Zaret & Suffern 1976, Gliwicz 1986, Lampert 1989). This predator-evasion hypothesis predicts that zooplankton will be distributed deeper in summer so that they are not exposed to high illumination when the risk of mortality from visual predators will be great. The observed seasonal pattern in *Chiridius armatus* was consistent with this prediction. While the day WMDs of *C. armatus* were fairly constant throughout the year (200 to 380 m), a seasonal trend

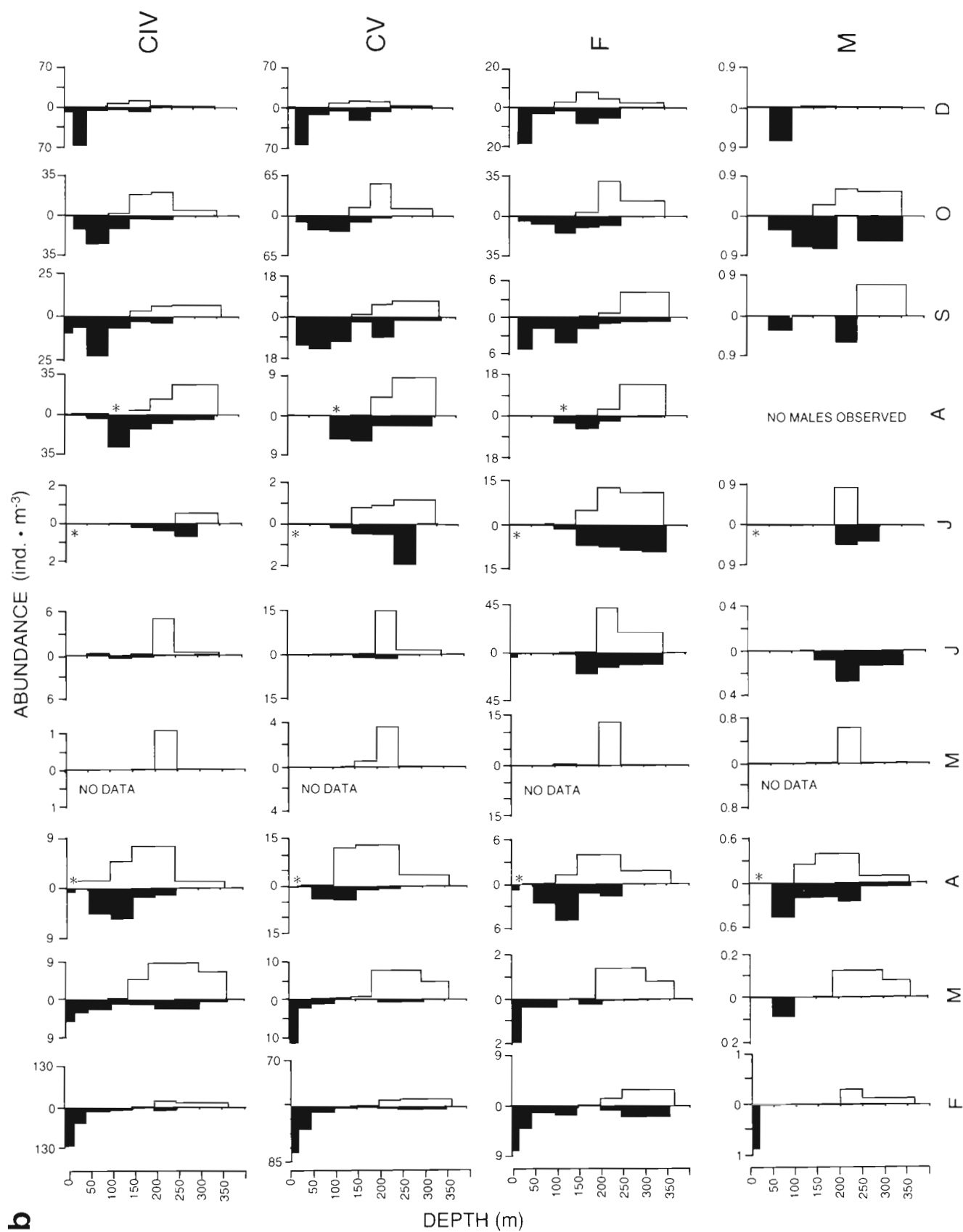


Table 1. Migration strength (V) of all copepodid stages of *Calanus finmarchicus*, *Metridia longa*, *M. lucens* and *Chiridius armatus* in Malangen, 1992. V is calculated according to Bollens & Frost (1989): $V = 1$ indicates maximum migration strength, while $V = 0$ indicates no diel vertical migration

	F	M	A	M	J	J	A	S	O	D
<i>Calanus finmarchicus</i>										
I	–	–	0.37	–	0.00	–0.02	–0.04	0.50	–	–
II	–	–	0.16	–	0.12	–0.23	–0.58	0.05	–0.76	–
III	–	–	0.15	–	0.22	–0.65	0.30	0.10	0.64	–
IV	0.03	–0.08	0.16	–	0.16	0.26	0.16	0.18	0.01	0.09
V	0.18	0.28	0.37	–	0.37	0.10	0.18	0.26	–0.03	0.13
Female	0.16	0.12	0.23	–	0.44	–0.11	0.33	0.50	0.44	0.23
Male	0.26	–0.16	0.00	–	0.08	–0.12	–0.36	0.81	–0.84	–
<i>Metridia</i> spp.										
I	–0.54	0.23	–0.02	–	0.14	–0.03	–0.19	–0.29	–0.29	–0.35
II	0.01	–0.47	–0.17	–	0.17	0.35	0.53	–0.58	0.20	0.48
III	–0.05	0.06	–0.07	–	0.37	0.35	–0.05	–0.30	–0.05	0.13
<i>M. longa</i>										
IV	–1.00	–	–	–	0.33	0.46	–	–	–	–
V	–0.66	–0.45	–	–	0.36	0.51	0.28	0.62	–0.11	0.53
Female	0.08	–0.04	0.45	–	0.26	0.51	0.21	0.84	–0.16	0.57
Male	–0.03	–0.12	–0.27	–	0.09	0.48	–0.67	0.04	0.00	0.54
<i>M. lucens</i>										
IV	0.23	0.45	–	–	–0.34	–0.32	–0.24	0.13	0.39	0.21
V	0.29	0.36	–0.64	–	0.21	0.43	0.52	0.41	0.29	0.42
Female	0.32	0.59	0.07	–	0.62	0.44	0.37	0.76	0.29	0.72
Male	0.14	–0.08	–0.11	–	–0.42	–0.19	–0.04	0.14	0.01	0.19
<i>Chiridius armatus</i>										
I	0.39	0.43	0.24	–	0.00	–0.17	0.31	0.54	0.33	0.05
II	0.34	0.30	0.27	–	0.22	–0.14	0.30	0.62	0.38	0.61
III	0.88	0.31	0.03	–	0.33	0.22	0.53	0.69	0.62	0.63
IV	0.87	0.41	0.45	–	0.82	0.48	0.66	0.80	0.78	0.68
V	0.76	0.74	0.43	–	0.00	–0.06	0.59	0.69	0.76	0.44
Female	0.58	0.77	0.48	–	–0.27	–0.07	0.47	0.81	0.53	0.60
Male	1.00	1.00	0.26	–	–0.04	–0.34	0.24	0.83	0.57	0.88

was seen in the night WMDs, which were deeper during the summer (below 100 m in June to August) than during the winter months (upper 100 m; Fig 8).

Furthermore, the relative change in light intensity is thought to be the most important proximate factor that initiates upward or downward swimming on a diel cycle (Russel 1927, Cushing 1951, Ringelberg 1964, 1991). DVM in zooplankton are thus expected to decrease during periods of small diel changes in light. The observed vertical distributions of *Chiridius armatus* are consistent with this prediction, since DVM in stage V and adults was strong in periods of large day/night contrast (spring and fall), but ceased during the period of midnight sun (Fig. 9). Similarly, the length of time *Metridia* spp. spent near the surface was found to vary seasonally with the length of night (Hays et al. 1995). *Calanus finmarchicus* did not perform DVMs during the midnight sun period in Malangen.

Depressed DVM in zooplankton in the absence of diel changes in light intensity has previously been observed in Arctic zooplankton (e.g. Bogorov 1946, Longhurst et al. 1984, Fisher & Wisbeck 1993, Loose 1993). Thus, changes in predation intensity need not be invoked to explain the major seasonal changes in the timing of DVM behaviour. While these results still support predator evasion as the ultimate cause of DVM, our results suggest that length of night is the proximate cue that causes seasonal changes in DVM of *C. armatus* in Malangen.

The seasonal variations observed in the vertical distributions of *Calanus finmarchicus* and *Metridia longa* were different from *Chiridius armatus*. *C. finmarchicus* was found in the shallow surface layers in March to May, and at the bottom of the fjord in the fall and winter. Besides, DVM was low and of variable strength on all dates. Bimodal distributions were observed for larger copepodid stages (CIV–CV) both day and night in summer, which has been considered as an indication of asynchronous vertical migration, where the amount of time spent in surface waters is determined

by individual foraging success (Rudjakov 1970, Pearre 1979). However, we suggest that bimodal vertical distributions were due to asynchronous seasonal migration, with one part of the population staying in the surface both day and night, while another part had migrated down to overwintering depths. Similarly, the bimodal distribution of *C. finmarchicus* adult females in the Canadian Arctic in August was interpreted as a post-reproductive situation (Longhurst et al. 1984). Periods of unimodal distributions of CIV and CV were connected with periods of high food abundance (April), when the majority of the population was concentrated above 150 m both day and night, and with the overwintering period (August and onward) when the population had migrated down to overwintering depths (150 to 380 m). A small proportion of the *C. finmarchicus* population in Malangen was found in the surface layers during the winter (Fig. 4b). This corrob-

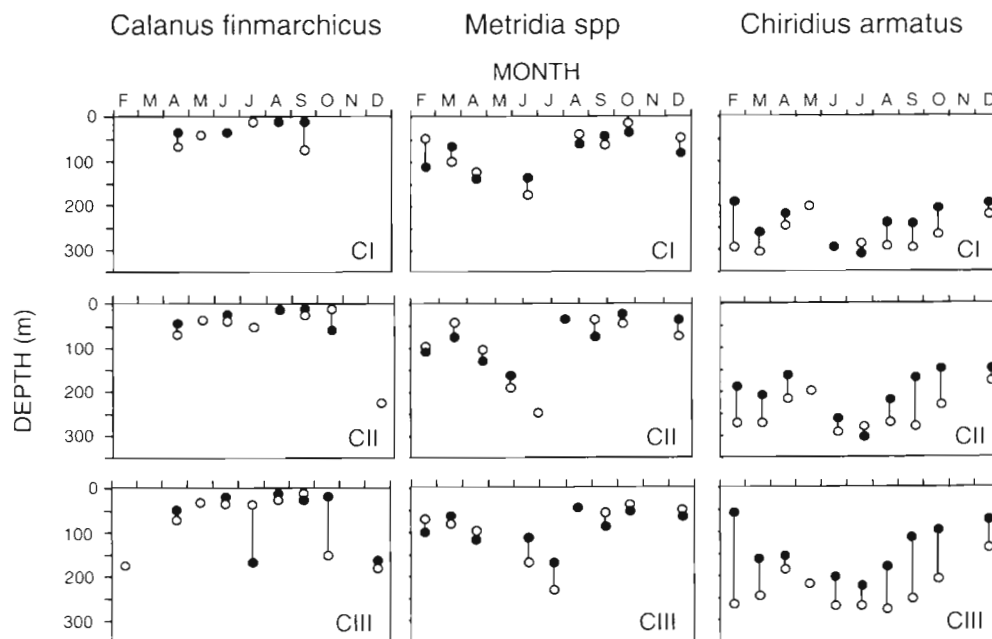


Fig. 7. Weighted mean depth during the day (○) and night (●) of *Calanus finmarchicus*, *Metridia* spp. and *Chiridius armatus* stages CI–CIII in Malangen, 1992

orates findings from other locations in the northern hemisphere (e.g. Herman et al. 1981, Bathman et al. 1990, Hirche 1991, Pedersen et al. 1995).

Both *Metridia longa* and *M. lucens* tended to avoid the surface during the day, with strong indications of

DVM, especially during the summer (Table 1). *M. lucens* showed no clear variations in vertical distribution with season in Malangen, while the daytime depths of CV and adult *M. longa* were deeper during winter (below 200 m) than in the summer (150 to 250 m

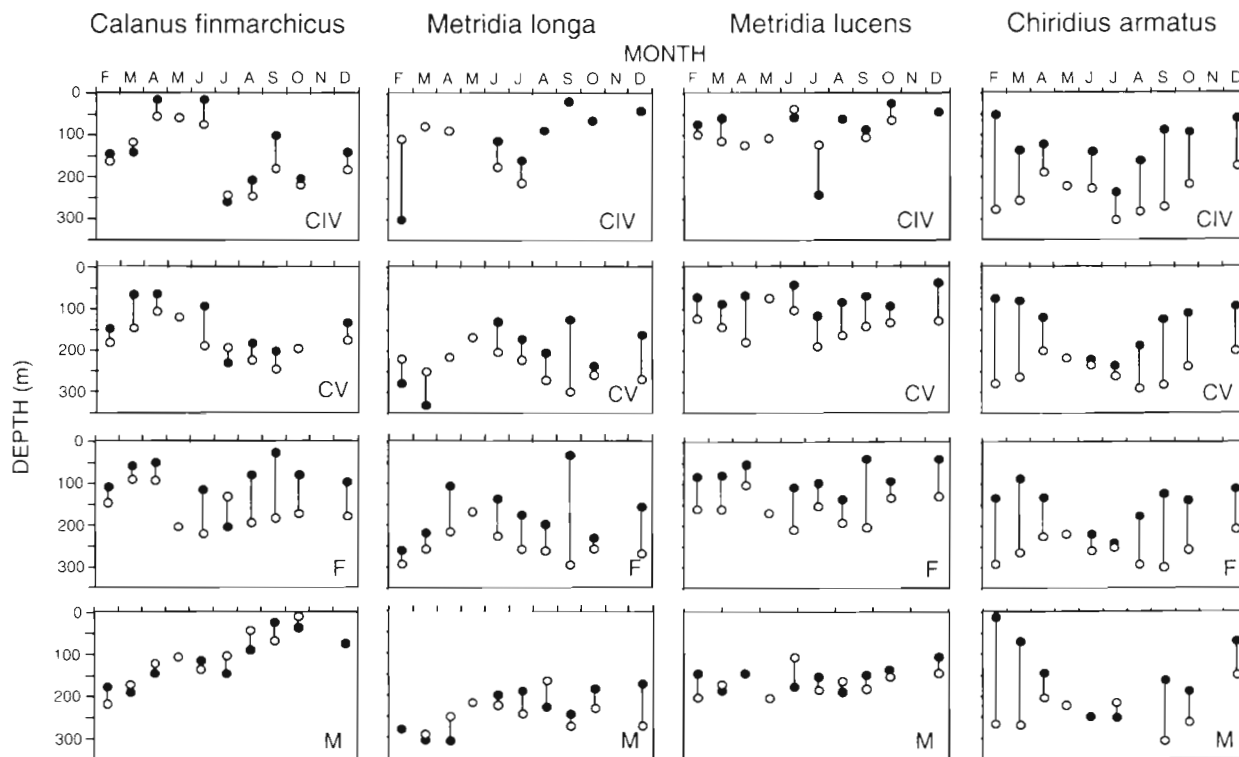


Fig. 8. Weighted mean depth during the day (○) and night (●) of *Calanus finmarchicus*, *Metridia longa*, *M. lucens* and *Chiridius armatus* stages CIV–CV, and CVI females (F) and males (M) in Malangen, 1992

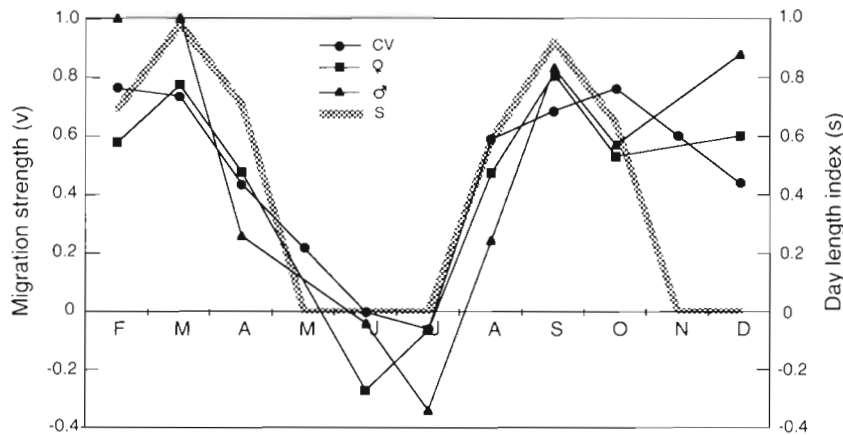


Fig. 9. Migration strength (V) of *Chiridius armatus* stages CIV–CV, and CVI females (♀) and males (♂) from February to December 1992. V is calculated according to Bollens & Frost (1989): $V = 1$ indicates maximum migration strength, while $V = 0$ indicates no diel vertical migration. Day length index (shaded line) is calculated as $S = 1 - (|D - N| / 24)$ where D and N are time for sun observed above (D) and below (N) the horizon per day. $S = 1$ indicates maximum light variability (12 h light and 12 h dark d^{-1}), while $S = 0$ indicates minimum variability (24 h light or 24 h darkness d^{-1})

from May to July). In the nearby Balsfjorden, *M. longa* (CIV–CV and adults) showed a clear tendency to nocturnal aggregation in the upper layer in September, but occurred within 50 m of the fjord bottom at noon throughout the year (Båmstedt et al. 1985). Balsfjorden is shallower (170 m) than Malangen (380 m), and if these copepods choose their depth according to light conditions, the animals will aggregate close to the bottom during the day in shallow areas.

In addition to light conditions, other variations in environmental conditions may also cause temporal variations in vertical behaviour: salinity gradients of more than 0.2 to 0.3‰ per 10 m have been found to prevent vertical migration of copepods (Banse 1964). Strong gradients in the top 50 m of Malangen waters from May to August may have contributed to the depression of DVM in *Chiridius armatus* and *Calanus finmarchicus* in this period. However, weak migration in these species was also observed in periods with no such physical barriers (Fig. 6b), indicating that other mechanisms are involved. Seasonal changes in predation intensity have previously been found to cause seasonal changes in the vertical behaviour of zooplankton (Ohman et al. 1983, Frost & Bollens 1992, Bollens et al. 1993). No quantitative data on seasonal variations in fish abundance in Malangen exist, but predation by planktivorous fish is probably highest in summer. Non-visual predators such as the carnivorous copepod *Euchaeta norvegica* and the chaetognaths *Sagitta elegans* and *Eukrohnia hamata* were regularly found in the fjord, with maximum abundances in February and December (unpubl. data). These predators themselves perform normal DVM in order to avoid visual preda-

tors. This may cause their own prey to perform reversed DVM, as has been observed in Dabob Bay (Ohman et al. 1983, Frost & Bollens 1992). Indications of reversed DVM (negative V -values in Table 1) occurred occasionally in all species studied, but since only a single tow was made at each station, these values could not be tested statistically. However, negative values were most often found in small stages of *Metridia* spp., which may be most sensitive to these predators (Osgood & Frost 1994). The zooplanktivorous ctenophore *Bolinopsis infundibulum* occurred in large quantities during the summer (May to August), but was restricted to the upper 50 m layer both day and night (Falkenhaus 1996). However, neither *C. finmarchicus* nor *Metridia* spp. showed any avoidance of the surface layer during this period. *C. armatus* stayed deep both day and night in summer, thus avoiding predation from both fish and ctenophores.

Inter- and intraspecific differences

The differences observed among the copepods in this study are consistent with the predator-evasion hypothesis which predicts that those species and developmental stages that are most susceptible to visual predation will spend the least amount of time near the surface. More conspicuous animals (e.g. large, pigmented, or highly active) are better detected by predators and are expected to be stronger migrators (e.g. Zaret 1980 and references therein, Greene 1988, Lampert 1989). We found that both migration amplitude and migration strength increased with the stage of development in all species studied in Malangen. This was most evident in *Chiridius armatus* where clear differences between day and night distributions were observed in all stages. Similar age-specific differences in DVM behaviour have previously been reported in *Calanus finmarchicus* (Clarke 1933, Nicholls 1933, Williams & Conway 1980), *C. pacificus* (Huntley & Brooks 1982), *C. sinicus* (Huang et al. 1992) and *Metridia lucens* (Osgood & Frost 1994). However, we found no obvious DVM in small copepodids (CI–CIII) of *Metridia* spp. and *C. finmarchicus*. Huntley & Brooks (1982) found small-amplitude (<1 m) diel migrations in the nauplii and small copepodid stages of *C. pacificus*. In our study, such small depth differences

may have gone unnoticed as a result of the larger depth intervals sampled, turbulence, or because of a general lack of synchrony with the light variation and thus a less obvious migration pattern (Pearre 1979).

This study is novel in describing the vertical distribution when the 2 sibling species of *Metridia* coexist: *M. lucens* were always more shallow than similar stages of *M. longa*, with smaller migration amplitudes. However, older stages of *M. lucens* (CV and adult females) performed DVM of more or less constant strength throughout the year ($V = 0.2$ to 0.6 , except from April), whereas similar stages in *M. longa* performed DVM only during the summer (June to September). *M. longa* and *M. lucens* differ markedly in body size (4.0 and 2.5 mm prosome length for adult stages respectively; cf. Sars 1903) and hence susceptibility to visual predators should be different. This is consistent with the observed deeper distribution of *M. longa* compared to *M. lucens*. However, as observed here and by Osgood & Frost (1994), similar sized stages of different species have different migration behaviour.

Metridia spp. showed a stronger tendency to avoid the surface during the day than did *Calanus finmarchicus*, and this species was found to perform DVM during the midnight sun period, while *C. finmarchicus* did not. *Metridia* has previously been reported to be a stronger migrator than *Calanus* in other areas (Krause & Radach 1989, Bollens & Frost 1992, Osgood & Frost 1994) and has been found to be more sensitive to light than *Calanus* (Clarke 1933, Dagg et al. 1989). During the midnight sun period the underwater irradiance does not remain constant during the day, since the solar angle varies. Thus, the observed differences in vertical behaviour may be due to different responsiveness to light among species. *Metridia* is a more continuously active swimmer than *Calanus* (Mackas & Burns 1986, Dagg et al. 1989), and hence susceptibility to predators should be greater. Stuart & Hugget (1992) found that *Euphausia lucens* ingested adult *M. lucens* at higher rates than other similar-sized prey. However, Bollens et al. (1993) found a greater electivity of zooplanktivorous fish for *C. pacificus* over *M. lucens*, while Yen (1985) found lower predation rates by *Euchaeta elongata* on adult *M. lucens* than on similar-sized *C. pacificus*. No information on the selective feeding of fish and other predators exists from Malangen.

Of the 4 copepod species studied, *Chiridius armatus* is the most highly pigmented, with a bright red intestine and white, opaque ovarian tubes. This copepod should thus be especially susceptible to visual predators, causing the observed strong DVM related to seasonal variations in light conditions.

The trade-off between feeding and predator avoidance is generally believed to be an important factor in

the evolution of vertical behaviour (e.g. Gliwicz 1986, Clark & Levy 1988). However, the value of food intake relative to reduced predation risk may be different for organisms with different generation times and fecundity (Aksnes & Giske 1990). As found in this study, younger stages remain at slightly lesser depths than older ones (Fig. 7), since younger stages have higher weight-specific metabolic rates and food requirements (McLaren 1963) and since smaller stages are less susceptible to visual predation (see above). However, in *Chiridius armatus*, younger copepodid stages were distributed more deeply than older ones (Fig. 8). Larger stages of this species may be more dependent on small copepods as food, which are distributed in the upper layers, whereas young *C. armatus* may avoid the upper layers, with their high risk of visual predation, by feeding on detritus in deeper layers. The vertical behaviour of calanoid copepods is closely linked to their trophic position (Marshall & Orr 1955). *C. finmarchicus* is considered to be predominantly herbivorous (see however Ohman & Runge 1994), with 1 generation yr^{-1} in these waters (Tande 1982, Tande et al. 1985). This species times its spawning to coincide with periods of high phytoplankton production, and remains near the surface both day and night to feed during the very short period of food abundance. DVM in this species would be costly as a result of reduced access to food. Similarly, daylight feeding in herbivorous copepods has been found during periods of short nights and greater food requirements (Williams & Lindley 1980, Atkinson et al. 1992). *Metridia* spp. do not enter the diapause phase (Grønvik & Hopkins 1984, Batchelder 1985), but become less active during the fall and winter in some areas (Båmstedt et al. 1985, Osgood & Frost 1994). Species of the genus *Metridia* certainly eat phytoplankton when it is abundant (Grønvik & Hopkins 1984, Båmstedt et al. 1985), but consume other food such as microzooplankton during the winter (Haq 1967). *C. armatus* is classified as an omnivore (Arashkevich 1969, Alvarez & Matthews 1975), feeding on small copepods, ciliates and possibly detritus (Ottesen 1995). The ability to utilize different types of food makes omnivores less vulnerable to vertical and seasonal variations in phytoplankton, which reduces the cost of DVM.

In conclusion, we suggest that the observed inter- and intraspecific differences in behaviour are related to life history, diet and conspicuousness. Each of the species studied responded differently to diel and seasonal variations in environmental factors. The vertical distribution of *Calanus finmarchicus* was thus dominated by seasonal rather than diel migrations, which seemed to be related to the seasonal change in primary production. *Metridia* spp. were generally consistent diel vertical migrators, *M. lucens* more so than *M.*

longa. The vertical behaviour of *Chiridius armatus* was related to the seasonal change in day length, which suggests that light is the main proximate cause of seasonal changes in DVM in this species. For studies made over short time scales these temporal variations may obscure intertaxa differences in the vertical behaviour. Accordingly, these observations emphasize that seasonal studies are needed to fully understand the proximate mechanisms that underlie the vertical behaviour of copepods. Quantification of different predator preferences for different stages and species, along with the distributions and abundances of the predators, would allow more definite conclusions to be drawn on why vertical behaviour varies from species to species and among the different stages of a single species.

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