

Vertical distribution and feeding of the carnivorous copepod *Paraeuchaeta norvegica*

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ABSTRACT: Adult females of *Paraeuchaeta norvegica* inhabited the lower part of a 200 m deep water column in winter and early spring, while their distribution became more shallow during summer and comprised both a deep and a shallow mode during autumn. Day and night profiles were fairly similar, although with slightly shallower population distributions at night. *P. norvegica* produced fecal pellets at all seasons. Enumeration of the egested pellets suggested greatest feeding activity during late autumn and least during winter. Pellets were produced at all depths. Feeding activity was greatest at night.

KEY WORDS: Diel vertical migration · Fecal pellets · Season

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INTRODUCTION

The carnivorous copepod *Paraeuchaeta norvegica* is a common constituent of the zooplankton of fjords and oceanic waters (Østvedt 1955, Bakke 1977, Mauchline 1995, Park 1995, Dale et al. 1999), and is assumed to play an important role in the pelagic food chain (Båmstedt & Skjoldal 1976, Bakke 1977, Bathmann et al. 1990, Eiane et al. 2002). Adult female *P. norvegica* attain prosome lengths >5 mm in Norwegian fjords (Kaartvedt et al. 2002), and such large copepods are susceptible to visual predators (O'Brien 1979). Typically, large copepods live relatively deep during daytime and migrate into shallow waters at night. This diel vertical migration may reflect the needs of avoiding predators and finding prey (Bollens & Frost 1991, Hays et al. 1994). However, little is known about diel or seasonal patterns in vertical distributions and feeding of *P. norvegica* (but see Fleddum et al. 2001, Kaartvedt et al. 2002).

Adult females of *Paraeuchaeta* spp. are most efficient in capturing smaller-sized prey like copepods of ~1 mm prosome length (Yen 1983, Greene & Landry 1985, Olsen et al. 2000). However, a range of prey sizes, including *Calanus* spp., can be handled (Båmstedt & Holt 1978, Øresland 1991, Øresland & Ward 1993). Small copepods prevail in near-surface waters during summer and autumn, possibly being preyed on at night (Kaartvedt et al. 2002). Organisms like *Calanus* spp., which spend parts of their life-cycle in deep water, may serve as food

for *Paraeuchaeta* spp. at depth (Fleddum et al. 2001). However, *Paraeuchaeta* spp. are tactile predators (Yen 1987) that may be unable to efficiently locate and exploit dormant copepods, and Yen (1991) suggested that *P. antarctica* might cease feeding during winter.

Fjords represent relatively deep and readily accessible near-shore habitats, thereby providing unique opportunities for studies of deep-living organisms. Here we address the vertical distribution and feeding of adult female *Paraeuchaeta norvegica* in the Oslofjord, Norway. The specific goals were to establish vertical distributions of *P. norvegica* during day and night throughout the year, and to describe feeding patterns in relation to time of day, season, and depth.

MATERIALS AND METHODS

The study was carried out at a 200 m deep location during 7 cruises in 1997–98 (5 March, 29 April, 12 June, 25 August, 21 October, and 20 November 1997; and 9 February 1998). The study site (59° 38' N, 10° 38' E) was located in the Drøbak Sound that separates the inner and outer Oslofjord (Fig. 1). Sampling was carried out from RV 'Trygve Braarud', except for June, when sampling was performed from RV 'Bjørn Føyn'.

Salinity and temperature were measured with a Neil Brown Mark III CTD, except for June, when we used a portable mini-CTD.

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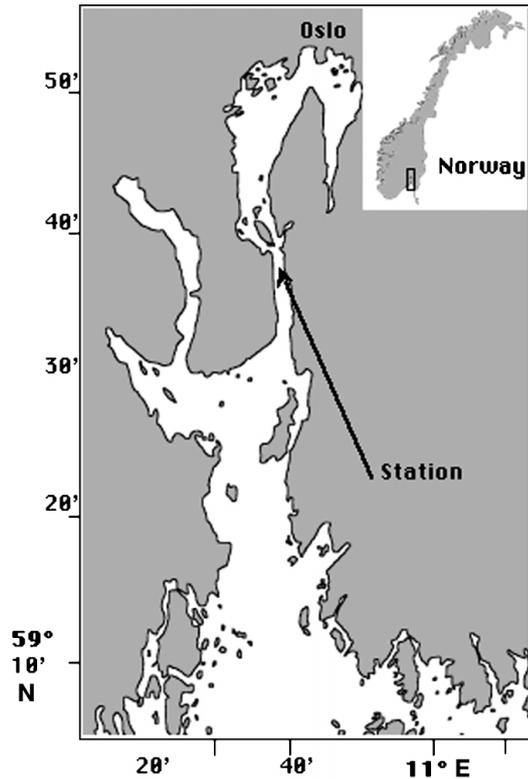


Fig. 1. Map of the study area

We assessed the vertical distribution of *Paraeuchaeta norvegica* and their potential prey by depth-stratified net-sampling covering the whole water column. Potential prey organisms were sampled with a WP-2 net (200 μm mesh size) in series comprising 4×50 m depth intervals. Two parallel series were obtained both day and night. Samples were preserved in 4% formalin. Biomass (wet weight of the preserved sample) was determined for 3 size categories, i.e. animals retained by sieves with mesh sizes of 2, 1 and 0.125 mm, respectively. Each subsample was filtered onto a pre-weighed (wet) GF/C filter before weighing.

Paraeuchaeta norvegica was sampled in the same 4 depth intervals by a modified Nansen net (mesh size 500 μm), equipped with a non-filtering cod-end. Four parallel series were taken both day and night, except for October, when only 2 daytime series were obtained before onset of darkness. All females in each sample were counted.

For comparisons of vertical distribution, weighted mean depth (WMD) was calculated as in Roe et al. (1984). We also estimated the average pellet production (see below) of *Paraeuchaeta norvegica* for the entire water column. Differences in WMD and pellet production between day and night, and between sampling dates, were tested by using 2-way ANOVA and subsequent Tukey's HSD post hoc test.

Feeding was assessed by enumerating fecal pellets

egested from freshly collected females. The number of egested pellets was assumed to be a representative measure for the feeding status at the time of capture. All captured females were included in the study, in total ~1000 individuals. Laboratory results have shown a strong linear relation between food intake and number of pellets produced (Yen 1987, 1991, Tiselius et al. 1997, Olsen et al. 2000), although the number of pellets egested in relation to amount of food eaten may depend on food types (Yen 1987).

Daytime sampling was always initiated several hours after sunrise in order to reduce the impact from previous feeding at night. Sampling at night was normally initiated more than 2 h after sunset. Immediately upon retrieval of the net, all adult females of *Paraeuchaeta norvegica* were rinsed with filtered seawater. They were transferred to 50 ml vials filled with filtered seawater and incubated in a refrigerator at ca. 6°C within ~10 min after capture. A maximum of 6 individuals were kept per vial. After 20 to 24 h, the copepods were removed and the water filtered onto GF/C or GF/F filters to retrieve pellets produced during the incubation. During 2 experiments measuring the gut evacuation rates (Skarra 1999), no pellets were found to be produced after 17 h, suggesting that guts would be emptied in the course of the incubation period. Filters were stored in individual petri dishes and frozen at -20°C. The filters were examined at 16 to 32 \times magnification, and the pellets were enumerated and measured for length using a micro-ocular. Variation in pellet size as a function of depth, season and time of day was tested by linear regression.

RESULTS

Hydrography

The surface temperature fluctuated between 2.5 (February) and 22°C (August), and the salinity varied between 21 (August) and 31 ppt (April) (Fig. 2). The temperature below 50 m was 6 to 7°C on most cruises, except for October, when the temperature was above 10°C in the uppermost 60 m, and in November, when there was a temperature maximum of 11.5°C at 75 m. Salinity below 50 m was always above 33 ppt, with the maximum value of 34.7 ppt occurring in February.

Zooplankton biomass

The abundance of zooplankton in the smallest size fraction was at a minimum in February (Fig. 3). Apart from this cruise, the smallest size fraction was most abundant in the upper 50 m. There was generally a biomass minimum at 50 to 100 m for this group, except

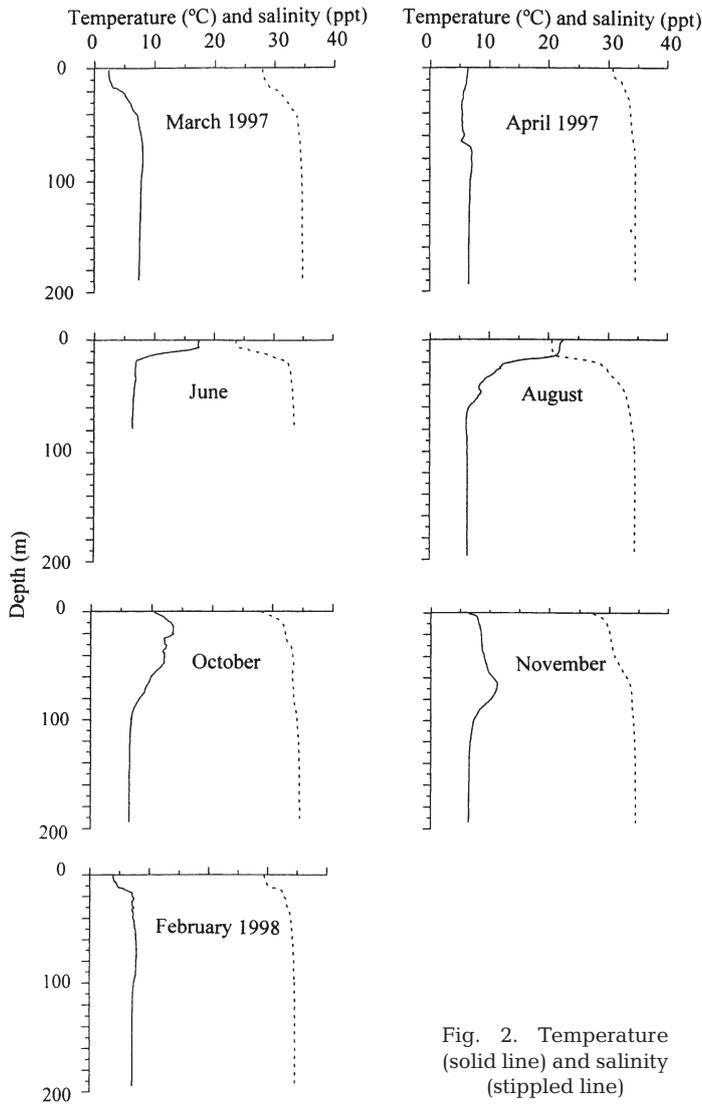


Fig. 2. Temperature (solid line) and salinity (stippled line)

for April, when the abundance decreased with depth. Organisms between 1 and 2 mm showed less variation in abundance between cruises, and were distributed more evenly throughout the water column, though usually with the highest catches in the 2 deepest intervals during the daytime. The largest size group was most abundant in deep water, with highest catches in April and June (Fig. 3).

Paraeuchaeta norvegica

Vertical distribution

Paraeuchaeta norvegica was most abundant between 150 and 200 m (Fig. 4). It stayed deepest early in the year (Figs. 4 & 5), and WMDs were significantly deeper in March and February than during all other

cruises ($p < 0.001$ to 0.031 , depending on cruise). The vertical distribution became more dispersed during summer and autumn (Fig. 4). A bimodal daytime distribution was indicated in October, when females mainly occurred between 200–150 m and 100–50 m.

Day and night profiles were fairly similar (Fig. 4). *Paraeuchaeta norvegica* was most abundant in the deepest interval day and night, and only few individuals were captured in the shallowest interval at night. However, for the whole data set combined, the WMDs were significantly shallower at night than during the day ($p < 0.001$), with amplitudes ranging between 0 and 31 m (June and April, respectively; Fig. 5).

Fecal pellets

Paraeuchaeta norvegica produced fecal pellets in all seasons (Figs. 4 & 6). The numbers were highest in November (significantly higher than during all other cruises; $p < 0.001$ to 0.023), while the lowest numbers were recorded in February. The number of pellets produced was higher for individuals captured at night than during the daytime (Fig. 6; $p < 0.001$). Pellets were produced at all depths (Fig. 4). By comparing all day and night profiles, respectively, maximum pellet production was recorded from all sampling depths on at least 1 cruise (except for the upper 50 m during the day), most frequently between 50 and 100 m at night. The greatest pellet production was recorded for individuals captured between 50 and 100 m at night in November (Fig. 4).

For all data combined, there was no difference between average pellet length from day (486 μm) and night (484 μm). Pellet lengths were fairly constant between cruises (Fig. 7), but still significantly shorter in February than in March and November ($p < 0.05$). Pellets in March were furthermore longer than in June ($p < 0.05$). There was a slight, but significant, increase in pellet length with depth ($p < 0.05$).

DISCUSSION

Paraeuchaeta norvegica lived deepest during winter. Their distribution became shallower during summer and comprised both a deep and a shallow mode during autumn. Fluctuations between surveys are not proof of systematic seasonal variations, but the trend appeared to be regular and the results concur with the few pre-

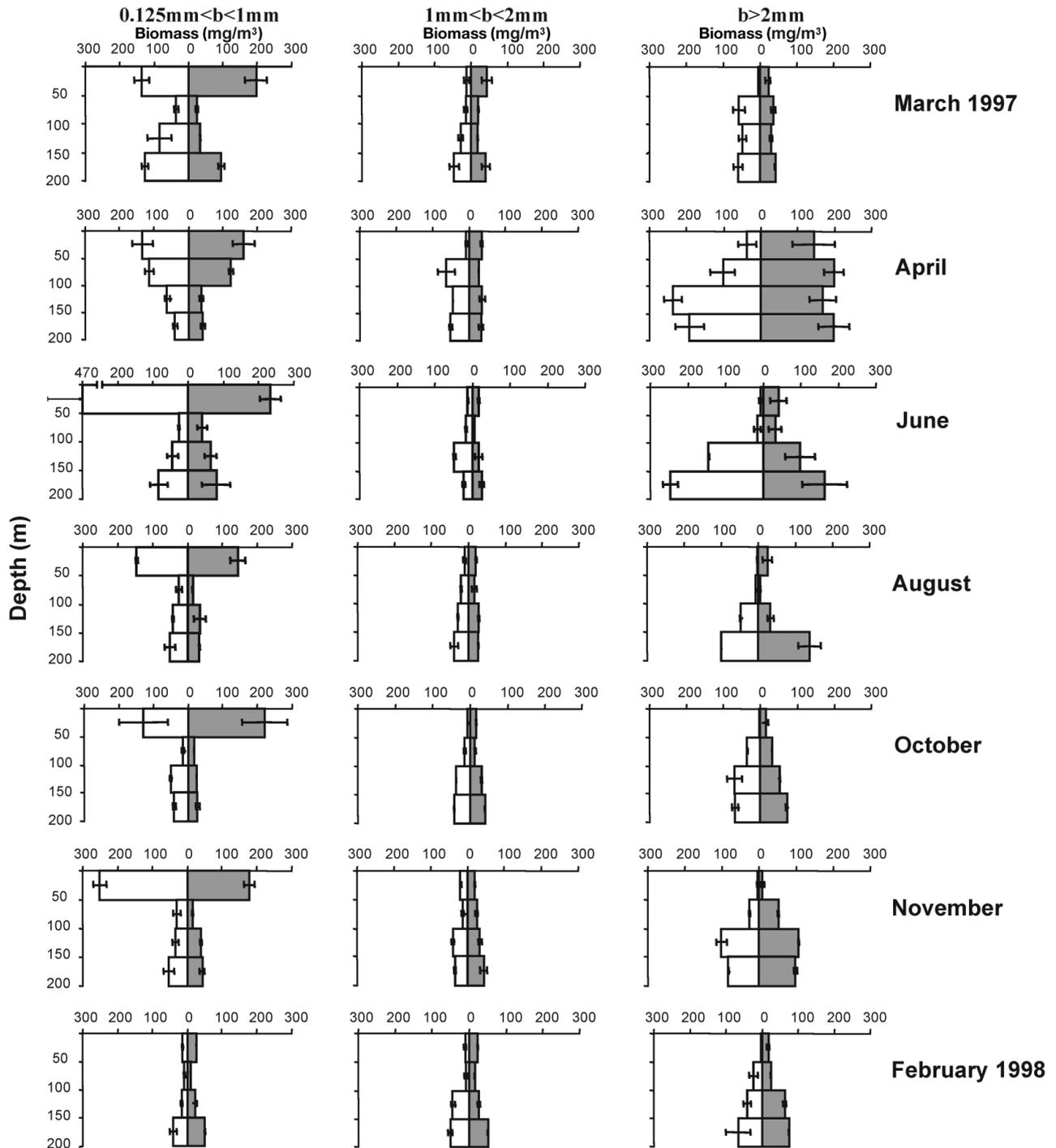


Fig. 3. Vertical biomass (wet weight \pm SE) distribution, during day- (open) and night- (filled) time, of potential prey allocated to size categories. b: mesh sizer

viously published records on this species from other Norwegian fjords. Data in Baliño & Aksnes (1993) reveal that adult *P. norvegica* stayed in deep water both day and night in January, and Kaartvedt et al.

(2002) documented bi-modal daytime distributions for *P. norvegica* during autumn. Diel vertical migration (DVM) was recorded for the shallow mode (Kaartvedt et al. 2002).

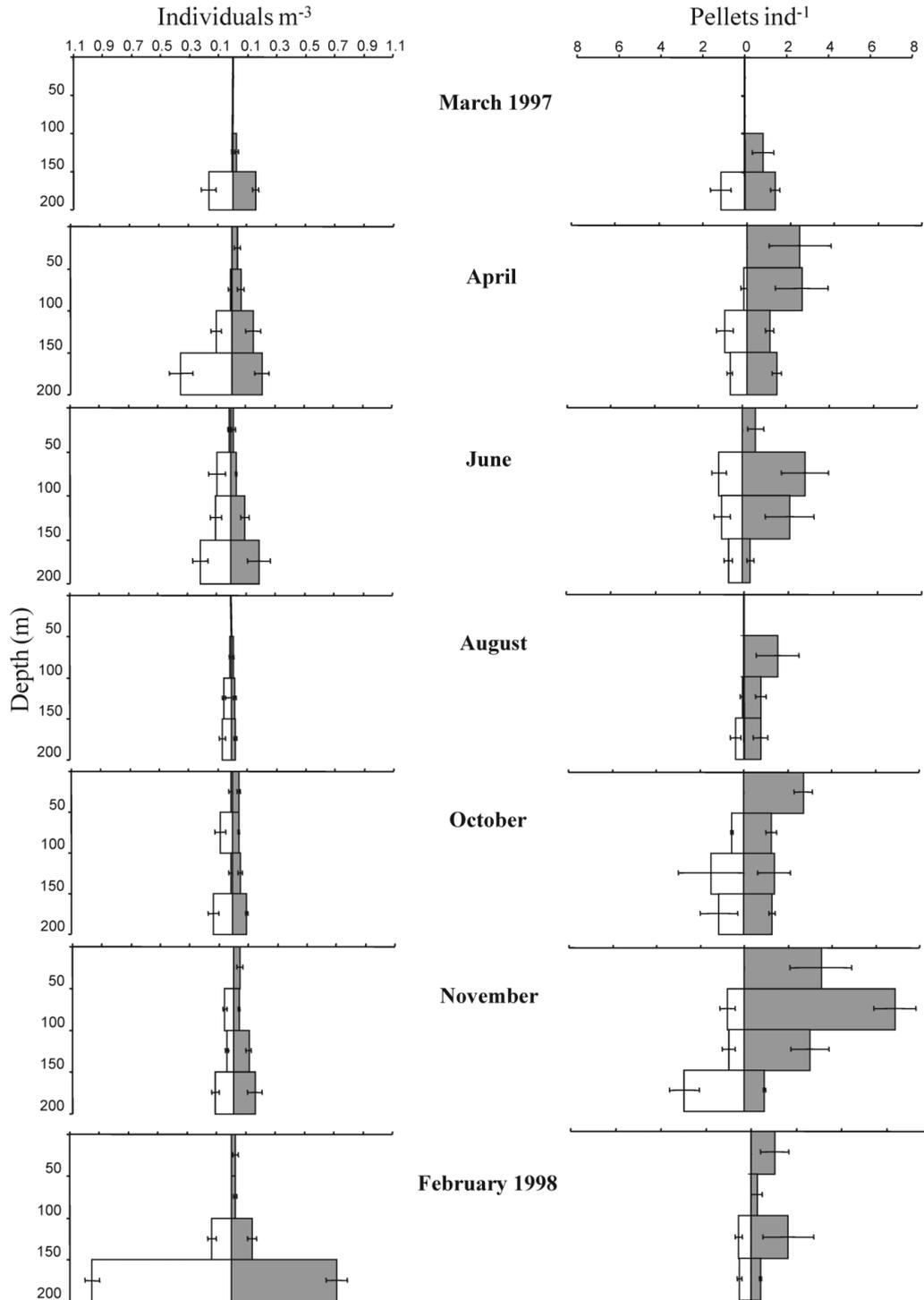


Fig. 4. *Paraeuchaeta norvegica*. Vertical distribution of adult females and pellet production during day- (open) and night- (filled) time. Bars denote \pm SE

We generally observed fairly similar day and night profiles, although with slightly shallower population distributions at night. Hays et al. (2001) reported that individuals of the copepod *Metridia pacifica* that migrated towards the surface at night had much

smaller oil sacks than individuals in the same population remaining at depth. This was ascribed to 'fat' individuals prioritizing predator avoidance in deep water rather than risky feeding in upper waters (Hays et al. 2001).

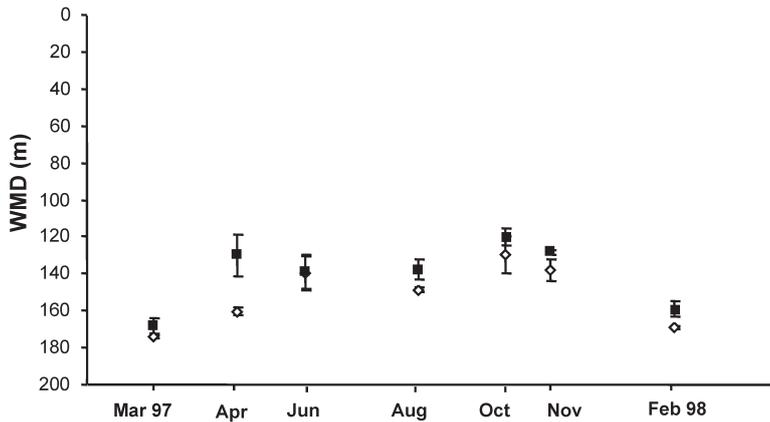


Fig. 5. *Paraeuchaeta norvegica*. Weighted mean depth (WMD) \pm SE during day- (open) and night- (filled) time

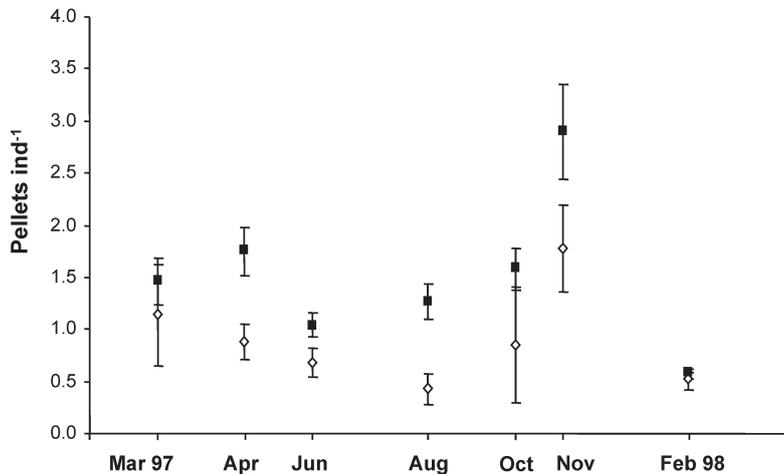


Fig. 6. *Paraeuchaeta norvegica*. Average pellet production (\pm SE) for the water column during day- (open) and night- (filled) time

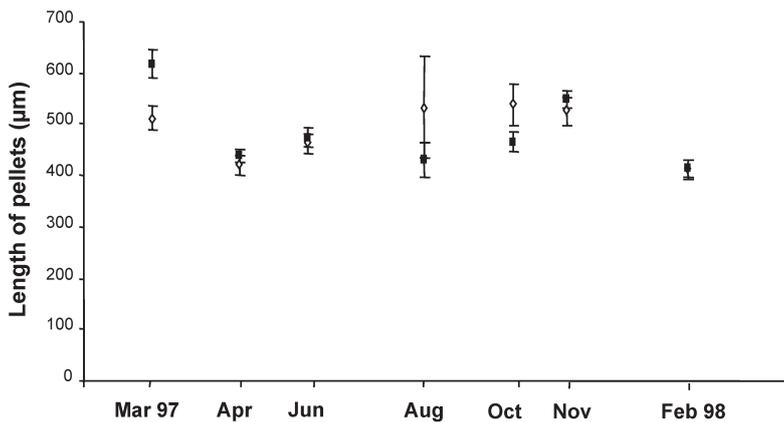


Fig. 7. *Paraeuchaeta norvegica*. Average length of pellets (\pm SE) during day- (open) and night- (filled) time

Paraeuchaeta norvegica was foraging throughout the year. Feeding was, however, apparently lowest in February, as derived from the combination of the lowest number and smallest size of the pellets. This concurred with the lowest potential prey abundance in the size class <1 mm, which is expected to represent the most relevant food organisms for *Paraeuchaeta* spp. (Yen 1983, 1985, Greene & Landry 1985, Olsen 1996). Also, juveniles of *P. norvegica* displayed the lowest feeding in February (results presented in Skarra 1999), and in that case pellet production was only recorded from individuals sampled at night.

Feeding activity appeared to peak in November, as derived from the greatest numbers of pellets and large pellet size at that time. However, prey availability (as expressed by biomass) did not exceed that during previous cruises, and the pellet production by juveniles assessed by Skarra (1999) did not show a corresponding peak. This specific response for adult females may be related to enhanced motivation for feeding. Other studies of *Paraeuchaeta norvegica* suggest maximal egg production in winter, supported by lipid reserves of the females (Bakke 1977, Båmstedt 1979, Hopkins 1982, Mauchline 1994), although reproducing females are present year-round in the Oslofjord (Wiborg 1940). Since accumulation of wax esters may permit production of eggs in *Paraeuchaeta* spp. during times of unfavorable food conditions in winter (e.g. Alonzo et al. 2000), a build-up of lipid reserves in autumn may be essential. Neither Yen (1982) nor Olsen (1996) found significant effects of female reproductive status in experimental studies of feeding in *Paraeuchaeta* spp.

Feeding was most prominent at night, but *Paraeuchaeta norvegica* also seemed to forage during the day, although results from daytime may have been influenced by remnants or initiation of nocturnal feeding. The greatest records of suggested daytime feeding were from October and November (Fig. 4). The short days at this time of year resulted in sampling close to sunset (Skarra 1999), and we cannot exclude that samples from late in the day actually reflected the beginning of nocturnal feeding in deep water. Since this potential bias will lead to overestimation of daytime feeding, our

conclusion of enhanced feeding at night is conservative. Olsen et al. (2000) experimentally demonstrated an endogenous rhythm of enhanced feeding at night in *Paraeuchaeta norvegica* from the same location as this study (see also Yen 1982). The search for food exposes copepods to predators (cf. Tiselius et al. 1997), and this may depress daytime feeding, even in deep water. In any case, the documentation of deep-living individuals with relatively high gut content late during the day (Skarra 1999) suggests that *P. norvegica* at times was foraging successfully in deep water.

On several occasions, high nocturnal production of pellets was measured at 50 to 100 m, even if this represented a stratum with minimum zooplankton biomass during most surveys. This could possibly be explained by short feeding excursions to upper layers, with a return to somewhat deeper, safer water for digestion (cf. Pearre 1979). Adult female *Paraeuchaeta* spp. may be vulnerable to visual predators even at night (Bollens & Frost 1991), and could therefore be prone to minimizing time spent in upper layers. In November, representing the most evident example of large production of pellets from individuals captured between 50 and 100 m, an additional bonus of sinking down after foraging would be enhanced digestion in the sub-surface temperature peak which occurred in this depth interval during that cruise (cf. Giske & Aksnes 1992, Loose & Dawidowicz 1994).

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