

## Spatial heterogeneity and niche differentiation in oceanic zooplankton

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### Abstract

The annual mean abundance (1958 to 1986) and geographical distributions of four of the major biomass species of copepod in the northern North Atlantic Ocean are shown together with their seasonal vertical distributions (1971 to 1974) from Ocean Weather Station I. The arcticboreal species *Euchaeta norvegica* and *Calanus finmarchicus* have sympatric distributions with their maximum numerical abundance in the cold water current system between Labrador and Greenland. The distribution of the temperate species *Pleuromamma robusta* and *Metridia lucens* are allopatric with respect to the two previous species but have sympatric distributions centering around the north-eastern oceanic region. The four species dominate the copepod biomass of the oceanic epiplankton and minimise interspecific competition by a) seasonal displacement of their main reproductive periods, b) occupying different trophic levels, c) having diverse reproductive strategies, d) residing in different positions in the water column and e) having different migratory behaviour throughout the year. The vertical distributions and migratory behaviour of these four copepods suggest a highly structured community with individual species occupying distinct niches with minimum overlap between competitors; even though the vertical distributions of the species are constantly changing through diel, ontogenetic and seasonal migrations.

### Introduction

The epipelagic and upper mesopelagic zooplankton community of the northern North Atlantic consists of an assemblage of over 500 species living and interacting together. In general terms the stability, persistence and species composition of this oceanic community is known but the species interactions and the mechanisms whereby individual species compete for, or partition, resources are less well understood. There are some planktologists who even find it difficult to accept the existence of structured communities within plankton. This view is maintained because of the paucity of information on behavioural

ecology and theoretical studies on population dynamics and community ecology from the marine pelagic environment; in comparison to freshwater and terrestrial ecosystems. The 'layered biocoenosis' described by Sorokin (1980) points to a structured community in the pelagic environment, especially where vertical variability in the physical environment is great; a point made by Longhurst (1985) and Sameoto (1986). The vertical spatial separation of species and their developmental stages has been known for many years which results in a patchy distribution of the biota but whether or not this reflects resource utilisation through species interactions is open for speculation. Ghilarov (1984) rejects that competi-

tive exclusion occurs between species with similar ecological requirements. Zooplankton do respond to changes in environmental variables such as temperature, oxygen, light, salinity, whereby their geographical boundaries and vertical distributions are defined. Species with different optimum requirements tend to succeed under different conditions and therefore come to occupy different niches in time and space.

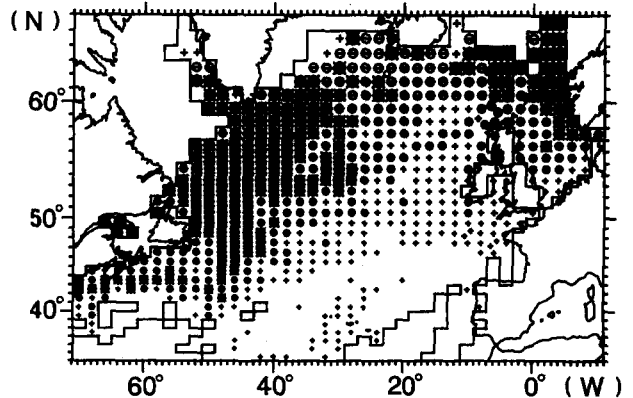
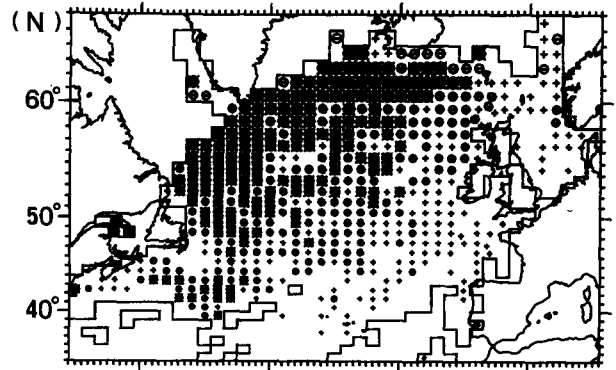
Of the hundred or so copepod species which are sampled regularly in plankton hauls taken in the northern North Atlantic Ocean, four species dominate (Williams & Robinson, 1973; Williams, 1974; Williams & Hopkins, 1975, 1976). These are *Euchaeta norvegica* Boeck, *Calanus finmarchicus* (Gunnerus), *Pleuromamma robusta* (F Dahl) and *Metridia lucens* Boeck. The available data on the spatial distribution (horizontal and vertical) and behaviour patterns of these four copepods were used to demonstrate the complexity of structure of the open ocean community and to pose the question whether or not specific niches occur in the habitat through the interaction of species or are just reflecting a patchy habitat structure.

### Materials and methods

From the Continuous Plankton Recorder (CPR) Survey (Glover, 1967; Colebrook, 1982) data on the four species of copepod were used to show their annual mean abundance, in rectangle 1° latitude by 2° longitude within the survey area, and their geographical distributions (Figs. 1 and 2). The figures are based on monthly horizontal sampling by the CPR at 10 m depth for a 29 year period, 1958 to 1986. The annual mean distributions of *Pleuromamma robusta* and *Metridia lucens* are based on night samples only. The survey area encompasses the majority of the oceanic region from 35° N to 64° N.

The vertical distributions and seasonal numerical abundance of the four species were determined from sampling carried out in the region of Ocean Weather Station 'I' (59° 00' N 19° 00' W) in the north-east Atlantic Ocean from March 1971 to October 1974. Ninety six oblique hauls (24–1971,

#### a) *Euchaeta norvegica*



#### b) *Calanus finmarchicus*

Fig. 1. a) *Euchaeta norvegica*, b) *Calanus finmarchicus*. Annual mean distribution and abundance from sampling at 10 m depth by the Continuous Plankton Recorder (CPR). Data for all months sampled were combined to show the mean abundance from 1958 to 1986. Samples were assigned to rectangles 1° lat. by 2° long. Rectangle means are represented by three graded symbols. The absence of symbols (in the sampled area) indicated that the species were not found in Plankton Recorder samples. The boundary of the sampled area is shown by straight lines.

26–1972, 24–1973, 22–1974) were taken with the Longhurst-Hardy Plankton Recorder (LHPR) (Longhurst & Williams, 1976), and a further 25 hauls in 1975. Only hauls taken during the daylight hours (1971 to 1974) were used in this study and these were spaced at approximately 7 d intervals over the sampling periods in each year. The

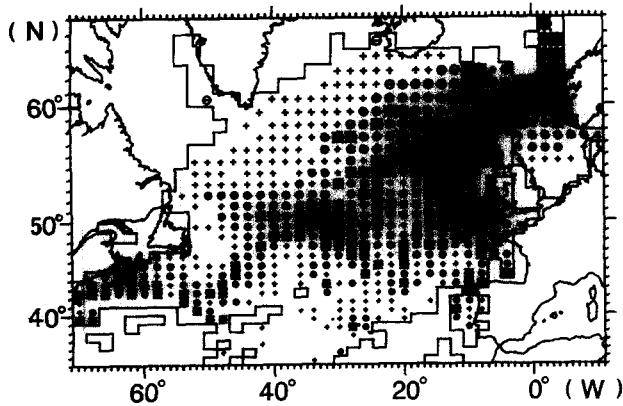
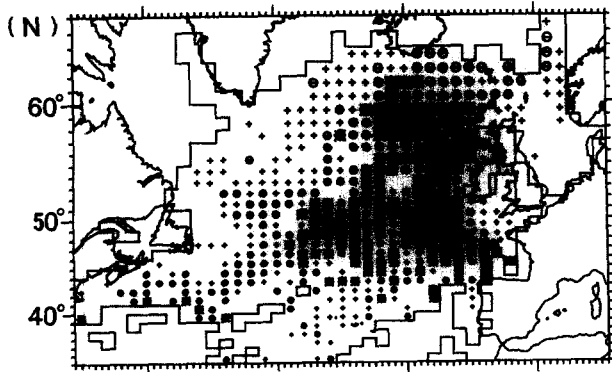
a) Pleuromamma robustab) Metridia lucens

Fig. 2. a) *Pleuromamma robusta*, b) *Metridia lucens*. Annual mean distribution and abundance from 1958 to 1986. Further details as in legend to Fig. 1.

net and filtering gauzes in the cod-end were 280  $\mu\text{m}$  mesh. Samples were collected on the ascent part of the haul and the winch speed was regulated to collect a sample every 10 m. Over 3500 samples were collected (1971 to 1974) and approximately 250 species, genera and higher taxa identified. The counts of the organisms per sample were converted to numbers  $\text{m}^{-2}$  over the depth range sampled, usually in excess of 500 m. The sea temperature was measured twice daily using mechanical bathythermographs as part of the meteorological programme on station and by

thermistor in the LHPR system (0–500 m) on each deployment.

Chlorophyll *a* was measured from water samples taken from 10 depths (0–200 m) sampled every day during the periods on station.

### Results and discussion

The vertical distribution (0 to 500 m) and seasonal numerical abundance of the four species *Euchaeta norvegica*, *Calanus finmarchicus*, *Pleuromamma robusta* and *Metridia lucens* from late March until early October (1971 to 1974), in day hauls only, are shown in Figs. 3, 4, 5 and 6. The distributions are composites of all the copepodite stages (CI to

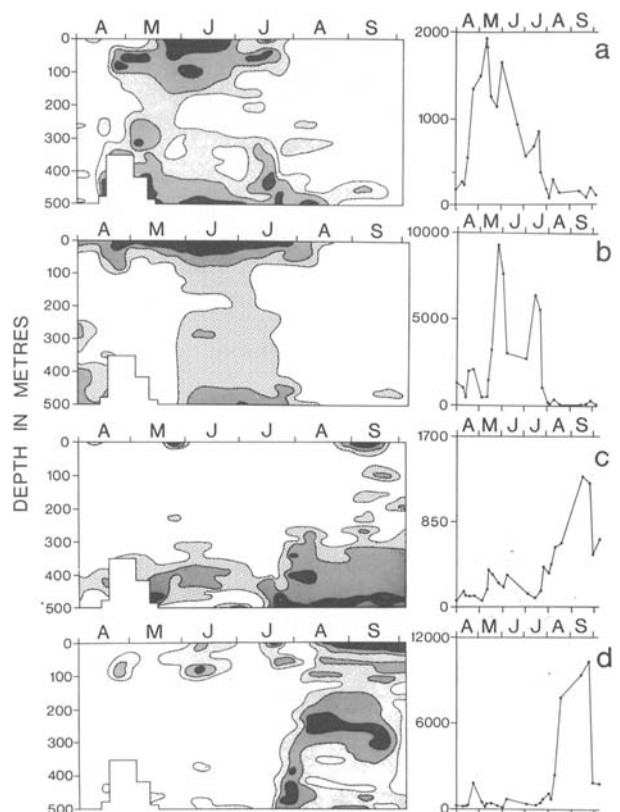


Fig. 3. a) *Euchaeta norvegica*, b) *Calanus finmarchicus*, c) *Pleuromamma robusta*, d) *Metridia lucens*. Vertical distributions and seasonal numerical abundance (Nos.  $\text{m}^{-2}$ , 0 to 500 m) at Ocean Weather Station 'P' in the north-east Atlantic Ocean from 31 March to 6 October, 1971.

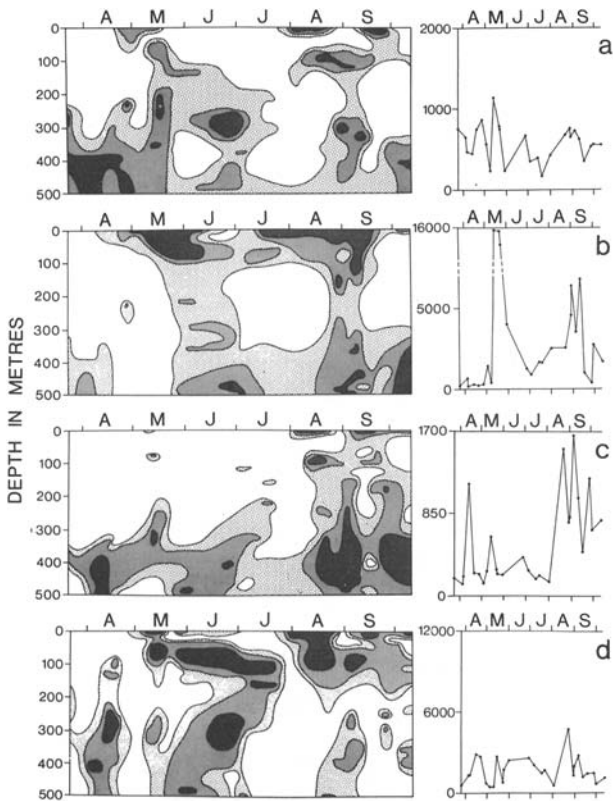


Fig. 4. a) *Euchaeta norvegica*, b) *Calanus finmarchicus*, c) *Pleuromamma robusta*, d) *Metridia lucens*. Vertical distributions and seasonal numerical abundance (Nos.  $m^{-2}$ , 0 to 500 m) at Ocean Weather Station 'I' in the north-east Atlantic Ocean from 24 March to 11 October, 1972.

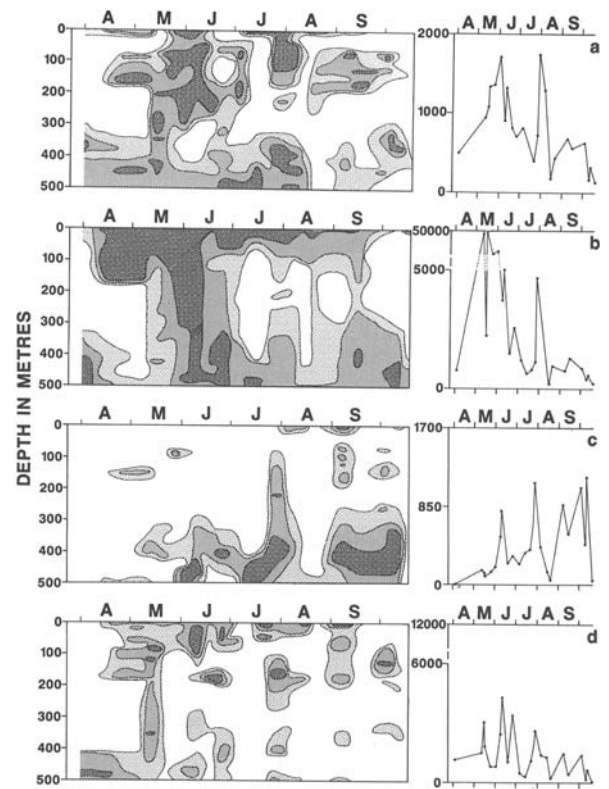


Fig. 5. a) *Euchaeta norvegica*, b) *Calanus finmarchicus*, c) *Pleuromamma robusta*, d) *Metridia lucens*. Vertical distributions and seasonal numerical abundance (Nos.  $m^{-2}$ , 0 to 500 m) at Ocean Weather Station 'I' in the north-east Atlantic Ocean from 2 April to 18 October, 1973.

VI) which were identified separately for each species. The values of the isolines in the contour figures were chosen to give evenly spaced contours and not to specifically highlight the maximum abundance. The ontogenetic changes in vertical distribution of the copepodite stages are not demonstrated by these figures neither are their diurnal changes in distribution. Over the four years studied these four species accounted for 34 to 57% by number and between 86 to 95% by dry weight of the total biomass of the copepods integrated over the sampling periods (March to October) from the surface to 500 m. Approximately 250 entities, species, genera and taxa, were identified in these profiles but a more detailed taxonomic study would probably have revealed more than 500 species.

The four species are geographically divided into a northern group and a south-eastern group. The northern group, *Euchaeta norvegica* (C1 to CVI, 1.06 to 8.36 mm total length) and *Calanus finmarchicus*, (C1 to CVI, 0.68 to 3.88 mm total length) have their main reproductive period in the spring. The south-eastern group of *Pleuromamma robusta* (C1 to CVI, 0.80 to 4.32 mm total length) and *Metridia lucens* (C1 to CVI, 0.68 to 3.56 mm total length) tend to have the peaks of their abundance in the early and late summer with the peak abundance of *P. robusta* occurring later. This seasonal displacement of the main breeding period is especially strong in northern latitudes and is a means by which competition between co-occurring species is reduced. The main breeding times are the periods when the species make their maximum

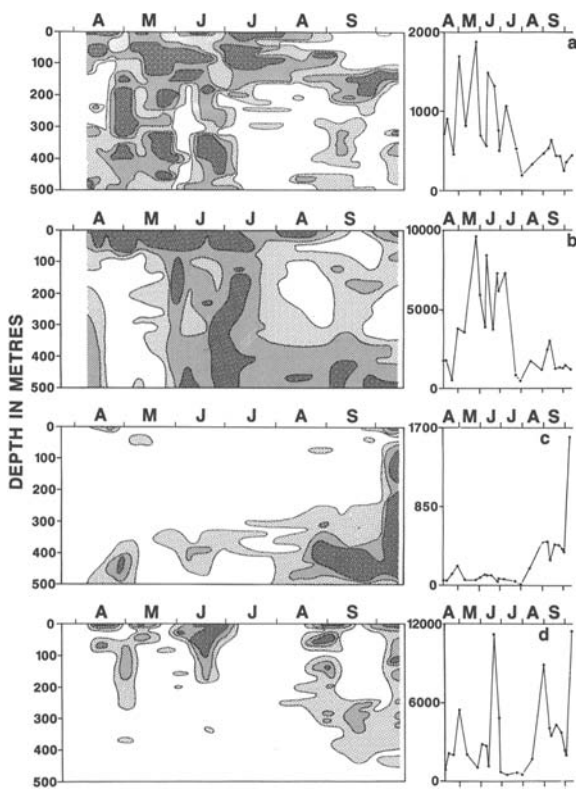


Fig. 6. a) *Euchaeta norvegica*, b) *Calanus finmarchicus*, c) *Pleuromamma robusta*, d) *Metridia lucens*. Vertical distributions and seasonal numerical abundance (Nos.  $m^{-2}$ , 0 to 500 m) at Ocean Weather Station 'T' in the north-east Atlantic Ocean from 9 April to 10 October, 1974.

demands from the habitat. In the northern group *E. norvegica* reproduces first with the females demonstrating batch reproduction and retaining their eggs in external egg sacs. The liberation of the nauplii and early development takes place deep in the water column prior to the spring phytoplankton bloom with the early copepodites migrating to the upper waters. In contrast, the reproduction of *C. finmarchicus* is keyed to the onset of the spring increase of diatoms (Fig. 7) with the eggs being released in the near surface waters and the development of the nauplii and young copepodite stages occurring in the upper 50 m (Williams, in prep). The peaks of chlorophyll *a* distribution (0 to 200 m) over the four years (1971 to 1974) occurred on 24 May ( $166.2 \text{ mg chl } a \text{ m}^{-2}$ ), 14 May ( $207.6 \text{ mg chl } a \text{ m}^{-2}$ ), 8 May

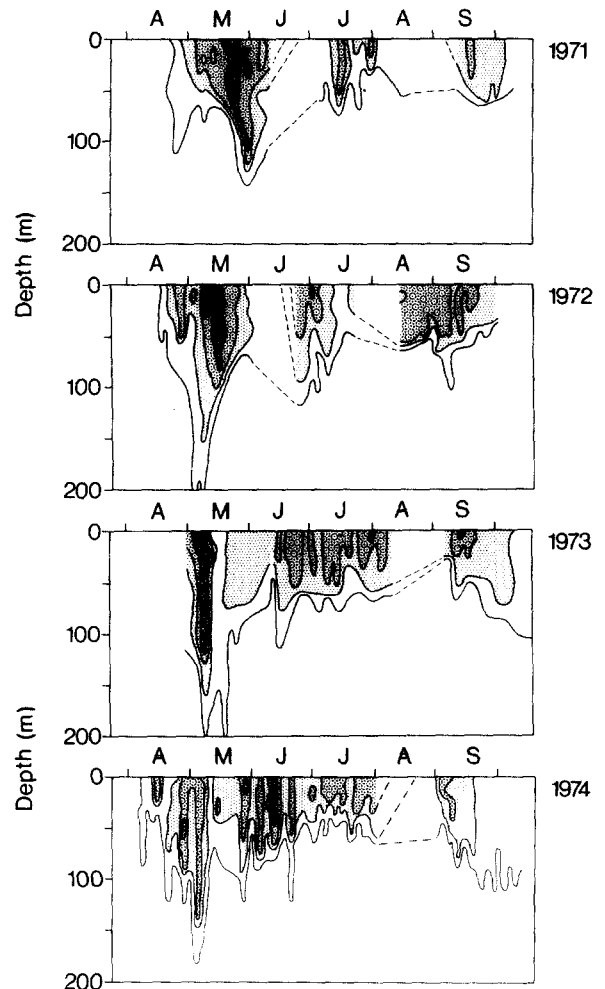


Fig. 7. Chlorophyll *a* in the upper 200 m at Ocean Weather Station 'T' the contour levels are drawn at 2.00, 1.00, 0.50 and  $0.25 \text{ mg Chl } a \text{ m}^{-3}$ .

( $257.5 \text{ mg chl } a \text{ m}^{-2}$ ) and 5 May ( $241.6 \text{ mg chl } a \text{ m}^{-2}$ ). Approximately 50% of this standing crop was present between the surface and 30 m over the sampling periods with over 95% of the primary production occurring in this depth horizon. These two northern species occupy different trophic levels. *C. finmarchicus* is an herbivore in spring while *E. norvegica* is primarily a carnivore. The adults and older copepodite stages of *E. norvegica* do interact with the younger stages of *C. finmarchicus* in a predator to prey relationship when the larger species migrate into the upper waters at night to feed (Williams, unpubl.). Even though the species have overlapping vertical dis-

tributions their main periods of abundance and depth distribution are spatially and temporally separated. This is demonstrated in the 1972 data (Fig. 4) where the two main generations of *C. finmarchicus* are essentially separated from the *E. norvegica* population. The later generations are not so evident in the vertical distributions observed in 1971 due to a large advection of mid-Atlantic water from the south in July. This event persisted throughout the summer months, and was responsible for nearly completely replacing the northern species with *Pleuromamma robusta* and *Metridia lucens*. The results of this advection can be seen in the changes of the seasonal thermal stratification and the deeper position of the 9 °C isotherm in 1971 when compared with the other three years (Fig. 8). The 1972 sequence of events is more 'typical' for this station than those seen in 1971. The vertical and seasonal spatial separation of the populations of these four species in the upper 500 m at OWS 'I' are even more evident when the numerical data from the day hauls are converted to dry weight biomass. This places emphasis on the distributions of the older copepodite stages. The dry weight distribution for the four species sampled in 1972 is shown in Fig. 9.

*Euchaeta norvegica* and *Calanus finmarchicus*, have similar geographical distributions with their main area of abundance within the colder waters between Labrador and Greenland. The vertical distributions, ontogenetic, diel and seasonal migrations of the two species contribute towards minimising interactions between the species. The vertical spatial separation of the populations and trophic relationships of these species should act as powerful stabilising factors allowing co-existence.

During the summer months *Pleuromamma robusta* and *Metridia lucens* make a greater contribution to the copepod biomass. Both species are omnivorous in feeding habits and the older copepodite stages (CV and CVI) make large amplitude vertical feeding migrations at night; the CPR horizontal distributions for these species, at 10 m (Fig. 2), are based solely on the CV and CVI copepodites identified in night samples. During

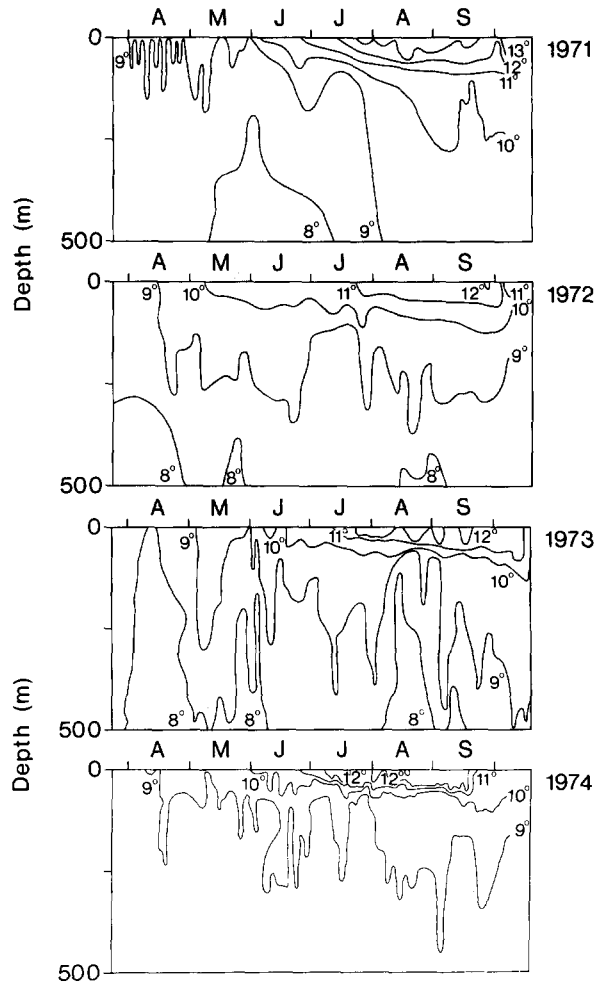


Fig. 8. Isotherms in the upper 500 metres at Ocean Weather Station 'I' from a) 31 March to 6 October, 1971, b) 23 March to 11 October, 1972, c) 24 March to 2 October, 1973 and d) 1 April to 10 October, 1974.

the day the major portion of the *P. robusta* population resides below 400 m (Figs. 3, 4, 5 and 6). The night migration of these two species is shown in Fig. 10, for two profiles taken in late March before the overwintering *C. finmarchicus* population has migrated to the upper waters. The copepodite stages (CI to CVI) of these two species at OWS 'I' have overlapping size ranges and probably utilize the same size spectra of particulates. The younger copepodites of *P. robusta* are found much deeper than those of *M. lucens* and both are deeper in the water column than *C. finmarchicus*. Because the two species have similar breeding periods, somewhat similar size ranges, and food

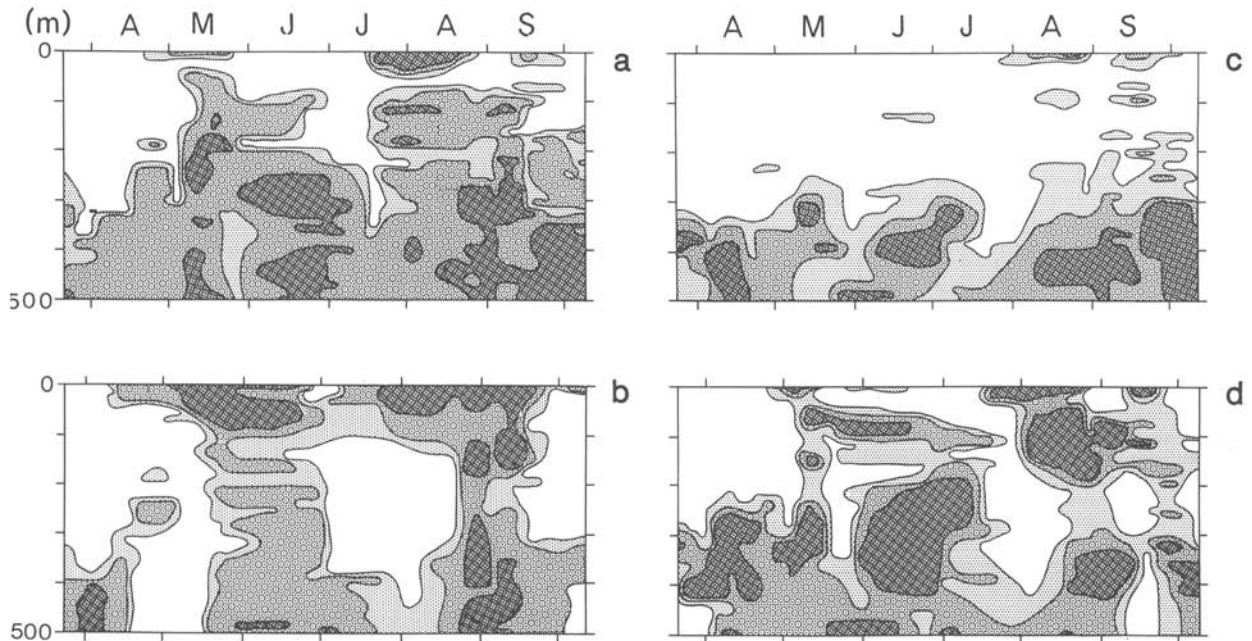


Fig. 9. a) *Euchaeta norvegica*, b) *Calanus finmarchicus*, c) *Pleuromamma robusta*, d) *Metridia lucens*. Dry weight biomass at Ocean Weather Station 'T' in the north-east Atlantic Ocean from 23 March to 11 October, 1972.

requirements then they could be expected to possess mechanisms which minimise and oppose the destabilizing effects of interspecific competition (Hassel, 1980). What can be seen from the vertical distributions of *P. robusta* and *M. lucens* (Figs. 3, 4, 5 and 6) is that the main depths of occurrence of the two species are different throughout the productive season. The species and their developmental stages partition the water column into distinct niches. The vertical distributions of the copepodite stages have different modal depths within these contoured figures, with the younger stages overlying the older copepodites (Longhurst & Williams, 1979). These developmental stages do not have static vertical distributions but are in a constant state of change with nocturnal migrations, breeding, ontogenetic and seasonal vertical migrations. This degree of complexity within the planktonic ecosystem was known previously, but can be effectively demonstrated for oceanic plankton using multiple-serial sampling systems such as the LHPR.

What has been observed in the vertical distribu-

tions of these copepods at OWS 'T' should be applicable to any sampling position within the oceanic geographical boundaries of these species; especially where the four species have sympatric distributions. In conclusion it has been shown for the four major biomass copepod species of the northern North Atlantic Ocean that they exist in a highly structured spatially organised community with each species and its developmental stages occupying preferred depth horizons which persist throughout the productive season. Whether this 'simple' community has been established after a succession of ecological fittings or whether its component species have evolved together in an evolutionary sense is still a very open question. Much more work is needed on the specific requirements of these species before any definite resource-utilisation patterns can be identified but the species are taking up specific patterns and this in itself suggest a level of interaction between the component species which point to organisation and not just a random response to a patchy resource distribution (Bradley & Bradley, 1985).

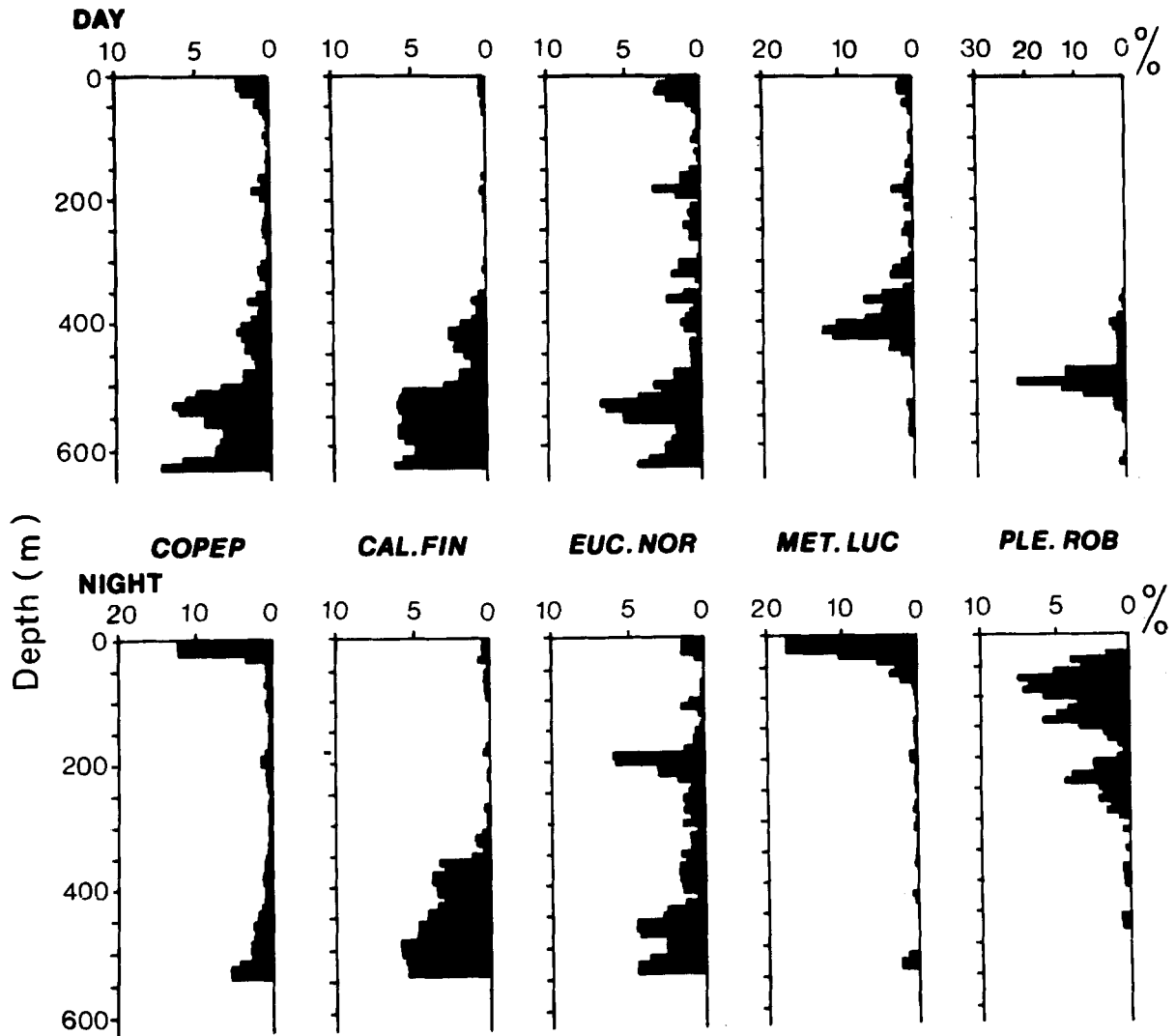


Fig. 10. Day and night percentage number profiles at Ocean Weather Station 'T' in late March 1975, (Copep - total Copepods).

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