

## The small-scale distribution of plankton at a shelf station off the northwest African coast

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**Abstract**—The small-scale distribution of zooplankton in the euphotic zone has aroused much interest in recent years, particularly with regard to which features of the water column structure might be causing or strongly affecting such distributions. At a station on the continental shelf off Mauretania pump sampling techniques were used to investigate the relation between the vertical distribution of various zooplankton taxa and the physical, chemical, and biological structure of the water column (water depth 60 m). Attention was focused on the very precise patterns of zooplankton distribution in the region of the pycnocline and its associated massive chlorophyll *a* and phytoplankton biomass maximum. The possible trophic relations of these taxa were considered with respect to the difficulties inherent in drawing meaningful conclusions about the ways in which resource or space might be partitioned, particularly when such trophic relations probably were indirect.

### INTRODUCTION

THE small-scale vertical distribution of zooplankton in the superficial waters of the oceans has been the subject of intensive study in the recent past, not least with regard to the possible relationships between such distributions and the physical structure of the water column, e.g., the depth of the pycnocline, and the depths of the chlorophyll *a* and primary production maxima (ANDERSON *et al.*, 1972; BOYD, 1973; LONGHURST, 1976; ORTNER *et al.*, 1980; SMITH *et al.*, 1981). However, the interdependence of the various parameters within the water column which may affect the vertical structure and distributions of zooplankton makes it difficult to establish meaningful, causative relations (SMITH *et al.*, 1981).

Several attempts have also been made to understand the distribution of the zooplankton with regard to their source of food. VENRICK *et al.* (1973) found that the biomass of total zooplankton was shoaler than the chlorophyll *a* maximum and concluded that differential grazing pressure was maintaining the observed depth distribution of the phytoplankton. Other studies have demonstrated, in contrast, a close correlation between the vertical distributions of chlorophyll *a* and of grazers (see review in HERMAN *et al.*, 1981). LONGHURST (1976) found that the zooplankton maximum lay at the base of the top mixed layer while the chlorophyll *a* maximum lay, on average, 25 m deeper in the pycnocline. He concluded that there was a close correspondence between the depth of the zooplankton maximum and that of the primary production maximum. HERMAN *et al.* (1981) inferred from these results a causal relationship between active primary production and grazers and suggested that the

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herbivores were reacting to biological or chemical cues associated with gradients in the production rates. They further demonstrated that the dominant herbivorous copepod species were more closely associated with the depth of the model-predicted primary productivity maximum than with the chlorophyll *a* maximum. Later studies led HERMAN (1983) to conclude that while some of the dominant copepod species were found in the region of the predicted primary productivity maximum, others aggregated in the chlorophyll *a* maximum, which lay only a few metres deeper.

Implicit in all these studies is the assumption that the zooplankton distributions are the result of active processes, i.e., that aggregations are formed as the result of a common behavioural response to some environmental cue. SMITH *et al.* (1976) found a maximum abundance of a wide range of zooplankton taxa in the top mixed layer, just above the thermocline. They concluded that physical processes probably were more important in controlling the observed distribution rather than biological ones. Thus, they ascribed the observed variability tentatively to the propagation of internal waves along the thermocline. HAURY (1976) also commented on the importance of internal wave activity and subsequently (HAURY *et al.*, 1979) found that tidally generated internal waves caused dramatic changes in the vertical and horizontal distribution of various organisms. KAMYKOWSKI (1976) has modelled successfully these effects.

FASHAM and PUGH (1976), whilst studying the horizontal coherence of chlorophyll *a* and temperature at a fixed depth and particularly in the region of the pycnocline, commented on the difficulty in separating the patchiness caused by internal waves from the true spatial heterogeneities in the phytoplankton distribution. Such fixed-depth sampling techniques also can be used to investigate the small-scale changes in the vertical distribution of the phyto- or zooplankton, particularly in the region of the pycnocline. Thus the relationship of the organisms to the vertical changes in the physical structure of the water column can be followed by studying their temporal variations as internal waves propagate past the instrumentation. In this case it would be necessary to separate the horizontal patchiness of the organisms from the vertical component, although the latter is likely to be more important in the pycnocline.

This paper describes an experiment where the distributions of various zooplankton taxa were investigated in the vicinity of the pycnocline/chlorophyll *a* maximum at a shelf station in the upwelling region off northwest Africa. Because of problems, such as spatial averaging (VINOGRADOV and SHUSHKINA, 1976), associated with such small-scale studies using nets and because of the inadvisability of using standard depth approaches to sampling (BANSE, 1964; OMORI and HAMNER, 1982) a pumped sampling system was used for zooplankton collection in conjunction with continuous monitoring of the physical parameters.

#### METHODS

'Discovery' Sta. 9529 was occupied on 7 April 1977 and was located at *ca.* 21°09'N, 17°18'W on the continental shelf off Mauretania, where the water depth was 60 m. The investigations were carried out using a Neil Brown Instrument System CTD (Conductivity, Temperature, Depth) probe, and a pumped water system, the inlet of which was attached to the CTD. The basic arrangement is similar to that described by FASHAM and PUGH (1976) with, in addition, an underwater irradiance meter (KAHN *et al.*, 1975). Seawater was pumped onto deck through 5-cm bore hosing at a rate of *ca.* 135 l min<sup>-1</sup>, of which the bulk was used for zooplankton collection. However, about 10 l min<sup>-1</sup> was diverted, through three 1.27-cm

diameter bleeds, and directed to: (a) a Turner Model III fluorometer; (b) a Hiac Model PC 320 automatic particle analyzer; and (c) an on-line nutrient analyzer and another Turner fluorometer. The fluorometric method of HOLM-HANSEN *et al.* (1965) was used to determine the *in situ* chlorophyll *a* concentrations from discrete, filtered samples taken at various times during the experiment, and these values were used to calibrate responses of the fluorometer. The concentrations of nitrate (+ nitrite) and silicate were measured continuously using the method of HOLLIGAN and HARBOUR (1977). The data from one of the fluorometers and the CTD, plus irradiance meter, were sampled by the shipborne IBM 1800 computer, using a standard suite of programs, and all the parameters, excluding salinity and irradiance, also were displayed on chart recorders. Particle counting was carried out according to the procedures outlined in PUGH (1978). Unfortunately, the particle concentrations at this station were so high that the counter became saturated and it was impossible to interpret the results. Phytoplankton cell concentration, species composition, and primary productivity were determined in two water samples, from 0- and 8-m depth. Barium carbonate contamination, however, rendered the productivity results useless.

The bulk of the pumped water supply was directed, alternately, onto two screens of 171- $\mu$ m mesh netting. The netting was clamped across the tops of powder funnels (24 cm diameter), the bases of which were push-fitted into the end of the 5-cm bore tubing. This system reduces the flow rate of water so as to minimize damage to the zooplankton during filtration. The pressure drop across the screens was reduced by immersing the funnels. Each filtration period lasted 60 s after which the flow was directed onto the other screen, the funnel removed and the sample back-washed onto a 5-cm disc of 171- $\mu$ m mesh netting, which was then placed in 5% formalin. The flow rate was monitored using an on-line E.M. flow meter. It was found that any minor fluctuations in the flow were averaged out over the 60-s sampling period and so it can be assumed that each sample represented the zooplankton from 125 l of water.

The vertical distribution of the various parameters was investigated by lowering the CTD, and pump inlet, from a depth of 3 to 56 m, and then raising it back to very close to the surface. The winch was run as slowly as possible. Zooplankton were collected during the lowering phase and the mean depth range spanned by the 60-s samples was  $3.87 \pm 0.67$  m (range 2.6 to 5.2 m). The very high concentrations of chlorophyll *a*, encountered at the base of the pycnocline, then were investigated by re-lowering the CTD to the approximate depth of this maximum. Sampling was continued for a further 139 min, whilst allowing the ship to drift. Slight adjustments were made to the CTD depth so as to sample different regions of the fluorescence peak. The computer crashed during this period and so a 100-min section of the data for temperature, chlorophyll *a* fluorescence, and nitrate was digitized at 6-s intervals from the chart records. Seventy-nine zooplankton samples were collected during part of this time. The major zooplankton taxa were enumerated and, whenever possible, specific identifications were made.

## RESULTS

### *Vertical profiling*

The results for the vertical profiling of the various physical, chemical, and biological parameters are shown in Figs 1 to 3. During the lowering of the CTD the density structure of the water column was closely mirrored by that for temperature, with a strong pycno/thermocline between 8- and 11-m depth (Fig. 1a). Salinity was relatively constant but with slightly

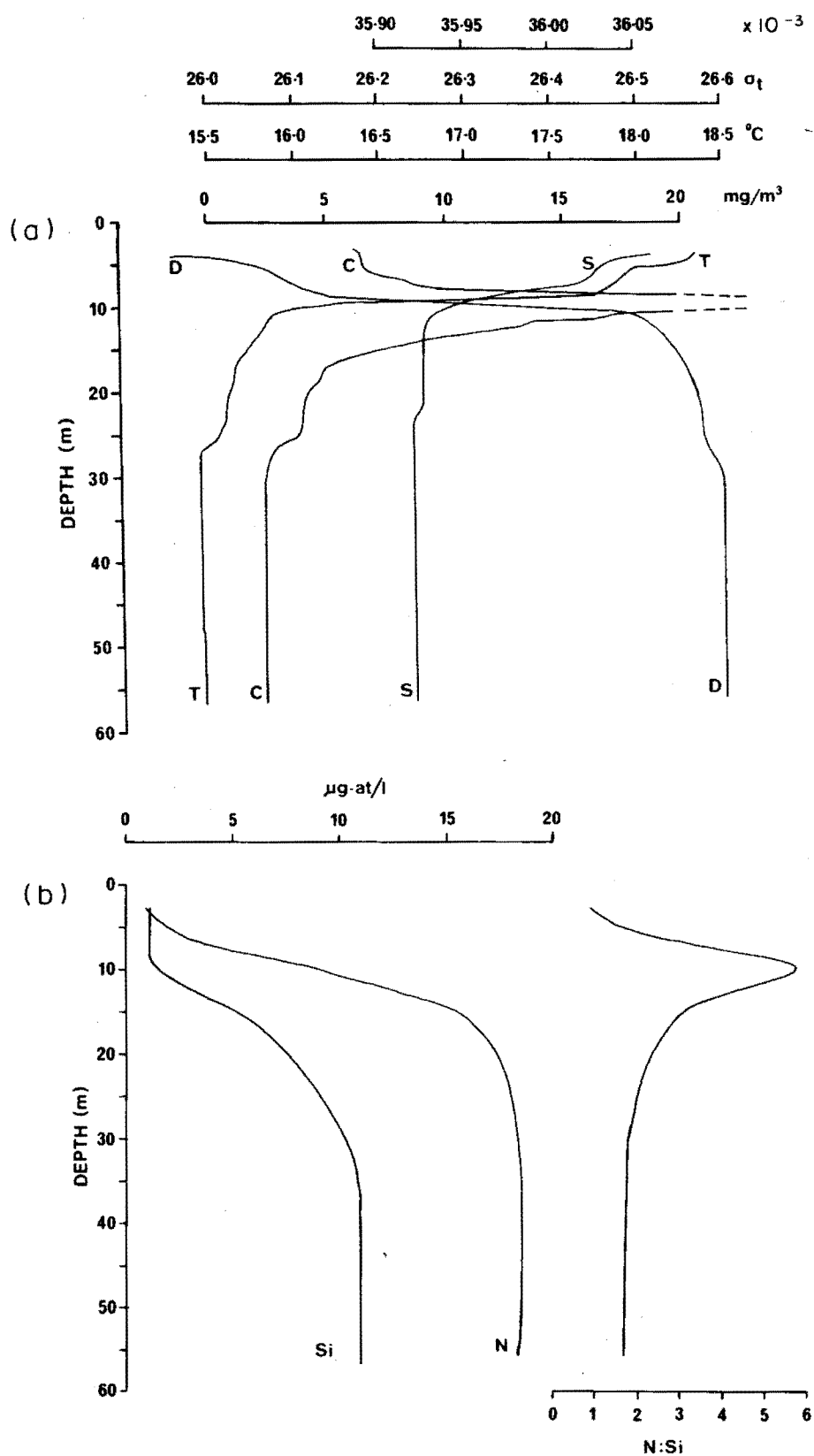


Fig. 1. The vertical distribution of various physical and chemical parameters measured during the lowering of the CTD. (a) Density (D), salinity (S), temperature (T), and chlorophyll *a* (C). (b) Nitrate (+ nitrite) (N), silicate (Si), and the N:Si ratio.

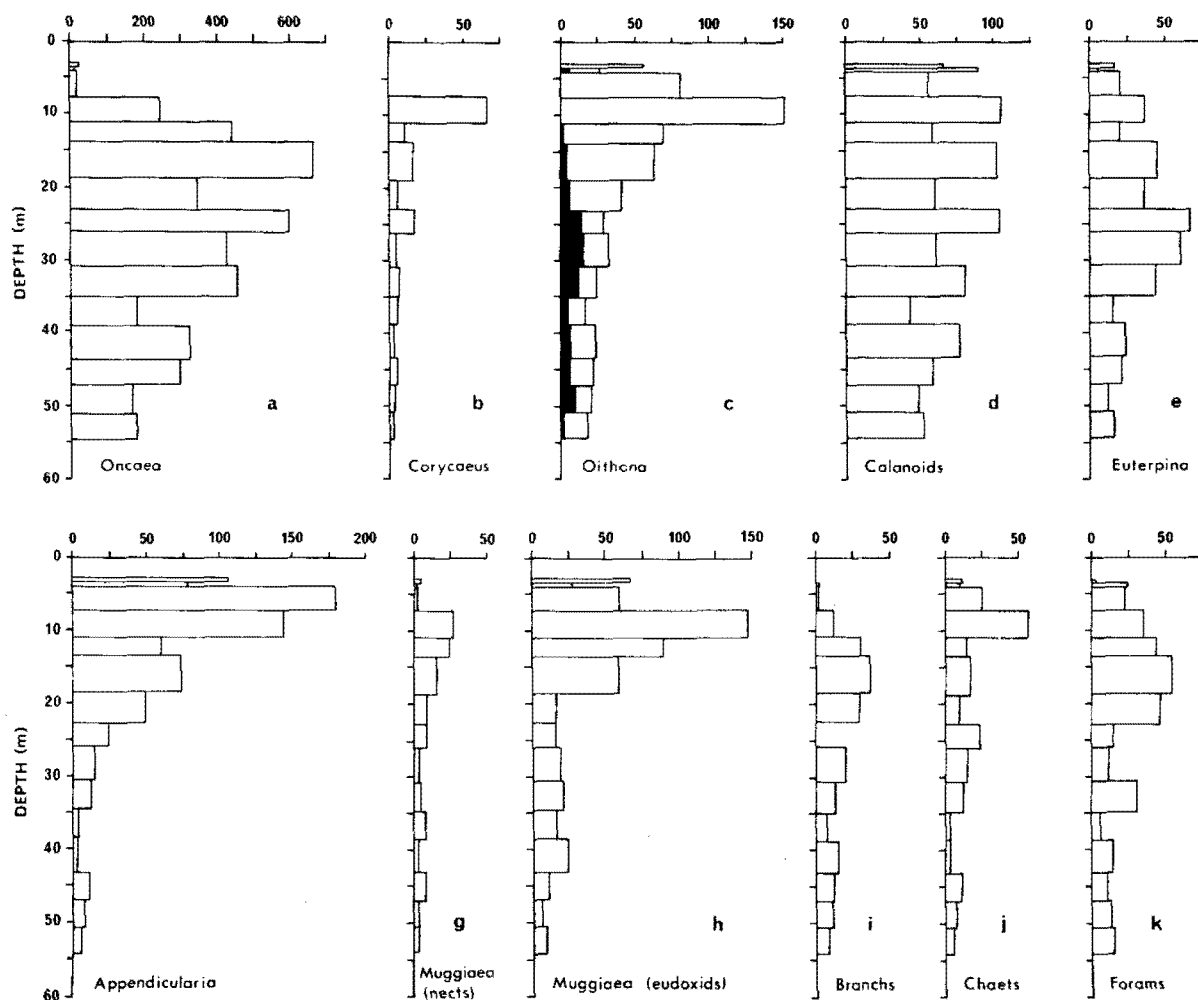


Fig. 2. The vertical distribution of zooplankton. (a) *Oncaea* spp., (b) *Corycaeus clausi*, (c) *Oithona nana* and other *O.* spp. (black), (d) Calanoid copepods, (e) *Euterpina acutifrons*, (f) Appendicularians, (g) *Muggiaea atlantica* nectophores, (h) *M. atlantica* eudoxids, (i) *Branchiostoma senegalense*, (j) larval chaetognaths, and (k) Foraminiferans.

elevated values in the surface waters. A feature of these profiles is the shoulder to the density/temperature structure, between 11 and 26 m. A slight but marked decrease of  $0.1^{\circ}\text{C}$  in temperature delimits this region from the isothermal bottom mixed layer below.

The vertical distribution of chlorophyll *a* was closely linked with the density structure of the water column. The surface values were erratic, ranging between  $2.5$  and  $10\text{ mg m}^{-3}$ , while in the pycnocline the concentrations rose rapidly and to such an extent that the fluorometers went offscale on the coarsest ( $\times 1$ ) range. This problem was overcome by inserting a piece of tracing paper in front of the red filter resulting in registerable values during the later horizontal profiling. Discrete samples taken at the fluorescence peak indicated that the chlorophyll *a* concentration was in the region of  $70\text{ mg m}^{-3}$ . This peak was situated at about 10-m depth, which was close to the base of the pycnocline, and below this depth the chlorophyll values decreased rapidly. The width of the 25% peak height was estimated to be  $<3\text{ m}$  although this is almost certainly an overestimate since there will be some turbulent mixing in the hosing. In accordance with the physical structure, there was a shoulder to the

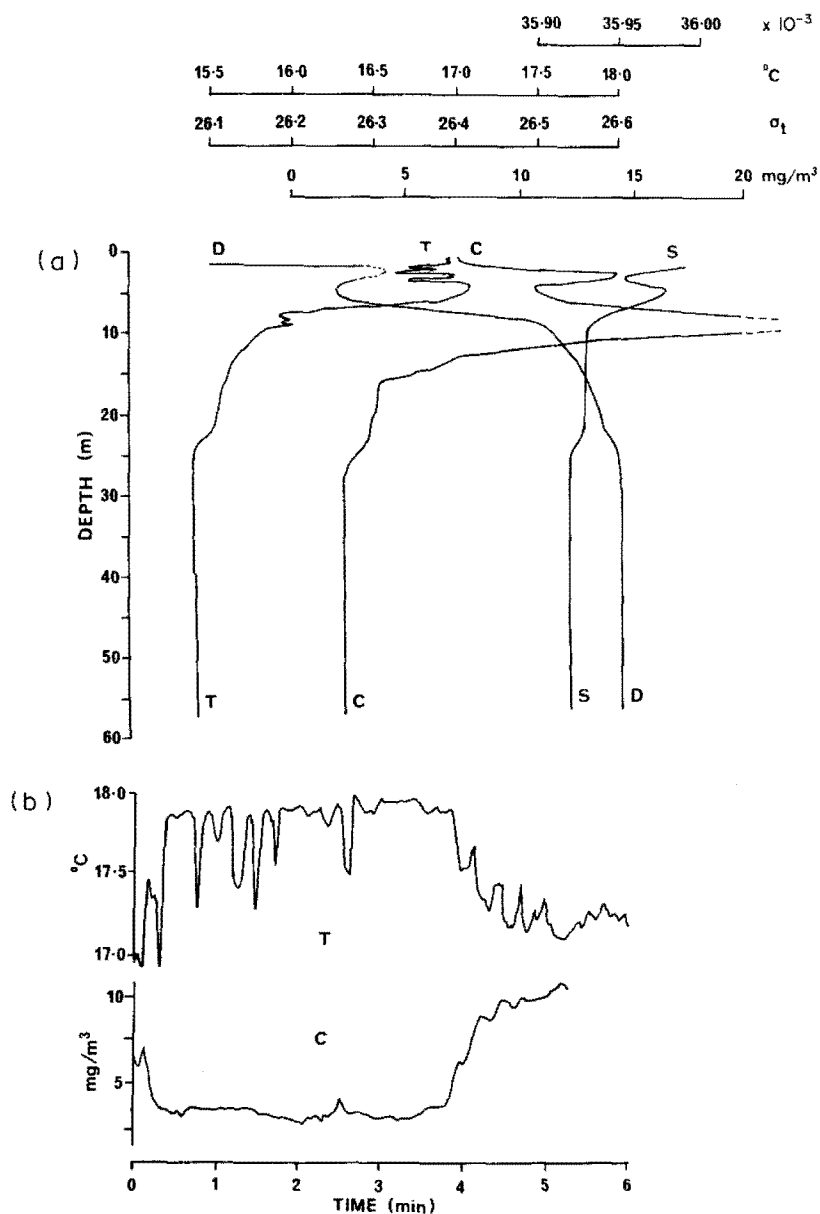


Fig. 3. (a) The vertical distribution of various physical and chemical parameters measured during the raising of the CTD; density (D), salinity (S), temperature (T), and chlorophyll *a* (C). (b) The temporal change in temperature (T) and chlorophyll *a* (C) close to the surface (see text for details).

fluorescence profile, with chlorophyll *a* concentrations of  $4.5 \text{ mg m}^{-3}$ , before the values dropped to a minimum in the bottom mixed layer.

Because of a malfunction in the surface photometer only the relative *in situ* values are available. These indicated a rapid decrease in light intensity ( $k_e$ , the vertical attenuation coefficient =  $0.73 \text{ m}^{-1}$ ) in the fluorescence maximum.  $k_e$  decreases to *ca.*  $0.12 \text{ m}^{-1}$  on the shoulder between 15 and 26 m, and further to  $0.09 \text{ m}^{-1}$  in the bottom mixed layer. By extrapolation the chlorophyll maximum was found to lie at *ca.* 2.5%  $I_0$  (the incident light intensity).

The nutrient profiles for silicate and nitrate (Fig. 1b) show that silicate was virtually

Table 1. The specific composition of the phytoplankton, cell Nos ml<sup>-1</sup> and plasma volume, in two samples from 0- and 8-m depth

	Depth (0 m)		Depth (8 m)	
	No.*	P.V.†	No.*	P.V.†
<i>Bacteriastrium</i>	0	—	6	—
<i>Chaetoceros</i> spp. (small)	134	6	1080	48
<i>Eucampia</i> sp.	0	—	20	—
<i>E. zodiacus</i>	0	—	28	—
<i>Hemiaulus</i> sp.	0	—	11	—
<i>Lauderia borealis</i>	32	14	20	9
<i>Leptocylindrus</i>	64	—	0	—
<i>Nitzschia 'seriata'</i>	11	—	31	3
<i>N. 'closterium'</i>	7	—	28	
<i>Rhizosolenia alata</i>	0	16	3	37
<i>R. delicatula</i>	18		6	
<i>R. fragilissima</i>	6		6	
<i>R. stolterfothii</i>	1		42	
<i>Skeletonema</i>	6	—	17	—
<i>Thalassiosira rotula</i>	13	13	1064	835
<i>T. subtilis</i>	6		126	
<i>Thalassiothrix frauenfeldii</i>	1	—	20	—
<i>Ceratium furca</i>	1	1	0	—
<i>Peridinium</i>	10		3	
<i>Scrippsiella trochoidia</i>	1		0	
Flagellates	4065	27	3360	22
Total	4376	91	5871	977

\* Cells Nos as Nos ml<sup>-1</sup>.† P.V. is plasma volume in units equivalent to 10<sup>4</sup> µm<sup>3</sup> ml<sup>-1</sup> (values of <3 × 10<sup>4</sup> µm<sup>3</sup> ml<sup>-1</sup> are not given).

undetectable above the pycnocline, while relatively high values of nitrate were found within the depth range of the chlorophyll *a* maximum. This implies that the phytoplankton population at the fluorescence peak was dominated by diatoms and is confirmed by the analyses of the phytoplankton composition from surface and fluorescence peak samples (Table 1). The total population numbers were similar at the two depths, due to the high densities of flagellates at both. However, the total plasma volume differed by an order of magnitude because of the large number of diatoms, particularly *Chaetoceros* and *Thalassiosira* spp. in the chlorophyll *a* maximum, with *T. rotula* contributing 85% of the total. This relates directly to the observed differences in the chlorophyll *a* concentrations, i.e., 2.5 mg m<sup>-3</sup> at the surface and 54.4 mg m<sup>-3</sup> in the 8-m depth sample.

Fifteen 60-s zooplankton samples were taken during the vertical profiling, of which two were collected from 3-m depth before lowering commenced. From these samples 21 major taxa of zooplankton were identified of which 10 only need be considered in any detail. The remainder, which included the cladoceran *Podon intermedius*, the harpacticoids *Microsetella* spp., and *Macrosetella gracilis*, various nauplii, ostracods, cyphonauts, tintinnids, and ophiuroid larvae, occurred only occasionally in the samples and showed no obvious trends. The vertical distribution of the 10 major taxa are shown in Fig. 2. The predominant animals were copepods of the genus *Oncaea*, mainly *O. media* f. *minor*, with other *Oncaea* species occurring only occasionally (Table 2). The females (ca. 0.5 to 0.6 mm in length) of *O. media* f. *minor* made up 95.3% of the total *Oncaea* catch and were widely distributed in and below

Table 2. The specific composition of the samples of *Oithona*, *Oncaea*, and *Corycaeus* collected during the vertical profiling experiment

Depth range (m)	<i>Oncaea media</i> f. <i>minor</i>			<i>Oncaea</i> spp.* ♀/♂	<i>Corycaeus</i> <i>clausi</i>			<i>Oithona</i> <i>nana</i>	<i>Oithona</i> <i>plumifera</i>	<i>Oithona</i> spp.
	♀	♂	Cop.		♀	♂	Cop.			
3.5	19	1	1	2	—	—	—	56	—	—
3.5–4.0	11	—	—	2	—	—	—	23	3	—
4.0–7.2	13	—	1	3	—	—	—	81	—	—
7.2–11.0	208	14	6	1	3	4	59	151	—	—
11.0–13.6	385	16	41	—	1	7	2	67	1	—
13.6–18.8	621	15	32	—	3	11	2	59	4	—
18.8–22.7	334	6	5	1	—	5	—	35	2	3
22.7–26.0	578	8	11	1	3	14	—	15	6	7
26.0–30.6	402	5	14	2	—	3	—	17	9	6
30.6–34.9	465	3	2	2	1	3	2	13	3	8
34.9–38.7	179	2	1	—	2	3	—	13	3	1
38.7–43.2	317	3	1	1	1	1	—	17	3	3
43.2–47.1	267	3	1	1	1	3	—	16	4	2
47.1–50.7	164	1	1	2	—	3	—	12	5	3
50.7–54.3	178	1	—	1	—	2	—	16	1	—

\* Species include *Oncaea mediterranea*, *O. tenella*, *O. similis*, and an unidentified species.



the thermocline. Maximum numbers, equivalent to *ca.* 5000 m<sup>-3</sup>, occurred just below the fluorescence peak (Fig. 2a). The males (*ca.* 0.4 to 0.5 mm length) of this species, although few in number, occurred mostly over a depth range which corresponded to the fluorescence peak and its lower slope (Table 2).

*Corycaeus clausi* was present in small numbers (Fig. 2b), but was noteworthy for being totally absent from the samples above the thermocline. Maximum numbers were reached in the upper part of the chlorophyll peak, but this population consisted of a large number of copepodids (0.4 to 0.8 mm in length), which occurred almost exclusively in this sample (Table 2). Adult *C. clausi* (body length 0.9 to 1.1 mm) were found mainly on the shoulder of the temperature/fluorescence profiles between 15- and 25-m depth, with lower numbers in the bottom mixed layer. The cyclopoid genus, *Oithona*, was well represented (Fig. 2c) and *O. nana* (body length 0.5 to 0.65 mm) predominated (Table 2), particularly in and above the fluorescence peak where maximum numbers of *ca.* 1200 m<sup>-3</sup> were found. The other species, which included *O. plumifera* (body length 1.0 mm), appeared mainly in the bottom mixed layer where together they constituted from 6 to 47% of the total *Oithona* population (Fig. 2c). Calanoid copepods were evenly distributed down through the water column (Fig. 2d), with a mean population of  $562 \pm 160$  m<sup>-3</sup>. These copepods were specifically identified only in a random selection of samples from the horizontal profiling series. In these, *Acartia clausi*, *Temora stylifera*, and other species were present in a ratio of 7:2:1. The only other crustacean species present in any numbers was the harpacticoid, *Euterpina acutifrons* (Fig. 2e), which was present throughout the water column, with a slight maximum of *ca.* 500 m<sup>-3</sup> at the top of the bottom mixed layer.

Appendicularians usually were the most abundant non-crustacean element in the samples, and these were dominated by two species, *Oikopleura dioica* and *O. longicauda*. The latter species was never abundant, forming <20% of the total appendicularians in the thermocline samples, while in the bottom mixed layer its abundance was similar to that of *O. dioica*, but the overall population density was low. Maximum numbers of *ca.* 1400 m<sup>-3</sup> were found at the top of the thermocline, above the fluorescence peak (Fig. 2f). The siphonophore, *Muggiaea atlantica*, also was well represented, particularly its eudoxid or reproductive stage (Fig. 2h). Peak abundance occurred in the region of the chlorophyll maximum, with the eudoxid bracts reaching 1200 m<sup>-3</sup> and the eudoxid gonophores, on average, being twice as abundant. The depth distribution of the anterior nectophores of the polygastric stage (Fig. 2g) was similar to that of the eudoxids, except for a virtual absence above the thermocline, where relatively high numbers of eudoxids were found.

Amongst the other major taxa present in the samples, larvae of the cephalochordate, *Branchiostoma senegalense*, with a mean size of  $2.24 \pm 0.26$  mm were common below the thermocline (Fig. 2i), with maximum numbers of up to 300 m<sup>-3</sup> on the shoulder of the temperature profile. Larval chaetognaths, too small to be specifically identified, reached maximum numbers in and above the thermocline (Fig. 2j), while a variety of foraminiferan species, including *Globigerina incompta*, *Globigerinella aequilateralis*, and *Globigerinoides* spp., were broadly distributed down the water column with maximum numbers on the shoulder of the thermocline (Fig. 2k). Overall, the zooplankton population in the pump samples closely resembled that found by BLACKBURN (1979) in net samples taken in a similar area on the northwest African shelf.

Some differences in the physical structure of the water column were noted during the raising of the CTD (cf. Figs 1 and 3), particularly in the top 10 m. The thermocline was found to be less pronounced, with a temperature rise of a little over 1°C, and at its base,

between *ca.* 9 and 7.5 m, the temperature fluctuated erratically around 15.95°C (Fig. 3a). Above the thermocline, the temperature also was very variable and there appeared to be instabilities in the density structure although these may have been artifacts caused by 'spiking' in the salinity measurements. The chlorophyll *a* profile was affected by these changes in the temperature structure (Fig. 3a) and its maximum lay in the region of erratic temperature fluctuations at the base of the thermocline. A secondary maximum was observed at 3 m, again where rapid temperature fluctuations occurred. During the profiling the ship drifted into a deep-brown coloured surface slick, and so the CTD and pump inlet were raised close to the surface to investigate this phenomenon. During the first 5 to 6 min of this near-surface sampling (Fig. 3b) the temperature fluctuated by more than 1°C and the chlorophyll *a* concentrations were inversely related to these changes.

### *Horizontal profiling*

The corresponding records for the temperature and chlorophyll *a* measurements made during the 139-min sampling period are shown in Fig. 4. For most of the time when the CTD was at 8 m the fluctuations in temperature and chlorophyll *a* concentration were inversely related, indicating that the sampling depth was in the upper slope of the chlorophyll maximum. The variations in the parameters probably are caused by internal waves propagating along the pycnocline. On occasions, and in the later part of the record when the CTD depth was increased, the vertical displacements of the thermocline were sufficient for the lower slope of the chlorophyll peak to be sampled so that the temperature and chlorophyll fluctuations were positively correlated. Over the 79 min of zooplankton sampling, between 1333 and 1453 GMT, several of these periods of positive correlation were observed (Fig. 5). The temporal changes in nitrate concentrations during this period (Fig. 5c) indicate the close proximity of the nitracline to the lower edge of the chlorophyll maximum.

Because of the alteration in the sign of the covariance between chlorophyll *a* concentration and temperature it is impossible to carry out any meaningful spectral or other statistical analyses, e.g., autocorrelation, of the data (cf. FASHAM and PUGH, 1976). Nonetheless it is obvious that the chlorophyll maximum lay not at a fixed depth but in a fixed region of the pycnocline. Because the relationship between the various parameters considered here is not necessarily monotonic, it is simplest and clearest just to plot the data for one parameter against another, as STAR and CULLEN (1981) have shown. Figure 6a shows the relationship between chlorophyll *a* and temperature. Maximum concentrations of chlorophyll *a* were reached at temperatures between *ca.* 16.0 and 16.15°C, at  $\sigma_t$  values of *ca.* 26.5. The decline in chlorophyll *a* concentration is more marked below the peak than above, but it should be remembered that the maximum lay at the base of a steep thermocline. The 75% peak height for the chlorophyll maximum spanned the temperature range 15.9 to 16.35°C which, from the vertical profiling series, represented a depth range of about 1 m. The relation between the nitrate concentrations and temperature (Fig. 6b) shows the rapid rise in nutrient levels at the lowest temperatures recorded, i.e., below the chlorophyll maximum. The scatter in the values at higher temperatures may be attributed, in part at least, to the smoothing effects of the sampling process which could not take account of the rapid nitrate fluctuations.

Twenty-six taxa of zooplankton were identified from the 79 samples analyzed. All those found during the vertical profiling were present, and in addition a single specimen of the *Athorybia* larva of an *Agalma* spp. (Siphonophora) and a few small tunicates, small lamellibranchs, and cirripede cyprids were found in the samples taken below the chlorophyll maximum. Tintinnids, which appeared in only one of the vertical profiling samples, also were

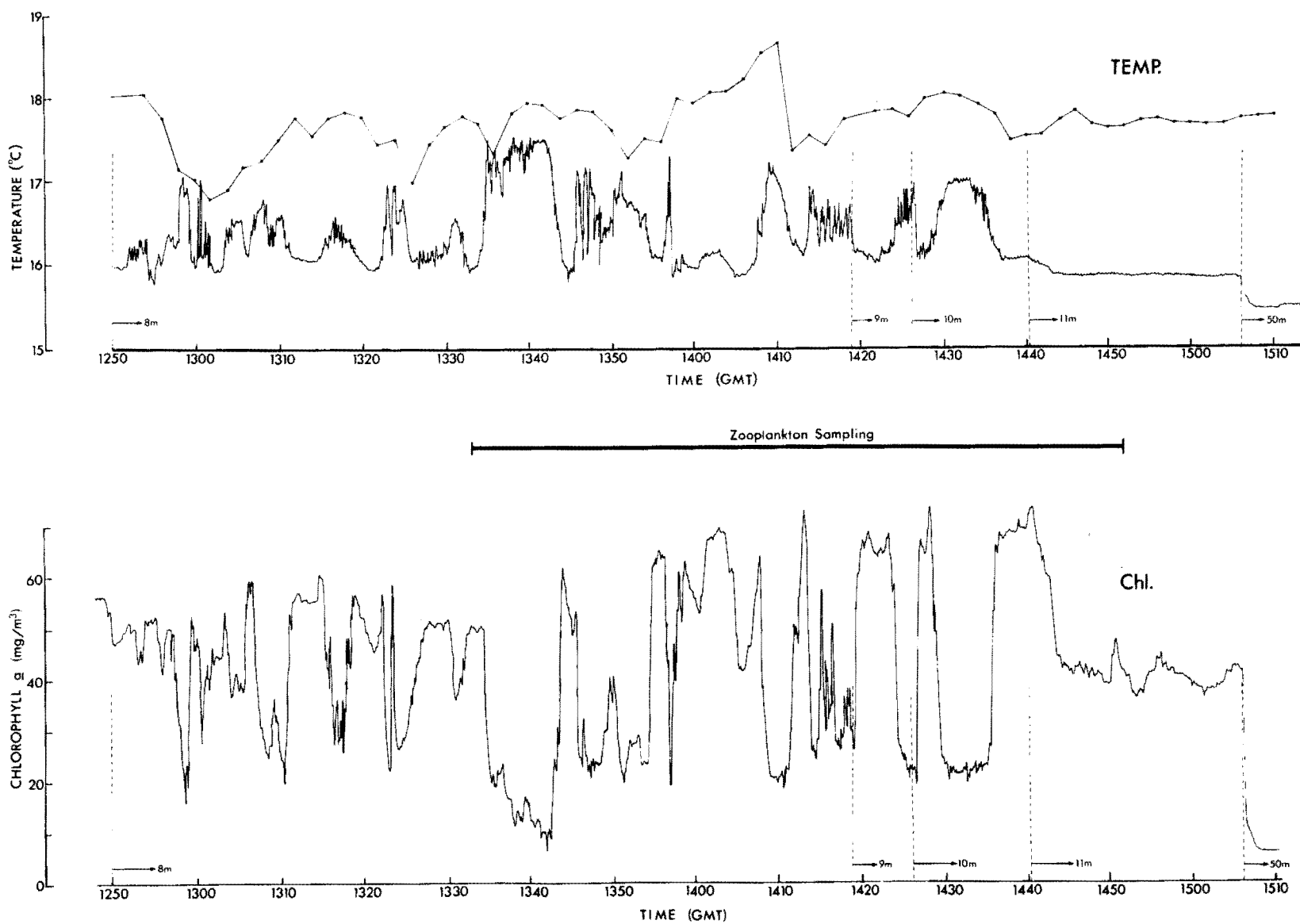


Fig. 4. Subsurface temperature and chlorophyll *a* measurements during the entire 139-min sampling period. The times at which the depth of the CTD and pump inlet was altered during the zooplankton sampling period are indicated. The surface temperature (2 min average, —●—) for this period also is shown.

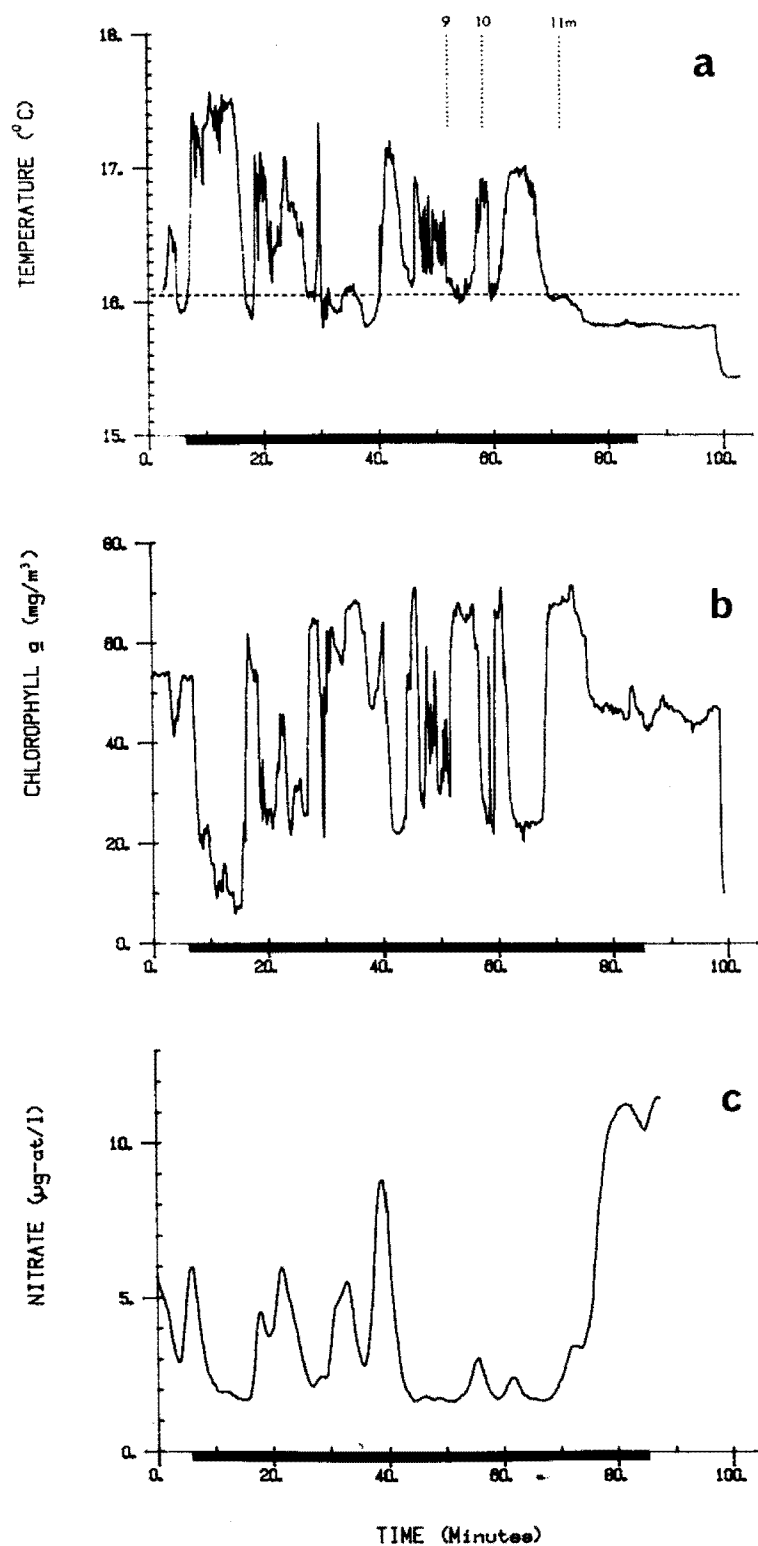


Fig. 5. The variations in the subsurface temperature (a), chlorophyll *a* (b), and nitrate (c) during the 100-min period (1327 to 1507 GMT) which spanned the zooplankton sampling (1333 to 1453 GMT). The times at which the CTD depth was changed are indicated in (a). When the temperature fell below *ca.* 16.05°C (dotted line in a) the variations in temperature and chlorophyll *a* were positively correlated.

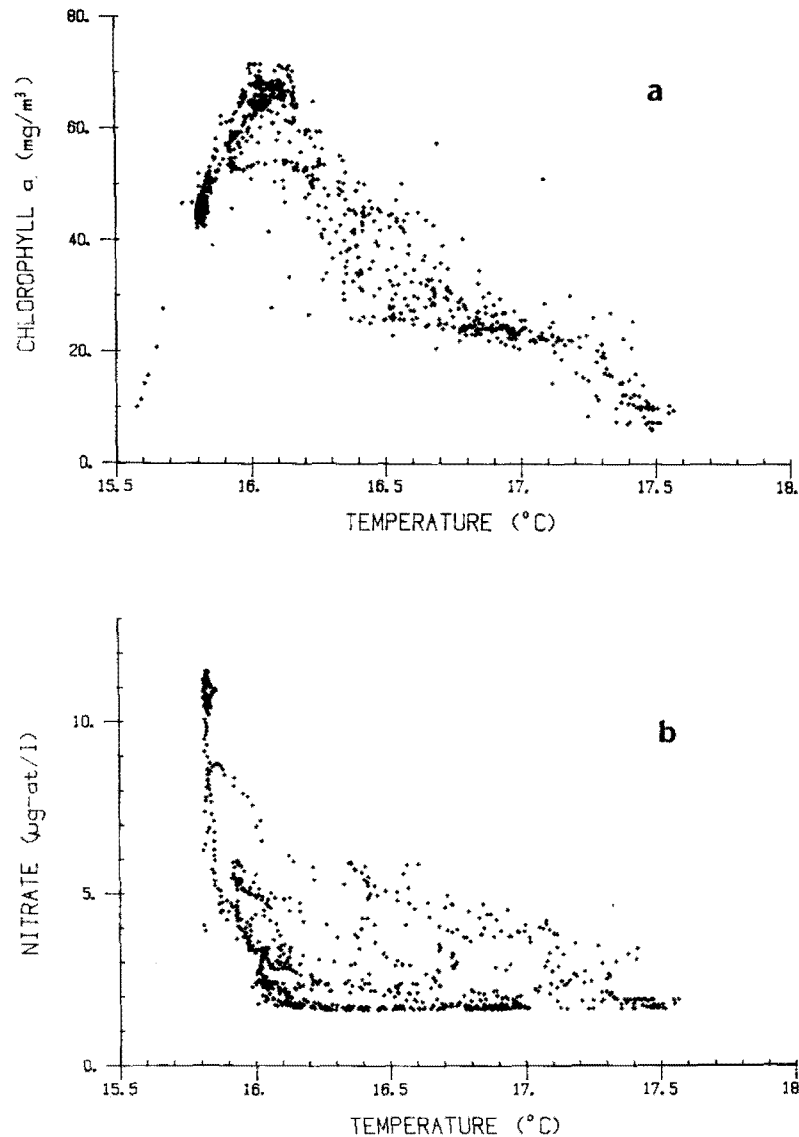
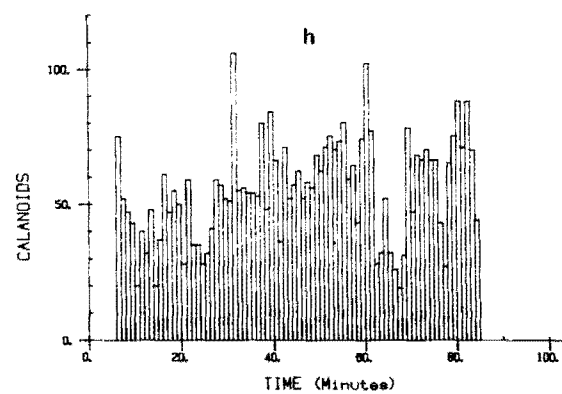
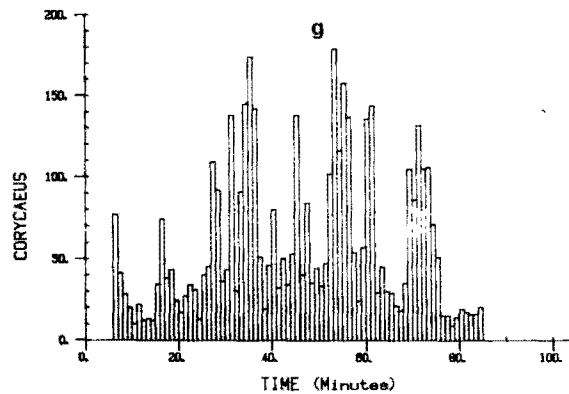
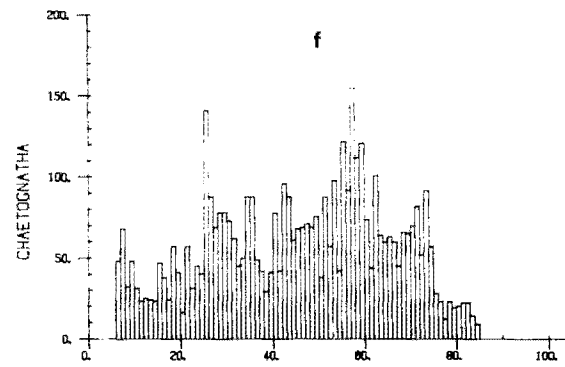
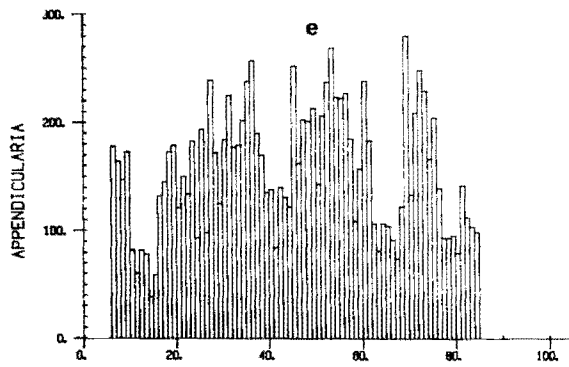
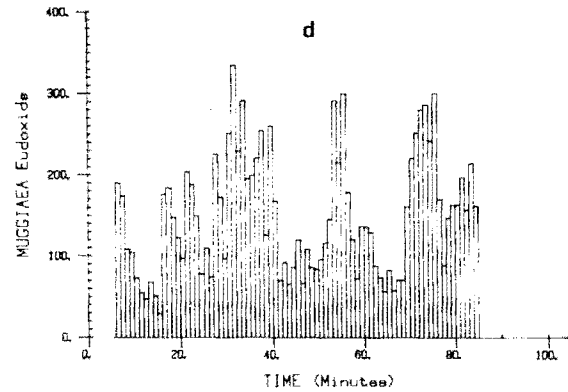
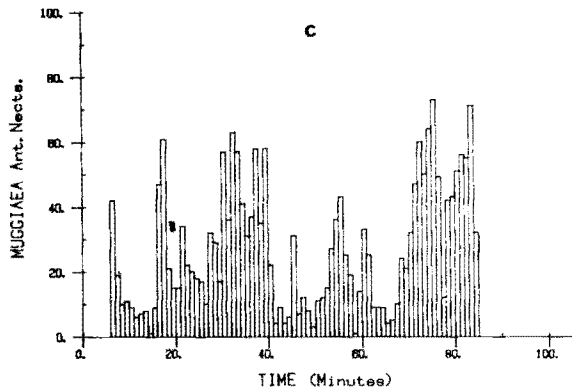
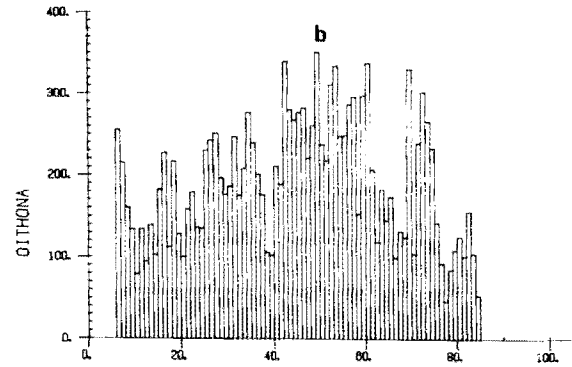
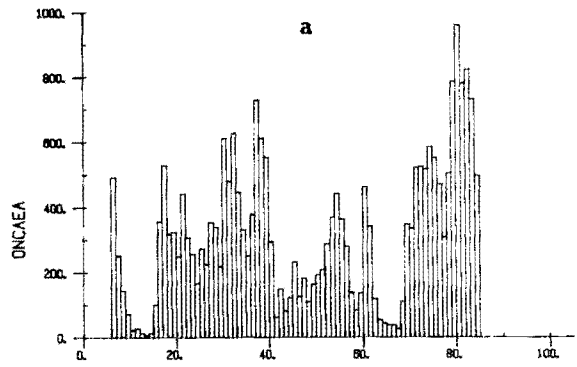


Fig. 6. Scattergrams showing the relationship between temperature and (a) chlorophyll *a*, and (b) nitrate.

common in these latter samples, reaching numbers of  $300 \text{ m}^{-3}$ , as were the harpacticoids *Microsetella* and *Macrosetella*, which previously had been found to be commonest in the bottom mixed layer. Ophiuroid larvae were found in greatest numbers at a temperature of *ca.*  $16.0^{\circ}\text{C}$ , on the lower slope of the chlorophyll maximum, while *P. intermedius* was commonest in the thermocline, in the  $16.3$  to  $17.0^{\circ}\text{C}$  temperature range.

The temporal variation in the numbers of the 11, numerically most significant, taxa are shown in Fig. 7, and the numbers per sample for each taxon are plotted against the mean temperature for that 60-s sampling period in Fig. 8. Because many of the taxa studied had a tendency to aggregate at or below the chlorophyll *a* maximum, i.e., at lower temperatures, the plots of numbers against mean chlorophyll *a* concentrations often are more difficult to interpret, but four examples are given in Fig. 9. The zooplankton data have been divided into two sets according to whether the mean temperature was  $\geq 16.05^{\circ}\text{C}$ , which is approximately



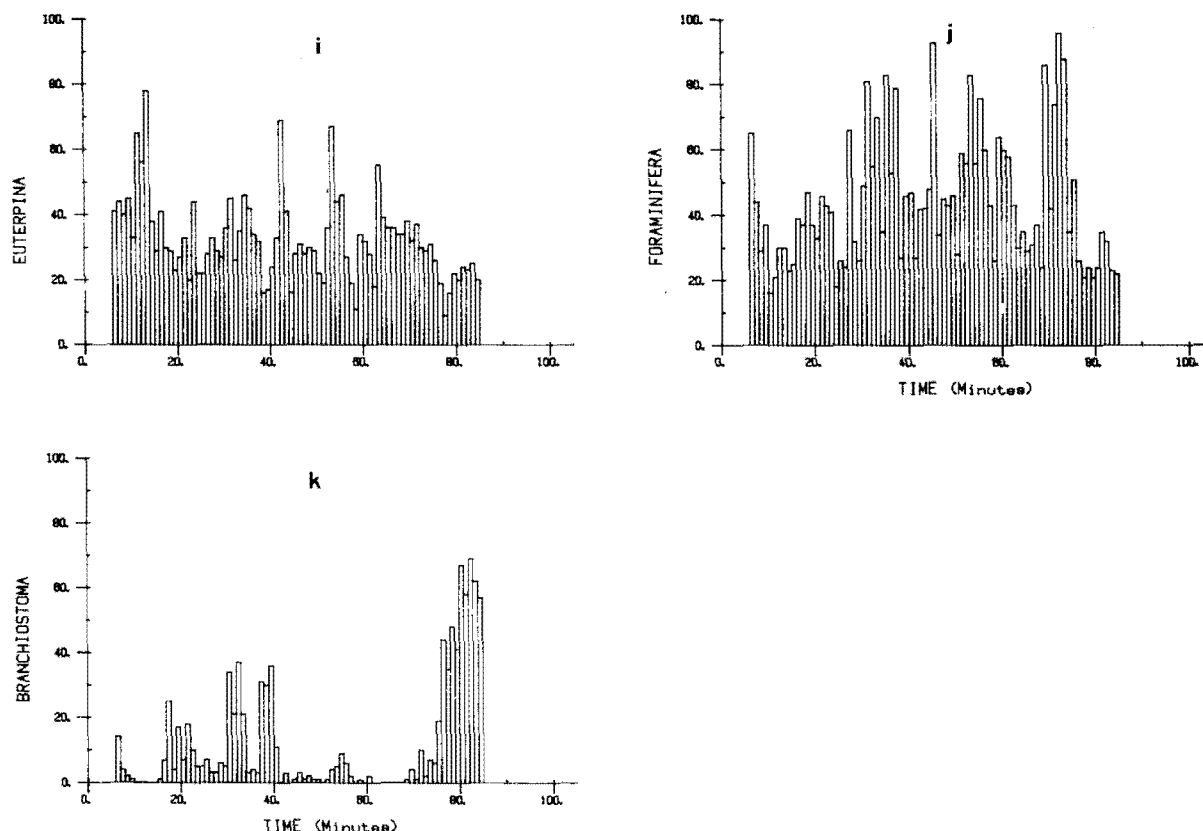
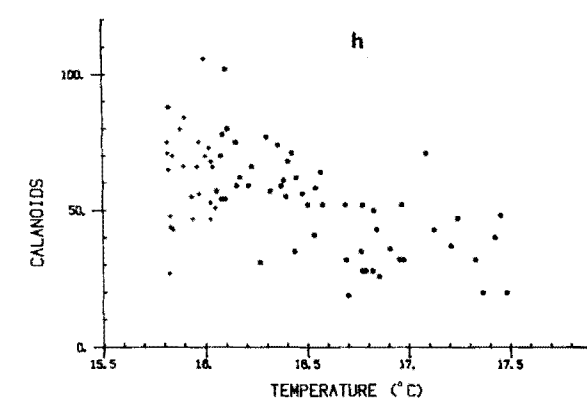
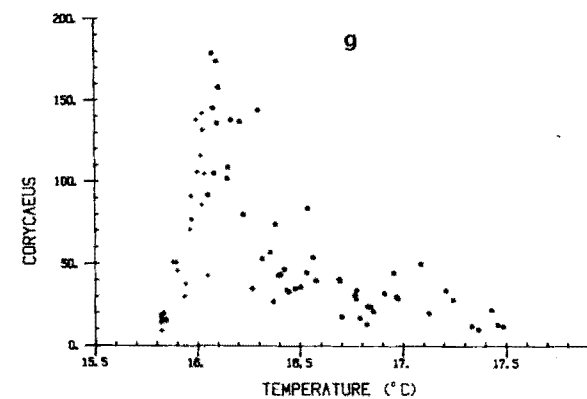
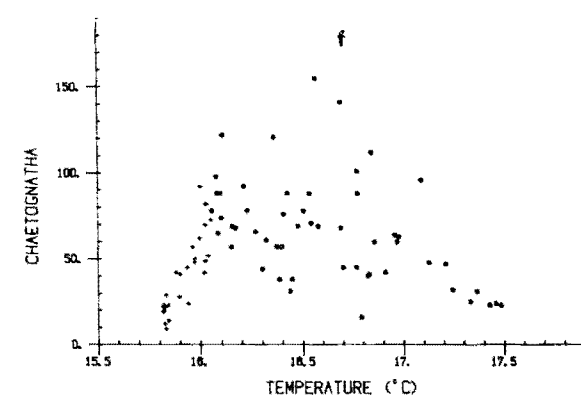
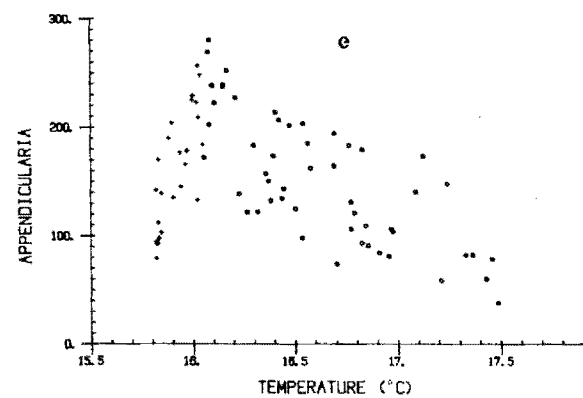
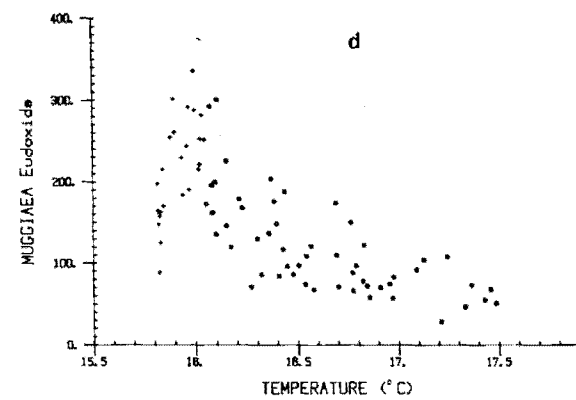
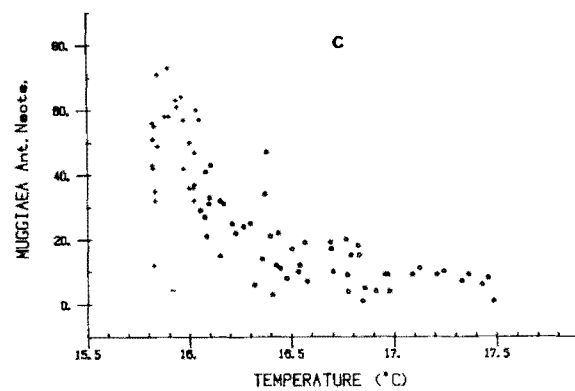
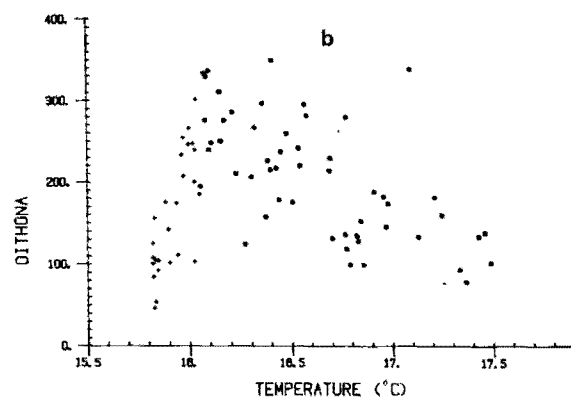
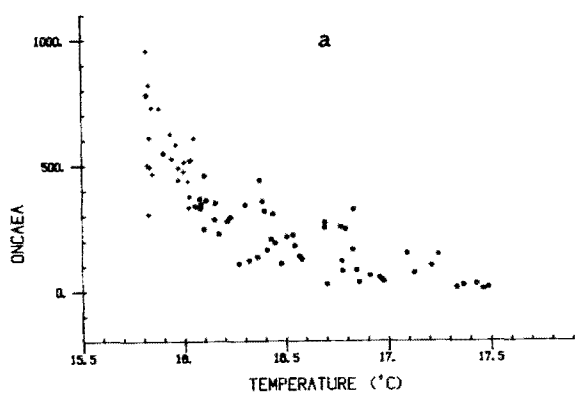


Fig. 7. Variations in the abundance of zooplankton (number per sample) during the horizontal profiling experiment. (a) *Oncaea* spp., (b) *Oithona* spp., (c) *Muggiaea atlantica* nectophores, (d) *M. atlantica* eudoxids, (e) appendicularians, (f) chaetognaths, (g) *Corycaeus clausi*, (h) calanoid copepods, (i) *Euterpina acutifrons*, (j) foraminiferans, and (k) *Branchiostoma senegalense*.

the temperature at which the highest chlorophyll *a* concentrations were found. The commonest taxon was the copepod, *Oncaea* spp. which was predominated by females of *O. media* f. *minor*. The mean density in the samples was  $2522 \pm 1768 \text{ m}^{-3}$ , with a range of  $48$  to  $7656 \text{ m}^{-3}$ . The population was greatly affected by the physical structure of the water column and there is a clear negative correlation with temperature (Fig. 8a). The plot of *Oncaea* numbers against chlorophyll *a* concentration (Fig. 9a) also clearly shows the increase in population numbers below the chlorophyll *a* maximum.

There was much less temporal variation in the numbers of *Oithona* spp. (predominantly *O. nana*) (Fig. 7b), but this apparent absence of patchiness in the data belies the actual distribution of the animals with respect to temperature (Fig. 8b), and to the chlorophyll maximum. Peak numbers appeared in the shoaler part of the chlorophyll maximum, with a rapid fall in numbers as the temperature decreased. Although there is some scatter in the results at higher temperatures, linear regressions, having split the data into the two sets as discussed above, have highly significant correlation coefficients ( $P \leq 0.001$ ).

The third most abundant taxon was the calycophoran siphonophore, *M. atlantica*, and the temporal variations of the polygastric (asexual) and eudoxid (sexual) stages are shown separately (Fig. 7c,d). The eudoxid bracts (mean  $1207 \pm 596 \text{ m}^{-3}$ ) were considerably more abundant than the nectophores (mean  $218 \pm 156 \text{ m}^{-3}$ ) and their coefficient of variation was higher. However, the plots against temperature (Fig. 8c,d) show that nectophores reached a





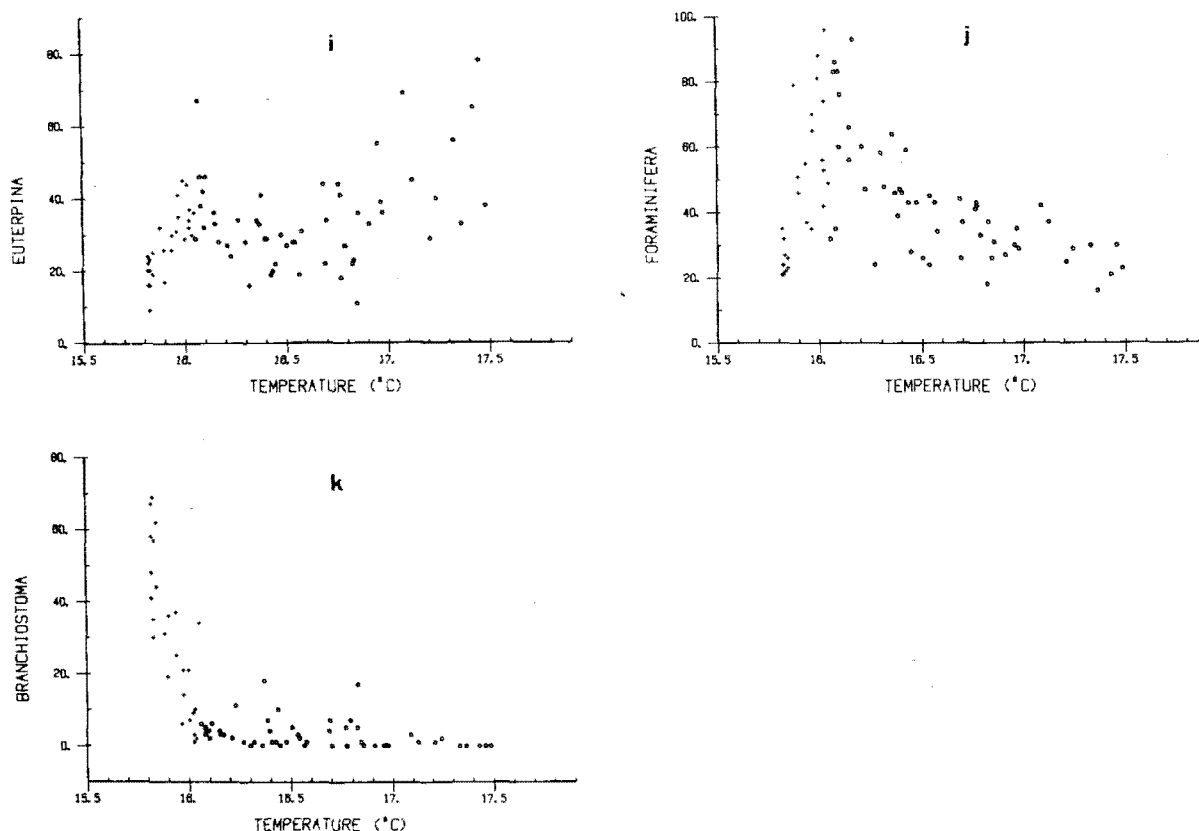


Fig. 8. Scattergrams showing the relationship between average temperature and zooplankton. (a to k) As in Fig. 7. Mean temperature:  $> 16.05^{\circ}\text{C}$  (O);  $< 16.05^{\circ}\text{C}$  (+).

maximum on the lower slope of the chlorophyll maximum at a temperature of *ca.*  $15.95^{\circ}\text{C}$  while numbers were low at temperatures in excess of  $16.4^{\circ}\text{C}$ . The distribution of the eudoxid stage was similar although their maximum occurred at a slightly higher temperature, *ca.*  $16.0^{\circ}\text{C}$ , and thereby on the lower edge of the chlorophyll maximum. The vertical profiling series has indicated a slightly shoaler distribution, exemplifying the difficulties inherent in making accurate assessments of small-scale distributions of zooplankton even with samples which span as little as 3- to 4-m depth.

Appendicularians, predominantly *O. dioica* (Fig. 7e) were as abundant as the eudoxid bracts of *M. atlantica* with mean numbers of  $1246 \pm 455 \text{ m}^{-3}$ . There was a marked peak of abundance at a temperature of *ca.*  $16.05^{\circ}\text{C}$  (Fig. 8e), coincident with the chlorophyll maximum. High numbers of appendicularians were found at higher temperatures, while there was a rapid decrease in the population below the chlorophyll maximum (Fig. 9b). However, the linear regressions of numbers against temperature and chlorophyll, for the two data sets, all had highly significant correlation coefficients ( $P \ll 0.001$ ).

Young, unidentifiable chaetognaths were common (Figs 7f and 8f) and maximum numbers were reached in the upper part of the thermocline with a rapid decrease in numbers below the chlorophyll maximum and relatively few specimens being found at the highest temperatures encountered. In contrast, *C. clausi*, which was present in similar numbers ( $461 \pm 362 \text{ m}^{-3}$ , Fig. 7g), showed (Fig. 8g) a very marked peak of abundance in the region of the thermocline where the chlorophyll maximum lay. This restricted distribution relative to

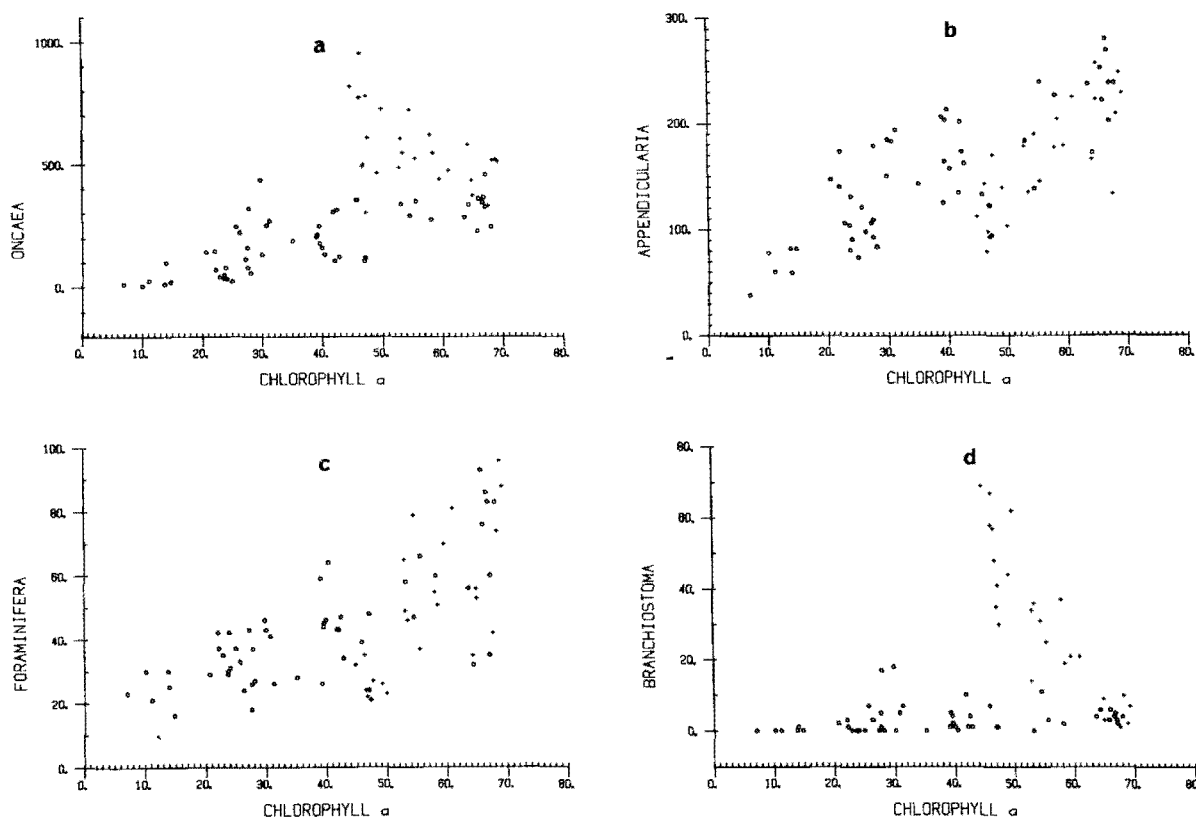


Fig. 9. Scattergrams showing the relationship between average chlorophyll *a* concentration ( $\text{mg m}^{-3}$ ) and zooplankton. (a) *Oncaea* spp., (b) appendicularians, (c) foraminiferans, and (d) *Branchiostoma senegalense*. Mean temperature:  $> 16.05^{\circ}\text{C}$  (O);  $< 16.05^{\circ}\text{C}$  (+).

temperature meant that 75% of the population in the main peak lay within a  $0.4^{\circ}\text{C}$  temperature range, equivalent to a 70-cm depth range. The vertical profiling series indicated that this *C. clausi* peak was mainly made up of copepodids. Also, in that series, this species was absent above the thermocline whereas, in the horizontal series, it was still found in comparatively low numbers at the highest temperatures sampled.

Although the temporal distribution of calanoids (Fig. 7h) appeared uniform with a low coefficient of variation (0.34), it is clear from the plot against temperature (Fig. 8h) that there is a significant trend ( $P < 0.001$ ) for these copepods to accumulate towards the base of the thermocline, around the chlorophyll maximum. The calanoids were mainly *A. clausi* with some *T. stylifera*. The coefficient of variation was similarly low for the harpacticoid *E. acutifrons*, with mean numbers of  $261 \pm 102 \text{ m}^{-3}$ , but the plot against temperature (Fig. 8i) showed that highest numbers were reached at the highest average temperatures sampled. Within the main thermocline the numbers were constant over the  $1^{\circ}\text{C}$  temperature change between  $17.0$  and  $16.0^{\circ}\text{C}$ , while below  $16.0^{\circ}\text{C}$  there was a rapid decrease in numbers. This distribution is in contrast to the vertical profiling data where peak numbers were found in the bottom mixed layer (not sampled during the horizontal profiling), while numbers were low above the thermocline.

Another discrepancy between the two sets of data is found with the foraminiferans (Fig. 7j) which had a widespread distribution in the vertical series. However, the horizontal profiling data (Figs 8j and 9c) indicated a very marked peak of abundance at the chlorophyll

Table 3. The Kendall Rank Correlation matrix showing the interrelation between the major zooplankton taxa, and temperature and chlorophyll *a*

	<i>Euterpina</i>	Chaetognatha	<i>Oithona</i>	<i>Corycaeus</i>	Foraminifera	Appendicularia	Mugeb	Mugan	<i>Oncaea</i>	Polychaetes	Calanoids	<i>Branchiostoma</i>	Nauplii	Temperature	Chlorophyll <i>a</i>
<i>Euterpina</i>	—	0.12	0.20	0.20	0.17	0.11	0.01	-0.10	-0.20	-0.23	-0.02	-0.25	-0.11	0.25	-0.03
Chaetognatha		—	0.51	0.44	0.33	0.32	0.04	-0.13	-0.15	-0.22	0.11	-0.25	-0.01	0.15	0.14
<i>Oithona</i>			—	0.57	0.46	0.48	0.13	-0.02	0.00	-0.08	0.38	-0.17	0.20	0.01	0.26
<i>Corycaeus</i>				—	0.60	0.58	0.37	0.21	0.18	0.02	0.39	-0.01	0.29	-0.20	0.51
Foraminifera					—	0.63	0.42	0.24	0.21	-0.09	0.43	0.05	0.25	-0.23	0.44
Appendicularia						—	0.44	0.27	0.28	0.12	0.40	0.11	0.35	-0.24	0.51
Mugeb*							—	0.69	0.63	0.48	0.41	0.48	0.48	-0.54	0.61
Mugan*								—	0.75	0.56	0.37	0.58	0.50	-0.66	0.53
<i>Oncaea</i>									—	0.65	0.44	0.71	0.57	-0.73	0.49
Polychaetes										—	0.33	0.67	0.44	-0.58	0.34
Calanoids											—	0.28	0.45	-0.41	0.41
<i>Branchiostoma</i>												—	0.44	-0.61	0.30
Nauplii													—	-0.58	0.55
Temperature														—	-0.58
Chlorophyll <i>a</i>															—

\* Mugan and Mugeb represent *Muggiaea atlantica* nectophores and eudoxids, respectively.

Significance levels 5%  $\tau = 0.150$ , 1%  $\tau = 0.198$ , 0.1%  $\tau = 0.252$ .

maximum with a rapid decline in numbers on either side. The regression lines have highly significant ( $P \ll 0.001$ ) correlation coefficients. Lastly, the larvae of the cephalochordate *B. senegalense* showed very marked temporal variations (Fig. 7k). Their distributions with regard to temperature (Fig. 8k) and chlorophyll (Fig. 9d) show clearly that this species is virtually absent in and above the thermocline but increases in numbers rapidly below the chlorophyll maximum, as was found in the vertical profiling series.

A Kendall Rank Correlation analysis was used to investigate the possible interrelations between the major zooplankton taxa observed, and the correlation matrix (Table 3) indicates that many pairs of taxa are highly correlated ( $P \ll 0.001$ ) with each other. If one extracts from this matrix those highly significant pairings ( $\tau > 0.40$ ) then two main groupings can be recognized. In addition *E. acutifrons* can be singled out as having a positive relationship with temperature, with peak numbers being reached at the highest temperature values, and as having no correlation, at the  $P = 0.1\%$  level, with any of the other taxa considered. One of the major groupings contains five taxa—*C. clausi*, *O. nana*, appendicularians, larval chaetognaths, and foraminiferans. All these taxa are strongly correlated with each other, except for chaetognaths with appendicularians and with foraminiferans, yet still both these pairs are correlated at the  $P < 0.1\%$  level. The other grouping includes six taxa—*M. atlantica* (nectophores and eudoxids), *O. media* f. *minor*, *B. senegalense*, the various nauplii, and polychaetes. Again the statistical relation between these taxa is strong, with no  $\tau$  values of  $< 0.40$ .

By referring these statistical groupings to the distribution of the taxa with regard to temperature and chlorophyll, as found during the horizontal profiling (Fig. 10), it can be seen that they included species which have their peaks of abundance either (a) in the region of the upper part of the chlorophyll  $\alpha$  maximum or slightly above this, in the main thermocline, or (b) on the lower slope of the chlorophyll maximum or at the lowest temperatures

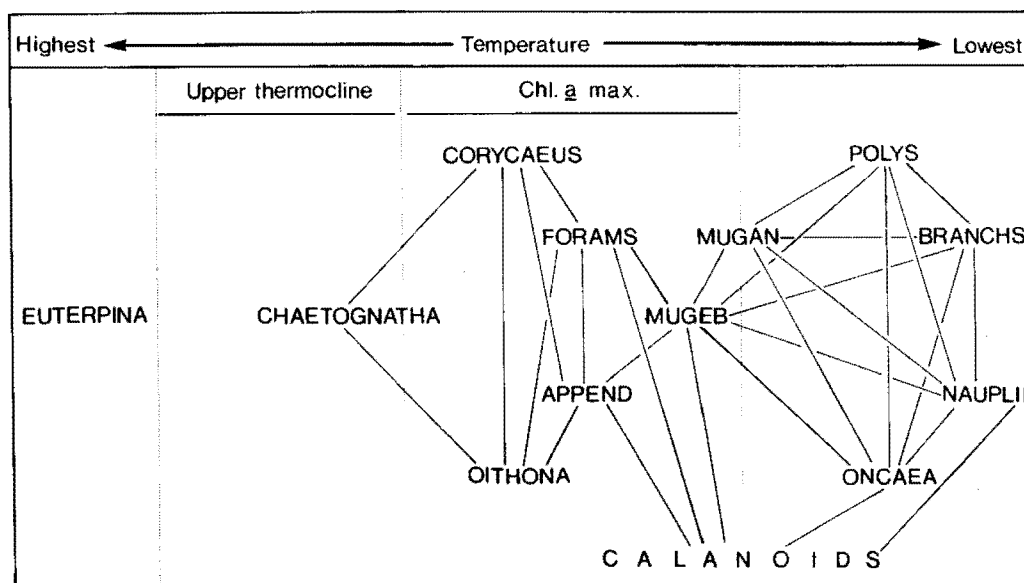


Fig. 10. The distribution of various zooplankton taxa with regard to temperature, as observed during the horizontal profiling experiment, and their interrelationship as indicated by the Kendall Rank Correlation analysis ( $\tau$  values  $> 0.40$ ). Abbreviations: *Append*, appendicularians; *Forams*, foraminiferans; *Mugan*, *Muggiaea atlantica* nectophores; *Mugeb*, *M. atlantica* eudoxids; *Polys*, polychaetes; *Branchs*, *Branchiostoma senegalense*.

encountered. At the chosen significance level there are only two interconnections between the above groupings—*M. atlantica* eudoxid bracts with the appendicularian and foraminiferans. The population maxima for these three taxa lie very close together in the region of the chlorophyll *a* maximum. At the  $P < 0.1\%$  significance level, there are five other interconnections between taxa in the two groupings, but the majority of pairings are not significantly correlated ( $P > 3\%$ ), and so in general the two groupings are distinct. This is exemplified further by the fact that all the taxa in the deeper living (colder temperature) grouping have very high ( $\tau > 0.40$ ) negative correlations with temperature, whereas none of those in the shallower grouping are correlated with temperature at the  $P < 0.1\%$  level. Most taxa from both groupings, with the notable exception of the chaetognaths, have highly significant correlations with the chlorophyll *a* concentration. However, for many of the taxa, their relation with temperature or chlorophyll is not monotonic, as can be seen from the scattergrams (Figs 8 and 9), so that the statistical analyses would not be expected to result in high correlation coefficients in these cases. One other taxon, the calanoid copepods, because of its widespread distribution in the lower part of the thermocline, has highly significant correlations ( $\tau > 0.40$ ) with certain taxa in both groupings (Fig. 10), and, at the  $P < 0.1\%$  level, with all the other relevant taxa, except chaetognaths.

#### DISCUSSION

Although the present results were obtained on the shelf region off northwest Africa where periodic upwelling occurs, it is clear that there was no active upwelling at the time of the experiment. BARTON *et al.* (1977) showed that periods of upwelling, lasting 5 to 10 days, were associated with strong northerly winds, and between these periods were intervals of 2 to 3 days when the winds were weak, from 230 to 315°, during which a strong pycnocline developed over the shelf and surface temperatures reached +18°C. The meteorological data for 'Discovery' Sta. 9529 are consistent with the latter observations. The ship drifted roughly northward (310 to 030°) probably with the tidal flow during the horizontal profiling at a rate between 10.7 m min<sup>-1</sup> at the start and 18.6 m min<sup>-1</sup> at the end of the experiment. The considerable heterogeneity in surface temperature (Fig. 4a), together with the observation of surface slicks of phytoplankton, also is consistent with patchiness resulting from a recent upwelling event. However, tidally generated internal waves may have had an effect, as HAURY *et al.* (1979) observed in the shallow waters of Massachusetts Bay. There they noted that the overturning and breaking of internal waves had a marked effect on the distribution of chlorophyll and zooplankton, with nutrients being mixed up from below. HUTHNANCE (1981) has reviewed the effects of breaking internal waves and notes that the consequent nutrient enrichment of the more superficial layers must greatly enhance the primary productivity of the region despite the absence of any major upwelling event.

When interpreting results from the temporal studies in one depth zone of the water column it is important to separate the effects of horizontal patchiness in the distributions of the phyto- and zooplankton from the vertical effects (STAR and MULLIN, 1981). A cross-correlation analysis, comparing the variation in numbers of each zooplankton taxon with the near-surface temperature, showed no significant correlations at the  $P = 10\%$  level. Thus, it is concluded that the effects of horizontal patchiness on the data are minimal and that the variability in zooplankton numbers is due mainly to vertical changes in the water column most probably caused by internal waves propagating along the pycnocline.

It is clear from the present results that many of the zooplankton taxa showed very precise depth distributions with respect to the steep pycno/thermocline, and in particular with reference to the chlorophyll *a* maximum that lay therein. However, SMITH *et al.* (1981) have drawn attention to the difficulties inherent in reaching meaningful conclusions as to which might be the controlling factor especially when the variables are so obviously interrelated. ORTNER *et al.* (1980) discussed this point further and observed that when the chlorophyll *a* maximum was erased by mixing, the associated zooplankton maxima persisted. Thus the animals either simply were responding to the existing physical gradient, or were exhibiting an habitual response, possibly conditioned by prior biological interactions. BOYD (1973) considered that the former response accounted for the observed zooplankton distributions in the pycnocline, despite the presence therein of a chlorophyll *a* maximum. Indeed, HARDER (1968) has shown that animals aggregate around density discontinuities in the absence of other stimuli, although different taxa reacted differently to the same discontinuity.

ORTNER *et al.* (1980) considered also the difficulty in interpreting unambiguously the co-distributions of carnivorous species in situations where the herbivores had vertical distributions apparently related to a pycno- or thermocline, since the carnivores themselves might be responding either to the physical gradient or to the distribution of their prey. Thus, the two groups of zooplankton found in the pycnocline during the present experiments (Fig. 10) do not necessarily indicate trophic relations between the constituent taxa, but again could result from differing responses to the physical environment. It is also possible that the various taxa studied undergo diel vertical migrations such that, at the time of the experiment, the observed distribution of predators bears little or no trophic relation to their prey. We have no data on such migrations at this station, but they are considered unlikely in such shallow water depths, especially as such precise depth distributions were observed. Certainly the concentration of the siphonophore, *M. atlantica*, in the region of the chlorophyll *a* maximum is not a direct response to the maximum *per se* since these animals are carnivores. However, their feeding strategy probably leads to an aggregation in regions of high prey density, and they have the potential to devastate the copepod population in their vicinity (PURCELL, 1982).

It is more difficult to make ecological sense of observed distribution patterns of trophically related taxa when this relation is indirect, as may be the case for the appendicularians and *Oncaea* spp. The presence of peak numbers of appendicularians in the chlorophyll *a* maximum is of interest since these animals feed mainly on nanoplankton, while larger particles ( $>8\ \mu\text{m}$ ) are retained on the incurrent filters of their houses (ALLDREDGE, 1977). Thus the large number of diatoms there present would be expected rapidly to clog these filters. An aggregation of appendicularians in more superficial waters, where indeed high numbers were found, might allow for more efficient feeding since there the phytoplankton population was predominantly small flagellates (Table 1). Such an avoidance of larger particles was found by PAFFENHÖFER (1983) for *Oikopleura* sp., but nonetheless the present results are similar to those of BINET (1976).

It is not certain whether any of the taxa considered here are predators on appendicularians, although *M. atlantica* has been reported to feed on them very occasionally (PURCELL, 1982). However, ALLDREDGE (1972) has noted that discarded houses may be a major source of food in the pelagic food web. Animals, such as *Oncaea* spp., feed on these houses, thereby enabling them to obtain a greater size range of particles than they could capture by filter feeding. Indeed, the mouthparts of *Oncaea* spp. are adapted for scraping surfaces and would be ineffective as a filter-feeding apparatus. The present results show that the peaks of abundance of appendicularians and *Oncaea* spp. do not coincide (Fig. 10).

However, since discarded houses most probably will sink, then any *Oncaea* feeding on them will be dispersed downwards into the bottom mixed layer. On reaching the sea bed the copepods could then swim back up to the base of the pycno/thermocline ready to repeat the cycle. The observed distribution of *Oncaea* (Fig. 2) is consistent with this hypothesis.

The copepod *C. clausi* displays a marked abundance peak fractionally above the chlorophyll *a* maximum, with a rapid decrease in numbers on either side (Fig. 8g). If the adults are visual predators, as for other species of *Corycaeus* (GOPHEN and HARRIS, 1981), then this strong association is presumably indirect and not indicative of any trophic relation. However, little is known of the developmental biology of *Corycaeus* species and it is possible that juveniles, which comprised the bulk of the abundance peak, are more omnivorous in their behaviour than the adults. Ontogenetic changes in feeding strategy from herbivorous juveniles to predatory adult have been reported from some *Oithona* species (PAFFENHÖFER, 1983), although LAMPITT and GAMBLE (1982) found the adults of *O. nana* to be omnivorous.

Another taxon whose depth distribution does not appear to relate directly to its potential food source is the larval cephalochordate, *B. senegalense*. These animals feed mainly on diatoms (GOSSELCK and KUEHNER, 1973), but their depth distribution (Fig. 2) lies below the chlorophyll *a* maximum. However, there is liable to be a considerable sinking out of diatoms from this maximum, as is indicated by the relatively high concentrations of chlorophyll *a* in the bottom mixed layer, that is sufficient to sustain the population. WEBB (1969) observed that low temperatures tended to trigger an upward swimming response in these animals, followed by passive sinking during which time they fed. It would appear, from the present results, that the discontinuity at the base of the pycno/thermocline is acting as a cue for the cessation of the swimming period. The avoidance of more superficial layers probably is advantageous in upwelling regions as the prevailing circulation might carry the animals offshore, whereas these animals eventually burrow into the bottom sediment in shallow waters.

Several previous authors (VENRICK *et al.*, 1973; LONGHURST and HERMAN, 1981) have concluded that differential grazing pressure must play a role in shaping the chlorophyll profile. However, CULLEN and EPPLEY (1981) and CULLEN (1982) believed that most chlorophyll profiles could be explained purely on the basis of an interaction between hydrography and the biology of the phytoplankton themselves. These latter authors drew attention to the important regional differences in the form of the deep chlorophyll maximum and cautioned against extrapolating conclusions from one region, such as the oligotrophic open ocean, to another, such as eutrophic shelf sea. Also, they noted that chlorophyll *a* fluorescence is a poor measure of biomass and gives no information on the size distribution of the phytoplankton population which probably changes with depth, as in the present results, and region. LONGHURST and HERMAN (1981) nevertheless expressed a confidence that grazing pressure had never been shown to be concentrated precisely at the chlorophyll *a* maximum. We feel that the present results indicate such a correspondence in the case of the major herbivores, e.g., appendicularians, calanoids, and *Oithona* spp. The possible reasons why other herbivores, such as the larval cephalochordates, occur below the chlorophyll maximum have been discussed above.

LONGHURST and HERMAN (1981) suggested that herbivores aggregated at a layer in the water column in response to another cue which covaried with the sub-surface chlorophyll maximum. HERMAN *et al.* (1981) suggest that this cue, by some unresolved biological or chemical means, is the primary productivity maximum that, in many cases and particularly in the open ocean, is predicted, from models, to lie above the chlorophyll maximum and in the top mixed layer. However, the concept of a productivity maximum in the top mixed layer

may be just a theoretical one for such a maximum can persist only if the specific growth rate of the phytoplankton exceeds the rate of eddy diffusive mixing, for otherwise the cells may become dispersed throughout this layer. DENMAN and GARGETT (1983) have begun to address this problem, and conclude that in the surface layers the time for cycling by turbulence, for vertical displacements of *ca.* 10 m, varies between 30 min and hundreds of hours, depending on wind speed, dissipation rate, and stratification. Further, diel changes in the shape of the chlorophyll maximum caused by vertical migration of part of the phytoplankton population to shallower depths by day (CULLEN *et al.*, 1983), and depth changes in the whole maximum caused by the passage of internal waves (KAMYKOWSK, 1976) will affect greatly the potential rate of primary production. Thus there are inherent problems in comparing observed vertical distributions of zooplankton with model-generated primary productivity curves, especially when the sensitivity of such models to predict these curves remains unresolved.

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