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Vertical distribution and partitioning of organic carbon in mixed, frontal and stratified waters of the English Channel

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ABSTRACT: The vertical distribution of plankton is described for 3 stations representative of stratified, frontal and vertically mixed regions of the western English Channel in summer. All components of organic carbon, representing dissolved and particulate organic carbon, phytoplankton, bacteria, protozoans, micro- and meso-zooplankton, were estimated independently. Major differences were found in the abundance and species composition of the phytoplankton, and in the relative proportions of different groups of heterotrophs. In the frontal region the phytoplankton (26.5 g C m^{-2}) was composed of an essentially monospecific, surface population of the dinoflagellate *Gyrodinium aureolum;* by contrast, under well-stratified conditions small naked flagellates (0.42 g C m^{-2}) forming a sub-surface chlorophyll maximum were dominant, and the tidally mixed waters were characterised by diatoms (7.91 g C m^{-2}). At each station the estimated standing stock of heterotrophs was between 2.3 and 3.2 g C m^{-2}, 10 to 30 % of which consisted of bacteria. Hence the phytoplankton was the dominant compartment in the frontal and mixed regions, whereas the zooplankton biomass considerably exceeded that of the phytoplankton in the well-stratified water. The ecological implications of these carbon distribution patterns are discussed.

INTRODUCTION

In the temperate shelf waters around the British Isles plankton distributions are determined directly by water movement (Southward, 1962; Fraser, 1965) and indirectly by the effects of tidal mixing and seasonal stratification (Pingree et al., 1978) on species succession and survival (see references in Holligan, 1981). Since the pioneering work of Lohmann (1908), Harvey (1950) and Krey (1956), no comprehensive study has been made of the structure of plankton communities in offshore waters. In this paper a quantitative comparison of the partitioning of organic carbon at stations in stratified, frontal and mixed waters is presented. Contemporary measurements of photosynthesis and respiration are described by Holligan et al. (1984). The observations were made in midsummer when the influence of the thermocline is most pronounced and when the distribution of carbon in the planktonic ecosystem is most likely to approach a steady-state condition.

Biomass data in units compatible with measured rates of production (e.g. autotrophic and heterotrophic carbon assimilation) are essential for calculating the specific growth rates of organisms or the potential for energy transfer from one trophic level to another. Despite the considerable effort given to numerical models of marine ecosystems (Platt et al., 1981) there is still little information available on the relative abundance of organisms at each trophic level especially for different hydrographic environments. Field studies have generally been confined to a part of the food-web (e.g. Smetacek, 1981; Beers et al., 1982), and the most complete set of published data is for the carbon biomass of bacteria, phytoplankton, ciliates and herbivorous and carnivorous zooplankton in the CEPEX enclosures (Grice et al., 1980).

In the present study, as in the CEPEX project, we have combined the work of a group of individuals using a variety of methods for estimating the numerical abundance and determining the carbon biomass of all the major taxonomic or size categories within the

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plankton. This approach, first applied over 70 y ago (Lohmann, 1908), provides the type of biological information required to elucidate trophic interactions within heterogeneous plankton communities. Indirect methods such as electronic particle counters (e.g. Sheldon et al., 1972; Herman and Mitchell, 1981) and biochemical measurements to distinguish living and non-living material (Hobbie et al., 1972), although less time-consuming, do not offer this important advantage.

SAMPLING AND ANALYTICAL METHODS

The positions of the sampling stations in stratified (E5), frontal (F) and mixed (M) waters are shown in Fig. 1 in relation to the surface temperature distribution for 0913 h GMT, 29 July 1981. The water depths were 120, 96 and 76 m respectively. Stations E5 and M were located in mid-channel, > 35 km from the nearest land, to either side of the mean predicted position (Pingree et al., 1978) of the Ushant tidal front. The site of Station F was selected during the cruise in a region with a relatively shallow (< 20 m) thermocline and with high surface chlorophyll *a* levels, features that are characteristic of frontal conditions. The periods of observations were: 1200 h, 23 July to 1730 h, 25 July at M; 0500 h, 26 July to 1300 h, 28 July at E5; and 0500 h, 30 July to 0830 2 h, August at F. At each station vertical pump profiles were made every 3 h for at least one 24 h period and at less frequent intervals for the remainder of the time. The position of each profile was corrected for tidal displacement, using information from Admiralty tidal charts, so that the horizontal distributions of hydrographic properties could be plotted.

Vertical profiles of hydrographic and biological properties were obtained by raising the intake hose (5 cm internal diameter) of the submersible pump (Flygt Pumps Ltd., Model B2051, giving an average flow rate of 160 l min^{-1}) from 60 m to 2 m in steps of 2 m min^{-1}. Temperature measurements were made with a platinum resistance thermometer (Rosemount Engineering Co. Ltd., Model E12767) positioned in the main outflow. The water was subsampled for a Turner Model III fluorometer, fitted with filters appropriate for detecting chlorophyll *a* fluorescence (Holm-Hansen et al., 1965), and a nutrient autoanalyser (Chemlab Instruments Mk III multi-channel colorimeter) giving continuous records of nitrate (Strickland and Parsons, 1972), as well as nitrite, ammonium and silicate. The remaining water was filtered through 200 µm and 80 µm nets in series to collect the zooplankton. The nets were suspended in a reservoir of sea water, and a valve system enabled samples to be taken as a continuous series through the water column. Each size fraction was subsampled by a stempel pipette for determinations of particulate carbon and nitrogen, the rest being preserved in 5 % neutral formalin for counting. Additional zooplankton samples were taken with paired 200 µm WP-2 nets (UNESCO, 1968), both for the whole water column and for the upper 60 m, to compare with the pump system.

In the laboratory, water from the outflow of the fluorometer was collected in 20 l carboys to give a series of integrated samples corresponding to successive depth intervals in the water column. After thorough stirring these were each sampled for analyses of particulate and dissolved organic material, and for plankton and particle counts.

Total particle volume and particle size distribution over a diameter range 2 to 100 µm were measured for fresh, untreated water samples with a model TA II Coulter Counter, using 100 and 400 µm orifices. Each analysis was performed in triplicate.

Chlorophyll *a* and phaeopigments were estimated by filtering 5 to 200 ml of sea water on to 0.45 µm membrane filters and measuring the fluorescence of 90 % acetone extracts before and after the addition of two drops of 10 % HCl (Lorenzen, 1966). The fluorometer was calibrated each day with a solution of pure chlorophyll *a* (Sigma Chemical Co.), the concentration of which was determined spectrophotometrically at the start and end of the cruise (Lorenzen, 1967).

Samples for particulate organic carbon (POC) and nitrogen (PON), and dissolved organic carbon measurements were obtained by screening sea water through a 200 µm mesh net to remove the larger zooplankton and then filtering 100 to 1000 ml, depending on the load of particulate material, through pre-ashed (400 °C for 6 h), 25 mm Whatman GF/C glass fibre filters under a vacuum of < 12 cm Hg. The filters were stored at −20 °C, and then oven dried at 55 °C prior to analysis with a Carlo Erba elemental analyser (Model 1106) calibrated with cyclohexanone or 1:5 diphenylcarbazide standards. Analyses of a series of duplicate samples gave standard deviations of ± 10 %, ± 22 %, and ± 18 % for the estimates of POC, PON and POC/PON from single determinations. Triplicate 8 ml samples of the filtrate were transferred to precombusted 15 ml glass vials, and 75 µl 1N HCl, made up in carbon-free distilled water prepared by ultra-violet irradiation, was added to dispel inorganic carbon as carbon dioxide. The vials were then sealed with Teflon-lined caps and stored at −20 °C. Dissolved organic carbon in the filtrates was measured by the ultra-violet photo-oxidation method of Collins and Williams (1977), as modified by Gershey et al. (1979). Potassium oxalate (Analar grade), dissolved in carbon-free distilled water, was used as a standard.

Water samples were preserved with Lugols iodine solution (Holligan and Harbour, 1977) and 0.5 % neu-

tralised formalin for counts of phytoplankton and protozoans, and in 2.5 % glutaraldehyde for counts of bacteria. The latter were stored at 5 °C in pre-sterilised scintillation vials.

Light measurements were made with 2 Underwater Quantum sensors 400 to 700 nm (Crump Scientific Products Ltd., Model 552), one fixed to the superstructure of the ship to give surface irradiance and the other lowered into the water column to 40 m to record downwelling irradiance.

SPECIES IDENTIFICATION AND CARBON BIOMASS ESTIMATES

Phytoplankton and protozoans

Cell counts were made on settled 10 to 100 ml samples (depending on the chlorophyll *a* concentration) with an inverted microscope using × 187 and × 750 magnifications. Carbon estimates for each species were derived from volume determinations (Kovala and Larrance, 1966) and the cell volume/carbon relationships given by Eppley et al. (1970) (see also UNESCO, 1974 – footnote on p. 11). The only exceptions to this procedure were that, for *Noctiluca scintillans* and for all ciliates, the carbon conversion factors given respectively by Dewey (1976) and by Beers et al. (1975) were applied.

To assess counting errors, and also the range in variation in cell volume for the major species, 5 replicates from the chlorophyll maximum layer at each of the 3 stations were counted and volumes for at least 40 cells of each of the dominant species determined (Table 1b). The replicate counts gave maximum standard deviations of ± 12 %, ± 3.4 % and ± 4.2 % for cell numbers of flagellates, *Rhizosolenia stolterfothii* and *Gyrodinium aureolum* respectively.

Bacteria

Bacterial numbers were estimated using an acridine orange epifluorescence direct counting technique after collection on 0.2 µm Nuclepore filters (Hobbie et al., 1977). The relative frequency and mean cell volumes of up to six size/shape categories of bacteria were obtained from enlarged photographs (Fuhrman, 1981). Bacterial carbon biomass was then calculated using the weighted mean cell volume estimates, a specific gravity of 1.1 g cm^{-3} (Doetsch and Cook, 1973) and a carbon to wet biomass ratio of 0.1 (Straškrabová and Sorokin, 1972).

Replicate bacterial counts and the relative frequencies of the main cell types gave maximum standard deviations between ± 4.5 % and ± 6.7 % whilst standard errors of biovolume estimates for each cell type ranged from ± 3.7 % to ± 9.3 % of the mean values.

Micro and mesozooplankton

Zooplankton species counts were made on subsamples examined under a stereomicroscope, and identifications were confirmed under higher magnification using an inverted microscope. The fraction retained by the 80 µm mesh and passing through 200 µm (80 to 200 µm) was used to obtain estimates of microzooplankton (copepod nauplii and early copepodites, invertebrate larvae).

Subsamples from this size fraction were typically about 1/100, giving counts of at least 100 individuals for dominant groups such as copepod nauplii. Mesozooplankton retained on a 200 µm mesh were estimated from a ¼ to ⅛ subsample, with the total sample being examined for some rarer groups. Counts of dominant copepods on replicate net samples gave a standard deviation of about ± 25 % of the mean.

Zooplankton carbon and nitrogen were estimated directly by filtering between ¼ and ⅛ of the fresh zooplankton samples onto pre-ashed GF/C pads. These aliquots were stored at −20 °C within 10 min of collection, and subsequently dried at 60 °C for 24 h before weighing on a Cahn Electrobalance. The zooplankton and filter were then ground in an agate ball mill and subsampled for analysis on the Carlo Erba elemental analyser (see previous section).

RESULTS

Summary of observations

Hydrographic observations

At the end of July 1981, the surface temperature structure in the western English Channel (Fig. 1) was characterised by anomalously warm water in the central region, and relatively weak horizontal gradients across the frontal boundary between cool mixed waters off the coast of France and the warmer stratified water to the north and west. The area of high surface temperatures (up to 18.2 °C on 28–29 July) corresponded to the distribution of a surface bloom of the dinoflagellate *Gyrodinium aureolum* which had developed to the stratified side of the frontal boundary during the preceding 4 wk (Holligan et al., 1983). Surface temperatures in the stratified water at E5, at the western edge of the bloom, were 16 to 17 °C and in the mixed water ranged from 13.0 °C north of Ushant to ~14.6 °C

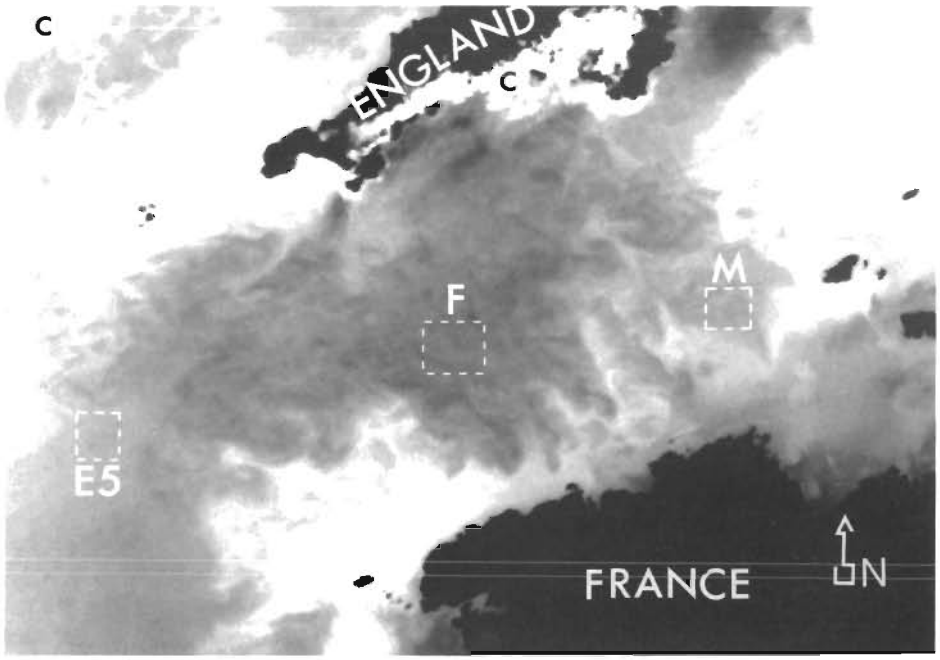

Fig. 1. Infra-red satellite (NOAA–7) image of western English Channel for 29 July 1981 (1353 h GMT), showing sampling regions in stratified (E5), frontal (F) and mixed (M) waters. Light areas off N. W. France, around the Scilly Isles and to the northwest of Station M indicate relatively cool surface water. C = clouds

around Station M. The variations in temperature of the mixed water are clearly shown in Fig. 1, and the position of the tidal front about half-way between Stations F and M could only be identified with certainty on the satellite image from the ship measurements of vertical temperature gradients.

At E5 the thermocline was typically 20 to 25 m deep, with a temperature change of 5 to 6 C°, and characterised by a subsurface chlorophyll maximum and a marked nitrate gradient from < 0.1 µM in the surface layer to ~ 4 µM in the bottom layer (Fig. 6). By contrast, in the mixed water at Station M the increase in temperature above 60 m was always < 0.3 C° and generally about 0.1 C°; profiles of chlorophyll fluorescence were uniform with depth, although measured concentrations of chlorophyll *a* usually decreased towards the surface, and nitrate levels were about 1 µM throughout the water column. The frontal region (F) showed an intermediate temperature distribution, with the main thermocline at about 16 m and a surface to bottom temperature difference of 3 to 5 C°, and high surface chlorophyll levels which extended into the thermocline layer on some profiles. The nitrate concentrations below the thermocline were remarkably low (< 0.3 µM compared to expected values of 2 to 3 µM for this degree of stratification in August), apparently due to assimilation by the dinoflagellate population (Holligan et al., 1984).

Offshore surface salinities increased from about 34.6 ‰ in the east (Station M) to 35.1 ‰ in the west (E5). Salinity differences between 60 m and the surface were < 0.02 ‰ at M and < 0.05 ‰ at F and E5, so that temperature changes were dominant in determining vertical density gradients.

Extinction coefficients for visible light (400 to 700 nm) in the surface layers were related to chlorophyll concentrations and ranged between 0.11 and 0.20 m^{-1} at E5, 0.44 to 0.85 m^{-1} at F, and 0.17 and 0.20 m^{-1} at M.

Spatial variability in the abundance of particulate material and plankton

Data on the standing stocks of chlorophyll *a* and particulate organic carbon (POC) in the upper 30 m of the water column for the 3 stations are shown in Fig. 2. Values for E5 and F include both the thermocline and surface layers (i.e. the effective euphotic zone) and show wide variations in phytoplankton abundance. Regression analyses, using the geometric mean method of Ricker (1973), yield POC to chlorophyll ratios of 81 and 74 respectively, although for both stations the correlation coefficients were relatively low. The data points for the mixed water are closely grouped and indicate no consistent relationship between the two parameters.

The variations in chlorophyll abundance show coherent patterns of horizontal distribution at each station (Fig. 3A) which are in good agreement with both the phytoplankton cell counts (e.g. Fig. 8B) and the satellite image of surface chlorophyll distribution on 29 July (Holligan et al., 1983). At the mixed water and frontal stations, where chlorophyll levels

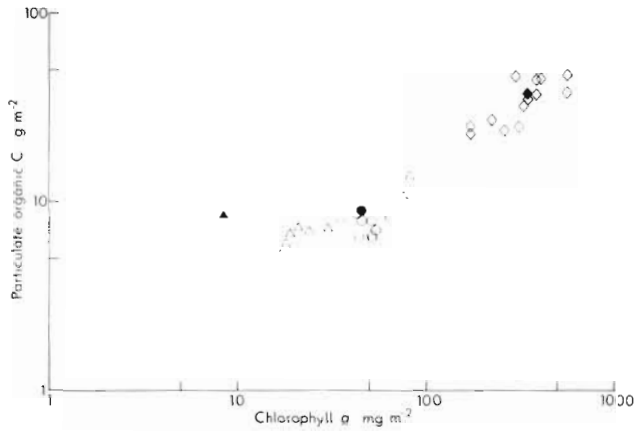

Fig. 2. Standing stocks of particulate organic carbon (<200 µm) and chlorophyll *a* in the upper 30 m of the water column, both plotted on log scales, at Stations E5 (△), F (◇) and M (○). Solid symbols: values obtained on reference profiles for which the detailed analyses of plankton samples were made. Geometric mean regression equations give for E5, POC = 0.0805 chl.*a* + 4.47 (r = 0.62, N = 18), and for F, POC = 0.0739 chl.*a* + 10.0 (r = 0.73, N = 14)

increased towards the north west, the dominant phytoplankton were, respectively, diatoms (mainly *Rhizosolenia stolterfothii*) and the dinoflagellate *Gyrodinium aureolum*. Station E5 exhibited a subsurface tongue of chlorophyll- and *Gyrodinium*-rich water extending between low chlorophyll regions to the southwest and northeast where the phytoplankton was composed mainly of small (< 10 µm diameter), naked flagellates.

Comparable data on zooplankton are presented in Fig. 3B for copepod nauplii in the surface 30 m, this group being chosen as an example of non-migratory organisms which feed mainly on phytoplankton. In the mixed water the distribution of nauplii was relatively uniform (variance to mean ratio 12.7), higher densities being found on the southern profiles. In the frontal region the mean densities differed by a factor of 6, giving a variance to mean ratio of 80.6, with the highest values towards the northeast. At Station E5, where the copepod nauplii were generally most abundant, the variance to mean ratio of 44.0 was intermediate. In no case was there any obvious relationship between the distribution of chlorophyll and nauplii.

Carbon to nitrogen ratios of particulate material

Measurements of POC and PON are summarised in Fig. 4. Geometric mean regression (Ricker, 1973) gives carbon to nitrogen ratios of 8.5 for the mixed water column, 8.1 for the frontal station and 7.7 (surface and thermocline layers) and 10.3 (bottom layer) for the stratified waters at E5. Each regression line yielded a positive POC intercept value, suggesting that some of the particulate carbon was not associated with nitrogen. The correlation coefficients were high for the samples from Station F, where phytoplankton formed the bulk of the particulate material, but relatively low at the other 2 stations. The increase in the carbon to nitrogen ratio for particulate material below the thermocline at E5 indicates some preferential removal of

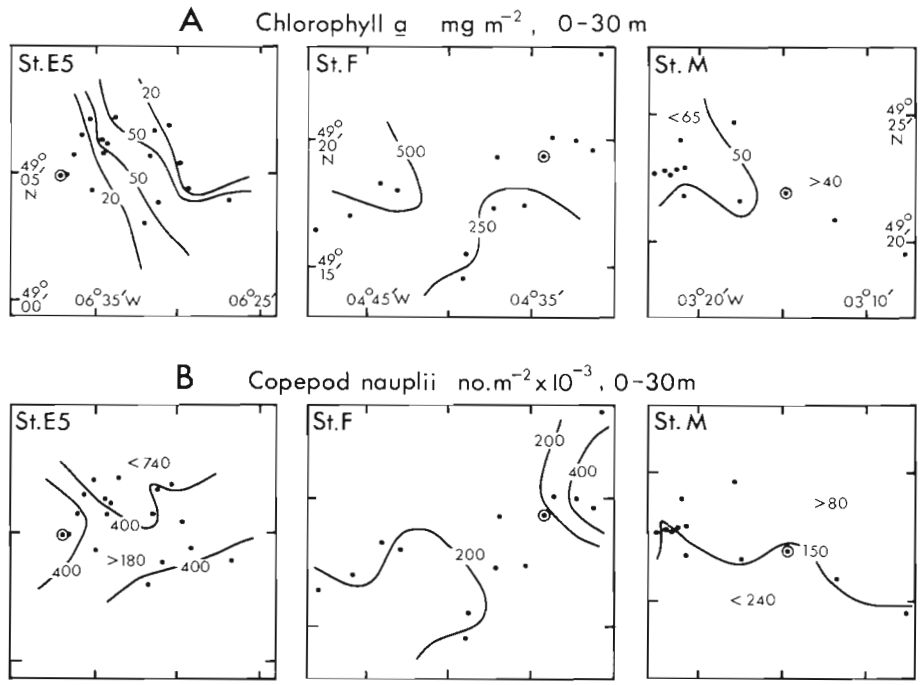

Fig. 3. Distributions of chlorophyll *a*, mg m^{-2} (A) and copepod nauplii, × 10^{-3} m^{-2} (B) in the upper 30 m of the water column at Stations E5, F and M. Dots show sampling positions, those enclosed by circles indicating reference profiles

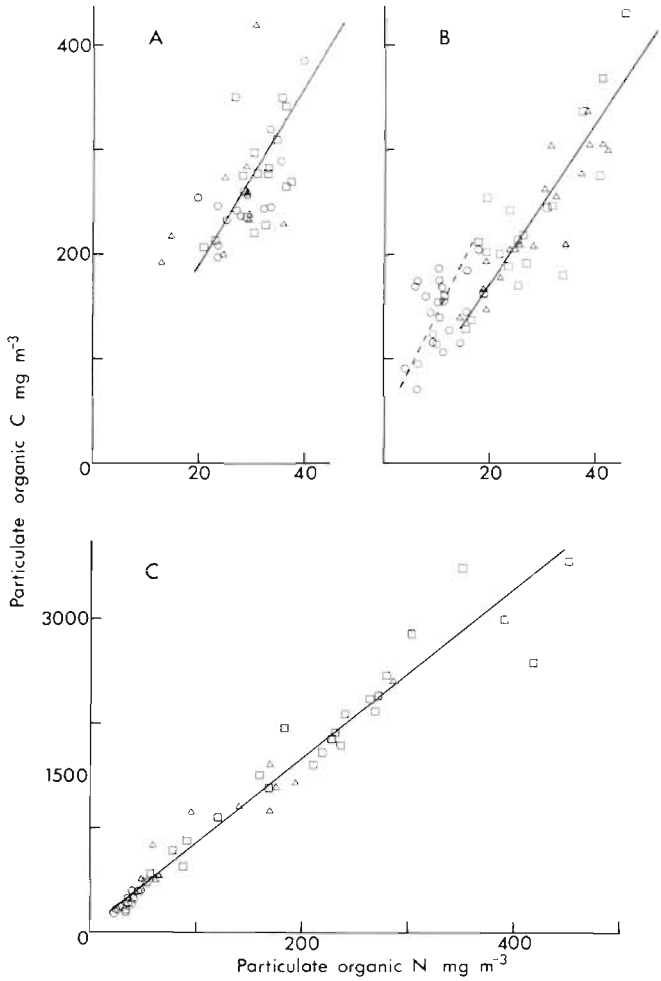

Fig. 4. Particulate organic C and N (<200 µm) analyses for (A). Station M (□, 2–20 m; △, 20–40 m; ○, 40–60 m); (B) Station E5 (□, 2–20 m; △, 20–30 m; ○, 30–60 m); (C) Station F (□, 2–10 m; △, 10–30 m; ○, 30–60 m). Regression equations are for M, all samples C = 8.51N + 19.61 (r = 0.57, N = 40); for E5, 2–20 m and 20–30 m samples C = 7.70N + 17.57 (r = 0.86, N = 39) and 30–60 m samples C = 10.31N + 40.87 (r = 0.51, N = 21); for F, all samples C = 8.12N + 47.38 (r = 0.98, N = 59)

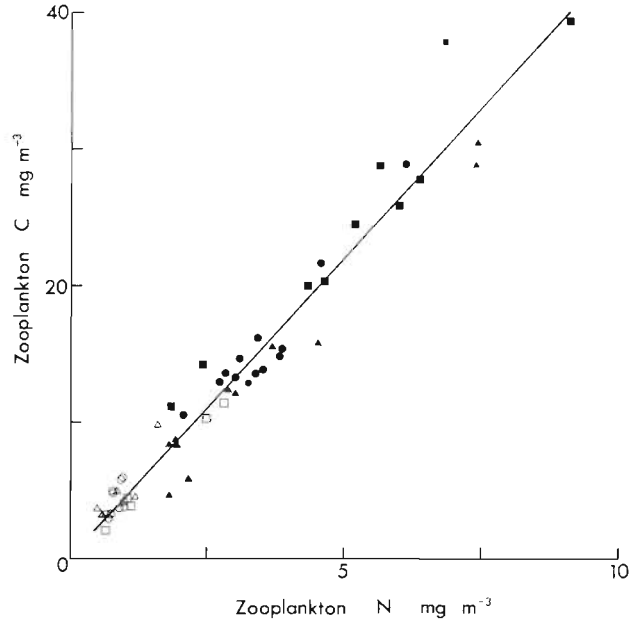

Fig. 5. Microzooplankton (80 to 200 µm, open symbols) and mesozooplankton (>200 µm, closed symbols) C and N analyses for Stations E5 (□), F (△) and M (○). The common regression equation is C = 4.40N + 0.103 (r = 0.98, N = 56)

nitrogen relative to carbon by recycling processes within the bottom water.

The micro- and mesozooplankton samples for all 3 stations showed a consistent carbon to nitrogen ratio of 4.4 (Fig. 5), almost half the value for the particulate materials available to the animals as food. This implies that for a wide range of grazing conditions, both in terms of the type and concentration of food and of herbivore species, the assimilation efficiency for nitrogen is about twice that for carbon. Furthermore, the good correlations between carbon and nitrogen for the plankton (Fig. 4C and 5) allow inferences to be made about the distribution of nitrogen from data on carbon alone.

Vertical distributions

A detailed comparison of the vertical distributions and relative abundance of the various components of the plankton was made for one reference profile (Fig. 3) at each of the 3 stations. The water was sampled over 5 intervals, each corresponding to a depth range of 12 m. At E5 the sampling was carried out in the chlorophyll-poor water to the west, where small flagellates dominated the phytoplankton, in order to make the comparison with the dinoflagellate and diatom populations at Stations F and M.

Hydrographic properties

The chlorophyll maximum at E5 was situated within the thermocline and associated with the nitrate gradient (Fig. 6). High concentrations of chlorophyll also extended to the base of the thermocline at Station F; the temperature inversions and related chlorophyll minima apparent on the profiles were probably caused by internal waves. In the mixed water slight variations in the vertical distributions of chlorophyll and nitrate were observed despite the absence of significant temperature (density) structure. The depth of the 1 % light level ranged from 36 m at E5, well below the thermocline and chlorophyll maximum, to < 10 m in the frontal region where *Gyrodinium aureolum* was abundant.

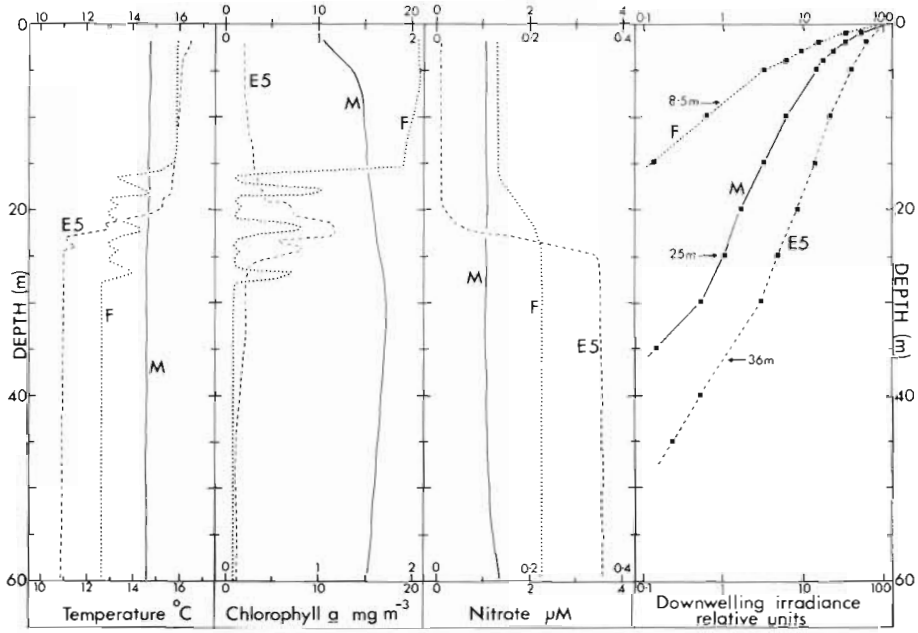

Fig. 6. Vertical distributions of temperature (°C), chlorophyll *a* (mg m^{-3}), nitrate (μM) and downwelling irradiance (relative to a maximum subsurface value of 100) in upper 60 m of the water column for the reference profiles at Stations E5 (dashed lines), F (dotted lines) and M (solid lines). The low scales for chlorophyll apply to E5 and M, and for nitrate to F and M. Arrows: depths of 1 % light levels

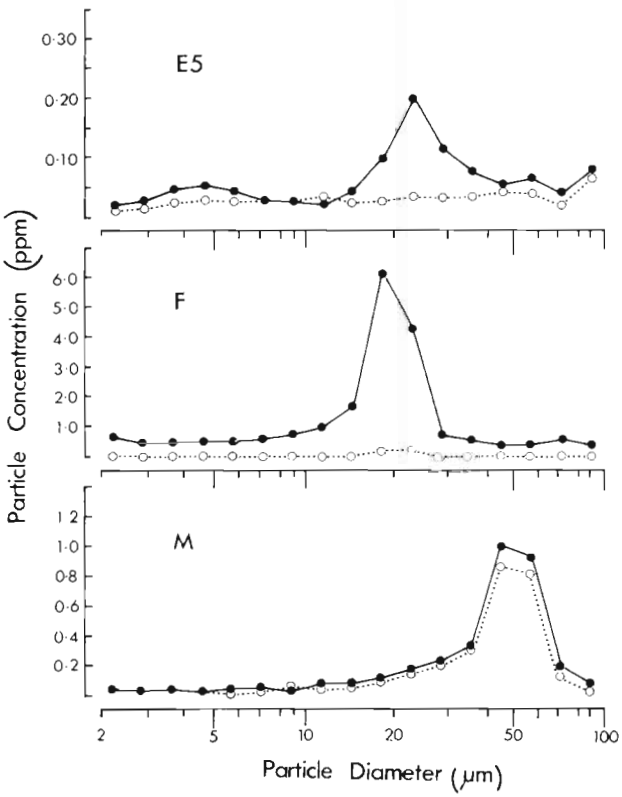

Fig. 7. Particle-size analyses, based on assumed spherical dimensions, for integral surface (0 to 24 m, solid lines) and sub-surface (24 to 60 m, dotted lines) water samples obtained for the reference profiles at Stations E5, F and M. Each data point represents the mean of 3 determinations

At the mixed water station intermediate conditions prevailed in terms of both light penetration and surface chlorophyll levels.

Particle concentrations were lowest throughout the water column at the stratified station, E5, being generally below 0.05 ppm across the entire size spectrum (Fig. 7). In the combined surface and thermocline layers there was a small peak in the range 3 to 6 μm, presumably representing the heterogeneous population of small flagellates, and a larger maximum between 20 and 25 μm apparently reflecting the presence of larger phytoplankton and protozooplankton in the thermocline (Table 1a). The particulate matter in the surface waters was relatively rich in carbon, 1 ppm being equivalent to 228.7 mg POC m^{-3} (1 μm^3 = 0.23 pg C). This may reflect the relatively high carbon per unit cell volume for the small flagellates, but is probably related to the large proportion of uncharacterised carbon or 'detritus' (Table 4).

In the surface 24 m at the frontal station F the total particle volume was over an order of magnitude higher than in surface stratified waters. The particle-size spectrum was dominated by the *Gyrodinium* population, with a biomass maximum of over 6 ppm in the 16 to 20 μm channel representing 2041 particles (cells) ml^{-1}. In addition, the background of small particles between 2 and 10 μm was considerably higher than at the other 2 stations, and the carbon content per unit volume of total particulate material was considerably lower than at E5, 1 ppm being equivalent to 79.2 mg POC m^{-3}. Below the thermocline total particle volume was over an order of magnitude lower, and was uniformly distributed with respect to particle size.

At the mixed water station, M the particle size distribution was similar throughout the water column and was dominated by a biomass maximum in the region of 50 μm, corresponding to the diatom population (Table

Table 1a. Vertical distribution of phytoplankton and protozoans (cells ml^{-1})

Taxa	Station	Depth (m) 2–12	12–24	24–36	36–48	48–60
Rhizosolenia stolterfothii	E5	–	–	–	–	–
	F	–	–	–	–	–
	M	40	42	47	46	51
Other diatom spp.*	E5	.09 (3)	.55 (10)	3.94 (10)	5.18 (12)	3.54 (13)
	F	3.3 (6)	.9 (3)	1.0 (2)	1.1 (6)	.7 (2)
	M	29.44 (24)	39.48 (22)	44.28 (25)	41.72 (24)	47.20 (24)
Gyrodinium aureolum	E5	.07	.08	.05	.03	.02
	F	2649	998	117	61	69
	M	–	.02	–	.01	.01
Other photosynthetic dinoflagellates*	E5	.72 (7)	4.49 (9)	.45 (5)	.15 (2)	.16 (3)
	F	12.4 (7)	6.2 (7)	1.0 (4)	1.0 (4)	.7 (3)
	M	17.46 (7)	.84 (5)	.52 (4)	.55 (6)	.34 (6)
Flagellates	E5	1848	1746	511	497	486
	F	3576	2160	535	475	421
	M	813	878	1175	969	1177
Non-photosynthetic dinoflagellates*	E5	1.02 (5)	.72 (6)	.27 (5)	.22 (4)	.59 (6)
	F	30.2 (10)	14.1 (9)	1.7 (7)	1.1 (5)	.9 (6)
	M	2.49 (12)	1.92 (9)	2.39 (12)	2.33 (10)	1.91 (10)
Ciliates	E5	1.31	6.61	.67	.41	.55
	F	3.3	2.1	.9	1.1	.6
	M	.79	1.27	1.22	1.36	.95

* Number of species found in 100 ml (M, E5) and 10 ml (F) samples are given in parentheses. The 2 groups of dinoflagellates were distinguished on a taxonomic basis

1a). The carbon content per unit volume of the particulate matter was comparable to that in the surface 24 m in the frontal region, 1 ppm representing 88.9 mg POC m^{-3}.

Phytoplankton and protozoans (Table 1)

At all 3 stations flagellates were numerically the most abundant phytoplankton although, in terms of carbon biomass, they were dominant only at E5. With the light microscope it was not possible to obtain useful taxonomic information about this group, or to determine whether individual cells contained chlorophyll. The count and biomass data for the flagellates include therefore unknown proportions of heterotrophic forms which, in a functional sense, should be assigned to the protozoans. In the surface layer at E5, the high phytoplankton carbon to chlorophyll ratio (Table 5) suggests that > 50 % of the flagellate carbon could have been attributable to non-photosynthetic species. The distribution of *Gyrodinium aureolum* corresponded to the extent of the surface bloom (~ 30,000 km^2) around Station F (see Holligan et al., 1983), with very low densities even in the thermocline at E5. The phytoplankton in the mixed water included many species of diatoms, in particular *Rhizosolenia stolterfothii* and *R. hebetata*. Among the protozoans, including the non-photosynthetic dinoflagellates, the most important species were the dinoflagellates *Noctiluca scintillans* (up to 8×10^6 cells m^{-2} in the *G. aureolum* bloom) and *Gyrodinium aff. spirale*, and the loricate tintinnid *Helicostomella* sp. which was most abundant in the thermocline at E5.

Vertical distribution patterns were consistent with the hydrographic data, with good correspondence between chlorophyll and phytoplankton counts (compare Fig. 6 and Table 1a) and with the main changes in species composition occurring at the level of the thermocline. Other notable features were the increase in diatoms below the thermocline at E5 (the benthic species *Paralia sulcata* was most abundant), the relatively high densities of flagellates below the thermocline at all 3 stations, and the increase in dinoflagellates in the upper 12 m at Station M contrasting with decreases in chlorophyll and diatom abundance in the same layer.

Measured cell volumes were very variable for the diatom *Rhizosolenia stolterfothii*, indicating that the population included both new and old lines of cells with respect to the formation of sexual auxospores. No

Table 1b. Volume and carbon data for dominant phytoplankton and protozoan species

Taxa (Station)	Depth range (m)	Mean volume* (μm^3)	Range in vol. (μm^3)	Mean carbon (pgC $cell^{-1}$)
Phytoplankton				
R. stolterfothii (M)	2–60	48400	11,259–100,800	1616
G. aureolum (F)	2–24	3847	3201–5121	589
	24–60	3511	2715–6177	540
Flagellates (E5)	2–12	44	2.4–398	8.8
	12–24	30	2.4–153	6.1
	24–60	20	2.4–102	4.2
Protozoa				
Gyrodinium sp. (F)	2–24	14900	14400–15100	2110
Noctiluca (F)	2–24	14,100,000	–	[38500]
Helicostomella sp. (E5)	12–24	13900	9500–25500	1100

* Dimensions of 40 to 100 cells of each taxon were measured

consistent variation in mean cell volume with depth was detected. By contrast, ranges in cell volume for *Gyrodinium aureolum* and *G.* aff. *spirale* were small, as expected for naked dinoflagellates undergoing asexual reproduction, although cells of *G. aureolum* below the thermocline were somewhat smaller than those above. The variations in size of the flagellates at E5 were probably related to changes in species composition within the water column. Mean volume appears to have been correlated with abundance so that the largest cells were found in the thermocline and the smallest in the bottom water.

Bacteria (Table 2)

The numbers of bacteria were highest at the frontal station, ranging from 1.7×10^6 cells ml^{-1} in the surface samples to $4.0–4.4 \times 10^5$ cells ml^{-1} at depths greater than 36 m where chlorophyll levels and phytoplankton densities were also low (Fig. 6, Table 1a). A similar distribution in relation to chlorophyll was observed at the stratified station where a maximum of 3.9×10^5 cells ml^{-1} was found in the thermocline. In the mixed waters bacterial numbers showed no obvious relationship with depth, varying from 5.5 to 6.8×10^5 cells ml^{-1}. The mean densities in the upper 60 m of the water column in general reflect differences in the phytoplankton standing stock at the 3 stations and ranged from 8.5×10^5 cells ml^{-1} at the frontal station (F), to 6.2×10^5 cells ml^{-1} at the mixed water station (M) and 3.0×10^5 cells ml^{-1} at the stratified station (E5).

The relative proportions of rods and cocci also differed with depth, rods predominating especially in the surface waters of the frontal station. These rods attained their largest size of 0.22 to 0.28 μm^3 at the depth where bacteria were most numerous, perhaps reflecting the availability of nutrients in the water column. Ferguson and Rublee (1976) have suggested that cocci are generally characteristic of low nutrient waters, and may represent dormant or 'starved' bacteria (also see Stevenson, 1978; Fuhrman et al., 1980).

Table 2. Numbers, proportion and cell volumes of bacterial rods* and cocci, as a function of depth (m)

Depth (m)	Bacteria ml^{-1} ($\times 10^5$) Relative proportion of rods*, (%) in brackets	Mean Volume Rods* (μm^3)	Cocci (μm^3)
	Station F		
2–12	16.5 (65)	0.219	0.110
12–24	11.5 (69)	0.130	0.050
24–36	6.5 (44)	0.107	0.046
36–48	4.0 (64)	0.105	0.041
48–60	4.4 (44)	0.101	0.038
	Station M		
2–12	6.5 (62)	0.183	0.052
12–24	5.9 (56)	0.134	0.046
24–36	6.5 (57)	0.131	0.057
36–48	6.8 (58)	0.221	0.045
48–60	5.5 (57)	0.091	0.045
	Station E5		
2–12	2.8 (60)	0.173	0.051
12–24	3.9 (58)	0.275	0.054
24–36	2.9 (61)	0.152	0.045
36–48	3.0 (56)	0.160	0.048
48–60	2.4 (47)	0.140	0.049

* Rods include cocco-bacilli

Zooplankton (Table 3)

Highest densities of microzooplankton at the stratified and frontal stations occurred in the upper 12 m, with copepod eggs and nauplii dominant at E5.

Table 3a. Vertical distribution of major microzooplankton groups (no m^{-3})

Taxa	Station	Depth (m) 2–12	12–24	24–36	36–48	48–60
Invertebrate larvae	E5	403	56	–	–	56
	F	1756	3342	1284	491	328
	M	672	1884	3766	2087	3206
Calanoid copepods	E5	7395	1009	56	–	112
	F	–	48	109	–	109
	M	1526	1578	814	611	612
Cyclopoid copepods	E5	3495	4314	1457	224	280
	F	3787	5901	1940	711	765
	M	489	1120	509	407	102
Copepod eggs and nauplii ($\times 10^{-3}$)	E5	39	25	6	2	3
	F	9	11	4	2	2
	M	7	6	4	4	4

At the mixed water station the vertical distribution of total microzooplankton was relatively uniform, although particular groups did show consistent trends with depth; copepod eggs and nauplii were dominant at densities similar to those observed at the frontal station.

The most significant feature of the vertical distributions of the major groups of mesozooplankton (> 200 µm) (Table 3b) was the influence of thermal stratification. At E5 the copepods were the most abundant group and showed maximum densities in the region of the thermocline (12 to 24 m) even in the daytime profiles, whereas invertebrate larvae, pteropods and euphausiids were all aggregated in the surface 12 m. In the frontal region numbers of copepods were relatively low throughout the water column, but amphipods were a more important component than at the other 2 stations. In the mixed water copepods dominated, with the highest densities in the surface layer and a relatively uniform distribution below 12 m. Also invertebrate larvae (predominantly gastropods, bivalves and echinoderms) were more numerous than in either the frontal or stratified waters.

Table 3b. Vertical distribution of major mesozooplankton groups (no m^{-3})

Taxa	Station	Depth (m) 2–12	12–24	24–36	36–48	48–60
Copepoda ($\times 10^{-2}$)	E5	49	92	41	6	5
	F	1	14	8	6	6
	M	48	33	31	36	33
Amphipoda	E5	–	–	–	3	1
	F	22	126	107	59	49
	M	12	–	20	20	61
Euphausiacea	E5	108	67	56	4	3
	F	7	111	84	24	15
	M	–	–	–	–	–
Pteropoda	E5	2366	134	22	11	311
	F	487	580	302	120	142
	M	37	20	31	10	71
Chaetognatha	E5	54	44	66	18	35
	F	48	32	36	66	57
	M	48	40	10	30	20

Data on the distributions of copepods (Table 3c) show that *Calanus helgolandicus* occurred at all 3 stations, but in low densities compared with the smaller calanoids *Paracalanus parvus* and *Pseudocalanus elongatus*. The first of these 2 species was concentrated in the region of the thermocline at E5 but was relatively evenly distributed with depth at the other 2 stations. *Pseudocalanus* similarly exhibited aggregations in the region of the thermocline in the well stratified water but was essentially absent from the surface layers at both Stations F and M. *Temora* was found in relatively small numbers only below 12 m at Stations F and M. By contrast, *Metridia lucens* was restricted to the well stratified waters where the population maximum was within and just below the thermocline. *Centropages* spp. were most important in the

Table 3c. Vertical distribution of dominant copepods (no m^{-3})

Taxa	Station	Depth (m) 2–12	12–24	24–36	36–48	48–60
Calanus helgolandicus	E5	134	12	90	99	99
	F	83	154	70	31	20
	M	–	51	61	41	61
Paracalanus parvus	E5	549	1533	–	12	13
	F	70	312	158	145	154
	M	598	591	672	293	310
Pseudocalanus elongatus	E5	3109	6131	2387	226	190
	F	8	–	193	218	287
	M	–	253	550	878	931
Temora longicornis	E5	–	–	–	–	–
	F	8	110	146	116	109
	M	–	61	81	122	61
Metridia lucens	E5	–	403	583	109	111
	F	–	–	–	–	–
	M	–	–	–	–	–
Centropages spp.	E5	27	–	–	6	–
	F	16	22	6	1	8
	M	500	305	254	295	214
Acartia spp.	E5	–	–	–	–	–
	F	31	82	23	4	3
	M	3542	1730	1415	1751	1588
Oithona spp.	E5	968	1098	1098	160	92
	F	705	665	122	26	42
	M	134	265	112	183	92

mixed water (predominantly *C. hamatus*) with the highest numbers in the surface 12 m. A similar pattern was observed for *Acartia*. *Oithona* spp. (predominantly *O. plumifera*) were most abundant in the surface layers at stations E5 and F, and the only group to show highest densities in the chlorophyll-rich frontal water were the cyclopoids including *Corycaeus* and *Oncaea*.

Partitioning of organic carbon

Evaluation of carbon determinations

Although the accuracy of direct measurements of carbon (DOC, POC, micro- and mesozooplankton) is difficult to specify in terms of the overall precision of the analytical and sampling methods, the results are internally consistent in terms of independent checks (e.g. POC versus TPV, carbon *versus* counts for zooplankton) and of trends relative to physical mixing processes (e.g. uniformity in tidally mixed water at Station M and below the thermocline at Stations F and E5) and to expected associations between parameters (e.g. POC and chlorophyll). For the surface (2 to 12 m) layers there is some uncertainty about the relatively high POC values at E5 and M since the corresponding increases in TPV were not proportional (other profiles also showed this feature at these 2 stations), and also about DOC measurements at F due to possible damage to the *Gyrodinium aureolum* cells during filtration.

Carbon values derived from microscope counts are more difficult to evaluate, but the patterns of vertical distribution are again consistent with other parameters. Good reproducibility of the microscope counts indicates that the main errors are likely to occur in the conversion of cell volume to carbon. However, some assessment of these is only possible for the phytoplankton. For Station F a comparison of the microscope data (Table 1) which yield a mean volume in the upper 24 m for *Gyrodinium aureolum* equivalent to 7 ppm and the particle counter results (Fig. 7) indicates that the former underestimate the cell volume of *G. aureolum* (this could occur as a result of cell shrinkage during preservation). On the other hand, the relationship between cell number and POC (Fig. 8) gives a carbon value of 345 pg cell^{-1} compared to 589 pg cell^{-1} (Table 1b) estimated from the microscope measurements. Although any correlation between POC and cell counts will underestimate cell carbon due to bias introduced by increasing properties of non-phytoplankton carbon at lower cell densities, these conclusions do appear contradictory. The diatom population at Station M gave good agreement between the particle size spectrum and the measured values of cell volume but, in this instance, phytoplankton carbon

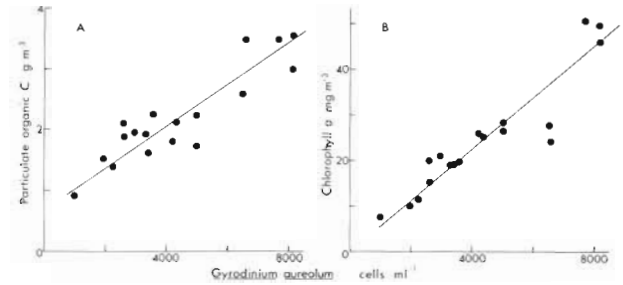

Fig. 8. Comparison of *Gyrodinium aureolum* cell counts with estimates of particulate organic C (A) and chlorophyll *a* (B) at Station F. Corresponding regression equations are C (mg m^{-3}) = 0.345 cells (ml^{-1}) + 682 (r = 0.90, N = 18); and chl.*a* (mg m^{-3}) = 0.00573 cells (ml^{-1}) − 0.243 (r = 0.93, N = 18)

cannot be compared directly with POC due to higher proportions of non-phytoplankton carbon.

Another type of variation to emerge from the analyses of particulate material was apparent diel changes in POC to chlorophyll ratios at the mixed and frontal stations (Fig. 9). Although the curves are based on

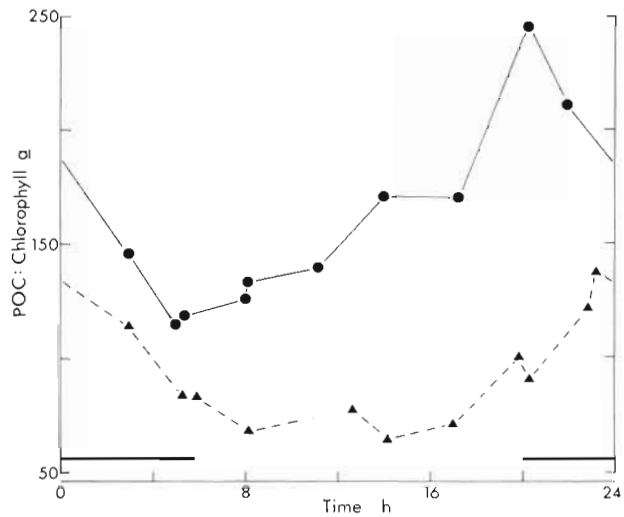

Fig. 9. Diel changes in particulate organic carbon to chlorophyll *a* ratios at Station F, 2 to 12 m (solid line) and Station M, 2 to 20 m (dashed line). Bars: dark period between sunset and sunrise

relatively few data points, the increase in the carbon to chlorophyll ratio during the daylight period when there is net photosynthetic production suggests that they are real. However, precise interpretation is difficult without information on changes in either POC or chlorophyll alone, especially for Station M where more than half the POC appears to be in the form of detritus (Table 4) and there is no correlation between POC and chlorophyll (Fig. 2). In the dinoflagellate bloom the good correlations between POC or chlorophyll *a* and cell counts (Fig. 8B) suggest that variations in the ratio

of the 2 parameters were due to diel changes in the composition of the dinoflagellate cells.

These difficulties in estimating the carbon content of planktonic organisms < 200 µm in diameter mean that the determination of detrital carbon by difference is subject to several sources of considerable potential error. Also, due to various statistical problems in comparing individual carbon (or chlorophyll) values (Banse, 1977), the differences in ratios of carbon in the various compartments can probably be considered significant only if they vary by an order of magnitude or more, or if they change consistently with the known distributions of organisms and hydrographic properties.

Comparison between stations (Table 4)

In the well stratified water at E5 chlorophyll concentrations exceeded 0.5 mg m^{-3} only within the thermocline at a depth of 19 to 25 m (Fig. 2). This layer was sampled mainly in the 12 to 24 m fraction and, in addition to the peak in phytoplankton carbon, gave maxima for bacteria and protozooplankton carbon as well as dissolved organic carbon (DOC). The micro- and mesozooplankton, on the other hand, were abundant throughout the upper 24 m. Notable features of the surface water were the high values for particulate organic carbon (POC) and total particle volume (TPV), apparently due to the presence of a large amount of

Table 4. Vertical distribution of organic carbon (mg m^{-3}), total particle volume (ppm) and chlorophyll (mg m^{-3}) at E5, F and M

Profile	Depth (m) 2–12	12–24	24–36	36–48	48–60
E5 (Profile 30, 0900 h)					
Dissolved organic carbon (DOC)	1367	1520	1117	1270	1280
Particulate organic carbon (POC)	404	209	190	143	228
Phytoplankton	17.7	17.2	4.2	4.0	4.2
Bacteria	3.8	7.9	3.5	3.6	2.5
Protozoa	1.8	8.0	0.9	0.5	0.9
Microzooplankton	13.7	10.1	2.1	0.2	3.9
Mesozooplankton	29.0	27.9	20.2	14.0	11.2
'Detritus'*	369	166	179	134	216
Chlorophyll *a*	0.17	0.39	0.16	0.14	0.12
Phaeopigment	0.05	0.11	0.04	0.07	0.06
Total particle volume (TPV)	1.44	1.25	0.92	0.59	0.61
F (Profile 47, 1530 h)					
Dissolved organic carbon	1703	1340	1250	1090	1133
Particulate organic carbon (POC)	2096	834	223	206	220
Phytoplankton	1604	604	79	40	42
Bacteria	35.2	13.4	5.4	3.7	3.2
Protozoa	57.9	25.0	3.4	4.1	3.0
Microzooplankton	5.5	9.9	5.0	3.3	3.8
Mesozooplankton	5.8	15.9	8.5	8.1	8.8
'Detritus'*	394	182	130	155	168
Chlorophyll *a*	19.94	7.62	1.23	0.64	0.58
Phaeopigment	0.34	1.80	0.08	0.20	0.29
Total particle volume (TPV)	25.56	11.41	1.37	1.50	1.33
M (Profile 13, 1230 h)					
Dissolved organic carbon (DOC)	1630	1570	1960	1410	1870
Particulate organic carbon (POC)	350	269	245	216	263
Phytoplankton	76	85	95	92	102
Bacteria	10.3	7.1	7.2	10.9	4.6
Protozoa	5.5	6.7	7.4	7.6	4.9
Microzooplankton	4.0	3.9	3.2	3.2	3.9
Mesozooplankton	16.3	15.5	13.0	13.9	14.9
'Detritus'*	255	166	132	102	148
Chlorophyll *a*	1.42	1.52	1.68	1.62	1.52
Phaeopigment	0.43	0.36	0.45	0.45	0.45
Total particle volume (TPV)	3.76	3.29	3.25	3.07	3.37

* Estimated by subtracting the < 200 µm plankton fractions from POC
Coccoid cyanobacteria, 0.8 to 1.2 µm in diameter, were present in all samples but are not included in biomass estimates. Densities were generally < 10^3 cells ml^{-1} except in the surface water at F which gave 2.7×10^4 cells ml^{-1}

detrital material. Below the thermocline, levels of POC and plankton carbon were generally low, and consistent with there being little or no growth of the autotrophs in the bottom water.

At Station F, the surface dinoflagellate bloom gave POC and TPV values in excess of 2 g m^{-3} and 25 ppm respectively in the 2 to 12 m fraction. DOC, bacteria and protozooplankton also showed pronounced maxima in this layer. By contrast, the zooplankton were relatively uniformly distributed with highest carbon values for 12 to 24 m, just below the main *Gyrodinium* population and associated with a peak in phaeopigment levels. Higher TPV values for the bottom water than at E5 seem to have been due to the phytoplankton (mainly *G. aureolum*) forming a greater proportion of the POC rather than to the sinking of detrital material from the bloom.

Both dissolved and particulate organic carbon were evenly distributed throughout the water column at Station M although some anomalies were apparent. For example, the lowest levels of phytoplankton carbon and chlorophyll were observed at 2 to 12 m, whereas both POC and TPV showed maximum values in this surface layer. Compared with water below the thermocline at Stations E5 and F, the mixed water had a similar POC content but gave higher TPV values. This was probably due to the abundance of diatoms which, on account of their vacuoles, have a high volume to carbon ratio. Also the average concentration of DOC at M exceeded that at either of the other 2 stations.

Relations between compartments of organic carbon (Table 5)

Particulate organic carbon, even with the inclusion of the >200 µm mesozooplankton carbon (Table 4), constituted generally 20 % or less of the dissolved organic carbon. The only exception to this was in the *Gyrodinium* bloom where the highest observed levels of POC, corresponding to chlorophyll *a* concentrations of ~ 50 mg m^{-3}, were about twice those of DOC. Note, however, that disruption of any fragile cells during filtration will have caused a reduction in POC and corresponding increase in DOC. In surface samples, the proportions of POC that could be attributed to the phytoplankton ranged from < 5 % at E5 to 70 % or more within the dinoflagellate bloom.

Phytoplankton carbon to chlorophyll ratios for Stations F and M showed no significant changes with depth. Previous estimates for *Gyrodinium aureolum* populations based on regression analysis (Pingree et al., 1982) have been somewhat higher (~ 100) but variations due to sampling at different times of the day (Fig. 9) and different stages of the bloom are expected. By contrast, the ratios for diatom populations at Station M were 3 to 4 times greater than those for spring diatom populations (Fasham et al., 1983) despite the low mean light levels to which they were being exposed. The increase in the phytoplankton carbon to chlorophyll ratio towards the surface at E5 may reflect real differences related to the light environment of the cells, or a greater proportion of heterotrophic flagel-

Table 5. Ratios between components of organic carbon at Stations E5, F and M

Component	Station	Depth (m) 2–12	12–24	24–36	36–48	48–60
POC/DOC	E5	0.29	0.14	0.17	0.11	0.18
	F	1.25	0.63	0.18	0.19	0.19
	M	0.21	0.17	0.13	0.15	0.14
Phytoplankton C/POC	E5	0.04	0.08	0.02	0.03	0.02
	F	0.77	0.72	0.35	0.19	0.19
	M	0.22	0.32	0.39	0.43	0.39
Phytoplankton C/Chlorophyll *a*	E5	104	44	26	29	35
	F	80	79	64	63	72
	M	54	56	57	57	67
Bacteria C/Heterotroph C	E5	0.09	0.15	0.13	0.20	0.14
	F	0.34	0.21	0.25	0.19	0.17
	M	0.31	0.21	0.24	0.30	0.16
Bacteria C/Phytoplankton C	E5	0.21	0.46	0.83	0.90	0.60
	F	0.02	0.02	0.07	0.09	0.08
	M	0.14	0.08	0.08	0.12	0.05
Mesozooplankton C/Phytoplankton C	E5	1.64	1.62	4.81	3.50	2.67
	F	0.004	0.03	0.11	0.20	0.21
	M	0.21	0.18	0.14	0.15	0.15

lates (which cannot be distinguished from autotrophic forms in the cell counts) above the thermocline.

Bacteria formed a substantial proportion, generally 10 to 30 %, of total heterotroph carbon at all depths at each of the 3 stations. Relative to the phytoplankton which probably forms the primary source of organic material for bacterial growth, they were most important in the stratified waters at E5, suggesting that phytoplankton growth rates were high at this station. By contrast, the bacteria to phytoplankton carbon ratio for the dinoflagellate bloom was more than an order of magnitude lower, even though the highest standing crops of bacteria were found in this situation (Table 4).

The ratios of mesozooplankton carbon to phytoplankton carbon in the surface water at Stations F and E5 varied by nearly 3 orders of magnitude. At F the mesozooplankton was scarce in both absolute (Table 4) and relative terms, suggesting that there may have been active avoidance of the dinoflagellates by copepods and other herbivores comparable to that reported by Fiedler (1982) and Huntley (1982) for *Gymnodinium* blooms off the coast of California. Below the dinoflagellate layer the mesozooplankton increased proportionately by almost two orders of magnitude to reach about 20 % of phytoplankton carbon. The relative abundance of mesozooplankton carbon at E5 also increased with depth, but for the upper 60 m of the water column exceeded the phytoplankton carbon by a factor of about 2. At night this dominance by the mesozooplankton would have been more marked due to the upward migration of organisms from below 60 m into the surface layers. In the mixed water at Station M the mesozooplankton carbon formed 15 to 18 % of the phytoplankton carbon at all depths.

CONCLUSIONS

The distributions of plankton carbon at the 3 stations are summarised in Fig. 10 and Table 6. In each case the proportions of plankton carbon were similar for the 0 to 24 m and 24 to 60 m layers, although below the thermocline at E5 and F the mean total concentration was relatively low compared to the surface and included a larger proportion of mesozooplankton. The main differences between the stations were in the vertical distribution, abundance and species composition of the phytoplankton and in the relative importance of the different groups of heterotrophs.

Previous studies of the phytoplankton and zooplankton communities in the western English Channel (Harvey et al., 1935; Digby, 1950; Grall and Jacques, 1964; Grall et al., 1971; Holligan and Harbour, 1977; Maddock et al., 1981) as well as investigations on the distributions of organisms in relation to the Ushant

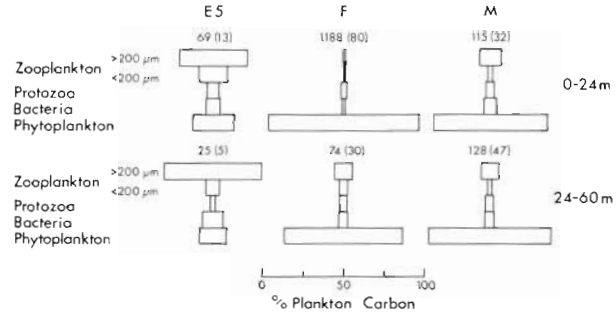

Fig. 10. Relative distributions of organic carbon in zooplankton, protozoans, bacteria and phytoplankton in the 0 to 24 m and 24 to 60 m layers on the reference profiles at Stations E5, F and M. The values for each histogram give the mean plankton carbon concentration (mg m^{-3}) and, in parentheses, the proportion of total particulate carbon (< 200 µm) that can be assigned to the plankton

Table 6. Total standing stocks (g C m^{-2}) of phytoplankton (autotrophs) and heterotrophs at E5, F and M

	E5	F	M
Water depth (m)	120	96	76
Phytoplankton[1,2]	0.42 (0.40)	26.50 (3.5)	7.03
Heterotrophs[2]	3.07	3.18	2.33

[1] The 2 values for Stations E5 and F correspond to surface + thermocline layers and, in parentheses, bottom layer
[2] Values for the whole water column were determined by extrapolation of data for the 48 to 60 m layer (Table 4) to the bottom

frontal system (Holligan, 1981 and cited references) confirm that the plankton observations at Stations E5, F and M in July 1981 (Tables 1 and 3) are typical of the midsummer period. Thus, in the stratified and frontal waters the dinoflagellates and flagellates had replaced the spring diatoms and the zooplankton included many intermediate or offshore species (Colebrook et al., 1961), whereas in the mixed water at Station M the diatoms had persisted and the zooplankton was neritic in character.

Values for the standing crops of chlorophyll generally fall within the ranges of previous measurements for the summer period (Holligan, 1981; Pingree et al., 1982) although those for the low chlorophyll profiles at E5 were more typical of the area of maximum stratification in the central Celtic Sea (unpubl. own observations). The *Gyrodinium aureolum* populations have been a characteristic feature of the frontal region since 1975. Comparative data for the standing crop of zooplankton are not available, although Harvey (1950) gives an annual average quantity of 1.5 g m^{-2} dry weight (equivalent to about 0.5 g C m^{-2}) for the waters off Plymouth, Steele (1956) quotes maximum values of 5 g C m^{-2} for the North Sea and English Channel which

presumably related to the period immediately after the spring diatom outburst, and Adams and Baird (1968) found average summer standing crops of 30 to 56 mg dry weight m^{-3} for the stratified waters of the northern North Sea. There are no earlier reports of bacterial numbers in the English Channel, but the standing stocks at Stations E5, F and M fall within the ranges previously reported for coastal waters (for a review see van Es and Meyer-Reil, 1982).

We suggest therefore that, despite possible modifications due to the patchiness of organisms, the plankton carbon distributions shown in Fig. 10 represent different types of food web which develop each year in response to different conditions of vertical (tidal) mixing. Their dynamic properties are considered by Holligan et al. (1984) in relation to experimental measurements of photosynthesis and community respiration. Here the ecological implications of widely varying autotroph to heterotroph biomass ratios are briefly discussed.

Variations in the relative proportions of autotrophs and groups of heterotrophs (Table 5, Fig. 10) reflect either imbalances between producers and consumers, as tend to occur at the time of the spring diatom outburst in temperate waters, or different production to biomass (P/B) ratios for the dominant species (Dickie, 1972; Banse and Mosher, 1980). For the phytoplankton populations, in particular, P/B ratios are likely to be variable due to the effects of light and nutrient availability on net carbon assimilation.

The dinoflagellate bloom at Station F appears to represent a special case of imbalance, in which the possible suppression of grazing and the capacity of *Gyrodinium aureolum* to sequester nitrate from below the seasonal thermocline (Holligan et al., 1984) lead to an increasing and persistent dominance of the plant cells in terms of biomass. This situation, however, is probably not stable in a given area for periods > 1 mo (Holligan et al., 1983) due to a combination of light and nutrient limitation of the plant growth rate and physical dispersion of the cells by water movement, but no studies have yet been made of the fate of the phytoplankton carbon when such blooms collapse.

Analysis of the photosynthesis and respiration data for Station M in relation to the vertical distribution of chlorophyll (Holligan et al., 1984) indicates that net production was restricted by the low photosynthesis to respiration ratio for the production as a whole, and was probably positive only on sunny days. In this situation the diatoms appear to survive through re-suspension by bottom tidal mixing, and fluctuations in production are likely to occur over time scales comparable to those in surface irradiance (i. e. sunny *versus* cloudy weather patterns). The large size of the plant cells will favour direct consumption by herbivorous mesozooplankton although, even if the latter show high P/B ratios, a relatively large standing crop of slow growing autotrophs will always be required to support grazing activity.

In the stratified water at E5, which is representative of summer hydrographic conditions for the greater part of the shelf area around the British Isles (Pingree et al., 1978), the seasonal thermocline creates a more favourable light environment for the phytoplankton so that positive net primary production is maintained even on low-light days. However, the factors that allow relatively high biomass of heterotrophs to persist for several months are not precisely understood, and numerical modelling (Vinogradov and Menshutkin, 1977) of this type of ecosystem is now required to show how the observed pattern of carbon distribution is likely to be maintained on the basis of present knowledge of growth efficiencies for the main groups of organisms. Although marine planktonic food webs are often assumed to be pyramidal with a given biomass of autotrophs supporting successively smaller biomasses of herbivores and carnivores, situations comparable to E5 (Fig. 10) are not uncommon (Raymont, 1980) and indeed may be typical of stratified conditions. For example, Mullin and Brooks (1970) showed that zooplankton to phytoplankton carbon ratios change from 0.3 in April/May to 2.1 in May/June and 1 to 2 during July and August in the coastal waters off California. Dominance by the heterotrophs indicates a more efficient utilisation of the plant carbon in stratified waters, with relatively small losses to the benthic community.

No comparative information on the role of bacteria in re-mineralisation processes and in the transfer of organic matter within the food web (Williams, 1981) under different hydrographic conditions is yet available. At E5, where the biomass of bacteria was comparable to that of phytoplankton (Table 5), consumption of bacteria by flagellates may make a significant contribution to secondary production at higher trophic levels. By contrast, at Stations F and M, the bacteria generally formed less than 10 % of the phytoplankton carbon and are likely to have been relatively more important in terms of nutrient regeneration. The lack of experimental evidence for such suggestions emphasises the need for quantitative observations on the transfer of carbon within the different food chains that develop in the English Channel each year as a result of differences in tidal mixing.

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