Process studies in eutrophic, mesotrophic and oligotrophic oceanic regimes within the tropical northeast Atlantic

A. Morel

Keywords: pelagic biomasses, primary production, benthic fauna, water-column carbon flux, time-series station, southeast North Atlantic, ecosystem models

Introduction

The aim of this review is chiefly to indicate how the EUMELI–JGOFS programme was set up and on what previous knowledge it was based, and then how it was carried out and for what specific JGOFS objectives. It is intended to provide, in a synthetic way, a general survey of the results already obtained and presently available. Another purpose is to inform the international JGOFS community, and its modellers in particular, of the parameters that were (successfully, or less successfully) monitored, and also to provide appropriate references to detailed studies that are already published or expected for the near future, and have resulted from the EUMELI programme.

If the present chapter fixes the general interdisciplinary frame of the programme, it does not intend to be exhaustive with regard to all of its aspects, nor definitely conclusive. Indeed at this stage of completion, drawing final conclusions for the whole four-year programme, and while many activities are still ongoing, is out of reach. For instance, the preparation of the sediment-trap samples for further analyses was only completed in January 1997, so that many analyses remain to be made or are yet to be validated. Thus, only partial results for the fluxes and related parameters are displayed in the tables in this chapter, and at present they do not encompass the entire period of data acquisition. Therefore, the presentation below represents an intermediate and provisional state of the work, before a global synthesis can be made. There is no explicit presentation of materials and methods in what follows, as specific papers already published, and referred to, provide this information.
Historical background and objectives

The earlier root of the EUMELI programme (acronym for EUtrophic, MEsotrophic and oLIgotrophic regimes) is to be found in the International Programme of Co-operative Investigation of the northern part of the Eastern Central Atlantic (CINECA). This programme, born and then co-ordinated under the auspices of CIESM, COI and FAO, consisted of multidisciplinary studies of coastal upwelling events associated with the western boundary currents. Its main goals were to analyse the physical, chemical and biological processes within and around a coastal upwelling system, and to determine the extent and effect of such a system upon the adjacent zones. The multi-nation, multi-ship surveys lasted about ten years, ending with a Symposium, held in Las Palmas in 1978, entitled The Canary Current, Studies of an Upwelling System. Under the same title, a series of papers were published in 1982, under the editorship of G. Hempel. The French group that contributed to this programme (the ‘Mediprod Group’) had still not been disbanded in 1985, about ten years after the last cruise (CINECA-5). Under the guidance of H. J. Minas, this group elaborated a new project based on one of the conclusions drawn at the issue of the Las Palmas Symposium: ‘Information on the near-shore area (along the African coast) is much better than that for the open ocean’ (Hempel, 1982). This new project, initially termed ‘upwelling dissipation’, was aimed at studying the progressive changes in the biogeochemical processes and the gradual decline of biological activity when the upwelled waters drift from their sources toward the open ocean. It quickly became the seed for a participation in the emerging international JGOFS Programme, and its initial objectives were accordingly amended.

The restructurings was made in accordance with the basic elements, as succinctly defined in the SCOR–JGOFS Report of the International Scientific Planning and Co-ordination Meeting, and held in Paris (1987). More precisely, two basic elements, ‘Process studies’ and ‘Modelling’, were identified as the main driving ideas for a revised programme. The statement in this Report, about the future need for satellite observation of ocean colour to achieve the JGOFS goals, was also taken into consideration. The adopted strategy for the EUMELI programme essentially consisted of:

1. Carrying out detailed studies of the main processes governing the particle flux, and particularly the carbon flux, from the upper oceanic layers where photosynthesis occurs, throughout the water column, to ultimate deposition on the sea floor, and finally to incorporation into the sediments;
2. performing such studies in three typical trophic regimes, differing as distinctly as possible in their nutrient availability, and therefore in their
primary production rate, in intensity of vertical transport, and ultimately in deposition rate;

3. developing a series of generic models allowing biogeochemical fluxes toward the interior, and then to the bottom of the ocean, to be related to near-surface properties, in particular those detectable through remote sensing techniques, such as chlorophyll concentration, sea-surface temperature, incident irradiation and wind;

4. validating these models (operated in uncoupled or coupled modes) in various regimes by using field data.

*Ab initio*, it was admitted that localised time series would be more appropriate for validation exercises, rather than successive cruises. A quasi-permanent sediment-trap deployment was planned and seen as an essential component of the EUMELI programme. Satellite data were also expected for the period of field activities. With these tools, it was believed that at least a certain continuity in observation could be preserved.

Initially, six regularly spaced cruises were planned (each about 7–8 months apart). This interval was optimal for collecting the captured sediments and re-deploying the traps, current-meters and benthic modules left on the bottom. Because of the multi-disciplinary approach, the diversity of experiments, and as a consequence the number of people involved, it was necessary to specialise and diversify the cruises. Emphasis was thus successively put on bathymetry and sedimentology, studies of benthic communities and processes, then on water-column chemistry and pelagic studies, including primary production and photophysiology. Apart from the first cruise, hydrography and sampling for the JGOFs core parameters were systematically performed during all cruises, whatever their main topics. A significant atmospheric sampling programme (for aerosols and sulphur compounds; see Putaud et al., 1993) was also implemented during cruises 3 and 4. Based on free-drifting sediment-trap deployments (at 200 m depth), the downward flux of detrital particulate dimethylsulphonio-propionate (DMSPp) was also studied (Corn et al., 1994).

The programme began with the first cruise (EUM#1) in July 1989 (Table 11.1). Because of funding problems, in particular for purchasing a sufficient number of traps, and because of limited ship time in the selected zone, the programme after the first cruise was delayed until January 1991 (EUM#2). It was then regularly pursued until cruise 5. The sixth cruise was cancelled for logistic reasons, and replaced by a study of another oligotrophic regime in the Pacific Ocean (during a cruise called OLIPAC). Nevertheless, the deployment of the sediment traps and current meters, ending with cruise 5, lasted about two years over three consecutive periods. Only the Oligotrophic and Mesotrophic sites were equipped with moorings. For various security reasons, the Eutrophic
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<tr>
<th>Site</th>
<th>Z (m)</th>
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<td>T2</td>
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<td>20°55'</td>
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site was never instrumented; it was not visited at all during EUMELI#3, owing to its inaccessibility during the Gulf war.

Selection of the sites

A pre-selection of the three sites was made under several constraints. Besides the practical constraint of minimising the distances between the three locations, a pre-requisite was to identify and locate in the tropical Northeast Atlantic the three typical trophic situations that were hoped for, with well-established regimes and sufficiently steady characteristics. The Mauritanian upwelling area and open-ocean stations at the same latitude were selected a priori on the basis of climatic considerations (see below), as well as on the examination of satellite ocean imagery interpreted in terms of chlorophyll concentration (by using the data from the Coastal Zone Color Scanner, CZCS).

At such latitudes (about 20°N), the amplitude of the winter deep convection is known to be considerably reduced, compared with that occurring at higher latitudes (Levitus, 1982). The subsequent occurrence of vernal bloom is unlikely, and the seasonality is reduced (Hastenrath & Lamb, 1977). The inter-tropical convergence zone does not reach these latitudes in summer, so that rather regular trade winds ensure a relative steadiness in external forcing and expected biological responses. More precisely, upwelling along the Northwest African coast experiences a seasonal oscillation in latitude with, nevertheless, a permanent activity around 20°N, near Cape Blanc (Speth & Detlefsen, 1982; Mittelstaedt, 1982). Consequently, coastal upwelling is a permanent feature at this location, in spite of a fluctuating intensity, as already revealed by the CZCS scenes analysed by Briculaud et al. (1987). The eutrophic site was thus positioned not too far from the source of upwelled waters (actually at about 140 km from Cape Blanc; see Fig. 11.1). However, it was far enough away to avoid coastal turbid waters (Morel, 1982), as well as the influence of Banc d’Arguin waters (Peters, 1976), and far enough to reach deep waters and bottom depths exceeding 2000 m. The chlorophyll (Chl) concentration at this site is always above 1 mg m⁻³, as recorded in the CZCS archive (see Morel, 1996).

This archive was also very helpful when selecting the position of the oligotrophic site. Indeed, the colour imagery showed that a permanent oligotrophic situation (with Chl below 0.1 mg m⁻³, and no seasonal signal) could only be observed offshore, at a minimal distance of about 1500 km from the coast. Such a location, at the periphery of the North Atlantic gyre, and northward of the North Equatorial current, is in a rather quiet zone. Meandering of this current and eddy formation generated by baroclinic
instabilities might induce some mesoscale variability near this area (Dadou et al., 1996).

The choice of a site expected to be representative of mesotrophic conditions was less easy, as such regimes seem to be essentially transient and zonally migrating within the Mauritanian zone. The general circulation in this area (the Canary Current offshore, and a Northward coastal countercurrent), as well as the presence of eddies and filaments detaching from the upwelling system (Bricaud et al., 1987; van Camp et al., 1991), leads one to think that complex situations and mesoscale structures are likely to occur (see Mittelstaedt, 1982). On average, however, mesotrophic conditions seem to prevail in a zone midway between the eutrophic coastal region and the Cape Verde islands, with chlorophyll concentrations remaining moderate and varying between 0.3 and 1.3 mg m$^{-3}$, approximately, according to CZCS data.

The bottom topography, the sediment stability, and the deposition rate were also considered before deciding on the final position of the sites. For this purpose, the first cruise was devoted to a detailed bathymetric survey around the sites. It also provided the opportunity for a preliminary study of the benthic community and activity. Around each site, the bottom topography was accurately mapped by using side-scan sonar, then visually analysed by using sea-floor acoustic imaging devices. Such precise knowledge was essential for the deployment of benthic instrumentation and mooring lines (Auffret et al., 1992; Sibuet et al., 1993). It was also necessary to verify that no significant
perturbation occurred near the selected sites, such as volcanic and hydrothermal activity, or turbidity events near the continental slope. A flat and extensive terrace, 2000 m deep, was selected for the eutrophic site. The mesotrophic site was located on the Cape Verde Terrace at an average depth of 3000 m, and the oligotrophic site on the abyssal plain (4600 m) far from the Cape Verde Islands rise, and from the mid-Atlantic ridge and scattered guyots. The sedimentation rates were found to be regular over the last post-glacial period and apparently correlated with the biological activity expected in the upper layers at the three sites (J.-L. Reyss, personal communication, 1991). The sites, as they were definitely selected after the first cruise, are shown in Fig. 11.1, as well as additional (intermediate) stations. Their geographical positions are given in Table 11.1. In what follows, the capitals O, M and E will be used to represent the oligo-, meso-, and eutrophic situations or sites.

Prevailing conditions at the three sites

The general climatology and main oceanographic features at these sites are summarised in Table 11.2. The seasonal variations to be expected at these latitudes can be found in the climatology of Hastenrath & Lamb (1977) (see also other estimates in Dadou & Garçon, 1993). The heat budget at the O site is in equilibrium over the year, whereas at the M and E sites a net oceanic heat gain (+40 and +70 W m⁻², respectively) results from increasing solar radiation and decreasing evaporation when approaching the coast. The amplitude in the annual cycle of the heat budget also increases eastward: the amplitude values are 120, 160, and 170 W m⁻² at the O, M, and E sites, respectively. The period of negative values (heat loss for the ocean) extends over 5 months (November–March) at the O site, 3 months (November–January) at the M site and only 1 month (December) at the E site. This site is almost permanently exporting energy through advection, whereas at the O site there is no net annual export. In spite of a rather long winter at the O site, the annual course of the upper-layer temperature (see Fig. 11.2) remains rather smooth. Winter values are not below 22.2 °C, and the narrow range of annual variation (by 3 °C) was fully confirmed by successive measurements. The temperature evolution at the M site, taken from Hastenrath & Lamb (1977), as well as the abundant oceanographic database for the CINECA region (Smed, 1982), spans a wider range.

The expected 5 °C change between early spring and fall was also confirmed during the successive cruises at this M site. At the E site, the annual amplitude is again of about 5 °C, but all values are shifted by 2 °C toward colder temperatures. The abrupt warming that starts in July probably results from the
Table 11.2. Climatological and other relevant information for the three sites

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<th>Oligotrophic</th>
<th>Mesotrophic</th>
<th>Eutrophic</th>
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<tr>
<td>*Short wave radiation year average</td>
<td>180</td>
<td>195</td>
<td>218</td>
</tr>
<tr>
<td>*Cloudiness index (tenth) min–max</td>
<td>5–7</td>
<td>4–6</td>
<td>3–5</td>
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<tr>
<td>*Net (short–long-wave) radiation (W m⁻²)</td>
<td>+ 110</td>
<td>+ 130</td>
<td>+ 145</td>
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<tr>
<td>Latent heat flux year average (W m⁻²)</td>
<td>- 110</td>
<td>- 90</td>
<td>- 75</td>
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<td>Ocean gain (W m⁻²)</td>
<td>0</td>
<td>+ 40</td>
<td>+ 70</td>
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<tr>
<td>†Mixed-layer depth (m) min–max</td>
<td>35–70</td>
<td>20–35</td>
<td>20–35</td>
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<tr>
<td>*Surface temperature (°C) min–max</td>
<td>22.2–25.6</td>
<td>20.2–25.0</td>
<td>18.8–24.0</td>
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<tr>
<td>‡Temperature at 100 dbar (°C) max–min</td>
<td>22.0–20.5</td>
<td>18.0–16.0</td>
<td>17.0–16.0</td>
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<tr>
<td>††Surface Chl (mg m⁻³) min–max</td>
<td>0.05–0.10</td>
<td>0.15–1.4</td>
<td>0.9–3.0</td>
</tr>
<tr>
<td>¶Primary production annual values (g C m⁻³)</td>
<td>110</td>
<td>260</td>
<td>535</td>
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<tr>
<td>Average per day (mg C m⁻³)</td>
<td>300</td>
<td>710</td>
<td>1500</td>
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Sources and symbols: * according to Hastenrath & Lamb (1977); † according to Levitus (1982); ‡ according to Maillard (1986); note that these temperatures are in opposite phase compared to those at surface, and thus are listed as max–min values, in correspondence with the min–max values for the surface; †† according to the CZCS–NASA climatological monthly maps (Feldman et al., 1989); ¶ predicted from CZCS surface-chlorophyll (Morel, 1996).

weakening of the trade winds and thus of the upwelling activity. Such a warming, observed during CINECA cruises (Smed, 1982), has not been documented during EUMELI.

At the depth corresponding to 100 dbar (see Maillard, 1986, and Table 11.2), the annual temperature variation is small. Interestingly, at the O site in March, minimal temperature, almost constant within the water column (about 22 °C), suggests that the mixed layer extends down to at least 100 m, and thus deeper than indicated in the Levitus (1982) atlas. At the M and E sites, even in winter, the surface temperature always exceeds that at 100 m by about 2 °C, and indicates that the stratification is maintained throughout the year.

The satellite-derived chlorophyll values leave no doubt about the permanent oligotrophic regime, and the seasonally modulated eutrophic regime, which
prevail at the corresponding selected sites. As anticipated for the M site, the algal biomass is much more variable, by a factor approaching 10, with erratic rather than well-defined seasonal patterns (see Fig. 2 in Morel, 1996). It can only be asserted that this regime is, on average, mesotrophic in terms of annual mean Chl content and of predicted primary production (Berthon, 1992).

Results

Water masses at the three sites

In contrast to the oligotrophic zone, which is rather poorly documented (see hydrographic stations compiled in Maillard, 1986, and in Lozier et al., 1995), the E and M sites were intensively studied. These sites were intensively studied during the CINECA era (Tomczak, 1981; Fiuza & Halpern, 1982; Minas et al., 1982; Manriquez & Fraga, 1982; Barton & Hughes, 1982; Mittelstaedt, 1982), and during several cruises afterwards (see, for example, Barton, 1987; Zenk et al., 1991; Ahran et al., 1994). Early observations (Fraga, 1974) showed that at
latitudes 21°–23°N a thermohaline front, without an appreciable density gradient, develops off Mauritania, with a complex meandering structure (see also Barton, 1987). Below the mixed layer, and down to about 800 m, the North Atlantic Central Water and the South Atlantic Central Water (NACW and SACW) are in contact. They interact along this front (named ‘Cape Verde Frontal Zone’ by Zenk et al., 1991) through isopycnal mixing, often resulting in interleaved layers (Barton & Hughes, 1982).

The E and M sites are expected to be mainly influenced by the northward intrusion of SACW. With a general NE–SW orientation of the central–water discontinuity, these sites might be exposed to fluctuations resulting from the frontal–zone meandering (see Fig. 2 in Zenk et al., 1991). The first intensive hydrographic survey (during the EUM#2 cruise; Vangriesheim et al., 1993) included 16 CTD casts made within a 30 × 60 km² box around the E site, and 13 others in a 30 × 45 km² box containing the M site. These measurements confirmed the predominance of SACW at both sites; however, spatial (actually east–west) nuances were detected within the boxes around the E and M sites (Pierre et al., 1994). The mixing proportions of SACW and NACW appeared more variable for the upper part of the water column (for z < 220 m and \(\sigma_\theta < 26.8\)), whereas for the deep part (down to 800 m and \(\sigma_\theta = 27.3\)) the \(\theta–S\) diagrams (potential temperature against salinity) were found to be steadily superimposed on that of ‘pure’ SACW.

The \(\theta–S\) diagrams for all cruises are separately shown in Fig. 11.3a–c for the three sites O, M and E. The seasonally changing upper–layer density profiles are displayed in Fig. 11.4a–c. Except for their upper parts, the \(\theta–S\) patterns at the O site were found to be remarkably stable during the two years of this study (Fig. 11.3a). The Antarctic Bottom Water, with a potential temperature of 2 °C or slightly less (Fig. 11.5), was present below 4000 m and progressively diluted upward with the North Atlantic Deep Water, which is characterised by a salinity maximum (with \(S > 35.05\) practical salinity units, psu). This maximum occurred at 1500, 1350, and 1250 m at the O, M, and E sites, respectively (see also the Salinity section in Fig. 11.6a). Above, namely at a depth of 925 m (O site), or 800 m (M and E sites), the relative salinity minima that were observed are the print of the Antarctic Intermediate Water, which forms a layer about 250 m thick (if demarcated by \(S < 35.00\) psu).

Central waters usually extend from \(\sigma_\theta = 27.3\) up to about 26.4, a value typical for the bottom of the mixed layer (see also Fig. 11.6b). At the O site, the central water was permanently of the NACW type, as expected. At the E site, a mixture, approximately 50–50%, of NA– and SACW was regularly present. At the M site, more complicated \(\theta–S\) properties were observed. Although generally dominated by SACW, various mixtures were encountered in the upper layers of this water mass (for \(z < 380\) m, and \(\sigma_\theta < 27.0\)). In contrast, the SACW was
Figure 11.3 Potential temperature – salinity (θ–S) diagrams for the three sites O (a), M (b) and E (c). All the deep CTD casts, down to the bottom (but only these) made during the cruises 2, 3, 4, and 5 are represented. The two straight lines represent the θ–S relations for the North Atlantic Central Water and the South Atlantic Central Water, as defined by Tomczak (1981). Note that, at the M site, the two superimposed curves (arrow) which differ from the others come from cruise 5, in December 1992.
almost pure within the deeper layers, down to 730 m, where $\sigma_\theta$ reaches 27.3; in December 1991, however, (during EUM#5), the deep SACW was slightly mixed with NACW. Above the central waters, the top layer, examined later, exhibited variable characteristics (Table 11.3) according to the period of the year (the successive cruises).

Time-averaged values, or range of variations, for the main properties at the three sites and various levels in the water column are given in Table 11.4. In relation to the water masses described above, in particular to the Central Waters, other parameters can be used as descriptors. As is well known (see, for example, Minas et al., 1982; Table 2 in Zenk et al., 1991), compared with

Figure 11.3b For legend see opposite.
NACW, SACW is characterised by higher nutrient contents and a more pronounced oxygen minimum. These features are clearly seen in Table 11.4. At the O site, the nitrogen maximum (occurring at about 800 m with $\sigma_\theta = 27.42$) is typical of the lower end of the NACW. In contrast, at the M and E sites, the N-maximum values are those of pure SACW; they were located around 600–650 m, with $\sigma_\theta = 27.2$, in correspondence with the lower end of this water mass. The oxygen minima were found 150 m above the N-maxima. The minimal concentration at the O site was close to 2.6 ml l$^{-1}$ in NACW, and thus almost twice that found in SACW, at both the M and E sites. A relative minimum in nitrogen (about 22.5 µM) was observed in the two sites (O and M) in the 2000–2500 m layer.
Figure 11.4 Typical examples of vertical profiles of potential density (density excess in kg m\(^{-3}\)) and of algal chlorophyll fluorescence (relative units) at each of the three sites and at various seasons (successive cruises). Dates are as follows (months identified by roman numbers). (a) O site: 14 II 91, 14 X 91, 24 VI 92, and 22 XII 92; note that the chlorophyll concentration (absolute units, mg m\(^{-3}\), Pujo-Pay & Raimbault, 1994), determined on discrete samples during EUM\#2 (17, 18, and 19 I 91), are given in inset. (b) M site: 09 II 91, 09 X 91, 16 VI 92, and 15 XII 92. (c) E site: 05 II 91, 13 VI 92, and 12 XII 92; the results for discrete chlorophyll determinations (station 50, April 3, 1974, CINECA 5 cruise) at about the same location are also shown. The chlorophyll concentrations (as mg m\(^{-3}\)) can be read with the same numerical scale used for fluorescence.
**Figure 11.4c** For legend see p. 351.

**Hydrographic section between the three sites**

From west to east, the replacement of NACW by SACW (or more precisely by NACW–SACW mixtures) is not progressive. A first salinity jump can be detected (Fig. 11.6a, showing EUMELI\#5 data) between stations MO-02 and MO-03. A second one, more abrupt, occurs near EM-03. These jumps in salinity have only a reduced impact on the essentially flat disposition of the isopycnals throughout the section (Fig. 11.6b). As already pointed out (Barton, 1987), when NACW replaces SACW, the concomitant changes in salinity and temperature are in opposite directions and thus leave the density practically unchanged. Very similar salinity and density fields were found during EUM\#4 (not shown), except perhaps for a steeper rise in salinity near the M site.

Concerning the large-scale circulation through the section displayed in Figs 11.6(a,b), the geostrophic currents computed in reference to the 3000 dbar level were found to be insignificant. The only exception was found between the M site and station MO-03, where velocities reaching 5 cm s\(^{-1}\) (towards S–SW) were derived within the upper 100 m layer. The orientation of the segments forming the section is admittedly not favourable for capturing the main circulation, which is essentially oriented southwest or westward in this zone. In addition, the distances between stations (about 280 km) are not appropriate for a detailed description of the velocity field at the mesoscale (Dadou et al., 1996).
Figure 11.5 θ-S diagrams for the deep waters, down to the bottom, at the oligotrophic site, as determined during the four cruises, from EUM#2 to 5. These curves show the internal consistency of measurements and calibrations (Tailliez, 1993): they slightly differ from the linear relation between S and θ proposed by Saunders (1986) for these waters. The two dashed lines are shifted by ± 0.002 psu, with respect to the Saunders reference line.

From the CTD measurements made at the triangular array enclosing the O site (namely at the stations T1, T2, and T3, separated by 65 km), a very slow, SW-orientated, geostrophic motion could be computed between 200 and 1000 m (or deeper). Significant speeds, up to 10 cm s⁻¹, were found in the upper layer. The corresponding fluxes, which cannot be balanced within the triangle, suggest mesoscale activity near the surface. The intermittent occurrence of lower salinities reinforces the possibility of such local drifts of fresher waters at the very surface.

Associated with some of the sediment traps, current meters (Aanderaa) were deployed at 250, 1000, and 2500 m, at the O site and the M site (never at the E site). With three consecutive periods (from EUM#2 to EUM#5), the total records lasted 665 and 630 d at the O and M site, respectively. At 250 m, predominantly SW-orientated currents were recorded at both sites (Bournot et al., 1995) with mean values over the entire period of 7.8 and 11.5 cm s⁻¹. Peak values were 38 and 50 cm s⁻¹, respectively, at the O site and the M site, even
Figure 11.6  (a) Vertical distribution of salinity, psu, and (b) potential density, density excess in kg m\(^{-3}\), along the two contiguous sections, from the O site to the M site, and from the M site to the E site. The continental slope is schematically shown near the E site. Results from the cruise EUM\#5.
with an exceptional event at the M site (reaching 98 cm s⁻¹ and lasting a few days). With such episodic current velocities, and values often exceeding 15 cm s⁻¹, the collection efficiency of the sediment traps at this depth is questionable (and is not yet clear). The energy spectra show pronounced maxima at frequencies corresponding to the semi-diurnal and diurnal tides, and to the inertial periods (32.5 and 37.8 h, at the latitudes of the O and M sites, respectively). At 1000 m, the currents were generally flowing westward with rather low mean speeds of 4.8 and 4.5 cm s⁻¹, and decreasing at 2500 m to 3.0 and 2.3 cm s⁻¹, at the O site and the M site, respectively, without clear orientations.

**Physical and biogeochemical properties within the upper layer at the three sites**

Typical examples of the density structure within the upper (300 m thick) layer are displayed at the three sites (Fig. 11.4a–c). Fluorescence vertical profiles are also plotted to show the close correlation between the vertical distribution of the algal biomass and the thickness of the mixed layer as well as the density gradient within the pycnocline. Biochemical information for these layers, and time variability detected by the successive cruises, are also provided in Table 11.3 for the three sites.

At the O site, internal waves of wide amplitude (at least ± 10 m) were always observed, resulting in vertical oscillations of the bottom of the mixed layer (ML), as well as of the deep chlorophyll maximum (DCM). Examples are provided by Partensky et al. (their Fig. 7, 1996), Lazzara et al. (their Fig. 1, 1996) and Morel et al. (their Fig. 7, 1996). Therefore the depths of the mixed layer and of the euphotic layer (denoted ZML and Zoe, respectively), which are given in Table 11.3, must be seen as representative mean values. The frequent occurrence of less saline waters drifting at the surface (probably owing to rains), often gave rise to two-step density profiles, in which the deepest one is the most significant (Fig. 11.4a–c). In mid-February (during EUM#2), about two weeks before the net heat budget returns to positive values, the winter deep convection was probably near its maximum and the mixed layer extended down to 120 m. This value greatly exceeds that given in Levitus (1982) (70 m). The minimal thickness of this layer (45 m), in coincidence with the warmest waters in October, agreed with the figure in Levitus (see also discussion and modelling in Dadou et al., 1993). With regard to the algal biomass, this O site was characterised by a permanent deep chlorophyll maximum, generally below 100 m, and actually at a level below the euphotic depth, when defined in reference to the 1% level of the PAR (photosynthetically active radiation) surface irradiance. Vertically integrated phytoplankton biomass was rather constant throughout the year (Table 11.3). Not surprisingly, the less structured
### Table 11.3. Upper ocean layer characteristics

<table>
<thead>
<tr>
<th>Cruise no.</th>
<th>Mixed layer</th>
<th>Chlorophyll a</th>
<th>Column at Z</th>
<th>Daily PP</th>
<th>Bacteria (0–200 m)</th>
<th>Zooplankton (0–200 m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Z&lt;sub&gt;ML&lt;/sub&gt;</td>
<td>T (°C)</td>
<td>σ&lt;sub&gt;θ&lt;/sub&gt;</td>
<td>[N] (μM)</td>
<td>Z&lt;sub&gt;eu&lt;/sub&gt; (m)</td>
<td>ML (mg m&lt;sup&gt;–3&lt;/sup&gt;)</td>
</tr>
<tr>
<td>Oligotrophic site</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>120</td>
<td>22.6</td>
<td>25.7</td>
<td>0.00</td>
<td>97</td>
<td>0.12</td>
</tr>
<tr>
<td>3 leg 1</td>
<td>45</td>
<td>26</td>
<td>24.5</td>
<td>0.06</td>
<td>0.28</td>
<td>110</td>
</tr>
<tr>
<td>3 leg 2</td>
<td>55(25)&lt;sup&gt;10&lt;/sup&gt;</td>
<td>26</td>
<td>24.7</td>
<td>&lt;0.003&lt;sup&gt;9&lt;/sup&gt;</td>
<td>95</td>
<td>0.08</td>
</tr>
<tr>
<td>4 leg 1</td>
<td>60(25)&lt;sup&gt;10&lt;/sup&gt;</td>
<td>23.3</td>
<td>25.6</td>
<td>0.06</td>
<td>0.25</td>
<td>120</td>
</tr>
<tr>
<td>4 leg 2</td>
<td>70</td>
<td>23.7</td>
<td>25.7</td>
<td>&lt;0.003&lt;sup&gt;9&lt;/sup&gt;</td>
<td>102</td>
<td>0.05</td>
</tr>
<tr>
<td>5</td>
<td>85</td>
<td>23.9</td>
<td>25.4</td>
<td>&lt;0.003&lt;sup&gt;9&lt;/sup&gt;</td>
<td>95</td>
<td>0.17</td>
</tr>
<tr>
<td>Mesotrophic site</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>55</td>
<td>19.9</td>
<td>25.8</td>
<td>0.04</td>
<td>50</td>
<td>0.2</td>
</tr>
<tr>
<td>3 leg 1</td>
<td>25</td>
<td>25.8</td>
<td>23.9</td>
<td>0.2</td>
<td>0.4</td>
<td>(40)</td>
</tr>
<tr>
<td>3 leg 2</td>
<td>30</td>
<td>25.3</td>
<td>24.3</td>
<td>0.01</td>
<td>0.3</td>
<td>1.3</td>
</tr>
<tr>
<td>4 leg 1</td>
<td>35</td>
<td>21.8</td>
<td>25.1</td>
<td>0.45</td>
<td>(H)&lt;sup&gt;12&lt;/sup&gt;</td>
<td>27.1</td>
</tr>
<tr>
<td>4 leg 2</td>
<td>40</td>
<td>21.7</td>
<td>25.2</td>
<td>0.7</td>
<td>25</td>
<td>1.25</td>
</tr>
<tr>
<td>5</td>
<td>40</td>
<td>21.5</td>
<td>25.4</td>
<td>0.03</td>
<td>30</td>
<td>0.8</td>
</tr>
</tbody>
</table>

<sup>1</sup> Mixed layer depth
<sup>2</sup> Chlorophyll a concentration
<sup>3</sup> Depth at which Chl a concentration is measured
<sup>4</sup> Primary production
<sup>5</sup> Phytoplankton production
<sup>6</sup> Bacterial abundance
<sup>7</sup> Zooplankton abundance
<sup>9</sup> Zooplankton biomass
<sup>10</sup> Data from previous study
<sup>12</sup> High concentration

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For detailed analysis and further study, please refer to the referenced sources.
<table>
<thead>
<tr>
<th>Layer</th>
<th>Depth (m)</th>
<th>Temp (°C)</th>
<th>Nitrate + Nitrite (mg/L)</th>
<th>Chlorophyll a (mg/L)</th>
<th>Depth (m)</th>
<th>Rate (mg/L/day)</th>
<th>Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>55</td>
<td>18.5</td>
<td>26.2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4 leg 1</td>
<td>40</td>
<td>18.5</td>
<td>25.8</td>
<td>1.5 (H)</td>
<td></td>
<td>59</td>
<td></td>
</tr>
<tr>
<td>4 leg 2</td>
<td>45</td>
<td>18.1</td>
<td>26</td>
<td>10</td>
<td>23</td>
<td>3.5 (H)</td>
<td>162</td>
</tr>
<tr>
<td>5</td>
<td>40</td>
<td>21</td>
<td>25.4</td>
<td>0.25</td>
<td>32</td>
<td>1.2 (H)</td>
<td>1151</td>
</tr>
<tr>
<td>C-5</td>
<td>70</td>
<td>17.1</td>
<td>26.5</td>
<td>9</td>
<td>30</td>
<td>1.2 (H)</td>
<td>65</td>
</tr>
</tbody>
</table>

1. Mixed layer depth ($Z_{ML}$), temperature, density excess ($\sigma_0$), nitrogen (NO$_3$ + NO$_2$) concentration (Pujo-Pay & Raimbault, 1994)
2. Depth of the euphotic layer, $Z_e$ (depth where PAR is reduced to 1% of its surface value)
3. Chlorophyll a concentration within the mixed layer (ML) at the deep chlorophyll maximum (DCM), and depth of this maximum; column-integrated chlorophyll (Claustre & Marty, 1994; H. Claustre, personal communication, 1996)
4. Daily primary production (Morel et al., 1996)
5. Pigment ratio, $F_p$, according to Claustre (1994)
8. Integrated (0–200 m) mesozooplankton biomass (WP-2 plankton net; S. Razoul & G. Gorsky, personal communication, 1996)
9. Below detection level (3 nM) using nanomolar method (Raimbault et al., 1990)
10. Depth of a first minute step in the density profile (see Fig. 11.4A)
11. April 3, 1974; station no. 50 at 25 nm in the NE of the Eutrophic site (CINECA-5, Cruise Report, 1976)
12. H, homogeneous vertical distribution, without deep maximum
Table 11.4. Main characteristics and fluxes at different levels for each site
Asterisks, relative numbers (n × *) used to compare the quantity in question (Sites M and E) with that observed at the reference site (Site O). Analyses of sediment trap collections are not presently completed (i.e. discrepancies remain between carbon flux and dry-mass flux measurements); daggers, cumulative deployment days for sediment trap collection.

<table>
<thead>
<tr>
<th>General information</th>
<th>Site O</th>
<th>Site M</th>
<th>Site E</th>
<th>EUM Cruise no. (reference)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bottom depth (m) and potential temperature (°C)</td>
<td>4600 (1.98)</td>
<td>3090 (2.38)</td>
<td>2030 (3.31)</td>
<td></td>
</tr>
<tr>
<td>Oxygen minimum (μM kg⁻¹)</td>
<td>115</td>
<td>60</td>
<td>70</td>
<td></td>
</tr>
<tr>
<td>(at Z, m)</td>
<td>(700)</td>
<td>(450)</td>
<td>(280–360)</td>
<td>3, 4, 5 (1)</td>
</tr>
<tr>
<td>(at σθ, kg m⁻³)</td>
<td>(27.33)</td>
<td>(27.05)</td>
<td>(26.9–26.95)</td>
<td></td>
</tr>
<tr>
<td>N maximum (NO₃ + NO₂, μM)</td>
<td>31</td>
<td>34.1</td>
<td>33.7</td>
<td>2, 3, 4 (2)</td>
</tr>
<tr>
<td>(at Z, m)</td>
<td>(800)</td>
<td>(600)</td>
<td>(650)</td>
<td></td>
</tr>
<tr>
<td>(at σθ, kg m⁻³)</td>
<td>(27.40)</td>
<td>(27.22)</td>
<td>(27.25)</td>
<td></td>
</tr>
<tr>
<td>pH minimum (at 25 °C)</td>
<td>7.595</td>
<td>7.506</td>
<td>3</td>
<td>3 (3)</td>
</tr>
<tr>
<td>(at Z, m)</td>
<td>(800)</td>
<td>(600)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mixed-layer depth (range) m</td>
<td>45–120*</td>
<td>25–55</td>
<td>40–70</td>
<td>2–5 (1, 4)</td>
</tr>
<tr>
<td>Upper layer (0–200 m depth)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N (NO₃ + NO₂, μM), ML range</td>
<td>0</td>
<td>0.01–0.7</td>
<td>0.2–10</td>
<td>(2)</td>
</tr>
<tr>
<td>Euphotic depth (m)</td>
<td>95–105</td>
<td>25–50</td>
<td>23–32</td>
<td>(5)</td>
</tr>
<tr>
<td>Near-surface Chl (mg m⁻²) (relative number)*</td>
<td>0.08 (1 × )</td>
<td>0.50 (2 × )</td>
<td>2 (25 × )</td>
<td>(5)</td>
</tr>
<tr>
<td>Chl a (mg m⁻²)</td>
<td>23.6 (1 × )</td>
<td>31.0 (1.3 × )</td>
<td>95 (4.0 × )</td>
<td>(5)</td>
</tr>
<tr>
<td>Primary production (mg C m⁻² d⁻¹)</td>
<td>330 (1 × )</td>
<td>870 (2.6 × )</td>
<td>1380 (4.2 × )</td>
<td>(5)</td>
</tr>
<tr>
<td>Particulate organic carbon (mg C m⁻²)</td>
<td>3600 (1 × )</td>
<td>7560 (2.1 × )</td>
<td>12 550 (3.5 × )</td>
<td>4 (2)</td>
</tr>
<tr>
<td>Heterotrophic bacteria (mg C m⁻²)</td>
<td>756 (1 × )</td>
<td>1693 (2.2 × )</td>
<td>3436 (4.5 × )</td>
<td>3, 5 (5)</td>
</tr>
<tr>
<td>Zooplankton (mg C m⁻²)</td>
<td>287 (1 × )</td>
<td>981 (3.4 × )</td>
<td>1151 (4.0 × )</td>
<td>3, 5 (5)</td>
</tr>
<tr>
<td>PG</td>
<td>Calculation</td>
<td>Units</td>
<td></td>
<td></td>
</tr>
<tr>
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<td>-------------</td>
<td>-------</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(1)</td>
<td>( × 6) 44</td>
<td>( × 6) 57,969</td>
<td>( × 5) 151,711</td>
<td></td>
</tr>
<tr>
<td>(2)</td>
<td>( × 6) 44</td>
<td>( × 6) 57,969</td>
<td>( × 5) 151,711</td>
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<td>( × 6) 57,969</td>
<td>( × 5) 151,711</td>
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<td>( × 6) 44</td>
<td>( × 6) 57,969</td>
<td>( × 5) 151,711</td>
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<tr>
<td>(5)</td>
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<td>( × 6) 57,969</td>
<td>( × 5) 151,711</td>
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<td>( × 6) 57,969</td>
<td>( × 5) 151,711</td>
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<td>(7)</td>
<td>( × 6) 44</td>
<td>( × 6) 57,969</td>
<td>( × 5) 151,711</td>
<td></td>
</tr>
<tr>
<td>(8)</td>
<td>( × 5) 3,690</td>
<td>( × 5) 3,690</td>
<td>( × 4) 1,476</td>
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<td>(9)</td>
<td>( × 6) 44</td>
<td>( × 6) 57,969</td>
<td>( × 5) 151,711</td>
<td></td>
</tr>
</tbody>
</table>

Other calculations:
- Total particulate organic carbon (g cm⁻²)
- Total bacterial + microeukarya (m² cm⁻²)
- Micro-eukarya (m² cm⁻²)
- Bacteria (mg C m⁻²)
- Sediments (0-10 cm)
- Cumulative deposition (days)
- Cumulative deposition (days)
- Cumulative deposition (days)
- Cumulative deposition (days)
- Dry mass flux (μg m⁻² d⁻¹) at 200 m above bottom
- Dry mass flux (μg m⁻² d⁻¹) at 200 m above bottom
- Dry mass flux (μg m⁻² d⁻¹) at 200 m above bottom

Notes:
- *Particulate organic carbon (μg C m⁻²)
- Heterotrophic bacteria (μg C m⁻²)
- Micro-eukarya (μg C m⁻²)
- Zooplankton (μg C m⁻²) (relative numbers)
- Water column (0-1000 m depth)
vertical Chl profile, with slightly higher values in the upper layer (0.15 instead of less than 0.10 mg Chl m\(^{-3}\)), and exhibiting a rather diffuse DCM, was observed at the moment of the deepest vertical convection (Fig. 11.4a).

The temporal change of the mixed layer thickness at the E site was rather weak. For the sake of completeness, a density profile typical of April (CINECA 5 cruise) has been added in Fig. 11.4c. It shows denser waters near the surface and a deeper extension of the ML (down to 60–70 m) at this period of the year. In all circumstances, including that of April 1974, the Chl profile was found to be featureless at this site and the algal biomass homogeneously dispersed throughout the mixed layer. It is worth noting that the depth of the mixed layer at this site always exceeded that of the euphotic layer.

At the M site, which was also affected by internal waves (see Fig. 1 in Lazzara et al., 1996), the relatively shallow thermocline was found to be permanent. It was extremely pronounced in October, with a thin ML (25 m); in this case only, a sharp DCM developed below the mixed layer, with short-term variations in chlorophyll concentration. Otherwise, as observed during the other cruises and seasons, a uniform algal biomass was maintained within the entire mixed layer, extending deeper than the euphotic level, as in the E site.

In summary, the O site and the E site were found typical of the two opposite situations that were hoped for, because of the highly contrasted nutrient levels and vertical distribution (Table 11.3). At the M site, the vertical distribution of the phytoplanktonic biomass tends, most of the time, to resemble that of the eutrophic regime, yet with lower pigment concentrations (and change in species composition, see below). The qualifier ‘mesotrophic’ is thus appropriate. During the period of the strongest stratification at this M site, which results in nutrient depletion within the mixed layer, the vertical algal profile conversely tends to resemble that of an oligotrophic regime. However, chlorophyll values are distinctly higher and the DCM is a rather ‘shallow’, compared with the situation in the O site. The regime remains of the mesotrophic type, even if its mode of functioning is different during such stable stratification periods.

**Biological structures in the upper layer at the three sites**

The vertical structure of the phytoplanktonic assemblages at the EUMELI stations has been thoroughly analysed by using flow cytometry and spectrofluorometry (Partensky et al., 1996; Lazzara et al., 1996). A spectrofluorimetric method was developed and used to quantify phycoerythrins (Lantoine & Neveux, 1997). The trophic status of the three main sites and their algal populations has been investigated by using a pigment biomarker approach (Claustre, 1994; Claustre & Marty, 1995; Lantoine & Neveux, 1997). Not surprisingly (Malone, 1980; Chisholm, 1992), large species, including diatoms in particular, predominate at the E site, with relatively high Chl c and
fucoxanthin concentrations. The pigment ratio, $F_p$, was found to be close to 0.9 (defined in Claustre, 1994). Note that $F_p$ is the ratio of the sum of fucoxanthin and peridinin pigments to the sum of all pigments. In brief, it expresses the relative contribution of diatoms and dinoflagellates to any algal assemblage, which in addition may comprise nano- and green flagellates, cryptophytes, cyanobacteria and prochlorophytes. Such $F_p$ values are typical of populations of diatoms and dinoflagellates, and indicate a predominance within the algal assemblage of algae directly involved in new production (Claustre, 1994). In agreement with the $F_p$ values, the contribution of small-sized cells was found to be minor, as revealed by flow cytometry and by the low value of the zeaxanthin:chlorophyll ratio, denoted $Z/C$ (see Table 11.3). Conversely, the lowest $F_p$ values and highest $Z/C$ values were observed at the O site. Cell counting consistently demonstrated the almost complete dominance of tiny species, essentially *Prochlorococcus*, *Synechococcus* and picoeukaryotes. They showed non-random vertical distributions, maintained through the seasons, which are similar to those found in the subtropical Pacific (Campbell & Vaulot, 1993; Campbell *et al.*, 1994). At the M site, a conspicuous feature is the relative importance of cyanobacteria, in the deep maximum when it existed (in October), or within the entire mixed layer, as it was observed in June and again in December. Exceptionally dense *Synechococcus* populations were observed at this location, as well as in its neighbourhood (station EM-02; see Partensky *et al.*, 1996). This predominance had important consequences for the optical properties of the water (Morel, 1997) as well as for the productivity at this site (Morel *et al.*, 1996). Prochlorophytes, also present at the M site, provided a minor contribution to the algal standing stock, so that the high $Z/C$ values were entirely due to the zeaxanthin-bearing cyanobacteria.

Somewhat surprisingly, a comparison of the seasonal values (Table 11.3) or mean values (as reported in Table 11.4) shows that the algal stocks are not markedly different at the M and the O sites. Indeed, the ratio of the vertically integrated Chl biomass at the M site to that at the O site is on average 1.3. This relative closeness mainly originates from the permanent presence at the O site of a deep chlorophyll maximum with algal populations often extending down to 200 m. In contrast, chlorophyll concentration was generally insignificant beyond 70–80 m at the M site. At the E site, the algal biomass is about 4 times larger than that observed at the O site. With relative numbers 1, 2.6, and 4.2 (Table 11.4), the mean primary production values are arranged as expected for oligotrophic, mesotrophic, and eutrophic regimes; in this way they differ from the biomass values themselves. The reason might be found in the photophysiological responses of the algal assemblages typical of the three sites. The photosynthetic parameters of algae have been studied in relation to the thickness of the mixed layer, the nitrogen availability, and the pigment
composition (Babin et al., 1996), and in effect, the photophysiological responses strongly differ in the three trophic situations. Before summarising these results, a first global approach is also informative.

In terms of photosynthetic capacity, the algal population at the M site is definitely more competent than those at the two other sites. This is made clear simply by forming the ratio of the integrated primary production to the integrated chlorophyll biomass, which turns out to be 14 g C g⁻¹ Chl d⁻¹ at both the O and E sites, whereas it is 28 g C g⁻¹ Chl d⁻¹ at the M site. A more accurate comparison must account for the variation in the incident PAR irradiation, from site to site and season to season. It consists of computing $\psi^*$, the bulk cross section for photosynthesis per unit of Chl (Morel, 1978, 1991). For the O site, it had already been shown (Claustre & Marty, 1995) that $\psi^*$ seems to be seasonally constant, with a value around 0.06 m² (g Chl)⁻¹ at the summer solstice as well as near the autumn equinox. The same value actually is found for the E site in June. In contrast, $\psi^*$ reaches 0.11 m² (g Chl)⁻¹ at the M site, a high, albeit common, value (Platt, 1986). These differences in bulk efficiency, and in particular the enhanced photosynthetic capacities at the M site, originate from the differences in photophysiology. Actually, it also reflects a weakness when photosynthetic efficiency is discussed based on chlorophyll only, as soon as other photosynthetically active pigments are abundantly represented, as is the case at the M site, with abundant phycoerythrin-bearing Synechococcus cells. The corresponding characteristics, namely the photosynthetic rate in the light-limited regime ($\alpha$), the maximum quantum yield for C-fixation ($\phi_{C_{\text{max}}}$), and the maximum rate at saturating irradiance ($P_{\text{b}_{\text{max}}}$), were determined through incubation experiments and fluorescence studies (Babin et al., 1996). In particular, the maximum quantum yield for carbon fixation has been found to decrease between the E site, the M site and the O site, with values about 0.05, 0.03 and 0.005 (mol C mol⁻¹ quanta absorbed). The latter is for the mixed layer at the oligotrophic site, where high values of 0.06 were also observed but only in the deep algal population. Part of the variation in quantum yield is clearly to be attributed to the variable contribution of non-photosynthetic pigments (such as zeaxanthin) to total pigments. Another part originates from changes in the fraction of functional PSII reaction centres, measured by using fast repetition rate fluorometry, and is to be related to nitrate availability. The $P_{\text{b}_{\text{max}}}$ values (Fig. 5 in Babin et al., 1996) at the M site are at least twice the values at the two other sites.

These photophysiological parameters were used for a posteriori computations of the vertical profiles of primary production via a modelling approach (Morel et al., 1996), and in this way, they allowed the differences in photosynthetic performances at the three sites to be understood. Only during cruise 3 and at the oligotrophic site were new and regenerated production determinations
performed. By using the $^{15}$N tracer technique, a comparison of nitrate and ammonium assimilation rates allows the $f$ ratio to be estimated (ratio of new to total production) (Dugdale & Goering, 1967; Eppley & Peterson, 1979). In the upper nutrient depleted layer in this site, the $f$ ratio was about 0.10, whereas it reached 0.15–0.18 at the bottom of the euphotic layer (P. Raimbault, personal communication, 1997).

Interestingly, the other (0–200 m) integrated biomass values, namely heterotrophic bacteria and mesozooplankton biomass, and even the particulate organic carbon standing stocks, are all increased by the same factor between the O and the E site, as already found for integrated chlorophyll (i.e. about 4). Such a likeness does not hold true, however, when the M site is compared to the O site. Although the factor for areal Chl content is 1.3, as stated before, those for the other trophic compartments and POC stock are definitely higher (from 2.1 to 3.4; see Table 11.4). If, instead of considering the Chl biomass, the primary production daily rates are compared, a factor of 2.6 is found between the M and O situations, which agrees well with the other factors. Inasmuch as the heterotrophic communities (or the detrital compartment) depend in a direct (or indirect) way on the organic matter synthesised by the primary producers, there is some logic in observing a better correlation with the algal productivity rather than with the algal standing stock itself. However, in the absence of knowledge about the carbon to chlorophyll ratio (not determined) within the phytoplanktonic assemblages investigated, it is difficult to go further into the above explanation supplied as a heuristic hypothesis.

In a global view, however, Dufour & Torréton (1996) found significant log–log regressions of bacterial biomass (expressed as carbon) on chlorophyll concentrations, when all the data for the three sites and depths were pooled together. Notwithstanding the above remark concerning the C: Chl ratio, if a tentative value of 50 is adopted for this ratio (as in Redalje, 1983), the bacterial C to algal C ratio would be 0.64, 1.09 and 0.72 within the 200 m thick upper layer at the O, M, and E sites, respectively. If the same computations are repeated for the water columns inhabited by phytoplankton (namely for the 200, 70, and 50 m thick layers, at the O, M, and E sites, respectively), the above ratios become 0.64, 0.38 and 0.18. Despite its approximate character, such a calculation clearly shows the regular increase of bacterial carbon biomass relative to algal carbon, when the trophic regime changes from eutrophic to oligotrophic (as already described; see, for example, Cole et al., 1988). It is also worth remarking that the ratio of bacterial carbon to POC for the (200 m thick) upper layer is almost constant, with a mean value of 24% (± 3%) at the three sites.

The heterotrophic bacterial production also differs at the three sites and would be significantly related to the photoautotrophic production (Dufour &
Figure 11.7  Dissolved organic carbon (DOC) concentration determined during EUM 4 at all stations along the two contiguous sections from the E site to the O site (re-drawn from Avril, 1995). Below 400 m (not shown), all the values are between 60 and 55 μmol l⁻¹.

Torréton, 1996). Within the upper layer, the measured production rates (via the tritium-thymidine incorporation method) lead to similar turnover times for heterotrophic bacteria (biomass/production) at the E and M site (2–6 d). These turnover times were distinctly increased at the O site, with values between about 8 and 20 d (Dufour & Torréton, 1996). Bacterial utilisation of glucose is also discussed in relation to bacterial biomass and production in the three sites (Bianchi et al., 1998).

Within the surface waters, a gradient in the partial pressure of CO₂ (pCO₂) occurs along the section between the three sites (Copin-Montégut & Avril, 1995). In the recently upwelled waters spreading at the E site, pCO₂ remains high, with values (computed for 25 °C) ranging between 550 and 600 μatm (compared with 353 in air). At the M site, outgassing and net biological consumption reduce the supersaturation, and pCO₂ values (at 25 °C) of 410 and 405 μatm were measured during the two cruises EUM#3 and 4. At the O site, pCO₂ values were found to be slightly above equilibrium (370 ± 5 μatm) in September–October, as well as in June.

Depth profiles of the dissolved organic carbon (DOC) were systematically determined with the high temperature catalytic oxidation method (Avril, 1995). In contrast to all the properties briefly examined above, the DOC distribution
appeared to be rather uniform (Fig. 11.7). In this vertical section, an increase by only 10 μmol l⁻¹ can be observed between the O and E sites; it appears to be weak compared with the gradient in productivity. This increase, related to the freshly produced, and presumably labile, DOC fraction, is confined to the near-surface layer (Z < 50 m). Once integrated over a layer 200 m thick, the DOC contents do not differ significantly between the three sites and amount to 190 g C m⁻² (mean concentration 0.95 g C m⁻³). Such a conservative behaviour tends to demonstrate that the biological production of DOC, related to phytoplankton abundance, is balanced by consumptive processes, in which bacterioplankton (see below) play a major role. These upper layer values exceed those uniformly found below 500 m and down to the bottom, steadily around 55 μM (or 0.67 g C m⁻³) at all stations of the E–M–O section. Changes in DOC concentration were insignificant and barely discernible between cruises 3, 4, and 5 (Avril, 1995). The above DOC concentrations are similar to those determined in the northwestern Mediterranean Sea (Copin–Montégut & Avril, 1993), and distinctly higher than those observed in the equatorial Pacific Ocean (Carlson & Ducklow, 1995). Similar conclusions can be drawn from a preliminary study (Pujo-Pay, 1995) of the dissolved organic nitrogen (DON) distribution. The concentrations (about 5–6 μM) in the upper layers were similar, whatever the site, and exceed those uniformly found (about 3 μM) at depth.

Water column characteristics and biomass at the three sites
The abundance, community structure, and vertical distribution of the macroplanktonic and micronektonic groups, as determined from oblique (0–1000 m) hauls, have been analysed at the three sites (Andersen et al., 1997). The diversity index and vertical migration amplitude both increase from the E site to the O site. Zooplanktonic C biomasses, integrated over the 0–1000 m water column, are distributed at the three sites according to the following numbers: 1, 3.6 and 6.8 (see Table 11.4). These values span an interval slightly wider than that characteristic of the upper (0–200 m) layer for parameters such as primary production rates, POC content, and even 0–200 m integrated zooplankton. This widening could indicate an increasing efficiency in the C transfer between the primary and the secondary producers, when changing from an oligotrophic to a eutrophic system. It is worth remarking that the zooplanktonic biomass, more abundant at the E site, is also more regularly spread out within the water column. The ratios of the 0–1000 m biomasses to the 0–200 m biomasses are 2.24, 2.34, and 3.80 at the O, M and E sites, respectively, and are to be compared with the value of 5 that would correspond to a uniform distribution. The diel variations and the effect of vertical migrations (G. Gorsky, personal communication, 1997) are smoothed out in these numbers, by averaging all the plankton net catches.
Heterotrophic bacterial carbon values, when integrated from surface to bottom, are almost equal at the E and M sites, and on average 2.4 times higher than that found at the O site. In terms of mean concentration, computed by dividing the biomasses by the bottom depths, the relative numbers (namely 1, 3.42, and 5.66) are more contrasted between the sites and arranged in the usual manner. Indeed, when the effect of the water column height is removed, these relative numbers fall into the range found for other relative numbers; in particular, they are close to those related to the 0–1000 m mesozooplankton compartment (amounting to 1, 3.6, and 6.8, respectively).

After the overwhelming DOC pool, particulate matter (POC) represents the second most important carbon pool. These particles, which include small living organisms (essentially bacteria), remain dominated by various organic detritus and small-sized, slowly sinking debris. The whole water-column POC contents are roughly the same (from 26 to 31 g C m$^{-3}$) for the three sites. Once converted to mean concentrations, as was done for bacterial C, the relative contrast between sites is restored; indeed, the relative numbers for the O, M and E sites are 1, 1.41, and 2.58, respectively. This inter-site contrast, however, is noticeably weaker than for other trophic compartments. This narrowing could be consistent with the hypothesis, made for oligotrophic environments, of the presence of smaller debris, generated by an ecological system based on picoplanktonic species and bacteria. In such a regime, the residence time within the water column of these tiny suspended particles would be increased accordingly. It is worth recalling that the POC pool represents a very small fraction of the total (POC + DOC) organic carbon pool. In the present case, the POC to DOC ratios are only 0.9, 1.2 and 2.2%, for the O, M and E sites, respectively.

**Fluxes and benthic responses**

As stated in the Introduction, the sedimenting material, sequentially collected by traps, has not yet been fully analysed for the entire deployment period and for all parameters. Nevertheless, detailed specific studies are published (Legeleux et al., 1994a,b, 1995, 1996; Relexans et al., 1996; Tachikawa et al., 1997; Hamelin et al., 1997). It is therefore unsafe and premature to relate the corresponding numbers or annual means to those pertaining to the upper layer or water column quantities.

With the available results, however, it can be noted that the mass fluxes, determined at 2500 m at the M and O sites (in a ratio of 5.1 to 1; Table 11.4), merely reflect the general tendency observed for other parameters. As a preliminary comment about the magnitude of these particle fluxes, it is worth remarking that they are well arranged within the general trend to be related to biogeochemical provinces with their peculiar planktonic ecosystems (Jickells et
al., 1996). These authors analysed the sediment trap data obtained along a N–S transect from 48° to 19°N, at about 20°W. Three sites of this transect, located off Mauritania, represent typical oligotrophic subtropical conditions, namely the sites studied by Lampitt (1992), by Kremling & Streu (1993) and by Jickells et al. (1996). The mass fluxes amounted to 33.4, 51.0, and 27.4 mg C m⁻² d⁻¹, respectively. Over two years, a very similar mean flux is observed at the O site, namely 36.2 mg C m⁻² d⁻¹. In addition, over a shorter period (120 d, analysed by Legeleux et al., 1996), the organic carbon fraction (4.7%) and the calcium carbonate fraction (66.7%) are practically confounded with the corresponding values given by Jickells et al. (1996; their Table I) for the three sites referred to above. For the M site, the present results can also be compared with those of Wefer & Fischer (1993). Their results were collected at nearby sites CB₁ and CB₂, located about 300 km off the Mauritanian coast at the latitude of the E site, in a regime presumably similar to that of the M site. The two successive time-series provided mean mass fluxes of 183 mg m⁻² d⁻¹ (during CB₁, trap depth 2195 m) and 148 mg m⁻² d⁻¹ (during CB₂, trap depth 3502 m); the fluxes recorded at the M site (2500 m) consistently result in a mean value of 178 mg m⁻² d⁻¹. Over a restricted period (120 d; see Legeleux et al., 1996), the organic carbon fraction at the M site amounted on average to 9.2%, with important fluctuations, compared with mean values of 4.1 and 3.0% for CB₁ and CB₂. The CaCO₃ fraction remained steadily around 56%, compared with 42.9% and 51.7% at CB₁ and CB₂. The lithogenic fraction varied between 11% and 35% at the M site, whereas it was 40.8% at CB₁ and 37.9% at CB₂.

Another, less direct, comparison is also possible for the site studied by Jickells et al. (1996), located at 19°N 20°W, which practically coincides with the EM-02 station (Table 11.1), intermediate between the E and M sites. As expected, the mass flux at this site, 245 mg m⁻² d⁻¹, at 2190 m as well as the organic carbon fraction, 12.6%, are both distinctly higher than the corresponding values at the M site.

The biomass of micro- and meio-benthos were measured and the benthic metabolic activities studied in parallel with determinations of the organic content and composition of the upper part of the sediments (see Relexans et al., 1996). According to the conclusions of these authors (see also Table 11.4), the benthic response to food supply from the upper layers is rather linear, to the extent that the relative numbers for benthic microbial biomass and primary production in the upper layers (at the O and M sites) are relatively close. In the same reference, it is also suggested that micro- and meio-benthos could be more efficient utilisers of the downwelling carbon supply than their counterparts in the eutrophic site.

The macrofauna community structure, the spatial patterns, and scale of the organisms’ aggregation were studied during three cruises (2, 3, and 4); 53 box
core samples were obtained by using a modified USNEL sampler (Cosson et al., 1997). The mean densities of the total benthic macrofauna, everywhere dominated by the Polychaeta, decreased significantly from the E site, to the M and O sites, as did the number of taxonomic groups (Sibuet et al., 1993; Cosson et al., 1997). The benthic response to primary productivity within the upper layers depends on both the organic matter flux exported downward and the bottom depth, or the distance travelled before deposition. It is worth recalling that for the EUMELI sites, the decrease in biological activity within the upper layers parallels the increase in bottom depth. A positive linear relation between the macrofaunal density at the three sites and the calculated organic carbon flux at the bottom level has been obtained (Rabouille et al., 1993). The organic carbon burial flux would represent an extremely small fraction of the flux that reaches the bottom, which means that this energy supply is efficiently exploited by the benthic organisms (Khripounoff et al., 1998; see also Table 7 in Cosson et al., 1997).

Perspective and conclusion

Studies are still ongoing in various fields, in particular those related to sedimentation or to the exchanges and partitioning of chemical species between the dissolved fraction, the minute particles (collected by in situ pumping), and the sinking larger particles (collected in the drifting and moored traps). Results have recently been presented about the distribution of rare earth and neodymium isotopic composition in the suspended matter (Tachikawa et al., 1997), and regarding the use of lead isotopes as tracers of exchange between the particulate and dissolved matter (Hamelin et al., 1997). The composition of the sedimentary organic matter and of the sedimenting material collected in the traps, and the relative importance of the lithogenic, opal, and calcite fluxes still deserve further studies. The susceptibility of biogenic elements to re-mineralisation during settling, and in general all the processes within the water column, are not yet analysed as completely as those occurring in the upper layer. The same can be said about the modelling of the complex and intricate processes involving various compartments and the whole water column.

In effect, with a series of papers published in a special section of Deep-Sea Research, Part I (vol. 43, no. 8), the algal and heterotrophic bacterial compartments in the upper layer are well documented and described in detail. The specific studies of the phytoplankton bio-optical and physiological properties (Babin et al., 1996) have also allowed a validation of the spectral primary production model to be performed (Morel et al., 1996). To the extent that the community structures and photophysiological responses of algae are
very different at the three sites, a meaningful assessment of the predictive skill of the carbon uptake model was attainable. The outputs of the model have been compared with in situ determinations at all levels, as well as with the resulting column-integrated primary productions. Because of this comparison, a 'version 2' of Morel's (1991) model was proposed. It differs from the previous version by a slight change within the set of standard photophysiological parameters, without modifying its general parameterisation. This version, adapted for general use (Antoine & Morel, 1996), was applied at a global scale (Antoine et al., 1996) to the monthly maps of the satellite chlorophyll concentration, as derived from the coastal zone color scanner data archive (Feldman et al., 1989). This model represents the initial segment of a series of models, dealing with the carbon flux from the surface down to the sediment. They are currently in progress and will be presented in their first versions at the JGOFS modelling symposium.

In reference to the initial strategy for EUMELI and to its main objectives, as summarised in the introductory section, several comments can be made. The general patterns expected for the zone and the three selected sites have been verified during the successive campaigns. Submitted to similar climatic conditions, the differing trophic regimes were characterised by mean primary production rate spanning a factor of 4 approximately. The other non-algal compartments and stocks related to the initial formation of particulate organic matter through photosynthesis are arranged roughly in the same way, as are the various fluxes within the water column and down to the bottom. This still preliminary conclusion tends to support the validity of hypotheses (necessarily made, but always questionable) underlying such a one-dimensional approach. Future detailed studies will probably discover some nuances. With abundant documentation in contrasted situations, and a databank available soon, the framework for further process studies, or for development and validation of models and use of future satellite data, is prepared.

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