Optical properties and radiant energy in the waters of the Guinea Dome and the Mauritanian upwelling area in relation to primary production

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Two water types may be distinguished according to their optical properties, themselves related to the nature of seston. For the first type, the optical properties are dominated by the influence of the algal biomass and associated detrital material. Belonging to this type are offshore waters in the Mauritanian upwelling zone and in the Guinea Dome region, especially in the deep productive layer. Nearshore waters along the Mauritanian coast are permanently turbid with a high load of resuspended sediment. They form the second type. Measurements of seston concentration and of particulate organic carbon corroborate this optical distinction.

For both kinds of waters, the Photosynthetic Available Radiation (PAR), the thickness of the euphotic layer, and the spectral composition of the remnant light are compared. The offshore and coastal waters also differ strongly with respect to their colour, which reflects their backscattering and spectral absorption properties.

The Photosynthetically Stored Radiant energy (PSR) stored as chemical energy, is compared with PAR. A dimensionless efficiency ε is computed, which may vary from 0-03 % to 8 % between the surface and the bottom of the euphotic layer in the Mauritanian zone and from 0-01 to 3 % in the Guinea Dome. For the whole layer, the energy storage through the photosynthetic process represents about 0-2 % of the incident energy in the case of coastal waters, and it is two to four times higher in the more productive waters offshore Mauritania. The corresponding value for the Guinea Dome is 0-04 % on average.

Introduction

The northeast tradewinds, blowing almost parallel to the coast from Morocco to Senegal, provoke a transport of the surface waters away from the shore, thus inducing an upwelling of deep water near the coast. The latitudinal position of these upwellings is dependent on the season (Wooster et al., 1976). Off Mauritania, in the vicinity of Cape Blanc and Cape Corbeiro, they are practically permanent, but particularly active in spring. The cruise CINECA 5 of "Jean Charcot" (Fig. 69B) took place during this season (1 March–20 April 1974). The following discussion is based on the results acquired during this cruise, and also on those results, although less numerous, obtained during the cruise CINECA–Charcot 2 (third part, 1–28 April 1971), off Cape Timiris.

Farther offshore and to the south of the Cape Verde Islands, a vast cyclonic gyre appears, when not opposed by the NE tradewinds, i.e., in summer when their southward extension is minimal. This gives rise to a hydrological dome-shaped structure. It is characterized by the presence of a surface layer of warm (T > 27°C) homogeneous water, which reduces in thickness towards the centre of the dome (15–25 m), and by a strong thermal gradient below this layer. This structure was studied during the cruise GUIDOM-Charcot (18 September–13 October 1976, Fig. 69A).

The aims of this paper are i) to present and discuss the results obtained in both these regions, concerning the optical properties of the waters and the penetration of solar radiation; ii) to study to what extent these properties are linked to and explainable by the amount and the nature of the seston present; and finally iii) to examine the consequences of the optical properties upon the photosynthetic activity within the euphotic layer.

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Measurements

The methods and instruments used for optical measurement during the cruises CINECA-Charcot 2 and 5 and GUIDOM-Charcot have been described and the results obtained presented earlier (Morel and Caloumenos, 1973; Morel and Prieur, 1976b,c; 1977b; Prieur and Morel, 1976; 1977). These measurements were:

Continuous measurements of surface radiation during daytime (Eppley pyranometer).

Profiles of the penetration of the Photosynthetic Available Radiation (PAR), measured in terms of quanta for the 370–700 nm band (CINECA 2: 10 stations; CINECA 5: 31 stations; GUIDOM: 11 stations).

Spectral analysis of downwelling, $E_d(\lambda)$, and upwelling irradiance, $E_u(\lambda)$, at various depths, at the same stations.

Vertical profiles of the scattering coefficient, $b$ (CINECA 5: 42 stations) simultaneously with temperature profiles (GUIDOM: 79 stations).

Spectral measurements of absorption by dissolved substances ("yellow substances") (CINECA 5: 11 stations).

Determination of the dry weight of seston (CINECA 5: 18 stations), and a CHN analysis carried out on the filters (Collos, personal communication).

Primary production measurements during these three cruises (Minas, 1976; Minas and Minas, 1977).

The two water types

From their optical properties, two water types can be distinguished. The nature and the abundance of the seston, so far as they govern the optical properties of the water body, constitute the real basis of this distinction. The optical effect of seston is different according to whether it is predominantly biogenous and organic or highly mineralized. Obviously the first situation is encountered offshore, the latter in the coastal zone.

Offshore waters with dominant biological material

In these waters the terrigenous influence is reduced to a minimum and the phytoplanktonic development becomes the main cause of variations in optical properties. With increasing biomass, their optical properties change gradually from those of the blue oligotrophic waters. This change is not only due to the presence of the algal cells, but also to the biogenous detrital material which derives from living cells by natural decay or grazing. To the extent that this material roughly covaries with the algal biomass, the variations in optical properties remain approximately correlated with the pigment content – even though these pigments, by their
specific and selective absorption, are only partly responsible for the variations actually observed.

These conditions where the seston is predominantly biogenous were encountered in the Guinea Dome and also off Mauritania beyond the coastal zone.

The Guinea Dome
At the centre of this zone, there exists in September a mixed layer of 15 to 30 m thickness, in which the temperature is slightly higher than 27°C. The nutrient concentration in this surface layer is very low and even nil in the case of nitrates. As remarked by Voituriez and Dandonneau (1977), the depleted nitrate layer is thicker than the mixed layer. Nitrates first become perceptible in the thermocline, more or less coinciding with the 18°C isotherm. So the appearance of nitrate occurs 15 or 20 m below the base of the homothermal layer, according to our observations (in September and October), instead of 6, on average, in August, when the dome structure is more pronounced (Voituriez and Dandonneau, 1977). At the same level, inside the thermal gradient, a small salinity feature reveals the intrusion of another water mass, the South Atlantic Central Water (see Fig. 70).

At this level, where the nitrate concentration increases rapidly from zero, the Photosynthetic Available Radiation is still sufficient, at least in the central part of the dome, and the phytoplankton finds conditions favourable for development. Chlorophyll as well as turbidity reach a maximum at this level (Fig. 70). The chlorophyll maximum is generally sharp, because a few metres farther down, light becomes the limiting factor. The turbidity maximum (measured by the total scattering coefficient) coincides approximately with the 1 μgat l⁻¹ N/NO₃ isopleth. It reflects the presence of phytoplankton and associated detrital particles. The pigment maximum often occurs a few metres below the turbidity maximum (Fig. 71).

The algal biomass and the seston content are very low in the surface layer (Chl a < 0.1 mg/m³; seston, dry weight < 0.05 g/m³) and the optical properties are those of clear oceanic waters. However, they are not as clear and blue as the truly oligotrophic waters such as those encountered in the Sargasso Sea and in some parts of the Mediterranean Sea. Below this layer appears the productive layer. Here the Chl a concentration varies between 0.3 and 1.5 mg/m³ and the seston content between 0.1 and 0.2 g/m³ (dry weight). The
For the stations surveyed in these waters, the chlorophyll $a$ content in the euphotic layer varied between 1 and 18 mg/m$^3$ and the seston content between 0-4 and 1-7 g/m$^3$ (Morel and Prieur, 1976a). The ratio POC/seston (Fig. 73), though lower than in the Guinea Dome since it varies between 20 and 30 %, still supports the organic nature of the particles. Five stations are chosen to show the possible variations of the optical properties of these waters (Table 6):

Station 70 is located beyond the upwelling zone;

Station 19 is within a newly upwelled water patch, where nutrients are abundant. Phytoplanktonic development is just beginning and the waters are still relatively clear;

Station 71 is an example where stabilization at the surface of the upwelled water has allowed an important algal growth (maximum chlorophyll content observed). Thus the thickness of the euphotic layer is reduced and the nutrient resources are almost exhausted;

All the other stations carried out offshore correspond to intermediary situations between the extreme cases of stations 19 and 71, and two examples are provided by stations 67 and 92.

**Coastal waters**

Off Mauritania, the continental shelf is 50 km broad and its edge coincides with the 100 m isobath. The extension of these shallow depths and the strong agitation induced by the tradewinds explain the permanent high turbidity of the coastal band. The present observations, as well as those by Kullenberg (1974; 1978) off Cape Timiris, systematically support this fact. The front between the milky-green coastal waters and the dark green offshore waters is often marked in a clear-cut manner. It coincides approximately with the 40 or 50 m isobath and does not reflect a hydrological structure or discontinuity. Vertical turbulence extends over a layer of at least 40 m thickness, and this agitation, churning up the sediment, brings back and keeps in suspension abundant detrital material. One may suppose that when the upwelling occurs over the inner shelf (weak winds), the cold waters along the coast would be clear. However, the opposite is found to be true (Fig. 72 right). The turbulence renders these waters turbid, as fast as they are upwelled.

The algal biomass is markedly less here than offshore (Chl $a$ varying between 1 and 3 mg/m$^3$), whereas the seston content appears higher (1-4 to 2-5 g/m$^3$). These detrital particles are highly mineralized$^2$, as evidenced

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$^2$ Since the terrigenous influx is small due to the arid climate, this particulate matter mainly originates from biological activity. However these particles are not newly formed, as offshore. The state of mineralization of this resuspended sediment is much more advanced.
by the low values (between 7 and 16 %) for the ratio POC/son (Fig. 73A). It should be noted that the carbon measured in these conditions is quite representative of the organic part, because the classical value of the order of 5-5 carbon atoms per nitrogen atom is preserved (Fig. 73B).

In spite of the difference in chemical composition, the relations between the light-scattering coefficient, \( b \), and the seston content are not significantly different for the coastal or offshore waters (Fig. 74). In coastal waters, \( b \) ranges from 1 to more than 3 m\(^{-1}\). On the other hand, the lowest values observed offshore, in newly upwelled waters, are around 0-35 m\(^{-1}\). However, when the algal biomass is important, \( b \) reaches values as high as 1-7 m\(^{-1}\), that is to say within the range of the coastal values.

Four stations are selected as representative of the coastal-type water (Table 7):

Stations 16 and 72 are very typical of these waters with milky appearance. Stations 6, 76 and 47 (although pigment concentration is higher at station 47) could have been taken as other examples;

Stations 35 and 63 are at the limit of the coastal zone and the special characteristics of these waters are less pronounced.

Comparison of optical properties
Photosynthetic available radiation (PAR)
PAR is defined as the amount of radiant energy, expressed as quantum units, available at a particular depth, within the approximate spectral range 350 to 700 nm (UNESCO/IAPSO Working Group 15 recommendations; Tyler, 1966). Figure 75 shows the relative decrease of PAR with depth, \( Z \), for the various stations of the cruises CINECA 5 and GUIDOM.

For the Guinea Dome, all the curves reveal the particular two-layer structure of this zone. Systematically, towards 35–40 m, a change of slope appears which cor-
responds to the productive layer where the diffuse attenuation coefficient, $K$, is higher. From 60 m downwards, the waters become clear again (see also Fig. 70) and the slopes are similar to those observed for the surface waters. The depth, $Z$ (1%), where PAR is reduced to 1% of its surface value, varies between 48 and 60 m.

For the offshore waters of the Mauritanian upwelling, $Z$ (1%) varies between 12 m for the waters richest in phytoplankton (station 71) and more than 30 m at the stations situated seaward and beyond the upwelling.

### Table 6. Data for selected offshore stations in the Mauritanian upwelling area

<table>
<thead>
<tr>
<th>Date</th>
<th>Station</th>
<th>Chl a (mg/m³)</th>
<th>N/NO₃ (µgat/l)</th>
<th>T (°C)</th>
<th>Z (1%) (m)</th>
<th>$b$ (m⁻¹)</th>
<th>$\bar{R}$ (%)</th>
<th>$\lambda_{dom}$ (nm)</th>
<th>$P$ (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1974</td>
<td>9 Apr</td>
<td>2.2</td>
<td>1.2-1.6</td>
<td>17.5</td>
<td>29</td>
<td>0.7-1.1</td>
<td>1.20</td>
<td>493</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td>17 Mar</td>
<td>1.0-2.0</td>
<td>12.9</td>
<td>15.9</td>
<td>24</td>
<td>0.4-0.5</td>
<td>0.75</td>
<td>495</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>6 Apr</td>
<td>10.3-4.7</td>
<td>3.4-5.7</td>
<td>16.9</td>
<td>19</td>
<td>0.7-1.2</td>
<td>0.73</td>
<td>504</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>17 Apr</td>
<td>9.9-8.0</td>
<td>2.5-7.0</td>
<td>16.1</td>
<td>15</td>
<td>0.9-1.1</td>
<td>0.71</td>
<td>537</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>11 Apr</td>
<td>12.0-18.4</td>
<td>0.1-1.5</td>
<td>16.4</td>
<td>12</td>
<td>1.5-1.7</td>
<td>0.55</td>
<td>560</td>
<td>35</td>
</tr>
</tbody>
</table>

### Table 7. Data for selected coastal stations in the Mauritanian upwelling area

<table>
<thead>
<tr>
<th>Date</th>
<th>Station</th>
<th>Chl a (mg/m³)</th>
<th>N/NO₃ (µgat/l)</th>
<th>T (°C)</th>
<th>Z (1%) (m)</th>
<th>$b$ (m⁻¹)</th>
<th>$\bar{R}$ (%)</th>
<th>$\lambda_{dom}$ (nm)</th>
<th>$P$ (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1974</td>
<td>16</td>
<td>1.1-1.9</td>
<td>7.1</td>
<td>17.5</td>
<td>10</td>
<td>3.7-3.0</td>
<td>7.98</td>
<td>510</td>
<td>15</td>
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<td></td>
<td>12</td>
<td>1.6-1.0</td>
<td>11.5</td>
<td>16.0</td>
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<td>23</td>
<td>1.5-1.9</td>
<td>10.2</td>
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<td>1.6-1.4</td>
<td>4.51</td>
<td>496</td>
<td>31</td>
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<td></td>
<td>5</td>
<td>2.3-3.1</td>
<td>8.4-10.6</td>
<td>15.8</td>
<td>23</td>
<td>0.87</td>
<td>2.50</td>
<td>494</td>
<td>33</td>
</tr>
</tbody>
</table>

*a If two numbers are given (for chlorophyll, nitrogen, and the scattering coefficient), they express the extreme values of the corresponding parameter, as observed within the layer extending from the surface to $Z$ (1%). A single value is given for temperature which is practically constant in the same layer (to within 0.2°C). The dominant wavelength, $\lambda_{dom}$, and the excitation purity, $P$, are computed from the spectral reflectance, $R(\lambda)$, for the surface layer. The mean value of $R(\lambda)$ calculated over the whole spectrum is written $\bar{R}$. #
zone where the algal biomass is less important (stations 70, 68). For the coastal waters, $Z\, (1\%)$ is generally smaller, varying from 10 m at the coast (station 16) to 23 m at the limit of this zone (station 63). However, the value of $Z\, (1\%)$ is not sufficient to discriminate between the offshore and inshore waters, any more than the value of $b$, as stated earlier. In fact, the thickness of the euphotic layer is more variable offshore than inshore, but thicknesses between 10 and 20 m can be observed in both zones.

The distinction between the two types of water appears if one studies the depth $Z\, (1\%)$ as a function of the average pigment content (Chl $a$ + Phaeo $a$) calculated for the euphotic layer (Fig. 76). When this content increases, $Z\, (1\%)$ decreases regularly in the case of the offshore water where the biogenous material determines the optical properties. In contrast, the coastal stations do not follow this general rule. For equal pigment concentrations, $Z\, (1\%)$ is markedly reduced as a result of the presence of resuspended sediment. The exceptional character of these coastal waters is clearly brought out by this representation.
Figure 76. Thickness of the euphotic layer, defined by Z (1%), depth where PAR is reduced to 1% of its surface value, shown as a function of the average pigment concentration (Chl a + Phaeo a) within this layer, expressed as mg/m². Crosses: GUIDOM stations; triangles: CINECA 2 stations; stars: CINECA 5 offshore stations; and circles: CINECA 5 inshore stations. The dashed curve is derived from Lorenzen's statistical expression (1972), transformed into

\[
\ln (\text{Chl a}) = 13.3 - 3.82 \ln Z (1\%)
\]

where (Chl a) is the average concentration in the euphotic column. In Lorenzen's equation, total chlorophyll is considered, i.e. the product (Chl a) × Z (1%).

Spectral composition of the radiative energy

Figure 77, which shows the spectral values of downwelling irradiance at diverse depths for station 43, is representative of all the measurements performed in the region of the Guinea Dome. For the surface layer the maximum is situated around 460 nm and the radiative energy for the blue-violet part of the spectrum (400–460 nm) remains important.

The spectral modification begins on entering the productive layer (between 30 and 35 m at this station). This is marked by a rapid attenuation of the blue radiations, mainly due to the presence of the pigments. The maximum shifts towards 490 nm and the radiative energy is concentrated in the 460–550 nm band.

For the Mauritanian region, two series of spectral measurements have been chosen (stations 71 and 16) because they are most typical of the water types, offshore and inshore respectively. It may be noted that even though the maxima of the spectral curves occur at the same wavelength (λ = 570 nm) in the two cases, the spectral compositions are quite different at approximately equal geometric depths (or also at approximately equal optical depths, since for both these stations, the total attenuation coefficients are similar).

The offshore waters (71) where the phytoplankton is abundant, have a much more pronounced filtering effect on light than the water charged with sediments (station 16). In the first case, the light tends to become monochromatic (green-yellow) and the energy is con-
centred in a narrow spectral band. At 12 m, 50% of the energy is within the 515–595 nm band. In contrast, at station 16, at 9 m, the blue radiations, strongly absorbed in the previous case, persist, and the spectral band containing 50% of the available energy is here much broader, extending from 465 to 595 nm.

This "narrow" or "broad" filter effect of the two water types is still more remarkable if one considers the upwelling irradiance \( E_u \) instead of the downwelling irradiance (not reproduced here, see Morel and Prieur, 1976b).

Stations 71 and 16 constitute for each of the two water types the extreme and most characteristic examples. In order to examine the possible variations within each category of water, without multiplying the figures, a synthetic approach is to study the spectral values of the diffuse attenuation coefficient \( K(\lambda) \) which governs the decrease of the irradiance with depth, and the modification of its spectral composition.

Spectral values of the diffuse attenuation coefficient \( K_d(\lambda) \)

For clear oligotrophic waters, the spectral values of \( K_d(\lambda) \) (see Appendix, note 1) are obviously minimal throughout the spectrum. For comparison, an example of such a \( K_d(\lambda) \) curve is shown which corresponds to the deep blue water of the Sargasso Sea (Fig. 78A, B).

The presence of diverse dissolved and particulate material increases the absorption and the scattering and, consequently, \( K \). According to the nature of these substances, or, as mentioned before, according to the zone, offshore or coastal, the \( K(\lambda) \) curves exhibit different shapes.

For the offshore waters, (Fig. 78A), the effect of the specific absorption of pigments and phaeopigments can be detected in the increase of \( K_d(\lambda) \) values: peak at 665 nm of chlorophyll \( a \), maximum from 410 to 440 nm due to phaeophytin and chlorophyll, shoulders of chlorophyll \( c \) at 630 nm and of carotenoids at 480 nm. These effects are very pronounced when the biomass is important (e.g. station 71). The detrital retinue also contributes to the increase in values of \( K_d(\lambda) \), but in a less selective manner. The modification of the spectrum is roughly related to the concentration of chlorophyll \( a \), taken as a biomass index. However, a strict linearity cannot exist since the relative proportions between the live cells and the diverse debris may vary according to the age of the population and the importance of grazing.

For the deep productive layer in the Guinea Dome, and off Mauritania (station 70) when the chlorophyll content is not too high, the minimum of \( K_d(\lambda) \) is situated around 530 nm. When the algal biomass increases, the "V" shape of the curve appears more and more pronounced. The \( K \) minimum becomes narrower and shifts towards 570 nm. It has been previously remarked that this maximum shifts from 450 nm up to 570 nm when the chlorophyll concentration increases from 0 to more than 10 mg·m\(^{-3}\) (Morel and Smith, 1974). In this type of water, where the properties are determined essentially by the biogenous material, it is not likely that the \( K \) minimum can pass beyond 570 nm. This limit is imposed by the combined effects of the absorption minimum of pigments which lies around 560–580.
nm, and the rapidly increasing absorption values of water beyond 580 nm.

For the coastal waters, where the algal biomass is relatively low, the attenuation is chiefly due to the resuspended sediment. Its influence on the spectral \( K \) values is quite different (Fig. 78B). The broad minimum passes from 490 to 560 nm (stations 63 and 16) with increasing seston content and these "U"-shaped curves remain very flat throughout this spectral band. This corresponds to the "broad" filter effect mentioned earlier.

It can be added that some intermediary situations have been observed in the frontal zone, between the coastal turbid waters and the offshore productive waters, where the biomass and sediment in suspension are equally important (e.g., station 47, CINECA 5; see Morel and Prieur, 1977a).

"Yellow substance" and classification of the waters

Two categories of waters have been defined here on the basis of the nature of the seston, essentially biogenous on the one hand, and highly mineralized on the other. These categories do not correspond to the water types of Jerlov's classification. In the revised presentation of this optical classification, Jerlov (1976) notes that his "coastal" waters (types 1 to 9) are defined on the basis of observations made near the Scandinavian and North American coasts, where the concentration of yellow substance is high, and constitutes the predominant cause for the increase in attenuation. Absorption of these substances gives a particular form to the spectral values of \( K_d(\lambda) \) (see Fig. 78C): a steep slope towards the violet region, relatively low values in the red region, and a minimum at 525–550 nm. In relation to the two categories considered here, these waters would form a third category within which the so-called types 1, 3, 5, 7, and 9 establish a gradation.

One of the reasons why the actual \( K_d(\lambda) \) curves differ from the curves of Jerlov's classification is the low quantity of yellow substance in the upwelling regions. Measurement of spectral absorption performed on filtered samples gave low values (Fig. 79: 0.10 to 0.18 m\(^{-1}\) at 400 nm and less than 0.05 m\(^{-1}\) beyond 500 nm. Compared with the \( K_d \) values, it can be concluded that the contribution of dissolved yellow substance to total attenuation remains weak, even though the slope towards \( UV \) is at least partly due to the presence of this substance.

Spectral reflectance \( R(\lambda) \) and "colour" of the water

\( R \) is defined as the ratio, at a given depth, of the upwelling irradiance \( E_u \) to the downwelling irradiance \( E_d \). The spectral values of \( R(\lambda) \) examined here are the values for the surface layer. They are obtained by taking the ratio of \( E_u(\lambda) \) values, measured just below the surface, to the \( E_d(\lambda) \) values of the incident irradiance, measured just above the surface. Figure 80 shows the spectral values of \( R(\lambda) \) corresponding to the stations listed in Tables 6 and 7.

The ratio \( R \) is particularly sensitive for establishing the distinction presented here between the two categories of waters. These results have already been presented in view to remote sensing applications (Morel and Prieur, 1977a). Some of the essential features and their interpretation are briefly reviewed.

With sufficient approximation, \( R \) can be considered to be proportional to the ratio \( b_b/a \), where \( b_b \) is the backscattering coefficient and \( a \), the absorption coefficient. This latter coefficient differs from \( K_d \) (cf. Appendix, note 1), but can be deduced from it. Absorption values, \( a(\lambda) \), are smaller than \( K_d(\lambda) \) values, but their spectral behaviour is similar. It is therefore logical that the \( R(\lambda) \) curves exhibit roughly the form of inverted \( K_d(\lambda) \) curves (if \( b_b \) were independent of wavelength, this proposition would be strictly true). Thus, the maximum and minimum of pigment absorption are seen as a minimum and maximum of \( R(\lambda) \) (at 440 and 565 nm respectively), which become more pronounced with increasing concentrations of chlorophyll. The second maximum at 685 nm is mainly due to the fluorescence of chlorophyll. The concave form of these curves between 400 and 565 nm and the pronounced maximum at 565 nm contrast with the convex form and the flat maximum typical of turbid coastal waters.
Figure 80. Spectral values of irradiance ratio (or reflectance), \( R(\lambda) \), for the surface layer, expressed in percentage. A) Offshore Mauritanian stations listed in Table 6, and station 43 in the Guinea Dome. B) Mauritanian coastal stations listed in Table 7.

Besides this difference in the spectral composition, the absolute values of \( R(\lambda) \) distinguish between the two water types in a significant manner. The organic material, predominant in the offshore productive waters, has a refractive index hardly higher than that of water. In this condition, the relative backscattering, i.e. \( r_p = b_b / b \) is low (less than 0.5 %), and consequently the \( R(\lambda) \) values are also low. Conversely, the mineralized particles are more refracting and present a higher value of \( r_p \) (1.5 % or more). This, along with the fact that the scattering coefficient, \( b \), is often considerably higher inshore than offshore, explains the high values of \( R(\lambda) \) observed here.

The values of the mean reflectance, \( \bar{R} \), computed for the whole spectrum, are presented in Tables 6 and 7. The effect of the nature of the seston on this quantity is clearly brought out by Figure 81, where \( \bar{R} \) is plotted as a function of the ratio POC/seston. The degree of mineralization appears as a cause inducing an increase in \( \bar{R} \) (at the other extreme, very clear and blue waters also present high \( \bar{R} \) values, but, in this case, the cause is low absorption values).

The impression of brightness to the human eye is related to the values of \( \bar{R} \). The offshore waters reflect-
Figure 82. Radiation utilization efficiency, $\varepsilon$, dimensionless quantity expressed in percentage, shown for each station as a function of integrated PAR for the incubation period, i.e., for the whole day, expressed as $(\text{quanta/m}^2\text{day}^{-1})$. A) Guinea Dome stations and B) Mauritanian upwelling stations. The solid curves are for the three coastal stations.
Such a reduced growth rate has also been observed, namely at stations 35, 63 and 76, but only for the surface samples and not for deeper samples. The effect of optical properties of the water upon the phytoplanktonic development has to be taken into consideration to account for the difference in biomass present.

Offshore, the development follows the classical scheme. The newly upwelled waters, when spreading at the surface, are initially clear. Afterwards, the gradual growth of the algal biomass becomes directly responsible for reducing the thickness of the euphotic zone. For these offshore waters, a regular decrease in $Z$ (1%) is observed with the increase in average pigment concentration (Fig. 76). Finally, when the biomass has become important, and as long as nutrients are available, the vertically compressed euphotic layer has a high capacity for the absorption and utilization of radiant energy, because of the abundance of pigments.

At the coast, on the other hand, the upwelled waters are permanently rendered turbid by agitation (Fig. 72). Before production starts, the conditions are already unfavourable because the euphotic layer is reduced in thickness (Fig. 76). Light is finally the limiting factor and the nutrients are not consumed.

This can be made clear by considering the efficiency factor which characterizes the utilization of available radiant energy by the phytoplankton. This efficiency factor, $\varepsilon$, which is dimensionless, expresses locally (i.e., for an elementary thickness $dz$) the ratio between the photosynthetically stored energy (PSR) and the energy removed from the radiant field by the physical and chemical processes together. This number is then simply defined (Morel, 1978) as the ratio $\varepsilon = k_b/K$, where $k_b$ is what Platt (1969) has called the “biological extinction coefficient”, and $K$ is the diffuse attenuation coefficient relative to the available energy.

The efficiency $\varepsilon$ has been calculated using the measurements of primary production (see Appendix, note 2). Figure 82B shows the variations of $\varepsilon$ at the diverse stations with the quantity of available energy integrated over the day, and at the depth of the experiment. This leads to a scale graduated in optical depth, and not geometric depth.

$\varepsilon$ has low and variable values at the surface and generally increases with depth. This is linked to the fact that the quantum yield defined as the number of carbon atoms fixed per quantum absorbed (not per quantum available), increases at low irradiance levels. The respective positions of the diverse curves reflect simultaneously the optical properties of the water (by $K$) and the photosynthetic activity of the biomass present (by $k_b$). The values of $\varepsilon$ at the coastal stations 35, 63, and 76 are among the lowest, showing that the conditions are less favourable here than offshore.

A value for total efficiency, $\bar{\varepsilon}$, can be obtained by integrating over the whole productive layer. Thus, $\bar{\varepsilon}$ represents that fraction of the energy incident at the surface which is converted into chemical energy through photosynthesis (it has to be noted that the total productive layer extends a bit below the depth $Z$ (1%)). Only the visible part of the radiant energy is potentially useful for photosynthesis. But if one takes as incident energy the total radiation, including infrared, one obtains, for stations 35, 63, and 76 respectively, $\bar{\varepsilon}$ values of 0.190, 0.163, and 0.094 %. For the 12 other stations typical of offshore waters, the mean value is 0.42 % (standard deviation 0.17). In conclusion, the existence of the extended continental shelf gives a particular character to this upwelling. Not only hydrologic, but also optical, properties, and consequently the production, are dependent on this topographic feature.

**Guinea Dome**

The particular conditions of the Guinea Dome, where photosynthetic activity only takes place at lower layers, result in $\varepsilon$ curves of a particular shape (Fig. 82A). At the layer of high available energy, the curves are depressed. But at the base of the euphotic layer (0.5 % < PAR < 5 %), the values of $\varepsilon$ are near those observed in the Mauritanian upwelling. For the total water column, the $\bar{\varepsilon}$ obtained by integration varies from 0.022 to 0.085 %. The mean value for the 8 stations is 0.042 % (standard deviation 0.020). It is thus ten times less than that obtained for the offshore Mauritanian stations.

With equal biomass, the photosynthesis is however approximately twice as efficient in the Guinea Dome system, considering that the biomass is twenty times smaller here than off Mauritania (Chl $a = 10^{-7}$ mg/m$^2$, standard deviation: 2.9, instead of 200 mg/m$^2$, standard deviation: 84). In this system, the photosynthetic activity takes place only at low irradiance levels where the quantum yield is increased. Moreover the quality of the radiations may also be responsible for the efficiency enhancement. In this two-layer system, the amount of blue and blue-green radiations reaching the deep productive layer is comparatively high. These radiations are easily absorbed by pigments and, therefore, the efficiency of this productive system would be increased.

**References**


