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PRIMARY PRODUCTION IN THE TROPICAL ATLANTIC OCEAN MAPPED FROM OXYGEN VALUES OF EQUALANT 1 AND 2 (1963)

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ABSTRACT

A relationship between primary production and the depth of 100% oxygen saturation is used to calculate the primary production in the tropical Atlantic Ocean during the Equalant 1 and 2 cruises (1963) and to improve the maps made previously from the measured ^{14}C data. The comparison between calculated and measured values shows a rather good agreement between them but the calculated values being much more numerous than the measured ones allow a more accurate mapping than the measured values can do.

The use of radioactive carbon to determine the rate of carbon fixation during photosynthesis (Steeman Nielsen, 1952) is a very sensitive method that can be applied to the most oligotrophic areas of the tropical ocean. It was a considerable improvement over the previous methods and it allowed intensive studies of the primary production in the oceans.

In 1963–1964 the International Cooperative Investigation of the Tropical Atlantic (ICITA) carried out a multivessel program named Equalant (Austin, 1963) to measure synoptically the physical, chemical and biological properties of the tropical Atlantic Ocean between 15°N and 15°S of latitude. It was the first attempt to get maps of primary production for the whole tropical Atlantic Ocean. However, to assess the actual carbon fixation in the water column, the *in situ* method needs too much time to be used in a multiship survey. Therefore, the simulated *in situ* method was used during the Equalant cruises. The results offered the first data in support of seasonal variation of primary productivity in the tropical Atlantic (Corcoran and Mahnken, 1969; Mahnken, 1969). However, for Equalant 1 (February–March 1963), in spite of the 93 measurements of the primary production, it was not possible to contour its distribution because of an insufficient areal cover. For Equalant 2 (August 1963) in spite of a good effort of standardization of the methods, the results show some evidence of discrepancy from one ship to the other (Fig. 1), and give little new information on the primary production compared to the results of Steeman Nielsen and Aabye-Jensen (1957) who have combined the measurements of organic production of the Galathea Expedition (1950–1952) with the planktonic algae standing stocks of the Meteor Expedition in 1925–1927 (Hentschel and Wattenberg, 1930).

In tropical areas the fertility depends on the rates of nutrient input into the euphotic zone which depends itself on the physical enrichment processes such as vertical mixing through the thermocline (Eppley, 1980). The relationship between thermal structure and the organic production is well known: Brandhorst (1958), Reid (1962) in the Pacific Ocean and Beardsley (1969) in the Atlantic, pointed out an inverse relationship between the depth of the thermocline and the organic production. In tropical areas the charts of the thermocline topography give in first approximation an image of the primary production. High productivity is located in the thermal ridges such as the equatorial divergence, the divergence between the North Equatorial Countercurrent and the North Equatorial Current, and the thermal domes. The lowest productions are located in the convergence zones corresponding to the central part of the large anticyclonic gyres.

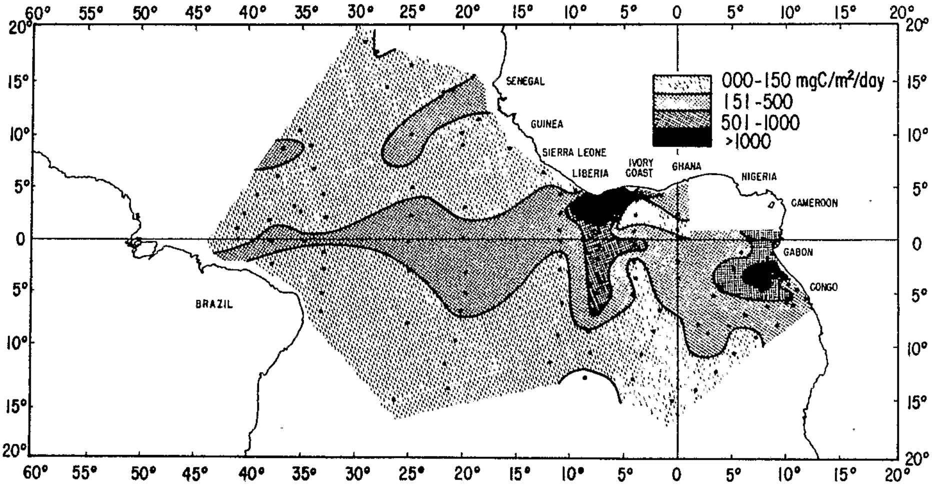

Figure 1. The distribution of integrated primary production from stations occupied during Equalant 2 (cold season) (from Corcoran and Mahnken, 1969).

Starting from the idea that the mapping of the physical and chemical parameters is easier than that of the primary production measurements because of the much greater number of values and of their better accuracy, Herbland and Voituriez (1979) tried to improve the qualitative relationship between thermal structure and organic production to derive charts of primary production from physical or chemical parameter measurements. Their results are used here to assess primary production in the tropical Atlantic Ocean during Equalant 1 and Equalant 2 from oxygen data.

Primary Production and Vertical Distribution of Nitrate and Oxygen

The vertical structure was precisely studied on selected stations covering the various depths of the thermocline (15–100 m) found in the tropical Atlantic during the R/V Capricorne cruises from 1970 to 1977. The methods of measurements, the position and the number of stations, and the statistical analysis were presented in a previous paper (Herbland and Voituriez, 1979). Some of the conclusions, valid only for the so called "typical tropical situations" (TTS), characterized by a nitrate depleted, mixed layer above the thermocline are the following:

First the "nitracline" (vertical gradient of nitrate) does not coincide with the thermocline (the distance between the top of each "cline" can reach 30 m), and the top of the nitracline has an important biological significance. At this level, the combination of the light and nutrient conditions is optimal so that the new production (Dugdale, 1967) which controls the overall production, and the nitrate uptake are maximum. The chlorophyll *a* maximum is also located at this level. All else being equal, the deeper the nitracline the less light would be present at the nitracline and therefore the less the primary production. Indeed an inverse relationship has been found between the integrated primary production (Pi) in the water column and the depth of nitracline (D_{NO_3}):

$$\text{Pi (mg C}\cdot\text{m}^{-2}\cdot\text{h}^{-1}) = -0.87 D_{NO_3}(\text{m}) + 90.2 \qquad (r = -0.84) \qquad (1)$$

The depth of the nitracline is defined by the first level where the nitrate concentration is different from zero.

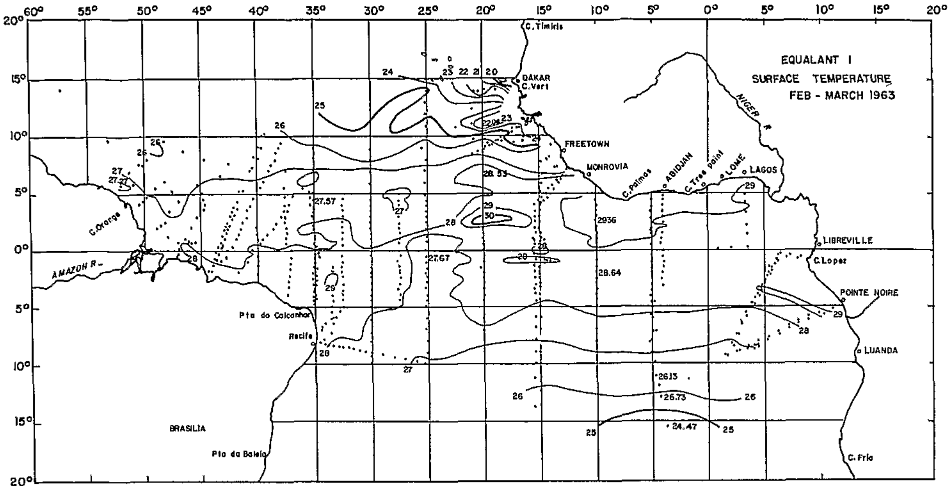

Figure 2. Sea surface temperature during Equalant 1 in February–March 1963 (Equalant Atlas, Kolesnikov, 1973).

Secondly in consequence of the stoichiometric relationship between oxygen and nutrients, according to the formula of the composition of phytoplankton (Redfield et al., 1963) in the processes of production and mineralization of organic matter, a very high significant correlation has been found between the depth of nitracline and that of the first non saturated oxygen value (D_{OX}):

$$D_{OX}(m) = D_{NO_3}(m) + 0.9 \qquad (r = 0.975) \tag{2}$$

The intercept 0.9 is not significantly different from zero and D_{OX} can be used in the place of D_{NO3} in relationship (1); it becomes:

$$Pi\ (mg\ C \cdot m^{-2} \cdot h^{-1}) = -0.87 D_{OX}(m) + 90.2 \tag{3}$$

The nitrate distribution (relationship 1) has been already used to evaluate the primary production in the Gulf of Guinea from the data of Cruise Guinée 1 of the R/V JEAN CHARCOT in May–June 1968 (Herbland and Voituriez, 1977). Because of the scarceness of the nitrate data of Equalant 1 and 2, the oxygen (relationship 3) has been preferably used for mapping the primary production in the tropical Atlantic Ocean.

PRIMARY PRODUCTION IN THE TROPICAL ATLANTIC DURING EQUALANT 1 AND 2

Application of the Relationship Primary Production—Oxygen

The relationships 1, 2, 3 are only valid in the TTS where the mixed layer is nitrate depleted, and in this paper all the other tropical areas where cooling and nitrate enrichment of sea surface occur will be called "upwelling" as opposed to TTS, independently of the enrichment processes. The sea surface temperature maps of Equalant 1 and 2 (Kolesnikov, 1973) (Figs. 2 and 3) show that the coastal upwellings occurred in the Senegal-Gambia area in February–March 1963 (Equalant 1) and off the Ivory Coast, Gabon and the Congo in August 1963 (Equalant 2).

The equatorial area is not so simple. The historical data of sea surface tem-

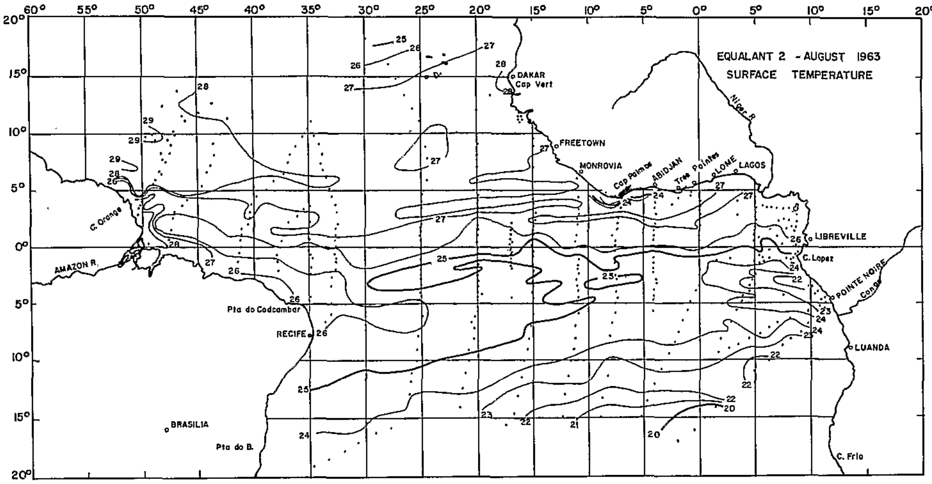

Figure 3. Sea surface temperature during Equalant 2 in August 1963 (Equalant Atlas, Kolesnikov, 1973).

peratures (Mazeika 1968a; Neumann et al., 1975; Hastenrath and Lamb, 1977; Merle, 1978) show clearly the occurrence of an equatorial cooling in summer* (T < 22°5′, Mazeika 1968a): the so-called equatorial upwelling (Fig. 4). The mechanisms of this phenomenon provoked intensive discussions (Adamec and O'Brien, 1978; Moore et al., 1978; Hisard, 1980; Merle, 1980) and will not be discussed in this paper. However the recent cruises of the R/V Capricorne from 1971 to 1979 show that significant nitrate concentrations occur on the surface in the eastern equatorial Altantic (Fig. 5) during the equatorial upwelling season in July–September (Voituriez, 1980). Therefore, the previous relationships should not be used to assess primary production in the equatorial area in summer. However, in the summer of 1963 the sea surface temperatures of Equalant 2 do not exhibit such a decrease in the Gulf of Guinea at the equator and everywhere along the equator the sea surface temperatures remain higher than 24°C (Fig. 3). Therefore the equatorial upwelling seems to have been nonexistent in the summer of 1963. Sedikh and Loutochkina (1971) have already noted the anomalous weakness of the equatorial upwelling during Equalant 2, and Hisard (1980) has confirmed the positive temperature anomaly of the 1963 cold season (July–August). The transequatorial transects of phosphate published by Corcoran and Mahnken (1969) and the charts of phosphate surface distribution (Kolesnikov, 1976), confirm this fact: the phosphate content of the sea surface is not higher in summer than in winter at the equator. Corcoran and Mahnken (1969) explain the equatorial planktonic enrichment in the summer of 1963 by a thermal anticline bringing the nutrient rich layer to a more illuminated level. This is a ridging and not an upwelling. Lastly, the transequatorial section of the R/V Pillsbury at 20°W during Equalant 2 shows no nitrate enrichment in the surface layer at the equator (Okuda, 1966). It can be concluded that the typical tropical structure was not disturbed at the equator during Equalant 1 as well as during Equalant 2. Therefore, the oxygen data (Figs. 6 and 7) can be used to estimate the organic production

* In this paper the terms winter and summer refer to the northern hemisphere season.

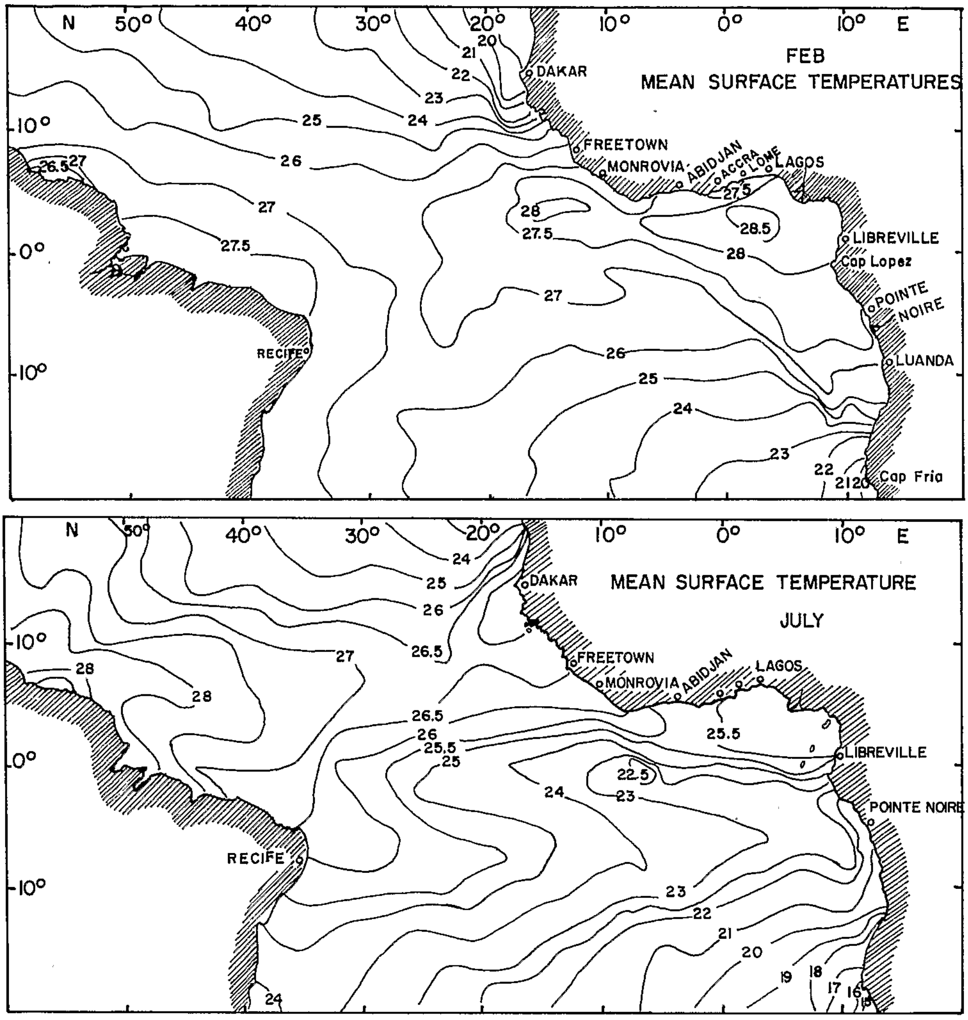

Figure 4. Mean surface temperature: a, in February; b, in July (Mazeika, 1968a).

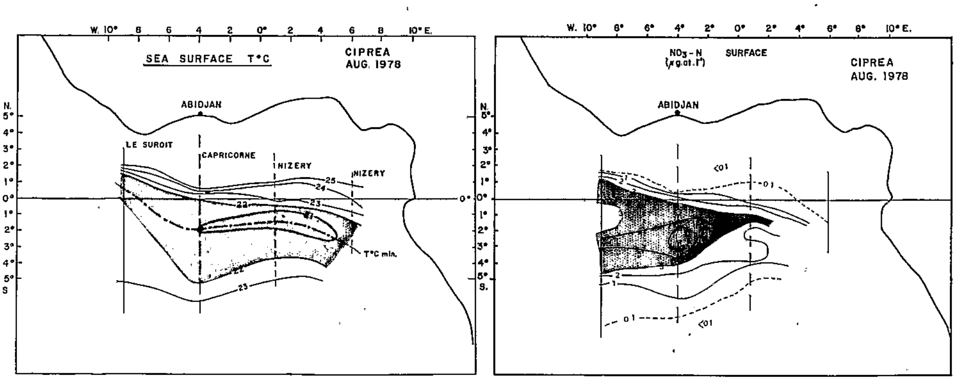

Figure 5. Temperature and nitrate distribution in surface in the Gulf of Guinea in August 1978 (upwelling season).

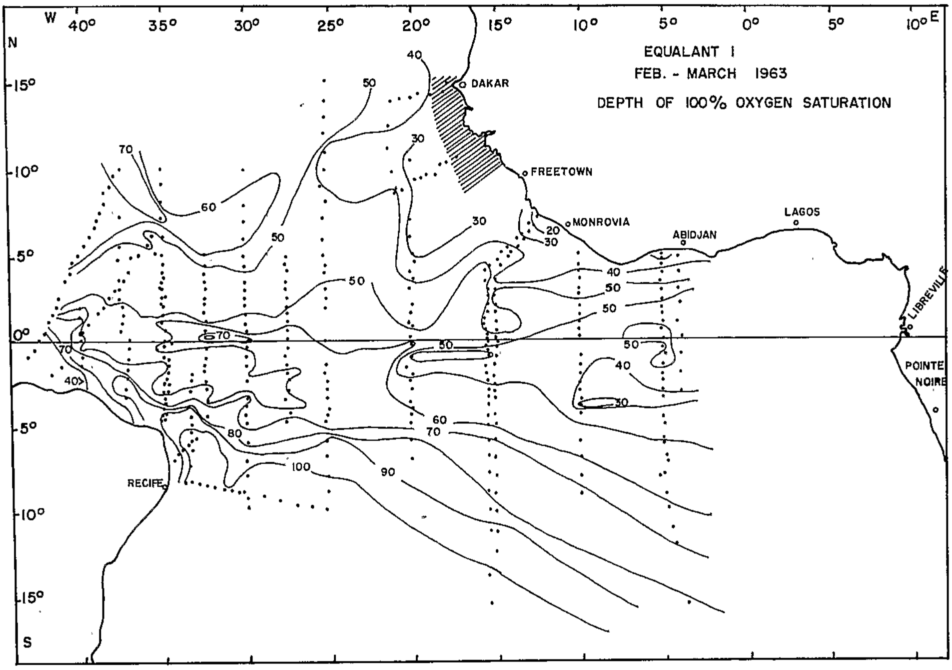

Figure 6. Depth of the 100% oxygen saturation level during Equalant 1 (February–March 1963). The hachured areas correspond to upwelling zones.

during the Equalant 1 and 2 cruises in all the oceanic tropical Atlantic except the coastal upwelling areas.

Distribution of Primary Production

The distribution of the calculated primary production (Figs. 8 and 9) corresponds to the main hydrological features shown by the temperature charts of the Equalant Atlas (Kolesnikov, 1973). The most productive areas are located off the Senegal-Gambia coast and south of the equator in the eastern part of the ocean. They correspond to two thermal ridges. The first one occurs between the North Equatorial Current and the North Equatorial Countercurrent and extends from Africa to South America along approximately 10°N. The second one, south of the equator (2–3°S) up to 20°W is, according to Voituriez and Herbland (1977), a permanent feature of the equatorial circulation in the Gulf of Guinea during the warm season. According to Hisard et al. (1977), the south equatorial ridge would correspond to the equatorial planetary divergence which is shifted south of the equator when the trade winds blow from the southeast in accordance with Cromwell's scheme (Cromwell, 1953). The less productive area is located in the southwestern part of the zone and corresponds to the very poor waters of the subtropical salinity maximum. A rather low production area occurs along 2–3°N through all the ocean in August and only in the Gulf of Guinea in February–March. This is the convergence between the South Equatorial Current and the North Equatorial Countercurrent prolonged by the Guinea Current. The decrease of the production in the equatorial area from east to west corresponds to the general increase of the thermocline depth from east to west shown in the Equalant Atlas (Kolesnikov, 1973).

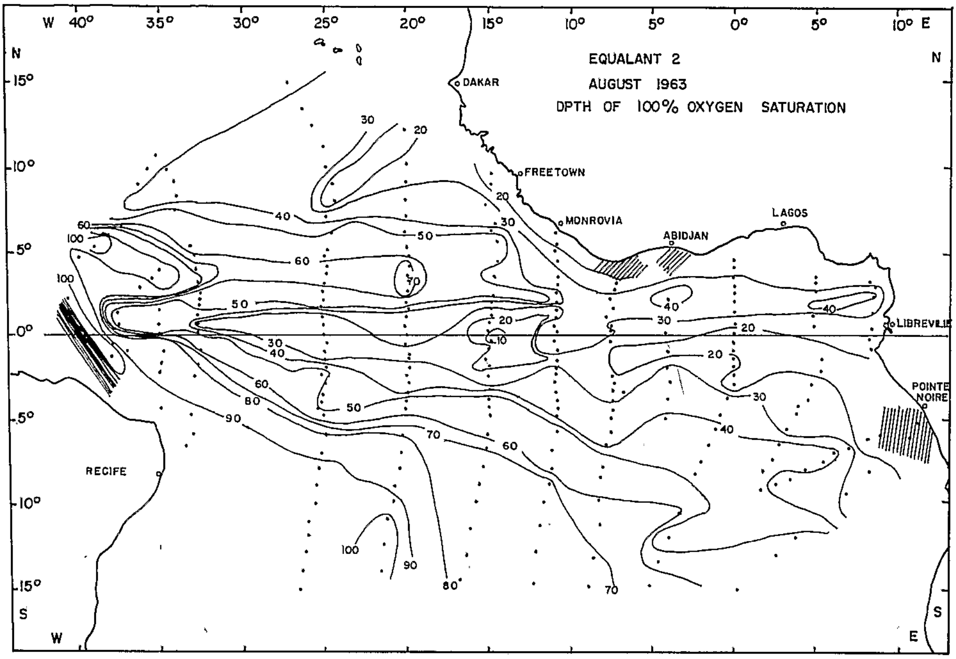

Figure 7. Depth of the 100% oxygen saturation level during Equalant 2 (August 1963). The hachured areas correspond to upwelling zones.

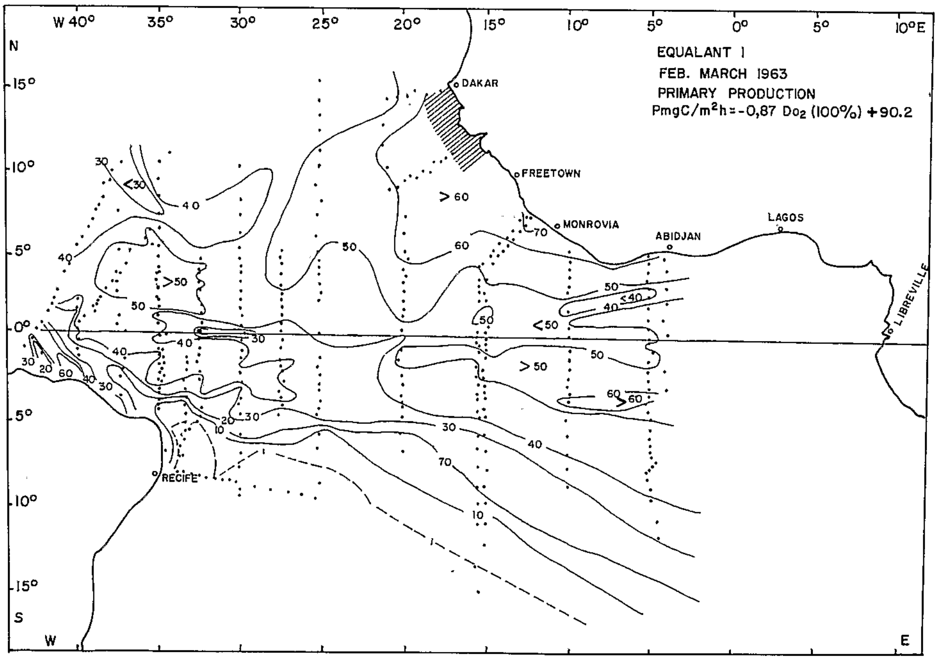

Figure 8. Primary production during Equalant 1 (February–March 1963) mapped from the oxygen distribution. The hachured areas correspond to upwelling zones.

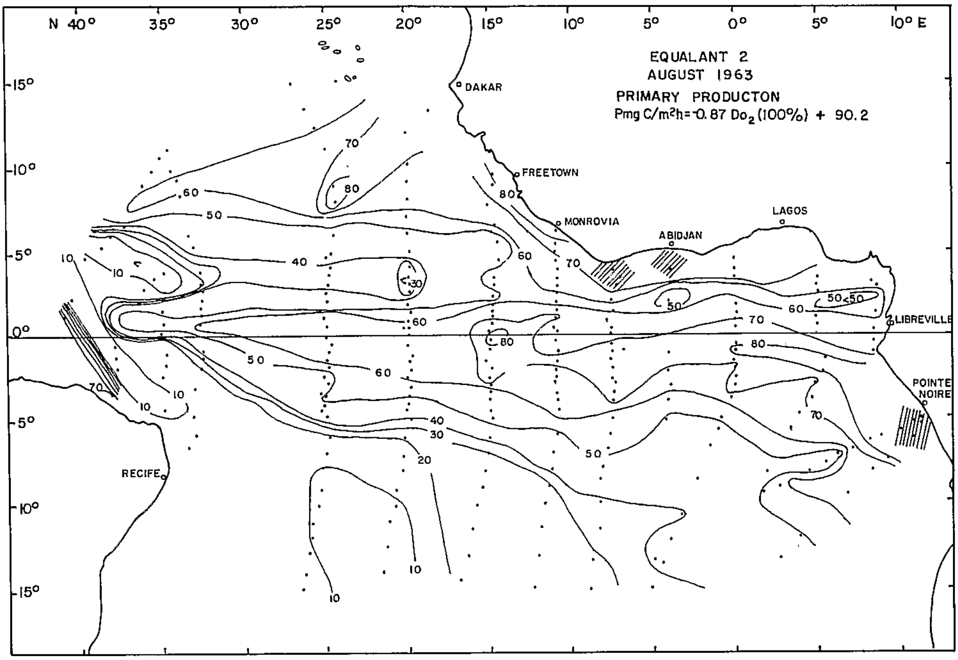

Figure 9. Primary production during Equalant 2 (August 1963) mapped from the oxygen distribution. The hachured areas correspond to upwelling zones.

The seasonal changes of the organic production are mainly due to the variations of the circulation which account for the changes of the thermocline topography. Two currents have mainly to be considered: the North Equatorial Countercurrent flowing eastward and the South Equatorial Current flowing westward at the equator.

The North Equatorial Countercurrent is fully developed at the surface between 5° and 10°N through the Atlantic and its speed is maximum in summer when the intertropical convergence zone is at its northernmost position. In winter this countercurrent is weak and disappears from the surface west of 20–25°W (Khanaichenko, 1974). This fact has two consequences: (1) the intensification in summer of the ridge at the northern boundary of the North Equatorial Countercurrent and the occurrence of the Guinea Dome at the eastern end of the ridge (Mazeika, 1968b; Voituriez and Dandonneau, 1974); (2) the summer intensification of the convergence at the southern boundary of the countercurrent and its extension through all the ocean, whereas in winter it is limited to the Gulf of Guinea where an anticyclonic circulation remains between the Guinea current and the South Equatorial Current (Hisard, 1975). Consequently, in summer there is an increase of the production in the Guinea dome (80 mg $C \cdot m^{-2} \cdot h^{-1}$) between 20–25°W and 10–15°N and an extension of the minimum of production in the convergence along 2–3°N from the African to the American coasts (Figs. 8 and 9).

The south equatorial ridge was also reinforced in the summer of 1963 because of the increase of the northward component of the trade winds which, according to Cromwell (1953), induce a divergence south of the equator in the South Equatorial Current. Consequently, the maximum of production in that ridge is higher in summer (80 mg $C \cdot m^{-2} \cdot h^{-1}$) than in winter (60 mg$C \cdot m^{-2} \cdot h^{-1}$). In the western part of the ocean where the northward component of the trade winds weakens, the ridge and the maximum of production were found nearer to the equator.

Discussion And Conclusion

If we consider a 10-h production period per day the values thus obtained are greater than the measured values reported by Corcoran and Mahnken (1969) (Fig. 1). In summer the equatorial measured values during Equalant 2 are less than 500 mg $C \cdot m^{-2} \cdot d^{-1}$ except between 5° and 10°W and in the coastal upwelling off Congo and Gabon, whereas, our calculated values are higher than 600 mg $C \cdot m^{-2} \cdot d^{-1}$ along the equator as far as 35°W. That difference can be easily explained by the differences in method. During Equalant cruises, the samples were incubated for 24 h at sea surface temperature at five simulated light levels while the production measurements used to provide our relationships (1) and (3) were made *in situ* at 8 or 10 levels from sunshine to sunset.

In summer (Equalant 2) there are no major contradictions in the distribution of the organic production between the measured and the calculated values (Figs. 1 and 9): the high production areas are the same. In winter (Equalant 1) the enrichment in the south equatorial thermal ridge (Fig. 8) was detected neither by Corcoran and Mahnken (1969) nor by Tchmir (1971). However, this thermal ridge is obvious on the temperature distribution at 50 m during Equalant 1 (Kolesnikov, 1973) and on the winter map (January–April) of the mean temperature at 50 m established by Mazeika from the historical data and published by Corcoran and Mahnken (1969). Furthermore, Voituriez and Herbland (1977) have shown that at 4°W this ridge is a permanent feature of the warm season to which high values of chlorophyll *a* correspond. However, during Equalant 1 the ridge was rather deep (it does not appear on the 30 m temperature chart of Equalant 1). Therefore, its influence on the production was weak, so that the resulting slight calculated maximum of production shown in Fig. 8 could be easily missed by an inadequate sampling.

In the summer of 1963 this method of evaluation of the primary production could be applied to the equatorial area because there was no appearance of upwelling. However, as far as the upwelling season is concerned, it was stated before that 1963 (Equalant 2) was really an exceptional year and the production maps of Equalant 2 (Figs. 1 and 9) cannot be considered as a reference of the equatorial production in summer. These maps give a minimum assessment of the equatorial production since the primary production measured when the equatorial upwelling occurs is higher (133 mg $C \cdot m^{-2} \cdot h^{-1}$ in July 1977) (Voituriez and Herbland, 1978).

The main advantage of the above proposed method is the possible biological valorization of the very numerous hydrological stations: in the typical tropical situations every station could be considered as a measurement of integrated primary production.

The above relationships established in the eastern tropical Atlantic should be tested in the other tropical oceans. If they could be generalized they would provide a very simple means of evaluation and comparison of the primary production in the tropical areas.

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