Primary production and phytoplankton biomass in the equatorial region of the Atlantic at 22° West

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ABSTRACT
Biological and chemical measurements were carried out in the equatorial Atlantic at 22°W, at ten sections between 3°N and 2°S, from February to June 1979. During this time two periods with low sea-surface temperatures, due to upwelling, were observed: one in February, the other in June. An increase in chlorophyll concentrations was measured during these periods, whereas an increase in primary production was observed only during the upwelling event in June. Small organisms dominated the phytoplankton composition in numbers as well as in biomass. Primary production was also highest in the small fraction (< 20 μm). Primary production values as estimated from the input of new nutrients into the productive zone showed the importance of regenerated production during periods without upwelling.


RÉSUMÉ
Production primaire et biomasse du phytoplancton dans l'Atlantique équatorial à 22° Ouest

De février à juin 1979, des mesures biologiques et chimiques furent effectuées en Atlantique équatorial au cours de dix trajets entre 3° Nord et 2° Sud le long du méridien 22° Ouest. Pendant ce temps, on a pu observer deux périodes avec des basses températures à la surface dues à l'upwelling : l'une au mois de février, l'autre en juin. Elles étaient accompagnées à chaque fois par une augmentation en chlorophylle. Par contre, la production primaire ne fut élevée que lors de la deuxième période d'upwelling, en juin. Le phytoplancton était dominé en nombre ainsi qu'en biomasse par des petites espèces appartenant au nanoplancton (< 20 μm). C'était aussi dans cette fraction que la production primaire était la plus élevée. Une estimation de l'apport des sels nutritifs nouveaux dans la couche productive, par mélange vertical, démontre l'importance de la production régénérée pendant les périodes sans upwelling.

INTRODUCTION

In the tropical oceans along the Equator, zones with higher productivity and plankton biomass exist. One of the first observations of this fact was made during the "Planktonexpedition" in 1889 (Krümmel, 1892). Since then, many expeditions have been carried out in this area to explore physical and biological processes: for a review, see Vinogradov (1981). During the past 25 years, intensive studies have been carried out by French scientists in the eastern equatorial Atlantic, e.g. Dufour, Stretta, (1973); Herbland, Voituriez, (1979); Herbland, Le Bouteiller, (1981); Voituriez, (1981); Voituriez et al., (1982). During the First Garp Global Experiment (FGGE) in 1979, the German RV „Meteor“ surveyed the equatorial Atlantic at 22°W, from 3°N to 2°S, from February to June. At ten sections, biological and chemical examinations were carried out, together with hydrographical and meteorological measurements. This study gives a short description of the biological situation at the time of investigation, a period usually described as the "warm" season without upwelling and with low productivity. More detailed studies on phytoplankton and zooplankton were done by Meyerhöfer (1980), Rolke (1981) and Bauerfeind (1983).

MATERIAL AND METHODS

Standard methods for the determination of planktological and chemical parameters were applied. Chlorophyll a was determined fluorometrically after acetone extraction. Whatman GF/C-filters, Ø 25 mm, were used for filtration.

Primary production measurements were done by the 14C-method according to the simulated in situ technique (incubation from noon to sunset, ~6 h). Solar radiation at the surface was measured continuously with a solarimeter (Kipp and Zonen integrator CC1). After incubation, the water was filtered through Sartorius membrane filters, pore size 0.45 µm, Ø 35 mm. After drying, the filters were stored in a desiccator. Activity on the filters was counted with a Geiger-Müller counter by the international 14C-agency in Hørsholm, Denmark. Production per day was calculated using the ratio of irradiance per day, irradiance per incubation time. Inorganic dissolved nutrients were determined with an autoanalyzer using the methods given in Grasshoff (1976). Water samples were taken with 101 Niskin bottles mounted together with the "Bathysonde". Sampling depths were chosen according to prior determination of the light levels (Secchi disk readings) in the euphotic zone (100%, 50%, 30%, 10%, 1%). In the deeper parts down to 250 m, samples were taken at depths of 75 m, 100 m, 125 m, 150 m, 200 m, 250 m. A detailed description of the methods, together with the data, is given in Bauerfeind et al. (1983).

Phytoplankton was counted in all samples at stations where primary production measurements were taken. Due to the low phytoplankton concentration, 100 ml sub-samples preserved with lugol's solution were sedimented for 48 h and counted with an inverted microscope. The organisms were determined and grouped in the following size classes: diatoms and dinoflagellates > 100 µm, 100-30 µm, 30-10 µm, and nanoflagellates (flagellates < 20 µm); the latter were grouped in organisms < 3 µm, 3-6 µm, 6-10 µm and >10 µm. The high amount of detritus in relation to cell numbers and biomass (often more than 95% of the measured particulate organic carbon was detritus), made it difficult to count the smaller organisms.

RESULTS

Hydrographical situation

In the area studied, a well mixed and nutrient-poor layer near the surface is separated from the deeper nutrient-rich but light-limited layer by the top of the thermocline. Within the thermocline, the equatorial undercurrent flows to the east at ~100 cm s⁻¹ whereas at the surface the south equatorial current flows in the opposite direction at ~25 cm s⁻¹. Vertical mixing due to the current shear causes spreading of the thermocline and nitraline. During the expedition, two periods with increased spreading of the thermocline were observed, together with lower sea-surface temperatures (Fig. 1). This cooling of the surface layer can only be explained by upwelling (Fahrbach, Bauerfeind, 1982; Fahrbach, 1983).

![Figure 1](image-url)  
Continuous temperature record at a depth of 15 m on the Equator (from Fahrbach, 1983). Dots represent temperatures measured with the CTD, bars show the time interval of the sections.

Low concentrations of nitrate were measured in the surface layer at stations near the Equator, only during upwelling (Fig. 2). Highest surface temperatures were measured in April/May at times when the Intertropical Convergence Zone (ITCZ) had reached its southernmost position. A similar change of the sea-surface temperatures in 1979 was reported by Molinari et al. (1983) for other areas of the equatorial Atlantic. In all areas, a decrease in temperature was observed shortly after the increase of the trade winds at the end of May.

Phytoplankton: cell numbers and biomass

During the period of investigation, cell numbers ranged from 10⁵ to 10¹³ organisms x dm⁻³. Higher numbers were found at the beginning of the expedition in February; they decreased in March/April and showed a slight increase at the end of May and beginning of June. Nanoflagellates were the dominating organisms, often accounting for more than 90% of the cell numbers. Species composition was uniform during the time of investigation with two exceptions:
1. *Rhizosolenia* mats were observed during the calm period in April.

2. Bundles of the nitrogen-fixing cyanophyta *Oscillatoria thiebautii* and *Oscillatoria coniotum* also appeared for the first time in April, and were present at all examined stations until the end of the expedition.

Cell volume and carbon content of the organisms were calculated according to the formulas given by Edler (1979). Integrated for the euphotic zone, phytoplankton-carbon (PPC) values ranged from 60-441 mg C m\(^{-2}\) with lower values in April and May. The average PPC for the whole period investigated was 178 mg C m\(^{-2}\) (n = 53). The PPC below the euphotic zone usually accounted for 30-50% of the total PPC within the water column. The quota of the different groups within the euphotic zone was calculated as follows:

- centric diatoms: 4%
- pennate diatoms: 2%
- dinoflagellates > 30 μm: 18%
- dinoflagellates < 30 μm: 19%
- nanoflagellates: 46%
- cyanophyta: 10%
- nanoflagellates < 30 μm: 37%
- dinoflagellates: 65%
- organisms < 30 μm: 6%
- diatoms: 6%

In the area investigated, phytoplankton biomass was dominated by small organisms. Dinoflagellates < 30 μm and nanoflagellates account for 65% of the biomass in the euphotic zone. But it should be borne in mind that the figures given are average values for the entire period of the expedition and that in several samples larger organisms dominated the plankton composition. This holds true especially for the *Oscillatoria* species mentioned above, which were encountered only during the second half of the expedition. The "Utermöhl" technique used for the evaluation of the phytoplankton biomass does not work satisfactorily for the small phytoplankton size fraction, especially the so-called picoplankton. It has been shown recently that organisms belonging to this size class form a considerable part of the phytoplankton in tropical and equatorial waters (Li et al., 1983; Herbland et al., 1985). Therefore the cell numbers and biomass given in this study may underestimate the real figures to a certain, as yet unknown extent. A more valid evaluation of phytoplankton biomass in future studies might be obtained by using epifluorescence microscopy in addition to the "Utermöhl" technique.

Simultaneously with the phytoplankton, protozooplankton (PZP) was counted in the samples. Cell numbers of these organisms (mainly naked ciliates and tintinnids) ranged from \(10^{3}-10^{4}\) organisms m\(^{-3}\). The biomass estimated from these numbers ranged from 1-45 mg C m\(^{-2}\) integrated for the euphotic zone. This is 1-32% of the phytoplankton biomass. The average biomass of PZP for the whole period was calculated to be 10% of the average phytoplankton carbon. Although these figures may underestimate the real PZP biomass — these organisms being very sensitive to fixation — they indicate the ecological importance of the protozooplankton in the equatorial region of the Atlantic.

**Chlorophyll concentration and primary production**

Chlorophyll \(a\), a measure of the plankton content of the water column, ranged from 5.6-38.7 mg Chl.a m\(^{-2}\) integrated for the euphotic zone. Higher values were found during periods of lower sea-surface temperatures (section 3 and section 9). The chlorophyll \(a\) content within the euphotic layer was three times higher in June than at the beginning of the expedition. During the other upwelling period in February, the increase was less pronounced (1.7 fold). The effect of upwelling is also obvious if one considers the sea-surface concentrations (Fig. 3). An increase of this parameter with its maximum near the Equator is evident at section 3 and section 9.

The vertical distribution of chlorophyll \(a\) showed a subsurface maximum in 50-80 m. This zone with higher chlorophyll \(a\) concentrations has a thickness of 20-30 m, is situated 10-20 m above the nitracline and parallels the thermocline. The nitracline and the chlorophyll \(a\) maximum are situated at the bottom of the euphotic layer and were usually found below the 10% light level.

The depth of the chlorophyll maximum did not show significant changes during the period of investigation and within the area studied, whereas the changes in chlorophyll concentrations are significant at the 95%
level (H-test, Kruskal and Wallis). Herbland and Voituriez (1979) reported a similar vertical distribution with a nitrate impoverished mixed layer and a subsurface chlorophyll maximum in the Eastern equatorial Atlantic at 4°W during the warm season. This situation is known as "typical tropical structure".

Primary production was always highest in the top 30 m of the water column in the central equatorial Atlantic at 22°W, separated from the chlorophyll maximum and from the nitracline. Figure 4 shows the typical vertical distribution of chlorophyll a, NO$_3^-$ and primary production obtained at a long-term station at the Equator. Integrated primary production ranged from 78-741 mg C m$^{-2}$ d$^{-1}$ in the period of investigation, with highest values in June when upwelling was observed. At the other upwelling period in February, however, no increase for this parameter was observed. The lowest primary production was measured in May along with low chlorophyll values. For the whole period of investigation, an average of 247 mg C m$^{-2}$ d$^{-1}$ (n = 53) was calculated. The results of size fractionated production measurements showed that the major part of the primary production (~90%) was due to organisms < 20 μm. Larger organisms were of minor importance which is supported by the results of the cell counts. These results of size fractionated primary production are similar to those reported by Herbland and Le Bouteiller (1981), and Herbland et al. (1985) for the region of the equatorial Atlantic.

As shown in Figure 4, the vertical distribution of primary production always showed a maximum in the top 30 m of the water-column, a zone where, during periods without upwelling, nitrate concentrations were below the detection limit of the method used. During this time vertical mixing was the most important source of input of nitrate into the layer near the surface. Using the vertical turbulent diffusion coefficient for dissolved substances $K_v = 2.7$ cm$^2$ s$^{-1}$ for the warm period, given in Fahrbach and Bauerfeind (1982), I estimated the flux of nitrate into the mixed layer within a zone 30° north and 30° south of the Equator. The input of new nutrients calculated by this method ranged from 0.6-2.0 mmol NO$_3^-$ m$^{-2}$ d$^{-1}$. Using these values, a primary production ranging from 43-137 mg C m$^{-2}$ d$^{-1}$ was calculated using a C/N ratio of 6. This result shows that on an average, ~42% of the measured primary production can be explained by the input of nitrate from the deeper
layers in the period without upwelling. Production based on the input of nitrate can be termed new production (Dugdale, Goering, 1967), whereas the remaining 60% of the total production may be based on recycled nutrients.

DISCUSSION

From February to June 1979, chlorophyll concentrations and to a lesser extent primary production in the equatorial region of the Atlantic at 22°W increased during the observed upwelling periods. This is different from the situation in the eastern part of the equatorial region at 4°W reported by Voruitiez et al. (1982). Primary production in this region was higher (~1 gC m⁻²d⁻¹ in 1978/79) than at 22°W; only small variations were observed and chlorophyll concentrations were the same in August and April (Voituriez, 1981). Another difference is obvious if one considers the vertical distribution of primary production. At 22°W, this is highest in the layer near the surface at a depth with low nutrient concentrations, whereas at 4°W the productivity maximum is present in the depth of the chlorophyll maximum close to the nitracline (Herbland, Voituriez, 1979; Voituriez et al., 1982). This difference between the two areas is certainly due to the discrepancy between the depths of the nitracline and the chlorophyll maximum in the two regions; this is caused by the tilt of the thermocline, which shallows in the eastern Atlantic (Merle, 1980; Henin, Hisard, 1987; Oudot, Morin, 1987). At 4°W the nitracline and the chlorophyll maximum are located in 30-40 m, whereas at 22°W these layers were observed in 50-80 m at a depth where light limitation may occur. This fact is supported by the results of experiments obtained on board during the FGGE-cruise. Samples from the depth of the chlorophyll maximum showed higher productivity when they were incubated at the 100, 50 and 30% light level than parallel samples incubated at light levels of the chlorophyll maximum (Bauerfeind, unpublished data). In the central equatorial Atlantic at 22°W, ~40% of the primary production during the warm season could be due to the input of new nitrogen into the productive zone, while about 60% may be regenerated production. A further hint towards the importance of regenerated production in the area investigated is given by the vertical distribution of zooplankton biomass. Rolke (1981) reported that higher zooplankton biomass was present at depths less than 100 m with a maximum in the depth range of 0-25 m. Numbers and biomass of bacteria derived from direct counts of samples stained with acridine orange also had a maximum in the layer near the surface (Bauerfeind unpublished data).

In conclusion, the following is assumed for the foodchain in the area of investigation. Phytoplankton composition is dominated by small organisms (nano-, plankton organisms and dinoflagellates < 30 µm). Primary production is to a great extent regenerated production, and ~90% are found in the size fraction <20 µm. The importance of small phytoplankton organisms in equatorial waters is stressed also by Herbland and Le Bouciller (1981) and Herbland et al. (1985). Due to the relatively high growth rate of the phytoplankton (an average doubling time of 22 h, range: 6-34 h, was calculated from the P/B values for the water column) a rapid turnover of the nutrients excreted by the micro- and mesozooplankton and remineralized by bacteria must exist. Primary producers are balanced by the grazing of micro- and mesozooplankton resulting in a more or less constant phytoplankton standing stock. Protozooplankton organisms are an important link between the small primary producers and the mesozooplankton. In times with upwelling and/or a shallow position of the nitracline high amounts of new nutrients are transported into the productive zone. This causes an increase in primary production and results in a surplus of phytoplankton biomass (Fig. 3) which, at least at the beginning of the upwelling season, is no longer controlled by the grazers and thus can be exported into other regions of the equatorial Atlantic.

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