Short-term upper ocean oxygen changes at a fixed station in the southwestern tropical Pacific (15°S, 173°E)

Oxygen
Oligotrophy
Tropical Pacific
Empirical
Orthogonal functions
Diel cycle

Oxygène
Oligotrophie
Pacifique Tropical
Fonctions orthogonales empiriques
Cycle journalier

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ABSTRACT

Oxygen concentrations were measured at discrete depths (0 to 250 m) at 20-day fixed station in an oligotrophic area (Proligo cruise of R/V *Jean Charcot,* 15°S, 173°E. September-October 1985). Measurements are available for both early morning and evening over a period of 14 days. Daily oxygen production (evening concentration minus morning concentration) is very variable, and does not permit a precise estimation of photosynthetic carbon fixation. Empirical orthogonal function analysis shows (first eigenvector : 74 % of total variance) that the variability of the oxygen concentration is null at the surface, increases evenly downwards, reaches a maximum at the depth of the nutricline and at the deep chlorophyll maximum, and decreases to null values at 187 m depth. These results suggest that the observed variations do not result from instrumental error, but are rather forced by biological processes. Absence of a pronounced daily periodicity of the oxygen concentration is attributed to horizontal advection and mesoscale variability, which make it impossible to estimate the photosynthetic production of oxygen with any degree of precision.

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RÉSUMÉ

Variations de la concentration en oxygène dans les couches superficielles de l'océan au cours d'une station fixe dans le Pacifique tropical sud-ouest (15°S, 173°E)

La concentration en oxygène a été mesurée à des profondeurs discrètes (0 à 250 m) pendant 20 jours en un point fixe d'une région oligotrophe. Les données disponibles ont été obtenues à la fois tôt le matin, et le soir, pendant 14 jours. La production diurne d'oxygène (différence entre la concentration du soir et celle du matin) est très variable et ne permet pas d'estimer avec précision la fixation photosynthétique de carbone. Une analyse en fonctions orthogonales empiriques montre que la variabilité de la concentration en oxygène est nulle à la surface, croît régulièrement avec la profondeur, atteint un maximum dans la nutricline et la couche du maximum profond de chlorophylle, puis décroît pour s'annuler à 187 m. Ceci suggère que ces variations ne résultent pas d'erreurs de mesure, mais plutôt d'un forçage biologique. L'absence de périodicité journalière nette est attribuée à l'advection horizontale et à la variabilité à moyenne échelle, qui empêchent d'estimer de façon fiable la production d'oxygène par photosynthèse.

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INTRODUCTION

Oxygen concentration in the sea has been routinely measured for a long time as a means of characterizing deep water masses, because it evolves slowly; respiration is indeed very slight in deep waters, where living organisms are not abundant and where their metabolism is reduced by low temperature. In the upper layers, and especially in the surface mixed layer, exchanges with the atmosphere, and photosynthesis, sustain important fluxes, so that the oxygen concentration cannot be considered as a conservative property. Despite this shortcoming, a large amount of data has been gathered from the upper oceanic layer, which thus serves as a source of information on these fluxes. Using such data bases, Minas (1970) and Shulenberger and Reid (1981) have estimated the net primary production in temperate areas below the seasonal thermocline. The later work launched a controversy which still impassions research in marine primary production. Oxygen accumulation below the thermocline can be assessed either when the oceanic system is periodically reset to initial conditions by winter mexing (Jenkins and Goldman, 1985), or when non-satured water evolves to oxygen saturation after drifting at the surface (Johnson *et al.*, 1979; Minas *et al.*, 1986; Oudot, 1989a). In tropical oligotrophic waters, a steady state is generally established and oxygen variations, if any, should be small and forced by the photosynthetic diel cycle. Johnson *et al.* (1981) have detected oxygen diel variations along the drift of a drogue in the Caribbean Sea; the low level of primary production which characterizes oligotrophic areas implies that diurnal oxygen production is small, and it is generally considered that the estimation of net primary production from oxygen variations calls for especially precise and accurate oxygen measurements (Oudot *et al.*, 1988). Quality of oxygen measurements alone may, however, prove insufficient : if oxygen concentrations are not spatially uniform, horizontal advection will cause a noise that may perturb the diel signal.

In the present study, the vairability of oxygen concentrations in an oligotrophic area is described and its main causes are investigated. The analysed data were collected during the Proligo cruise (Dandonneau and Lemasson, 1987) on board R/V *Jean Charcot* (September-October 1985). During this cruise, a 22-day fixed station was occupied, and oxygen concentration was measured in 40 casts, most of which were done early in the morning or in late evening, at discrete depths ranging between 0 and 250 m. The position of the fixed station (15°S, 173°E) corresponds to an oligotrophic area, with a permanent thermocline (mean depth of SST-1°C = 75 m according to Levitus, 1982) and low sea-surface chlorophyll concentration at all times (Dandonneau and Gohin, 1984).

METHODS

Oxygen measurements were done in duplicate according to the Winkler method. The end-point was detected by potentiometry. Samples were taken at discrete depths between the surface and 250 m with a rosette multisampler (NISKIN, 12 × 1.7 L bottles). Precision of the résults is ± 0.015 mL.L^{-1} (one standard deviation). The concentration of the thiosulphate solution was calibrated at each 12-bottle cast.

Temperature and salinity were measured with a CTD probe, and were used to compute the sea water density

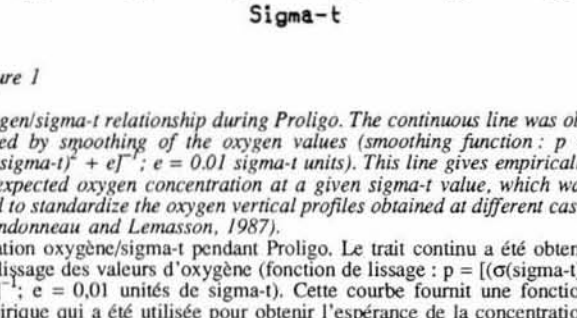

Figure 1

Oxygen/sigma-t relationship during Proligo. The continuous line was obtained by smoothing of the oxygen values (smoothing function : p = [(σ(sigma-t)^2 + e]$^{-1}$; e = 0.01 sigma-t units). This line gives empirically an expected oxygen concentration at a given sigma-t value, which was used to standardize the oxygen vertical profiles obtained at different casts (Dandonneau and Lemasson, 1987).

Relation oxygène/sigma-t pendant Proligo. Le trait continu a été obtenu par lissage des valeurs d'oxygène (fonction de lissage : p = [(σ(sigma-t)^2 + e]$^{-1}$; e = 0,01 unités de sigma-t). Cette courbe fournit une fonction empirique qui a été utilisée pour obtenir l'espérance de la concentration en oxygène à une valeur donnée de sigma-t, de façon à standardiser les profils verticaux d'oxygène (Dandonneau et Lemasson, 1987).

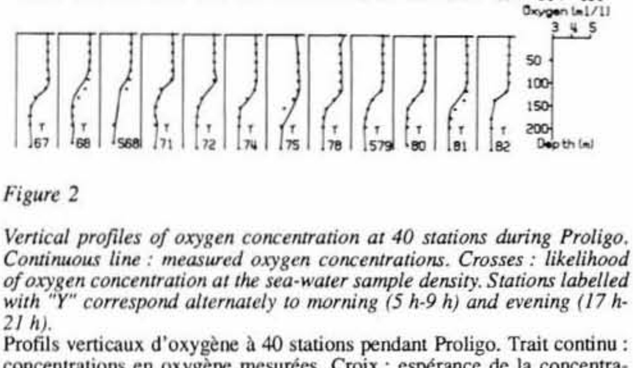

Figure 2

Vertical profiles of oxygen concentration at 40 stations during Proligo. Continuous line : measured oxygen concentrations. Crosses : likelihood of oxygen concentration at the sea-water sample density. Stations labelled with "Y" correspond alternately to morning (5 h-9 h) and evening (17 h-21 h).

Profils verticaux d'oxygène à 40 stations pendant Proligo. Trait continu : concentrations en oxygène mesurées. Croix : espérance de la concentration en oxygène à la densité du prélèvement. Les stations marquées par un «Y» correspondent alternativement au matin (5 h à 9 h) et au soir (17 h à 21 h).

(expressed as sigma-t) at each sampling depth. Oxygen concentration is depth- (and sigma-t-) dependent: low-density waters in the surface mixed layer are close to saturation, or sometimes slightly supersaturated, while respiration processes below the photic layer tend to depress the oxygen content. A scatterplot of oxygen concentration versus sigma-t, together with an empirical sigma-t/oxygen relationship (obtained by moving the average of the data points) are presented on Figure 1. Large discrepancies can result from different choices of the sampling depths and from internal waves which may produce discordant situations, such as station 63 with a 125 m-thick oxygen-saturated mixed layer, and station 59 when this layer was only 90 m thick (Fig. 2). The sigma-t/oxygen relationship provides the likelihood of oxygen concentration at a given sigma-t value. The ratio of

- integrated (0 to 150 m) vertical profiles of observed oxygen concentrations to
- integrated vertical profiles of the oxygen likelihood permits us to correct the oxygen content of the water column (Dandonneau and Lemasson, 1987).

The main oxygen variations during Proligo are described by means of empirical orthogonal function (EOF) analysis (Lorenz, 1956). For this purpose, a 28 × 18 matrix of oxygen concentrations was constructed, as follows:

- 28 columns representing a selection of 14 days for which data from both a morning and an evening cast are available;
- 18 lines corresponding to different depths ar regular sigma-t spacing.

Each column of the matrix was filled by interpolation of the observed oxygen concentration from the corresponding cast. Interpolation (in the sigma-t dimension) was made on oxygen anomalies (the oxygen field minus the sigma-t-dependent oxygen likelihood); the likelihood of oxygen concentration was then added.

It must be kept in mind that only the first line of this matrix represents the surface mixed layer, and can be affected by air-sea oygen exchanges; the 17 remaining lines describe the waters at or below the thermocline, and variations of oxygen concentration due to short-term exchanges with the atmosphere can be neglected.

EOF analysis uses a covariance matrix derived from the 28 × 18 matrix, and diagonalization of this matrix. The results are expressed as a sum of functions of sigma-t-(σ) and time (t) in the form:

$$O_2(\sigma, t) = O_{2,\,mean}(\sigma) + \sum_{i=1}^{18} F_i(t) \times O_{2i}(\sigma) \quad (1)$$

where $O_{2,mean}$ is the mean vertical profile of oxygen, O_{2i} is a pattern of oxygen vertical variations, modulated by F_i. The first vertical patterns, $O_{2i}(\sigma)$, and time-functions $F_i(t)$ generally extract most of the total variance, so that only these patterns (which, in best cases, each correspond to a distinct and significant phenomenon) are summed in equation (1). We thus obtain a decomposition of a complicated field into a few independent (orthogonality) dominant phenomena, each being empirically given by an eigenvector (vertical pattern) and an empirical function of time.

RESULTS

Integrated values

As already mentioned, the Proligo fixed station lasted 22 days, but only 14 days, provide two daily measurements (one cast in the morning and the other in the evening). These 14 days (28 casts) will be artificially presented as a continuous series (Fig. 3), but it should be kept in mind

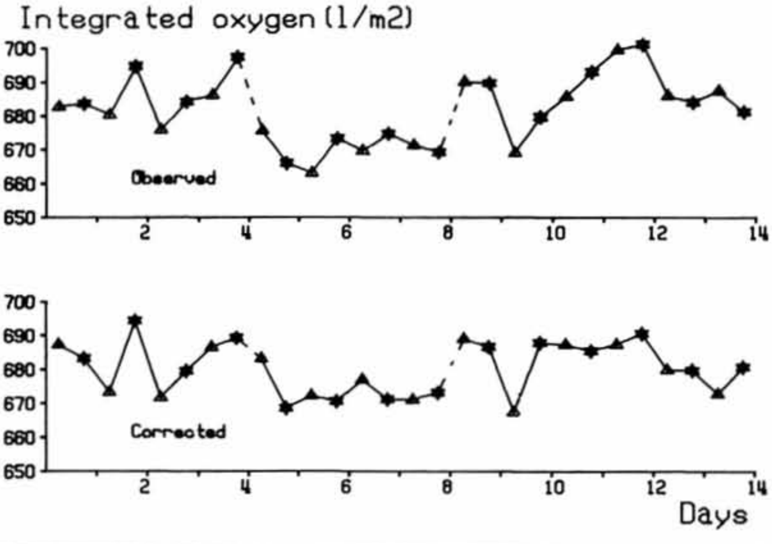

Figure 3

0-150 m integrated oxygen during Proligo. Top: observed oxygen concentrations integrated according to the trapezoidal rule. Bottom: same, after correction according to Dandonneau and Lemasson (1987). Triangles correspond to morning casts (5 h-9 h). Stars correspond to evening casts (17 h-19 h).

Oxygène intégré de 0 à 150 m pendant Proligo. Haut: concentrations en oxygène observées intégrées selon la méthode des trapèzes. Bas: même chose, après correction (Dandonneau et Lemasson, 1987). Les triangles correspondent aux mesures effectuées le matin (5 h à 9 h) et les étoiles à celles effectuées le soir (17 h à 21 h).

that one day was skipped between the fourth and fifth days of the series, and six days were skipped between the eighth and ninth days of the series. The oxygen content of the water column (0-150 m) has been computed for the 28 casts, by integration of the measured oxygen concentrations according to the trapezoidal rule. No clear diel periodicity appears (Fig. 3). The oxygen was generally more abundant in the evening than in the morning, but a net decrease occurred during the 5th and 14th days, and an increase during the nights from the 7th to 9th, 10th to 11th, and 11th to 12th days. Oxygen production in the water-column during the day (water-column oxygen content in the evening minus that in the morning) is very variable (Fig. 3). The mean difference is 3.57 $L.m^{-2}$; standard deviation is high : 7.21 $L.m^{-2}$. If the difference is imputed to photosynthesis, net carbon fixation would be 1915 $mg.m^{-2}.day^{-1}$. The need to correct the water-column oxygen content can be understood from the data presented on figures 2 and 3 : cast 81 (i.e. 14th day, morning) has a high content due to a thick saturated mixed layer, and cast 72 (i.e. 11th day, morning) has a low content due to a shallow saturated mixed layer. Figure 2 shows, however, that cast 81 gave lower than expected oxygen concentrations, while cast 72 gave higher ones. After correction, the oxygen content in the 14th day, morning, is indeed lower than in the 11th day (Fig. 3). Yet, most of the abnormalities (daily oxygen decrease, or night increase) persist after correction, and diel periodicity does not appear more clearly. The mean evening minus morning oxygen content difference is now 2.54 $L.m^{-2}$, and standard deviation increases to 9.65 $L.m^{-2}$; the corresponding photosynthetic net carbon fixation would still be very high for an oligotrophic area : 1360 mg m^{-2} day^{-1}.

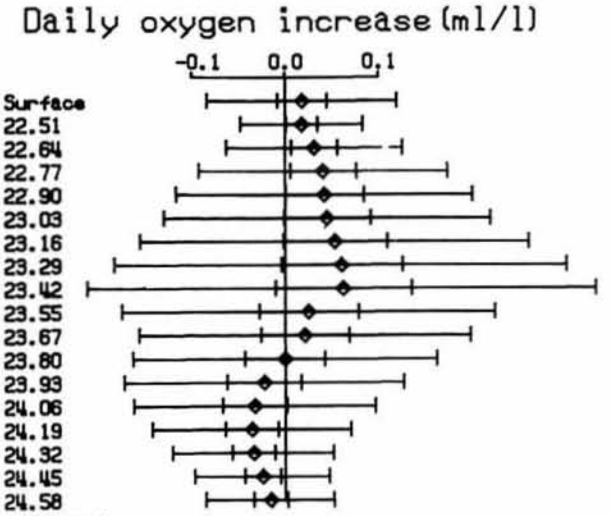

Figure 4

Oxygen concentration in the evening (17 h-21 h) minus oxygen concentration in the morning (5 h-9 h) at fixed densities, from 28 casts during Proligo. Squares represent the mean daily oxygen increase. Horizontal bars on both sides of the mean represent the error on the mean (closer tick marks) and one standard deviation of the observed daily increases (more distant tick marks).

Différence entre la concentration en oxygène le soir (17 h-21 h) et celle du matin (5 h-9 h) à des densités fixées, d'après 28 stations de la campagne Proligo. Les carrés représentent la moyenne de la production diurne d'oxygène, les barres horizontales de chaque côté de la moyenne représentent l'erreur sur cette moyenne (premières marques) et un écart type des productions diurnes observées (marques éloignées).

Vertical distribution

At fixed water densities, the evening minus morning oxygen concentration difference is very variable. A vertical pattern is however, suggested (Fig. 4) : at low sigma-t values, in the surface mixed layer, the mean daily oxyhen increase is near zero. Higher values are progressively found until sigma-t = 23.42 where the daily oxygen increase peaks at + 0.06 mL L^{-1}. A rapid decrease then gives slightly negative values in dense, deep waters. At all seawater densities, and especially at the maximum of the mean dailly oxygen increase, standard deviation of the observations is high, and the daily oxygen production does not significantly differ from zero.

The first EOF of the 28 × 18 matrix of oxygen concentrations accounts for 74 % of the variance of the residuals (oxygen concentrations minus mean vertical profile). The vertical pattern shown by the first eigenvector (Fig. 5) looks similar to the vertical profile of mean daily oxygen production (Fig. 4). with quasi null values at the surface and a maximum at sigma-t = 23.42; at depth, however (sigma-t = 24.58), the first eigenvector is near zero. The time function of the first EOF is very similar to the variations with time of the corrected daily oxygen production of the water column (Fig. 3). The second eigenvector (15 % of total variance) has a "S" shape and the corresponding time function has only two high values, at casts 16 (evening) and 75 (morning). The third EOF is not significant : it shows a more complicated pattern, with three maxima; its time function is low during the whole series, and it only extracts a negligible fraction of the variance.

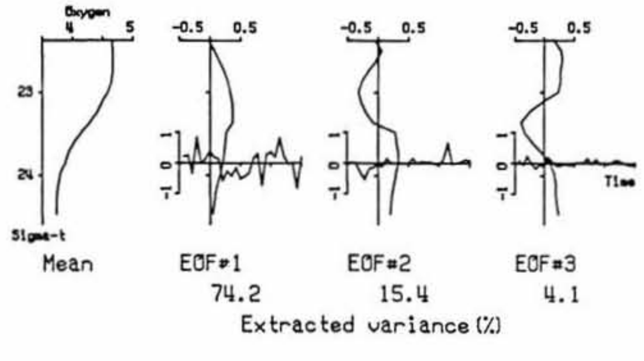

Figure 5

EOFs of oxygen variations with density and time. The oxygen concentration at sigma-t = σ and time t can be computed back by multiplying the value of the first eigenvector at σ (vertical graph); repeating this operation until EOF#18 (the two first EOFs which account for 90 % of the variance and give a quasi-complete representation of the observations may be sufficient); and adding the result to the mean oxygen concentration at σ (leftmost graph).

EOFs des variations de l'oxygène avec la densité et le temps. La concentration en oxygène à sigma-t = σ et au temps t peut être retrouvée en mulplifiant la valeur du premier vecteur propre à σ (graphique vertical) par celle de la première fonction du temps à t (graphique horizontal); en répétant cette opération jusqu'à l'EOF#18 (toutefois, les deux premières EOF qui extraient 90 % de la variance et donnent une image à peu près complète des observations peuvent suffire); et en ajoutant les résultats à la concentration moyenne en oxygène à σ (graphique le plus à gauche).

DISCUSSION

The Proligo oxygen data are not obviously shaped by the diel forcing caused by photosynthesis. Unlike Johnson *et al.* (1979), or Oudot (1984, 1989), we do not observe owygen concentrations in the evening to be all cases higher than those in the morning (Fig. 3), although on the average, evening concentrations are greater than morning ones. Photosynthetic oxygen production might be an unrealistic explanation of the mean increase during daylight hours : 3.57 L m^{-2} day^{-1} (i.e. net carbon fixation = 1915 mg m^{-2} day^{-1}) or , if correction is made according to Dandonneau and Lemasson (1987) 2.54 L m^{-2} day^{-1} (i.e. 1363 mg m^{-2} day^{-1}) are probably overestimations of the daylight net community production (NCP). The ^{14}C experiments carried out during Proligo gave carbon fixation between 134 and 992 mg m^{-2} day^{-1}, far less than the former values, despite the fact that oxygen budgets give estimates of the NCP, corrected for respiration, while the ^{14}C method gives the gross production. It would be tempting to consider that these results confirm that the ^{14}C technique strongly underestimates primary production (Shulenberger and Reid, 1981: Jenkins and Goldman, 1985). Standard deviation of our data is very high, however (Fig. 4), and makes any conclusion uncertain. It also renders illusory any attempt to isolate photosynthetic oxygen production from other oxygen fluxes : plankton respiration and exchanges with the atmosphere or with deeper waters.

Nonetheless, the vertical patterns of oxygen variations shown by the mean evening minus morning oxygen concentrations (Fig. 4) or by the first EOF (Fig. 5) strongly suggest that photosynthesis might play an important role. The bell-curves displayed by these vertical patterns present a maximum at sigma-t = 23.42; the mean depth of this isopycnal during Proligo was 129 m (Fig. 6), which is very close to the mean depth of the deep chlorophyll maximum (128 m) and to the mean depth of the nutricline (125 m) (Dandonneau and Lemasson, 1987). High variability of the oxygen concentration at this depth would thus be caused by the maximum of primary production which, in oligotrophic areas, is generally associated with the deep chlorophyll maximum (Herbland and Voituriez, 1979; Cullen and Eppley, 1981). Zooplankton respiration may further contribute to this variability since the zooplankyon maximum is often located near the maximum of primary production (Longhurst, 1976). Oudot (1984, 1989b) pointed out that warming of the surface layer and subsequent diminution of oxygen solubility could produce an oxygen maximum below the mixed layer, where temperature remains quite unchanged. The record of sea-surface temperature (Anonymous, 1985) at the position of the Proligo fixed station does not show a significant warming in September and October 1985, so that this process could not play a major role. Measurement error cannot be considered as the main cause of the observed variations : random imprecision, or biased casts due to errors in thiosulphate calibrations, would both give an even variance at all depths. This is not the case : at the surface, variance is lower (Fig. 4) and the vertical pattern shown by EOF#1, which accounts for most of the variance, has a small amplitude (Fig. 5). The surface mixed layer is indeed always near oxygen saturation, and gains or losses are rapidly resorbed by exchanges with the atmosphere. At the bottom of the layer under study, EOF#1 also shows an amplitude of variations near zero, in agreement with the low biological activity which prevails at the mean of sigma-t = 24.58 (Fig. 6 : 187 m). The negative mean oxygen daily production at this depth (Fig. 4) results from cast 16 (Fig. 2 : oxygen concentration at the bottom slightly lower than expected in the evening) and cast 75 (Fig. 2 : oxygen concentrations higher than expected in the morning) : these two casts are the only ones for which EOF#2 gives high values in deep waters. They can be considered as exceptions, and the characterization of a more reliable vertical signal by EOF#1 illustrates the superiority of EOF analysis versus more simple statistics.

If the high variability of oxygen concentration at the level of the deep chlorophyll maximum is forced by photosynthesis, it is puzzling that the well-known photosynthesis diel cycle only emerges from the variations of water-column oxygen content in the poor form of a non-significant mean evening-minus-morning value. The attempt to relate the vertical variations of oxygen at a given point to local processes assumes that advection, if present, introduces waters with the same properties as waters carried away. Current measurements during Proligo have shown speeds of about 30 cm s^{-1} (Dandonneau and Lemasson, 1987); advection cannot thus be neglected. Water masses however did not change during the Proligo cruise : temperature-salinity curves remained constant through the fixed station, which was made at a position far away from oceanic fronts, in a region of smooth

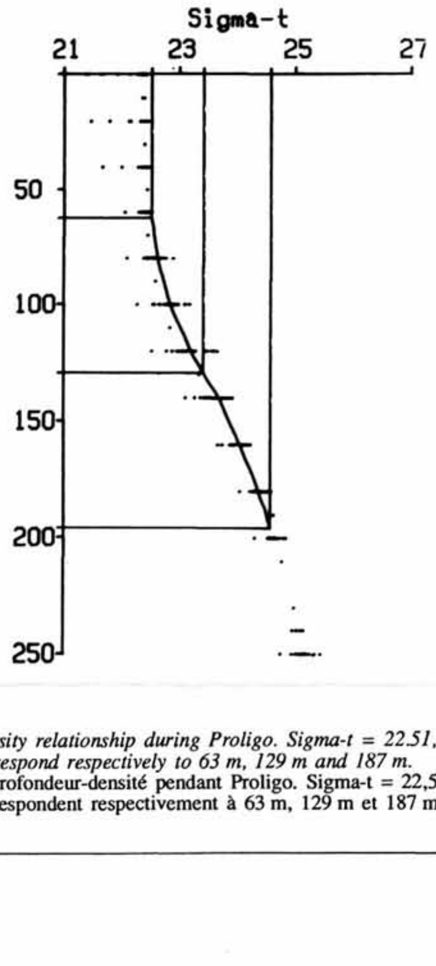

Figure 6

Depth-density relationship during Proligo. Sigma-t = 22.51, 23.42 and 24.58 correspond respectively to 63 m, 129 m and 187 m.
Relation profondeur-densité pendant Proligo. Sigma-t = 22,51, 23,42 et 24,58 correspondent respectivement à 63 m, 129 m et 187 m.

gradients. The only observed change was the appearance of low-salinity waters at the surface after heavy rains during the last three days. This change however only concerned the surface mixed layer, which, in the matrix submitted to EOF analysis, is only represented by the first line. The oxygen variations described above thus probably occurred in steady water masses, and may be partly caused by mesoscale variability which perturbs the diel cycle. Isolating the diel cycle from the oxygen variations is then a problems of signal and noise, which cannot be solved for the Proligo data because :

- sampling (two casts per day) was too widely spaced to describe either the diel signal or the noise;
- and EOF#1 does not separate the diel cycle and the noise, which have the same vertical signal.

The time variations of the water-column oxygen content (Fig. 3) and the time function of EOF#1 present similarities. Resemblance is less pronounced with the observed water-column oxygen ($r = 0.68$, $n = 28$) than with the corrected water-column oxygen ($r = 0.89$). This improvement of the correlation calls for several remarks :

- correction was done to remove the effect of dilatation or contraction of some water layers under the influence of internal waves. We have approached this result, since the corrected values of integrated oxygen converge with the 18×28 matrix built at fixed densities;
- presentation of results in the form of vertically integrated amounts per surface unit is very attractive, because primary production, exchanges at the interface and flux of solar energy are also given in this way;
- reliable integrated water-column oxygen contents are analogous to average values. The associated error is then equal to instrumental error divided by $\sqrt{n}$, where n is the number of sampling depths. This can contribute to solve the problem of precision in oxygen-based production studies.

CONCLUSION

We have described a bell-shaped vertical pattern of oxygen variations, with a null amplitude at the surface and at depth ≈ 187 m, and a maximum amplitude at about 129 m, where the deep chlorophyll maximum and the nutricline were also found during Proligo. These aspects suggest that the main forcing is probably represented by photosynthesis; the diel cycle of photosynthesis does not yet clearly appear. It is proposed that horizontal advection coupled with mesoscale variability of oxygen distribution masks the diel oxygen cycle, which one can expect to have a low amplitude in tropical oligotrophic areas. Mesoscale variability may be the result of phases of phytoplankton growth, as described by Dandonneau and Lemasson (1987), occurring in patches. Existence of this variability in an oligotrophic area poses the question of new production in these areas : if new production were very low, and if biological processes were at a steady state, spatial heterogeneity would tend to decrease. The Proligo data analysed here reveal a rather high variability in agreement with coexistent forcing.
To draw a conclusion remains, however, an uncertain exercice because it was not possible to single out a diel oxygen cycle from the ambient noise. In such oligotrophic areas, it would appear very important to measure the oxygen concentration more than twice a day, in order to obtain a time series at closer intervals, permitting isolation of the diel cycle from random mesoscale variability.

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REFERENCES

Anonymous (1985). Climate Diagnostics Bulletin, Global analyses and indices, NOAA, National Weather Service, National Meteorological Center, Climate Analysis Center, September 1985 and October 1985.
Cullen J.J. R.W. Eppley (1981). Chlorophyll maximum layers of the southern California Bight and possible mechanisms of their formation and maintenance, *Oceanologica Acta*, **4**, 23-32.
Dandonneau Y., F. Gohin (1984). Meridional and seasonal variations of the sea-surface chlorophyll concentration in the southwestern tropical Pacific (14 to 32°S, 160 to 175°E), *Deep-Sea Res.*, **31**, 1377-1393.
Dandonneau Y., L. Lemasson (1987). Water-column chlorophyll in an oligotrophic environment : correction for the sampling depths and variations of the vertical structure of density, and observation of a growth period, *J. Plankton Res.*, **9**, 215-234.
Herbland A., B. Voituriez (1979). Hydrological structure analysis for estimating the primary production in the tropical Atlantic Ocean, *J. mar. Res.*, **37**, 87-101.
Jenkins W.J., J.C. Goldman (1985). Seasonal oxygen cycling and primary production in the Sargasso sea, *J. mar. Res.*, **43**, 465-491.
Johnson K.S., R.M. Pytkowicz, C.S. Wong (1979). Biological production and the exchange of oxygen and carbon dioxide across the sea surface in Stuart Channel, British Columbia, *Limnol. Oceanogr.*, **24**, 474-482.
Johnson K.M., C.M. Burney, J. McN. Sieburth (1981). Enigmatic marine ecosystem metabolism measured by direct diel ΣCO_2 and O_2 flux in conjuction with DOC release and uptake, *mar. Biol.*, **65**, 49-60.
Levitus S. (1982). Climatological Atlas of the World Ocean, *NOAA Prof. pap.*, **13**, US Governement Printing Office, Washington DC.
Longhurst A.R. (1976). Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean, *Deep-Sea Res.*, **23**, 729-754.
Lorenz E. (1956). Empirical orthogonal functions and statistical weather prediction, Rep. N° 1, Statistical Forecasting Program, MIT, 49 pp.
Minas H.J. (1970). La distribution de l'oxygène en relation avec la production primaire en Méditerranée nord-occidentale. *Mar. Biol.*, **7**, 181-204.
Minas H.J., M. Minas, T.T. Packard (1986). Productivity in upwelling areas deduced from hydrographic and chemical fields, *Limnol. Oceanogr.*, **31**, 1182-1206.
Oudot C. (1984). Echange physique d'oxygène et production primaire dans la couche homogène en zone équatoriale de l'Océan Atlantique est, *Oceanogr. Trop.*, **19**, 95-109.
Oudot C. (1989). The shallow oxygen maximum in the tropical Atlantic Ocean (Guinea dome area) : physical or biological origin ? *Global Biogechem. Cycles*, **3**, 163-178.
Oudot C. (1989). O_2 and CO_2 balances approach for estimating biological production in the mixed layer of the tropical Atlantic Ocean (Guinea Dome area). *J. mar. Res.*, **47**, 385-409.
Oudot C., R. Gérard, P. Morin, I. Gningue (1988). Precise shipboard determination of dissolved oxygen (Winkler procedure) for productivity studies with a commercial system, *Limnol. Oceanogr.*, **33**, 146-150.
Shulenberger E., J.L. Reid (1981). The Pacific shallow oxygen maximum, deep chlorophyll maximum and primary production, reconsidered, *Deep-Sea Res.*, **28**, 901-919.