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Journal of Plankton Research Vol.9 no.1 pp.215–234, 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

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Abstract. The chlorophyll content of a water column (*WCC*), which is commonly used as an index of the phytoplankton abundance, is affected by the choice of the sampling depths and by the variations of the vertical structure of density. For instance, the thickness of the water layer, between two sigma-*t* values, which contains the deep chlorophyll maximum, can vary with internal waves. The resulting noise often dominates the mesoscale variations of the observed water-column chlorophyll (*OWCC*).Sigma-*t* dependent statistics (mean, standard deviation) of the chlorophyll concentration are computed using the observations at 29 casts from a 22-day-long fixed station in an oligotrophic environment at 15°S, 173°E. For each cast, these statistics, the sampling depths, and the water density at these sampling depths, allow the estimation of a station-dependent 'expected water-column chlorophyll' (*EWCC*). The ratio of *EWCC* to the overall likelihood of *WCC* during the fixed station (i.e. the mean of all *OWCC*) is a measure of the effect of sampling and variable density structure at each cast. When this effect is removed, the noise in *WCC* estimates decreases significantly. The time variations of *WCC* during the fixed station then show a trend with relatively high values during the first days, followed by a 12-day-long period with low values. A regular increase occurred from 1 October, which was accompanied by high carbon fixation rates and was mainly due to an increase of the chlorophyll concentration between the surface and the deep chlorophyll maximum. New production during this active phase was estimated to be 535 mgC m^{-2} day^{-1}, corresponding to 62% of the total production. Breaking of internal waves which were recorded at the beginning of the growth phase and vertical mixing of nutrients can explain the observation.

Introduction

Tropical oligotrophic areas are generally in a near steady state (Sharp *et al.*, 1980) and variations at the scale of a few days, or tens of kilometers are expected to be low (Hayward *et al.*, 1983). The occurrence of vertical mixing events which pump nutrients from below into the surface mixed layer has however been taken into consideration (McGowan and Hayward, 1978). Such short events are of considerable importance for the biogeochemical fluxes in the oceans, because they carry out in a few days a large fraction of what occurs over much longer periods (Platt and Harrison, 1985). Mixing events have been documented in coastal waters (Cullen *et al.*, 1983) but the phytoplankton growth phase after these events has never been described in oligotrophic areas because observations at a fixed station have generally not been more than a few days long: among others, a 10-day station has been occupied at 28°N in the Pacific in 1969 (Venrick *et al.*, 1973), and a 6-day station in the Atlantic at 16°N (Voituriez and Dandonneau, 1974). The probability of observing (i) a mixing event and (ii) the resulting increase of the phytoplankton biomass, is very small in such short periods. The French research vessel *Jean Charcot* occupied a 22-day fixed station at 15°S, 173°E (PROLIGO expedition, September–October 1985) during which many physical and biological observations were made. The results of these observations are used to examine whether the ecosystems in this region remained in a steady state, or if the steady state was interrupted by growing phases, resulting in an increased phytoplankton biomass.

One of the most commonly used indicators of the abundance of phytoplankton is the total amount of chlorophyll in a vertical water column with a m^2 section, limited upwards by the sea surface and downwards by an arbitrary depth Z_m. This total amount is named 'chlorophyll content of the euphotic layer' (Lorenzen, 1970), 'integrated chlorophyll' (Hayward and Venrick, 1982) or 'water column chlorophyll' (Platt and Herman, 1983). Z_m can be taken as the depth of the photic layer, but is often fixed at an arbitrary depth, large enough to include the entire layer of the deep chlorophyll maximum (*DCM*) and minimize the amount of chlorophyll which exists below. Z_m being fixed, the observed water column chlorophyll (*OWCC*) can be represented by:

$$OWCC = t\overline{WCC} + e$$

where : t is the effect of a possible mesoscale trend: e is the small-scale error; $\overline{WCC}$ is the large-scale expectation of the water column chlorophyll in the region.

If this equation is used to estimate the effect of the trend, which we expect to be small in oligotrophic areas, the unknown error e will cause uncertainty. This error is partly due to the measurement error, and to the small-scale variability of the chlorophyll concentration in a given water mass. When *OWCC* is computed, we also introduce 'column' errors which are due to the choice of discrete sampling depths, and to short-term variations of the relative amounts of various water masses which make up the water-column. Inadequate sampling schemes can lead to biased estimates of the *WCC* (Venrick, 1978) especially if the *DCM* is missed. The concept of water column admits an often neglected source of variations: water columns are strict boxes which contain a stratification of moving water masses with different densities, but the relative amounts from various water masses change rapidly, mostly with internal waves. For instance, the thickness of the chlorophyll-poor layer can decrease substantially between two stations a few hours part, while the thickness of the intermediate water layers which carry the *DCM* can increase. *OWCC* will then be temporarily high due to a reversible physical process. Water columns are not an absolute reference and special procedures must be developed in order to remedy the looseness of this concept. If c is the effect of these 'column' errors, the equation becomes:

$$OWCC = tc\overline{WCC} + e \quad (1)$$

e, which is now free of 'column' errors, is smaller, and the estimation of the effect of the trend gains in precision.

Principle of OWCC correction and hypothesis

A single chlorophyll concentration measurement, C, can be used to infer the *WCC* at a station, provided that the chlorophyll concentration in the region is statistically known, using:

$$WCC = \overline{WCC}\ C\ \overline{C}^{-1} \quad (2)$$

where *WCC* is the water-column chlorophyll estimate, $\overline{WCC}$ is the expectation of the water-column chlorophyll in the region, and $\overline{C}$ is the expectation of C in the same water mass. Genin and Boelhert (1985) obtained $\overline{C}$ as a function of temperature using a chlorophyll–temperature diagram in which they defined temperature intervals. For each interval, corresponding to a water mass, they computed a mean chlorophyll concentration $\overline{C}$ and its standard deviation, to which individual measurements were then compared. We likewise opted for density-defined water masses and $\overline{C}$ was drawn from the chlorophyll–sigma-*t* relationship. The existence of such a relationship is based on the reasonable hypothesis that mixing processes or vertical motions are weak and do not upset the vertical structure of the photic layer.

The error on *WCC* in equation (2) is given by the error on *C*, and if we only have one chlorophyll measurement, this error will be important. If we have *n* measurements C_i at different depths Z_i on a station, equation (2) becomes:

$$WCC = \overline{WCC}\left(\frac{1}{n}\sum_{i=1}^{n} C_i\right)\left(\frac{1}{n}\sum_{i=1}^{n} \overline{C}_i\right)^{-1} \quad \text{or} \quad WCC = \overline{WCC}\, C_{st}\left(\frac{1}{n}\sum_{i=1}^{n} \overline{C}_i\right)^{-1}$$

where $\overline{C}_i$ are drawn from the chlorophyll–sigma-*t* relationship and C_{st} is the mean value of the observed C_i. The error is now given by the error on C_{st} and is proportional to $(n-1)^{-0.5}$, provided that the measured C_i are independent. Independence of the C_i values at different depths Z_i implies that the superimposed water masses have different horizontal motions, which is our second hypothesis. A further improvement consists of weighting the C_i and $\overline{C}_i$ values to account for the variable thickness of the water layers which they represent. We adopted:

$$WCC = \overline{WCC} \sum_{i=1}^{n} [\tfrac{1}{2}(Z_{i+1}-Z_i)(C_i+C_{i+1})] \Big/ \sum_{i=1}^{n} [\tfrac{1}{2}(Z_{i+1}-Z_i)(\overline{C}_i+\overline{C}_{i+1})] \qquad (3)$$

If Z_1 corresponds to the sea surface and $Z_n = Z_m$, the two sums in equation (3) are respectively *OWCC* and an expected, station-dependent, water-column chlorophyll (*EWCC*) computed with the expectation of the chlorophyll concentration at the sea water densities measured at the sampling depths and with the sampling depths' intervals. Then, equation (3) becomes:

$$WCC = OWCC\ \overline{WCC}\ EWCC^{-1} \qquad (4)$$

If the error resulting from measurement and small-scale noise is not considered the ratio *WCC* to $\overline{WCC}$ represents the effect of mesoscale trends: $WCC = t\overline{WCC}$.

Combining (1) and (4) gives:

$$\frac{WCC}{\overline{WCC}} = \frac{OWCC}{EWCC} = t$$

which expresses that the effect of mesoscale trends is the same on the (a) regional or (b) station-dependent water-column chlorophyll, and:

$$\frac{OWCC}{WCC} = \frac{EWCC}{WCC} = c$$

which expresses that the 'column' error has the same effect on the (a) estimated or (b) expected water-column chlorophyll.

This technique requires that sigma-*t* dependent statistics of the chlorophyll concentration in the region be known, allowing the expectation of the water-column chlorophyll in the region ($\overline{WCC}$) and the station-dependent expected water-column chlorophyll (*EWCC*) to be computed.

Materials and methods

Choice of the site

The position (15°S, 173°E) occupied during the PROLIGO expedition was chosen for the low sea surface chlorophyll concentrations which are observed there, and for being far enough from the Vanuatu and Fiji islands, and free of possible island mass effects (Dandonneau and Charpy, 1985). Furthermore, no seasonal variations have been detected at 15°S in the western Pacific in a 5-year period (Dandonneau and Gohin, 1984). Climatological analysis of the few existing historical data in this region (Levitus, 1982) shows that the surface mixed layer is ~75 m thick and has a temperature of 27°C. Below, temperature slowly decreases until 150 m depth (24.73°C) and then decreases more quickly (21.61°C at 200 m). A deep and not well-defined thermocline has been mentioned as a characteristic of the southwestern tropical Pacific (Dandonneau, 1979). Oligotrophy of the region is confirmed by Venrick *et al.* (1973) who reported a weak *DCM* at 150 m depth at 15°S, 155°W in October.

Measurements

The measurements which lasted from 16 September to 7 October, 1985 were interrupted from 26 to 30 September during which the ship put into Suva. Temperature, salinity and density (expressed in sigma-*t*) were obtained on 82 casts from a Bisset-Berman CTD probe calibrated with water samples at least once every day. Currents were measured with an Aanderaa current meter mounted on a current profiler. In order to avoid an important bias due to ship drift caused by the wind, the current profiler was allowed to sink along a wire hanging from under a spar buoy. Seven profiles were obtained on 24 and 25 September, one on 5 October and two on 7 October. The zonal and meridional components of the currents were averaged on 20-m intervals and averaged values have been used to compute the vertical shear. An Aanderaa thermistor chain with sensors at 10-m intervals was launched and allowed to drift from 17 to 20 September (maximum depth = 150 m) and from 1 to 4 October (maximum depth = 180 m). Temperature measurements were taken at 10-min intervals.

Samples for chlorophyll determinations were taken on 29 casts using a rosette attached to the CTD probe, generally at 20-m intervals between the surface and 200 m depth, plus one sample at 250 m. Filtration was made on Whatman GF/F filters and chlorophyll measurements were made with a fluorometer after mechanical grinding and extraction by 90% acetone, according to Holm-Hansen *et al.* (1965). *OWCC* was computed by integration of the chlorophyll−depth curve from the surface to 250 m depth, with linear interpolation. No duplicates were taken to determine the precision of the chlorophyll measurements. However, on 21 stations, 3−6 sampling depths corresponded to the surface mixed layer (within an interval of 0.04 sigma-t units); assuming that mixing was efficient, so that the chlorophyll concentration has the same value at all these depths, we can estimate the standard deviation of the error at each of the 21 stations. The mean of the standard deviations was 0.0082 mg chlor m^{-3} which can be considered as an estimate of the measurement error. The resulting error on *OWCC* computed between 0 and 250 m using 12 sampling depths is then:

$$S_m = 0.0082 \times 250 \quad 12-1 = 0.62 \text{ mg chlor m}^{-2}$$

Primary production has been measured by the ^{14}C technique after *in situ* incubations of 280 ml water samples with 10 μCi of $^{14}CO_3$ for ~6 h. Carbon fixation has been computed assuming that the concentration of carbonates in sea water was constant and equal to 90 mg l^{-1}. Samples were then filtered on Whatman GF/F glass fiber filters and stored until measurement of the radioactivity by liquid scintillation.

Estimation of the expected water-column chlorophyll (EWCC)

EWCC has been estimated using the sampling depths, and chlorophyll concentrations given by a chlorophhyll−sigma-t relationship (with the sigma-t values found at these depths), instead of the measured chlorophyll concentrations. The first step in the computations consisted of fitting a function to the observed pairs (X_i = sigma-t, Y_i = chlorophyll concentration). Abbot *et al.* (1984) used a Gaussian curve to represent the deep chlorophyll maximum. We adopted a similar form:

$$F1 = C_m e^{-A(X-X_m)^2}$$

where C_m is the chlorophyll maximum, X = sigma-t is the variable, X_m is the sigma-t value at the depth of the maximum and A is a constant which controls the sharpness of the chlorophyll maximum. This form satisfies the chlorophyll decrease to negligible values in dense, deep waters (Figure 1), but fails to represent the more or less low and even concentrations above the maximum. We meet this requirement by addition of a hyperbolic tangent:

$$F2 = \tfrac{1}{2} C_s \,[1 + \tanh\,(X_p - X)]$$

where C_s is the chlorophyll concentration in the surface layer and X_p is the sigma-t value at the point of inflexion. $Y(X) = F1(X) + F2(X)$ tends to constant values on both sides of the observations: C_s in low density waters and zero in deep waters (Figure 1), and for this advantage, this model was preferred to an easier-to-fit linear one. The five constants C_m, X_m, A, C_s, and X_p were determined simultaneously by a continuous approach computing technique (derived from the method of Fletcher-Powell, in Cea, 1971) which minimized the sum of squares $(Y - Y_i)^2$. It must be noted that C_m and X_m, which correspond to the maximum of $F1(X)$, do not exactly correspond to the maximum of $Y(X)$ after addition to $F2(X)$. The mean chlorophyll concentration, Y, at a given sigma-t, X, is then:

$$Y = C_m e^{-A(X-X_m)^2} + \tfrac{1}{2}\,[1 + \tanh\,(X_p - X)] \qquad (5)$$

Subtracting $Y(X_i)$ from the observations Y_i produces residuals which have been used to compute the sigma-t dependent standard deviations S of the chlorophyll concentration. Only the residuals $Y(X_i) - Y_i$ which satisfied $X - \Delta X < X_i < X + \Delta X$ were taken

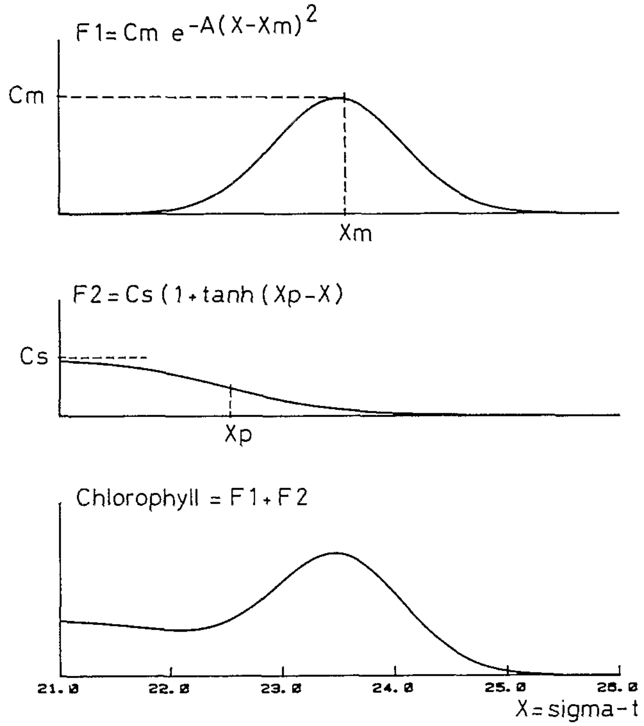

Fig. 1. Schematic representation of the function of sigma-*t* fitted to the chlorophyll observations.

into account to compute $S(X)$ at sigma-t = X. We used $\Delta X = 0.3$; smoothing was achieved by weighting factors $p_i = 0.15(|X_i - X| + 0.5)^{-1}$.

Knowing the mean of the chlorophyll concentration at a given water density makes it easy to simulate vertical profiles of chlorophyll and to compute station-dependent water-column chlorophyll:

for each station, the sampling depths Z_i and corrresponding water densities X_i from 0 to 250 m are kept unchanged;

at each sampling depth, an expected chlorophyll concentration is obtained by $Y(Z_i) = F1(X) + F2(X_i)$;

a simulated water-column chlorophyll is computed using the expected $Y(Z_i)$ instead of the observed Y_i. The result gives *EWCC* which is the likelihood of *OWCC* under the assumption of a steady state, in the conditions of sampling and vertical structure of density which prevailed at the station.

Another solution has been attempted to estimate *EWCC*: the central idea is that the measured chlorophyll concentrations are only individual values among all the possible ones at the same water density, and that *OWCC* is only one realization among all the possible ones. *EWCC* could then be defined as the mean of a large number of such realizations simulated at random. Random chlorophyll concentrations with the same distribution as during the PROLIGO expedition were obtained by

$$Y(Z_i) = F1(X_i) + F2(X_i) + H\, S_0^{-1} S(X_i)$$

where H is drawn at random from a series of numbers with a log-normal distribution, zero mean, and standard deviation S_0, and $S(X_i)$ is the standard deviation of the chlorophyll concentration at sigma-t = X_i. This procedure was abandoned because it uses too much computer time. We present however the results of 1000 such simulations made for each station, which provide interesting information on the potential dispersion of the water-column chlorophyll at each station.

Results

The hypothesis that the chlorophyll concentrations on a station at various depths are independent from one another due to isopycnal advection of water masses from various directions can be tested using the results of the current measurements: the vertical shears of the currents averaged on 20-m thick layers are shown in Figure 2. The mean shear value is 4.4 10^{-3} s^{-1}. Considering two water masses sampled at 20-m intervals at a station, this mean shear gives a horizontal distance of 3.8 km after drifting for 12 h, which was in most cases the time between two successive stations. Similarly, the observed extreme shear values, 0.5 10^{-3} s^{-1} and 26.5 10^{-3} s^{-1} give horizontal separations equal to 0.43 km and 22.9 km. These estimates correspond to the assumption of steady currents; however, the results of a series of seven current profiles over a 24-h period (24–25 September) indicate that the short-term variability of the currents was high. Trajectories of water particles at different depths between 20 and 180 m during this 24-h period have been put together in Figure 3. They show that the sea water samples taken at station 61 may have been scattered over a 16-km wide zone when station 60 was made (11 h before) and over 9 km when station 62 was made (11 h later).

Chlorophyll concentrations during the PROLIGO expedition ranged between 0 and 0.42 mg m^{-3}. The high density of observations at sigma-t = 22.4 corresponds to the 80-m thick surface mixed layer where about five samples were taken at each station. Values in the surface mixed layer were usually between 0.03 and 0.12 mg m^{-3}, and values at 250 m depth were close to zero. A deep chlorophyll maximum was observed at each station; its depth ranged between 100 and 150 m, with a mean value at 128 m, very close to the mean value of the depth of the nitricline (Table I). The best fit of

$$Y = C_m e^{-A(X - X_m)^2} + \tfrac{1}{2} C_s [1 + \tanh (X_p - X)]$$

where X is the sea water density (in sigma-t) and Y is the chlorophyll concentration, was obtained for $C_m = 0.28$, $A = 1.43$, $X_m = 23.46$, $C_s = 0.16$ and $X_p = 21.55$ (Figure 4). The continuous approach program used to fit the curve has been run several times with different starting values of C_m, A, X_m, C_s and X_p, giving each time the same final result for these constants. The standard deviation, estimated from the observed chlorophyll concentration minus $Y(X)$, shows a maximum at sigma-t = 23, while the chlorophyll maximum is at sigma-t = 23.46. The standard deviation decreases evenly towards dense waters but looks unstable at densities less than sigma-t = 22.2 where few observations are available (Figure 4). Sigma-t values <22.2 occurred only at stations 75, 77, 78 and 80 at the sea surface, and reached 80 m depth at station 81 and 40 m depth at station 82. They were caused by low salinities which were observed after a rainy period which started on 4 October, with heavy rains on 5 and 7 October.

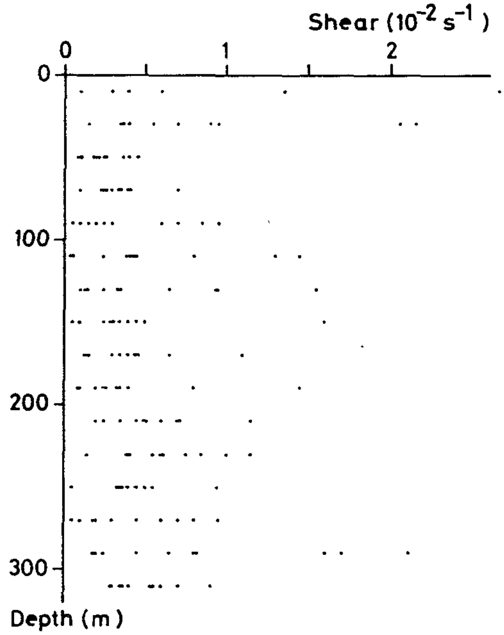

Fig. 2. Vertical shears averages at 10 current profiler stations during the PROLIGO expedition.

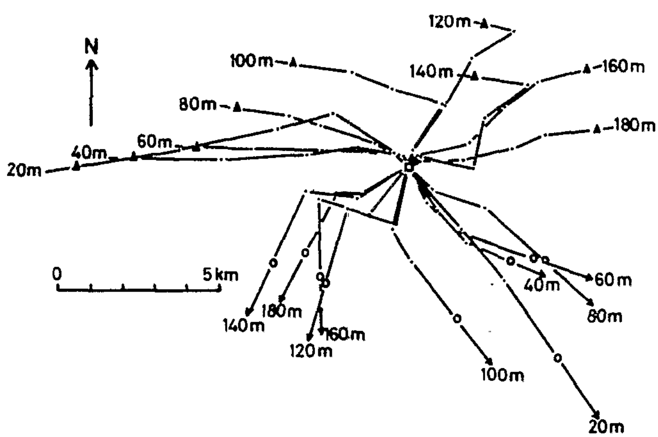

Fig. 3. Trajectories of water particles during a 24-h series of currents observations (PROLIGO expedition). Triangles indicate the position of the particles at the cast of station 60 (24 September, 19.10h) and circles at the cast of station 62 (25 September, 15.35h). The square indicates the position of station 61 (25 September, 6.37h).

The mean *OWCC* and *EWCC* for all stations are nearly equal (Table I). We then adopted:

$$\overline{WCC} = 27.58 \text{ mg chlor m}^{-2}$$

as the expected water-column chlorophyll in the region. Equation (4) can then be written: $WCC = 27.58\ OWCC\ EWCC^{-1}$. Conforming to the principle of *OWCC* correc-

Table I. Water-column chlorophyll (observed: *OWCC*; expected: *EWCC*; corrected: *WCC*) and some aspects of the photic layer during the PROLIGO expedition. Z_n is the depth of the nutricline, defined as the depth where nitrate concentration is 0.1 μmol l^{-1}.

Station	Date	Time	*OWCC* (mg m^{-2})	*EWCC* (mg m^{-2})	*WCC* (mg m^{-2})	Z_n (m)	Sigma-*t* at Z_n	Depth of *DCM*(m)	Surface chlor. (mg m^{-3})
1	16 Sept	10.45	30.50	25.95	32.42	139	23.52	140	0.06
502	17	06.20	32.95	27.45	33.11	129	23.62	100	0.08
3	17	17.45	27.40	25.80	29.29	123	23.36	120	0.05
16	18	17.30	32.10	28.72	30.83	141	23.53	140	0.03
28	19	05.00	24.35	29.08	23.09	125	23.21	140	0.04
40	19	17.05	25.35	27.24	25.67	127	23.23	140	0.04
552	20	07.30	23.20	28.36	22.56	125	23.38	100	0.04
53	20	21.11	25.75	27.07	26.24	140	23.43	140	0.04
54	21	19.00	22.50	26.62	23.31	121	23.23	120	0.04
55	22	07.00	23.60	32.09	20.28	108	23.33	120	0.01
56	22	19.05	27.55	28.59	26.58	105	23.08	120	0.04
57	23	07.10	26.10	28.70	25.08	104	23.20	120	0.05
58	23	18.45	32.05	31.49	28.07	120	23.27	100	0.07
60	24	19.10	26.70	27.60	26.68	123	23.24	140	0.00
61	25	06.37	25.70	28.67	24.72	121	23.30	120	0.04
62	25	15.35	29.35	33.38	24.25	120	23.43	120	0.05
63	1 Oct	16.13	22.95	27.33	23.16	125	23.26	140	0.03
564	2	05.50	25.95	27.95	25.61	122	23.22	120	0.07
67	2	18.00	24.60	25.45	26.66	123	23.17	140	0.05
568	3	05.46	29.95	27.93	29.57	107	23.05	120	0.08
71	3	17.50	23.70	27.30	23.94	107	23.18	120	0.05
72	4	05.00	29.80	26.01	31.60	124	23.37	140	0.07
74	4	20.39	26.25	24.82	29.17	141	23.50	140	0.07
75	5	05.00	23.30	25.63	25.07	150	23.57	150	0.02
77	5	12.50	37.30	28.88	35.62	141	23.43	140	0.09
78	5	17.50	31.85	26.31	33.39	141	23.39	140	0.08
80	6	18.00	36.05	25.14	39.55	129	23.33	100	0.09
81	7	05.00	23.25	26.96	23.78	120	22.52	140	0.04
82	7	17.50	29.60	23.52	34.71	123	23.24	140	0.09
Mean values			27.58	27.59	27.27	125	23.30	128	0.06

tion, $OWCC - WCC$ is the 'column' error due to the variations of the vertical structure of density and to the choice of the sampling depths. The standard deviation of this error can then be estimated using the results listed in Table I:

$$S_c = 2.16 \text{ mg chlor m}^{-2}$$

This error is greater than the measurement error which we estimated to be $S_m = 0.62$ mg chlor m^{-2}.

The probable water-column chlorophyll generated by the random process covers a wide range at each station (Figure 5). The mean standard deviation of the results is about 3.3 mg chlor m^{-2}, arising from the dispersion of the chlorophyll concentrations at a given sigma-*t*, i.e. from measurement error, small-scale noise, and possible trends. Since the variations due to the measurement error are small, the two latter causes are

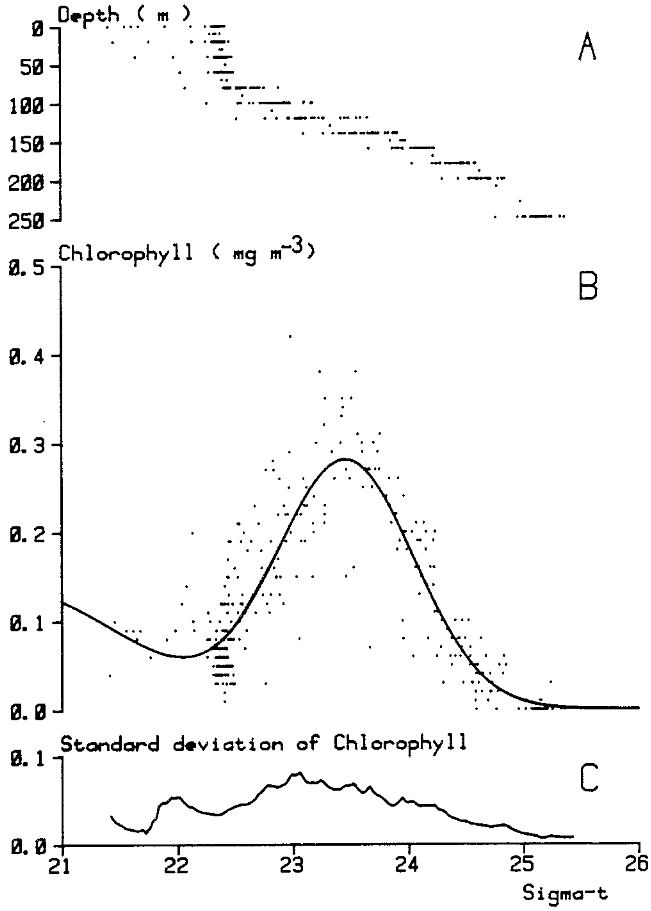

Fig. 4. (A) Sigma-t versus depth during the PROLIGO expedition. (B) Observed sigma-*t*—chlorophyll pairs and best fit of

$$Y = C_m e^{-A(X-X_m)^2} + ½\ C_s[1 + \tanh\ (X_p - X)]$$

(C) Standard deviation of the observations from the fitted curve.

thus important sources of variance for the water-column chlorophyll. At 11 stations (3, 16, 40, 53, 56, 58, 60, 564, 67, 568, 74 and 75) *OWCC* and *EWCC* do not differ strikingly. But for many stations, discrepancies appear: *OWCC* falls in the 5% largest water-column chlorophyll simulated values at five stations (1, 77, 78, 80 and 82) and in the 5% smallest ones at station 55. Six stations out of 29 are significantly different at the 95% confidence level from what is expected suggesting that something other than isopycnal motions of independent water layers might act.

The time variations of *OWCC* during the 22-day fixed station look uncertain (Figure 6a). Only the periods 19–22 September with evenly low *OWCC*, and 5–6 October

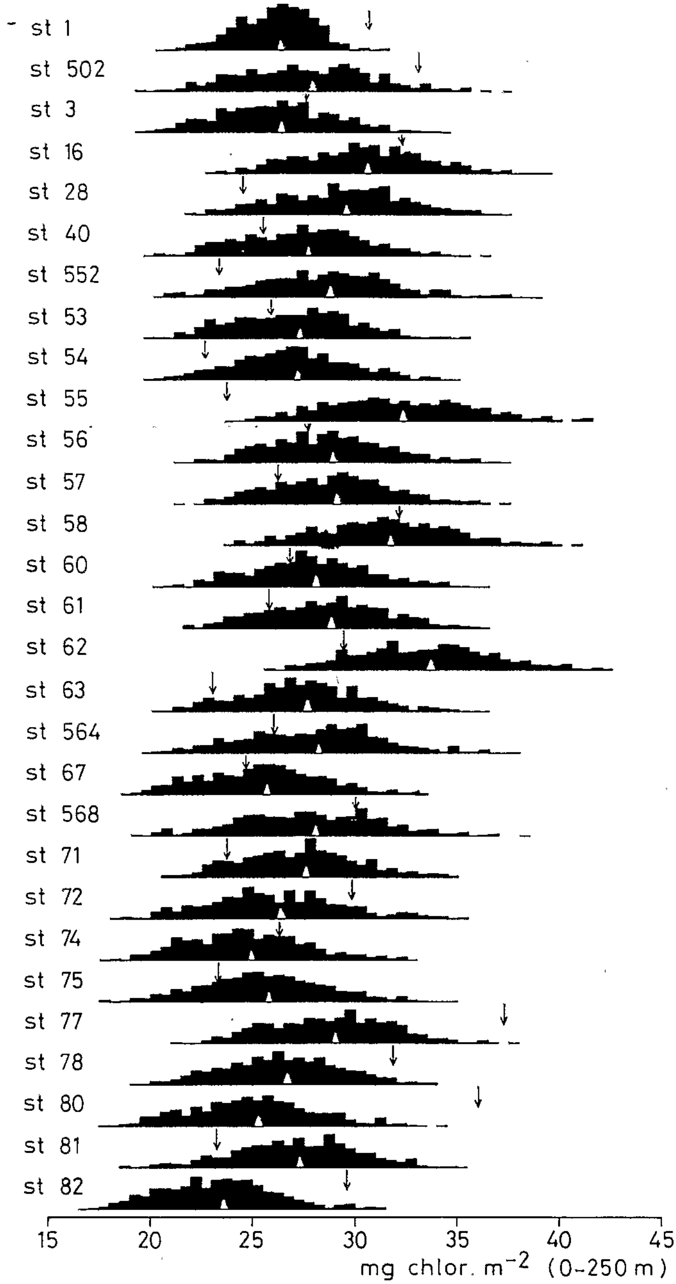

Fig. 5. Distributions of the results of 1000 water-column chlorophyll simulations. For each station, the arrow pointing downwards indicates the observed water-column chlorophyll (*OWCC*). The white triangle indicates the mean result of the simulations.

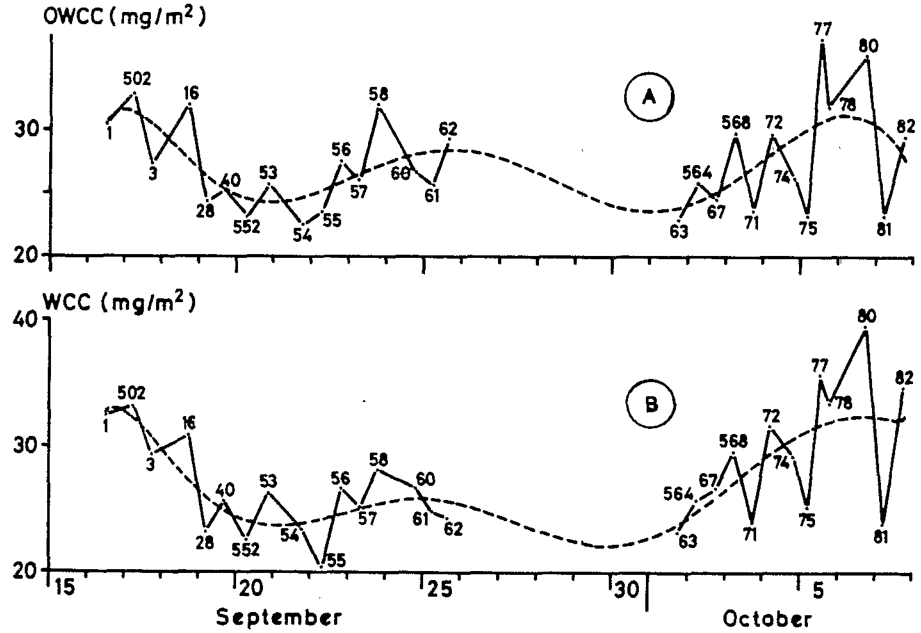

Fig. 6. (A) of *OWCC* during the PROLIGO expedition. (B) Evolution of $WCC = OWCC\ \overline{WCC}\ EWCC^{-1}$ where $\overline{WCC}$ is the mean value of *OWCC* for the 29 stations. The labels are the station numbers.

with high *OWCC* stand out against noisy variations. The variance of *OWCC* is 16.16. Our series of results only consists of 29 observations irregularly spaced in time, making it difficult to distinguish a trend from the ambient noise. The most commonly used techniques are Fourier analysis, low-pass filters or best fits of functions. We adopted a polynomial fit; the coefficient of determination stabilized from degree seven, and the fraction of extracted variance was then $r^2 = 0.349$. The standard deviation of the variations due to the trend (derived from the polynomial approximation) is then $(16.16 \times 0.349)^{-0.5} = 2.37$ mg m^{-2}, and the standard deviation of the small scale noise (represented by the residuals) is $[16.16\ (1-0.349)]^{-0.5} = 3.24$ mg m^{-2}. We have then:

$$\text{signal-to-noise-ratio of } OWCC = 2.73/3.24 = 0.73$$

If *WCC* is plotted instead of *OWCC* (Figure 6b), a trend appears more clearly, with high values from 16 to 18 September, low values from 19 September to 2 October, and high values again until the end of the expedition with downward spikes at stations 71, 75 and 81. The variance of *WCC* is 21.07. A seven-degree polynomial fit applied to the 29 time–*WCC* pairs gives $r^2 = 0.520$. The standard deviations of the trend and of the residuals become respectively 3.31 and 3.18 mg m^{-2}, and we now have:

$$\text{signal-to-noise-ratio of } WCC = 1.04$$

Correction of *OWCC* for sampling depths and variations of the vertical structure of density has thus increased the signal-to-noise ratio.

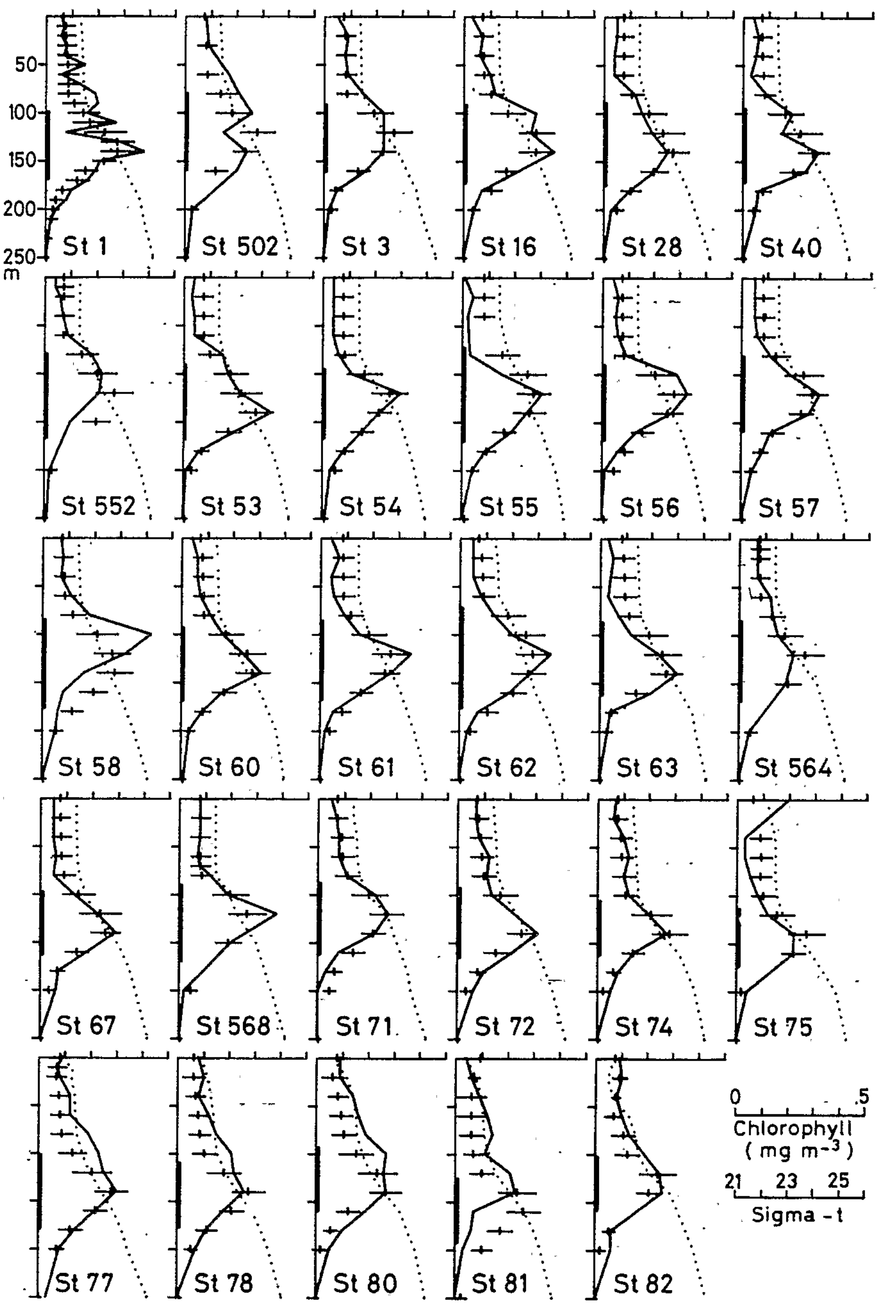

Fig. 7. Vertical profiles from the PROLIGO expedition. Solid line: observed chlorophyll concentration. Horizontal bars: two standard deviations of the chlorophyll concentration at the sigma-*t* of the sampling depth; the short vertical bar indicates the associated mean. Dotted line: sigma-*t*. Vertical reinforced bars on the ordinate indicate the interval between sigma-*t* = 22.7 and sigma-*t* = 24.2 where the deep chlorophyll maximum is located.

Discussion

WCC was derived from *OWCC* using a correction factor $\overline{WCC}\ EWCC^{-1}$. The expectation of the water-column chlorophyll in the region was considered to be a constant. The trend which appears in Figure 6 implies that $\overline{WCC}$ might be a function of time, in which case our corrected *WCC* results would be underestimated at the beginning and at the end of the fixed station, and overestimated from 19 September to 2 October. On the other hand, *EWCC* is derived from $\overline{C}$ (a function of sigma-*t*) which might equally be a trend-like function of time, and compensate for the variations of $\overline{WCC}$ with time. It is not possible to appreciate exactly the consequences of adopting constant statistics over the length of the fixed station. $\overline{WCC}$ can be considered as the water-column chlorophyll of an assumed standard water column. *EWCC* is the water-column chlorophyll which would be observed under these standard conditions, given the same sampling depths and given the same vertical structure of density as at the station under study. The correction factor $WCC\ EWCC^{-1}$ is then based on a unique reference, and can be considered as valid as far as this reference fits the observations. During the fixed station, the depth of the *DCM*, the depth of the nutricline and the water density at the depth of the nutricline did not indicate important changes which would require a revision of this reference (Table I). The form given to equation (5) is only one among other possible ones. A bias in $\overline{WCC}\ EWCC^{-1}$ may result from this choice, especially because the effect of equation (5) is present in $EWCC^{-1}$ and not in $\overline{WCC}$ which was arbitrarily fixed at 27.58 mg m^{-2}, i.e. the mean value of *OWCC*. This bias however would be very small because the mean values of *EWCC* and *WCC*, in which equation (5) interferes, are very close to the mean of *OWCC* (Table I).

The trend cannot be seen as clearly on *OWCC* which is perturbed by small-scale noise. The correlation between *OWCC* and corrected *WCC* is high ($r = 0.88$), which means that corrections are small and do not produce an upset of the data. Clarity of the trend in the *WCC* values results mostly from the increase allotted to stations 1, 80 and 82, and from the decrease allotted to stations 16, 58 and 62 (Figure 6). The correction factor $\overline{WCC}\ EWCC^{-1}$ is >1 when *EWCC* is low, which was the case at stations 1, 3, 67, 74, 75, 80 and 82. Low values of *EWCC* during the PROLIGO expedition probably do not result from inadequate sampling because samples were generally taken at 20-m intervals, which seems satisfactory for a description of the vertical profile of chlorophyll in a region where all the sea water properties exhibit low vertical gradients (Figure 7). They result rather from a reduced vertical extension of the water layer with sigma-*t* values between 22.7 annd 24.2, where the *DCM* is observed (Figure 4). The mean thickness of this layer during the whole PROLIGO expedition was 78 m; at stations 1, 3, 67, 74, 75, 80 and 82, this layer was only 72, 70, 68, 58, 63, 68 and 59 m thick (Figure 7). On the contrary, high *EWCC* at stations 16, 55, 58 and 62 results from enhanced vertical spreading of the same water mass which was respectively 80, 97, 95 and 106 m thick at these stations. Such short-term variations of the vertical density structure of the water column are confusing, and the correction factor $\overline{WCC}\ EWCC^{-1}$ sets the observations under mean physical conditions of the water column. At station 1, 24 samples were taken instead of 12 as at the other stations. This more intense sampling gives a smaller dispersion of the simulated water-column chlorophyll values which are recorded in the histogram of station 1 in Figure 5. This result is an expected one since water-column chlorophylls are analogous to mean chlorophyll concentrations between 0 and 250 m, and the variance of the mean of n individuals is proportional to n^{-1}.

Low corrected *WCC* values are obtained at stations 28, 552, 54, 55, 62, 63, 71, 75 and 81 (Figure 6). They generally result from abnormally low chlorophyll concentrations in the mixed layer above the *DCM*, except at stations 552, 71, and 81 where they proceed from abnormally low chlorophyll concentrations below the *DCM* (Figure 7). Higher *WCC* values at stations 1, 502, 72, 77, 78, 80 and 82 result from abnormally high chlorophyll concentrations above the *DCM* except at station 72 where deep water is the main cause. In most cases, the water between the surface and the DCM is thus responsible for the main variations in the results. Another mark of the predominance of this water layer is given by the greater dispersion of the chlorophyll concentration at low sigma-t values (Figure 4). Interest in the relationships between the sea surface chlorophyll concentration and the water-column chlorophyll has increased due to the possibilities which are offered by satellite-borne sea color sensors. Hayward and Venrick (1982) observed no relationships in the oligotrophic North Pacific central gyre. In our results, the sea surface chlorophyll concentration is not significantly correlated with *OWCC* ($r = 0.26$, $P > 0.05$) but is significantly correlated with the corrected *WCC* ($r = 0.39$, $P < 0.05$), in spite of the confusing station 75 which has a high sea surface chlorophyll concentration and low water-column chlorophyll (Figure 7).

The ^{14}C incubation experiments made during the PROLIGO expedition confirm the trend of the corrected *OWCC* shown on Figure 6. During the first part of the cruise, carbon fixation was low: 134, 435 and 210 mg m^{-2} day^{-1} at stations 502, 552 and 559 (24 September). Carbon fixation was still low at the beginning of the second part (343 mg m^{-2} day^{-1} at station 564) but rapidly increased later: 992 mg m^{-2} day^{-1} at station 568 and 739 mg m^{-2} day^{-1} at station 579 (6 October). *WCC* reached particularly high values from station 77, 2 days after the increase of carbon fixation. Assuming that the 'new production' during the steady-state phase (stations 28–71) was not greatly different from zero (Sharp *et al.*, 1980), we can tentatively estimate the 'regenerated production' as the mean of the production measurements made at stations 552, 559 and 564, i.e. 330 mg C m^{-2} day^{-1}. The mean *WCC* value during this phase is 25.05 mg chlor m^{-2}, giving a productivity index equal to 13.17 mg C (mg chlor)$^{-1}$ day^{-1} which can be compared to the value 15.7 found by Sharp *et al.* (1980). Considering that the regenerated production remained constant, and that total production during the growth phase was $(992+739)/2 = 865$ mg C m^{-2} day^{-1}, new production during the growth phase was then 535 mg C m^{-2} day^{-1}, i.e. 60% of the total production. Missing such events when oligotrophic areas are studied can thus lead to incomplete views concerning the dynamics of these ecosystems (Platt and Harrison, 1985).

The cause of the increase of the phytoplankton biomass and productivity does not appear in the variations of the depth of the nutricline (defined as the depth of NO_3 concentration = 0.1 μmol l^{-1}) which was influenced by semi-diurnal internal waves (Table I). Presence of nitrates in the mixed layer, or in the upper part of the *DCM*, which would indicate recent vertical mixing events, could not be significantly detected. The vertical profiles of chlorophyll, sigma-t, nitrates and Brunt–Väisälä frequencies at stations 552 (low *WCC* episode) and 568 (growth phase) do not differ strikingly, but carbon fixation at station 568 is much higher than at station 552 (Figure 8). The occurrence of such mixing events must be considered in spite of the absence of measurable nutrients

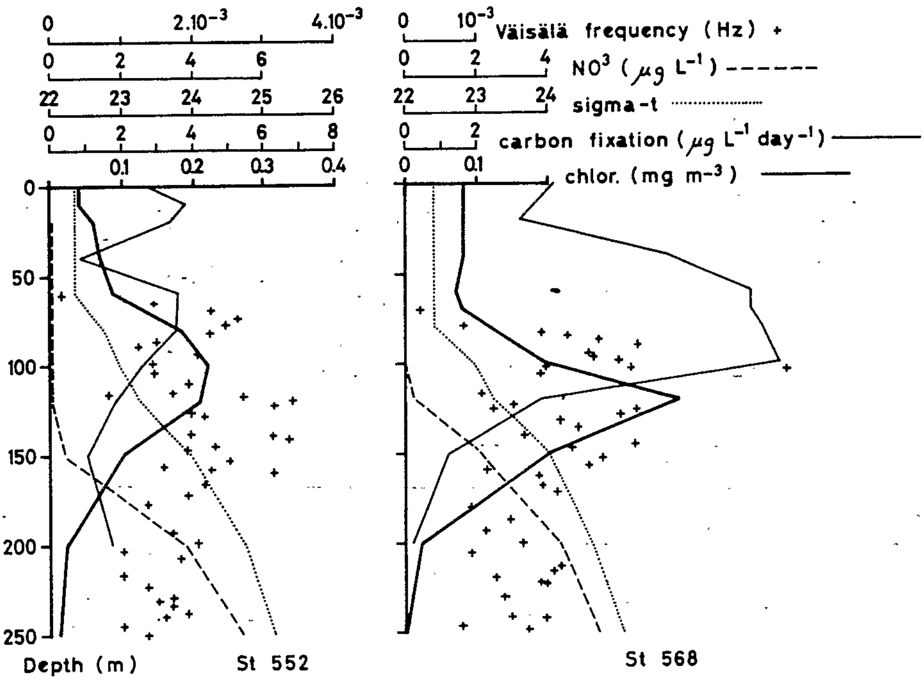

Fig. 8. Vertical profiles at station 552 (20 September, resting phase) and 568 (3 October, growth phase).

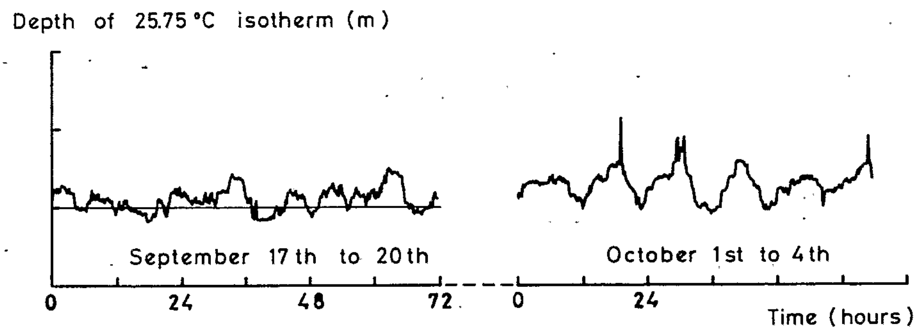

Fig. 9. Internal waves during the PROLIGO expedition. The depth of the 25.75°C isotherm has been obtained by linear interpolation of the temperatures measured by a thermistor chain. Depths >150 m during the first series of data have been obtained by extrapolation, using the mean value of the vertical temperature gradient between 25° and 26°C.

in the mixed layer, because of the rapid uptake by the phytoplankton (McGowan and Hayward, 1978). The nutricline does not greatly depart from waters at sigma-t = 23.3 (Table I), except at stations 56, 568 and 81 where the nutricline is found in less dense waters. Such rises of the nutricline might be due to small vertical mixing events. The two series of temperature data given by a thermistor chain allow the internal waves during the PROLIGO expedition (Figure 9) to be described. The thermistor chain was first launched from 17 September at 15.00 h to 20 September at 15.00 h; this period

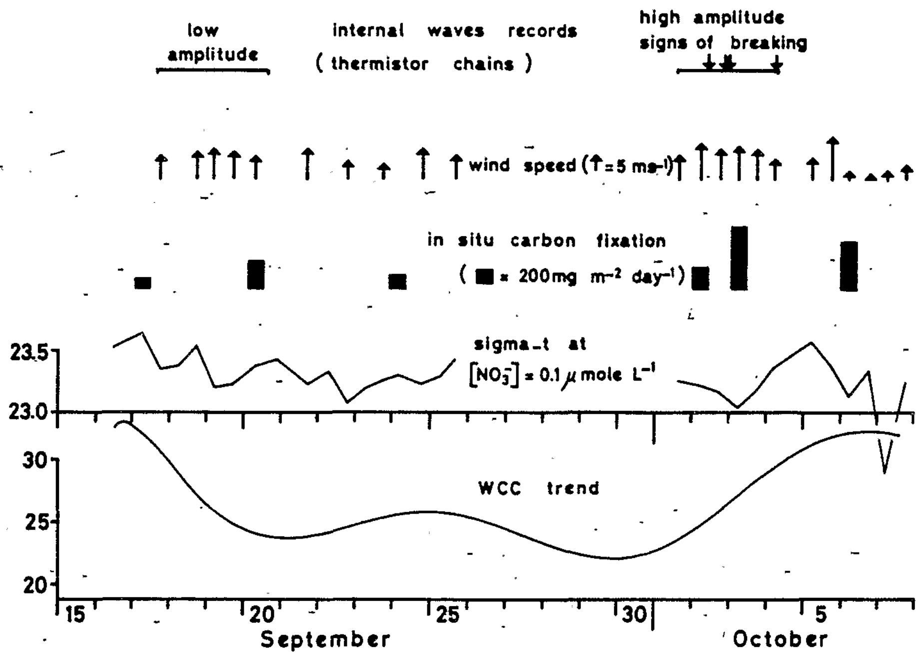

Fig. 10. Summary of the conditions which prevailed during the PROLIGO expedition.

included stations 3, 16, 28, 40 and 552 preceding the low *WCC* episode which lasted until 2 October (Figure 6). Internal waves then had a maximum amplitude of <15 m and their period was doubtful. The second series of measurements from 1 October at 14.00 h to 4 October at 08.00 h which included stations 63, 564, 76, 568, 71 and 72 shows well-defined, semi-diurnal internal waves with a 18 m mean amplitude. The wind speeds then were noticeably higher than during the first series of measurements (Figure 10). Spikes are superimposed at the crests of the second, third and last waves described by this series (Figure 9). It is noteworthy that the spikes at the second and third waves occurred just before an intrusion of nitrates in waters at sigma-t = 23 and just between stations 564 and 568, 24 h apart, where primary production was respectively 343 and 992 mg C m^{-2} day^{-1} (Figure 10). The pycnocline during the PROLIGO expedition was dim. Brunt–Väisälä frequencies at the depth of the nutricline are $N/2\pi = 2.5 \times 10^{-3}$ Hz (Figure 8) corresponding to a mean period of ~7 min. Such low frequencies do not exclude the possibility of vertical mixing. Averaged values of the Richardson number *Ri* between 110 and 150 m depth are greater than 0.25 (Table II) which is often considered as the upper limit of *Ri* for conditions of vertical turbulence. However, a few values are smaller than unity, and smaller than those found by Cullen *et al.* (1983) who documented a vertical mixing event. Conditions for vertical mixing are thus within reach and could probably be met sometimes during the fixed station.

Vertical mixing of nutrients by breaking internal waves appears then to be a plausible explanation for the *WCC* increase which distinguishes the second part of the PROLIGO expedition. During this phase of active growth, *WCC* kept low at stations

Table II. Richardson numbers at 10 vertical profiles of current, calculated with the mean sea water density and current in the 90–110, 110–130, 130–150 and 150–170 m water layers.

Day	Time	110 m	130 m	150 m
24 Sept	18.20	9.58	13.9	0.89
24	21.55	8.02	210	22.9
25	00.40	0.78	31.7	7.24
25	03.15	398	2.01	20.2
25	05.55	521	4.13	22.1
25	09.30	0.72	14.5	15.4
25	12.00	1.80	57.0	7.24
5 Oct	13.20	10.2	0.59	139
7	11.45	8.99	105	6.44
7	15.00	34.8	2.77	1076

71, 75 and 81 (Figure 6). This does not contradict the hypothesis of an enhanced growth subsequent to mixing events because the breaking of internal waves is likely to be patchy, so that some water masses may remain unaffected. Furthermore, the low *WCC* value at station 81 is due to low chlorophyll concentrations below 150 m while relatively high chlorophyll concentrations above the *DCM* at this station are in agreement with an input of nutrients in the surface layers (Figure 7).

No explanation can be put forward for the relatively high *WCC* at the beginning of the expedition (stations 1–16) because the time of response of *WCC* is of the order of a few days and the cause must be sought in the period before the observations began. Neither can we assess the consequences of the pronounced nitrate intrusion into low density waters on 7 October, when the fixed station came to an end (Figure 10). The period from 22 to 26 September shows a slight *WCC* increase which is not accounted for by the other results: primary production was low on 23 September, and the wind conditions were about normal over the period (Figure 10); a nitrate intrusion up to waters at sigma-t = 23.08 on 22 September might perhaps explain this slight increase, but evidence of the causality is small.

Conclusion

The studied area which has a chlorophyll maximum at depths greater that 100 m, chlorophyll concentrations below 0.45 mg m^{-3} and a 100–150 m thick nutrient-exhausted mixed layer, can be compared to other tropical oligotrophic areas. Furthermore, its position at 15°S and 173°E does not correspond to any divergence or doming (Wyrtki and Kilonsky, 1984; Oudot and Wauthy, 1976), so that an important supply of nutrients from below cannot be expected. The results of the 22-day-long fixed station made during the PROLIGO expedition show however that a mixing event, probably due to breaking of internal waves, was followed by a period of growth and an increase of the water-column chlorophyll. Whether such an observation was likely or not within a 22-day period cannot be determined, unless several such long fixed stations be made. Existing biological data from long fixed stations in oligotrophic areas are few, and generally do not cover a period long enough to include a phase of increased growth. Relatively high *WCC* at the beginning of the PROLIGO expedition is perhaps indicative of a similar period a few days before. If that was the case, vertical mixing events are not exceptions at 15°S, 173°E, and the concept of a steady state in this region must be revised. Exchanges between the surface (0–150 m) water which support the photosynthesis and deeper waters where remineralization occurs would then be important. Conditions for an intermittent mixing regime are more favourable in the South Tropical Pacific where the thermocline is broad (Wyrtki and Kilonnsky, 1984) than in the North Pacific central gyre where it is sharper (McGowan and Hayward, 1978). The variations in water-column chlorophyll that result from these mixing events however are small, and do not emerge strikingly from the ambient noise. The method developed in this work to eliminate the effects of sampling and density structure variations proved to be efficient in reducing the noise and showing up the trend in water-column chlorophyll.

Acknowledgements

We thank Gerard Eldin for watching over the physical data collection at sea, and processing of these data, and Henri Walico for the chlorophyll measurements. We are also grateful to the captain and crew of R.V. *Jean Charcot* for their kind assistance at sea.

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Received April 1986; accepted October 1986