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Subsurface chlorophyll maximum and hydrodynamics of the water column

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ABSTRACT

The vertical distributions of chlorophyll *a* (*in vivo* fluorescence) and hydrodynamic properties were monitored in the Gulf of St. Lawrence (Canada) from 6 to 10 August 1983, using an automatic yo-yo profiling system and a chain of 4 current meters. Spectral analyses of temperature and *in vivo* fluorescence series showed that dominant frequencies were associated with internal waves (~16 h inertial frequency). A subsurface chlorophyll maximum was continuously observed in the lower part of the 20 m thick photic layer, at a depth corresponding with maximum vertical stability of the water column, just above the nutricline.

The depth of maximum phytoplankton production, at least on sunny days, corresponded to that of the subsurface chlorophyll maximum and of the maximum in vertical stability. This close association persisted despite strong horizontal advection and vertical movements caused by internal waves. Photosynthetic adjustment did occur in the water column: higher vertical stability at depth favored shade adaptation of the phytoplankton in the layer of maximum stability, as compared to the more light-adapted cells of the upper well-mixed layer. At our sampling station, vertical turbulent diffusion seemed to be high enough to replenish nutrients in the photic layer, so that they never became completely exhausted, even in surface waters. Therefore, the observed subsurface chlorophyll maximum not only resulted from environmental conditions more favorable for phytoplankton accumulation and growth, but it also involved active photosynthetic responses of phytoplankton.

1. Introduction

During the summer months, stratified coastal waters are generally characterized by the presence of a subsurface chlorophyll maximum (Hobson and Lorenzen, 1972; Pingree *et al.,* 1978; Cullen and Eppley, 1981; Holligan *et al.,* 1984a). The mechanisms at the origin of such maxima have been reviewed by Cullen (1982). Among various mechanisms, decreased sinking rates of phytoplankton cells at the pycnocline (Steele and Yentsch, 1960; Derenbach *et al.,* 1979; Pingree *et al.,* 1978) and behavioral responses, such as the active aggregation of free-swimming cells (Smayda, 1970; Kamykowski, 1976; Falkowski *et al.,* 1980; Cullen, 1982) have most often been invoked to explain the accumulation of cells into subsurface chlorophyll

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maxima. However, these mechanisms cannot fully account for the persistence of those maxima. The coincidence often observed between the subsurface chlorophyll maximum and the nutricline suggests that active nutrient uptake, and therefore phytoplankton growth, play an important role in the maintenance and development of chlorophyll maxima (Herbland and Voituriez, 1979; Eppley *et al.*, 1979). It has been shown by Herbland and Voituriez (1979) that, when light and nutrients are nonlimiting, the growth of phytoplankton favors the development of a chlorophyll maximum. The photic zone is often a two-layer system, with a nutrient-depleted surface layer and deeper water where light limits phytoplankton growth (Dugdale, 1967). In that context, subsurface chlorophyll maxima would occur at an intermediate depth where both light and nutrient conditions offer the best compromise for phytoplankton growth.

Following this idea, Legendre *et al.* (1986) have proposed that unhanced biological production occurs at nutriclines, and also at other aquatic interfaces (ergoclines: Legendre and Demers, 1985), as the consequence of the matching or resonance of physical scales with biological scales. Interpreting the horizontal scales of phytoplankton in terms of physical processes goes back to Platt (1972), and the idea was generalized in oceanography by Platt and Denman (1975). As subsurface chlorophyll maxima are concerned, Lewis *et al.* (1983) have shown that their very presence can cause the depth stratum containing the deeper portion of the maximum to increase its thermal stratification with time, which may permit the maintenance and development of the chlorophyll maximum, hence possible resonance of physical scales with biological scales.

Despite a large number of field studies, the relative importance of physical and biological factors in the maintenance and development of the subsurface chlorophyll maximum remains to be ascertained (Holligan *et al.*, 1984a, Fasham *et al.*, 1985). There is some debate in the literature as to whether the depth of maximum chlorophyll concentrations corresponds or not to that of maximum vertical stability. For instance, Holligan *et al.* (1984a) have observed dinoflagellate maxima that were located below the depth of maximum stability. On the contrary, Pingree *et al.* (1975) have explained sharp dinoflagellate maxima by increased characteristic mixing time in the pycnocline. This opens two questions. First: is the vertical distribution of phytoplankton production independent from the scales in the vertical physical structure? If these are not independent, then: is biological production in the chlorophyll maximum caused (at least in part) by changes in the physiological state of the organisms? If not, only physical mechanisms are probably responsible for the subsurface maximum. The contrary may indicate that phytoplankton have evolved mechanisms not only to cope with physical variability, but to actively exploit it, as suggested by Harris (1980). Whether maximum production corresponds or not to the depth of maximum vertical stability is therefore the first point to be examined when studying a subsurface chlorophyll maximum.

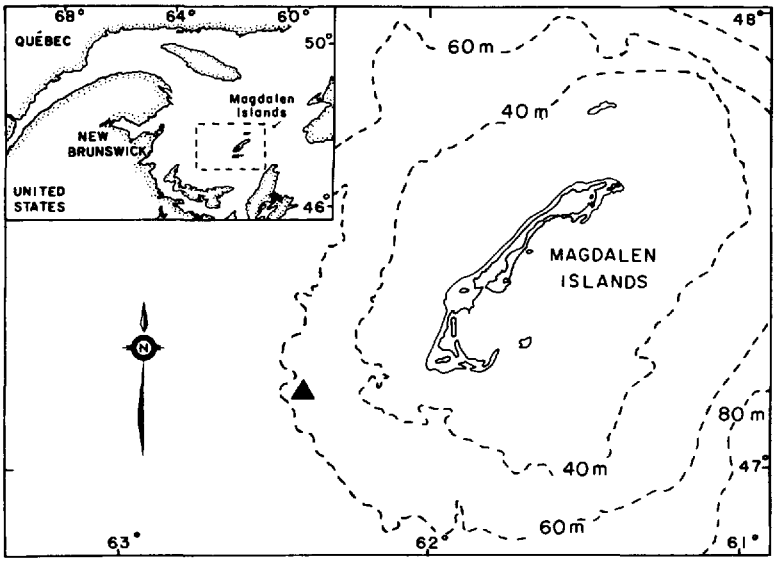

Figure 1. Map showing the location of the sampling station. Isobaths in meters.

The vertical structure of phytoplankton cannot be investigated by only sampling state variables, either biological (e.g. biomass) or physical (e.g. temperature or salinity) (Platt *et al.*, 1981; Legendre and Demers, 1984). If mechanisms are to be addressed, on the vertical, rate variables must be measured simultaneously, for both biological and physical properties. Accordingly, the vertical distributions of photosynthetic activity and phytoplankton production, together with hydrodynamic rates, were sampled in the stratified waters of the Gulf of St. Lawrence, with the purpose of investigating the mechanisms responsible for formation and maintenance of the subsurface chlorophyll maximum. The discussion of these mechanisms will be conducted with reference to the questions above.

2. Materials and methods

a. Sampling. Sampling was conducted in the Gulf of St. Lawrence from 6 to 10 August 1983, at an anchor station (47° 10'N, 62° 25'W; 60 m depth) located 23 km west off the Magdalen Islands (Fig. 1). An automatic yo-yo profiler interfaced with a computer was used to record more than 1200 multivariate profiles (0–30 m) of temperature and salinity (Guildine CTD probe Model 8770), photosynthetically active radiation (PAR: Biospherical Quantum Scalar Irradiance Meter), light beam transmission (Sea Tech transmissometer) and *in vivo* fluorescence. Water was continuously pumped, from the depth of the probes, into a Turner Designs fluorometer (on deck) for the measurement of *in vivo* fluorescence as an index of *in situ* chlorophyll concentra-

tion (Lorenzen, 1966). Measurements recorded on the computer were discretized every 0.5 m, after shifting back the fluorescence data by a time lag corresponding to the estimated travel time between the pump and the fluorometer; this time lag was measured using a fluorescent dye, and the flow was periodically checked with a flow meter at the outlet of the fluorometer. In order to later transform the *in vivo* fluorescence into chlorophyll *a,* 500 ml of sea water were periodically sampled at the outlet of the fluorometer and filtered on Whatman GF/C glass fiber filters. After 24 h extraction in acetone 90%, the concentration of chlorophyll *a* was determined using the fluorometric method of Strickland and Parsons (1972). One chain of 4 Aanderaa current meters with conductivity and temperature probes (located at average depths of 12, 14, 16 and 18 m) was anchored near the ship.

Every hour, water samples were collected using Niskin bottles at 0, 10, 15, and 20 m. These depths were chosen after examination of the first few multivariate profiles, with the purpose of sampling the layer of the subsurface chlorophyll maximum while simultaneously covering the whole photic layer. Photosynthetic characteristics of the phytoplankton, and concentrations of chlorophyll *a* and of dissolved nutrients (filtered frozen samples stored and analyzed within one month in the laboratory using a Technicon autoanalyser: Strickland and Parsons, 1972) were determined for each depth. Finally, 200 ml of water were fixed with gluteraldehyde and cacodylate for later cell examination.

From 7 to 9 August, photosynthesis *versus* irradiance relationships were determined hourly on the Niskin water samples with photosynthetron incubators (Lewis and Smith, 1983). Due to a technical problem with one of the incubators, there are no data at 0 m on 7 August. Parameters of the photosynthesis *versus* irradiance curves were fitted using the equation of Platt *et al.* (1980), after normalizing the activities per unit chlorophyll *a* (B). These parameters are the initial slope (α^B), the light-saturated photosynthetic rate (P^B_{max}), the photoinhibition parameter (β^B), $I_k = P^B_{max}/\alpha^B$, and the light intensity at which P^B_{max} is reached (I_m). Rates of primary production were estimated according to the method of Harrison *et al.* (1985), using the photosynthetic parameters and the *in situ* irradiance. The models of Jassby and Platt (1976) and of Platt *et al.* (1980) were compared in computing normalized production rates P^B(mgC mgChla^{-1} h^{-1}); the second model takes into account photoinhibition at high light intensity, while the first does not. These P^B values, multiplied by B, gave hourly production rates (mgC m^{-3} h^{-1}). Daily production rates (mgC m^{-3} d^{-1}) were obtained by summing the corresponding 24 hourly rates.

b. Data analyses. Due to problems with the control system of the yo-yo profiler, the time interval between successive vertical profiles could not be kept constant during the whole cruise. On the average, there were about 15 profiles per hour, except between 15h00 and 20h00 on 7 August when only one profile per hour is available. A standard time interval of 1 h was therefore used for the whole series, each of the 83 hourly profiles being the average of all the profiles 30 min before and after the hour.

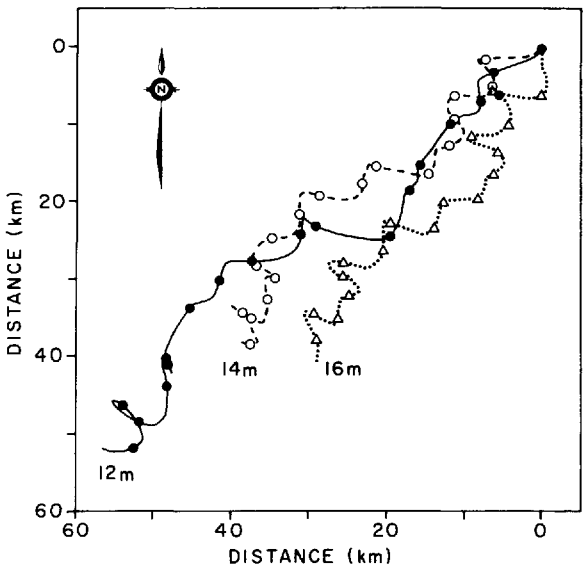

Figure 2. Progressive vector diagrams of currents at 12, 14 and 16 m. There is a 6 h interval between each point.

The Richardson number was used to estimate the dynamic stability of the water column (e.g. Krauss, 1981):

$$Ri = \frac{(\sigma_{z+1} - \sigma_z)\,\Delta_z\ 10^{-3}\,g}{(U_{z+1} - U_z)^2 + (V_{z+1} - V_z)^2}$$

where σ is sigma-t; Δ_z is the difference between depths $z + 1$ and z; U and V are the two horizontal components of the current velocity.

This number compares the stabilizing effect of buoyancy to the destabilizing influence of vertical shear in the horizontal velocity field, over a given depth interval (Turner, 1973). Larger values thus indicate greater potential stability over the depth interval. Data from the 4 current meters were used to compute Ri over 3 depth intervals. The static stability (N: Brunt-Väisälä frequency) was estimated as:

$$N^2 = g\,\frac{(\sigma_{z+1} - \sigma_z)\ 10^{-3}}{\Delta_z}$$

and the vertical shear was estimated as:

$$[(U_{z+1} - U_z)^2 + (V_{z+1} - V_z)^2]/\Delta_z^2.$$

Spectral analyses of temperature and *in vivo* fluorescence series were conducted according to Jenkins and Watts (1968), using the method of Blackman and Tukey with the spectral window of Tukey. Confidence intervals for coherence spectra were

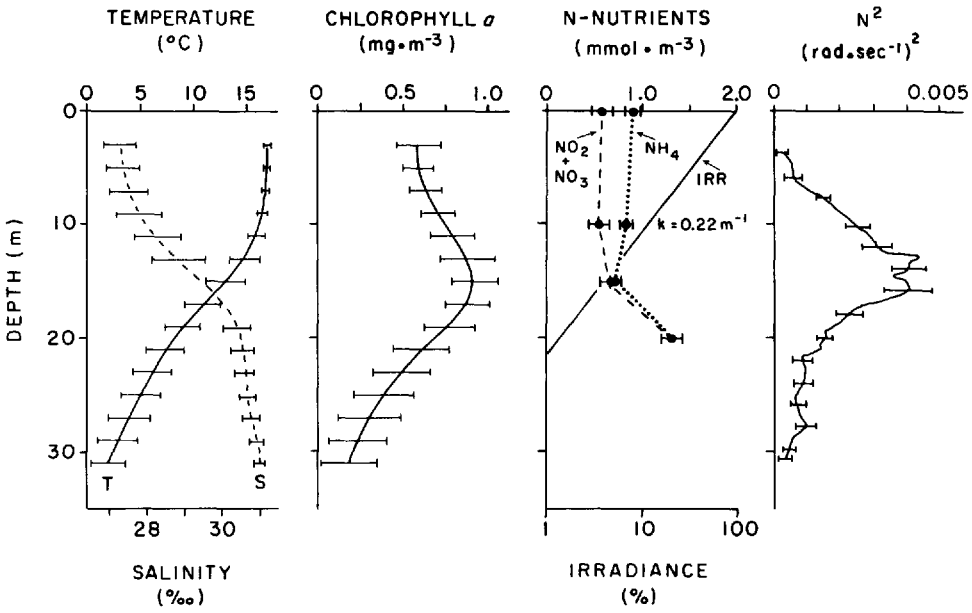

Figure 3. Mean profiles of temperature, salinity, chlorophyll *a*, nitrate (NO_2 + NO_3), ammonia (NH_4), irradiance and squared Brunt-Vaïsälä frequency (N^2). Irradiance plotted on a logarithmic scale. Standard errors are drawn for all the variables except irradiance.

computed according to Bendat and Piersol (1971), on Fisher's z transformed coherence estimates [$\tanh^{-1}$ (coherence)].

3. Results

a. Hydrodynamics. Progressive vector diagrams of currents (Fig. 2) show that the residual current at the sampling station was generally SW, with an average velocity of 0.2–0.3 m s^{-1}. The whole sampling period was therefore characterized by relatively strong surface advection. The vertical structure of the water column (Figs. 3 and 4) was characterized by a well-mixed surface layer, extending down to about 12 m and isolated from deeper water by a thick thermohalocline. Distinctive internal waves were traveling in the thermohalocline (Fig. 4). Garrett and Munk (1972) have shown that the frequencies of such internal waves should range between the inertial frequency (0.061 cycle h^{-1}, at 47N) and the Brunt-Vaïsälä frequency (N). Accordingly, spectral analyses of temperature series (Fig. 5) showed a peak in spectral density at around 0.0648 cycle h^{-1}, which is slightly higher than the calculated inertial frequency at our sampling station. In shallow waters, the presence of oscillations at/or near the inertial frequency is well known (Webster, 1968). Such oscillations had already been observed near our sampling station, by Tang (1979).

Table 1 gives the mean values of static stability (N^2), vertical shear and Richardson number (Ri), for 3 depth intervals between 12 and 18 m. The high values of dynamic

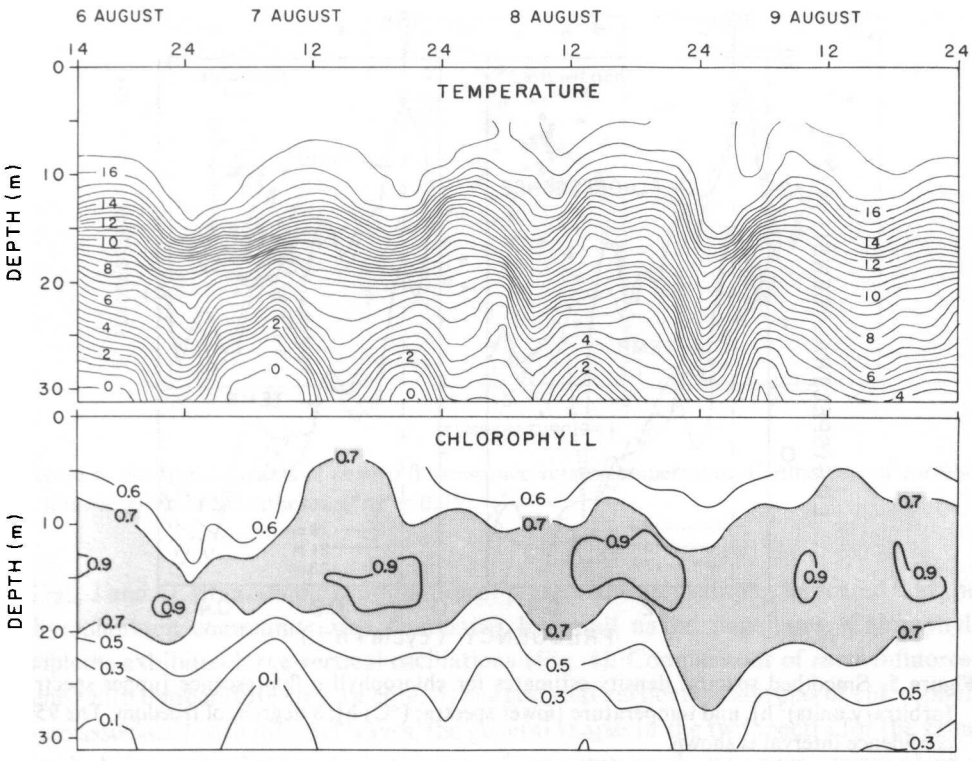

Figure 4. Temporal variations of isotherms (°C), and chlorophyll *a* isopleths (mg m^{-3}).

stability (*Ri*) between 14 and 16 m, and the correspondingly low values of vertical shear indicate that current shear was not strong enough to cause vertical instabilities over this depth interval. The average profile of the squared Brunt-Väisälä frequency (Fig. 3) shows that the layer of maximum stability was located, on the average, between 13 and 16 m. Vertical shear increased between 16 and 18 m (Table 1).

b. Light and nutrients. Coefficients (k) of light extinction were computed from irradiances measured at 1 and 20 m, assuming the usual exponential profile of light extinction. The average coefficient was $k = 0.22$ m^{-1} (Fig. 3). Nitrate + nitrite, as well as ammonia concentrations (Fig. 3) were, on the average, higher than 0.5 mmol m^{-3} in the mixed layer (upper 10 to 15 m). The increase in concentrations at 15 to 20 m (the nutricline) did parallel the decrease in vertical stability with depth, from about 15 m downward (Fig. 3). Phosphate concentrations remained above 0.2 mmol m^{-3}.

c. Vertical distribution of chlorophyll. In vivo fluorescence and chlorophyll *a* are both dependent variables, so that a Model II linear regression must be used to transform fluorescence measurements into chlorophyll *a* concentrations (Ricker, 1973; Laws and Archie, 1981). Four separate regressions were computed, for the days and nights of

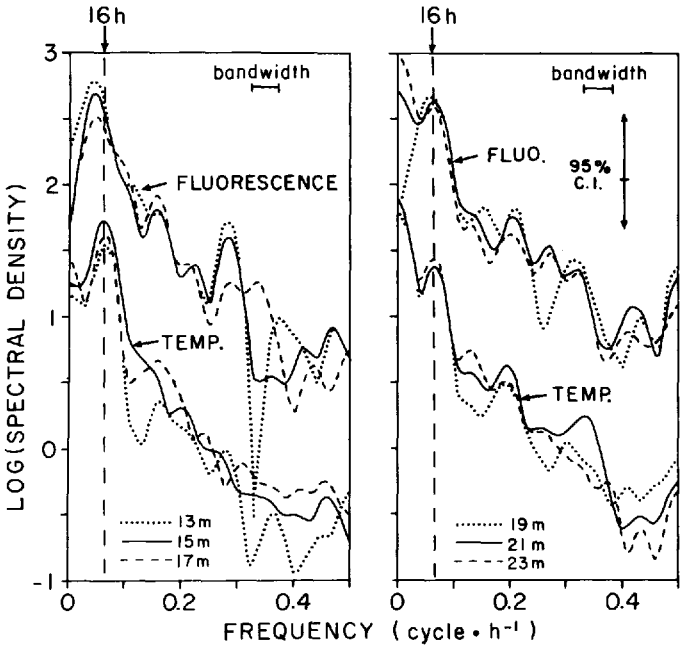

Figure 5. Smoothed spectral density estimates for chlorophyll *a* fluorescence [upper spectra; (arbitrary units)^2 h], and temperature [lower spectra; (°C) h]; 8 degrees of freedom. The 95% confidence interval is shown.

6 to 8 August, using the reduced major axis model (Sokal and Rohlf, 1981). According to the equation of Clarke (1980), there were no significant differences ($p > 0.05$) between the slopes of the 4 regressions, so that the following overall equation was used for the whole series:

$$\text{Chl}a = -0.184 + 0.023\ \text{Fluor}\ (r = 0.91, P \leq 0.001).$$

At the sampling station, there was a characteristic subsurface chlorophyll maximum at an average depth of about 15 m, that is just below the well-mixed surface layer

Table 1. Mean values for static stability (squared Brunt-Väisälä frequency), vertical shear and Richardson number for the 83 h sampling period and the 3 depth intervals.

Depth (m)	Mean static stability (N^2) 10^{-3} (rad s^{-1})^2	Mean vertical shear-squared 10^{-4}s^{-2}	Mean dynamic stability (Ri)
12			
14	3.852	9.00	4.28
16	3.679	1.68	21.90
18	2.721	18.25	8.90

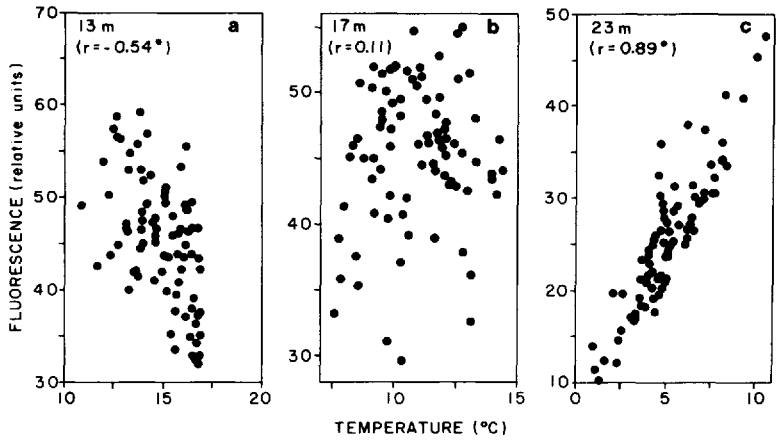

Figure 6. Scatter diagrams of *in vivo* fluorescence versus temperature. Coefficients of correlation are given in parentheses. (*: $P \leq 0.05$).

(Figs. 3 and 4). Microscopic examination of preserved water samples indicated that the phytoplankton community was dominated by small naked flagellates. Chlorophyll isopleths exhibited large vertical oscillations (Fig. 4). Comparisons of *in vivo* fluorescence with temperature spectra (Fig. 5) suggest that vertical oscillations of chlorophyll were associated with internal waves, the general shapes of the two spectra for the same depths being quite similar. As in the case of temperature, fluorescence spectra show a peak in spectral density near the inertial period $T = 16.4$ h, with perhaps slight shifts in the fluorescence spectra toward longer periods ($T \sim 20$ h) at 13, 15, and 17 m (Fig. 5).

Cross-spectra were computed between fluorescence and temperature series, after checking for linear relationships (Fig. 6a, c) as recommended by Star and Cullen (1981). In the lower part of the chlorophyll maximum, the coherences between fluorescence and temperature were generally high, as illustrated for the 23 m series (Fig. 7a), and significantly different from zero ($P \leq 0.05$). In the upper part of the chlorophyll maximum, the relationship between fluorescence and temperature was more complex, as shown in Figure 7b for the 13 m series. Table 2 gives the squared coherence and Fisher's z transformed coherence estimates, near the inertial period, for depths between 13 and 29 m. Between 19 and 29 m, the coherence at $T = 16$ h is always significantly different from zero. At 13 m, it is lower but still different from zero. At 15 and 17 m, it is even lower and not significantly different from zero, and there is no linear relationship between fluorescence and temperature (Fig. 6b).

The phase remained very stable and near 0° over the whole range of resolved frequencies between 19 and 29 m (Fig. 7a), while it fluctuated around 180° at 13 m (Fig. 7b). This corresponds to the positive correlation between fluorescence and temperature in the lower part of the chlorophyll maximum at 23 m (Fig. 6c), and to the

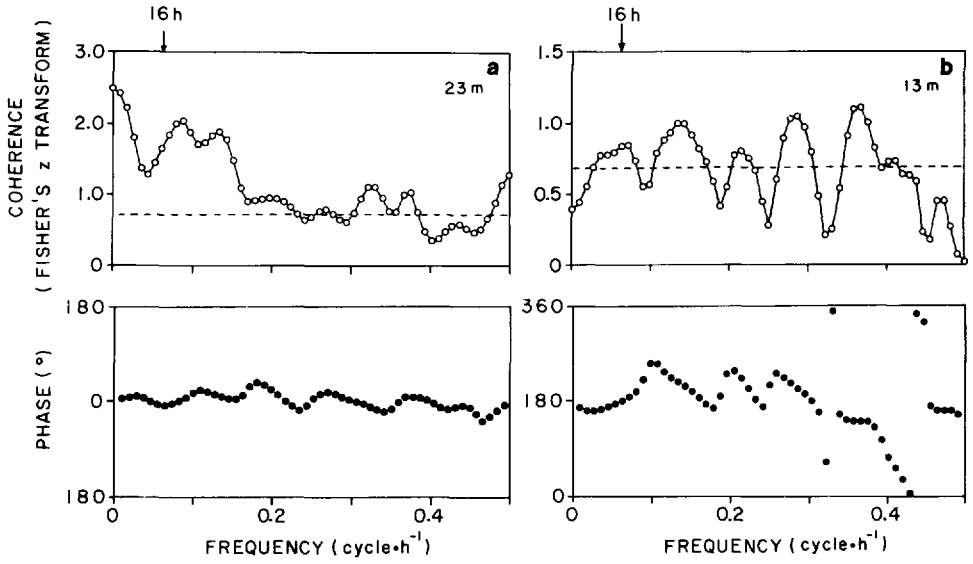

Figure 7. Fisher's z transformed coherence estimate and phase between *in vivo* fluorescence and temperature at (a) 23 m and (b) 13 m. The lower limit of the approximate 95% confidence interval is shown.

negative correlation at 13 m (Fig. 6a). This change in sign is due to the fact that temperature decreases monotonically with depth, while chlorophyll increases from the surface down to the maximum, from where it decreases downward.

d. Photosynthesis and phytoplankton production. Mean values of the photosynthetic parameters are given in Table 3 for the 4 sampled depths. One-way analyses of variance were used to compare mean values from the 4 depths for each parameter

Table 2. Squared coherence and Fisher's z transformed coherence estimates [$\tanh^{-1}$(coherence)] between *in vivo* fluorescence and temperature, for the period T = 16 h, at depths between 13 and 29 m; 8 degrees of freedom.

Depth (m)	Coherence^2	$\tanh^{-1}(co)$
13	0.470	0.838*
15	0.238	0.532
17	0.225	0.515
19	0.632	1.08*
21	0.736	1.28*
23	0.865	1.66*
25	0.952	2.20*
29	0.850	1.59*

*Coherence significantly different from zero, $P \leq 0.05$.

Table 3. Mean values for the parameters of the photosynthesis *versus* irradiance curves, standard errors (in parentheses) and number of cases. Photosynthetically active radiation (PAR) near midday.

Depth	P^B_{max}	α^B	β^B	I_k	I_m	PAR
0 (m)	13.1 (1.06)	0.160 (0.017)	0.004 (0.0007)	147 (25)	491 (46)	876
	43	43	43	43	42	
10 (m)	13.6 (0.78)	0.161 (0.014)	0.005 (0.0006)	181 (38)	495 (35)	121
	72	72	72	72	70	
15 (m)	11.8 (1.04)	0.312 (0.026)	0.004 (0.0006)	49 (5)	209 (13)	65
	72	72	72	72	68	
20 (m)	12.5 (0.90)	0.305 (0.022)	0.007 (0.0006)	53 (5)	208 (14)	19
	69	69	69	69	68	

P^B_{max} in mgC mgChl a^{-1} h^{-1}; α^B and β^B in mgC mgChl a^{-1} h^{-1} · $(\mu E\ m^{-2}\ s^{-1})^{-1}$; I_k and I_m and PAR in $\mu E\ m^{-2}\ s^{-1}$.

(Table 4). P^B_{max} was high at all depths, and showed no significant differences between depths. All the other measured parameters showed significant differences between depths. Using the *a posteriori* test of Student-Neuman-Keuls, significant differences were evidenced between 20 m and the upper depths for β^B, and between 0–10 m and 15–20 m for α^B, I_k and I_m. Thus, except for P^B_{max} which was vertically homogenous, the photic layer can be divided into two relatively homogenous photosynthetic layers, located above and below 10–15 m. In the 0–10 m layer, the light intensity of maximum photosynthesis (I_m) was about 500 $\mu E\ m^{-2}\ s^{-1}$, which roughly corresponds to the average light intensity to which the vertically mixed cells were exposed at mid-day in this layer (PAR from ~900 $\mu E\ m^{-2}\ s^{-1}$ at 0 m to ~100 $\mu E\ m^{-2}\ s^{-1}$ at 10 m). The I_m values at 15–20 m were higher than the corresponding PAR values. Platt *et al.* (1982) explained a similar difference observed between I_m and *in situ* irradiance, at the bottom of the photic layer, by the energetic cost for the phytoplankton of adapting to low light intensities.

Hourly and daily rates of phytoplankton production were computed according to Harrison *et al.* (1985). Figure 8 gives an example of hourly production rates computed

Table 4. One-way analyses of variance (mean squares) for each photosynthetic parameter *versus* depth. Degrees of freedom: between groups = 3; within groups = 252 for all parameters except I_m, and 244 for I_m. α^B, I_m and I_k were log-transformed to homogenize variances between groups.

	P^B_{max}	β^B	α^B	I_k	I_m
Between depths	42.2	0.0001333	12.14	19.49	14.23
Within depths	57.8	0.000035	0.52	0.79	0.25
F ratio	0.73	4.25*	23.47*	24.67*	55.64*

*$P \leq 0.05$.

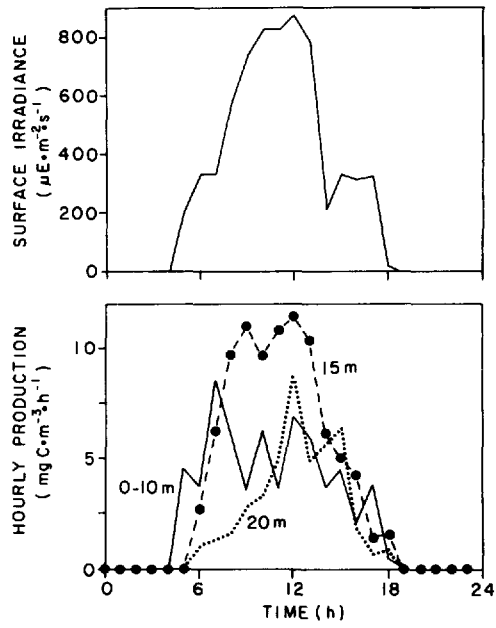

Figure 8. Hourly subsurface irradiance and rates of primary production on August 8, computed according to Harrison *et al.* (1985) using the exponential model of Platt *et al.* (1980).

at 0–10, 15 and 20 m, using the exponential model of Platt *et al.* (1980). Changes in irradiance obviously drive changes in production, especially at shallower depths. Daily rates were calculated by adding together 24 hourly rates. Figure 9 shows that computed daily production was about the same whether using the model of Jassby and Platt (1976) or that of Platt *et al.* (1980). During the 3 sampling days, daily production

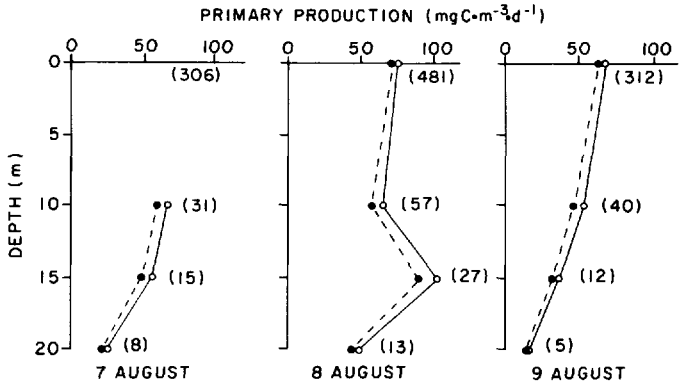

Figure 9. Daily rates of primary production at 0, 10, 15 and 20 m. Solid lines: hyperbolic tangent model (Jassby and Platt, 1976); dotted lines: exponential model (Platt *et al.*, 1980). Mean integrated values of PAR (μE m^{-2} s^{-1}) are given in parentheses.

was quite homogenous from the surface down to ~15 m, except on the most sunny day (8 August) when production was maximum at 15 m.

4. Discussion

a. Biological production and physical scales. Despite strong horizontal advection at the sampling station (Fig. 2), a subsurface chlorophyll maximum did persist during the whole sampling period (Fig. 4). This suggests that, during the summer months, stratified waters in the Gulf of St. Lawrence are characterized by a subsurface chlorophyll layer, of wide extent and strong persistence. Holligan *et al.* (1984b) have documented a similar structure in the Gulf of Maine.

A major effect of internal waves is to force vertical oscillations of the chlorophyll maximum (Fig. 4) (Kamykowski, 1974, 1976; Cullen *et al.*, 1983; Haury *et al.*, 1983). Our results suggest that most of the observed variations in chlorophyll were due to internal waves rather than to horizontal advection of anomalies or patches past the observing site. Firstly, fluorescence and temperature at the same depths were significantly correlated as one might expect for variations due to vertical displacements by internal waves (Table 2). Secondly, strong correlations also exist, between the depth of the center of mass of chlorophyll (F: fluorescence)

$$\left[\int_{1.5}^{29.5} z \cdot F(z) \cdot dz \Big/ \int_{1.5}^{29.5} F(z) \cdot dz\right]$$

and the depths of either temperature or fluorescence isopleths. For example (Fig. 4), the correlation between the depth of the center of mass of chlorophyll and the depth of the 6°C isotherm is $r = 0.70$; similarly, $r = 0.75$ for the 30.0 fluorescence isopleth (~0.5 mg chl m^{-3}). Such high correlations are expected in the presence of large amplitude internal waves. Between 19 and 29 m, vertical movements can explain most of the variability recorded in the *in vivo* fluorescence series, as indicated by the similar fluorescence and temperature spectra (Fig. 5) and also by the high coherences between the two variables (Fig. 7a and Table 2). At these depths, which are below the photic layer (Fig. 3), chlorophyll thus behaves as a passive contaminant of the water column.

In the upper part of the subsurface maximum, between 13 and 17 m (Fig. 3), the variability in chlorophyll cannot be explained solely in terms of internal waves. The coherences between the *in vivo* fluorescence and temperature series, even if significant at some depths (Table 2 and Fig. 7b), are lower than those recorded below 19 m. There are several possible explanations for these observed low coherences. First, differences in the vertical distributions of temperature and chlorophyll can be invoked. Indeed, it is around 15–17 m (Fig. 3) that the relationship between chlorophyll and temperature shifts from negative ($\leq$13 m, Fig. 6a) to positive ($\geq$19 m, Fig. 6c), with correspondingly nonsignificant coherences at 15 and 17 m (Table 2). As these lower coherences occur in the photic layer ($\leq$17 m: Fig. 3), phytoplankton growth may also contribute to

disrupt the coherence between the two variables. If this is so, chlorophyll cannot be taken, in the photic layer, as a passive contaminant of the water column.

Our computed estimates of hourly phytoplankton production (Fig. 8) are within the range (1.0–8.2 mgC m^{-3} h^{-1}) of simulated *in situ* values published by Bulleid and Steven (1972) for the same area. The depth of maximum phytoplankton production, at least on sunny days (Fig. 9), corresponded to that of the subsurface chlorophyll maximum and also to the nutricline (Fig. 3). There is some discussion in the literature as to whether the depth of maximum biomass is the same or not as the depth of maximum production (Herbland and Voituriez, 1979; Cullen and Eppley, 1981; Herman *et al.*, 1981; Herman and Platt, 1986). However, most of the studies (including our own) do not have enough vertical resolution to critically test the hypothesis of a vertical discrimination between the two maxima. At our sampling station, the depths of both the subsurface chlorophyll maximum and the production maximum (on sunny days) corresponded to those of both maximum static (N^2) and dynamic (Ri) stabilities (Table 1 and Fig. 3). This is not what Holligan *et al.* (1984a) have observed in the Gulf of Maine, where dinoflagellate maxima were centered at depths of zero to slightly positive N. This, however, agrees with the explanation given by Pingree *et al.* (1975) for the occurrence of high concentrations of dinoflagellates within sharp pycnoclines, in terms of a longer characteristic mixing time of the water column. At our sampling station, the close association between subsurface maxima of phytoplankton and stability persisted despite relatively strong horizontal advection (Fig. 2) and also the vertical movements caused by internal waves (Fig. 4). In reference to our first question (Introduction), we can therefore reject the idea that the vertical distribution of chlorophyll, and probably also that of phytoplankton production, was independent from the scales in the vertical physical structure.

b. The mechanisms of the subsurface maximum. In an environment dominated by small naked flagellates, as was our sampling station, behavioral factors probably have only a minor impact on the vertical distribution of chlorophyll. This is contrary to subsurface maxima dominated by dinoflagellates, where it has been hypothesized that vertical migrations might play a significant role (e.g. Kamykowski and Zentara, 1977; Holligan *et al.*, 1984a).

In a stratified environment, such as the Gulf of St. Lawrence in the summertime, the vertical structure of the water column is characterized by a thick thermohalocline (Figs. 3 and 4), in which vertical stability is maximum (Table 1, Fig. 3). In this layer of minimized turbulent diffusion, phytoplankton growth can potentially lead to the development of biomass heterogeneities, as long as light and nutrients are nonlimiting and as grazing pressure does not regulate the biomass. On the contrary, the high vertical mixing in the upper part of the water column would prevent the accumulation of biomass into discrete layer(s). This is quite similar to the mechanism leading to the formation of horizontal phytoplankton patches. In the KISS model (Kierstead and

Slobodkin, 1953; Skellam, 1951), when horizontal patches are above a characteristic size, the growth rate of phytoplankton is high enough to maintain the integrity of patches against horizontal diffusion. More elaborate models of horizontal phytoplankton patches have also incorporated horizontal diffusion and phytoplankton growth rate (e.g. Platt and Denman, 1975; Wroblewski *et al.*, 1975; Denman and Platt, 1976; Okubo, 1978). Similarly, diffusion and growth rate can be invoked here to explain the observed vertical heterogeneity. In addition to this mechanism, the increased density gradient in the pycnocline can lower the sinking rate of phytoplankton cells, and thus favor their concentration in the chlorophyll maximum (Steele and Yentsch, 1960; Ignatiades, 1979). Where this occurs, the subsurface chlorophyll maximum accumulates biomass resulting from its' own production and also from that of upper waters. It is also possible but not likely that the vertical chlorophyll structure could be influenced by zooplankton grazing.

Physiological adjustment of the organisms to vertical environmental gradients does not play any role in the above mechanisms. However, hydrodynamical processes are known to act on phytoplankton production in the water column through the proximal agency of both light and nutrients (Legendre and Demers, 1984). Mean concentrations of $NO_2 + NO_3$ and NH_4 at our sampling station were above 0.5 mmol m^{-3} at all depths (Fig. 3). This indicates that the growth of phytoplankton was generally not limited by nutrients, even in the upper part of the water column. The high photosynthetic capacities at all depths (P^B_{max}: Table 3) support the idea that the environment was not nutrient deficient (Curl and Small, 1965). The nutricline was closely associated with the observed decrease in vertical stability (N^2), just below the photic layer, and with the chlorophyll maximum (Fig. 3). This suggests that nutrients were actively assimilated by phytoplankton in the subsurface maximum, as they diffused upward. Even if our nutrient profiles are not adequate for computing vertical nutrient fluxes, we can assume that vertical mixing, at the boundary between the vertically stable layer and the underlying nutrient-rich water, was enough to replenish nutrients in the photic layer. Similar upward nutrient transport has been ascribed to semidiurnal tides and internal waves (Cullen *et al.*, 1983; Kahru, 1983; Sandstrom and Elliott, 1984). Holligan *et al.* (1984b) indicated that the input and assimilation of nitrate, in the subsurface chlorophyll maximum, could account for as much as 50% of net phytoplankton production during the summertime, in areas where the thermocline was well developed and where the biomass of chlorophyll was not too high. This leads to the conclusion that, at our sampling station, vertical turbulent diffusion was probably high enough to replenish nutrients in the photic layer, but not strong enough to destroy the vertical structure of stability (Table 1 and Fig. 3) and chlorophyll (Figs. 3 and 4).

Since the growth of phytoplankton was not limited by nutrients, any control exerted by hydrodynamics on phytoplankton physiology would be through the proximal agency of light. Vertical mixing determines the light intensities to which phytoplankton are exposed in the water column. Even in layers where vertical mixing is weak, the cells can

be vertically displaced across light gradients by internal waves (Fig. 4). Phytoplankton can sometimes adjust their photosynthetic characteristics to the environmental light conditions. The time required for such an adjustment is shorter than the generation time (Lewis *et al.*, 1984), but it is not negligible. In laboratory, periods of 10 h (Marra, 1980) and 12 h (Prézelin and Matlick, 1980) have been reported for cultures to adjust to decreased light intensities. Lewis *et al.* (1984) report that P^B_{max} responds within a few hours to changes in light intensity. They conclude that the adjustment of phytoplankton cells to a given light intensity, in the water column, is a function of vertical mixing. Thus, the critical hydrodynamic characteristic that concerns photosynthetic adjustment of phytoplankton is the time of residence at given depths.

The various photosynthetic characteristics of the phytoplankton at our sampling station were not the same in the mixed layer (0–10 m) and in the more stable layer (15–20 m) (Tables 3 and 4). The slight (nonsignificant) decrease in P^B_{max}, the strong increase in α^B and the decrease in I_k and I_m all indicate that phytoplankton in the 15–20 m layer were shade-adapted relative to the more light-adapted cells of the 0–10 m layer. When vertical mixing is intense and persistent, changes in environmental conditions are more rapid than the adjustment time of the phytoplankton, so that the cells acclimate to the average light conditions in the mixed layer; on the contrary in conditions of moderate or weak vertical mixing, changes in environmental conditions are slower than physiological adaptation by the phytoplankton, so that the cells can continuously adjust to the new conditions (Savidge, 1979; Falkowski, 1980; Demers and Legendre, 1981, 1982). Following this model, phytoplankton in the 0–10 m layer would be light-adapted to the average intensities in the mixed layer, while those in the 15–20 m layer would be shade-adapted to the ambient light intensities. The homogeneity of photosynthetic characteristics in the 0–10 m layer supports light-adaptation to the average intensity, especially that I_m roughly corresponded to the average maximum light intensity in this layer (Table 3). Similar photosynthetic characteristics in the 15–20 m layer may be interpreted as reflecting maximum shade-adaptation of phytoplankton to the low irradiances prevailing at these depths. This is contrary to Holligan *et al.* (1984a), who reported poor adjustment of phytoplankton to low light intensities in the subsurface chlorophyll maximum. Shade-adaptation of phytoplankton in the 15–20 m layer probably occurred at our sampling station, as a consequence of longer residence time at depths of maximum stability.

As pointed out by Cullen (1982), a subsurface chlorophyll maximum does not necessarily correspond to a maximum in phytoplankton biomass, as chlorophyll per unit biomass increases when the cells become shade adapted (e.g. Prézelin, 1981). At our sampling station, shade adaptation of phytoplankton at 15–20 m (doubling of α^B) is accompanied by only a slight decrease in P^B_{max}, so that we can be confident that the observed chlorophyll maximum observed at around 15 m (Figs. 3 and 4) does not only reflect shade adaptation (increased chlorophyll per cell) but rather represents a real increase in phytoplankton biomass. Vertical profiles of light beam transmission (not

shown) evidenced that fluorescence maxima were always associated with transmission minima, which confirms that increased biomass was associated with the chlorophyll maximum. The overall result of the above photosynthetic adaptation (Fig. 3) was relatively high primary production at all depths from 0 to 15 m (Fig. 9). With only three days of sampling, it is not possible to assess whether the situation encountered on 8 August, with maximum production at 15 m, was more frequent or not than a more uniform vertical production profile as observed on 7 and 9 August. High production near the bottom of the photic layer (15 m) suggests a good adaptation to low light intensities. It can therefore be concluded (a) that phytoplankton were well adapted to the ambient light intensities over the whole photic layer, conducive to high primary production at all depths, and (b) that, some days, primary production at depth contributed to increase the subsurface chlorophyll maximum relative to phytoplankton concentrations in the upper waters.

The mechanisms of the subsurface chlorophyll maximum we observed in the Gulf of St. Lawrence are somewhat different from those reported by Holligan *et al.* (1984a) in the Gulf of Maine. There, the aggregation and growth of motile organisms (dinoflagellates) were the most important factors, without consideration of vertical mixing. In the Gulf of St. Lawrence, on the contrary, hydrodynamics plays a major role in demarcating a layer of vertical stability (a) where phytoplankton can accumulate and grow and (b) where they can photosynthetically adapt to the ambient low light intensities. This answers our second question (Introduction), as we can conclude that the subsurface chlorophyll maximum was (in part) caused by changes in the physiological state of the organisms.

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