Primary production rates in tidally mixed coastal waters : the eastern English Channel case study

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Abstract : Homogeneity hypothesis has been often made on vertical distribution of biological parameters in coastal area dominated by the tide. In studies of ecosystem fluxes, primary production variability at short and medium scales of space and time has been generally rather considered. However, it appears after some field and modelling works in typical coastal waters periodically mixed by the tide (the eastern English Channel) that photosynthetic properties of phytoplankton can be related to the vertical gradient of light. Photoadaptation processes can so occur in mixed coastal water column, and these processes can be controlled by vertical mixing intensity at two typical time scales : the high-low tidal cycle scale and the neap-spring tidal cycle scale. If photoadaptation is not considered in daily primary production estimates, potential underestimation or overestimation can vary between 2.6 and more than 100 %. By another way, phytoplankton response times to reciprocal light shift gives some evidence on the extent of photoadaptation in mixed, but not permanently mixing, coastal waters.

Key words : Phytoplankton, primary production, photoadaptation, coastal waters, Eastern English Channel, tidal mixing, light shift, Lagrangian model.

1. Introduction

It is well recognized that photosynthetic fixation of carbon is a fundamental biological process in marine systems. This process is the main source of organic carbon and supports the greatest part of marine biomass. According to teledetection studies and compilations of many data related to phytoplankton concentration (chlorophyll *a*) and photosynthetic parameters (physiological parameters used to estimate primary production rates), it seems that marine net primary production would be in the same order as terrestrial net primary production (LURIN *et al.*, 1994; LONGURST *et al.*, 1995).

With regard to marine primary production, some great distinctions can be made between coastal waters and the open ocean. If coastal waters represent only ten percent of marine systems, primary production can be ten times higher (or more according to the season) in coastal waters than in the open ocean (FALKOWSKI and RAVEN, 1997; JOINT and GROOM,

2000). Coastal waters can show extremely high events of productivity corresponding to algae blooms which are known to have large ecological and economical impact on the actors of the food chain (from micro-organisms to fish), on fishery farms and tourism ; especially in the case of toxic algae bloom (HORNER *et al.*, 1997; TURNER and TESTER, 1997; ROUSSEAU *et al.*,2000). Coastal waters are also much more marked than deeper waters by a high variability of chemical and physical environmental variables influencing primary production, due to river inputs that may be governed by meteorological conditions and increasing anthropogenic activities such as agriculture, industries and urbanization (KNAUER, 1993; HAMASAKI *et al.*, 2001). By another way, a chain of event relationship between climatic changes and biological production at all trophic levels (including primary production) has been shown in coastal waters (SAKSHAUG, 1997; OTTERSEN and STENSETH, 2001; HAMASAKI *et al.*, 2001). Coastal phytoplankton primary production is so a fundamental ecological process and could have a major place in the carbon cycle, not only at local or regional scales, but also at a global scale.

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Despite many years of research, from first STEEMAN-NIELSEN studies in 1952 until today, there are still great uncertainties about phytoplankton primary production rates in coastal seas. It is particularly difficult to estimate primary production rates in shallow coastal waters, because forcing or limiting factors of phytoplankton production are numerous and can display different variation or heterogeneity patterns in space and time, in relation with physical characteristics encountered in these waters : river run-off, horizontal and vertical tidal current, coastal up- and down-welling, bathymetry, roughness of the bottom and wind on the sea surface. Most of these physical variables can not always control directly primary production rates in coastal waters, but variations in quality and intensity of light, in suspended matter, in nutrients, in pollutant concentrations and in temperature, through complex combinations. In a second place, variations of light, turbidity, nutrients, pollutant etc. act on primary production rates. However, in a consistent way with the photoadaptation theory (FALKOWSKI and OWENS, 1980), vertical mixing can also directly control primary production rates via the cell exporting through the water column.

Many studies on the interactions between phytoplankton primary production and hydrodynamical conditions focused on the primary production control by vertical mixing of waters inducing nutrients inputs from deep layer into the euphotic layer (FORTIER and LEGENDRE, 1979; DEMERS and LEGENDRE, 1981; LEVASSEUR et al., 1984; LEGENDRE and DEMERS, 1984, 1985; LEGENDRE et al., 1986; Le FÉVRE and FRONTIER, 1988; BISSET et al., 1994). In this point of view, vertical mixing allow cell production and are considered as auxiliary (or covariance) energy (MARGALEF, 1978). In these previous works, it has been shown that the frequency of disturbances from external forces, or the tuning between physical and biological processes, are responsible for primary production level of a marine system, but also for the diversity of a biotic community as exposed in the intermediate disturbance hypothesis (IDH) (CONNELL, 1978; PADISAK et al., 1993; LINDENSCHMIDT and CHORUS, 1998). Such effects occur especially at

medium and great scales of space (from 1 to 100 km) and time (from several days to 1 year) (HARRIS, 1980). Phytoplankton responses to fluctuating light resulting from vertical excursions throughout the water column are in compensation identified at small scales of space (from 1 m to 100 m) and time (from second to several hours) (HARRIS, 1980). Evidences of these physical-biological interactions are given by many works (LEWIS and SMITH, 1983; FALKOWSKI, 1983; GALLEGOS et al., 1983; LEVASSEUR et al., 1984; LEWIS et al., 1984a; CULLEN and LEWIS, 1988; MALLIN and PAERL, 1992). These works have been conducted after it has been demonstrated that the relationship between photosynthesis and light energy (PE, see Fig. 1) is in control of cell physiological adaptations to light (FALKOWSKI and OWENS, 1980; FALKOWSKI, 1981). For example, phytoplankton photoadaptation at short time scales is characterized by thylakoid stacking in chloroplasts (cell organelles where are located light-harvesting pigment-protein complexes), chloroplast position in cells, interconvertion of carotenoid pigments (i.e. the xanthophylls cycle), changes in the number of photosynthetic reaction centers, in the functional size of the antennae serving the reaction centers (i.e. in photosynthetic pigment concentrations), in enzymatic activity and in in vivo fluorescence yield (FALKOWSKI and RAVEN, 1997). These complex physiological processes that depend on nuclear gene regulation by irradiance (ESCOUBAS et al., 1995), can be easily estimated by the PE relationship variations, if PE relationships are measured at a precise "t" time. Such physiological photoadaptations are used by phytoplankton to optimise or minimize variations in growth rate, in relation with environmental condition fluctuations.

LEWIS et al.(1984b) showed in this way, for the first time, with simultaneous measurements of PE relationships and of turbulent kinetic energy, that phytoplankton photoadaptations occur according to the vertical mixing intensity of waters. This last study and most of the previously cited woks have been conducted in stratified waters where vertical mixing are often generated by the wind, a determinist physical factor. In such a case,
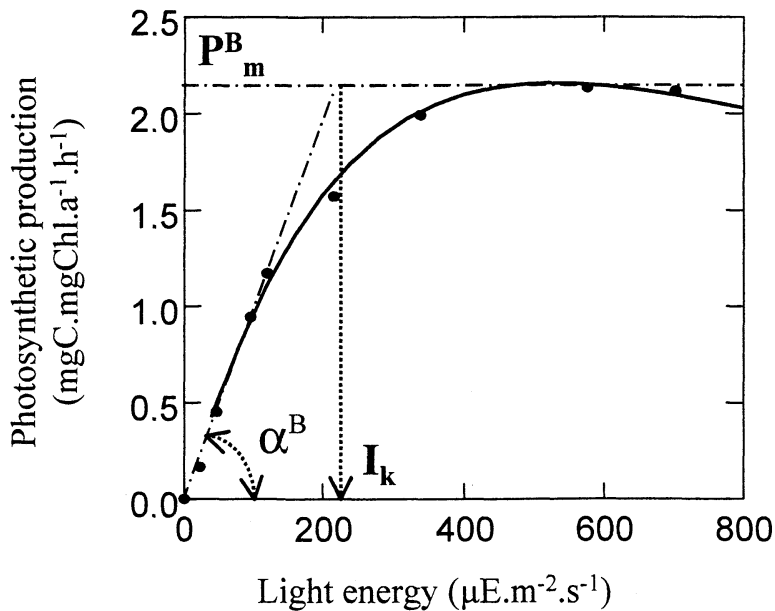
Fig. 1. An example of Photosynthesis-Energy relationship (PE) showing the three main photosynthetic parameters (P_m^B, photosynthetic capacity or light-saturated uptake rate; α^B, photosynthetic efficiency; I_k, light saturation parameter) derived from the equation of optimal curve adaptation as presented by PLATT *et al.* (1980).

vertical mixing takes place at low frequencies in a more or less deep layer according to the wind speed (DENMAN and GARGETT, 1983), preventing more or less cell physiological adaptation to light. Photoadaptations of phytoplankton actually depend on the time scales of vertical mixing that induce fluctuating light, and on cell response times. When vertical mixing is moderate, light conditions change at a slower rate than the physiological adaptation times of phytoplankton. Cells can continuously adjust their physiological activity to the vertical gradient of light. So, parameters of the PE relationships would be non uniformly distributed in the water column. If mixing processes occur on a shorter time scale than the adaptation time of phytoplankton, parameters describing the PE relationships would be expected more uniformly distributed in the water column. In this case, photoadaptation can not take place (FALKOWSKI and OWENS, 1980).

Now, it is well recognized that significant wind speed variations, or wind speed events sufficently high to homogeneize a coastal water column, occur at higher time scales (several days) than vertical mixing due to the tide (FRONTIER *et al.*, 1992), a systematic physical factor. As a matter of fact, current speed generated by the M_2 tidal wave can display maximum values every 6 h. Currents interact then with the bottom to produce turbulence with tend to mix the entire water column in the case of shallow coastal waters. Although rapid response times of physiological photoadaptations have been shown (CULLEN and LEWIS, 1988), any study before our works in the English Channel has considered that interactions between vertical tidal mixing and phytoplankton photoadaptation could exist in shallow coastal waters, vertically homogeneous with respect to temperature and salinity. According to SHAY and GREGG (1986), this does not necessarily mean that mixing events are always high and continuous. Also, between two high current speed values, especially in neap tide, vertical gradients in photoadaptation properties of phytoplankton can be hypothesized in relation to low mixing events, despite an homogeneity in hydrological parameters.
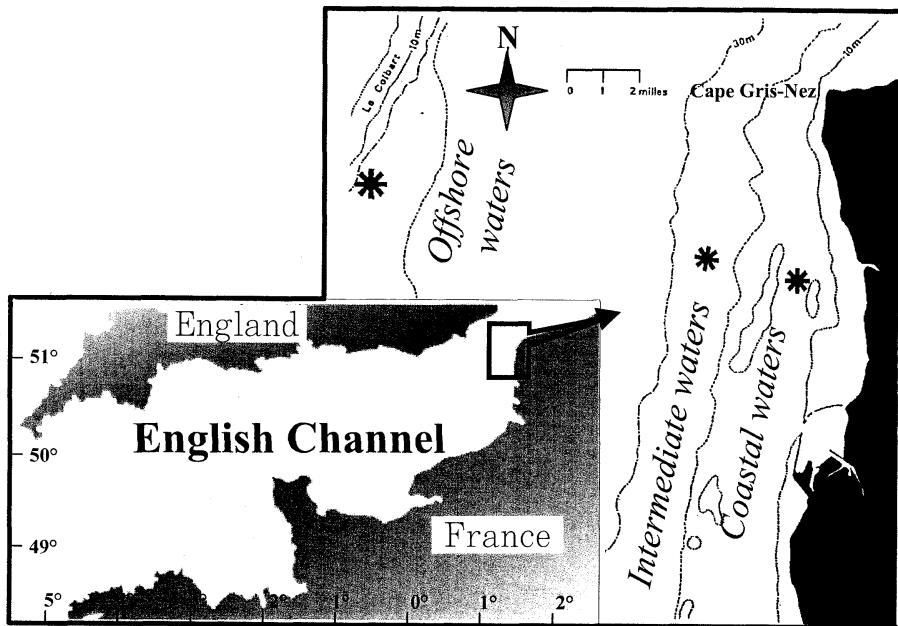
Fig. 2. The study area showing the anchor stations, and the coastal (or near-shore waters), the intermediate and the offshore waters of the eastern English Channel.

In order to test this hypothesis, we have measured parameters of the PE relationship of marine phytoplankton and environmental parameters, during several hours, in different tidal conditions and in different water masses of a typical coastal sea mixed by the tide, the eastern English Channel. In the present paper, we (i) first review the main characteristics of photoadaptation processes that have been observed and their consequences on daily primary production rates, (ii) compare cell response times and mixing time scales with the results of light shift experiments of natural phytoplankton populations, (iii) review the main results of a Lagrangian models that have been developed to test theoretically our hypothesis on photoadaptation in a turbulent water column.

2. Photoadaptation and consequences on daily primary production rates
2.1.   Methods
To test our hypothesis on phytoplankton photoadaptation in a tidally mixed water, we have worked in the eastern English Channel (Fig. 2) where the tidal range is one of the highest in the world (ranging from 3 to 9 m). The dissipation of tidal energy causes homogenization of the shallow waters (50 m maximum depth); and occur at two typical time scales : at the scale of high-low tidal cycles (with a period of 6 h), and at the scale of neap-spring tidal cycles (with a period of 14 days). Tides generate so vertical mixing and a residual circulation parallel to the coast, drifting coastal waters and river inputs from the English Channel to the North Sea (Fig. 2). Coastal waters are then separated from offshore waters (Atlantic waters) by a tide controlled frontal area (BRYLINSKI and LAGADEUC, 1990).

Several sampling were conducted in coastal, intermediate and offshore waters of the English Channel (Fig. 2), in neap and spring tide period, during several tidal cycles. At 2 h intervals, water samples were collected at four different depths varying according to the three sampling stations. In each case, the surface, the bottom and the middle part of the water column were sampled using Niskin bottles. Every hour, a Sea Bird 25 CTD probe was used to measure temperature, salinity, photosynthetically active radiation (PAR, 400

−700nm) and *in vivo* fluorescence. Current direction and velocity were also measured with an Aanderaa current meter.

For all our sampling, chlorophyll *a* (Chl. *a*) analyses were performed after filtration of samples on Whatman GF/F glass fiber filters and after 24 h extraction in 90 % acetone at 5°C using the spectrophotometric method. Primary production was estimated by the ^{14}C incorporation method (STEEMAN–NIELSEN, 1952). For each sampling, PE measurements were conducted in a radial "photosynthetron" (BABIN *et al.*, 1994) equipped with an halogen dysprosium lamp (Osram, HQI–T 250 W/D) that provided a day light spectrum from about $850 \mu E \ m^{-2} s^{-2}$ in front of the first subsample, to about $10 \mu E \ m^{-2} s^{-2}$ at the last one. All subsamples (50ml) were inoculated with 74kBq NaH^{14}CO$_3$ and incubated during 30 or 40 min (see § 2.2. below for further informations, or LIZON and LAGADEUC, 1995). After incubation, samples were filtered on glass fiber filters (GF /F) which were rinsed with filtered seawater (HARRISON *et al.*, 1985) before being dropped in vials containing the scintillation cocktail. The activity was later measured on a liquid scintillation counter (L. K. B. Wallac 12–14 Rackbeta), the efficiency of which was determined with an external standard channels ratio method.

Primary production was calculated according to PARSONS *et al.* (1984). Photosynthetic parameters (Fig. 1) P_m^B (light−saturated uptake rate), α^B (photosynthetic efficiency at low irradiance) and I_k (light saturation parameter) were derived from the equation of optimal curve adaptation as presented by PLATT *et al.* (1980). The superscript "B" denotes that these parameters have been normalized to chlorophyll *a* concentrations.

2.2. Preliminary study

Before testing our hypothesis and conducting specific sampling, we have realized a preliminary study to determine if bias could occur (and under which conditions) in daily primary production rate estimates according to the cell incubation time, a necessary stage in phytoplankton production measurements. Different incubations times are often considered in such studies : from 30 min. to 24 h. Now, it

would be unusual for phytoplankton to experience constant irradiance during several hours in shallow coastal systems. So, we have first estimated primary production with the ^{14}C incorporation method (STEEMAN – NIELSEN, 1952) from long term simulated *in situ* incubations (SIS) of 4 h and 24 h, and we have compared these estimates with values of primary production based on photosynthetic parameters determined on short incubation durations (40min). Sampling was conducted under different conditions of vertical mixing in the English Channel (LIZON and LAGADEUC, 1995).

In this work, it has been shown that daily primary production rates computed from 24 h incubation durations are the lowest at each sampling station, whereas differences between daily production rates estimated from 4 h and 40 min. incubation durations, depend on the sampling stations. Vertical mixing and available light intensity could control differences between the computed daily production rates on 4 h and 40 min. incubation durations. In fact, it has been demonstrated(LIZON and LAGADEUC, 1998) that under conditions of non limiting light intensity for photosynthesis, photoadaptation processes could occur in long term SIS incubations, which do not take into account vertical mixing, and enhance (until 40 %) primary production estimates. So, it can be recommended to use short incubation durations several times a day in order to estimate primary production measurements in a perturbed hydrodynamic system. As the total loss rates increase with incubation times (due to cell respiration and excretion), long−term and short term incubations approximate respectively net and gross primary production, whereas a mean incubation duration approximate something between net and gross production.

2.3. Photoadaptation in a water column

With the sampling strategy described to test our main hypothesis, we have shown that phytoplankton photoadaptation can occur in a shallow coastal sea dominated by the tide, since vertical heterogeneity of photosynthetic parameters consistent with the vertical gradient of light have been observed in the eastern English Channel (Fig. 3). Phytoplankton have

$$\alpha^B$$

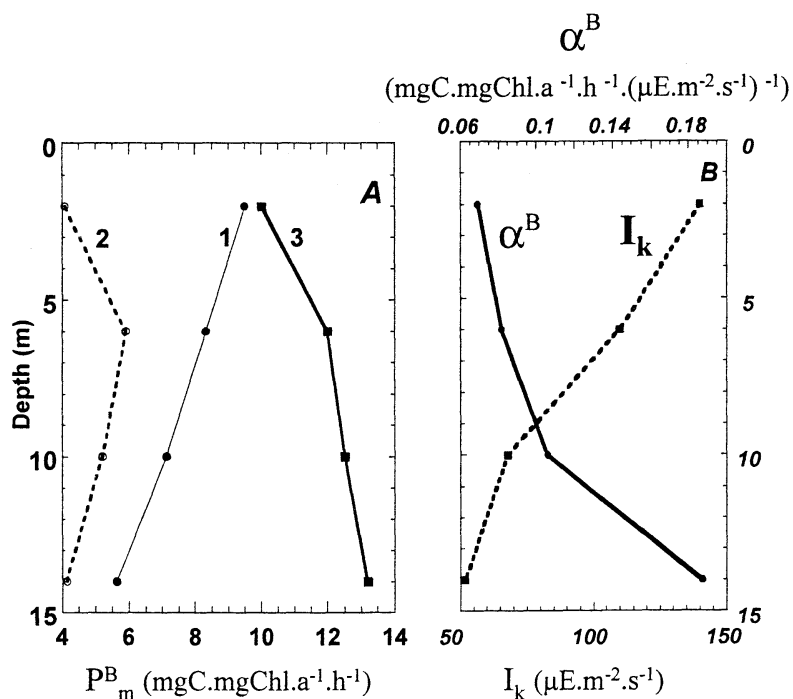$$(\text{mgC.mgChl.a}^{-1}.h^{-1}.(\mu E.m^{-2}.s^{-1})^{-1})$$

Fig. 3. The different typical vertical profiles of photosynthetic parameters observed in our sampled water columns (the number 1, 2 and 3 made reference to three vertical gradients. See the text for further details).

generally displayed three typical vertical gradients of photosynthetic parameters in the sampled water columns.

The first gradient consists in a vertical decrease of the photosynthetic capacity (P_m^B) and of the light saturation parameter (I_k), but also in an increase of the photosynthetic efficiency (α^B) (Fig. 3). Such photosynthetic parameter variations are encountered for each sampling conditions and are characteristics of classical photoadaptation processes on looking at the decreasing light intensity with depth. Most of cell physiological processes stated in introduction of this paper are then implemented. However, P_m^B shows also two other vertical variation profiles.

The second vertical gradient of P_m^B shows first low values in the upper layer of the water column (*i.e.* from the surface to more or less 5 m depth according to the water turbidity) and then, decreasing value to the bottom. A parabolic variation of P_m^B with depth generally mean a photoinhibition of phytoplankton. As a

matter of fact, strong light intensity about midday in subsurface waters can destroy some protein–complexes of the photosynthetic units and depress photosynthesis (HARRIS, 1978; FERRIS and CHRISTIAN, 1991). Photoinhibition is a light and time dependent process that is commonly observed in stratified waters (VINCENT et al., 1984; DEMERS et al., 1991; FALKOWSKI and KIEFER, 1985) but rarely in our case studies (at midday and in neap tide conditions, LIZON et al., 1995).

The third vertical gradient of of P_m^B consists in concomitant and increasing variations of P_m^B and α^B with depth (Fig. 3). In this particular case, it has been observed increasing values of chlorophyll a concentrations with depth (LIZON et al., submitted). This kind of vertical gradient can be explained with a shade type algal community located in the lower part of the water column, and formed by microphytobentic or tychoplanktonic algae that have been resuspended by vertical mixing (HUAULT et al., 1994). It is well recognized that shade type
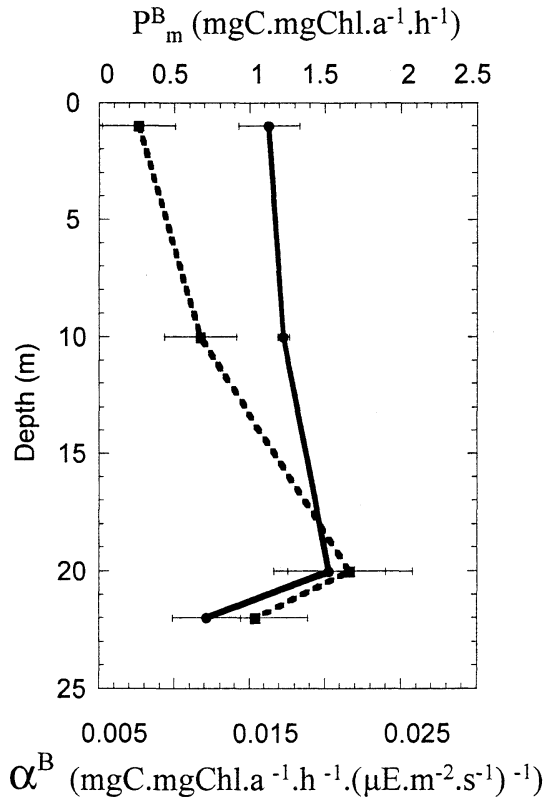
Fig. 4. Mean vertical profiles (and standard errors) of photosynthetic capacity (P_m^B) and efficiency (α^B) in our coastal (or near-shore) water column, and in the sediment (data presented at 22 m depth on the picture).

algae, as microphytobenthos, can use low light intensity with high efficiency (MACINTYRE *et al.*, 1996). However, high values of P_m^B for microphytobenthos, as for phytoplankton in the water column, can appear surprising. These results are nevertheless consistent with some other measurements of microphytobenthos production (BLANCHARD and CARIOU-LE GALL, 1994; MACINTYRE and CULLEN, 1995), and with primary production measurements realized at the sediment water interface and on sediments suspended in filtered sea–water (according to the technique of MACINTYRE and CULLEN, 1995) from our sample site. Despite low light intensity, it appears that microphytobenthos of our area can show P_m^B values of the same order of magnitude than cells located at the sediment water interface (Fig. 4). Since resuspension and settling occur on time–scales of minutes to

hour (ANDERSON, 1976; WARD, 1985), it can be so hypothesized that microphytobenthos maintain here high levels of potential photosynthetic capacity, or develop very fast response times to changing light, in order to optimise their production when they are periodically exported through the water column by physical events.

In addition, all vertical profiles of observed photosynthetic responses support the hypothesis according to which cells can stay long enough at a given depth and can adapt their photosynthetic characteristics to the ambient light in a coastal sea. These results are also consistent with measurements of size–class and biomarker pigment distributions in water columns of our study area (BRUNET and LIZON, submitted).
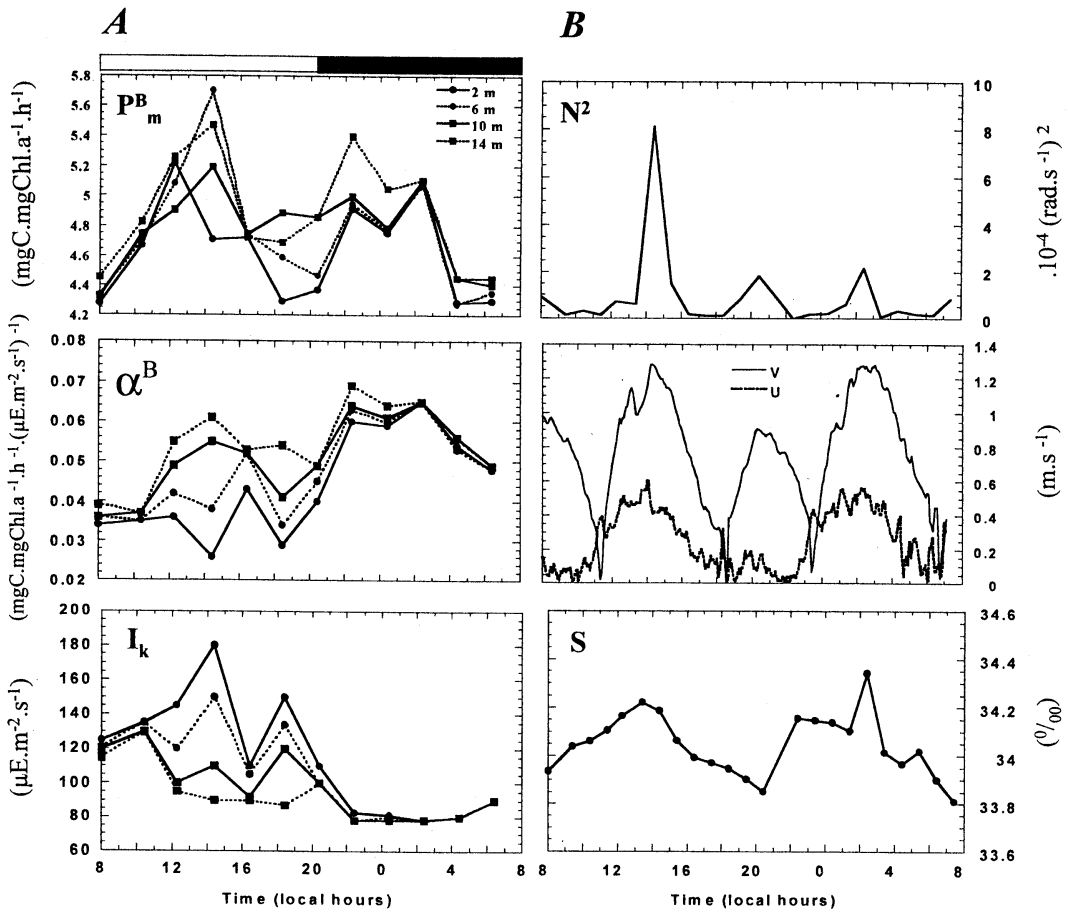
Fig. 5. (A) Temporal variations of the three main photosynthetic parameters measured at four depths (2, 6, 10 and 14 m) in a coastal water column and in neap tide condition. (B) Temporal variations of the Brunt Väisälä frequency (N^2), current speed (according to the north-south component (V) and the east-west component of current (U)), and salinity in the same time as photosynthetic parameters.

2.4. Photoadaptation in relation with vertical tidal mixing

Considering photosynthetic parameters in the water column during the daylight period, it appears from our sampling that photo-adapatation is not always a continuous process in time in a coastal sea dominated by the tide. The dissipation of tidal energy that takes place at two typical time–scales (several hours and several days), controls the occurrences and levels of photoadaptation processes.

First, at the high–low tidal cycle scale, a general temporal variation pattern of photosynthetic parameters with depth have been observed in coastal and intermediate water columns of the English Channel (LIZON et al., submitted). The general variation pattern consists in a temporal alternation of homogeneous and heterogeneous vertical profiles of PE parameters (P$_m^B$, α^B, I$_k$), occurring respectively after each high current speed periods and during each low current speed periods (Fig. 5A and 5B for an example). Such time variation pattern means that photoadaptation can take place and that the water column is relatively stable. On the opposite, when vertical mixing increase due to high current speed, photosynthetic characteristics are the same in the water column.
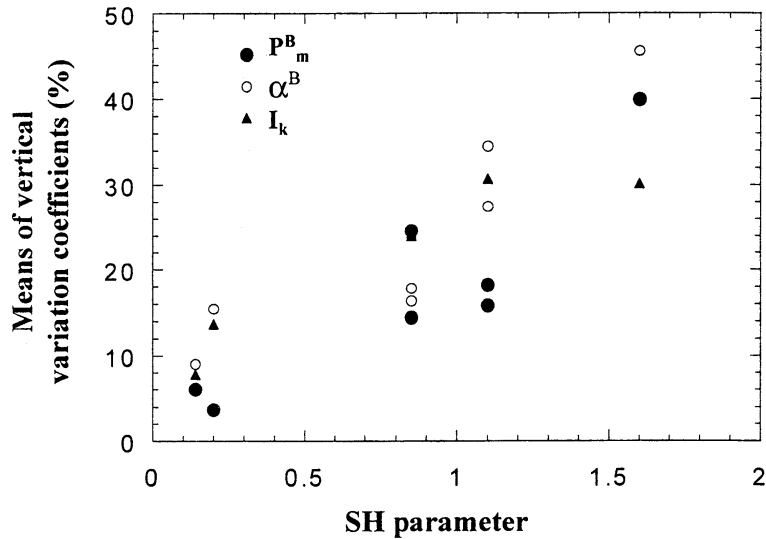
Fig. 6. Relationship between the Simpson and Hunter (SH) parameters and the mean vertical variation coefficients of the three main photosynthetic parameters for the different sampling periods conducted in the different water columns of the eastern English Channel.

Cell light history become similar at the scale of the water column. This result is consistent with the time fluctuations of the Brunt Väisälä frequency computed for the whole water columns in the same time (Fig. 5B). This physical parameters (related to the vertical density gradient of waters) allow to identify relative stable and mixing periods in a water column (DEMERS and LEGENDRE, 1981). These periods occur respectively before and after high current speed values (Fig. 5B). Significant correlations (Spearman rank coefficient) between (i) the variation coefficients (VC) of the three PE parameters (computed between the four sampling depth) and (ii) the Brunt Väisälä frequency (N^2) are also noted ($r = 0.716$, $p < 0.01$ for P_m^B; $r = 0.687$, $p < 0.05$ for α^B; $r = 0.704$, $p < 0.05$ for I_k). So, biological and physical processes considered here display good temporal interactions. It can be hypothesized that photoresponse times of phytoplankton in a tidally mixed coastal sea could be very fast.

However, this general temporal variation pattern of photosynthetic parameter distributions with depth can be more or less different according to some factors as the sampled water masses (LIZON et al., submitted). Since depth of

offshore waters (30-50 m depth) are greater than depth of coastal waters (0-20 m depth), vertical tidal mixing induced by tidal current interacting with the bottom are lower in offshore waters than in nearshore waters. As a consequence, we can explain that the temporal alternation of homogeneous and heterogeneous vertical profiles of photosynthetic parameters are not observed in offshore waters in neap tide condition (LIZON et al, 1995). The offshore water column being relatively stable, photoadaptation can take place without interruption during the daylight period. The general variation pattern of vertical photosynthetic parameter profiles can also be different with regard to resuspension processes of microphytobenthos that can occur from the bottom. Being given that sediment distribution display great variations in space in the English Channel (AUGRIS et al., 1997), it can be hypothesized that microphytobenthos is not homogeneously distributed in space. This can explain that the third category of vertical photosynthetic parameter profiles previously described is not observed for all sampling stations, but more specially in neashore waters.

Secondly, at the neap-spring tidal cycle scale, the order of magnitude of photosynthetic

parameter vertical variations (*i.e.* of photo-adaptation processes) depends on the intensity of vertical mixing (LIZON *et al.*, submitted). As a matter of fact, considering all our sampling periods and stations, significant correlations have been found between the distributions of vertical variation coefficients (VC) of the three PE parameters and the Simpson and Hunter (SH) stratification parameters. The SH parameters were calculated following BATH and LEGENDRE (1985) using depth of the water column, mean tidal stream velocity and a drag coefficient. This parameter was used in our study to characterize and compare the general vertical stability of the different water columns that have been sampled in different area and tidal conditions. The correlation coefficients between mean vertical VC of P_m^B, α^B, I_k and SH are respectively r = 0.800 (p < 0.05), r = 0.981 (p < 0.01), r = 0.781 (p < 0.05). These significant correlations have been so obtained between mean values of VC distributions of PE parameters (computed for each sampling period) and SH. So, when SH is high (or close to the standard value of 1.5 which is often used to identify the transition between highly stratified and mixed waters), means of vertical VC of PE parameters for a sampling period are also high (Fig. 6). An opposite result is obtained when SH is low (Fig. 6). In addition, vertical mixing intensity varying at the neap spring tidal cycle scale can control the extent of phytoplankton photoadaptation processes in a tidally mixed coastal sea.

However, no significant relationship or correlation has been found between hydrodynamical conditions of sampled waters and the order of magnitude of photosynthetic parameters. Such a relationship was expected since the aim of phytoplankton photoadaptation is to optimise primary production and its growth rate. This can be easily explained with sampling periods conducted in different seasons, from spring to autumn. At this scale, it is well recognized that different phytoplankton populations consistent with species successions can be sampled (HARRIS, 1980), and that environmental parameter changes (temperature, nutrient concentrations...) can also control photosynthetic parameter values of encountered phytoplankton cells (PRÉZELIN *et al.*, 1977, CÔTÉ and PLATT, 1983; FERRIS and CHRISTIAN, 1991). In the same way, but at smaller scale, we can explain photosynthetic parameter variations according to the high or low tide conditions. Generally, P_m^B and α^B display greater values in high tide period than in low tide period (Fig. 5A). This can be due to horizontal advection of different populations (in specie and physiological point of view) that are characteristics of offshore and nearshore waters, as shown by salinity variation (Fig. 5B).

2.5. Estimation of daily primary production rates

Several estimates of daily primary production rates considering or not the general temporal and vertical variation patterns of photosynthetic parameters have been computed for each sampling day to determine if bias could occur when short term variability of photosynthetic parameter is neglected. Briefly, daily production rates were calculated using all measured photosynthetic parameters (method A), using only maximum or minimum PE parameters obtained on the same profile (method B), using only values measured at 2 m during the day (method C), and around noontime at 2 m (method D). These different methods are consistent with different sampling strategy encountered in the literature and allow the display of potential errors due to under sampling.

In this way, we can show that potential underestimations or overestimations that result from calculating daily production rates without taking into account all photosynthetic parameter variability, vary between 2.6 and most of 100 % (LIZON *et al.*, submitted). Greatest differences are obtained between A and B methods, more particularly if homogeneous vertical profiles of photosynthetic parameters are used in B method (*i.e.* when photoadaptation in the water column is completely neglected). HARDING *et al.* (1982) and VANDEVELDE *et al.* (1989) also showed differences of 19–39 % and 25–56 %, respectively, for integral daily rates, but considering or not circadian cycles at one depth. Photoadaptation

with depth was not considered in their both studies. So, many production rates reported in the literature could be in error, especially in tidally mixed coastal area for which homogeneity hypothesis are made on vertical profiles of biological parameters. No extrapolation of photosynthetic parameters in order to estimate primary production rates at large scale (by remote sensing for example) must not be made in coastal waters without assessing the variability of these fundamental physiological parameters.

3. Response times of natural phytoplankton to light shifts

Since our field measurements have not allowed to conclude directly on the control of daily production rates by vertical mixing intensity (varying at the scale of the neap–spring tidal cycle), we have conducted a theoretical study on the interactions between vertical mixing (which change according to high–low tidal cycles and neap–spring tidal cycles) and photoadaptation processes. In this aim, we have had to make first some experiments to determine photoresponse times of natural phytoplankton populations from the eastern English Channel.

Light shift experiments have been so conducted on natural phytoplankton population collected in coastal waters of the eastern English Channel. Such experiments consist first in phytoplankton sampling (with Niskin bottles) in surface and deep waters (20 m depth). Secondly, surface phytoplankton cells are shifted to low light simulating light intensity of deep waters, and deep phytoplankton cells are shifted to high light similar to light intensity in subsurface waters. Photosynthesis irradiance relationships (PE) and chlorophyll a concentrations have been then measured (according to the same methods as in our field studies) at different times during 10 after the shifts. The temporal variations of each photosynthetic parameters have been adjusted with first–order kinetic equations (CULLEN and LEWIS, 1988) in most of the case, in order to calculate photoresponse times of phytoplankton to reciprocal light shifts (*i.e.* from low to high light (LH) and from high to low light (HL)).

As expected, light shift experiments have shown that natural phytoplankton displays photoresponses to reciprocal light shifts that are consistent with the photoadaptation theory (FALKOWSKI and OWENS, 1980), and other results obtained from experiments on mono–specific phytoplankton culture (PRÉZELIN and MATLICK, 1980; CULLEN and LEWIS, 1988). As a matter of fact, P_m^B (in a first time before to decrease) and I_k increase for a LH light shift, while a^B decreases in the same time (Fig. 7). On the opposite, P_m^B and I_k decrease for a HL light shift, while a^B increases (Fig. 7). With regard to the light shifts, variation patterns of photosynthetic parameters are so similar to variations observed in a water column. Decreasing values of P_m^B 3h after the LH light shift can be here easily explained by photoinhibition processes. Such phenomenon are well documented in stratified waters (HARRIS, 1980; VINCENT *et al.*, 1984; NEALE and RICHARDSON, 1987; FERRIS and CHRISTIAN, 1991) and are some times encountered near the sea surface in the English Channel (LIZON *et al.*, 1995). However, it is interesting to see here that photoinhibition is not instantaneous but can begin with several hour's delay. Evidence of photoinhibition is given here by a photo-protective index : the ratio between diatoxanthin (Dt) pigment concentrations and diadinoxanthin (Dd) plus diatoxanthin concentrations (Fig.7). Diadinoxanthin is involved in the photodependant xanthophyll cycle of chromophyte algae as precursor of diatoxanthin, which is the photoprotective pigment (BRUNET *et al.*, 1993; CLAUSTRE *et al.*, 1994). In our experiment, the Dt/(Dd + Dt) ratio increase after the third hour in the case of the LH light shift, indicating so that cells must dissipate light energy received in excess. This is typical of a photoinhibition situation.

However, the most important results of these experiments are the response times of photosynthetic parameters (deduced from kinetic constants) which are lower than the time between two high current speed events (Fig. 8). Half response times ($T_{0.5}$) of photosynthetic parameters ranging between 0.7 h and 2.5 h show that significant responses of photosynthesis can occur during a 6h period. This is
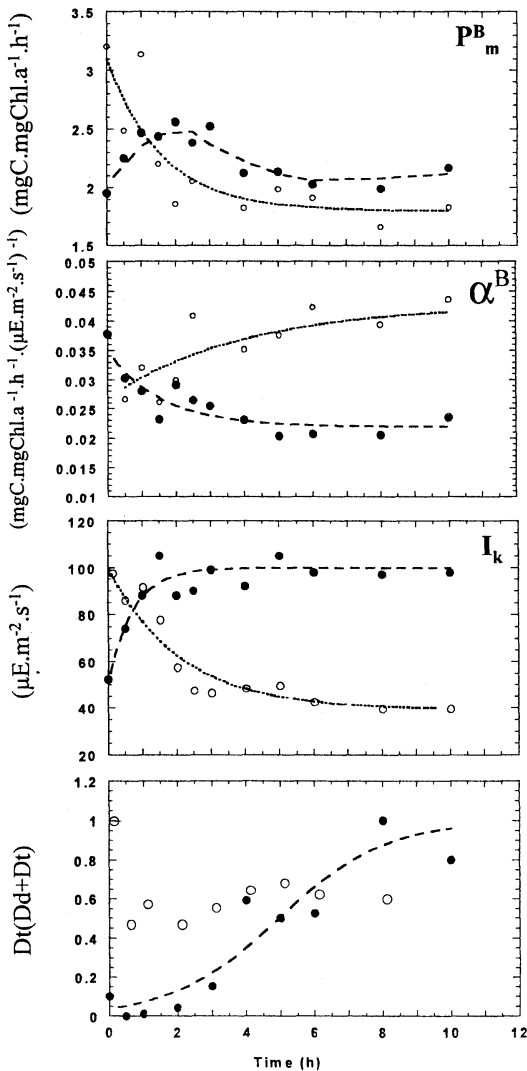
Fig. 7. Temporal variations of the three photosyn-
thetic parameters and the ratios between
diatoxanthin (Dt) pigments and dia-
dinoxanthin (Dd) plus diatoxanthin, after
light shifts (i) from high to low light (HL)
(white points) and (ii) from low to high light
(LH) (black points). Data were adjusted with
a first order kinetic equation (see CULLEN and
LEWIS, 1988), excepted in the case of (i) P_m^B for
the LH light shift (data were simply fitted),
and (ii) the Dt(Dd + Dt) ratios (data were here
adjusted with a logistic model for the LH light
shift).

consistent with our field results on the occur-
rence of photoadaptation processes. In our ex-
periments, photosynthetic parameters response

times appears to be very fast; faster than many
values reported in the literature (LEWIS et al.,
1984a; POST et al., 1985; CULLEN and LEWIS, 1988)
and obtained from laboratory culture. For ex-
ample, P_m^B and α^B make most often a complete
transition between 6–10 h and 3–5 h respec-
tively. In our case, response times of P_m^B and
α^B are smaller than literature values, or close to
the low values of these intervals. This could be
explained by hydrodynamical conditions en-
countered in tidally mixed coastal waters. As
JUPIN and LAMANT (1997) says, the habit of ag-
gressions allows to "form the character" of
natural microalgae, by an unidentified way,
and allows them to acquire effective adapta-
tions more rapidly than culture growing in
comfortable room.

In these light shift experiments on natural
phytoplankton, different half response times
($T_{0.5}$) for each photosynthetic parameters have
also been obtained from low to high light shift
and the reciprocal light shift (Fig. 8). Natural
phytoplankton photoresponse times are so not
symmetrical with regard to reciprocal light
shifts, as for CULLEN and LEWIS (1988). More
precisely, response times of P_m^B are faster for a
HL light shift and response times of α^B and I_k
are faster for a LH light shift. Even if these re-
sults are consistent with some other results on
mono–specific culture (PRÉZELIN and MATLICK,
1986), they are surprising for natural popula-
tion sampled in periodically mixed coastal wa-
ters. As a matter of fact, light shifts displaying
fastest photoresponse times here are not those
that allow phytoplankton to optimise their pro-
duction after a shift from low to high light, or
high to low light in the natural environment.
For example, a fast response time of α^B was ex-
pecting for a light shift from high to low light
and not in the opposite case (Fig. 8). Even if
this question must be investigated, these sur-
prising results suggest that a cell photo-
adaptative strategy relating to the fastest
response times with respect to LH or HL light
shifts (in order to optimise production in a tur-
bulent environment) can be rejected.

In addition, first–order kinetic constants esti-
mated in this preliminary study for natural
phytoplankton are different for each photosyn-
thetic parameters and each kind of light shift.
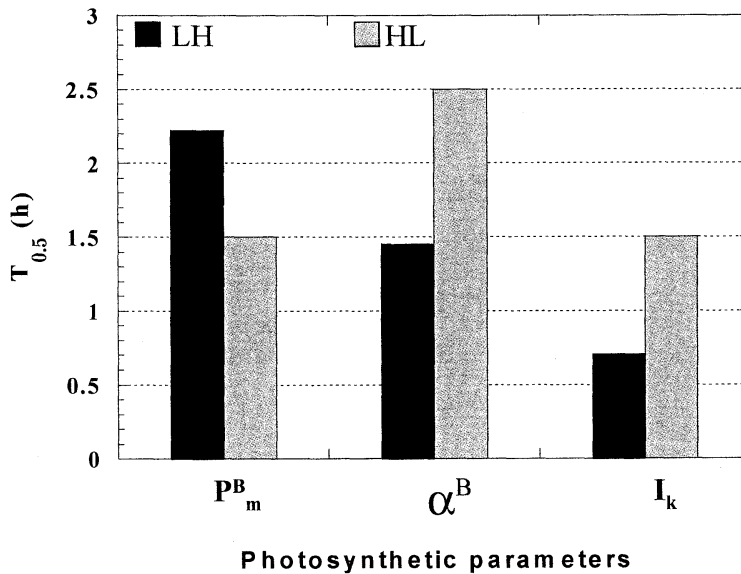
Photosynthetic parameters

Fig. 8. Half response times ($T_{0.5}$) of the three main photosynthetic parameters for the Low-High light shift (LH) and the High-Low light shift (HL).

Therefore, these results have been taken into account in our modelling study presented in the following section.

4. Lagrangian modelling of photoadaptation in a tidally mixed water column

Since difficulties of sampling and the variability of environmental conditions involved in primary production control can hide a possible relationship between vertical mixing intensity and daily primary production rates (see § 2.5 for more details), we have conducted a theoretical study on the interactions between vertical mixing (which changes according to the high–low tidal cycles and neap–spring tidal cycles) and both photoadaptation processes and daily production rates. The model used is a Lagrangian model (LIZON *et al.*, 1998). It describes individual physiological properties of cells instead of cell concentrations. It takes into account different photoresponse time constants for each PE parameters and each light shift (cf. § 3. above), and a depth dependent diffusion coefficient (K_v) that is a function of current speed measurements collected in the eastern English Channel (see LIZON *et al.*, 1998 for further details). For more clarity, non-mobile phytoplankton cells are considered. The sinking rate of cells and wind driven turbulence are neglected. Simulation have been made for different typical water columns (in depth and turbidity point of view) found in the English Channel, along an inshore–offshore transect.

The overall result of our simulations is an increase in the daily primary production rates between spring and neap tide conditions (Fig. 9A and 9B). It can be stated that the control of daily production rates by vertical mixing intensity is realized via photoadaptation processes occurring at short time scales. As a matter of fact, differences in daily primary production rates between spring and neap tide conditions are, for example, in the order of 40 % when photoadaptation processes are taken into account in a nearshore water column, whereas they are in the order of 4.2 % only if photoadaptation processes are not considered (Fig. 9C). From our simulations, it follows that daily primary production rates relating to short term photoadaptation processes are not only a function of light intensity, nutrient concentrations and phytoplankton biomass (AGOUMI, 1985 ; MOLONEY *et al.*, 1986 ; HOCH, 1995; HOCH and MÉNESGUEN, 1995 ; MÉNESGUEN and HOCH, 1995), but also of vertical mixing intensity.
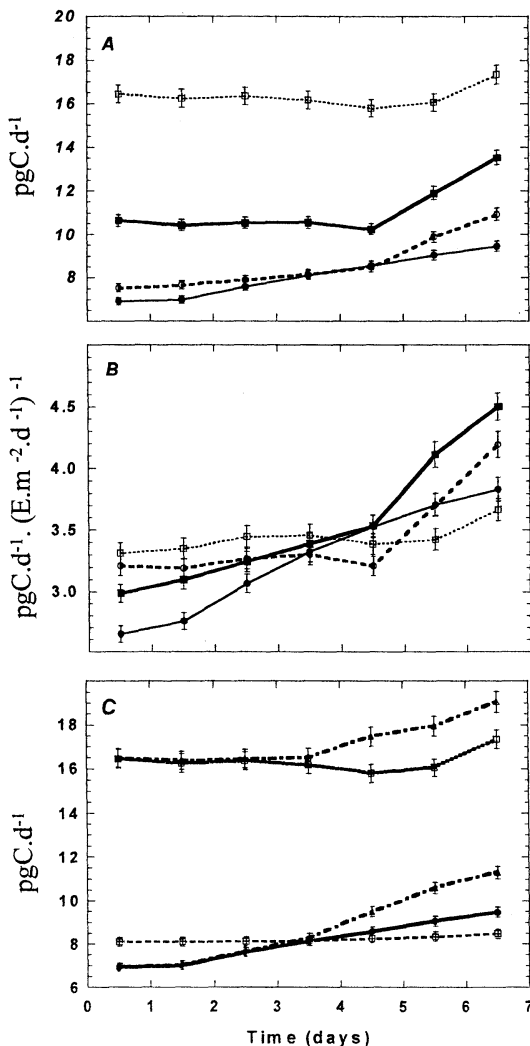
Fig. 9. (A) Daily primary production rates in nearshore (●), intermediate (○), offshore (■) and $Z_e/Z_m = 1$ (□) water columns between spring (first day) and neap tide (seventh day) conditions, (B) ratios between the daily production rates and the mean daily light intensites of each considered mixed layer, (C) daily primary production rates considering photoinhibition processes (● and □) or not (▲ and △), in coastal (● and ▲) and $Z_e/Z_m = 1$ (□ and △) water columns, and daily primary production rates obtained by turning off photoadaptation processes (⊞) in coastal waters (adapted from Lizon et al., 1998).

However, the previous relationship between daily production rates and vertical mixing intensity are also related to the water column

considered along an inshore–offshore transect (Fig. 9A and 9B). Actually, this relationship depend on the value of the ratio between depth of the euphotic zone (Z_e) and depth of the mixed layer (Z_m). Statistically significant increases, in the order of 40%, are observed in the course of the semi–neap–spring tidal cycle, for coastal $(Z_e/Z_m = 0.49)$ and intermediate $(Z_e/Z_m = 0.53)$ water columns (Kendall's coefficients of rank correlation are respectively 0.970 and 0.852 with $p < 0.01$). On the contrary, for offshore $(Z_e/Z_m = 0.68)$ and $Z_e/Z_m = 1$ water columns, the increase tendencies of daily production rates are not significant in a statistical point of view (Kendall's coefficients are respectively 0.335 and 0.231 with $p > 0.05$). In these two last cases, the increases in daily rates occur late in the course of the semi–neap spring tidal cycle, and all the more weakly that the Z_e/Z_m ratios are near to the unit (Fig. 9B). If a relationship between daily primary production rates and vertical mixing intensities was expected, the influence of the euphotic zone depth on this relationship was not. This last remark could be explained by the fact that the vertical heterogeneity of three photosynthetic parameters decreases (in the simulation results), when the depth of the euphotic zone increases (Lizon et al., 1998). It can then be hypothesized that the low VC of photosynthetic parameters in a $Z_e/Z_m = 1$ water column would be insignificant compared with the vertical gradients of light considered in the computation of the cell primary production rates. So, in a $Z_e/Z_m = 1$ water column, low photoadaptation processes would have a weak effect on daily production rates between spring and neap tide conditions, for which the vertical gradients of light are similar. Since photoadaptation processes displayed by simulation results in offshore waters are contrary to field results (cf. § 2.4), new experimentations must be made in order to study cell–specific constants of photoadaptation processes, for water columns of different Z_e/Z_m ratios.

5. Conclusion

From the combination of field, laboratory and modelling study, our work give some insights into the variability of photosynthetic

activity in a typical coastal sea (the eastern English Channel), periodically mixed by the tide and generally considered as being always homogeneous with respect to temperature and salinity profiles.

With reference to our hypothesis, we can conclude that photoadaptation processes to the vertical gradient of light can occur in coastal mixed waters, and that photoadaptation can be controled by vertical mixing intensity at two typical time scales : the high–low tidal cycle scale and the neap–spring tidal cycle scale. About the control of daily primary production rates by vertical mixing intensity, we cannot completely conclude because the relationship is just supported by simulation results of a Lagrangian model on the interactions between the time scales of these biological and physical processes. According to simulation results, the relationship between daily primary production rates and vertical mixing could consist in a significant increase (40%) of daily production while vertical mixing intensity decrease between spring and neap tide conditions. At this scale, it has been difficult to identify from field studies such a relationship since biological and physical fluctuations in our coastal systems can occur faster than the biweekly neap–spring tidal cycles, owing to horizontal advection processes of different water masses, as in other studies(VÉZINA et al. 1995; BRYLINSKI et al. 1996).

Therefore, the validation of the relationship between daily production rates and vertical mixing at the neap–spring tidal time scale will be difficult and will require probably experiments in mesocosm where all "environmental" parameters will be controlled (GERVAIS et al., 1997). With regard to our works, the knowledge of such relationship appears however to be of prime interest in order to give new estimates of coastal primary production rates, considering (i) all the variability of photosynthetic activity (photosynthetic parameters, response times to changing light, etc.) and (ii) biological–physical interactions at different scales; not only at the scale of the day or at the neap–spring tidal cycle scale (as with our field and modelling studies), but also at greater time scales, as seasonal, annual and inter–annual time scales. Even if we have shown two

example of scale dependence (see BARRY and DAYTON (1991) for more details) between vertical tidal mixing and photosynthetic activity, we must be aware of scale transfer processes (FRONTIER et al., 1992) that can be significant in phytoplankton primary production estimates of a tidally mixed coastal system. In scale transfer processes, variability of a biological factor occurring at a given scale could influence a biological signal that is a priori typical of another scale (STEELE, 1988). So, production rate variability, that characteristic scale is most often the mesoscale (see JOINT and GROOM (2000) for example), could depend on process taking place at the scale of the cell (YAMAZAKI, 1993; LEVIN, 1994). Such considerations in research on phytoplankton production could be of great interest in order to best estimate coastal primary production and carbon flux at relevant scales, in a context of global climatic change and its influence on coastal phytoplankton (KNAUER, 1993; OTTERSEN and STENSETH, 2001).

Acknowledgments

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