Vol. 102: 69–77, 1993 | MARINE ECOLOGY PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published December 9

In situ variations of the xanthophylls diatoxanthin and diadinoxanthin: photoadaptation and relationships with a hydrodynamical system in the eastern English Channel

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ABSTRACT: Photosynthetic pigments from phytoplankton were measured by high performance liquid chromatography (HPLC) along inshore-offshore transects and vertical profiles in the southeastern English Channel. An inverse relationship between the (Dd+Dt)/chl *a* and Dt/(Dd+Dt) ratios (Dt = diatoxanthin, Dd = diadinoxanthin, chl *a* = chlorophyll *a*) and light penetration was found, indicating a photoadaptative response of phytoplankton to high light irradiances. High ratios are present in less turbid, clearer offshore waters, in comparison to coastal waters influenced by river inputs. This response can be caused both by seasonal changes in mean irradiances or by different amounts of turbidity, which affect light penetration. The lack of variation along the vertical profiles with respect to the surface is interpreted as an indicator of a recent vertical transport of phytoplankton by the high-energy tidal currents present in the study area. In addition, a diel cycle was noted, with a decrease in the concentrations of diatoxanthin at night. The use of this pigment as a marker of water masses must be cautious, since pigment concentration and composition are dependent on the physiological state of the cell, on the environmental conditions and dynamics, and on seasonal and diel cycles.

KEY WORDS: HPLC · Phytoplankton · Pigments

INTRODUCTION

Recent phytoplanktonic studies have used biochemical constituents as markers for biological processes: lipids (e.g. Claustre et al. 1990, Nichols et al. 1991), aminoacids (e.g. Madariaga & Joint 1992), nucleic acids (e.g. Sakshaug & Andersen 1986, Madariaga & Joint 1992), and photosynthetic pigments (e.g. Abayachi & Riley 1979, Mantoura & Llewellyn 1983, Gieskes & Kraay 1986). A major advance has been made by the use of high performance liquid chromatography (HPLC), which, when applied to pigment analysis, allows the precise identification and quantification of chlorophylls, carotenoids and phycobilins in photosynthetic organisms. Carotenoids act as light-harvesting molecules inside the cell, allowing an efficient utilization of the light from the blue region of the spectrum. Beside this light-harvesting function, the carotenoids play an important role in protecting the pigment-protein complexes and the chloroplast itself against photooxidation (Young & Britton 1990).

This study is concerned with diatoxanthin (Dt) and diadinoxanthin (Dd) pigments, which are acetylenic carotenoids of the xanthophyll family. These pigments are specific markers for the Chromophyte algae and, in the marine phytoplankton, are present in diatoms, dinoflagellates and prymnesiophytes (Liaaen-Jensen 1978, Demers et al. 1991). The 2 pigments are converted from one to the other by a photo-dependent reversible reaction of de-epoxidation. The formation of diatoxanthin (the epoxy-free form) is induced by high light intensities, while the inverse reaction takes place when light intensities decrease. An equivalent strategy involving violaxanthin, antheraxanthin and zeaxanthin

also exists in higher plants and prochlorophytes (Siefermann-Harms 1990, Demers et al. 1991).

Studying photoinhibition in 2 Chromophyte algae, Caron et al. (1992) have shown that a photoprotective role depends on the ratio between the epoxidated and de-epoxidated forms of both the violaxanthin ↔ zeaxanthin and the diadinoxanthin ↔ diatoxanthin interconversions. The photoadaptation strategy (Falkowski & LaRoche 1991) and the underlying molecular mechanisms (Santus 1983) are known. These mechanisms are postulated to involve in a decrease of efficiency of the antenna-pigment in the presence of high levels of de-epoxidated xanthophylls. This decrease could be caused by the aggregation of light-harvesting complexes (Ruban et al. 1991), deactivation of triplet-state chlorophyll and singlet oxygen (Young & Britton 1990) or non-radiative energy dissipation (Demmig & Winter 1988).

Some authors consider diatoxanthin as the only pigment acting as a photoprotectant (Jeffrey 1980, Paerl et al. 1983), while others also invoke the same role for diadinoxanthin (Bidigare et al. 1987, Kerherve 1991). Controversies also exist about the duration of the de-epoxidation reaction, i.e. the transformation of diadinoxanthin in diatoxanthin. Welschmeyer & Hoepffner (1986) report a duration of seconds, Willemoës & Monas (1991) of minutes, Caron et al. (1992) of half an hour, and Mortain-Bertrand & Falkowski (1989) and Demers et al. (1991) of even 1 hour. The discrepancy could be due to the different biological material used in the different studies: algal cultures vs natural samples, or to different light conditions (quantity, quality, photoperiod). All of these studies agree that the reverse reaction (Dt to Dd) is slower.

Thus, the measurements of diadinoxanthin and diatoxanthin contents can give an indication of the ecological past of the cells (light conditions, water turbidity) and could become an indicator of the movements of the water masses and of their turbulence (Lewis et al. 1984, Cullen & Lewis 1988, Therriault et al. 1990, Kerherve 1991).

The aim of this work is to study the adaptation of natural phytoplankton populations to the hydrological environment, on both a seasonal and diel scale. We analysed subsurface samples from several inshore-offshore transects at different times of the year for 2 yr, and vertical profiles from 2 stations located inside the coastal and the offshore water masses, respectively. This study is a contribution to the research on biochemical markers of the dynamics of water masses.

MATERIAL AND METHODS

As shown by previous hydrobiological studies, the southeastern English Channel is characterized by a net separation between inshore and offshore water masses (Brylinski et al. 1984, Gentilhomme 1988, Brylinski et al. 1991). The 2 systems are separated by a frontal area which is tide dependent (Brylinski & Lagadeuc 1990). Samples were taken during 10 oceanographic cruises between March 1990 and June 1992 along inshore-offshore transects across 2 water masses (Fig. 1). At each sampling station (every 0.3 nautical miles), vertical profiles of salinity, temperature and chlorophyll fluorescence were taken using a CTD profiler (Seabird SBE 19) and an underwater fluorimeter (Sea Tech, Inc.). Light irradiances at different depths were measured with a quantameter (Li-Cor, Inc., model Li 185 B). Samples for pigment analyses were taken at a depth of 2 m between 11:00 and 16:00 h. During 2 cruises, in March and May 1992, continuous measurements of hydrological parameters and chlorophyll *a* (chl *a*) fluorescence were taken along Transects 3 to 11 (Fig. 1) at a depth of 2 m. At the same time, turbidity was also measured with a turbidimeter (Hach, model 43900) and water samples for pigment analysis were taken ca every 2 miles. During the March and May 1990 cruises, 2 stations, representative of the inshore and offshore waters, respectively, were sampled at 10 depths along Transect 1.

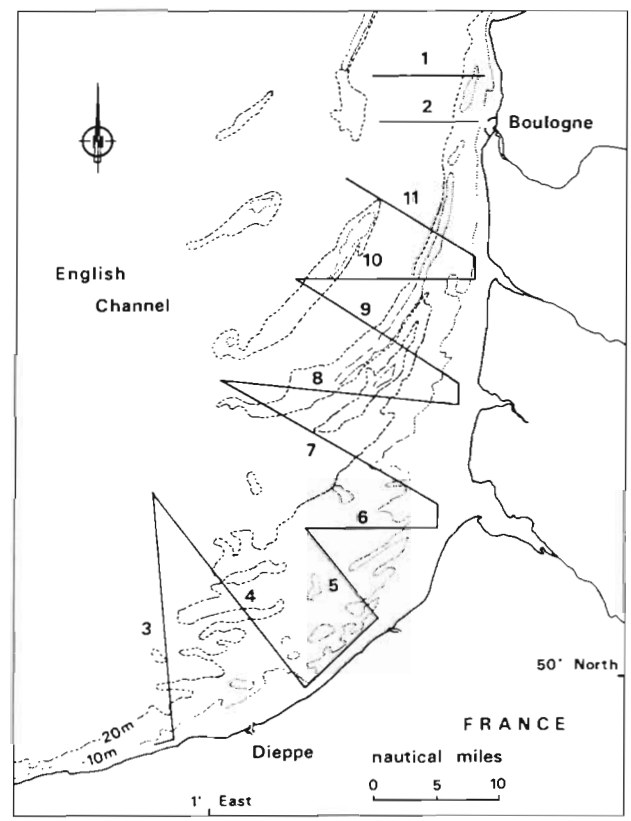

Fig 1. The study area showing the different inshore-offshore transects. Samples were taken: 28 Mar, 10 & 14 May, 8 Nov 1990; 4-5 Mar, 6-7, 22, 25 & 26 May 1992

Phytoplankton pigment composition and concentrations were analysed by HPLC. One liter samples were filtered onto Whatman GF/C filters which were stored in darkness and deep-frozen. The filters were disrupted by mechanical pounding for 3 min in 4 ml of 90% acetone. The 2 h long extraction was done at 4°C. A Beckman ultrasphere RP 18 column (ODS 5 µm, 250 × 4.6 mm, IP) was used for separation. Two solvent mixtures were used: (A) methanol:water:P solution (80:10:10) and (B) methanol:ethyl acetate (80:20) (modified from Klein & Sournia 1987). The P solution (ion-pairing) is the same as that used by Mantoura & Llewellyn (1983). The solvent flux was constant (1.5 ml min^{-1}), and the gradient was programmed as follows: the proportion of solvent B in the mobile phase increased from 20 to 60% during the first 7 min, then stabilized at 60% for 5 min and increased again to 100% in the following 8 min. Finally, pure solvent B was injected for 18 min. The detection of pigments was both spectrophotometric (440 nm, with Beckman Gold system model 167) and fluorimetric (excitation: 407 nm, emission: 420 to 700 nm, with a Kontron SFM 25). The extinction coefficients used to calibrate our system for quantification of diatoxanthin and diadinoxanthin were those of Johansen et al. (1974).

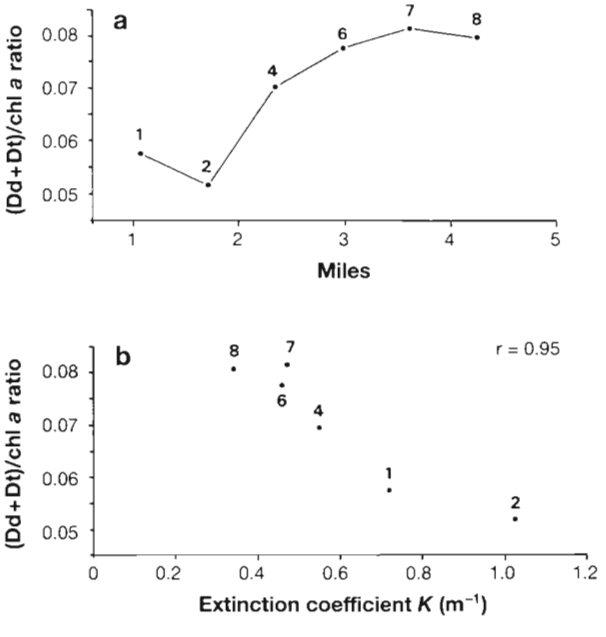

Fig. 2. (a) Variation of (Dd+Dt)/chl *a* along inshore-offshore Transect 2 on 22 May 1992 and (b) correlation (significance 1%, r = −0.95) between this ratio and extinction coefficient *K* (m^{-1}). Miles correspond to distance from Boulogne harbour in nautical miles

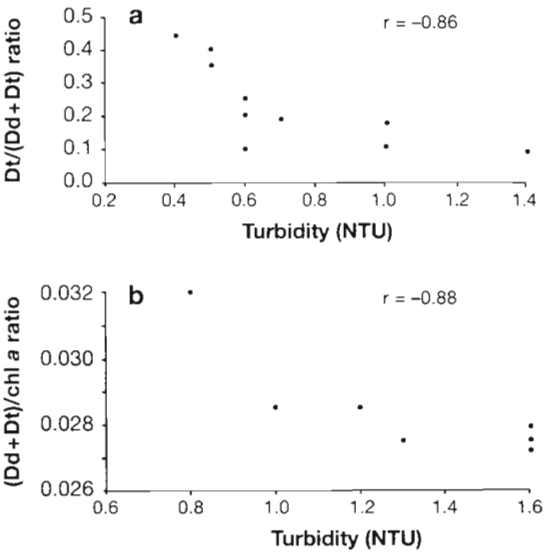

Fig. 3. Correlations (significance 1%) between (a) (Dd+Dt)/chl *a* and turbidity (r = −0.88) and (b) Dt/(Dd+Dt) and turbidity (r = −0.86) for the inshore-offshore Transects 5 & 6 and 3 & 4, respectively, on 4 May 1992. Miles correspond to distance from the coast in nautical miles

RESULTS

We followed the variations of 2 parameters: the Dt/(Dd+Dt) and (Dd+Dt)/chl *a* ratios.

Inshore-offshore variations

Along the inshore-offshore transects (2 m depth), the (Dd+Dt)/chl *a* ratio increased between inshore and offshore stations (Fig. 2a) and was directly related to the light penetration in the water column, expressed by the extinction coefficient *K* (m^{-1}; Fig. 2b) and, obviously, inversely related to the turbidity of the water. The same observations are valid for the Dt/(Dd+Dt) ratio (Fig. 3).

An exception to this relation was found in some coastal stations where a high Dt/(Dd+Dt) ratio (Fig. 4) or (Dd+Dt)/chl *a* ratio was found (see Fig. 10b). A peak of the Dt/(Dd+Dt) ratio also corresponded to a thermal (Fig. 5) or haline (Fig. 6) front. Also, in March 1990, no diadinoxanthin was measured between 2.4 and 3.9 nautical miles from the coast (Fig. 7).

Vertical variations

At the 2 stations sampled along a vertical profile, the Dt/(Dd+Dt) ratio did not vary with depth (Fig. 8): it remained low (<0.1) at the inshore station, while it maintained high values (>0.85) at the offshore

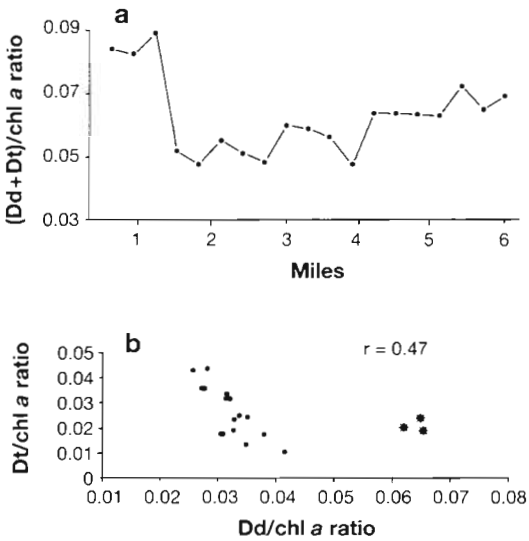

Fig. 4. (a) Variation of (Dt+Dd)/chl *a* and (b) relationship between Dt/chl *a* and Dd/chl *a*, along inshore-offshore Transect 1, on 8 November 1990. Correlation significance at 5% ($r = -0.47$, excluding the 3 coastal stations marked by •

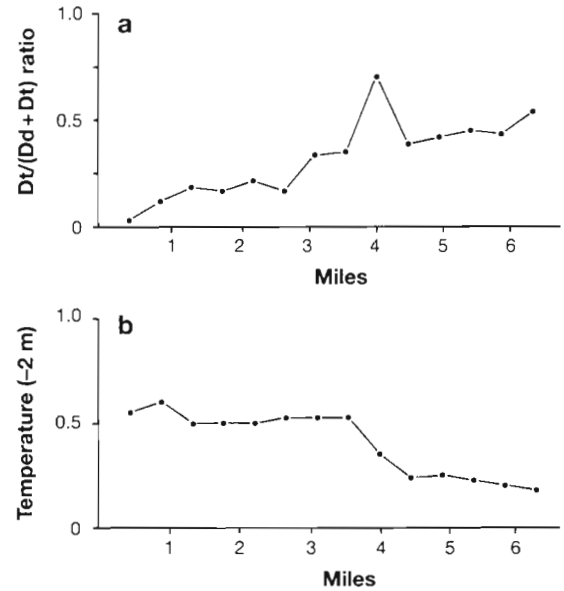

Fig. 5. Variation of (a) Dt/(Dd+Dt) and (b) temperature at 2 m along inshore-offshore Transect 2 on 25 May 1992. Miles correspond to distance from the Boulogne harbour in nautical miles

one, both in the upper layer directly exposed to solar irradiance, and below the thermocline (7 m depth), when this was present (Fig. 8). The Dt/(Dd+Dt) ratio seems therefore to be independent of the light attenuation along the water column in both coastal and offshore stations and the amplitude of variations of these 2 ratios according to the depth is lower than along the inshore-offshore transects (Fig. 8, Table 1).

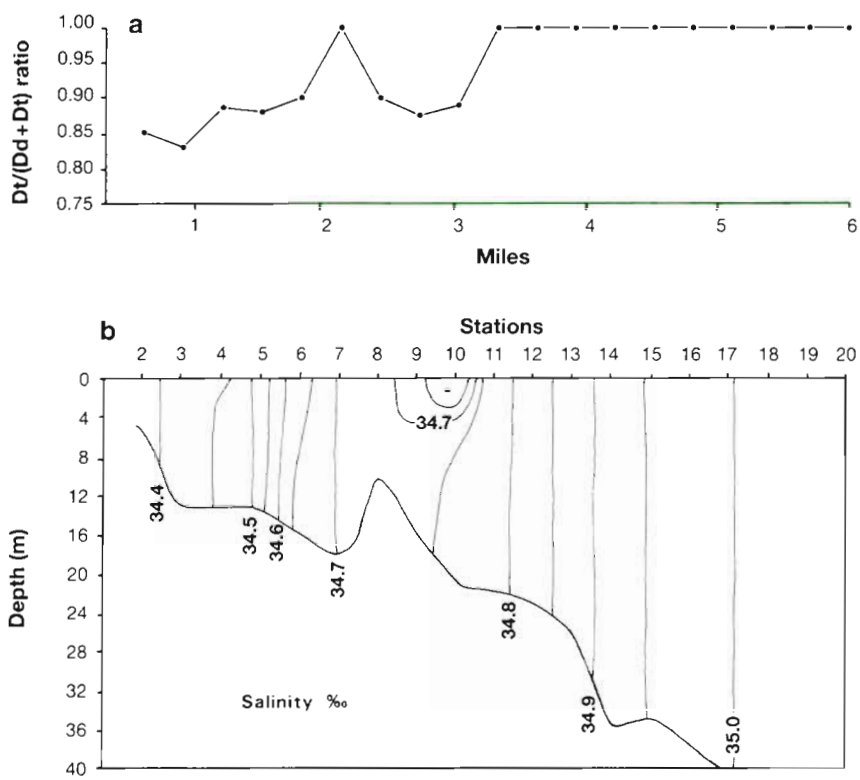

Fig. 6. Variation of (a) Dt/(Dd+Dt) and (b) salinity along inshore-offshore Transect 1 on 14 May 1990. Miles correspond to distance from the coast in nautical miles

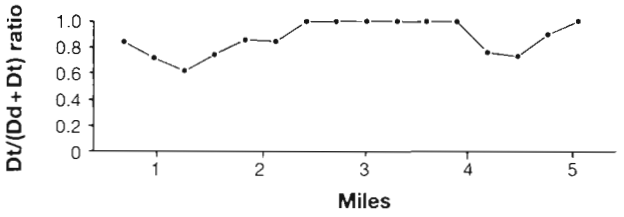

Fig. 7. Variations of Dt/(Dd+Dt) along the inshore-offshore Transect 1 on 28 March 1990. The absence of inshore-offshore gradient (also on 29 March, see Table 1) can be explained by low turbidity of the coastal station due to lower river discharges during this sampling period. Miles correspond to distance from the coast in nautical miles

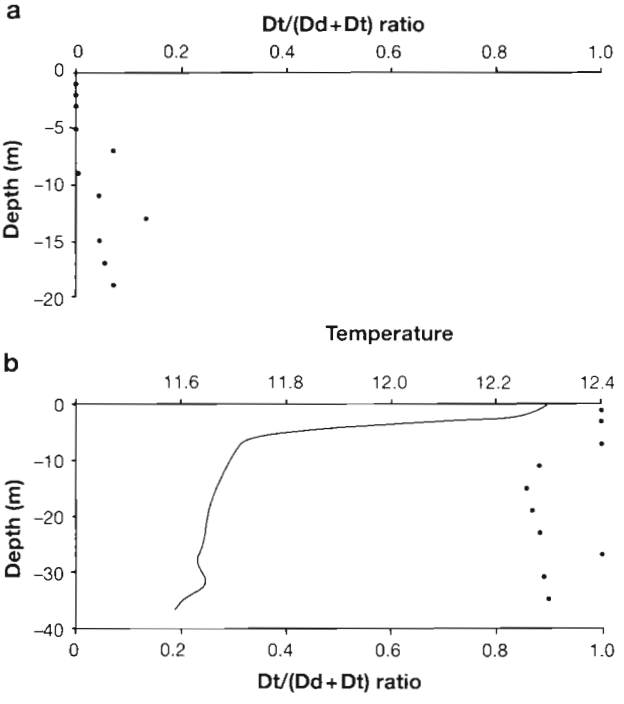

Fig. 8. Variation of the Dt/(Dd+Dt) in the vertical profiles of (a) Stn 6 and (b) Stn 20 on 10 May 1990 along Transect 1. Temperature profile (line in b) is shown for the open-sea station (stratification at 7 m)

Table 1. Irradiance (μE m^{-2} s^{-1}) at 1 m depth (measured with a quantameter during the sampling time) and means of pigment ratios in the water column at coastal (n = 5) and offshore (n = 5) stations on 28 Mar 1990; and at the same stations (coastal, n = 12; offshore, n = 10) on 10 May 1990

	29 Mar 1990		10 May 1990	
	Inshore	Offshore	Inshore	Offshore
Irradiance (1 m)	120	380	800	550
(Dt+Dd)/chl *a*	0.040	0.050	0.070	0.080
Dd/chl *a*	0.034	0.040	0.067	0.060
Dt/chl *a*	0.010	0.018	0.001	0.071
Dt/(Dt+Dd)	0.210	0.320	0.038	0.930

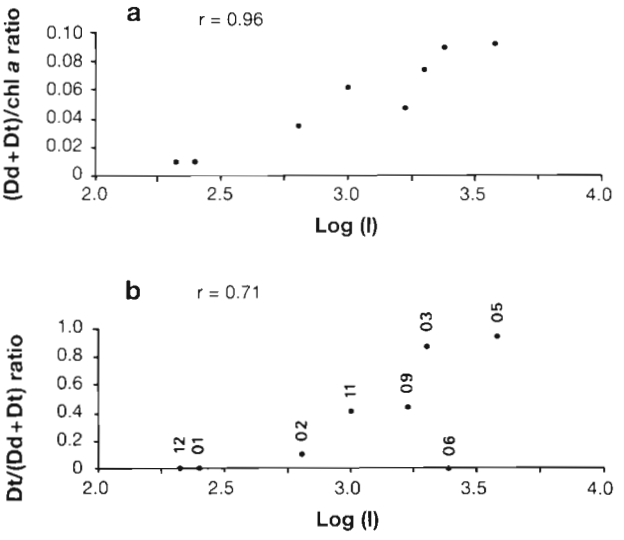

Fig. 9. Correlation between (a) (Dd+Dt)/chl *a* (at 2 m depth) and irradiance and (b) Dt/(Dd+Dt) (at 2 m depth) and irradiance. The irradiance values (measured in air, μE m^{-2} s^{-1} on a log scale) are means of weekly values (Grossel & Hitier 1991)

Annual variations

The (Dd+Dt)/chl *a* and Dt/(Dd+Dt) ratios increased with the mean irradiance during the year (Fig. 9). The logarithmic correlations between the (Dd+Dt)/chl *a* and Dt/(Dd+Dt) ratios and irradiance were significant to 1 % (r = 0.96) and 5 % (r = 0.72), respectively.

Diel variations

We found a systematic decrease or a disappearance of diatoxanthin at night along the inshore-offshore transects (Fig. 10), indicating a physiological adaptation of the phytoplankton to the natural light-dark cycle. This phenomenon was particularly discernible in the offshore waters where this pigment was very abundant during the day.

At nightfall on 5 May 1992 (Fig. 10a), diatoxanthin was present in open-sea samples taken at 20:30 h. The concentration progressively decreased, reaching zero at about midnight (i.e. in about 3.5 h). In March 1992 (Fig. 10b) the duration of this decrease to zero was shorter; Dt was absent in the offshore stations within 1 h after nightfall.

DISCUSSION

The influence of environmental factors such as temperature, nutrients or light on the pigment pool of phytoplankton has already been shown by several

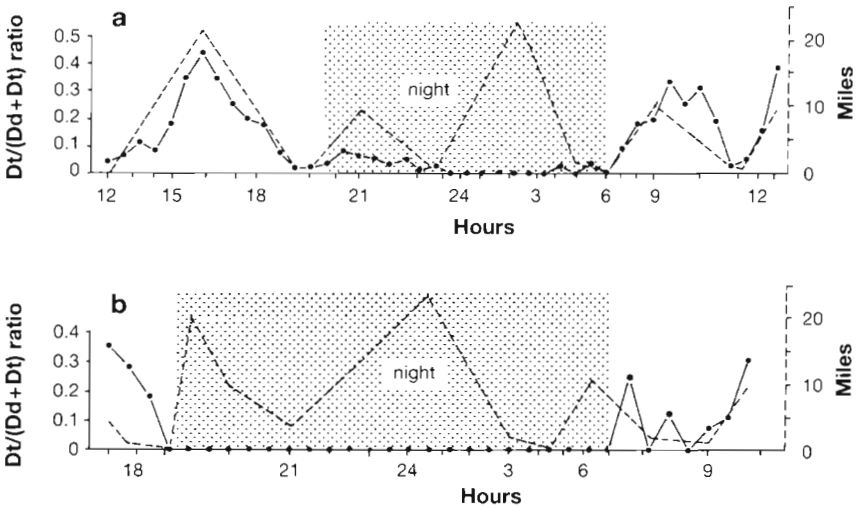

Fig. 10. Variations of Dt/(Dd+Dt) along 2 series of inshore-offshore transects on (a) 6–7 May 1992 (Transects 3 to 11) and (b) 4–5 March 1992 (Transects 4 to 11). Time in local hours. Dashed lines: miles (corresponding to distance from the coast in nautical miles)

authors (Carreto & Catoggio 1976, Gallagher & Alberte 1985, Kana et al. 1988, Klein 1988, Olaizola et al. 1992), but only the last study was realized *in situ*, like ours. On cultured species, Demers et al. (1991) already reported an increase in Dt under high irradiances and Sakshaug & Slagstad (1991 and references therein) observed an increase of Dd+Dt in cells adapted to high light intensities. Klein (1988) did not detect photoadaptation in benthic diatoms but he used irradiances too low (20 $\mu E\ s^{-1}\ m^{-2}$) to induce photoprotection even in the absence of a photoperiod, which should, on the contrary, induce it (Willemoës & Monas 1991). When adaptation to irradiance occurs, it always corresponds to an increase in photoprotectant pigments, i.e. diatoxanthin in chromophyte algae (Demers et al. 1991, Willemoës & Monas 1991).

Our data show a direct relationship between light and both (Dd+Dt)/chl *a* and Dt/(Dd+Dt) ratios, indicating an adaptation of phytoplankton cells to local irradiances. The distribution of the chosen markers shows a clear gradient from the coast to the open sea, with the higher levels present in offshore stations (Figs. 2, 3, 5 & 6). The higher requirement of photoprotection in the offshore community with respect to the coastal one is due to the high turbidity of the coastal area, which limits the penetration of light. The turbidity in this area is due to terrigenous inputs from rivers and to active resuspension of matter (Brylinski et al. 1984, Dupont et al. 1991). In May 1990 the inshore-offshore gradient of the Dt/(Dd+Dt) ratio (Fig. 6a) was disrupted by low values because an isolated water mass with coastal characteristics (Fig. 6b) was present, thus showing the reliability of this ratio as a marker of water masses.

The variations in the values of the Dt/(Dd+Dt) ratio with depth (Fig. 8) are smaller than those seen along the inshore-offshore transects (Table 1), although the light gradient is higher. This is due to the fact that the vertical transport inside the water column is too fast to allow the cells to photoadapt. Since we measured a time of ca 3.5 h in May (Fig. 10a) for the decrease (or disappearance) of diatoxanthin after nightfall, we infer that the phytoplankton sampled near the bottom were in the upper layers less than 3.5 h before the sampling. Based on this hypothesis, we calculated vertical transfer rates of more than 5 $m\ h^{-1}$, i.e. 12 $min\ m^{-1}$. This result agrees with that of Denman & Gargett (1983), who found vertical transfer rates of 10 m for cells by turbulence ranged between some minutes to several hundred hours. The relationship between vertical mixing and photoadaptation has been studied with the aid of physical models (Lewis et al. 1984, Cullen & Lewis 1988, Yamazaki & Kamykowski 1991, Prézelin et al. 1991), or with variation of *in vivo* fluoresence (Therriault et al. 1990) but this is the first example of a pigment marker for such a relationship.

The use of pigments as indicators of water movements needs indeed to be cautious, since different factors, as the physiological state of cells, or environmental stresses, can cause errors. In our case, high values of (Dd+Dt)/chl *a* (Fig. 4) or Dt/(Dd+Dt) (Fig. 10b) were found at some coastal stations. In the first case, these values of Dt and Dd disrupt the relationship between Dd/chl *a* and Dt/chl *a* found at any other station (Fig. 4b). The high concentrations of degradation products (0.16 and 2.20 $mg\ m^{-3}$ of chlorophyllid *a* and phaeophytin *a*, respectively) indicate a situation of senescence of the phytoplankton community of these stations, in agreement with culture experiments (Klein 1988) showing an increase of xanthophyll concentrations (especially diatoxanthin) following senescence of the cells. These stations present other parameters which distinguish them from the typical coastal ones (Brylinski et al. 1984).

Hydrological or nutritional stresses can enhance the effects of high irradiances (for a review see Ferris & Christian 1991) and therefore speed up the conversion of diadinoxanthin into diatoxanthin (the reaction can take up to a few seconds; Welshmeyer & Hoepffner 1986). The hypothesis of an influence of environmental parameters (especially the temperature) on the xanthophyll cycle has been already proposed (Olaizola et al. 1992).

The Dd amount can be used as a marker of the transfer of cells across 2 water masses with different characteristics, as seen in May 1992 (Fig. 5a) when a peak of the Dt/(Dd+Dt) ratio was found to correspond with the external area of a thermic front (Fig. 5b), where a situation of physiological stress, due to the transfer of cells from coastal to offshore waters, has been already demonstrated (Brunet et al. 1992).

In March 1990, no Dd was detected at some stations between 2.4 and 3.9 miles from the coast (Fig. 7), in correspondence with the area of oscillations of the front in spring tide (Brylinski & Lagadeuc 1990), i.e. of an area of high hydrological stress.

The use of pigment ratios as markers is also influenced by seasonal or daily variations. From our data, it is clear that the ratios increase with the light intensities on a seasonal scale (Fig. 9). Olaizola et al. (1992) found no such a relationship, but their study was realized on a short temporal scale and in the presence of a weak gradient of irradiances. It has been demonstrated that light plays a role on the species succession (Levasseur et al. 1984, Rijstenbil 1987) but in our study area the photoadaptation process seems to be independent of the seasonal phytoplanktonic succession probably since the major part of the phytoplankton community is composed of 2 groups of algae: diatoms and prymnesiophytes (with *Phaeocystis* sp. dominating the spring bloom; Grossel & Hitier 1991). A high pigment similitude exists between these 2 groups (Stauber & Jeffrey 1988), with diatoxanthin and diadinoxanthin as major pigments (Liaaen-Jensen 1978).

The existence of a circadian rhythm in the intracellular production of xanthophylls is clearly indicated by the decrease in diatoxanthin at night (Fig. 10), with no equivalent increase of diadinoxanthin. This agrees with observations concerning the turnover of xanthophylls in a marine diatom by Goericke & Welschmeyer (1992) who suggest a synthesis of fucoxanthin from the diadinoxanthin pool. This diel cycle of de-epoxydation adds to the endogenous rhythms of chlorophyll synthesis and photosynthetic activity already shown by several authors (Sournia 1974, Legendre et al. 1988).

In May 1992 the diatoxanthin pool was consumed in ca 3.5 h (Fig. 10a), but we cannot infer a general duration, since the velocity of the reaction involved in the transformation of diatoxanthin in diadinoxanthin is dependent on the phytoplankton species and the light regime and intensity. In March of the same year it seemed that the epoxidation rate was faster (ca 1 h; Fig. 10b).

Our levels of Dt/(Dd+Dt) ranged between 0 and 1, and are higher than those previously reported. However, Demers et al. (1991) and Caron et al. (1992) report values of 60% for the Dt and Willemoës & Monas (1990) of 80%. These studies were realized on cultures under controlled conditions. Our results, obtained from the natural environment, evidently reflect different conditions, and are also influenced by seasonal and yearly variations. The inter-annual variability of the phytoplanktonic community (Reid et al. 1990) and the influence of seasons on the total pigment pool (Buma et al. 1990) are known. In addition, our lowest value of Dt (Dt = 0), agrees with results on cultures adapted to low irradiances (Demers et al. 1991, Caron et al. 1992).

Acknowledgements. The authors thank D. Hilde for his assistance during the cruises, N. Degros for his help for pigment analysis, D. Menu for iconography, and the sailors of Sepia II and Pluteus II. The authors are grateful to R. Casotti for a critical revision of this manuscript and the 3 anonymous referees for their remarks.

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This article was submitted to the editor

Manuscript first received: February 16, 1993
Revised version accepted: July 15, 1993