

## SHORT NOTE

## Water Column Stability and Photosynthetic Capacity of Estuarine Phytoplankton: Long-Term Relationships\*

Serge Demers\*\* and Louis Legendre

GIROQ, Département de biologie, Université Laval, Québec, Canada G1K 7P4

**ABSTRACT:** In estuaries, the intensity of vertical mixing due to tides varies over a broad range of time scales. In the St. Lawrence Estuary, Canada, increased stability of the water column has 2 effects on the phytoplankton: (1) a physiological effect in the form of a light-dependent increase in the photosynthetic capacity; (2) a population response in the form of an increase in chlorophyll *a* variability.

Phytoplankton cells must be able to adjust their metabolic activities to highly fluctuating environmental conditions. Previous experimental studies demonstrate that they can adjust rapidly to changing light intensities through variations in chlorophyll content, thus allowing utilization of available light with maximum efficiency (Owens et al., 1978; Riper et al., 1979; Falkowski, 1980; Harris, 1980). If physiological adjustment by the phytoplankton is faster than changes in environmental conditions, the cells continuously adjust their metabolic activities to the new conditions (Vincent, 1980); if not, the cells can only adjust to mean environmental conditions (Savidge, 1979; Falkowski, 1980). An example of such a physiological adjustment is that of the photosynthetic capacity of phytoplankton which should respond to fluctuating environmental conditions, since it is influenced by light conditions to which the cells were previously exposed (Prézelin et al., 1977; Prézelin and Sweeney, 1977, 1978).

In estuaries, the intensity of vertical mixing due to the tides varies over a broad range of frequencies: monthly ( $M_m$ ), fortnightly ( $M_f$ ) and semidiurnal ( $M_2$ ) tidal harmonics, and slack waters. Vertical mixing not only affects nutrient and oxygen redistribution in the

water column (Webb and D'Elia, 1980), but also the distribution of plankton organisms in the mixed layer. Since tidally-induced vertical mixing is highly prevalent in estuaries, they provide a unique experimental opportunity to study the effects of vertical mixing on phytoplankton. In the St. Lawrence Estuary, Québec, a research program (ECOVARIATE) was conducted on estuarine variability between 1975 and 1977. Results on phytoplankton were published by Fortier et al. (1978), Fréchette and Legendre (1978), Demers et al. (1979), Demers and Legendre (1979), Fortier and Legendre (1979), Lafleur et al. (1979), Roy and Legendre (1980), Demers and Legendre (1981), and Fréchette and Legendre (in press).

In the present study, the influence of varying degrees of vertical mixing on estuarine phytoplankton is examined, both at individual (physiological) and population (distributional) levels, over a 2-month period.

During summer 1975, sampling was conducted at an anchor station (1 m depth) in the Middle St. Lawrence Estuary (the portion between the Saguenay Fjord and Québec City). This station was occupied during 14 to 18 June, 5 to 12 July, and 1 to 8 August. Hourly measurements were made of chlorophyll *a* concentration per volume ( $B$ ), photosynthetic capacity (under saturating light intensity of  $375 \mu\text{Ein m}^{-2} \text{s}^{-1}$ , in an Hawaiian-type incubator: Doty and Oguri, 1959) normalized for chlorophyll *a* ( $P_{\text{max}}^B$ ), and the vertical density structure of the water column. For more information about the Methods, see Demers and Legendre (1979, 1981). The difference between the densities at 5 m and 35 m depths ( $\Delta\sigma_t$ ) was used as an index of the vertical stability, in order to include the whole mixed layer. Under conditions of intense vertical mixing (spring tides), Demers and Legendre (1979) have found circadian variations in the photosynthetic capacity of

\* Contribution to the program of GIROQ (Groupe interuniversitaire de recherches océanographiques du Québec)

\*\* Centre Champlain des Sciences de la mer, Sciences et levés océaniques, C.P. 15 500, 901 Cap Diamant, Québec, Canada G1K 7Y7

St. Lawrence Estuary phytoplankton. The intense vertical mixing causes all the cells in the mixed layer to experience similar average light conditions (Demers and Legendre, 1981). In order to eliminate these 24-h variations from the long-term trend studied here, the photosynthetic capacity was integrated over periods of 24 h. In addition, mean values of  $\Delta\sigma_t$  over 24 h were also computed.

A linear increase of daily photosynthetic capacity was found with increasing mean daily density gradient (Fig. 1A). This linear relationship is independent of the sampling dates, since the various conditions of stability were encountered at different times during the 2-month sampling period. There is an apparent linear relationship of both chlorophyll a concentrations and photosynthetic capacity with the density gradient (Table 1). However, when partial correlations are com-

Table 1. Coefficients of linear correlation (upper right,  $v = 13$ ) and of partial correlation (lower left,  $v = 12$ ) between daily photosynthetic capacity, daily mean chlorophyll a concentrations, and daily mean density gradient (index of vertical stability of the water column)

|                  | $P_{max}^B$ | Chl a   | $\Delta\sigma_t$ |
|------------------|-------------|---------|------------------|
| $P_{max}^B$      |             | 0.684** | 0.789**          |
| Chl a            | 0.213       |         | 0.759**          |
| $\Delta\sigma_t$ | 0.568*      | 0.489   |                  |

\*  $0.01 < P \leq 0.05$ ; \*\*  $P \leq 0.01$

puted, only the photosynthetic capacity and the density gradient remain significantly correlated.

Growth rates of phytoplankton are controlled by light intensity, temperature, and nutrient concentrations in the euphotic zone. In the St. Lawrence Estuary, nutrients are seldom limiting (Sinclair, 1977; Fortier and Legendre, 1979), especially in the Middle Estuary where the vertical mixing is high (d'Anglejan and Smith, 1973). On the other hand, seasonal temperature variations are known to influence the photosynthetic capacity of phytoplankton, particularly in lakes (Jones, 1977, 1978) and in shallow coastal estuaries (Eppley, 1972). In the St. Lawrence Estuary, the partial correlation between temperature and  $P_{max}^B$ , when controlling for the density gradient, is not significantly different from zero ( $r = 0.188$ ) while that between  $P_{max}^B$  and  $\Delta\sigma_t$ , when controlling for temperature, remains different from zero ( $r = 0.515$ ): the range of observed temperatures (7–11 °C) is too small to account for the large variations observed in the photosynthetic capacity. Similarly, Sinclair (1977) finds no relationship between surface temperature and  $P_{max}^B$  in the Lower Estuary.

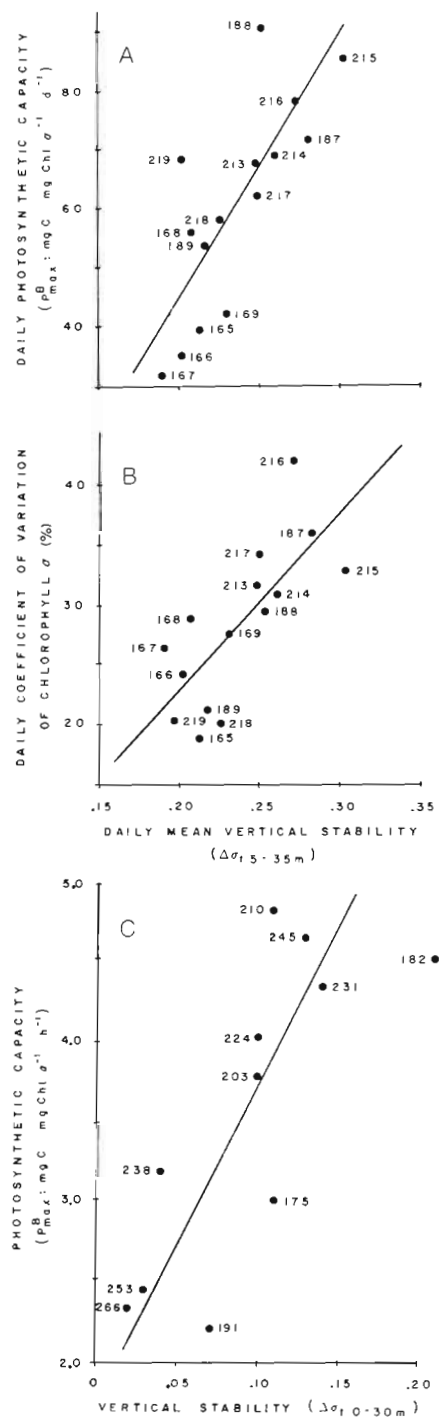


Fig. 1 (A) Daily photosynthetic capacity and (B) daily coefficient of variation of chlorophyll a as a function of daily mean vertical stability of the water column (density gradient), in the Middle St. Lawrence Estuary. (C) Photosynthetic capacity as a function of water column stability, in the Lower Estuary:  $P_{max}^B$  read on saturation curves from Sinclair (1978: Fig. 12) at  $15 \text{ cal cm}^{-2} \text{ h}^{-1}$  ( $175 \text{ W m}^{-2}$ ), and  $\Delta\sigma_t$  from Fig. 6 of the same. Sampling dates indicated as Julian days

Under well-mixed conditions, the phytoplankton may be carried under the euphotic zone, so that light becomes the limiting factor. This is the case in the Middle St. Lawrence Estuary, where the average extinction coefficient  $k = 1.7 \text{ m}^{-1}$  (Cardinal and Bérard-Therriault, 1976). Thus, the mixed layer is always deeper than the euphotic zone. Due to the short residence time of the phytoplankton cells at any given depth, their photosynthetic capacity cannot become adjusted to any one light intensity; rather it adjusts to the mean light intensity in the mixed layer (Savidge, 1979; Falkowski, 1980). Since the mean light intensity is determined by the degree of vertical mixing in the mixed surface layer, increased vertical mixing will result in a lower  $P_{\text{max}}^{\beta}$ . The linear relationship observed between  $P_{\text{max}}^{\beta}$  and  $\Delta\sigma_t$  (Fig. 1A) is therefore a unique example of long-term physiological adjustment of phytoplankton photosynthetic capacity to varying environmental light intensity. A similar relationship ( $r = 0.769$ ) was found between  $P_{\text{max}}^{\beta}$  and  $\Delta\sigma_t$  (0–30 m), observed weekly in the Lower St. Lawrence Estuary in the summer of 1974 (Fig. 1C). However, these data are not strictly comparable to those from the Middle Estuary, since there is only one  $P_{\text{max}}^{\beta}$  available for each sampling day. Nevertheless, they corroborate the relationship between photosynthetic capacity and the density gradient seen in Fig. 1A.

Our data show that the only partial correlation coefficient which significantly differs from zero is that of the relationship between the photosynthetic capacity of phytoplankton and the density gradient of the water column (Table 1). Using path analysis, 2 causal models (De Neufville and Stafford, 1971: 257–284) can account for the computed correlations between the 3 observed variables ( $P_{\text{max}}^{\beta}$ , chlorophyll *a* and  $\Delta\sigma_t$ ). For both models, the density gradient must be in the middle of the 3 variables. In the first model, chlorophyll *a* concentrations and photosynthetic capacity are both influenced independently by the density gradient. In the second model, the density gradient, partially influenced by chlorophyll *a* concentrations, affects  $P_{\text{max}}^{\beta}$ . Obviously, only the first causal model is appropriate so that there is no direct relationship between chlorophyll *a* concentrations and photosynthetic capacity (normalized for chlorophyll *a*),  $P_{\text{max}}^{\beta}$  being directly influenced by the density gradient.

Furthermore, the daily coefficients of variation of chlorophyll *a* concentrations show a significant linear increase ( $r = 0.776$ ) with increasing vertical stability (density gradient) (Fig. 1B). This result supports the hypothesis of Harris (1980) that 'the stratified period, with all possibilities of ephemeral thermal structure and internal motions, has more spatial and temporal variability than periods of continuous mixing and turnover'. Increased vertical mixing leads to a more

Table 2. Coefficients of variation of chlorophyll *a* and cell numbers (hourly sampling), from 5 to 12 July 1975. (Data from Demers et al., 1979)

|             | Neap tides<br>(5 to 8 July) | Spring tides<br>(9 to 12 July) |
|-------------|-----------------------------|--------------------------------|
| Chlorophyll | 16.0 %                      | 11.7 %                         |
| Cell counts | 53.1 %                      | 37.7 %                         |

homogeneous distribution of static properties such as phytoplankton biomass (chlorophyll and cell numbers), as observed from 5 to 12 July, between neap and spring tides (Table 2). The partial correlation between  $P_{\text{max}}^{\beta}$  and the coefficient of variation of the chlorophyll, when controlling for the vertical stability, is not significantly different from zero ( $r = 0.132$ ) whereas that between  $P_{\text{max}}^{\beta}$  and  $\Delta\sigma_t$ , when controlling for the coefficient of variation of chlorophyll, is significantly different from zero ( $r = 0.674$ ). Therefore,  $P_{\text{max}}^{\beta}$  and the coefficient of variation of chlorophyll are not linearly related.

In conclusion, over a 2-month period, changes in the vertical stability of the water column are reflected in both the photosynthetic capacity and the variance of the chlorophyll *a* concentration. In the St. Lawrence Estuary, there is a direct relationship between photosynthetic capacity and the mean light intensity in the mixed layer as affected by the vertical stability of the water column (Fig. 1A, C). The strength of this relationship results from the fact that, in the Middle Estuary, the photic layer is always shallower than the mixed layer. Also, over a long period the variance, rather than the daily concentration of the chlorophyll, is directly related to the vertical stability (Fig. 1B). Therefore, there is a direct long-term relationship between vertical stability and the response of the phytoplankton: (1) a physiological effect, a light dependent increase in the photosynthetic capacity, and (2) a population response, an increase in the variance of the chlorophyll concentrations.

#### LITERATURE CITED

- Cardinal, A., Bérard-Therriault, L. (1976). Le phytoplancton de l'estuaire moyen du Saint-Laurent en amont de l'Île-aux-Coudres (Québec). *Int. Revue ges. Hydrobiol.* 61: 639–648
- d'Anglejan, B. F., Smith, E. C. (1973). Distribution, transport and composition of suspended matter in the St. Lawrence Estuary. *Can. J. Earth Sci.* 10: 1380–1396
- Demers, S., Lafleur, P. E., Legendre, L., Trump, C. L. (1979). Short-term covariability of chlorophyll and temperature in the St. Lawrence Estuary. *J. Fish. Res. Bd Can.* 36: 568–573
- Demers, S., Legendre, L. (1979). Effets des marées sur la variation circadienne de la capacité photosynthétique du phytoplancton de l'estuaire du Saint-Laurent. *J. exp. mar. Biol. Ecol.* 39: 87–99

- Demers, S., Legendre, L. (1981). Mélange vertical et capacité photosynthétique du phytoplancton estuarien (estuaire du Saint-Laurent). *Mar. Biol.* 64: 243–250
- De Neufville, R., Stafford, J. H. (1971). *Systems analysis for engineers and managers*, McGraw-Hill, New York
- Doty, M. S., Oguri, M. (1959). The carbon-fourteen technique for determining primary plankton productivity. *Pubbl. Staz. zool. Napoli* 31: 70–74
- Eppley, R. W. (1972). Temperature and phytoplankton growth in the sea. *Fish. Bull., U.S.* 70: 1063–1085
- Falkowski, P. G. (1980). Light and shade adaptation in marine phytoplankton. In: Falkowski, P. G. (ed.) *Primary productivity in the sea*. Plenum Press, New York, pp. 99–119
- Fortier, L., Legendre, L. (1979). Le contrôle de la variabilité à court terme du phytoplancton estuarien: stabilité verticale et profondeur critique. *J. Fish. Res. Bd Can.* 36: 1325–1335
- Fortier, L., Legendre, L., Cardinal, A., Trump, C. L. (1978). Variabilité à court terme du phytoplancton de l'estuaire du Saint-Laurent. *Mar. Biol.* 46: 349–354
- Fréchette, M., Legendre, L. (1978). Photosynthèse phytoplanctonique: réponse à un stimulus simple, imitant les variations rapides de la lumière engendrées par les vagues. *J. exp. mar. Biol. Ecol.* 32: 15–25
- Fréchette, M., Legendre, L. (in press). Phytoplankton photosynthetic response to light in an internal tide dominated environment. *Estuaries*
- Harris, G. P. (1980). Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, models, and management. *Can. J. Fish. aquat. Sci.* 37: 877–900
- Jones, R. I. (1977). Factors controlling phytoplankton production and succession in a highly eutrophic lake (Kinnego Bay, Lough Neagh). III. Interspecific competition in relation to irradiance and temperature. *J. Ecol.* 65: 579–586
- Jones, R. I. (1978). Adaptations to fluctuating irradiance by natural phytoplankton communities. *Limnol. Oceanogr.* 23: 920–926
- Lafleur, P. E., Legendre, L., Cardinal, A. (1979). Dynamique d'une population estuarienne de Diatomées planctoniques: effet de l'alternance des marées de morte-eau et de vive-eau. *Oceanol. Acta* 2: 307–315
- Owens, T. G., Riper, D. M., Falkowski, P. G. (1978). Studies of delta-aminolevulinic acid dehydrase from *Skeletonema costatum*, a marine plankton diatom. *Plant Physiol.* 62: 516–521
- Prézelin, B. B., Meeson, B. W., Sweeney, B. M. (1977). Characterization of photosynthetic rhythms in marine dinoflagellates. I. Pigmentation, photosynthetic capacity and respiration. *Plant Physiol.* 60: 384–387
- Prézelin, B. B., Sweeney, B. M. (1977). Characterization of photosynthetic rhythms in marine dinoflagellates. II. Photosynthesis-irradiance curves and *in vivo* chlorophyll a fluorescence. *Plant Physiol.* 60: 388–392
- Prézelin, B. B., Sweeney, B. M. (1978). Photoadaptation of photosynthesis in *Gonyaulax polyedra*. *Mar. Biol.* 48: 27–35
- Riper, D. M., Owens, T. G., Falkowski, P. G. (1979). Chlorophyll turnover in *Skeletonema costatum*, a marine plankton diatom. *Plant Physiol.* 64: 49–54
- Roy, S., Legendre, L. (1980). Field studies of DCMU-enhanced fluorescence as an index of *in situ* phytoplankton photosynthetic activity. *Can. J. Fish. aquat. Sci.* 37: 1028–1031
- Savidge, G. (1979). Photosynthetic characteristics of marine phytoplankton from contrasting physical environments. *Mar. Biol.* 53: 1–12
- Sinclair, M. (1977). Phytoplankton distributions in the Lower St. Lawrence Estuary. Ph. D. thesis, University of California, San Diego
- Sinclair, M. (1978). Summer phytoplankton variability in the lower St. Lawrence estuary. *J. Fish. Res. Bd Can.* 35: 1171–1185
- Vincent, W. F. (1980). Mechanisms of rapid photosynthetic adaptation in natural phytoplankton communities. II. Changes in photochemical capacity as measured by DCMU-induced chlorophyll fluorescence. *J. Phycol.* 16: 568–577
- Webb, K. L., D'Elia, C. F. (1980). Nutrient and oxygen redistribution during a spring neap tidal cycle in a temperate estuary. *Science, N.Y.* 207: 983–985