Photoadaptation of sea-ice microalgae in springtime: photosynthesis and carboxylating enzymes*

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ABSTRACT: Photoadaptive responses of sea-ice microalgae in springtime were observed in southeastern Hudson Bay (Canadian Arctic). The responses included changes in pigment composition (chlorophyll a, carotenoids), photosynthetic parameters (Pmax, Ik, α, β) and carboxylating enzymes. The complete transition from shade to light adaptation took place over 1 generation time while susceptibility to photoinhibition decreased more rapidly. Activities of carboxylating enzymes were never the rate-limiting step of photosynthesis. At low irradiances, increased pigments in the cells and modifications of the photosynthetic parameters suggest that photosynthesis did depend on the trapping of light energy and on the rate of electron transport. With increased irradiances, light energy harvested by the cells exceeded their energetic requirements, so that photosynthesis was only related to the rate of electron transport. These results emphasize the ability of sea-ice microalgae to photoadapt to the seasonally increasing under-ice irradiance, showing that they are not an obligate shade flora in southeastern Hudson Bay.

INTRODUCTION

The successful development of microalgae in polar waters, under conditions of very low light and temperature, has been the subject of several studies in the past few decades (e.g. Appolonio 1961, 1965, Bunt 1968, Neori & Holm-Hansen 1982, Jacques 1983, Cota 1985, Palmisano et al. 1987).

Light has been identified as a critical factor for the growth of ice algae (Meguro et al. 1967, Bunt & Lee 1970, Horner & Schrader 1982). The investigations of Cota (1985) in the High Arctic and of Palmisano et al. (1985) in the Antarctic have suggested that ice algae are markedly shade-adapted. On the other hand, Gosselin et al. (1985), Rochet et al. (1986) and Barlow et al. (1988) found that ice algae in Hudson Bay were not an obligate shade flora, and that they adapted to the seasonally increasing irradiance. In Hudson Bay, Gosselin et al. (1985) have reported a critical value of 7.6 μEin m^{-2}s^{-1} below which there was no population

growth. At higher light intensities (up to 9.0 μEin m^{-2}s^{-1}) ice algae seem to photoadapt by improving the trapping of light energy and simultaneously increasing the density of reaction centers of photosystem I (RCI) and that of plastoquinones; above 9.0 μEin m^{-2}s^{-1} the density of reaction centers and plastoquinones is reduced but electron transport through RCI becomes faster (Barlow et al. 1988).

In addition to modifications in the photosynthetic apparatus itself (size and number of photosynthetic units, electron transport components), the photoadaptive strategies of algae could also involve changes in activities of photosynthetic enzymes (Steemann Nielsen & Hansen 1959, Beardall & Morris 1976, Falkowski & Owens 1980). For higher plants, Berry & Björkman (1980) and Berry & Raison (1981) have shown that photosynthesis depends on electron transport capacity when temperature conditions are optimal; at suboptimal temperatures, photosynthesis is likely to be limited by enzyme reactions. Considering the very low temperatures prevaling in polar waters, carboxylating reactions can be expected to limit photosynthesis.

This paper describes the succession of photoadaptive events experienced by microalgae at the ice-water interface during the springtime in southeastern Hud-

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son Bay. Observations concern changes in carboxylating enzymes and photosynthetic parameters, which allows assessment of the relative importance of enzyme reactions versus electron transport in limiting the photosynthetic capacity of these algae. Moreover, since activities of 3 carboxylating enzymes (RuBPC, PePC and PePCk) were measured, the contribution of β-carboxylation relative to C_3-carboxylation can be estimated for a natural population of ice microalgae.

MATERIALS AND METHODS

Sampling was conducted from 3 April to 15 May 1986, on the first-year ice of Hudson Bay (55° 30.1' N, 77° 44.9' W) 22 km off Kuujjuarapik (Fig. 1). Every second day, free-floating ice algae at the ice-water interface were collected by SCUBA divers using a 2 l syringe sampler. These were rapidly brought to a shore laboratory in Kuujjuarapik for further analyses. The samples did not contain ice. Under-ice irradiance at the interface was measured with a scalar irradiance meter moored at the ice-water interface (Biospherical MER 1010), and temperature and salinity were recorded with a guildline CTD probe.

Microalgae were filtered on 2.5 cm Whatman GF/F glass-fiber filters, for the spectrophotometric determination of chlorophyll a and carotenoid pigments after 24 h extraction in 90 % acetone at 5 °C, using the equations of Jeffrey & Humphrey (1975). Cell identification and enumeration were done with an inverted micro-

Fig. 1. Location of the sampling station off Kuujjuarapik in Southeastern Hudson Bay

scope (Lund et al. 1958) on samples preserved in acidic Lugol.

Beginning on 9 April, photosynthesis was measured on 25 1-ml aliquots, each one inoculated with 1 µCi $NaH^{14}CO_3$ and incubated for 20 min under different irradiances, as described by Lewis & Smith (1983). Incubations were performed at −1.5 °C and under blue-green light, in order to simulate the under-ice light conditions (Maykut & Grenfell 1975). Incubations were conducted at the same temperature throughout the season, as temperature at the ice-water interface remained very constant (x = −1.3 °C, s = 0.18), except for the last 2 d of biological sampling (Fig. 2). At the end of incubations, 0.5 ml 6N HCl was added to each sample and excess ^{14}C was evaporated during 40 min. After evaporation, 12 ml of an Aquasol-methanol mixture (10 : 1 vol : vol) were added to the samples, which had been neutralised with 0.5 ml 6N NaOH. Samples, stored in the dark, were counted on a LKB WALLACK scintillation spectrometer (Mini Beta Model 1211), using the channels radio method. Parameters of the photosynthesis versus irradiance curves were estimated according to the model of Platt et al. (1980). These are the maximum photosynthetic rate (Pmax), the slope of the initial portion of the curve (α), the slope of the inhibited portion of the curve (β), and Ik = Pmax/α, the photoadaptive index described by Talling (1957). For each curve, the initial activity of the ^{14}C solution was estimated, and there were 2 controls treated with DCMU (Legendre et al. 1983) which is known to block electron transport near photosystem II.

Activities of RuBPC, PePC and PePCk were determined using the ^{14}C technique described by Smith et al. (1983) and modified by Li et al. (1984). Similar enzyme assays have been carried out in other laboratories (e.g. Storrø & McFadden 1983). For each sample, 5 aliquots of seawater, including 2 blanks, were filtered on 2.5 cm Whatman GF/F filters. Volumes filtered varied during the sampling season, according to the concentration of algae at the ice-water interface. In early April, 100 ml of sea water were filtered, while in May when chlorophyll a concentrations were maximum, only 20 ml were filtered. The filters were rinsed with a solution made of Tris buffer (0.1 M, pH 7.5), $MgCl_2 \cdot 6H_2O$ (20 mM), EDTA (0.78 mM), reduced glutathione (10 mM), dithiothreitiol (DTT) (5 mM), $NaHCO_3$ (25 mM) and α-lysophosphatidylcholin (0.2 mg l^{-1}) (Miller et al. 1978, 1979). In PePCk assays, $MgCl_2 \cdot 6H_2O$ was replaced by $MnCl_2 \cdot 4H_2O$ (2 mM), and ADP (5 mM) was added to the solution. Each filter, placed in 1 ml of this solution made to 1.5 M with glycerol (Syrett 1973), was preincubated at 0 °C during 40 min. At the end of the preincubation, the filters received 100 µl of the rinse solution to which were added 2 mg of RuBP (Na_4 salt, Sigma) for the RuBPC
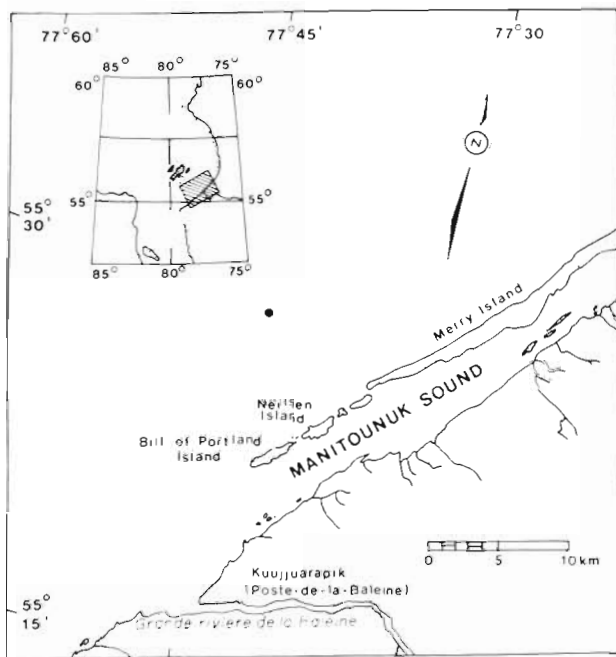
assays, and 5 mg of PeP (Na_3 salt, Sigma) for the PePC and PePCk assays. Blanks received the rinse solution without reagents. After 3 additional minutes of preincubation, the samples were inoculated with $NaH^{14}CO_3$ (100 μl, 5 μCi) and incubated at 20 °C for 40 min. This temperature is adequate for enzyme activities according to the results of Li et al. (1984) for 3 carboxylating enzymes in Arctic phytoplankton, and Descoslas-Gros & De Billy (1987) and Smith & Platt (1985) for RuBPC in respectively cultures of Antarctic diatoms and Arctic phytoplankton. The reaction was stopped by the addition of 0.5 ml 6N HCl. Evaporation, neutralisation with 6N NaOH, and counting of samples were the same as for photosynthesis.

Physiological parameters were normalized to unit chlorophyll a and to cellular volume. Total cellular volumes were estimated using average cell volumes, measured for the most abundant species, together with the numbers of enumerated cells (Smayda 1978). Normalizing physiological parameters to unit cellular volume is the logical approach for natural populations, even if it is relatively time consuming. With laboratory cultures, physiological parameters can be normalized to unit cell, but this is not possible with natural populations in which cell sizes are distributed over wide ranges. In this paper, parameters normalized to cellular volume and to chlorophyll a are respectively identified by v or b, as for example P^vmax and P^bmax.

In order to facilitate visual interpretation of data, moving averages were drawn on figures showing time series. However, results reported below were computed on the original data, not the moving averages.

RESULTS

Average irradiance under the ice was 4.0 μEin $m^{-2} s^{-1}$ (s = 1.0) before 25 April, after which it rapidly increased to an average of 17.9 μEin $m^{-2} s^{-1}$ (s = 7.3) (Fig. 2A). Temperature and salinity at 0.5 m under the ice were quite stable until 12 May (T = −1.3 °C, S = 27), after which there was a slight increase in temperature (to 0 °C) and an important decrease in salinity (to 7) (Fig. 2B, C). Under-ice irradiance was related to the thickness of the snow cover; the rapid increase of under-ice irradiance after 25 April corresponded to snow melt and the decrease that occurred from 1 to 7 May was associated with a snowfall (Fig. 2A, D). Changes in water salinity and temperature after 12 May were associated with ice melt (Fig. 2B, C, E).

During the sampling period, chlorophyll a concentration of ice-algae collected at the ice-water interface (Fig. 3A) increased from 0.8 mg m^{-2} to a maximum of 23.6 mg m^{-2}; at the time of ice melt (15 May), cells were
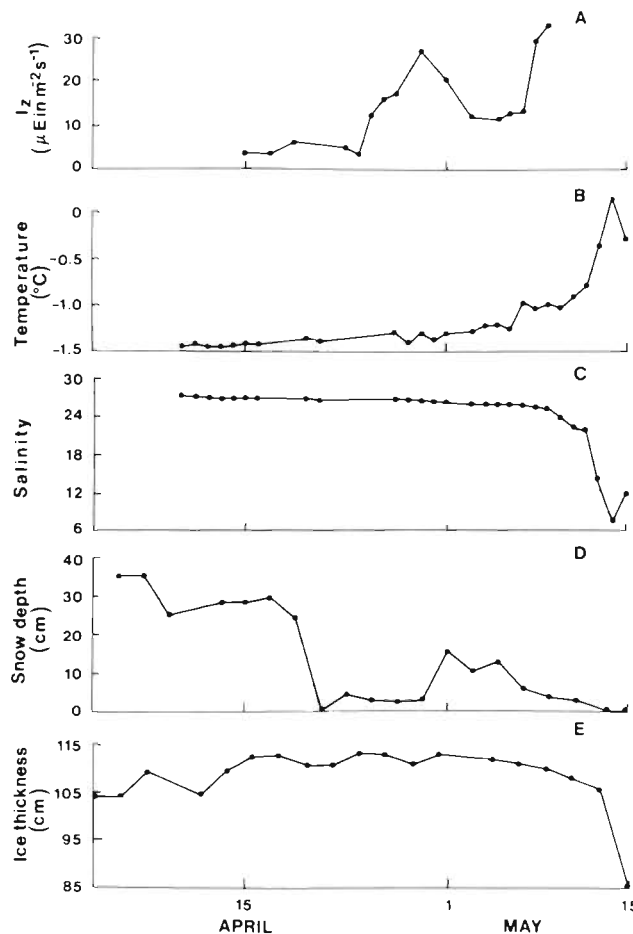

Fig. 2. Seasonal variations of (A) under-ice irradiance, (B) water temperature, (C) salinity, (D) snow depth, and (E) ice thickness

flushed from the interface, and chlorophyll a dropped to 0.6 mg m^{-2}. Cell numbers varied in correlation with chlorophyll a (r = 0.94, p < 0.01), reaching a maximum value of 5.8×10^9 cells m^{-2} on 12 May (Fig. 3B). Changes in total cellular volume (Fig. 3C) followed the seasonal trend already noted for chlorophyll a and cell numbers (Fig. 3A, B). The ice-algal community was numerically dominated by Nitzschia frigida (41 %), followed by Navicula pelagica (14 %), 2 unidentified species of Nitzschia (14 %), flagellates (14 %) and Chaetoceros spp. (5.1 %) (Fig. 4). Fig. 5A shows the seasonal decrease of chlorophyll a normalized to unit cellular volume. Carotenoids followed a similar trend as chlorophyll a (Fig. 5B), but the ratio carotenoids: chlorophyll a increased slowly from around 21 April (Fig. 5C).

Fig. 6 shows the variations of photosynthetic parameters Pmax, α, β, and Ik. P^bmax increased rapidly after the beginning of May (Fig. 6A), this increase being correlated with a 4 d lag to the under-ice irradiance Iz (r = 0.80, p < 0.01). The same lag-correlation was found
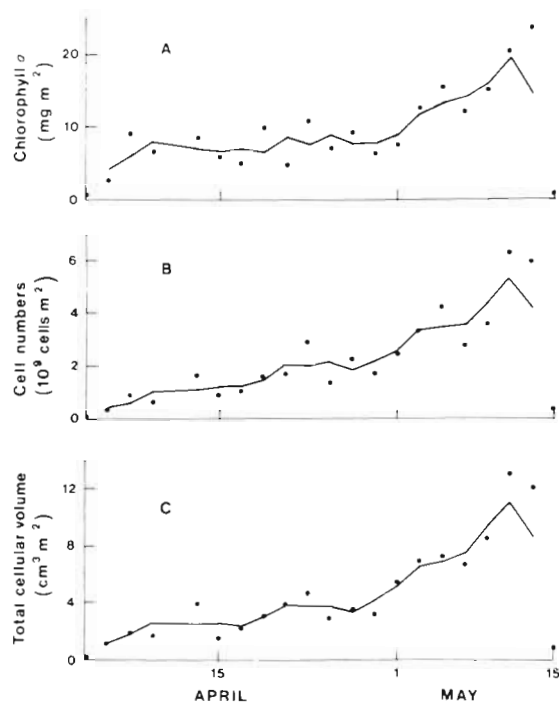
Fig. 3. Seasonal variations of (A) chlorophyll a, (B) cell numbers, and (C) total cellular volume. Observed data and moving average ($n = 3$)

Fig. 5. Seasonal variations of (A) intracellular chlorophyll a, (B) intracellular carotenoids, and (C) carotenoids:chlorophyll a ratio. Observed data and moving average ($n = 3$)
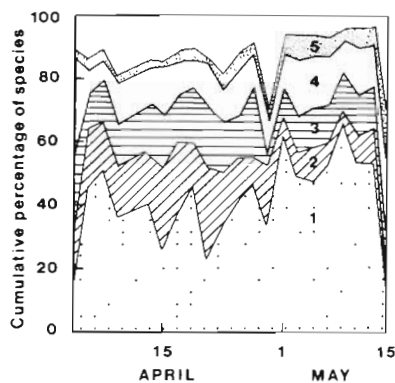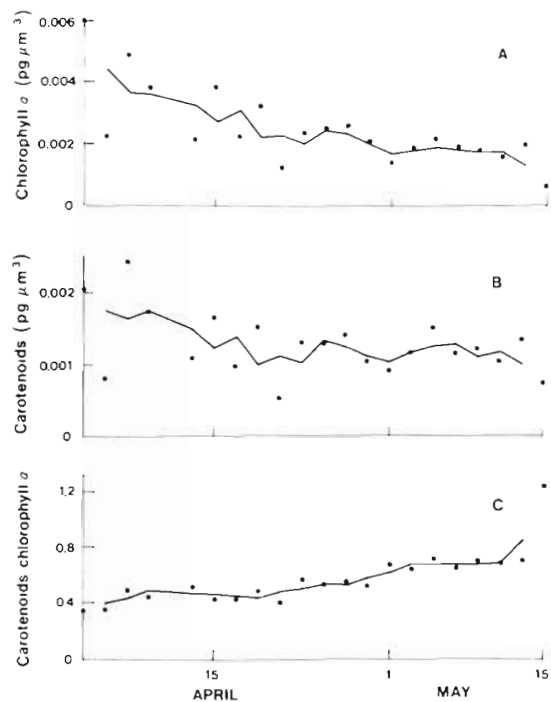

Fig. 4. Species composition of the sea-ice microalgal community at the ice-water interface: (1) *Nitzschia frigida*, (2) *Nitzschia* spp., (3) *Navicula pelagica*, (4) flagellates, and (5) *Chaetoceros* spp.

between Iz and P^vmax, even if this last parameter decreased at the beginning of the season (Fig. 6B) (r = 0.80, $p < 0.01$). Photosynthetic efficiency, α^b and α^v, had no seasonal trend, and did not respond to the rapid change in under-ice irradiance that occured on 25 April (Fig. 6C, D). The photoadaptive index (Ik) had clearly 2 different levels. Before 27 April it averaged 13.4 µEin $m^{-2} s^{-1}$ (s = 6.5), after which it increased to 29.5 µEin $m^{-2} s^{-1}$ (s = 17.7) (Fig. 6E); difference between the 2 means was significant (t-test, $p < 0.05$). As in the cases

of P^bmax and P^vmax, there was a 4 d lag between the changes in Ik and in the under-ice irradiance (r = 0.86, $p < 0.01$). Finally, the photoinhibition parameter (β^b) dropped drastically on 25 April (Fig. 6F); β^v (not shown) was almost the same as β^b. Changes in photosynthetic parameters and enzyme activities normalized to cellular volume were not significantly correlated to changes of in situ temperature.

The activity of $RuBPC^b$ increased seasonally (Fig. 7A) while the activities of $PePC^b$, $PePC^v$ and $PePCk^b$ (Fig. 7B, C, E) did not show any definite seasonal trends. There were increased activities of $PePC^b$ and $PePC^v$ at the beginning and the end of the sampling season. On a volume basis, RuBPC activity had no seasonal trend but PePCk showed a slight decrease (Fig. 7B, F). Pmax was only correlated with RuBPC (r = 0.86, $p < 0.01$) and PePCk (r = 0.78, $p < 0.01$). Finally, the seasonal increase of the ratio Pmax:Σcarboxylating enzymes indicated a growing divergence between enzyme activities and the maximum photosynthetic rate (Fig. 8).

DISCUSSION

Light and shade adaptation

It has been shown (Falkowski 1980, 1981, Côté & Platt 1984) that photoadaptation in phytoplankton is best characterized by the parameters of the photosyn-
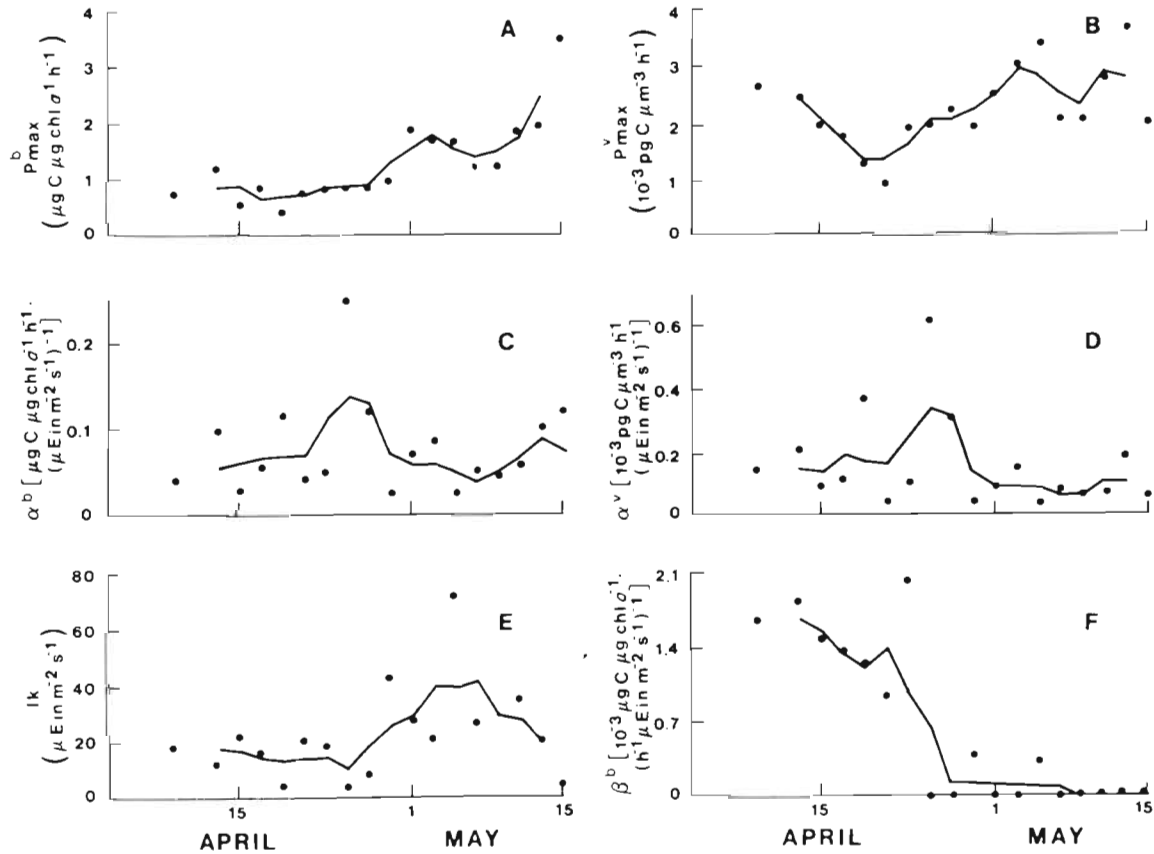
Fig. 6. Seasonal variations of the photosynthetic parameters. Maximum photosynthetic rate normalized (A) to chlorophyll a, and (B) to cellular volume; photosynthetic efficiency normalized (C) to chlorophyll a, and (D) to cellular volume; (E) photoadaptive index Ik, and (F) photoinhibition parameter normalized to chlorophyll a. Observed data and moving average ($n = 3$)

thesis versus irradiance curves, and especially the maximum rate of photosynthesis Pmax.

The rapid increase of under-ice irradiance on 25 April (Fig. 2A) clearly divided the growth season of ice algae in 2 distinct periods. Before 25 April, irradiance was very low (<7 µEin m^{-2}s^{-1}) and microalgae were characteristically shade-adapted, with low Pmax and Ik (Fig. 6A, B, E) and high cellular chlorophyll content as well as β (Fig. 5A, 6F) (Steemann Nielsen & Hansen 1959, Yentsch & Lee 1966, Jørgensen 1969, Prézelin 1981, Falkowski & Owens 1980, Perry et al. 1981). Two sets of observations can be used to identify mechanisms involved in this shade adaptation. First, the decrease of P^{v}max observed during this period (Fig. 6B) can be related to the decrease in cellular chlorophyll (Fig. 5A), suggesting that the maximum photosynthetic rate did depend on the trapping of light energy (Falkowski & Owens 1980). Second, the fact that α^v did not follow the same trend as Pmax and cellular chlorophyll a implies that absorption of photons at low irradiance was not linked to an increased efficiency in the utilisation of light energy, thus suggesting possible limitation at the levels of either carboxylating reactions or elec-

tron transport. The seasonal increase in the ratio Pmax : Σcarboxylating enzyme activities (Fig. 8) indicates that carboxylating activity explained only part of the variations in maximum photosynthetic rate, as observed by several authors (Mukerji & Morris 1976, Senger & Fleishhacker 1978, Glover & Morris 1979). It follows that enzyme activity, at low irradiances, was not the rate-limiting step of photosynthesis. This leaves the rate of electron transport, and also the trapping of light energy, as mentioned above, as the major control mechanisms of photosynthesis before 25 April.

After 25 April, ice algae adapted to the increased irradiance. This is shown by the rapid decrease in β (Platt et al. 1980, Smith et al. 1983) and the increase 4 d later in Ik, P^{b}max and P^{v}max (Fig. 6A, B, E, F) (Steemann Nielsen & Hansen 1959, Steemann Nielsen & Park 1964, Yentsch & Lee 1966, Prézelin & Sweeney 1978, Richardson et al. 1983, Palmisano et al. 1987). The first step of the photoadaptive response was a decrease in susceptibility to photoinhibition (decrease in β, Fig. 6F), that occurred at the time of irradiance increase. This rapid response is in agreement with the results of Samuelsson & Richardson (1982), who
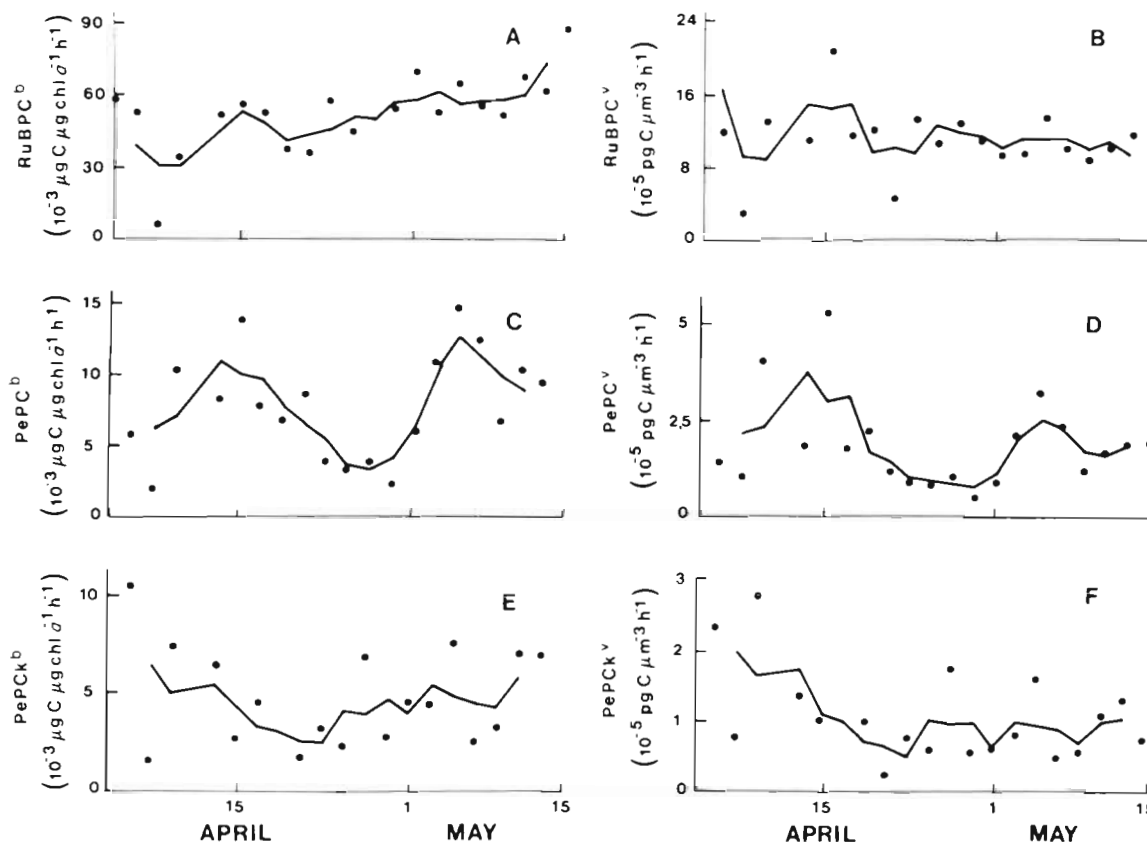
Fig. 7. Seasonal variations of enzyme activities. RuBPC normalized to (A) chlorophyll a, and (B) to cellular volume; PePC normalized (C) to chlorophyll a, and (D) to cellular volume; PePCk normalized (E) to chlorophyll a, and (F) to cellular volume. Observed data and moving average (n = 3)

showed for *Amphidinium carterae* reversible photo-inhibition within 2 h following an exposure to high irradiance. In their paper, the photoinhibitory response was a decrease of photosynthetic activity with exposure to high light; in the present study, photoinhibition is characterized by the slope β of the inhibited portion of P vs I curves. This is not the same as in Samuelsson & Richardson (1982), but changes in β lead to a similar conclusion, which is that photoinhibition appears to be controlled by fast response mechanisms. Pmax and Ik also adjusted to the new

Fig. 8. Seasonal variations of the ratio of maximum photosynthetic rate to carboxylating enzyme activities. Observed data and moving average (n = 3)

light conditions, but with a few days lag. This lag corresponds to cell division times, which varied from 2 to 23 d during the season and were about 4 d around 25 April (M. Gosselin unpubl.). Adaptation to higher irradiance took about one generation, contrary to photoinhibition response which was rapid.

After the ice algae had developed their light-adapted character (following 25 April), only $P^{v}max$ continued to increase (Fig. 6A), while the cellular chlorophyll content remained constant (Fig. 5A) thus indicating the stability of the light-larvesting component. Moreover, the increase of the carotenoids : chlorophyll a ratio (Fig. 5C) suggests that light energy absorbed by the cells exceeded their energetic requirements, since carotenoid pigments are known to provide photoprotection to chlorophyll a by storing excess energy harvested by the cells (Prézelin 1981). As the under-ice irradiance increased, photosynthesis probably became limited only by the rate of electron transport. In that context, the augmentation of $P^{b}max$ and $P^{v}max$ with increasing light intensities (Fig. 6A, B) can be explained by a shortening of electron transport times, as shown by Barlow et al. (1988) for sea-ice microalgae at a nearby station in southeastern Hudson Bay.
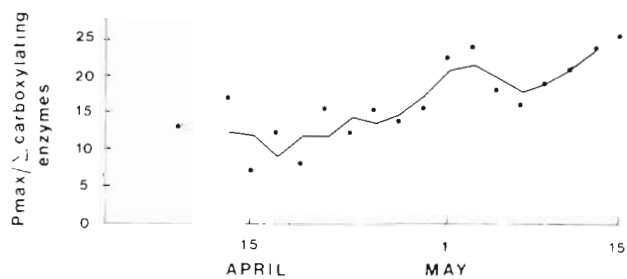
Enzyme activities

Carboxylating enzyme activities did not account for the total photosythetic capacity of ice-algae (Fig. 8). Values similar to those of Fig. 8 have been reported by Glover & Morris (1979) who observed ratios Pmax: carboxylating enzyme activities up to ca 25 for natural phytoplankton. Other studies reported a contribution of carboxylating enzymes from less than 10 % of photosynthesis (Mukerji & Morris 1976) to 15 % of the maximum photosynthetic rate (Smith et al. 1983).

In higher plants, changes in photosynthetic capacity have often been related to changes in carboxylating enzyme activities (Björkman 1968, Bowes et al. 1972, Blenkinsop & Dale 1974). Concerning marine phytoplankton, Glover & Morris (1979) reported increasing ratios of Pmax: carboxylating enzyme activities with higher Pmax. Also, Senger & Fleishhacker (1978) observed that, whereas photosynthetic capacity of *Scenedesmus obliquus* tripled in high light, activity of RuBPC only doubled. These authors suggested that such changes could be interpreted as a partial limitation of photosynthetic capacity by dark enzyme reactions. The increasing ratio Pmax: Σ carboxylating enzymes indicates that enzyme reactions explained a seasonally decreasing fraction of the maximum photosynthetic rate (Fig. 8). The high activity of RuBPC compared to PePC and PePCk clearly shows that C_3-carboxylation dominated over β-carboxylations. This corresponds to data of Smith & Platt (1985), who showed for Arctic phytoplankton that RuBPC was the only enzyme tightly linked to photosynthetic capacity. For marine phytoplankton, Appleby et al. (1980) and Descolas-Gros & Fontugne (1985) observed that RuBPC dominated over the PePC and PePCk. Descolas-Gros & Fontugne (1985) also showed that PePC and PePCk never occurred simultaneously in the same algal species, PePC being found in flagellates and PePCk in diatoms. The simultaneous activities of PePC and PePCk measured in ice algae was probably due to the species composition of the ice community, which comprised both diatoms and flagellates (Fig. 4). Also, the increased activity of PePC at the beginning and at the end of the sampling season (Fig. 7C, D) may be related to increased proportions of flagellates at these periods (Fig. 4). The fact that only RuBPC and PePCk were correlated with the maximum photosynthetic rate supports the view that PePCk, rather than PePC, is active in diatoms that dominate the ice-algal biomass.

Photoadaptive processes have been proved to be important for both Arctic and Antarctic algae (Palmisano & Sullivan 1982, Gosselin et al. 1985, Palmisano et al. 1986, 1987, Sakshaug & Holm-Hansen 1986). Our results support these findings and emphasize the view that the ability of sea-ice microalgae to photoadapt as the under-ice irradiance seasonally increases contribute to their high productivity in springtime and early summer.

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