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Photoadaptive strategies in sea-ice microalgae*

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ABSTRACT: Sea-ice microalgae photosynthesize and grow under conditions of very low in situ photon fluence rates and temperature. We sought to determine the mechanisms whereby natural sea-ice algal cells in Hudson Bay adapt to changing photon fluence rates at the ice-water interface at the end of the Arctic winter. It was found that the cells positively adapted to the seasonal increase in photon fluence rates by increasing their maximal photosynthetic rate (P_{max}) and the saturating photon fluence rate (I_m). Under low photon fluence rates (7.6 to 9.0 μEinst m^{-2} s^{-1}), photosynthesis was optimized by increasing the number of photosynthetic units, and at higher photon fluence rates, the algal cells decreased the number of units as well as the concentration of plastoquinone. An effective absorption cross section was maintained by increasing the size of photosynthetic units through a reduction in the number of reaction centres while the concentration of the light-harvesting pigments chlorophyll *a*, chlorophyll *c* and fucoxanthin remained essentially constant. Estimates of the turnover time of photosystem I reaction centres revealed that there was a faster flow of electrons through the electron transport chain in response to the increase in under-ice photon fluence rates.

INTRODUCTION

Photon fluence rate is one of the major environmental variables that influences the growth and physiology of photosynthetic organisms. Sea-ice microalgae, in particular, occupy a habitat that is characterized by very low photon fluence rates (Sullivan et al. 1982, Cota 1985) and temperature (Legendre et al. 1981, Gosselin et al. 1985), and a distinctive psychrophilic adaptation has been demonstrated for these algal cells as a response to the increasing sensitivity of photosynthesis to the ambient freezing temperature caused by the seasonally increasing photon fluence rate (Rochet et al. 1985). Previous photoadaptation studies have indicated that ice algae are extremely shade adapted and Antarctic species can be photoinhibited at photon fluence rates above 25 μEinst m^{-2} s^{-1} (Palmisano et al. 1985). In the Canadian Arctic, Cota (1985) was able to measure photosynthesis at under-ice photon fluence rates as low as 5 μEinst m^{-2} s^{-1} and concluded that photosynthesis was optimal at photon fluence rates close to the maximum ambient light but inhibited at higher fluence rates. Horner & Schrader (1982) report a critical photon fluence rate of 7.7 μEinst m^{-2} s^{-1} for Alaskan ice microalgae, while Antarctic communities appear to have a much lower critical rate of 0.3 μEinst m^{-2} s^{-1} (Palmisano & Sullivan 1983). Investigations in Hudson Bay reveal that seasonal photosynthetic activity does not commence before the photon fluence rate reaches 7.6 μEinst m^{-2} s^{-1} (Gosselin et al. 1985). As the under-ice photon fluence rate increases, there is a concomitant increase in photosynthesis (Gosselin et al. 1986) which suggests that there is a definite adaptation by the ice microflora to the seasonal change in photon fluence rates.

Sea-ice microalgae appear, therefore, to be unique in being able to adapt to the extreme conditions of light and temperature in the polar regions. However, their photoadaptive strategies have not yet been studied in detail. In the open ocean, phytoplankton adapt to variable photon fluence rates by altering their cellular content of light-harvesting pigments and/or reaction centres. When exposed to low photon fluence rates, phytoplankton usually increase their pigment concentration (Beardall & Morris 1976, Barlow & Alberte 1985) and change the organization of these pigments within their photosynthetic units (PSU) (Falkowski & Owens

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1980, Perry et al. 1981, Gallagher et al. 1984, Barlow & Alberte 1985, 1987, Gallagher & Alberte 1985). By altering PSU size, numbers of reaction centres and photosynthesis versus irradiance (P-I) characteristics, cells can maximize light energy capture and transfer so that optimal photosynthesis is maintained under a wide range of light regimes (Richardson et al. 1983). In order to further understand the response of sea-ice microalgae to light, we examined the changes in P-I relationships, PSU size, photosystem I reaction centre (P700) and plastoquinone in a natural algal community. Our objective was to determine the physiological mechanisms used by these organisms to adapt to the seasonal change in photon fluence rate.

METHODS

Sample collection. Sampling was conducted during April and May 1985 at a field station located on the first-year ice (1 m thick) 27 km off Kuujjuarapik (55° 30.1' N, 77° 44.5' W), Hudson Bay, Canadian Arctic. Using a 2.0 l syringe sampler (Slurp Gun), SCUBA divers collected the microalgae at the ice-water interface. The microalgal suspension was decanted into opaque, light-proof bottles and rapidly transferred by helicopter to a shore laboratory in Kuujjuarapik for analysis. Under-ice photon fluence rate (PAR) was measured with a Biospherical under-water 4 π quantum sensor and water temperature as well as salinity were recorded at a depth of 2.5 m from the ice under surface using an Aanderaa current meter. Salinity of water samples from the ice-water interface was measured with a Hytech 6220 salinometer.

Biomass estimates. Subsamples of the microalgal suspension were filtered onto Whatman GF/F filters for the spectrophotometric determination of chlorophyll *a* using the equations of Jeffrey & Humphrey (1975), after 24 h extraction in 90 % acetone at 5 °C. Additional subsamples were preserved with acid Lugol for cell counts and species enumeration.

Photosynthesis measurements. Rates of photosynthesis were measured by ^{14}C assimilation in a photosynthetron incubator as described by Lewis & Smith (1983), under light transmitted through blue-green plexiglass which simulated the under-ice light spectrum (Maykut & Grenfell 1975). Parameters of the P-I curves were computed according to the equations of Platt et al. (1980) using a Gauss-Newton algorithm (Jennrich & Sampson 1968). The parameters were the maximal photosynthetic rate (P_{max}), photosynthetic efficiency (α) and the saturating photon fluence rate (I_m). P_{max} and α were normalized to both cell number and chlorophyll *a*.

P700 and pigment determinations. Subsamples of the microalgal suspension were filtered onto Nuclepore polycarbonate membrane filters (pore size 0.8 µm, comparable to Whatman GF/F filters) and stored in liquid nitrogen until analysed for P700. Thawed cells were gently washed off the Nuclepore filters and suspended in 150 m*M* Tris-HCl (pH 8.0) containing 4 m*M* $MgCl_2$. The cell suspension was disrupted by 2 passes at 110 × 10^3 kPa in a French pressure cell and photosynthetic membranes solubilized in 0.1 % Triton X-100 (Perry et al. 1981). P700 was assayed by light-dark difference spectroscopy on an Aminco DW-2 dual-wavelength spectrophotometer at 697 nm using a reference beam of 725 nm as described by Shiozawa et al. (1974). A differential extinction coefficient of 64 mM^{-1} cm^{-1} (Hiyama & Ke 1972) was used to calculate the concentration of P700. The chlorophyll *a* concentration in P700 samples was estimated using the equations of Jeffrey & Humphrey (1975) after an aliquot of the solubilized membranes was extracted into acetone. The ratio of chlorophyll *a* to P700 was calculated as a molar ratio (PSU size).

Further subsamples were filtered onto Whatman GF/F filters, frozen in liquid nitrogen, lyophilized, and later

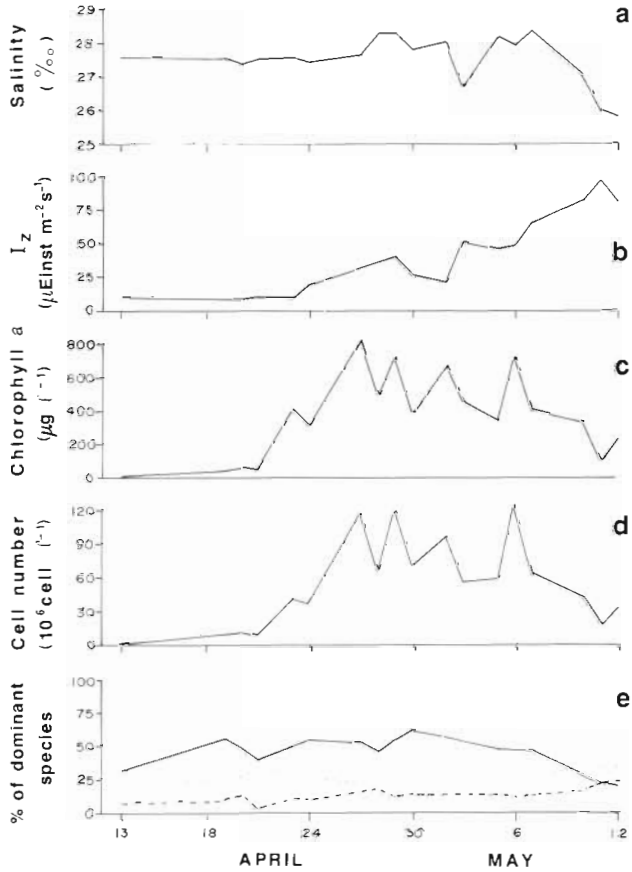

Fig. 1. Seasonal variation of a salinity (a), under-ice photon fluence rate I_z (b), chlorophyll *a* concentration (c), cell number (d), and the dominant species *Nitzschia frigida* (—·), *Navicula* spp. (· ·), *Nitzschia* spp. (– – –) (e), at the ice-water interface

analysed for the major light-harvesting pigments, chlorophyll *a*, chlorophyll *c* and fucoxanthin, by reverse-phase ion-pairing high performance liquid chromatography according to Mantoura & Llewellyn (1983). The ratios of chlorophyll *a* to chlorophyll *c* and chlorophyll *a* to fucoxanthin were determined and used together with the chlorophyll *a*/P700 ratios to estimate the molar ratio of total pigments (chlorophyll *a* + chlorophyll *c* + fucoxanthin) to P700 (PSU size).

Plastoquinone analysis. Microalgal subsamples were filtered onto Nuclepore filters and stored in liquid nitrogen until analysed for plastoquinone by the method of Redfearn & Friend (1962). Thawed cells were extracted with 100 % MeOH at −20 °C overnight and the supernatant was adjusted to 90 % MeOH before extraction (2×) with petroleum ether (40 to 60 °C). The combined petroleum ether extracts were further partitioned with successive aliquots of 95 % MeOH to remove the chlorophylls and hypophasic carotenoids until the MeOH layer was clear. The petroleum ether layer was evaporated to dryness under a stream of N_2 and the residue dissolved in EtOH (3 ml). The absorbance of the EtOH solution was determined before and after reduction with $NaBH_4$ at 255 nm. The plastoquinone concentration was calculated from the difference in absorbance at 255 nm, using a differential extinction coefficient of 14.8 mM^{-1} cm^{-1} (Redfearn & Friend 1962).

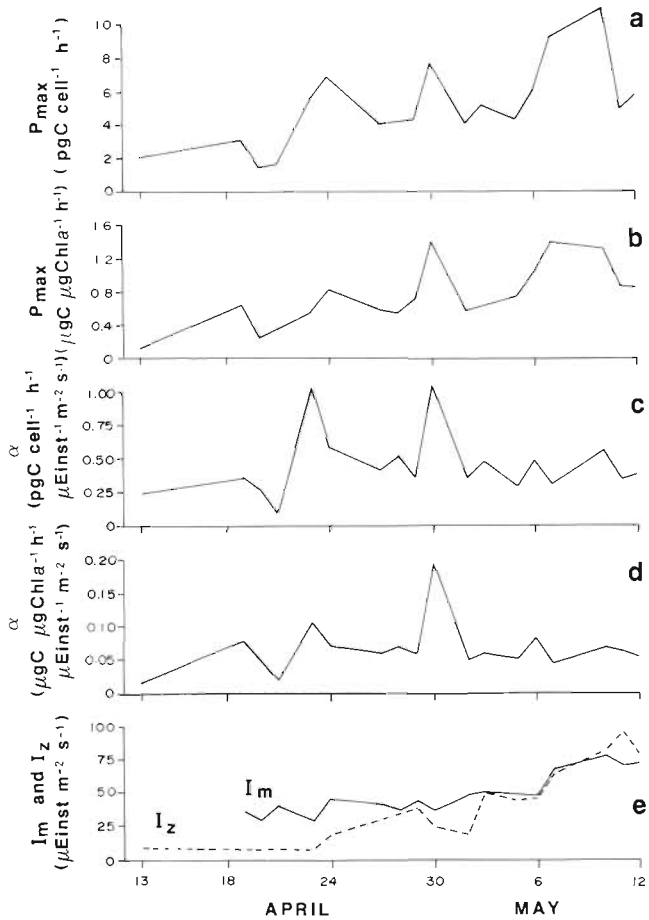

Fig. 2. Seasonal variation of the maximal photosynthetic rate (P_{max}) normalized to cell number (a) and chlorophyll *a* (b), photosynthetic efficiency (α) normalized to cell number (c) and chlorophyll *a* (d), and the saturating (I_m) and under-ice (I_z) photon fluence rates (e)

RESULTS

The water temperature at 2.5 m below the ice surface was constant at −1.5 °C during April and warmed to −1.2 °C in May. Under-ice photon fluence rates (I_z) varied between 7.6 and 9.0 µEinst m^{-2} s^{-1} until 23 April, thereafter exhibiting a seasonal increasing trend during the rest of the study (Fig. 1b). Algal biomass (chlorophyll *a* and cell numbers) was low while I_z was low, increased significantly during the second half of April as I_z increased, and then remained more or less constant until 10 May (Fig. 1c, d). From 10 to 12 May, chlorophyll *a* and cell numbers decreased concomitantly with the decrease in salinity at the ice-water interface (Fig. 1a, c, d). Pennate diatoms of the genera *Nitzschia* and *Navicula* dominated the ice microalgal community (67 to 93 %), with *Nitzschia frigida* accounting for about 50 % of the species present (Fig. 1e). Other diatoms were also present and flagellates <5 µm in size were observed in all samples, but these small cells accounted for <5 % of the total cell count. During the decline of the bloom (10 to 12 May) the percentage of *N. frigida* cells decreased noticeably and the *Navicula* species then became dominant (Fig. 1e).

The P-I characteristics of the ice algal community are presented in Fig. 2, and it may be observed that P_{max}, normalized to both chlorophyll *a* and cell numbers (Fig. 2a, b), exhibited a generally increasing trend during the study. Photosynthetic efficiency (α) (Fig. 2c, d) was low at the beginning of the study (13 April), increased between 13 and 23 April, then remained essentially constant during the remainder of the sampling programme except for noticeable increases on 23 and 30 April. The initial increase in efficiency of photosynthesis coincided with the period of under-ice photon fluence rates of 7.6 to 9.0 µEinst m^{-2} s^{-1} (Fig. 2e), indicating that the microalgae rapidly assimilated carbon when I_z was equal to or just greater than the critical photon fluence rate of 7.6 µEinst m^{-2} s^{-1} reported by Gosselin et al. (1985). The peaks on 23 to 24 and 30 April in Fig. 2a, b, c, d do not seem to be attributable to any dramatic changes in I_z (Fig. 2e) or temperature and may be due to processes related to tidal variations in water column stability (see Gosselin et al. 1985). The

saturating photon fluence rate for maximal photosynthesis (I_m) was usually greater than or approximately equal to I_z during the sampling period, except for 10 to 12 May when I_m was slightly lower than I_z (Fig. 2e).

The cellular concentrations of chlorophyll *a*, chlorophyll *c* and fucoxanthin were low on 13 April but increased in the period to 23 April (Fig. 3a). P700 concentration also increased during this period (Fig. 3c) and both the P700 and pigment increases are

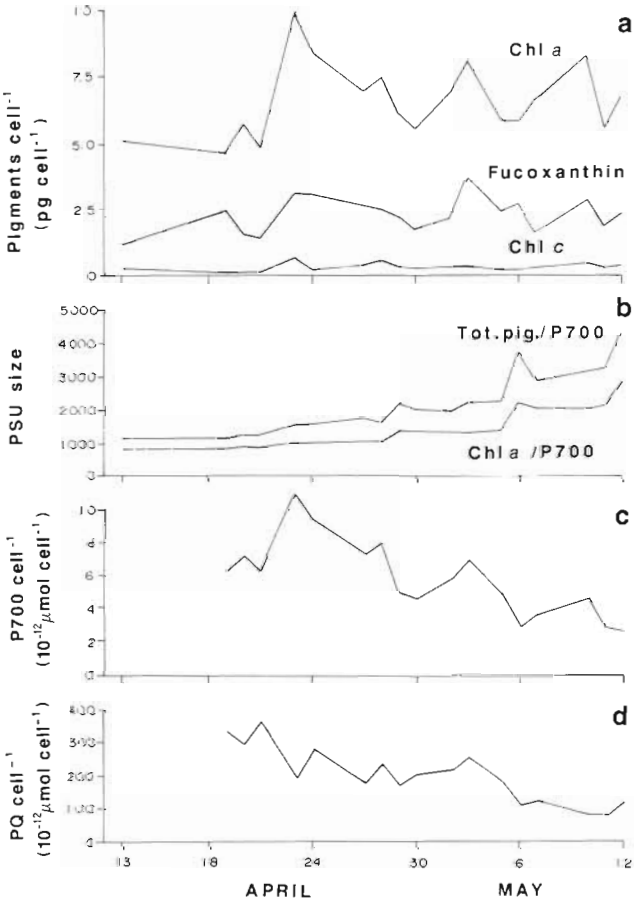

Fig. 3. Seasonal variation of cellular pigment content (a), PSU size based on P700 (b), P700 content per cell (c), and plastoquinone (PQ) content per cell (d)

reflected in a slight increase in the size of the PSU (Fig. 3b). PSU sizes continued to increase from 23 April until 12 May (Fig. 3b) and during this period the concentration of pigments remained essentially constant (Fig. 3a) while the P700 content per cell decreased (Fig. 3c). There was also a concomitant decrease in the cellular content of plastoquinone (Fig. 3d), an important component of the electron transport chain that accepts electrons from photosystem II.

In order to elucidate the effects of under-ice photon fluence rate on photosynthesis, we examined the relationship between I_z and P_{max}, between I_z and the Chl/P700 ratio, and between I_z and the electron transport components, P700 and plastoquinone. P_{max} increased with I_z (Fig. 4a), confirming that under-ice photon fluence rate is a major environmental variable influencing the photosynthetic performance of sea-ice microalgal cells. There was an increase in the Chl/P700 ratio (Fig. 4b) and a decrease in the P700 and plastoquinone content per cell (Fig. 4c, d) as I_z increased. These observations indicated that the increase in under-ice photon fluence rate resulted in the formation of apparently larger PSUs. This was due to the decrease in the number of photosystem I reaction centres (P700) since there was no increase in light-harvesting pigments (Fig. 3a). The algal cells also required less plastoquinone to utilize the changing photon fluence rate.

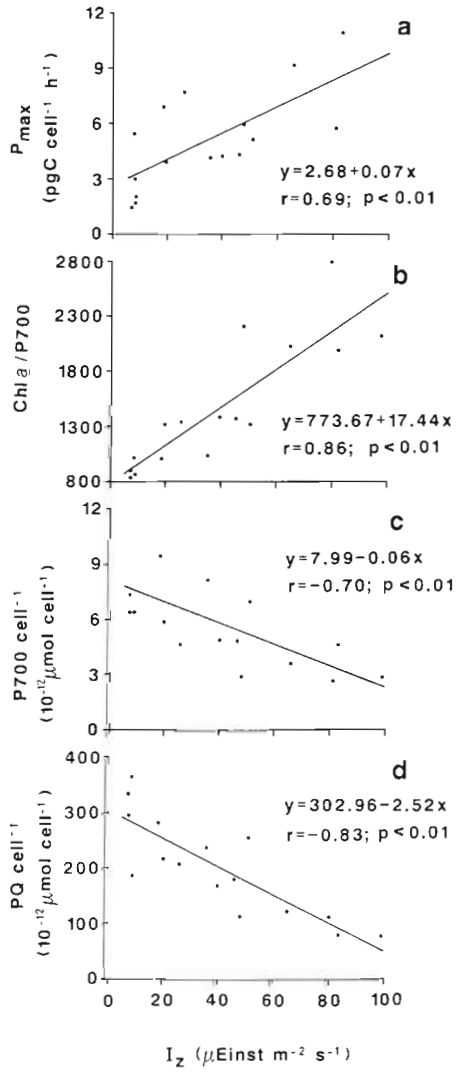

Fig. 4. Relationships between I_z and P_{max} per cell (a), chl *a*/P700 ratio (b), P700 per cell (c), and plastoquinone (PQ) per cell (d)

DISCUSSION

Sea-ice microalgae constitute an important component of the primary biomass of polar seas (Horner & Alexander 1972, McConville & Wetherbee 1983) and salinity, temperature, light and nutrients have been identified as the main environmental variables regulating the growth of these algal cells (Demers et al. 1986). Unlike phytoplankton, ice algae usually grow under relatively stable conditions of temperature and salinity and are not subjected to high frequency fluctuations in photon fluence rate (Legendre et al. 1986). Nutrient replenishment at the ice-water interface, however, is most influenced by hydrodynamical variations and Maestrini et al. (1986) noted that nitrogen may limit the biomass yield of sea-ice microflora in southeastern Hudson Bay even when nutrients were not exhausted. Since the photon fluence rate at the ice-water interface is only about 0.1 % of that incident to the ice surface, light can be considered to be a critical factor regulating the growth of ice algae (Horner & Schrader 1982, Gosselin et al. 1985). Therefore, it is of interest to elucidate the photoadaptive strategies employed by ice algal communities in response to the seasonal change in photon fluence rate.

Nitzschia and *Navicula* species usually dominate the community during the ice-algal blooms in Hudson Bay, as evidenced by the results of this study (Fig. 1e) and those of Rochet et al. (1985). The high concentration of fucoxanthin in the ice-algal cells and the detection of chlorophyll *c* provided further chemotaxonomic evidence for the overwhelming presence of diatoms (Fig. 3a). Chlorophyll *a*, chlorophyll *c* and fucoxanthin are the major light-harvesting pigments in diatoms (Prézelin 1981) and are organized into discrete pigment-protein complexes in the photosynthetic membrane (Alberte et al. 1981, Friedman & Alberte 1984). In this study, chlorophyll *a* was found to be the dominant light-harvesting pigment accounting for about 50 % of the total pigment content (Fig. 3a). The ratios of chlorophyll *a*:fucoxanthin and chlorophyll *a*:chlorophyll *c* varied between 2.2 and 4.2 and between 13.2 and 45.6, respectively. These values are significantly higher than the values of 1.6 and 7.6 reported by Vesk & Jeffrey (1977) to be characteristic of diatoms. This suggests that the pigment ratios observed here are a reflection of the extreme light and temperature conditions at the ice-water interface where blue-green light dominates the under-ice light field (Maykut & Grenfell 1975). Our pigment determinations differ significantly from those of Rochet et al. (1986) who report high concentrations of carotenoids and chlorophyll *c* in ice algae from Hudson Bay, yielding chlorophyll *c*: chlorophyll *a* ratios >1. These differences in pigment concentration may be attributed to the different techniques employed to measure pigments. Rochet et al. (1986) used a spectrophotometric method, whereas we used a more sensitive and accurate chromatographic procedure.

These ice diatoms are well acclimated to the freezing temperatures (Rochet et al. 1985) and as the under-ice photon fluence rate increased above the I_{crit} level of 7.6 μEinst $m^{-2} s^{-1}$ (Gosselin et al. 1985) the cells rapidly increased their photosynthetic activity (Fig. 2). While the efficiency of photosynthesis (α) remained essentially constant after an initial increase (Fig. 2c, d), the maximal photosynthetic rate increased at higher photon fluence rates (Fig. 2a, b, e, 4a). I_m also progressively increased as I_z increased (Fig. 2e) and the algal cells therefore saturated photosynthesis at photon fluence rates above or equal to the under-ice photon fluence rate. The increase in P_{max}, together with the change in I_m with respect to I_z, indicated that the ice microalgae progressively adapted to the seasonal change in under-ice photon fluence rates. Rochet et al. (1986) also observed that I_m was greater than I_z and we concur with their conclusion that the sea-ice microalgal communities in Hudson Bay are not obligate shade flora, contrary to the suggestion by Cota (1985) for the high Arctic.

At the end of the study, we noted a decrease in salinity (Fig. 1a) and in algal biomass (Fig. 1c, d) and I_m was estimated to be slightly lower than I_z (Fig. 2e). These observations suggested that the microflora were being flushed out from the ice-water interface by fresh water produced from melting ice and that the community was possibly susceptible to photoinhibition at the same time. It is also interesting to note that the number of *Nitzschia frigida* cells declined noticeably during this period and *Navicula* spp. then dominated the community (Fig. 1e). *N. frigida* may be susceptible to the detrimental effects of lower salinity (see Poulin et al. 1983) and possibly to photoinhibition as well, while *Navicula* spp. may be more tolerant of these conditions. Further research is required, however, to elucidate the response of these species to environmental perturbations.

The mechanisms employed by the ice microalgae to adapt to the changing photon fluence rates seemed to be flexible and depended on the under-ice light conditions. Under low photon fluence rates (7.6 to 9.0 μEinst $m^{-2} s^{-1}$), which prevailed at the beginning of the study, the increase in P_{max} was accompanied by an increase in RCI and slight increases in PSU size and plastoquinone content (Fig. 3b, c, d). As the photon fluence rates increased above 9.0 μEinst $m^{-2} s^{-1}$, the continued increase in P_{max} (Fig. 4a) corresponded to a reduction in RCI and plastoquinone activity (Fig. 4c, d) and to an apparent increase in PSU size (Fig. 4b). Using current terminology, this means that the ice algal cells main-

tained photosynthesis under low photon fluence rates by increasing the number of PSUs. This has also been observed in various cyanobacterial species by Kawamura et al. (1979), Vierling & Alberte (1980), Raps et al. (1983) and Barlow & Alberte (1985). Centric diatoms, on the other hand, reduce the number of PSUs under low photon fluence rates while increasing the size of these units (Falkowski & Owens 1980, Falkowski et al. 1981, Perry et al. 1981, Gallagher et al. 1984). At higher photon fluence rates, the ice algal cells increased P_{max} by reducing the number of PSUs, thus effectively increasing the size of these units. This response is contrary to that generally observed in phytoplankton in which numbers of PSUs increase, and PSU sizes decrease, with increased photon fluence rates (see Prézelin 1981, Richardson et al. 1983). Ice algae appear, therefore, to be highly efficient in harvesting the increasing light energy as they maintained an effective absorption cross section by reducing the number of reaction centres instead of expending energy in synthesizing larger PSUs. This conservation of cellular energy for other metabolic processes and cell division would ensure continued growth of the population under the ice.

The adaptation to higher photon fluence rates by increasing P_{max} and reducing the number of reaction centres and plastoquinone implies a faster transport of photosynthetically derived electrons. The minimum turnover time of photosystem I reaction centres may be calculated from P_{max} and the concentration of reaction centres. P_{max} values were expressed as moles CO_2 mole $P700^{-1}$ ms^{-1} and then converted to number of electrons mole $P700^{-1}$ ms^{-1} by assuming that, at light saturation, 4 electrons are required to reduce each assimilated CO_2 molecule (Ort et al. 1983). No account was made for any cyclic electron flow around photosystem I. Turnover times estimated in this way for the ice microalgal community decreased from about 190 ms e^{-1} at the beginning of the bloom to less than 20 ms e^{-1} later in the season. If the changing turnover times are plotted against I_z (Fig. 5), then a significant decrease in the turnover time of RCI is observed as I_z increased. This means that there was a faster flow of electrons through the electron transport chain in response to the increase in photon fluence rates. Similar phenomenon have also been observed in other microalgal cells by Falkowski et al. (1981), Raps et al. (1983) and Post et al. (1985).

Since light-saturated photosynthetic rates are related to the concentration of photosynthetic units and their minimal turnover rate (Falkowski et al. 1981, Raps et al. 1983), our results suggested that photosynthesis in sea-ice microalgae was limited by electron transport. However, a recent study by Sukenik et al. (1987) on the pool sizes of components of the electron-transport chain and carbon fixation enzymes in the marine chlorophyte

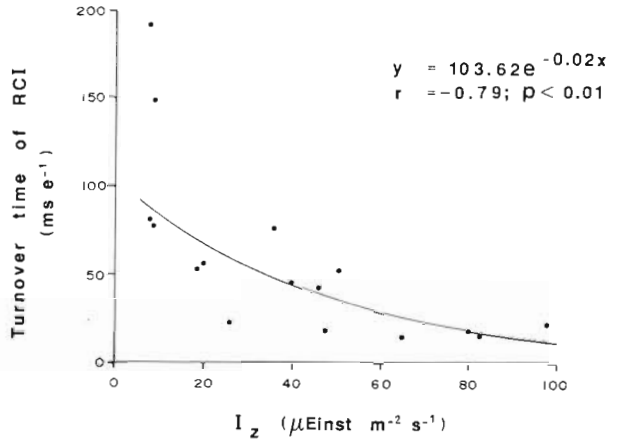

Fig. 5. Relationship between I_z and the turnover time of photosystem I reaction centres (RCI)

Dunaliella tertiolecta indicated that carbon fixation rather than electron transport is the rate-limiting step. Similar conclusions were also arrived at by Stitt (1986), who investigated the pool sizes of carbon fixation metabolites in spinach leaves. Whether or not carbon fixation limits photosynthesis in ice microflora, this investigation reveals that Hudson Bay communities have developed a successful strategy for harvesting energy and increasing the flow of photosynthetically derived electrons to maintain photosynthesis under extreme conditions of light and temperature in a polar region.

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