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Ultra-algae (<5 µm) in the ice, at the ice-water interface and in the under-ice water column (southeastern Hudson Bay, Canada)*

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ABSTRACT: In ice-covered southeastern Hudson Bay (Canada), the plume of the Great Whale River determines onshore-offshore gradients in salinity, concentrations of suspended particles and of dissolved nutrients, and stratification of the water column. Because of the snow and ice cover, irradiance in the water column is low, and it is further attenuated by the turbidity of water in the plume. Ultra-algae (0.4 to 5 µm) were found primarily in the sea-ice bottom, and they also occurred at the ice-water interface and in the water column. This is the first time such algae have been directly observed in the sea-ice environment. Concentrations ranged between 36×10^3 and 63×10^6 cells l^{-1}, and the contribution to total chlorophyll *a* varied from 9 to 96%. Concentrations of ultra-algae in this subarctic environment and their contribution to total algal biomass were much higher than previously hypothesized for high-latitude marine waters. Ultra-algal abundances varied primarily with depth, but also with distance from shore and with time. The ice bottom, the ice-water interface and the water column formed distinct habitats, which were colonized by different taxonomic assemblages. These comprised chlorophyll-rich eucaryotes (35 to 93%), procaryotic cyanobacteria (phycoerythrin-rich, 2 to 51%; and phycocyanin-rich, 4 to 24%) and eucaryote cryptomonads (0 to 6%). Eucaryotes were dominant in the ice bottom and at the ice-water interface. Their importance increased with distance from shore, following the onshore-offshore salinity gradient. Procaryotes dominated in the water column near the mouth of the river. Total abundances were well correlated with salinity at the bottom of the ice (which determined ice structure), and with light attenuation at the ice-water interface and in the water column (which reflected particle load). It is concluded that the main factor controlling ultra-algal abundances, in the studied environment, is the availability of solid substratum (i.e. ice structure and particle load).

KEY WORDS: Ultra-algae · Distribution · Sea ice · Water column · Salinity · Particle load

INTRODUCTION

In the literature, small phytoplankton are usually referred to as picoplankton (<2 µm; Sieburth et al. 1978, Caron et al. 1985, Stockner & Antia 1986, Olson et al. 1989, Hall & Vincent 1990) or, less often, as ultraplankton (<5 µm; Sverdrup et al. 1942, Murphy & Haugen 1985). Actually, the definition of picoplankton is based on cell volume, the group being mainly composed of cyanobacterial procaryotes such as *Synechococcus*. In contrast, ultraplankton may be seen as a functional group, containing procaryotic cells and <5 µm eucaryotic algae. Recently, several studies on carbon cycling in marine waters have focused on the quantitative and qualitative contribution of ultraplankton to total primary production, particularly in comparison to that of large cells such as diatoms (e.g. Azam et al. 1983, Cushing 1989, Legendre & Le Fèvre 1989,

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1991). The importance of ultraplankton in the cycling of carbon has been demonstrated for temperate as well as tropical marine and fresh waters (e.g. Sorokin 1971, Banse 1974, Herbland & Le Bouteiller 1981, Li et al. 1983, Fahnenstiel et al. 1986, Fogg 1986, Stockner & Antia 1986, Pick 1991, Søndergaard et al. 1991).

Temperature, irradiance and nutrients are hypothesized to be the main determinants of picoplankton productivity and biomass. The development of cyanobacteria is apparently favoured by warm waters (e.g. Caron et al. 1985, El Hag & Fogg 1986, Jochem 1988, Weisse 1988, Kuosa 1990), whereas low concentrations have been reported at high latitudes (Gradinger & Lenz 1989, Walker & Marchant 1989, Legendre et al. 1993). Murphy & Haugen (1985) found a positive relationship between the relative abundance of eucaryotes and latitude, but Kuosa (1991) argued that the concentration of eucaryotes bears no clear relation to surface temperature. Concerning light, picoplankton cells have a higher photosynthetic efficiency at low irradiance than larger cells (e.g. Glover & Morris 1981, Platt et al. 1983, Glover et al. 1985b, Joint & Pomroy 1986). Yet high concentrations of picoplankton in surface waters (Joint & Pomroy 1986, Kudoh et al. 1990, Søndergaard et al. 1991) and in coral reef waters (Legendre et al. 1988, Charpy & Charpy-Roubaud 1991) indicate that small cells can also thrive at high irradiances (Pick 1991). Concerning nutrients, concentrations of picoplankton in oligotrophic temperate and tropical oceanic waters range between 10^5 and 10^8 cells l^{-1} (e.g. Platt et al. 1983, Murphy & Haugen 1985, Joint & Pomroy 1986, Olson et al. 1990, Søndergaard et al. 1991). Their contribution to total chlorophyll *a* varies from 20 to 100%, and it is generally >50% (e.g. Platt et al. 1983, Glover et al. 1985a, Putt & Prézelin 1985). The dominance of picoplankton in these waters could be linked to their ability to use very low nutrient concentrations (Friebele et al. 1978, Raven 1986). Yet, nutrient supply does not seem to be always important for the dynamics of picoalgae (Kuosa 1991). As an alternative hypothesis to the importance of irradiance, temperature and nutrients, it has also been proposed that the abundance of picoplankton is determined by the availability of particles suspended in the water column (Silver et al. 1986, Walker & Marchant 1989).

In arctic and subarctic waters, environmental conditions in and under the ice are extreme, i.e. near-freezing temperature, low irradiance and high concentrations of dissolved nutrients. River runoff is also a major characteristic of the Arctic Ocean (Aagaard & Carmack 1989), so that coastal areas are often subjected to influx of fresh water and suspended particles. The presence of picoplankton in such extreme environments is poorly documented but, based on the size-fractionation of chlorophyll *a*, Legendre et al. (1987) and Probyn & Painting (1985) gave indirect evidence for the occurrence of picoplankton in the cold waters of subarctic Hudson Bay (Canada) and the Antarctic Ocean, respectively. There is no report, so far, of direct observations of ultra-algae in the ice bottom or at the ice-water interface.

In the present study, the term ultra-algae refers to photosynthetic organisms in the size range 0.4 to 5.0 µm, which can be found in the water column (ultraplankton) as well as in the ice-bottom matrix. The abundance, taxonomic composition and contribution of ultra-algae to total chlorophyll *a* were quantified at 5 stations along an onshore-offshore transect in ice-covered southeastern Hudson Bay. The transect was located in an area influenced by the plume of the Great Whale River, which determines large inshore-offshore gradients in salinity, nutrient concentrations and particle load. The present paper shows that the concentrations of ultra-algae in the ice bottom and at the ice-water interface are not negligible, in spite of the prevailing extreme environmental conditions. It also compares the ecological response of procaryotes and small eucaryotes to temperature and salinity gradients, irradiance and particle load, and nutrient concentrations.

MATERIALS AND METHODS

Samples were collected from 22 April to 20 May 1990, off Kuujjuarapik (55° 30.1' N, 77° 44.5' W) in southeastern Hudson Bay. Five stations, located along a south-north transect, were sampled on the first-year sea ice. The transect covered the salinity gradient corresponding to the plume of the Great Whale River (Fig. 1). Stns B and D were sampled every second or third day, and Stns BC, C and CD every fifth or seventh day.

At each station, vertical profiles of temperature and salinity in the water column were recorded with a SEACAT instrument (model SBE 19). Under-ice irradiance (photosynthetically active radiation, PAR: 400 to 700 nm) was measured by a SCUBA diver using a Biospherical Instruments quantum meter with an underwater probe (4π). A reference sensor was positioned above the ice cover. Vertical profiles of irradiance were recorded away from apertures in the ice. The coefficient of diffuse light attenuation (k), which reflects particle load, was calculated according to the Beer-Lambert equation $k = (\log I_{z_1} - \log I_{z_2})/(z_2 - z_1)$, where I_z is the irradiance measured at depth z. Snow depth and ice thickness (average of 5 values) were also measured at each sampling time. Water samples were collected at the ice-water interface and in the water

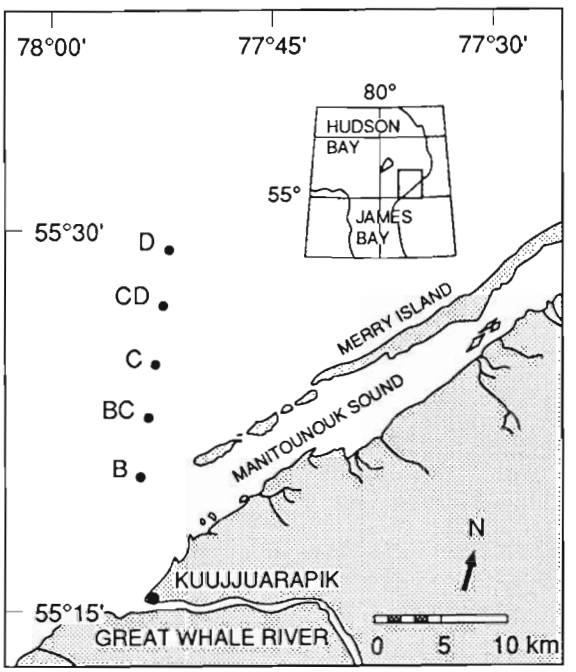

Fig. 1. Location of the sampling stations off the mouth of the Great Whale River, southeastern Hudson Bay, Canada

column for the determination of nutrients [$NO_3 + NO_2$, PO_4, $Si(OH)_4$]. Water samples were filtered on pre-combusted Whatman GF/F glass-fiber filters (50 ml syringes equipped with Sweenex filter holder) before being frozen (–60°C) for later determination of nutrient concentrations with a Technicon AutoAnalyser II.

Ice algae were collected from the ice bottom by SCUBA divers using a submersible ice core. Each ice-bottom sample consisted of 5 ice cores (each 3 cm long × 6 cm diam.), which were melted at room temperature. SCUBA divers also sampled free-floating algae at the ice-water interface using a 2 l syringe 'slurp-gun' sampler. Each sample from the interface consisted of five 2 l samples. Phytoplankton samples were collected at 2.5, 5 and 10 m with a Little Giant submersible pump. All algal samples were kept in the dark until treated in the laboratory. The field samples were transported without delay to the shore laboratory in Kuujjuarapik. Size-fractionated chlorophyll *a* was determined fluorometrically (Parsons et al. 1984) on subsamples filtered in parallel on Poretics polycarbonate filters of 5.0 and 0.4 µm, respectively. $MgCO_3$ was added during the filtration. Filters were stored at –60°C until they were ground and pigments extracted for 24 h in 90% acetone at 4°C in the dark, followed by centrifugation and filtration on Poretics 0.4 µm filters. Fluorescence of the extracts was measured using a Turner Designs fluorometer. For the enumeration of ultra-algae, subsamples (1 to 10 ml for ice samples and 2 to 100 ml for water samples) were fixed in 0.2% formaldehyde for at least 24 h (Hall 1991). These samples were then filtered onto Poretics polycarbonate 0.4 µm black filters, after serial prefiltration on 5 µm filters. The filters were mounted in immersion oil, on slides which were sealed and stored frozen in the dark at –20°C. Ultra-algae were enumerated using an epifluorescence microscope (Leitz Dialux 22; 788×). The characteristic fluorescence emitted by different taxa allowed their identification, i.e. under blue excitation light, chlorophyll-rich eucaryotes are far-red, phycoerythrin-rich cyanobacteria are yellow and cryptomonads are larger and orange; under green excitation light, all cyanobacteria show bright red-orange fluorescence (MacIsaac & Stockner 1993). Four taxa could thus be distinguished, i.e. chlorophyll-rich eucaryotes (EUC), cryptomonads (CRYPT), phycoerythrin-rich cyanobacteria (PEC) and phycocyanin-rich cyanobacteria (PCC) (i.e. total cyanobacteria minus PEC). EUC plus CRYPT gives the total eucaryotes (EUCT), while PEC plus PCC makes up the procaryotes (PROC). A minimum of 100 to 200 cells were counted on each slide for the abundant taxa, whereas for scarce taxa all cells were entirely enumerated (Hall & Vincent 1990).

RESULTS

Environmental conditions

Snow depth decreased progressively until 17 May when the snow cover was completely melted. The river freshet occurred on 23 May, and the breakup of the landfast sea ice cover in Hudson Bay started on 4 June. Ice thickness varied from 120 to 140 cm and decreased during the study period. Sea ice was slightly thicker at Stn BC (125 to 150 cm) than at other stations.

Time-depth sections of temperature and salinity at each station illustrate the inshore-offshore development of the Great Whale River plume in the upper 15 m (Fig. 2). The low-salinity and slightly warmer waters of the plume were present during the entire sampling period at Stns B and BC, but they reached Stn C, CD and D only after the spring freshet in mid-May. Where present, the pycnocline was located at ca 5 m depth. The temperature gradient generally paralleled the salinity gradient.

Water transparency remained relatively high until the spring freshet in mid-May, when the advection of plume waters caused an abrupt increase in turbidity (as measured by k, the coefficient of diffuse light attenuation) (Fig. 3a, b). Before the freshet, light attenuation in the surface layer (0 to 5 m) was higher at Stn B than at Stn D. Depending on station and time in the season, between 1 and 15% of the radiation at the upper surface of the ice (E_0) reached the ice-water interface, and

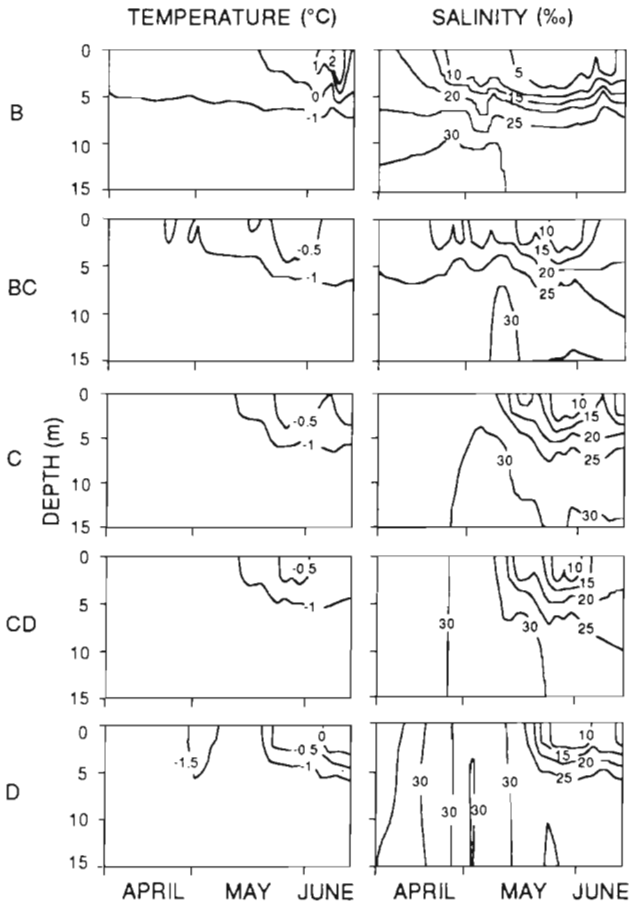

Fig. 2. Seasonal variations of isotherms (°C) and isohalines (‰), at Stns B (inshore) through D (offshore), from 7 April to 14 June 1990

<0.5% of E_0 reached the depth of 15 m (Fig. 3c, d). Over the sampling period, PAR at the ice-water interface increased from ca 5 µE m^{-2} s^{-1} in April to >100 µE m^{-2} s^{-1} in early June (Fig. 3e, f), in response to the melting of snow and, later, to the dislocation of the ice cover. Thus, despite the increase in water turbidity, both PAR (Fig. 3e, f) and the percentage of E_0 (Fig. 3c, d) increased in the water column over the sampling period. Underwater irradiance was generally slightly higher at Stn D than at Stn B.

Snow depth, ice thickness and total pigments (chlorophyll *a* plus phaeophytin, from microalgae plus ultra-algae sampled at the bottom of the ice and at the ice-water interface) explained 63% of the variation in percent irradiance at the ice-water interface (multiple linear regression, $\%E_0$ = 15.99 – 0.43 snow depth – 0.09 ice thickness – 0.04 pigments; R = 0.79, n = 13, $p < 0.05$). k was calculated for the snow-ice sheet, the ice-water interface down to 2.5 m, and 2 strata in the water column (2.5 to 5 and 5 to 10 m). For the snow-ice layer, a multiple regression, with snow depth and ice thickness as independent variables, explained 74% of the variation in k (k = –4.77 + 0.15 snow depth + 0.06 ice thickness; n = 13, $p < 0.05$). Adding the biomass of ice algae to the regression increased the coefficient of multiple determination by 2% only (R^2 = 76%). Light attenuation was maximum in the layer immediately under the ice (i.e. from the ice-water interface down to 2.5 m), which corresponded to the plume of the Great Whale River (Fig. 3). In the water column, including the ice-water interface, the variability in k was correlated with salinity (r^2 = 61%), but not with total chlorophyll *a* (r^2 = 1.6%).

Several silicate data are missing due to technical problems at the time of analysis. Nutrient concentrations tended to decrease at Stns B and D as the season progressed. All nutrients were less abundant at the ice-water interface than in the underlying water column. Vertical gradients in nutrient concentrations were stronger at Stn B than at Stn D. Concentrations of phosphate and silicate were higher at Stn D than at Stn B, while those of nitrate were similar at the 2 stations.

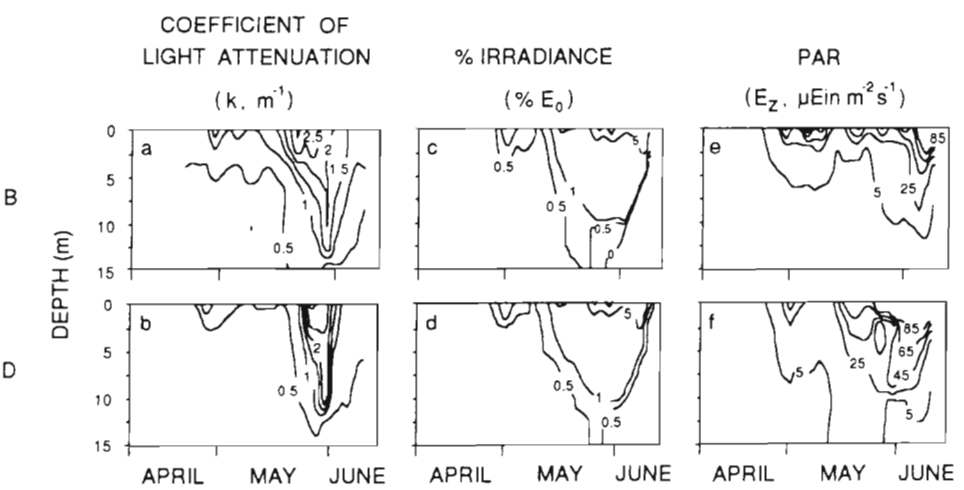

Fig. 3. Seasonal variations of isopleths for the coefficient of diffuse light attenuation (k), percent ice-surface irradiance ($\%E_0$), and irradiance under the ice (E_z), at Stns B (inshore) and D (offshore), from 22 April to 14 June 1990. E represents the photosynthetically active radiation (PAR, 400 to 700 nm)

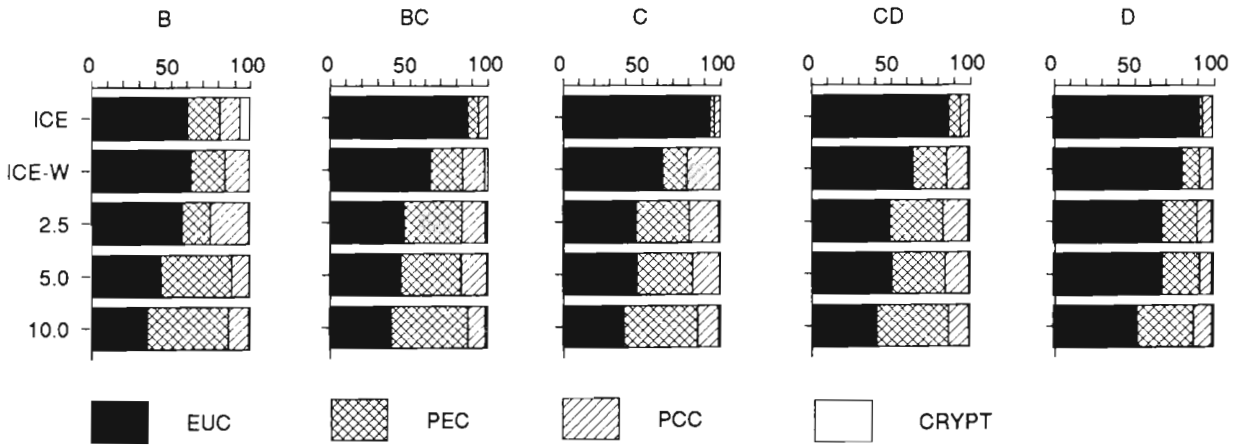

Fig. 4. Taxonomic composition (%) of ultra-algae in each depth stratum, at Stns B (inshore) through D (offshore), from 22 April to 20 May 1990. Shown are percent chlorophyll-rich eucaryotes (EUC), phycoerythrin-rich cyanobacteria (PEC), phycocyanin-rich cyanobacteria (PCC) and cryptomonads (CRYPT) in the ice, at the ice-water interface, and at the 3 sampled depths (given in meters) in the water column

Taxonomic composition of ultra-algae

Overall, chlorophyll-rich eucaryotes were the most abundant taxonomic group in the ultra-algal assemblage (35 to 93%), followed by phycoerythrin-rich cyanobacteria (2 to 51%) (Fig. 4). Phycocyanin-rich cyanobacteria were not negligible (4 to 24%), whereas cryptomonads represented a very small fraction of total cell numbers (0 to 6%). At all stations, chlorophyll-rich eucaryotes were dominant in the ice, at the ice-water interface and at 2.5 m. The proportion of phycoerythrin-rich cyanobacteria was highest at 5 m at Stn B and at 10 m at Stns BC, C and CD. The highest percentages of phycocyanin-rich cyanobacteria were always recorded in the water column. As a general trend, total eucaryotes were dominant in the ice and in the plume at all stations (58 to 93%), and their proportions in the water column increased with distance from shore (Fig. 5). Procaryotes in the water column were more important nearshore, with maxima at Stns BC and C (52 to 60%).

Spatio-temporal distribution of ultra-algae

At each station and during the entire sampling period, ultra-algae were found in the ice, at the ice-water interface and in the water column (Table 1). Concentrations ranged between 36×10^3 and 63×10^6 cells l^{-1}. Cells primarily occurred in the ice bottom, but their abundances were never negligible at the ice-water interface or in the water column down to 10 m.

A 3-factor (Date × Station × Depth) unbalanced analysis of variance (ANOVA) without replication was applied to the log-transformed abundance data in order to determine the relative importance of each sampling axis in explaining the spatio-temporal distribution of ultra-algae. For each taxon as well as for total eucaryotes and procaryotes, the variance in abundances associated with each sampling axis was significantly larger than the interaction between the 3 axes, which is the term for uncontrolled variation in the

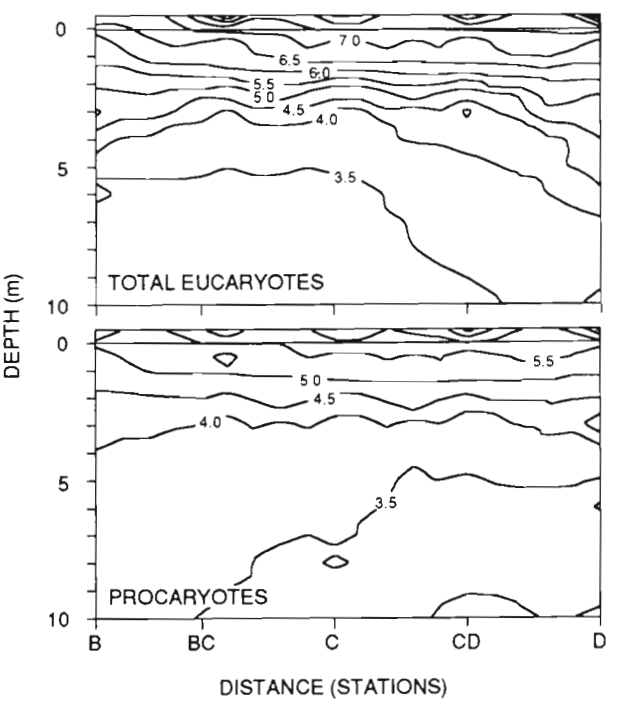

Fig. 5. Distance-depth sections for the abundances (log of cells l^{-1}) of total eucaryotes and procaryotes, from 22 April to 20 May 1990

Table 1. Mean concentrations of ultra-algae (10^3 cells l^{-1}) and standard deviation at the 5 stations (B through D), from 22 April to 20 May 1990, in the ice, at the ice-water interface, and at 2.5, 5 and 10 m in the water column. n: number of samples

Depth	B	BC	C	CD	D
Ice					
Mean	1385	26766	24697	25304	17664
SD	886	25844	14884	10419	9664
n	7	3	4	3	6
Ice-water interface					
Mean	265	365	764	552	1358
SD	283	101	526	467	1237
n	9	10	5	6	10
2.5 m					
Mean	107	80	77	67	143
SD	33	28	29	14	77
n	9	10	4	5	11
5 m					
Mean	61	61	65	58	154
SD	17	13	8	20	104
n	9	9	4	5	9
10 m					
Mean	70	52	53	64	101
SD	45	7	6	28	73
n	10	6	6	4	10

model (Table 2). Depth proved to be the most important factor (vertical gradient), followed by station (horizontal gradient, i.e. distance from shore) and date (temporal variation).

The abundance of ultra-algae was always maximum in the ice matrix, and it decreased exponentially with depth (Table 1). In the water column, the abundance of eucaryotes was associated with the salinity gradient of the Great Whale River plume, and procaryotes were more abundant near the mouth of the river (Fig. 5). For all taxa except the cryptomonads, concentrations in the ice were significantly higher than those at the ice-water interface, which were significantly higher than those in the water column (Table 3). In summary, except for cryptomonads, the ice, the ice-water interface and the water column constituted distinct compartments as far as abundances were concerned.

Table 3. Student-Newman-Keuls (SNK) multiple comparison test. Comparisons among the mean concentrations (cell counts were log transformed) of chlorophyll-rich eucaryotes (EUC), cryptomonads (CRYPT), phycoerythrin-rich cyanobacteria (PEC), and phycocyanin-rich cyanobacteria (PCC) by depth stratum. Mean abundances (log of 10^3 cells l^{-1}) and numbers of observations are given for each taxon in the ice, at the ice-water interface and at the 3 sampled depths in the water column. Vertical lines identify depth strata in which cell concentrations were not significantly different

Depth	EUC Mean	EUC n	CRYPT Mean	CRYPT n	PEC Mean	PEC n	PCC Mean	PCC n
Ice	3.76	23	0.69	23	2.52	23	2.63	22
Ice-water interface	2.57	25	0.50	25	1.72	25	1.53	25
2.5 m	1.72	32	0.28	32	1.43	32	1.12	32
5 m	1.57	31	0.23	32	1.37	31	0.91	31
10 m	1.41	32	0.16	31	1.35	32	0.87	32

Between 3 and 11 May at Stns B and D (periods and stations for which total chlorophyll *a* data are available), ultra-algae accounted for 9 to 96% of total chlorophyll *a* (Table 4). The contribution of ultra-algae to total chlorophyll biomass was generally lower at coastal Stn B than at the more marine Stn D. It was minimum at the ice-water interface and maximum in the water column where it almost always exceeded 50%. In the ice, contribution to total chlorophyll *a* was intermediate between that found for the other environments, with more than one-third of the chlorophyll *a* belonging to ultra-algae.

Table 2. Unbalanced 3-factor ANOVA without replication, showing relative contribution (*F*-ratio) of date, station and depth of sampling to the variance in the abundance (10^3 cells l^{-1}) of chlorophyll-rich eucaryotes (EUC), cryptomonads (CRYPT), total eucaryotes (EUCT = EUC + CRYPT), phycoerythrin-rich cyanobacteria (PEC), phycocyanin-rich cyanobacteria (PCC), and total procaryotes (PROC = PEC + PCC). Cell counts were log transformed

Source of variance	df	EUC	CRYPT	EUCT	PEC	PCC	PROC
Model	83	28.05**	2.68**	13.72**	8.02**	7.22**	12.93**
Date	9	6.88**	3.43**	3.38**	3.16**	3.67**	4.82**
Station	4	33.39**	3.38*	14.29**	2.27*	1.05^{ns}	2.10*
Depth	4	201.13**	4.68*	88.86**	58.97**	48.63**	91.26**
Date × Station	19	2.37**	1.50^{ns}	2.75**	1.27^{ns}	1.30^{ns}	1.72*
Date × Depth	31	2.63**	2.26**	2.57**	1.71*	1.05^{ns}	1.86*
Station × Depth	16	5.48**	2.68**	2.70**	1.63*	1.12^{ns}	1.90*

* $p < 0.1$, ** $p < 0.01$, $^{ns}p > 0.1$

Table 4. Chlorophyll *a* biomass (mg m^{-3}) of ultra-algae (0.4–5.0 µm) and microalgae (>5 µm), and percent contribution of ultra-algae to total chlorophyll *a* biomass (%U/TOT)

Depth	Date	Stn B			Stn D		
		0.4–5 µm	>5 µm	%U/TOT	0.4–5 µm	>5 µm	%U/TOT
Ice	3 May	120.43	218.35	36	–	–	–
	6 May	21.65	29.58	42	–	–	–
	9 May	25.86	30.08	46	–	–	–
Ice-water interface	3–4 May	14.86	98.60	13	26.17	37.09	41
	6–7 May	6.66	22.78	23	7.28	50.35	13
	9–10 May	3.03	31.24	9	–	–	–
2.5 m	3–4 May	0.71	0.36	66	0.33	0.01	96
	6–7 May	0.08	0.25	26	0.15	0.11	58
	9–10 May	0.11	0.20	36	0.23	0.12	65
5 m	3–4 May	0.15	0.10	61	0.17	0.06	73
	6–7 May	0.08	0.04	68	0.13	0.10	57
	9–10 May	0.13	0.06	68	0.33	0.08	81
10 m	3–4 May	0.80	0.10	89	–	–	–
	6–7 May	0.02	0.03	46	0.24	0.06	74
	9–10 May	0.04	0.02	65	0.34	0.08	77

Environmental conditions and ultra-algal abundances

Multiple partial correlations, which allow quantification of the relationship between 2 variables while keeping all others constant, were used to assess the relations between different environmental factors and the abundances of ultra-algae. Data for the ice matrix were excluded from the analysis, because physical and chemical variables were not available for this environment. Environmental variables were considered to be redundant when their coefficient of linear correlation was $r > 0.80$ (Scherrer 1984). Thus, underwater irradiance and temperature were excluded because of their redundancy with $\%E_0$ and salinity, respectively. Partial correlations (Table 5) between abundance and k were highly significant for all ultra-algal taxa. Abundances of procaryotes were significantly correlated with k only, whereas those of total eucaryotes (chlorophyll-rich eucaryotes + cryptomonads) were correlated with k, $\%E_0$, salinity and phosphate.

Table 5. Partial correlations (excluding data from the ice bottom) of the abundances of chlorophyll-rich eucaryotes (EUC), cryptomonads (CRYPT), total eucaryotes (EUCT = EUC + CRYPT), phycoerythrin-rich cyanobacteria (PEC), phycocyanin-rich cyanobacteria (PCC) and total procaryotes (PROC = PEC + PCC), with the concentrations of phosphate (PO_4), nitrate (NO_3), and silicate [$Si(OH)_4$], the percentage of ice-surface irradiance ($\%E_0$), the coefficient of light attenuation (k) and salinity (S). For each taxon, the correlation is computed with the given oceanographic variable holding all the others constant. The abundances of ultra-algae, percent irradiance, and coefficient of light attenuation were log transformed

		PO_4	NO_3	$Si(OH)_4$	$\%E_0$	k	S
EUC	r	−0.121	−0.127	0.032	0.236	0.400	0.246
	n	134	134	67	134	134	134
		ns	ns	ns	••	•••	••
CRYPT	r	−0.226	0.019	0.217	−0.097	0.310	0.283
	n	134	134	68	134	134	134
		••	ns	•	ns	•••	••
EUCT	r	−0.128	−0.100	0.024	0.277	0.377	0.235
	n	132	132	66	132	132	132
		•	ns	ns	••	•••	••
PEC	r	−0.072	0.102	0.046	−0.129	0.386	0.099
	n	135	135	69	135	135	135
		ns	ns	ns	ns	•••	ns
PCC	r	−0.247	0.052	0.127	−0.076	0.280	0.087
	n	133	133	68	133	133	133
		••	ns	ns	ns	••	ns
PROC	r	−0.108	−0.018	0.087	−0.137	0.467	0.055
	n	136	136	69	136	136	136
		ns	ns	ns	ns	•••	ns

•$p < 0.1$, ••$p < 0.01$, •••$p < 0.001$, ns: $p > 0.1$

Table 6. Partial correlations between the abundances of chlorophyll-rich eucaryotes (EUC), cryptomonads (CRYPT), total eucaryotes (EUCT = EUC + CRYPT), phycoerythrin-rich cyanobacteria (PEC), phycocyanin-rich cyanobacteria (PCC) and total procaryotes (PROC = PEC + PCC) in the ice bottom, with the concentrations of phosphate (PO_4), nitrate (NO_3), the percentage of ice-surface irradiance ($\%E_0$), the coefficient of light attenuation (k) and salinity (S) at the ice-water interface. For each taxon, the correlation is computed with the given oceanographic variable holding all the others constant. The abundances of ultra-algae, percent irradiance, and coefficient of light attenuation were log transformed. n = 23

		PO_4	NO_3	$\%E_0$	k	S
EUC	r	0.048	0.222	−0.33	−0.384	0.458
		ns	ns	ns	ns	•
CRYPT	r	−0.388	0.432	−0.326	−0.205	0.238
		ns	•	ns	ns	ns
EUCT	r	0.092	0.205	−0.375	−0.41	0.460
		ns	ns	ns	ns	•
PEC	r	−0.473	0.365	−0.353	−0.363	0.555
		•	ns	ns	ns	•
PCC	r	−0.264	0.275	−0.017	−0.157	0.451
		ns	ns	ns	ns	•
PROC	r	−0.392	0.355	−0.370	−0.383	0.656
		ns	ns	ns	ns	••

•$p < 0.1$, ••$p < 0.01$, ns: $p > 0.1$

To study the relationships between environmental conditions and ice-bottom ultra-algae, abundances were correlated with physical and chemical data from the ice-water interface. Silicate was excluded from the analysis because of missing data. The partial correlation between abundance and k was not significant, but a negative correlation was found with salinity for all taxa except the cryptomonads (Table 6). The abundances of cryptomonads were negatively correlated with nitrate, and those of phycoerythrin-rich cyanobacteria with phosphate.

DISCUSSION

Ultra-algae in ice-covered seas

Our results for the water column support the general idea of a paucity of picoplankton in arctic and subarctic waters (Waterbury et al. 1986, Gradinger & Lenz 1989). In southeastern Hudson Bay, the biomass of ultraplankton was low, but their contribution (26 to 96%) to total chlorophyll *a* in early May was comparable to that measured in other environments. For example, Stockner (1988) reports that freshwater and marine picoplankton (0.2 to 2.0 µm) make up between 1 and 90% of the chlorophyll biomass, and values varying from 20 to 100% have been published for cells <3 µm in tropical, subtropical and temperate waters (Bienfang & Szyper 1981, Herbland & Le Bouteiller 1981, Platt et al. 1983, Takahashi & Bienfang 1983, Takahashi & Hori 1984, Glover et al. 1985a, Putt & Prézelin 1985, Takahashi et al. 1985, Hall & Vincent 1990).

In the ice matrix and to a lesser extent at the ice-water interface, our results clearly indicate that ultra-algae can be important in terms of both biomass and contribution to total chlorophyll *a*. In the ice matrix, where the concentration of the ultra-algae reached 63×10^6 l^{-1}, their contribution to total chlorophyll *a* was substantial (36 to 46%). The value was lower (9 to 41%) at the ice-water interface. Based on size-fractionated chlorophyll *a*, Legendre et al. (1987) suggested the existence of ultra-algae in sea ice. To our knowledge, the present study is the first confirmation, by direct observation, enumeration and identification, of the presence of ultra-algal cells in sea ice.

Legendre et al. (1987) measured the photosynthetic activity of size-fractionated samples collected at the ice-water interface in southeastern Hudson Bay. They found that photosynthetically active cells were present in the <1 µm fraction. Similar measurements were not conducted during the present study, since efforts were devoted instead to careful sampling and detailed taxonomic analysis of small algae. However, significant changes in cell numbers during the course of the study, for all taxa (Table 2), indicate that these organisms were indeed active over the whole sampling period.

Concentrations observed in the water and in the sea ice may not be representative of all arctic or subarctic waters, since the study area is influenced by a river plume. However, it has already been mentioned (see 'Introduction') that river runoff is a major characteristic of the Arctic Ocean (Aagaard & Carmack 1989), so that many arctic and subarctic coastal areas are subjected to influx of fresh water and suspended particles. It follows that values reported for southeastern Hudson Bay may have significance for many other similar areas. Eucaryotes dominated the high concentrations of ultra-algae in the ice and at the ice-water interface, and this dominance increased with distance from shore. Procaryotes dominated the low concentrations of ultra-algae found in the water column. Their relative importance increased with depth and decreased with distance from the mouth of the Great Whale River. Thus, procaryotes were mainly associated with the diluted waters of the Great Whale River plume and the overlying ice cover

Environment and ultra-algae

Particle load

When controlling for the effects of other environmental variables, the concentrations of all ultraplankton taxa, at the ice-water interface and below, were positively correlated with k, the coefficient of diffuse light attenuation, which reflects the suspended particle load. Variations in k were negatively correlated with salinity ($r = -0.78$), because an increasing k is indicative of an increased contribution of particle-loaded freshwaters from the Great Whale River. This suggests that particle load (i.e. turbidity as measured by k) was the main factor favoring ultraplankton in southeastern Hudson Bay. This observation supports the idea of Silver et al. (1986) that suspended particles may favor the development of ultraplankton by supplying the small cells with an alternative habitat to open water. The association of cyanobacteria with suspended particles was also observed by Walker & Marchant (1989) in Antarctic waters, by Caron et al. (1986) in the North Atlantic, by Kaltenbock & Herndl (1992) in the northern Adriatic Sea and by Rogerson & Laybourn-Parry (1992) in the Clyde Estuary (Scotland). Similarly, numerous studies have shown the association of heterotrophic bacteria with particles, e.g. Kottmeier et al. (1985) for Antarctic waters, and Palumbo et al. (1984) for estuarine and coastal water.

Percent irradiance

When controlling for the effects of light attenuation and the other environmental factors, the concentrations of chlorophyll-rich and total eucaryotes were significantly correlated with percent ice-surface irradiance. In ice-covered seas, irradiance is drastically reduced by the snow and ice cover, which often limits photosynthesis (Harrison & Platt 1986, Gosselin et al. 1990). The significant partial correlation between concentrations of eucaryotes and percent irradiance suggests that eucaryotes might be more dependent than procaryotes on light availability. This is confirmed by the significant positive relationship between the ratio of eucaryotes to procaryotes (EUCT/PROC) and percent ice-surface irradiance (Fig. 6a). Thus, procaryotes might be more competitive at low light intensities (as in the ice-covered study area; Fig. 3) than eucaryotes. The opposite has been reported for various other environments by Lewis et al. (1985), Murphy & Haugen (1985) and Glover et al. (1986), but eucaryotes are a diverse group with a variety of photosynthetic characteristics, so they may exhibit a wide range of responses to light intensity and quality. The ratio of phycocyanin-rich to phycoerythrin-rich cyanobacteria (PCC/PEC) was also positively related to percent irradiance (Fig. 6b). According to Lewis et al. (1985) and Pick (1991), the shift between eucaryotes and procaryotes as well as the shift between phycoerythrin-rich and non-phycoerythrin-rich cyanobacteria would be linked not only to changes in total irradiance, but also to changes in the spectral quality of light. If this was the case in Hudson Bay, the overall structure of the ultraplankton assemblage could reflect competition among different pigment types. This would explain (1) the dominance of eucaryotes in the ice and at the ice-water interface, and that of procaryotes in the water column, and (2) the increasing preponderance of eucaryotes with distance from shore, as well as the association of procaryotes with the turbid waters of the Great Whale River plume.

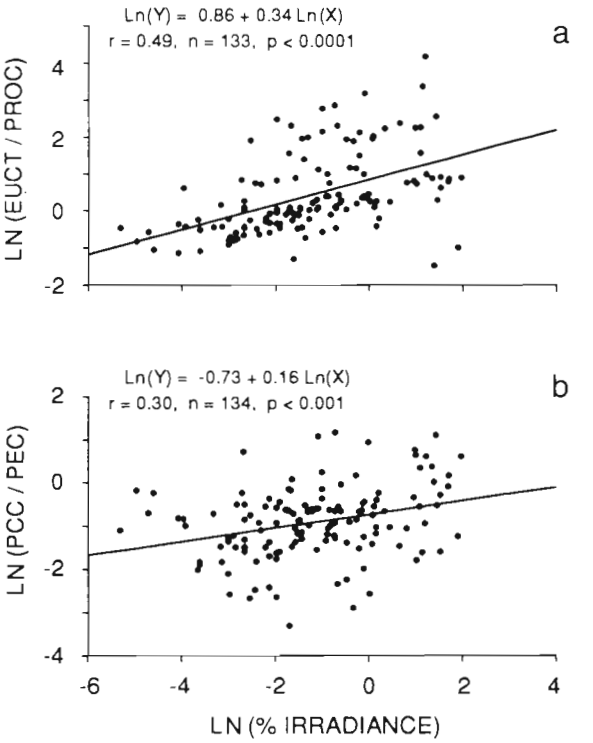

Fig. 6. Ratios of (a) eucaryotes to procaryotes (EUCT/PROC) and (b) phycocyanin-rich to phycoerythrin-rich cyanobacteria (PCC/PEC) plotted as functions of percent ice-surface irradiance, for the 5 stations and the whole sampling season (22 April to 20 May 1990)

Salinity and temperature

In the present study, salinity and temperature were highly correlated ($r = -0.98$). Water temperature varied from −1.60 to +0.09 °C while corresponding variations in salinity ranged between 1.29 and 31.13‰. Ice tem-

peratures measured on 21 April at 140 cm (from the snow-ice interface) and on 3 May at 115 cm were, respectively, -8.65 and -2.25°C (Éric Hudier pers. comm.). Because the respective effects of salinity and temperature on ultra-algae cannot be separated, the significant partial correlations between salinity and ultra-algal abundance may reflect ecophysiological effects of temperature as well as of salinity.

For ultraplankton in general, the maximum numbers of ultra-algae, eucaryotes and procaryotes occurred in the ice matrix. The concentration of all ultra-algal taxa was positively correlated with salinity measured at the ice-water interface and, likely, with salinity of the ice, since the salinity of melted ice exhibits a positive inshore-offshore gradient which parallels the salinity gradient at the ice-water interface (Legendre et al. 1991). Salinity of the ice is positively correlated with the rate of ice growth, which was identified by Legendre et al. (1991) as the most important factor controlling ice algal biomass. Moreover, salinity and the rate of ice growth determine ice structure (volume of brine and gas pockets). Ultra-algae did thrive at the coldest temperatures, presumably taking advantage of the favourable substratum offered by porous sea ice.

Eucaryotes were most abundant in the ice, where they showed some (positive) dependency on salinity. At the ice-water interface and below, concentrations of chlorophyll-rich eucaryotes, cryptomonads and total eucaryotes were positively correlated with salinity. Thus, at the ice-water interface and below it, salinity or temperature would primarily affect the eucaryotic component of the ultra-algal assemblage. This is in accordance with the negative temperature dependence of eucaryotes in the North Atlantic (where temperatures ranged between 5.4 and 27.5°C; Murphy & Haugen 1985) and the Greenland Sea (where temperatures varied from -0.8 to 0.6°C; Legendre et al. 1993). Yet, in the northern Baltic Sea, eucaryotes are abundant throughout the year, showing no clear correlation with surface water temperature (Kuosa 1991).

Similarly to eucaryotes, procaryotes were most abundant within the sea-ice. However, their abundances were not significantly correlated with salinity or temperature. This does not agree with the positive relationship between cyanobacteria abundance and temperature suggested in several studies (Murphy & Haugen 1985, Waterbury et al. 1986, Marchant et al. 1987, Gradinger & Lenz 1989; however, these results were for temperatures higher than those measured in the present study) and supported by examples from oceans (El Hag & Fogg 1986, Jochem 1988, Kuosa 1990, Legendre et al. 1993) and lakes (Caron et al. 1985, Weisse 1988). Nor does it agree with the very low growth rate found for heterotrophic bacteria at near-freezing temperature (Christian & Wiebe 1974). An explanation might be the existence of a cold-water race or species of cyanobacteria, as suggested by Shapiro & Haugen (1988) for the North Atlantic. An interesting alternative, which does not exclude the previous hypothesis, is offered by the positive relationship between procaryotes and substratum (i.e. particles) observed in the water column. Substratum provided by the ice matrix and the ice-water interface could favor cyanobacteria, thus balancing the negative effect of cold temperature.

Nutrients

Partial correlations between the concentrations of ultra-algal taxa and those of nutrients, when significant, were generally negative. According to Stockner (1988), small cells have rapid nutrient uptake rates, which enable them to compete successfully with large cells at very low nutrient concentrations (Raven 1986). This may explain why picoalgae generally dominate primary production in nutrient-depleted waters (Søndergaard et al. 1991), although exceptions to this pattern may be found (Hall & Vincent 1990, Kuosa 1991). In southeastern Hudson Bay, the water column in spring was not oligotrophic. It follows that nutrient availability had apparently little to do with the dynamics of ultra-algae under the ice cover, unless nutrients could compensate for the negative effect of low temperature on growth rate, as was observed for organic substrates in the case of heterotrophic bacteria (Pomeroy & Wiebe 1988, Pomeroy et al. 1991, Wiebe et al. 1992).

Conclusions

In the area of southeastern Hudson Bay influenced by the plume of the Great Whale River, the main factor controlling the development of ultra-algae, in spring, is the availability of solid substratum as measured in the water column by the coefficient of diffuse light attenuation (i.e. particle load) and, for the ice, as a result of ice structure. This would explain why these algae are most abundant in the ice matrix and at the ice-water interface and why concentrations in the water column are positively correlated with sediment-loaded river water.

Note added to proofs. According to Wood et al. (1985), there are 2 types of phycoerythrin-rich cyanobacteria. In the present study, type II PRC were not identified as such (under green light). Some PEC cells may have thus been counted as phycocyanin-rich cyanobacteria. In some cases, the ratio PCC/PEC could then have been slightly overestimated, which would not, however, change the conclusions of the study.

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