

Horizontal distribution of sea-ice microalgae: environmental control and spatial processes (southeastern Hudson Bay, Canada)*

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ABSTRACT: Microalgae from the ice bottom and the ice-water interface were collected in southeastern Hudson Bay (Canada) along inshore-offshore transects during April and May 1989 and 1990. The transects extended from the mouth of the Grande rivière de la Baleine (Great Whale River; almost fresh waters) to 25 km offshore (saline waters). Salinity and nutrients at the ice-water interface exhibited marked horizontal gradients which were more pronounced in 1990 than in 1989. Algal concentrations as well as species diversity and evenness also presented horizontal structures. Canonical Correspondence Analyses (CCA) showed that a large part of the variation in species abundances (i.e. 43 to 50 %) could be explained by environmental variables, especially salinity. Given the spatial structure of salinity, Partial CCA were used to assess the direct relationships between environmental variables and algae, independent of purely spatial processes. In 1990 (strong inshore-offshore gradient), most of the effect of salinity on algal abundances reflected the spatial structure determined by the river plume. At the interface, there was a strong increase of taxonomic richness and diversity and of biomass at the edge of the under-ice plume, which reflected an ecotone situation. The significant positive relationship between species richness and algal biomass, at the ice-water interface, suggests that the interdispersion of habitats, which characterizes ecotones, had a direct impact on the production of organic matter in the under-ice plume.

KEY WORDS: Algae · Sea ice · Spatial process · Ecotone

INTRODUCTION

In polar seas, large concentrations of microalgae often develop in the bottom of the first-year sea ice and at the ice-water interface. It has been hypothesized that these microalgae are instrumental in seeding phytoplankton assemblages at the time of ice melt (Horner 1976, 1985, Horner & Schrader 1982, Michel et al. 1993). The organic matter synthesized by ice algae may be important for marine polar food webs, and also for the global flux of carbon (Legendre et al. 1992).

However, the relationships between algal assemblages in the ice bottom, at the ice-water interface and in the underlying phytoplankton are not well known.

Because of the ecological importance of ice-algal production, the environmental factors controlling abundance, growth and composition of algal assemblages have already been the subject of a number of studies. Factors invoked include nutrient limitation at the ice-water interface (Maestrini et al. 1986, Cota et al. 1987, Demers et al. 1989, Gosselin et al. 1990), growth rate of the ice (Legendre et al. 1991), irradiance in the ice bottom (Gosselin et al. 1986), cumulative seasonal effect of surface light in relation to snow depth (Welch et al. 1991), salinity (Poulin et al. 1983, Legendre et al. 1992), and time/space variability of conditions in the microenvironment of ice algae (Cota et al. 1991, Legendre et al. 1991).

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The present study was conducted at the mouth of the Grande rivière de la Baleine (Great Whale River), near Kuujjuarapik (northern Québec, Canada; see Fig. 1), which is one of the major rivers flowing into southeastern Hudson Bay. The expanse of the under-ice plume of this river during the spring may reach 1000 km² (Lepage & Ingram 1991). Its extent and location vary as the result of river runoff, tides and currents. The general circulation in Hudson Bay is cyclonic, with current speed reaching 0.19 m s⁻¹ near the sampling site (Prinsenbergh 1986). The present paper investigates the structure of algal assemblages in the ice bottom and at the ice-water interface, along an inshore-offshore transect across the under-ice plume of the Great Whale River. The paper (1) quantifies the fraction of the variability in species assemblages which is explained by environmental factors, and (2) assesses the role of purely spatial processes (i.e. independent of measured environmental variables) and their importance relative to environmental variables.

MATERIALS AND METHODS

Sampling and laboratory analyses. Sampling was conducted from 9 April to 2 May 1989 and from 22 April to 8 May 1990, on the first-year sea ice of southeastern Hudson Bay, Canada. The 5 stations sampled each year (Fig. 1) were located along south-north transects that extended from the mouth of the Great Whale River (almost fresh waters) to ca 25 km offshore in Hudson Bay (saline waters). Samples were collected by SCUBA divers from the ice bottom (submersible ice corer: 3.5 cm long × 6 cm diameter) and at the ice-water interface (2.2 l syringe 'slurp gun' sampler). Samples from the interface were free of ice. Subsamples were filtered in the field on Whatman GF/F filters

(syringes equipped with Sweenex filter holders), and frozen in cryovials at -60°C for later determination of dissolved inorganic nutrients. In addition, water samples from 2.5 and 10 m depths were collected using a Little Giant submersible pump. All water samples were kept in dark thermos bottles, and transported by helicopter to a shore based laboratory (Centre d'études nordiques, Kuujjuarapik) within 20 min of collection. Vertical profiles of temperature and salinity were recorded using a Seacat SBE 19 CTD. Irradiance incident at the surface of the ice (I_0) and in the water at the undersurface of the ice (I_z) were measured with a Biospherical scalar irradiance meter (PAR: 400 to 700 nm).

Sampling dates at the 5 stations are given in Table 1. Whole transects (i.e. the 5 stations) were sampled 3 times during each of the 2 seasons. In the remainder of the present paper, only these complete 5-station transects are considered when dealing with biological variables, while all the available samples (i.e. complete and incomplete transects) are used when examining environmental variables.

Subsamples (25 to 115 ml for melted ice, and 20 to 100 ml for the ice-water interface) were filtered on Poretics 5 µm polycarbonate membranes and on GF/F glass fiber filters, for the spectrophotometric determination of chlorophyll *a* (chl *a*) after 24 h extraction in 90% acetone at 4°C (Parsons et al. 1984), using the equations of Jeffrey & Humphrey (1975). Since the present paper focusses on algae counted under light microscopy (generally >5 µm), chl *a* concentrations given here are only for the >5 µm fraction. Additional subsamples (20 ml for melted ice, and 200 ml for the interface and the water column) were preserved with acidic Lugol's solution for further identification and enumeration of algae >5 µm under the inverted microscope (Lund et al. 1958). Concentrations of phosphate (PO₄) and nitrate (NO₃ + NO₂) were determined using an autoanalyzer (Technicon in 1989, and Alpkem in 1990; Parsons et al. 1984).

Data analysis. The various environmental measurements were interpolated over the sampled spatio-temporal domain, using a squared inverse distance algorithm. Species diversity (*H*) and evenness (*J*) were calculated as: $H = -\sum p_i \log_2 p_i$ (Shannon & Weaver 1963) and $J = H/H_{\max} = H/\log_2 S$ (Pielou 1975), where p_i and *S* are the proportions of the various species (*i*) and the total number of species, respectively, in a given sample. Microflagellates were excluded from these

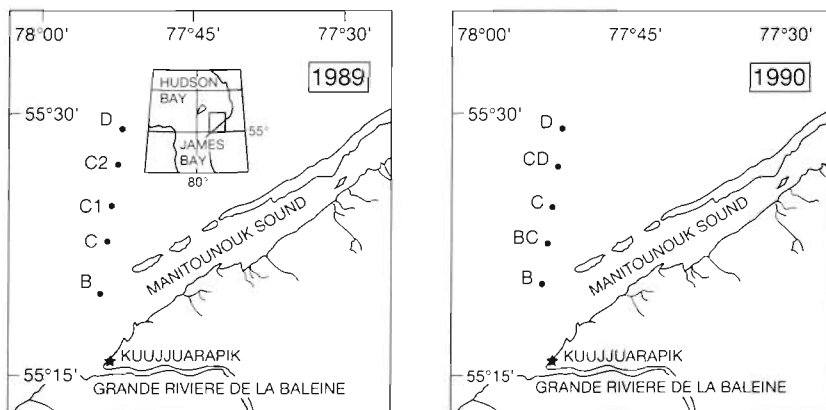


Fig. 1. Map of southeastern Hudson Bay (Canadian Arctic) showing the positions of the sampling transects (Stns B to D) near the mouth of the Great Whale River, in 1989 and 1990

Table 1 Sampling dates in 1989 and 1990 (Julian days), and timing of the 3 inshore-offshore 5-station transects (t_1 , t_2 and t_3). (1) Data on environmental variables, but not on chl *a* concentrations; (2) data on chl *a* concentrations, but not on environmental variables; (3) data on chl *a* concentrations at the ice-water interface only, and not on environmental variables; (4) data on environmental variables, and on chl *a* concentrations at the ice-water interface only; (5) data on environmental variables, and on chl *a* concentrations in the ice bottom only; and (6) complete data set

Date in 1989		Station					Date in 1990		Station				
		B	C	C1	C2	D			B	BC	C	CD	D
99		1	–	–	–	1	112		1	–	–	–	–
101	t_1	–	6	6	6	–	113	t_1	–	–	–	–	4
102	t_1	6	–	–	–	6	114	t_1	4	4	4	4	4
104		6	–	–	–	3	115	t_1	4	–	–	–	–
107		2	–	–	–	6	116		–	–	–	–	4
108		–	6	–	6	–	118		6	–	–	–	–
109		6	–	–	–	6	119	t_2	–	–	–	–	4
111		6	–	–	–	6	120	t_2	–	6	6	6	–
113		6	–	–	–	6	121	t_2	6	–	–	–	–
114	t_2	–	6	6	6	–	122		–	–	–	–	6
115	t_2	6	–	–	–	6	124		6	–	–	–	–
117		1	–	–	–	–	125	t_3	–	–	–	–	4
119	t_3	6	–	–	6	6	126	t_3	–	5	6	6	–
120	t_3	1	6	6	4	6	127	t_3	6	–	–	–	–
							128		–	–	–	–	6
							130		1	–	–	–	–
							132		–	–	1	1	1

computations because they were not identified to the same taxonomic level as other cells (i.e. they were lumped into a single, supraspecific group). The indices of diversity and evenness were combined to calculate trend surfaces using an inverse squared distance algorithm (SYGRAPH; Wilkinson & Leland 1989).

The links between environmental variables and the observed abundances of microalgae were quantified using Canonical Correspondence Analysis (CCA; Ter Braak 1986a, b, 1987). In this technique, which is an extension of reciprocal averaging (Hill 1973), the ordination axes are linear combinations of the environmental variables. Species and environmental variables are plotted in the same space, which is defined by the chi-squared distance. In the ordination plots, species are represented by dots and environmental variables by vectors. The direction and length of each environmental vector are determined by the correlation of the environmental variable with the ordination axes and by the eigenvalues of the axes. CCA selects the linear combination of variables that maximizes dispersion of species in the ordination space. This is termed 'constrained ordination' (for more information see Hill 1973, Ter Braak 1985, 1986a, b, 1987, Jongman et al. 1987). The orthogonal projection of species dots on environmental vectors reflects the approximate ranking of the weighted averages of species with respect to each environmental variable (Ter Braak 1987). In other words, this projection specifies the position of the center (optimum) of the unimodal distribution of each species on each environmental variable. The multi-

collinearity among environmental variables was assessed by the Variance Inflation Factor, $VIF = 1/(1-R_j^2)$ (Montgomery & Peck 1982), where R_j is the coefficient of multiple linear correlation between environmental variable j and the other environmental variables included in the analysis. The 95% confidence intervals for the 2 groups of diatoms (pennate and centric) are represented on the ordination plots by ellipses (Sokal & Rohlf 1981).

The influence of purely spatial processes was estimated using Partial Canonical Correspondence Analysis (PCCA; Ter Braak 1988, Borcard et al. 1992). Using this method, it is possible to remove the effects of space, treated as a covariate, by means of multiple linear regression. Computations were done with the CANOCO programme of Ter Braak (1988). In order to do so, the potentially explanatory variables were subdivided into 2 sets: the environmental variables, and 2 covariates characterizing the spatial influence, i.e. $V_1 = 1/D$ and $V_2 = 1/D^2$ (D = Euclidean distance between stations; $R^2 = 0.90$ and 0.86 between the first axis and the combination of V_1 and V_2 , for the ice and the interface, respectively). Borcard et al. (1992) have shown that the total variation of a species data matrix can be partitioned into 4 fractions (see Fig. 8): (1) non-spatial environmental variation in the species data, (2) spatial structuring in species data shared by environmental data, (3) spatial patterns in species data that are not shared by environmental data, and (4) fraction of the species variation explained by neither the spatial coordinates nor the environmental data.

RESULTS

Environmental conditions and biomass of microalgae

Conditions at the ice-water interface were largely determined by variations in the horizontal extent of the under-ice plume of the Great Whale River (Fig. 2). Overall, the horizontal salinity gradient was much more pronounced during most of 1990 than during 1989. Horizontal variations in the depths of isohalines show marked differences between the 2 years (Fig. 2). Both the horizontal extent and the depth of the under-ice plume (boundary at isohaline 25 psu) were greater in 1989 than in 1990. In 1989, the plume was 7.5 m thick and it reached Stn C2, whereas in 1990, the plume was only 5 m thick and it did not extend beyond Stn C. In 1990, and to a lesser extent in 1989, the inshore-offshore distributions of both nitrate and phosphate isopleths paralleled those of salinity (Fig. 3a, c, d). Irradiance at the undersurface of the ice exhibited more coherent spatio-temporal patterns during 1990 than during 1989 (Fig. 3b).

Spatio-temporal distributions of chl *a* in the ice bottom and the ice-water interface were plotted on the same coordinates as those used for the environmental variables (Fig. 3e, f). In the 2 years considered, the ice-bottom algal biomass exhibited an overall inshore-offshore gradient, the highest values of chl *a* being observed at offshore stations (Stns C1 to D in 1989, and C to D in 1990). At the ice-water interface, the distribution patterns of chl *a* were mostly independent of the

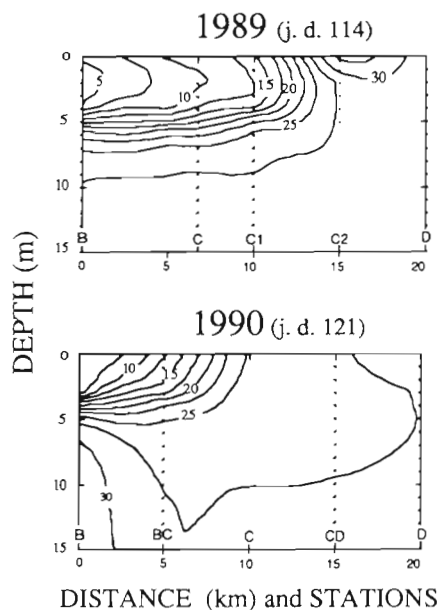


Fig. 2. Horizontal variations in the depths of isohalines (psu) at midseason (Transect t_2 ; Table 1)

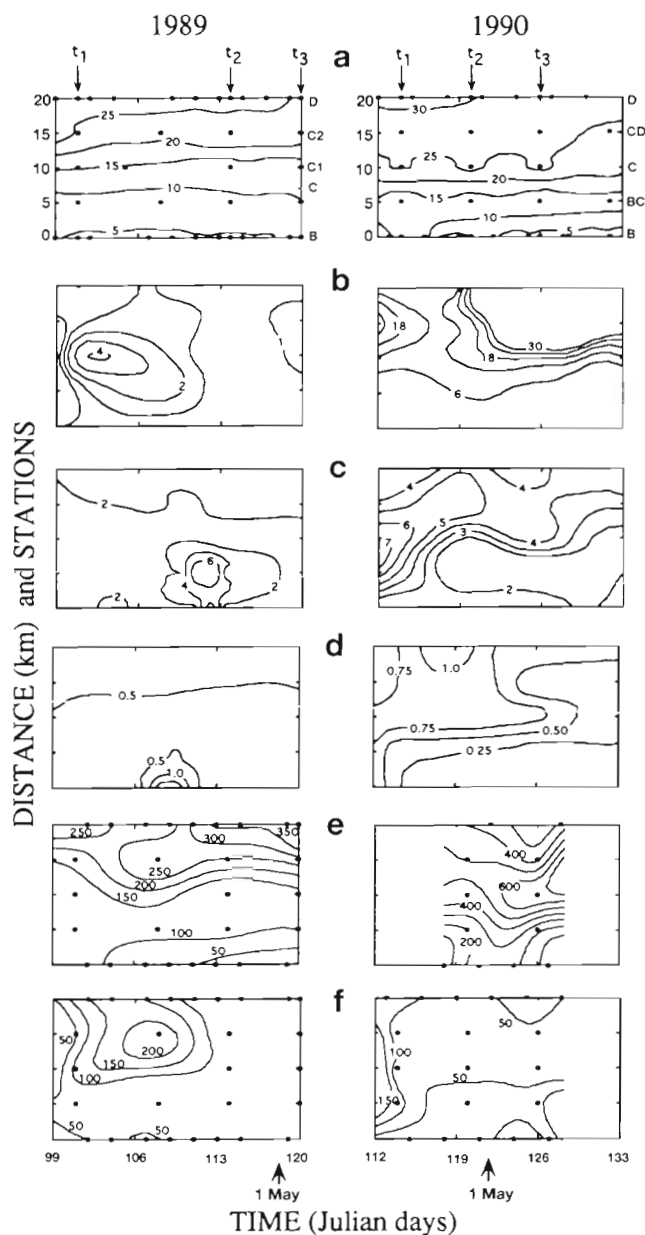


Fig. 3. (a) Spatio-temporal changes in the isopleths of salinity (psu) at the ice-water interface; (b) irradiance at the undersurface of the ice ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$); (c) nitrate and (d) phosphate (mmol m^{-3}) at the interface; and chl *a* (mg m^{-2}) (e) in the ice bottom and (f) at the ice-water interface. Sampling points are indicated by dots in (a), (e) and (f)

distance to shore. The distribution of chl *a* was quite patchy, the highest values being either offshore (Stn C2 in 1989) or inshore (Stn B in 1990).

The algal biomass ($\text{mg chl } a \text{ m}^{-2}$ for algae $>5 \mu\text{m}$; Fig. 4) in the ice bottom in 1989 exhibited an inshore-offshore gradient which became more pronounced as the season progressed. Chl *a* reached a maximum value of 21.4 mg m^{-2} at offshore Stn D. In 1990, the

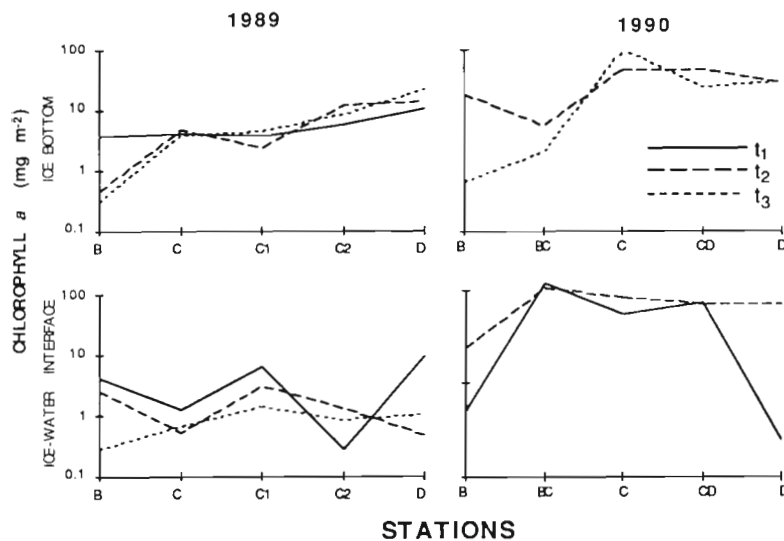


Fig. 4. Spatio-temporal variations of microalgal biomass ($\text{mg chl } a \text{ m}^{-2}$; algae $> 5 \mu\text{m}$) in the ice bottom and at the ice-water interface in 1989 and 1990

concentrations of ice-algal chl *a* at all stations (maximum of 2.4 mg m^{-2}) were of the same order of magnitude as those observed at the inshore stations in 1989 (0.3 to 4.8 mg m^{-2} , at Stns B, C and C1), and the highest values occurred at intermediate stations along the transect. Concentrations of algae at the ice-water interface in 1989 were generally higher offshore than inshore but, contrary to the situation observed in the ice bottom, they progressively decreased as the season progressed. In 1990, algal concentrations at the interface were much higher than in 1989 (maximum of 100.6 mg m^{-2} in 1990 at Stn C, and 9.2 mg m^{-2} in 1989 at Stn D) and, as in the case of the ice bottom, the highest values were observed at intermediate stations.

Taxonomic richness, diversity and evenness

The total number of taxa varied from 76 to 92 in the ice bottom, and from 38 to 96 at the interface where interannual variability was higher (Table 2). The main taxonomic groups in the ice bottom and at the ice-water interface were pennate diatoms (66 to 70 % of the total number of species in 1989, and 52 to 64 % in 1990, all stations pooled) and microflagellates (16 to 23 and 23 to 27 %), with much lower proportions for centric diatoms (5 to 6 and 5 to 8 %) and dinoflagellates (4 to 6 and 4 to 8 %).

The average diversity of algae in the ice bottom and at the ice-water interface increased from inshore to offshore (Fig. 5). At the offshore stations (Stns C2 and D in 1989 and Stns C to D in 1990), diversity was higher for algal assemblages in the ice and at the interface than for the phytoplankton assemblages at 2.5 and 10 m. In 1990, the highest diversities at the ice-water interface occurred at intermediate stations. In 1989, there was a

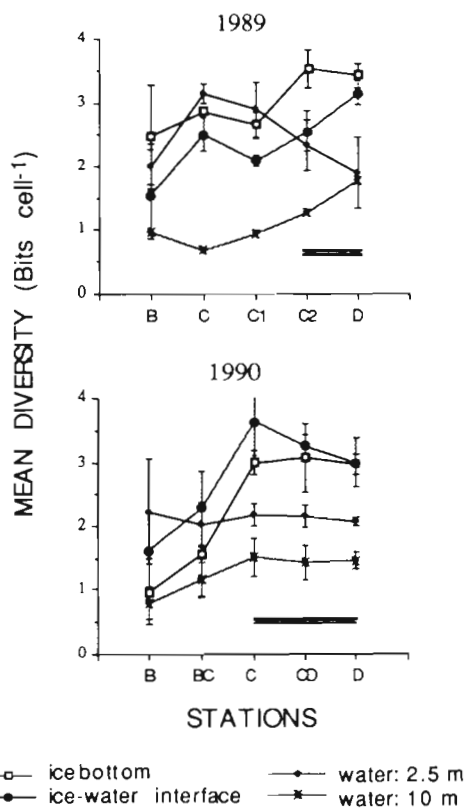


Fig. 5. Variations of mean taxonomic diversity (microflagellates excluded) along the transect, in the ice bottom, at the ice-water interface and at 2 depths in the upper water column. Underlined: stations where the diversity of algae in the ice and at the interface is higher than that of water column phytoplankton

Table 2. Numbers of algal taxa in the ice bottom and at the ice-water interface along the 3 inshore-offshore 5-station transects (t_1 , t_2 and t_3) in 1989 and 1990

Transects	Ice bottom		Ice-water interface	
	1989	1990	1989	1990
t_1	84	86	57	67
t_2	76	92	60	91
t_3	85	92	38	96
Average	82	90	52	85

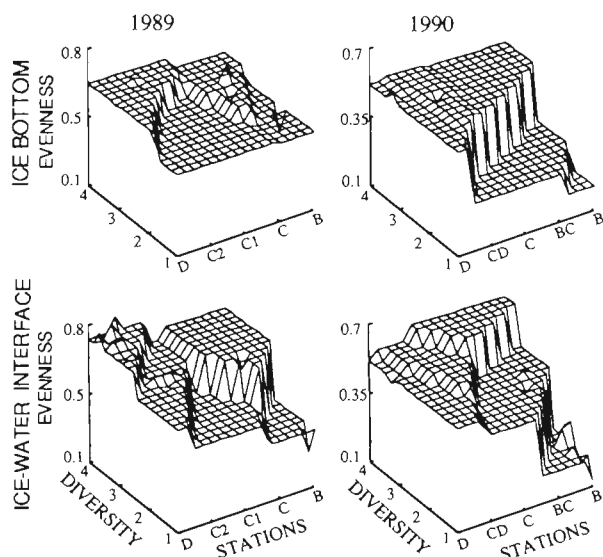


Fig. 6. Trend surfaces combining mean taxonomic diversity and evenness, along the transects, for the ice bottom and the ice-water interface

phytoplankton bloom in coastal waters (Stns C to C2), which corresponded to the observed high species diversities at 2.5 m depth.

Trend surfaces combining evenness and diversity are shown in Fig. 6. For both the ice bottom and the ice-water interface, there was a general increase of the 2 indices in the offshore direction, which resulted in a slope in the trend surfaces. At the ice-water interface in 1990, this tendency was not monotonic, since the intermediate stations developed a combination of high evenness and diversity.

Environmental variables and species diversity

Physical and chemical variables

Fig. 7 (Canonical Correspondence Analyses) shows the relationships between measured environmental variables and species composition. A large fraction of the variation in the abundances of species can be explained by the environmental variables, i.e. 43% in 1989 and 44% in 1990 for the ice bottom, and 45% in 1989 and 50% in 1990 for the ice-water interface.

Algal species from the ice bottom were positioned in 1989 in a space defined primarily by nitrate ($r = -0.57$ with the first axis), while the second axis was mainly correlated with salinity, nitrate, phosphate and the coefficient of light attenuation ($r = -0.48, -0.54, -0.66$ and 0.54 , respectively). The species were mainly dispersed along this second axis. The 95% confidence intervals for the 2 groups of diatoms were wide. In 1990, the first axis was mainly correlated with phosphate and salinity ($r = -0.65$ and -0.90), and the second axis with nitrate ($r = -0.71$). The dispersion of species was narrower than in 1989, and mainly along the first axis. The 95% confidence intervals for the 2 groups of diatoms were clearly distinct, and the dispersion of centric diatoms was highest along the first axis.

Algal species from the ice-water interface were, in 1989, dispersed in a space defined primarily by a first axis which was significantly correlated with phosphate, irradiance and salinity ($r = -0.48, -0.50$ and 0.39 , respectively). The second axis was equally correlated with all the environmental variables. The species

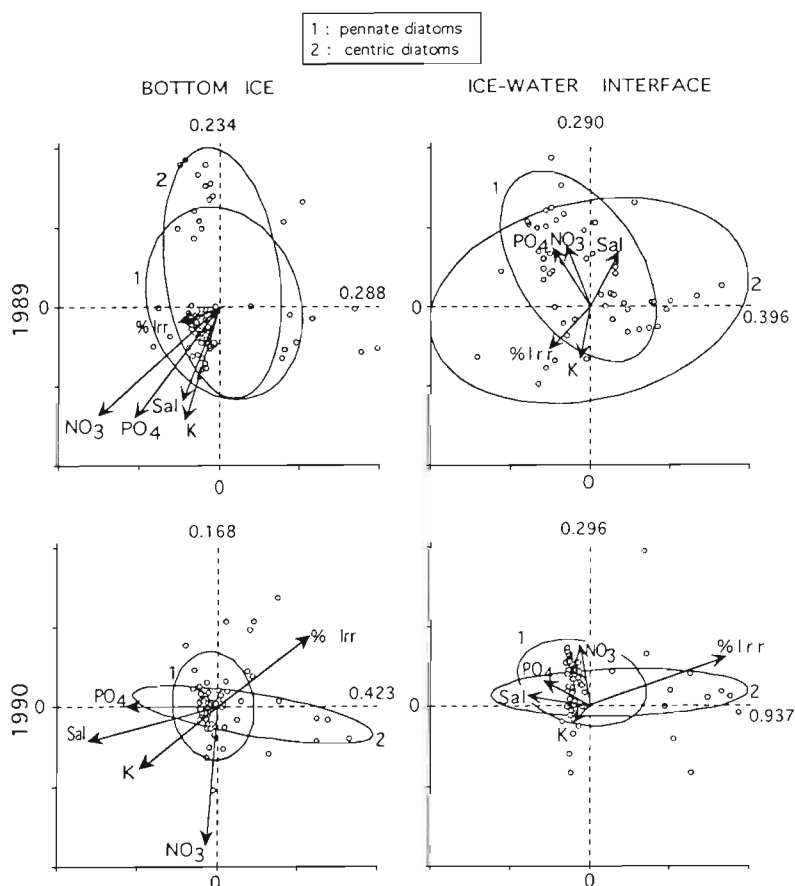


Fig. 7. Canonical Correspondence Analyses. Positions of environmental variables (vectors) and species (dots) in the space of the first 2 canonical axes, and 95% interval ellipses for (1) pennate and (2) centric diatoms. Eigenvalues are given for each axis

were almost equally dispersed along the 2 axes. The 95% confidence intervals for the 2 groups of diatoms were wide. During 1990, the first axis was defined by salinity ($r = -0.97$) and also irradiance ($r = 0.71$), while the second axis was mainly correlated with nitrate ($r = 0.61$). The first axis explained 30% of the total variation in species, whereas it accounted for 16 to 20% in the other 3 cases. The dispersion of species was lower than in 1989. The 2 groups of diatoms were well separated, with the centric diatoms being mainly dispersed along the first axis.

Results of the CCA analyses separate the 2 groups of diatoms well, for both the ice bottom and the ice-water interface, especially in 1990. Overall, centric diatoms were mostly correlated with salinity. A much stronger salinity gradient was observed in 1990 than in 1989, with parallel differences in algae, i.e. lower dispersion of species on the environmental vectors, and better separation between the 95% confidence intervals for the 2 groups of diatoms.

Spatial processes

The existence of parallel inshore-offshore gradients for several environmental variables raises the possibility that spatial processes, which would influence these variables but are not included in the analyses, are present. If a large part of the variation in species data could be explained by spatial processes, the correlations with environmental variables would be spurious. In order to assess the direct and separate effect of environmental factors on the distribution of algae in the ice bottom and at the ice-water interface, Partial CCA (PCCA) were conducted, with the environmental variables and space used in turn as covariates.

Fig. 8 shows that the environmental and spatial variables ($a + b + c$) always explained more than half the total variation in species abundances. In 1989, 34 and 35% of the variation in the abundances of algal species in the ice bottom and at the ice-water interface, respectively, were explained by the nonspatial environmental variation (a), while only 9 to 10% was explained by the spatial structuring in the species data shared by the environmental data (b). Approximately one quarter (23 and 27%) of the variation was explained by the distance from the shore (i.e. the purely spatial processes, c). In 1990, the nonspatial environmental variation (a) explained a smaller fraction of the variation in algal species than in 1989 (29 and 25% for the ice bottom and the ice-water interface, respectively), while the spatial structuring shared by the environmental data (b) increased to 15 and 25%, respectively. At the ice-water interface, the spatial structuring in species shared by the environmental

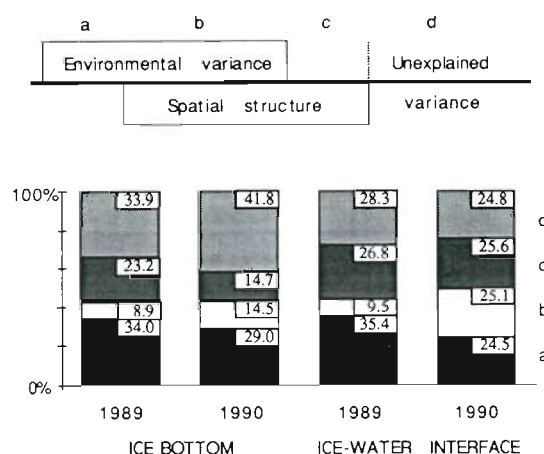


Fig. 8. Upper panel: partitioning the variance of a species data matrix into 4 fractions (a–d), using Partial Canonical Correspondence Analysis (after Borcard et al. 1992). Lower panel: percentage variation of the bottom-ice and ice-water interfacial algal species explained by the environmental variables and by space, respectively (a–d as in the upper panel)

variables and the purely spatial pattern ($b + c$) explained a larger fraction of the variance in species abundances during 1990 (51%) than in 1989 (36%), but the share of the purely spatial processes (c, 26%) was similar to that of 1989.

Salinity was identified as one of the main environmental factors related to the distribution of species assemblages, especially under conditions of strong inshore-offshore gradients (1990; Fig. 7 and corresponding results). In order to investigate whether the effects of salinity on species are direct or linked instead to the spatial structure, PCCA were computed for the ice-water interface, with salinity and space used in turn as covariates. Results (Fig. 9) show that, in the presence of a strong inshore-offshore gradient (1990), most of the effect of salinity was spatial. Under conditions of a smoother gradient (1989), the direct effect of salinity on species assemblages is slightly more evident, and the spatial structuring of the species shared

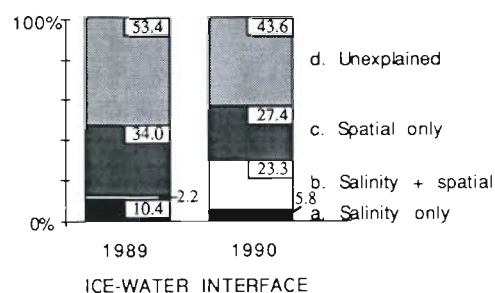


Fig. 9. Percentage variation of the algal species at the ice-water interface explained by salinity and by space, in 1989 and 1990 (a–d as in Fig. 8)

by salinity is very small. In both cases, the direct effect of salinity on species is small ($\leq 10\%$), and the spatial processes identified account for more than one third (36 to 51 %) of the variation in algal species at the ice-water interface.

For each year, species at the ice-water interface were pooled over the sampling season for each station, and the ranges of distribution along the transect were ordered according to the relative abundances of species (Fig. 10). In 1989, few species were present at all stations, the 5 most abundant ones (at the bottom of the figure) being restricted to only one or a few stations. Species richness was similar at all stations, and there was no trend in replacement of species along the transect. In 1990, the situation is different. The most abundant species are present at all stations, without discontinuities, and there is a marked difference in species richness between the inshore (Stns B to BC) and the offshore (Stns C to D) domains. High species richness in the transition zone (Stns C to CD) is caused by the combination of inshore and offshore species and also by the presence of species that are not found elsewhere, i.e. they are highly specialized.

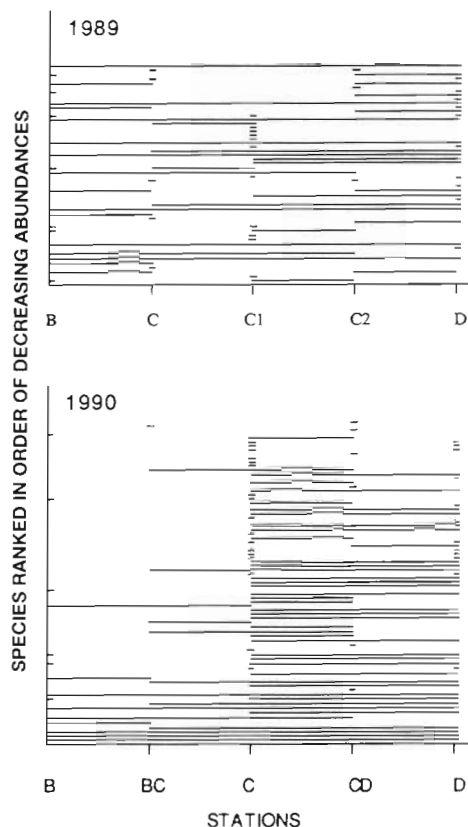


Fig. 10. Spatial ranges of the various species along the transects at the ice-water interface, pooled over the whole sampling season. Species are ordered according to their relative abundances

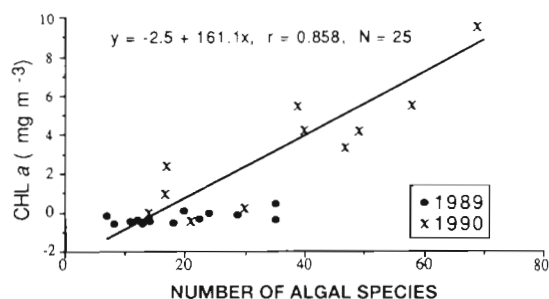


Fig. 11. Relationship between the number of algal species at the ice-water interface and chlorophyll a biomass. Model II regression; data pooled for all stations and the 2 sampling years

Fig. 11 shows the scatter diagram and model II linear regression between algal biomass ($\text{mg chl } a \text{ m}^{-3}$) at the ice-water interface and the number of algal species, at each station and time, in 1989 and 1990. There is a strong positive relationship between the 2 variables ($p < 0.01$). This indicates that algal biomass at the interface is strongly related to the number of algal species.

DISCUSSION

Environmental control of algal biomass and species abundances

The observed variations in the spatio-temporal distributions of environmental variables (Fig. 3a–d) and of algal biomass (Fig. 3e, f) suggest that the control exerted on biomass was not the same in the ice bottom and at the ice-water interface. In the ice bottom, the highest algal biomasses were found, in 1989 and 1990, at offshore stations (Fig. 3e). Their distributions generally followed the salinity gradient and, in some respect, the nutrient gradients (Fig. 3a, c, d). In 1989, the distributions were independent of irradiance (Fig. 3b) and they were not strongly related to the inshore variations of nutrient concentrations (Days 107 to 119; Fig. 3c, d). This indicates that, in 1989, irradiance was not the main factor that limited algal growth in the ice bottom. At the ice-water interface in 1989, the highest biomasses were distributed over a narrow spatio-temporal domain (Fig. 3f) that corresponded to the highest under-ice irradiances (Fig. 3b). In 1990, the patterns of salinity, irradiance and nutrients were quite similar, but they did not correspond to that of the algal biomass. Moreover, there was a strong increase in biomass at the interface for stations located midway along the transect (Fig. 4), i.e. at the edge of the river plume. Similar chl *a* maxima have often been observed in fronts. Holligan (1981) concluded that the high bio-

masses in frontal areas are not the result of a simple physical accumulation, within convergent or divergent flows, and that the coupling between high biomasses of phytoplankton and similarly distributed zooplankton suggests an overall balance between primary and secondary production.

It could be imagined that algae in the ice bottom should influence the distributions of algal biomasses at the ice-water interface, through either light attenuation or direct export of cells. However, the very different distribution patterns of algal biomass in the environments (Figs. 3e, f & 4) suggest that this is not the case. Therefore, in terms of biomasses, the ice bottom and the ice-water interface appear to be uncoupled.

Previous studies have generally reported higher diversities for the ice-algal assemblages than for under-ice phytoplankton (e.g. Margalef 1977, Horner 1985, Hsiao 1988, 1992). This classical scheme was observed at the offshore stations (underlined in Fig. 5), where the diversity of assemblages in the ice bottom and at the ice-water interface was higher than that of phytoplankton. In contrast, patterns at coastal stations were more complex, mainly because of the variability in diversity at 2.5 m depth. The highest species diversities for the ice bottom assemblages were observed offshore, whereas for the ice-water interface in 1990, these occurred in mid-salinity waters (15 to 25 psu; Fig. 2) where the diversity reached a very high value ($H = 4.4$ at Stn C, before the freshet; Fig. 5).

Algal differences between the ice bottom and the ice-water interface are summarized in Table 3. These concern species richness (Table 2), the spatio-temporal distribution of biomass (Figs. 3e, f & 4), diversity (Fig. 5), and other characteristics discussed below. Overall, the ice bottom and the ice-water interface appear to be 2 distinct ecological compartments.

Horizontal distributions of species

A 'mature' biological system is characterized by high diversity and evenness (e.g. Frontier 1985, 1990). The combination of these 2 indices (Fig. 6) indicates that the maturity of the assemblages in the ice bottom increased from inshore to offshore. Since increases in diversity are often controlled by spatial heterogeneity (e.g. Frontier 1990), changes observed for the ice bottom assemblages (Figs. 5 & 6) may have been linked to changes in the structure of the ice. Indeed, the number and size of brine cells increase as a function of both sea water salinity and the rate of ice growth (Weeks & Lofgren 1967). This increases the surface available for colonization by algae, and may be the main factor regulating the dynamics of algal populations in the ice bottom (Poulin et al. 1983, Legendre et al. 1991). However, at the ice-water interface in 1990, there was a zone of high maturity for stations located at the edge of the under-ice plume, within the range of salinities 15 to 25 psu (Figs. 2, 5 & 6). Local discontinuities between adjacent systems, in the rate of change for the structure or composition of species assemblages, are typical of ecotones (Wiens 1992). van der Maarel (1990) distinguished between 2 types of ecotones, i.e. those where the diversity is less than that of adjacent communities (stress zones), and those where the diversity is higher than that of adjacent communities. The concept of ecotone was defined by Odum (1971) as 'an intersection between plant communities where there is a relatively abrupt change in vegetation structure or composition'. The term has been recently redefined as a 'zone of transition between adjacent ecological systems. Ecotones have a set of characteristics defined by space and time scales, and by the strength of interactions between adjacent ecological systems' (Holland & Risser 1992). In such places, biotic interactions are

Table 3. Main characteristics of biomass and species abundances in the ice bottom and at the ice-water interface. Summary for 1989 and 1990

Characteristic	Ice bottom	Ice-water interface	Data
Richness	Short-term variability: low Interannual variability: low	Short-term variability: high Interannual variability: high	Table 2 Table 2
Diversity	Highest diversities in high-salinity offshore waters	Highest diversities in mid-salinity waters	Fig. 5
Maturity	Inshore-offshore gradient with no strong heterogeneities	High maturity in mid-salinity waters	Fig. 6
Biomass	No gradient, or gradient parallel to that of salinity	Highest biomasses in mid-salinity waters	Figs. 3e, f & 4
Spatial structure	Weak	Strong	Fig. 8
Explanatory factors	Nonspatially structured environmental variables; $a \geq (b + c)$	Spatially structured environmental variables + purely spatial process; $a < (b + c)$	Fig. 8

strong and highly complex (Allen & Starr 1982). Such an abrupt change in spatial patterns of species assemblages contrasts with gradual changes referred to as ecoclines or true gradients (van der Maarel 1976).

In 1989, changes in the characteristics of species assemblages were gradual, with the diversity and maturity progressively increasing from inshore to offshore (Fig. 6). This situation could reflect the fact that environmental gradients were smoother in 1989 than in 1990 (Fig. 2) and, from a biological point of view, corresponded to an ecocline. The high diversity and maturity observed at the ice-water interface in 1990 (Stns C and CD; Figs. 5 & 6) are typical of ecotones. The ecological theory predicts that at an ecotone, there should be a drastic change in the composition of species assemblages. This is exactly what happened along the transect in 1990 (Fig. 10), where a major increase in species richness occurred at Stns C and CD relative to the more inshore and offshore stations. This increase is caused by the combination of species belonging to both the inshore and offshore environments, and also of highly specialized species occurring only within the ecotone. This is known as the edge effect (Leopold 1933, Gates & Gysel 1978), i.e. the enhancement of species diversity in response to the interdispersion of habitat and resources which characterizes ecotones. The ecotone at the ice-water interface could act as a barrier between the inshore and offshore algal assemblages, and thus regulate the spatial pattern of changes in species composition along the transect (Di Castri & Hansen 1992).

Concerning the effect of space, variations in the abundances of algal species exhibited a strong spatial structure (b + c) for the assemblages both in the ice bottom and at the ice-water interface (Fig. 8). The unexplained variance (d) ranged between 25 and 42%, which is low when compared to the study of Borcard et al. (1992) on assemblages of oribatid mites and on a forest community. In 1989 and 1990, the spatial component of the total explained variation in species assemblages ($(b + c) / (a + b + c)$) was $\geq 50\%$, reaching 67% for the ice-water interface in 1990, which corresponded to strong environmental gradients (Figs. 2 & 3). However, purely spatial processes (c) explained less than 27% of the total variation, so it is legitimate to consider the measured environmental variables when interpreting variations in algal species assemblages. Assemblages at the ice-water interface were more sensitive than those in the ice bottom to the spatial structuring by environmental gradients (Fig. 8). Thus, especially for the assemblages at the interface, the interpretation of correlations as direct relationships between species and environmental variables would neglect an important spatial component. Concerning the effects of salinity on species, the question is whether these were direct (e.g. physiological) or linked to the spatial struc-

ture. Results in Fig. 9 show that, when the inshore-offshore gradient is strong, the distributions of salinity and of the species assemblage reflect the general horizontal structure determined by the river plume. Thus, there was no detectable direct effect of salinity on species assemblages.

Overall ecological significance

Results of the present study suggest that the combined effects of hydrodynamics and horizontal processes largely determine the dynamics of algal assemblages in the ice bottom and at the ice-water interface. At the interface, there is a significant relationship between species richness and algal biomass (Fig. 11). This indicates that the interdispersion of habitats which characterizes ecotones has a direct influence on the production of organic matter in the under-ice plume of the river. In the area of the Great Whale River, during the springtime, fish larvae are older near the mouth of the river than offshore (Ponton & Fortier 1992), which stresses the role of the under-ice plume for the feeding of larvae and the development of their prey items (i.e. copepods, eggs and nauplii; Drolet et al. 1991, Gilbert et al. 1992).

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