The link between precipitation, river runoff, and blooms of the toxic dinoflagellate *Alexandrium tamarense* in the St. Lawrence

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Abstract: Blooms of the toxic dinoflagellate *Alexandrium tamarense*, which is responsible for paralytic shellfish poisoning, are annually recurrent events in the Estuary and Gulf of St. Lawrence, Québec, Canada. The analysis of abundance data for this algal species between 1989 and 1998 at Sept-Îles, a presumed initiation site in the northwestern Gulf of St. Lawrence, revealed yearly fluctuations in the onset, duration, and magnitude of toxic *A. tamarense* blooms. Hydrological and meteorological data for the region indicate that rainfall, Moisie River runoff, and wind are highly related to the pattern of bloom development each year. Results from the 10-year data set reveal that in this system: (*i*) high Moisie River runoff from a prolonged spring freshet or from heavy rainfall events in the summer and fall can initiate *A. tamarense* blooms; (*ii*) high Moisie River runoff combined with prolonged periods of weak winds ($<4\ \mathrm{m\cdot s^{-1}}$) favour the continued development of blooms; and (*iii*) winds $>8\ \mathrm{m\cdot s^{-1}}$ disrupt blooms. Salinity, which reflects the general state of the water column in terms of freshwater input and stability, had a strong negative correlation with the probability of observing *A. tamarense* cells at this station and could thus be used as a predictive tool for the presence of cells in this system.

Résumé : Les floraisons du dinoflagellé toxique *Alexandrium tamarense*, responsable de l'intoxication paralysante par les mollusques, sont des événements annuels récurrents dans l'estuaire et le golfe du Saint-Laurent, Québec, Canada. L'analyse des données d'abondances de *A. tamarense* entre 1989 et 1998 à Sept-Îles, un site présumé d'initiation des floraisons dans le nord-ouest du golfe du Saint-Laurent, montre que l'initiation, la durée et l'ampleur des floraisons toxiques de *A. tamarense* varient d'une année à l'autre. Les données hydrologiques et météorologiques indiquent que les précipitations, le débit de la rivière Moisie et le vent sont étroitement liés au patron annuel de floraisons. Les 10 années de résultats démontrent que dans ce système : (*i*) un débit élevé de la rivière Moisie dû à une importante crue printanière ou à de fortes précipitations durant l'été et l'automne peut déclencher des floraisons de *A. tamarense*, (*ii*) un débit élevé de la rivière Moisie combiné à une période de vents faibles ($<4\ \mathrm{m\cdot s^{-1}}$) favorise le développement continu des floraisons et (*iii*) des vents $>8\ \mathrm{m\cdot s^{-1}}$ dispersent et mettent fin aux floraisons. La salinité, qui reflète l'état général de la colonne d'eau en terme d'apport d'eau douce et de stabilité, démontre une forte corrélation négative avec la probabilité d'observer des cellules de *A. tamarense* à cette station. Ce paramètre pourrait donc être utilisé comme outil pour prédire la présence de *A. tamarense* dans ce système.

Introduction

Harmful algal blooms and the phycotoxins they produce represent a significant and increasing threat to human health, fishery resources, and marine ecosystems throughout the world. These blooms result from a combination of physical, chemical, and biological mechanisms and interactions that have not yet been well established. Several studies have shown that toxic blooms are often associated with freshwater plumes (Franks and Anderson 1992*a*; Taylor and Haigh 1993; Hallegraeff et al. 1995). For example, the timing and spread of shellfish toxicity in the waters of the Gulf of Maine was linked to the alongshore transport of *A. tamarense* in a buoyancy current originating from several rivers that empty into

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the Gulf (Franks and Anderson 1992*a*, 1992*b*). Similarly, in the Strait of Georgia, British Columbia, the first appearance of substantial numbers of the marine raphidophyte *Heterosigma* coincides with maximum runoff from the Fraser river (Taylor and Haigh 1993). A number of studies have also indicated that toxic dinoflagellate blooms often coincide with enhanced rainfall and freshwater runoff, as well as with a stable water column (Ryther 1955 and references therein; Hallegraeff et al. 1995; Giacobbe et al. 1996). The association of toxic dinoflagellate blooms with freshwater runoff has not yet been elucidated but may be due to more favourable temperature and salinity conditions (Prakash 1967), the supply of humic substances (Granéli and Moreira 1990), increased water column stability (Margalef et al. 1979), or a combination of these factors that might be physiologically important for optimum cell growth.

In the St. Lawrence (Fig. 1), the species *Alexandrium tamarense* (Lebour) Balech, which is responsible for paralytic shellfish poisoning (PSP), produces extensive recurrent blooms during the summer months (Blasco et al. 1998). The factors controlling bloom dynamics are not yet fully understood, but previous studies in the lower St. Lawrence Estuary (LSLE) have emphasized the importance of freshwater runoff and water-column stability as the major factors controlling bloom dynamics (Therriault et al. 1985; Cembella et al. 1988; Larocque and Cembella 1990). Therriault et al. (1985) found that the pattern of PSP outbreaks and the spatial distribution of *A. tamarense* cells in the LSLE closely corresponded to the extent of the freshwater plume produced by the Manicouagan and Aux-Outardes rivers. However, the exact nature and the precise mechanisms underlying the freshwater *A. tamarense* relationship could not be clearly defined owing to the complex circulation pattern in the LSLE, which is characterized by eddies and transverse currents (Vezina et al. 1995; Savenkoff et al. 1997). We suspect that local populations of *A. tamarense* exist within the Estuary and Gulf, each with their own unique set of environmental and hydrological conditions that determine the timing and extent of bloom development. Until now, no study has examined in detail and over an extended period of time the association of *A. tamarense* blooms and river plumes in the St. Lawrence.

In this study, we examine the interannual variability of *A. tamarense* blooms over a 10-year period at Sept-Îles, in the Gulf of St. Lawrence (GSL). Sept-Îles, where significant *A. tamarense* concentrations are often observed, is an ideal site to examine the effects of freshwater runoff on bloom dynamics. First, Sept-Îles is located in an area where sources of freshwater are restricted to north shore rivers as a result of the general circulation pattern in the GSL with no direct influence from the St. Lawrence Estuary (Fig. 1). Second, the nearby Moisie River, the most important river in terms of discharge rate, is not regulated by hydroelectric dams. Thus, a more natural relationship is expected between variations in yearly snowmelt, precipitation, river runoff, and subsequent *A. tamarense* blooms. The objective of this study was to assess how variations in precipitation, river runoff, and wind affect the bloom dynamics of *A. tamarense* at Sept-Îles using the analysis of the biological, meteorological, and hydrological data between 1989 and 1998.

Materials and methods

Study area

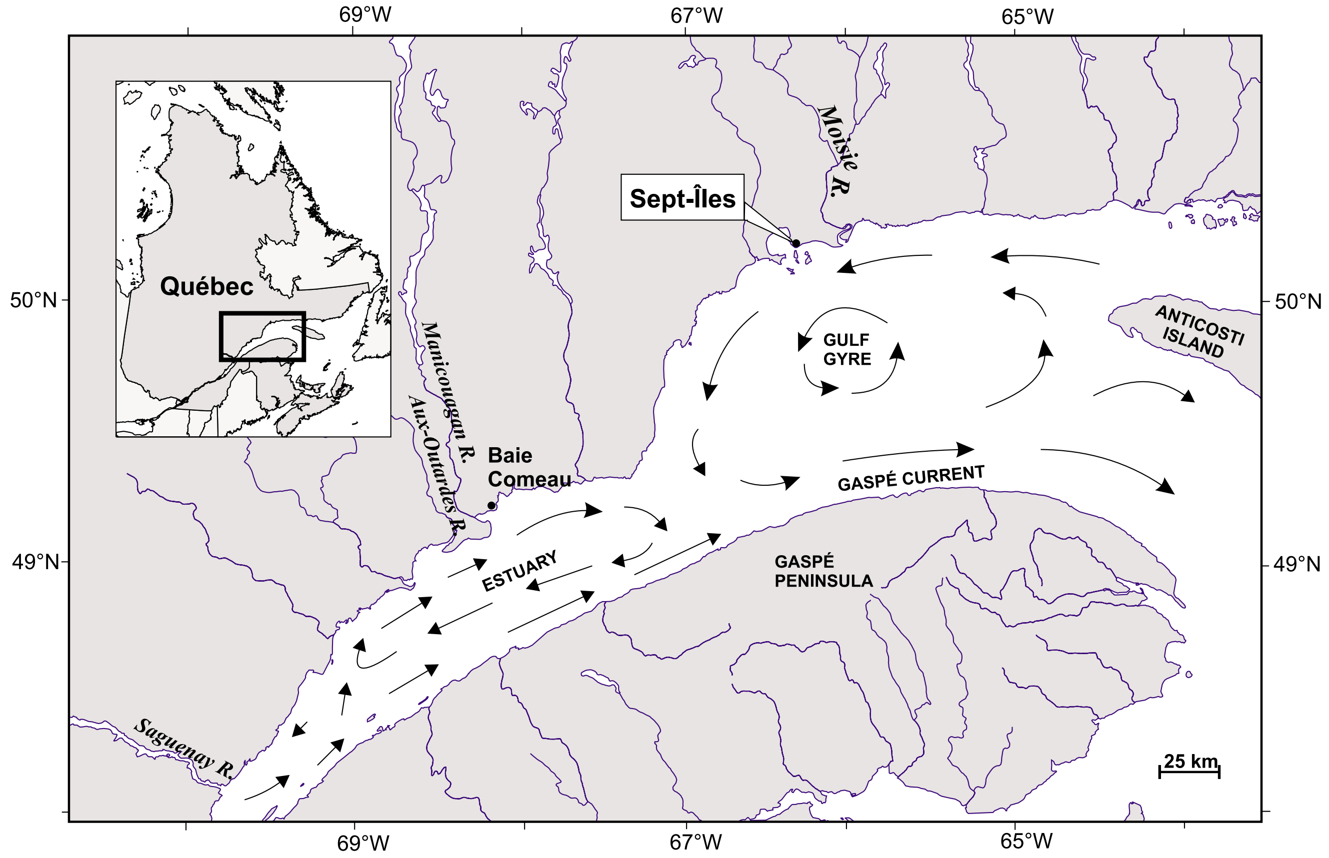
The Sept-Îles monitoring station is located at the eastern entrance of the Sept-Îles Bay, in the northwestern GSL (Fig. 1). The GSL is a semi-enclosed sea and is forced at various temporal and spatial scales by tides from the Atlantic Ocean, local and large-scale meteorological seasonal and transient events, freshwater runoff and heat flux, and perturbations at the continental shelf (see review by Koutitonsky and Bugden 1991). The continuous supply of freshwater from the St. Lawrence River and other tributaries in the GSL watershed maintains a density-driven circulation with an outflow of lighter waters near the surface and a penetration of Atlantic waters in deeper layers (Koutitonsky and Bugden 1991). Figure 1 illustrates the main features of the summer surface circulation pattern in the St. Lawrence, which is characterized by the Gaspé current, a strong coastal jet flowing seaward along the Gaspé Peninsula, and by the presence of a quasi-permanent anti-clockwise gyre west of Anticosti Island (El-Sabh 1976, 1979). In the northwest sector of the Gulf, an offshore pressure gradient along the northern Québec shore created by lateral runoff induces a coastal current ($5–10\ \mathrm{cm \cdot s^{-1}}$) towards the west (Koutitonsky and Bugden 1991). The Moisie River, located approximately 20 km east of Sept-Îles, is the most important river near Sept-Îles in terms of discharge rate. The freshwater plume produced by this river is expected to influence our sampling station owing to the dominant westward surface currents created by the anticlockwise Anticosti gyre (refer to Fig. 1).

Oceanographic, hydrological, and meteorological data

Data presented in this paper were collected at Sept-Îles between 1989 and 1998 through the toxic algae monitoring program of the Department of Fisheries and Oceans Canada (Maurice Lamontagne Institute, Mont-Joli, Québec). Details of the field and laboratory analyses have already been fully described (Blasco et al. 1998). To summarize, surface water samples were collected at high tide from the Sept-Îles dock on a weekly basis between mid-May and the end of October of each year using a Niskin bottle (General Oceanics Inc., Miami, Fla.) or a bucket. In situ surface-water temperature was measured with a mercury thermometer. A subsample was fixed with acidic Lugol's iodine solution for later identification and enumeration of phytoplankton cells using the Utermöhl (Utermöhl 1931) technique with a Leitz phase contrast inverted microscope (Leica Microsystems (Canada) Inc., Richmond Hill, Ont.). Another subsample was taken for later analysis of salinity using a Guildline salinometer (model Autosal 8400T, Ocean Scientific International Ltd., Hampshire, U.K.). To test whether the presence of *A. tamarense* cells could be predicted from the surface salinity data at Sept-Îles, we tabulated the presence or absence of cells at the monitoring station between 1990 and 1998 for 13 salinity classes and converted this to the percent occurrence of cells per salinity class. The same analysis was carried out for Baie Comeau, located in the lower St. Lawrence Estuary (Fig. 1).

The daily Moisie River discharge, recorded about 35 km upstream from the mouth of the river, was supplied by Envi-

Fig. 1. Map of the Estuary and Gulf of St. Lawrence, Canada, showing the location of the Sept-Îles monitoring station, and the general summer surface circulation pattern (adapted from El-Sabh 1976, 1979).



ronment Canada and the Ministère de l'Environnement et Faune Québec. We classified our 10-year data set into years of "low" and "high" summer Moisie River runoff relative to the 30-year average (1968–1997) to assess how variations in freshwater runoff affect the bloom dynamics of *A. tamarense* at Sept-Îles. Total daily rainfall and hourly winds (direction and speed) recorded at the weather station near Sept-Îles were supplied by Environment Canada.

Results

Oceanographic data

The analysis of the 10-year data set (i.e., weekly samples from mid-May to the end of October of each year between 1989 and 1998) revealed year-to-year variations in the timing and magnitude of *A. tamarense* blooms. Cells (≥20 $\text{cells}\cdot\text{L}^{-1}$) were present as early as the week of 14 May and as late as the week of 22 October, but were recorded almost each year during a 3-week period between the week of 18 June and the week of 2 July (data not shown). This corresponds to a period when water temperatures are generally warm (12.0 ± 1.9°C) and salinity values relatively low (26.3 ± 2.6‰). Temperatures ranged from 2 to 18°C between mid-May and the end of October, 1989–1998, and followed the seasonal warming and cooling cycle each year (Fig. 2*a*). Salinity ranged between 20 and 31‰ during the same period, but exhibited significant interannual variability (Fig. 2*b*). Years during which low salinity values were recorded generally corresponded to years of high cell concentrations (Figs. 2*b* and 2*c*). Cells were detected each year, but exceeded 1000 $\text{cells}\cdot\text{L}^{-1}$ (the concentration at which shellfish generally become toxic in the St. Lawrence) during 1992, 1994, 1995, 1996, 1997, and 1998. The highest concentration was recorded in 1994, with 38 735 $\text{cells}\cdot\text{L}^{-1}$, followed by 1996 and 1997, with 17 760 and 8480 $\text{cells}\cdot\text{L}^{-1}$, respectively (Fig. 2*c*). Although *A. tamarense* cells were recorded in a wide range of temperature and salinity values, the highest cell concentrations were mainly associated with warm (≥12°C) and brackish (20–26‰) waters (Fig. 3).

Moisie River runoff, salinity, and *A. tamarense* blooms

The monthly Moisie River runoff and salinity values were averaged over each month between June and September, 1990–1998 (Fig. 4). We found a significant correlation ($r^2 = 0.58$, $P < 0.0001$) between Moisie River runoff and salinity recorded at Sept-Îles.

Years of low and high summer Moisie River runoff relative to the 30-year average (1968–1997) are presented in Fig. 5 along with associated salinity anomalies and *A. tamarense* cell concentrations. All six low-runoff years (1989, 1990, 1991, 1993, 1995, and 1998) were characterized by an earlier and (or) lower than average spring freshet, which translated into lower than average river runoff during June (Fig. 5*a*). These years, with the exception of 1993 and 1998, were also characterized by 5–32% less rainfall when compared with the average total rainfall recorded for the June to

Fig. 2. Interannual variability of (*a*) temperature (°C), (*b*) salinity (‰), and (*c*) *Alexandrium tamarense* cell abundance (cells·L^{-1}) at Sept-Îles between mid-May and the end of October, 1989–1998. Data were only available as of mid-June 1990 and mid-July 1989 and 1992. The dotted line at 1000 cells·L^{-1} represents the concentration at which shellfish generally become toxic in the St. Lawrence (80 µg STX eq·100 g meat^{-1}).

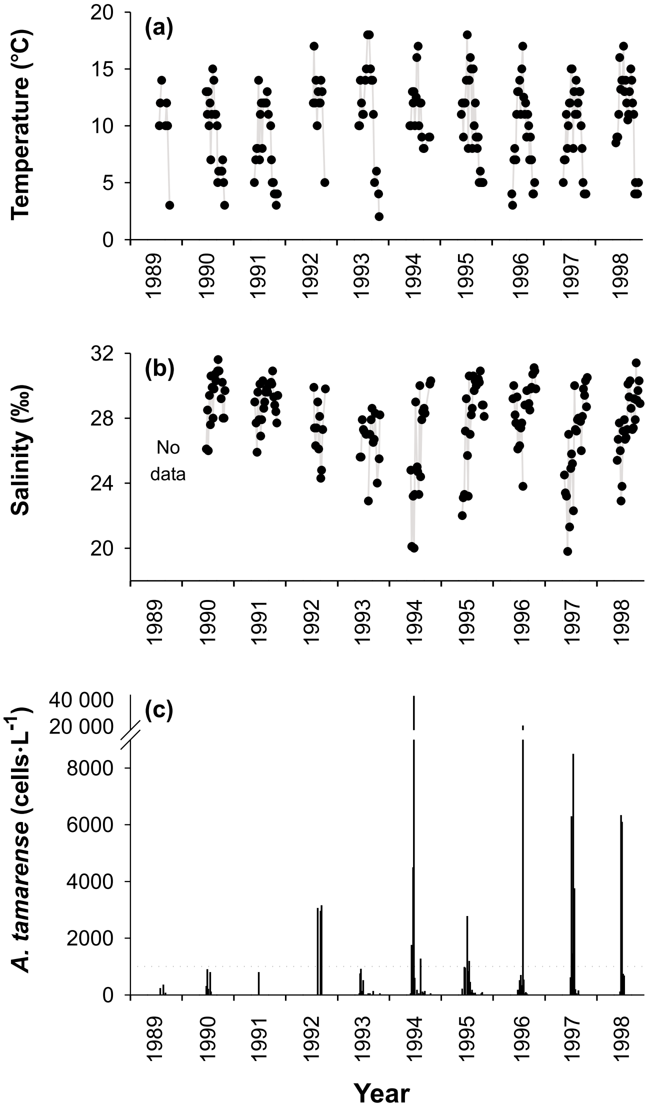


Fig. 3. Abundance ranking of *Alexandrium tamarense* vs. temperature (°C) and salinity (‰) at Sept-Îles between mid-May and the end of October, 1990–1998. No salinity data were available for 1989. The circle encompasses most of the highest cell concentrations.

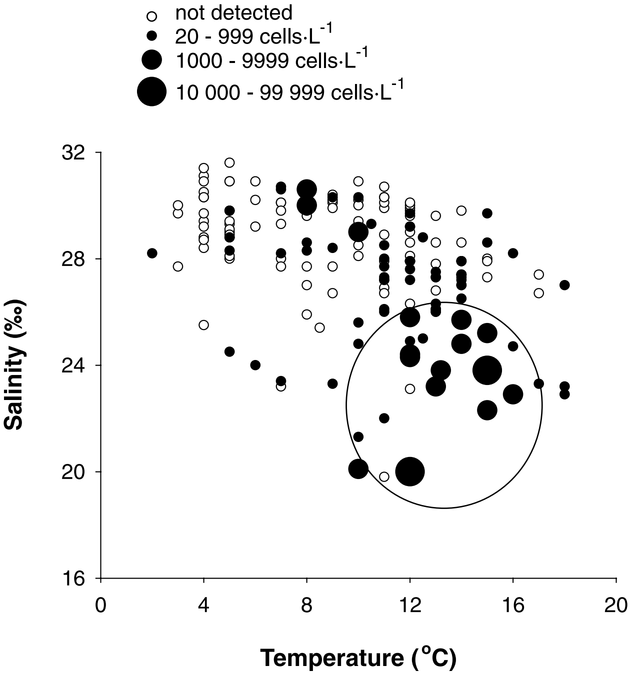
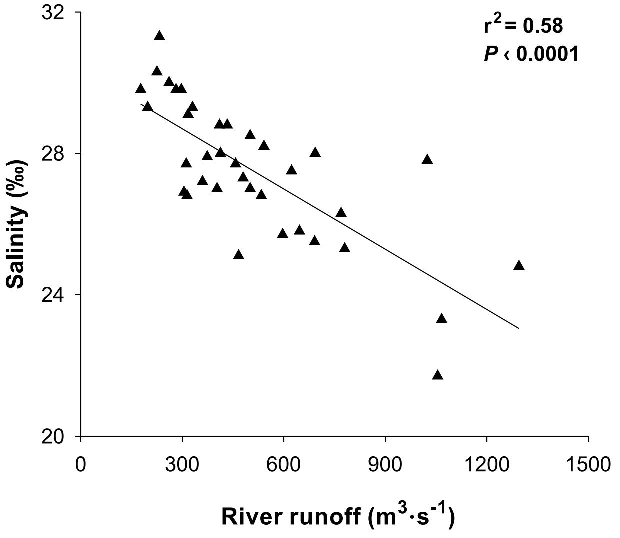
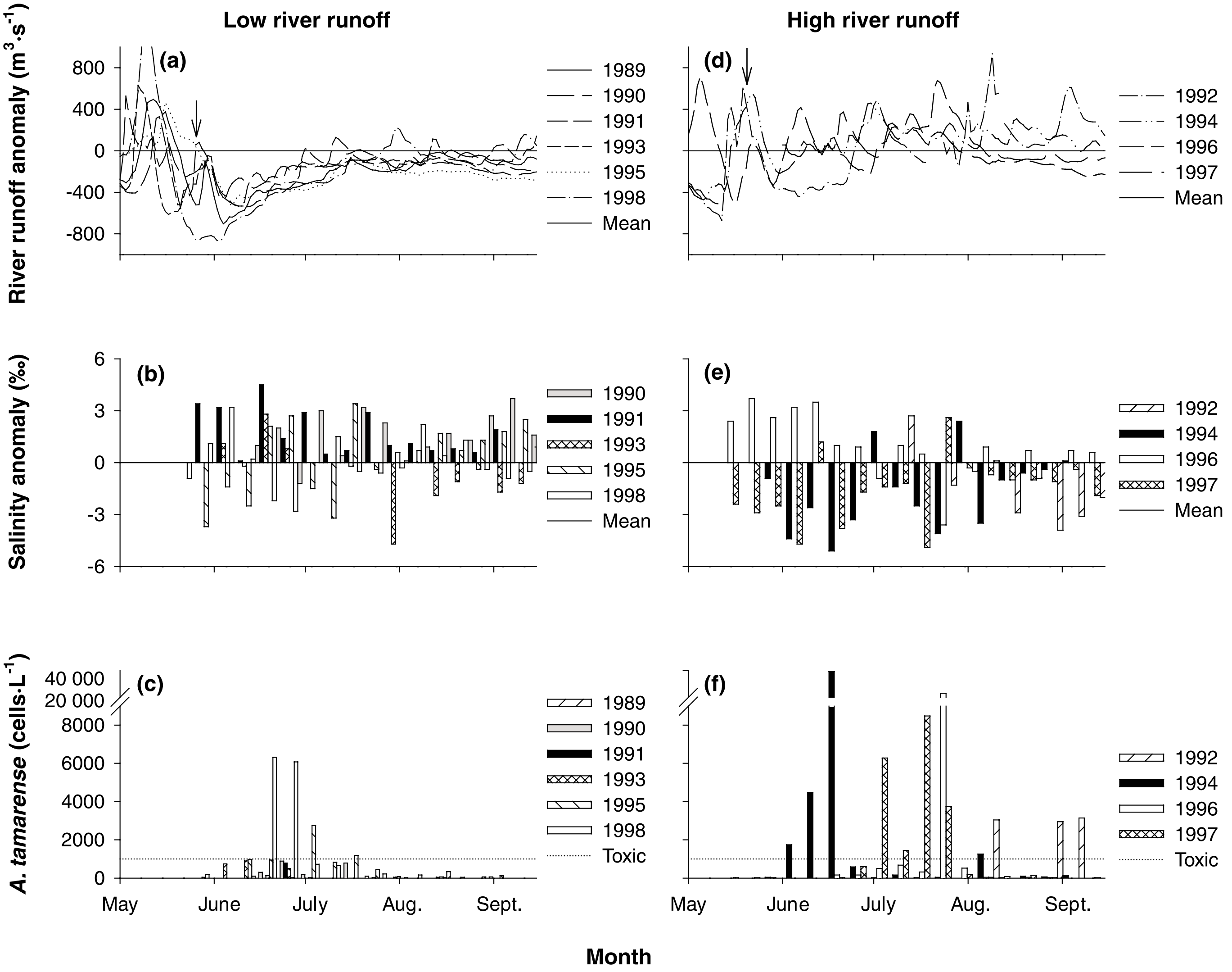


Fig. 4. Monthly salinity values (‰) recorded at Sept-Îles vs. the monthly Moisie River runoff (m^3·s^{-1}) from June to September, 1990–1998. No salinity data were available for 1989.



August, 1961–1990 period by Environment Canada (1993). Mainly above-average salinity values, relative to the 10-year average (Fig. 5*b*), and low *A. tamarense* cell concentrations (Fig. 5*c*) were associated with these six low-runoff years. When an exceptionally strong rainfall event occurred during an otherwise low runoff summer, substantial *A. tamarense* cell concentrations were recorded. For example during mid-June 1998, 91.8 mm of rain fell within seven days, which is almost the total average June rainfall (92.3 mm) recorded between 1961 and 1990 by Environment Canada (1993) (data not shown). This resulted in a negative salinity anomaly (Fig. 5*b*) and more than 6000 *A. tamarense* cells·L^{-1} (Fig. 5*c*). Years of high summer river runoff (i.e., 1992, 1994, 1996, and 1997) were characterized by a strong spring freshet occurring at approximately the same time as the 30-year average (Fig. 5*d*). Furthermore, during 1992 and 1994, 28–50% more rainfall was recorded for the June to August period than the average recorded by Environment Canada (1993). The four high-runoff years were characterized by mainly lower than average salinity values (Fig. 5*e*) and high *A. tamarense* cell concentrations (Fig. 5*f*). Thus, in general, years of low cell concentrations were associated with low

Fig. 5. The 10-year data set was classified into years of (*a*) low and (*d*) high summer Moisie River runoff relative to the 30-year average (1968–1997). The arrow indicates the timing of the 1968–1997 average spring freshet maximum ($m^3 \cdot s^{-1}$). The deviations (anomaly) with respect to the 1990–1998 mean weekly salinity (‰) in (*b*) and (*e*) for low and high runoff years, respectively. *Alexandrium tamarense* cell concentrations ($cells \cdot L^{-1}$) in (*c*) and (*f*) for low and high runoff years, respectively. No salinity data were available for 1989. Salinity and cell abundance data were only available as of mid-June 1990 and mid-July 1989 and 1992.



runoff, whereas high *A. tamarense* cell concentrations were associated with high runoff.

We illustrated the relationship between rainfall, Moisie River runoff, salinity, and *A. tamarense* blooms (Fig. 6). Both 1992 and 1996 were marked by exceptionally heavy rainfall during the summer months. Between 15 and 20 July 1996 a total of 95.2 mm of rain fell within only six days at Sept-Îles (Fig. 6*a*), which is more than the total monthly average of 90.8 mm recorded at this station during July (1961–1990) by Environment Canada (1993). This heavy rainfall event was followed by a sharp increase in Moisie River runoff by more than 400 $m^3 \cdot s^{-1}$, reaching a peak of 1150 $m^3 \cdot s^{-1}$ on 22 July. By 29 July, the salinity had decreased from 28‰ to 24‰ and more than 17 000 *A. tamarense* $cells \cdot L^{-1}$ were recorded (Figs. 6*b* and 6*c*). Similarly, high cell concentrations were recorded following two heavy rainfall events in 1992. The first event occurred during early August, when 54.0 mm fell within just three days (Fig. 6*d*). This is more than half the total rainfall usually recorded during the month of August by Environment Canada (Environment Canada 1993). The rainfall event was followed by a substantial increase in river runoff and the subsequent presence of more than 3000 *A. tamarense* $cells \cdot L^{-1}$ (Figs. 6*d* and 6*f*). The second event occurred during late August – early September (74 mm within 12 days) and resulted in increased Moisie River runoff by 600 $m^3 \cdot s^{-1}$, a drop in salinity by 4‰, and close to 3000 *A. tamarense* $cells \cdot L^{-1}$ the following week (Figs. 6*d*–6*f*). No cells were recorded above our level of detection at any other time during 1992.

An attempt was made to determine whether the first annual appearance of cells was triggered by a heavy rainfall event. The data from 1991, 1996, and 1998 suggest that the first appearance of cells is indeed preceded by strong rainfall and is followed by a period of weak winds, which is associated with a drop in salinity and a rise in temperature at the sampling station (Table 1). For example, *A. tamarense* cells

Fig. 6. Association between heavy rainfall, river runoff, salinity, and *Alexandrium tamarense* blooms at Sept-Îles during 1992 and 1996. Daily Moisie River runoff ($m^3 \cdot s^{-1}$; solid line) and rainfall (mm; bars) during (*a*) 1996 and (*d*) 1992; salinity (‰) during (*b*) 1996 and (*e*) 1992; *A. tamarense* cell concentrations ($cells \cdot L^{-1}$) during (*c*) 1996 and (*f*) 1992. Salinity and cell abundance data were only available as of mid-July 1992.

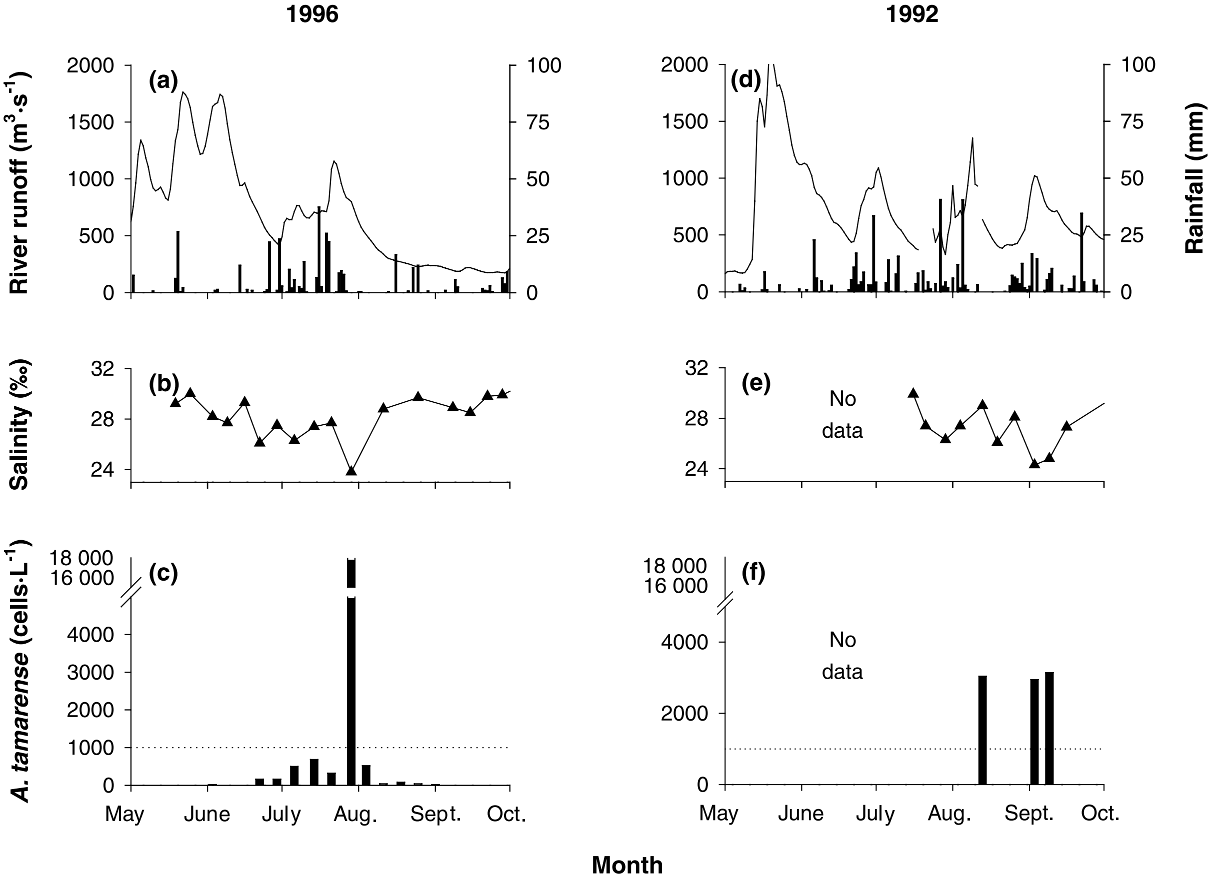


Table 1. Environmental conditions preceding the first appearance of *Alexandrium tamarense* cells in surface water samples in 1991, 1996, and 1998 at Sept-Îles.

Date of sample	*A. tamarense* concentration ($cells \cdot L^{-1}$)	Rainfall (mm)	Salinity (‰)	Temperature (°C)	Wind speed ($m \cdot s^{-1}$)
27 May 1991	0	0.8	29	5	5.0 ± 2.6
5 June 1991	0	5.6	28	7	4.7 ± 1.7
12 June 1991	0	18.4	26	8	4.8 ± 2.3
17 June 1991	0	16.8	30	8	6.0 ± 2.2
25 June 1991	785	13.1	28	14	3.8 ± 2.1
19 May 1996	0	0	29	4	4.9 ± 2.2
25 May 1996	0	35.6	30	3	5.1 ± 3.0
3 June 1996	20	0	28	7	4.0 ± 2.1
24 May 1998	0	32.4	25	9	3.0 ± 1.6
31 May 1998	0	16.0	27	9	3.6 ± 1.8
7 June 1998	0	51.4	28	9	4.1 ± 2.0
14 June 1998	100	8.0	26	11	2.7 ± 1.2

Note: For the first sampling day of each year, the total rainfall and average wind speed were calculated from the seven preceding days.

were first recorded on 25 June 1991 following a week of low wind speeds (3.8 ± 2.1 $m \cdot s^{-1}$) and 16.8 mm of rain. During this time, the salinity dropped from 30 to 28‰, the temperature rose from 8 to 14°C, and 785 $cells \cdot L^{-1}$ were recorded. Similar patterns were observed in 1996 and 1998. During 1993, 1994, 1995, and 1997, *A. tamarense* cells were already present as of the first sampling day (mid-May to early June) and were associated with low salinity values (22–25‰), and with the exception of 1997, warm temperatures (10–11°C). The years 1994 and 1995 were among the three years where average wind speeds during the month of May (4.0 ± 2.1 and 4.1 ± 2.2 $m \cdot s^{-1}$, respectively) were the lowest in the 10-year period. Furthermore, the month of May in 1994 and 1997 received 20 and 65% more rain, respectively, than the 1961–1990 average recorded by Environment Canada (1993). As for 1989, 1990, and 1992, sampling data was only available later in the season (end of June or mid-July). Thus, the first appearance of cells appears to be preceded by strong rainfall and a period of weak winds, the timing varying from year to year.

Development and dissipation of blooms—the influence of wind

Although *A. tamarense* cells were often observed over several consecutive weeks during the summer months, high concentrations were generally only observed at Sept-Îles for a short period of time. In contrast, in 1994, the bloom period lasted several weeks and produced high cell concentrations that allowed us to investigate the hydrological and meteorological conditions responsible for the development, persistence, and dissipation of the bloom. We illustrated the combined influence of rainfall, river runoff, and wind on this *A. tamarense* bloom (Fig. 7). The runoff from the Moisie River remained high throughout the month of June following the spring freshet (Fig. 7*a*). An exceptionally long period of weak winds that averaged 3.3 ± 1.8 $m\cdot s^{-1}$ and lasted for three weeks was associated with low salinity values (20–23‰) in June (Figs. 7*b* and 7*c*). On 30 May the concentration of *A. tamarense* cells was 40 $cells\cdot L^{-1}$ and gradually increased to reach 38 735 $cells\cdot L^{-1}$ on 22 June (Fig. 7*d*), the highest concentration recorded throughout the 10-year period. The dissipation of the bloom coincided with strong wind events, that is: (*i*) speeds of 8–11 $m\cdot s^{-1}$ lasting for 15 h on 26 June and (*ii*) speeds of 9–13 $m\cdot s^{-1}$ lasting for 18 h on 28 June.

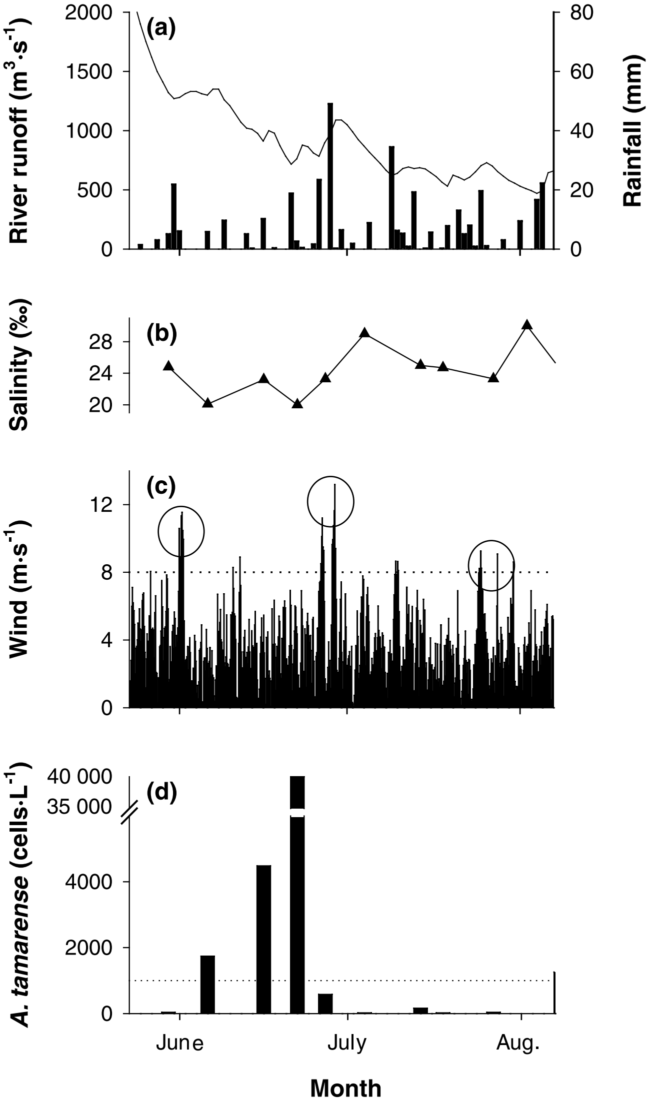
Salinity index

Because surface salinity reflects the general state of the water column in terms of freshwater input and water column stability, we examined the relationship between salinity and the occurrence of *A. tamarense* cells at Sept-Îles. We present the percent occurrence of *A. tamarense* cells in relation to salinity for the 1990–1998 period (Fig. 8). For example, for a salinity of 28‰, *A. tamarense* was present in 16 of 32 samples, i.e., 50% of the time; for a salinity of 23‰, cells were present in 8 of 10 samples, i.e., 80% of the time (Fig. 8). The regression of all data points results in $r^2 = 0.77$ ($y = -7.7x + 259.6$, $n = 175$) and when data points of three samples or less are omitted from the regression, we obtain $r^2 = 0.86$ ($y = -10x + 328.63$, $n = 168$) for the 23–31‰ salinity range, which comprises 96% of samples from the study period. One can clearly see that the probability of observing *A. tamarense* cells at Sept-Îles increases with decreasing salinity values. The same analysis carried out at Baie Comeau (refer to Fig. 1 for location) between 1990 and 1998 revealed a similar negative correlation ($r^2 = 0.72$, $y = -6.5x + 218.5$, $n = 175$) between salinity and the occurrence of *A. tamarense* cells for the 21–31‰ salinity range, comprising 94% of samples from the study period (Fig. 9).

Discussion

The strong correlation between salinity and the occurrence of *A. tamarense* cells at Sept-Îles highlights the importance of freshwater runoff for *A. tamarense* bloom dynamics in the St. Lawrence. Indeed, a previous study conducted in the St. Lawrence Estuary found that the spatial distribution of *A. tamarense* cells coincided with the brackish waters of the plume produced by the Manicouagan and Aux-Outardes rivers (Therriault et al. 1985). The present study, more in-depth and over a 10-year period (1989–1998), shows that this type of relationship also exists in the Gulf of St. Lawrence because *A. tamarense* blooms near Sept-Îles were mainly associated with low-salinity waters, essentially those of the plume produced by the Moisie River.

Fig. 7. Environmental conditions preceding the 1994 bloom at Sept-Îles. (*a*) Daily Moisie River runoff ($m^3\cdot s^{-1}$) (solid line) and rainfall (mm) (bars), (*b*) salinity (‰), (*c*) wind speed ($m\cdot s^{-1}$), and (*d*) *A. tamarense* cell abundance ($cells\cdot L^{-1}$).



In general, few *A. tamarense* cells were recorded during years of low summer river runoff. Because there are no hydroelectric dams on the Moisie River, river runoff during the summer months is principally influenced by the timing and duration of the spring freshet and rainfall over the region. When the spring freshet occurred early, i.e., before mid-May, few *A. tamarense* cells were usually recorded. In con-

Fig. 8. The probability of observing *A. tamarense* cells at Sept-Îles vs. salinity. The percentage was calculated by tabulating when cells were present in samples for each salinity class, and converting this to a percent occurrence of cells. (○), Salinity classes consisting of three samples or less; (●), salinity classes consisting of between 5 and 36 samples. The linear regression of all data points is represented by the dotted line (r^2 = 0.77, y = –7.7x + 259.6, n = 175). The linear regression of points with four or more samples per salinity class (●) is represented by the solid line (r^2 = 0.86, y = –10x + 328.63, n = 168) and comprises 96% of samples from 1990 to 1998.

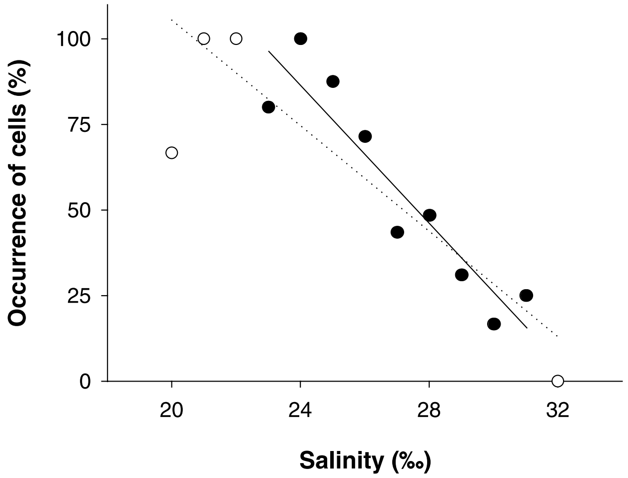
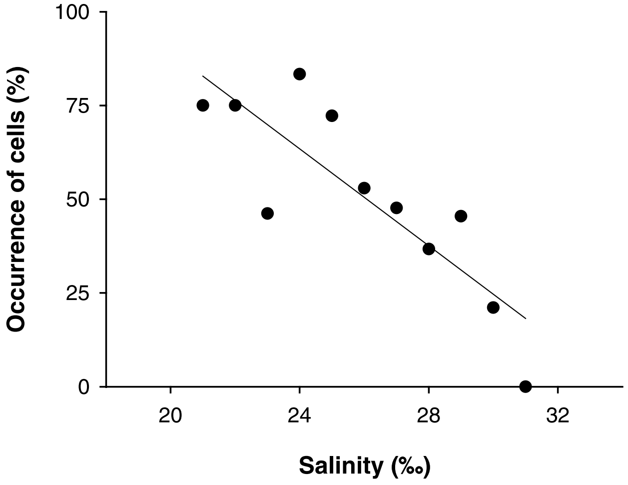


Fig. 9. The probability of observing *A. tamarense* cells at Baie Comeau vs. salinity. The percentage was calculated by tabulating when cells were present in samples for each salinity class, and converting this to a percent occurrence of cells. The linear regression of data points with four or more samples per salinity class is represented by the solid line (r^2 = 0.72, y = –6.5x + 218.5, n = 175) and comprises 94% of samples from 1990 to 1998.



trast, an *A. tamarense* bloom developed in June 1994 when the spring freshet lasted for a long time, either because of more snow or slower melting. The June 1994 bloom was the earliest bloom recorded during the 10-year period, exceeding 1000 cells·L^{-1} as of the first week of June and reaching close to 40 000 cells·L^{-1} by mid-June. Although the timing and duration of the spring freshet may influence *A. tamarense* blooms early in the summer, day-to-day variations in precipitation appear to be more important in controlling *A. tamarense* bloom dynamics throughout the remainder of the summer.

Heavy rainfall events resulted in strong freshwater pulses from the Moisie River, a drop in salinity at Sept-Îles, and the subsequent presence of high *A. tamarense* cell concentrations. This is the first time that it is shown in the St. Lawrence that *A. tamarense* blooms can be initiated by heavy rainfall in the summer and fall. Previous studies have loosely associated rainfall events with phytoplankton blooms, such as that of an *Alexandrium minutum* bloom in a Mediterranean lagoon (Giacobbe et al. 1996) and a *Gyrodinium aureolum* bloom in a sea loch in Scotland (Jones et al. 1982). However, the timing and quantity of rainfall involved were not specified in these studies. Our results concord with those of Blanco et al. (1985) who reported that an *A. tamarense* red tide developed during a period of heavy precipitation, more than 2.75 times the average monthly rainfall, in the Ria de Ares and Betanzos, Spain.

The association between freshwater plumes and toxic phytoplankton blooms has been observed in several coastal areas of the world (Franks and Anderson 1992*a*; Taylor and Haigh 1993; Hallegraeff et al. 1995). However, it is unclear whether this association is principally caused by the direct effects of low salinity and high temperature on cellular growth rate, the supply of nutrients, dissolved organic matter, trace elements or other materials that might serve as growth stimulants, and (or) increased water column stability that favours the proliferation and retention of cells. Humic substances, which are supplied in freshwater runoff from heavily forested watersheds, such as those found on the Québec North Shore, may play a role in the bloom dynamics at Sept-Îles. Humic substances have been shown to have a positive effect on the growth rates and biomass production of several toxic dinoflagellates (Granéli and Moreira 1990; Carlsson et al. 1995; Doblin et al. 1999) and favour the growth of dinoflagellates over diatoms in culture (Granéli and Moreira 1990). Although no data on humic substances was available for this data set, recent laboratory studies carried out with *A. tamarense* cultures isolated from the St. Lawrence Estuary have shown that the addition of humic substances from three different sources (including a humic and a fulvic extract from the Manicouagan River) significantly enhanced overall cell density and growth rates relative to control treatments (R. Gagnon, Maurice Lamontagne Institute, Fisheries and Oceans Canada, Mont-Joli, Québec, personal communication).

Increased *A. tamarense* cell concentrations from one week to another at Sept-Îles are most likely the result of combined biological growth, vertical migration, and (or) advection of cells. If we assume only in situ biological growth, we obtain net population growth rates ranging between 0.1 day^{-1} and 0.5 day^{-1} throughout most of the sampling period (84%), which is within the 0.3–0.5 day^{-1} range of maximum growth observed in laboratory studies for this species (Levasseur et al. 1995; MacIntyre et al. 1997; Parkhill and Cembella 1999). However, the highest growth rate that we obtained was 0.7 day^{-1}, which is unrealistically high for this species. In addition to growth, increased cell concentrations could be the result of high-density patches formed owing to the swimming behaviour of this species (Cullen and MacIntyre 1998 and references therein). Moreover, in frontal systems, vertical migration and convergent circulation can combine to accumulate cells (Franks 1992). In the Sept-Îles area, *A. tamarense* cells may be concentrated in convergence zones of the Moisie River plume front and advected to our coastal monitoring station. The increase in *A. tamarense* cell concentrations associated with high river runoff and low salinity may thus be the result of a combination of biological and physical processes.

Dinoflagellates are particularly well adapted for life in relatively calm, stratified conditions (Margalef 1978). They are active swimmers and are able to maintain themselves in the euphotic zone with comparative ease and access nutrients at depth if depleted in surface waters, whereas less-motile phytoplankton may sink out of the euphotic zone or become nutrient limited (Margalef 1978; Cullen and MacIntyre 1998). At our coastal monitoring station, prolonged periods of calm, stratified conditions favoured the continued development of *A. tamarense* blooms. For example, the June 1994 bloom was associated with high river runoff and an exceptionally long period of low wind speeds averaging 3.3 ± 1.8 $m \cdot s^{-1}$ over a 3-week period. Although 1996 and 1997 had a similar river runoff pattern during June, such a long and continuous period of low wind speeds was not observed and did not result in an *A. tamarense* bloom as in June 1994. These observations are in accordance with those of Hallegraeff et al. (1995) who noted that continuous periods of low wind speed ($<5\ m \cdot s^{-1}$ for five days or more) were associated with PSP. Similarly, Blanco et al. (1985) reported that an *A. tamarense* bloom developed during a month of heavy precipitation and weak winds averaging 4 $m \cdot s^{-1}$ that was progressively destroyed following winds of 7 $m \cdot s^{-1}$. Although wind speeds greater than 8 $m \cdot s^{-1}$ accounted for only 5% of occurrences during the June–August period (1989–1998) at Sept-Îles, our results suggest that increased mixing of the water column, reflected in an increase in salinity and decrease in temperature, are associated with these winds. The wind-induced processes involved in the decline of blooms still remain uncertain. Mixing associated with turbulent conditions may discourage the formation of blooms because of the physical dispersion of cells. Dinoflagellate growth may also be negatively impacted by turbulence through the direct effects of fluid shear on cell physiology as demonstrated by several laboratory experiments (Thomas and Gibson 1990; Berdalet and Estrada 1993; review by Smayda 1997). Recently, Juhl et al. (2001) demonstrated that the net population growth of *A. fundyense* in cultures decreased with shear flow similar to levels expected in near-surface waters on a windy day for exposures greater than 1 $h \cdot day^{-1}$, and became negative with exposures greater than 12 $h \cdot day^{-1}$.

The analysis of this 10-year data set indicates that the timing of *A. tamarense* blooms at Sept-Îles is related to a combination of key environmental variables, notably temperature, salinity, rainfall, Moisie River runoff, and wind, whereas the magnitude of blooms is controlled by the duration of these favourable conditions promoting bloom development. The fact that significant interannual variability in both the timing and magnitude of *A. tamarense* blooms is observed over the 10-year period demonstrates that this proper combination of factors is not met every year. Our results reveal that there was a “window” when *A. tamarense* cells were present in the surface waters every year, i.e., the last two weeks of June and the first week of July. This is a period when the water column has warmed substantially and is more likely to be stratified. Nonetheless, our results indicate that other factors, such as high river runoff and low wind speeds that further intensify vertical stratification, are required for an *A. tamarense* bloom to fully develop at Sept-Îles. Year-to-year variations in the timing of the spring freshet, occurrence of heavy rainfall events, and periods of low wind speeds will thus influence *A. tamarense* bloom dynamics, as will climate changes that affect these forcing factors.

In summary, local oceanographic, hydrological, and meteorological conditions are important for the initiation, development, and maintenance of *A. tamarense* blooms at Sept-Îles. Salinity can be considered an indication of freshwater input and water column stability and the importance of both these factors is inferred by the strongly significant negative correlation between surface salinity and the occurrence of *A. tamarense* cells at Sept-Îles, as well as at Baie Comeau, during the study period. We suspect that a similar relationship exists between *A. tamarense* blooms and other rivers along the Québec North Shore. Finally, this simple index, whereby the presence of cells can be predicted from the surface salinity data, could be a very useful tool to predict toxic blooms.

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