Climate change and abundance cycles of two sympatric populations of smelt (*Osmerus mordax*) in the middle estuary of the St. Lawrence River, Canada[1]

M. Mingelbier, F. Lecomte, and J.J. Dodson

Abstract: Commercial catches of two ecologically distinct sympatric smelt (*Osmerus mordax*) populations segregated along the two shores of the St. Lawrence middle estuary exhibited inverse patterns with periodicities on the order of 30 years. The influence of water level in the St. Lawrence River and air temperature, chosen to reflect variations in hydrology and climate, differed markedly between the two populations. Analyses revealed that both water level and temperature were generally positively related with north-shore smelt landings and negatively related with south-shore smelt landings. For both populations, a number of significant climatic factors contributing to variance in smelt landings were lagged by one to three years relative to the year of landings, indicating that climatic variables influenced smelt recruitment. The contrasting role of hydroclimatic variables in driving these abundance cycles is likely related to differential exploitation of estuarine habitats; the south-shore population is associated with shallow shoal habitat, whereas the north-shore population is associated with deep channel habitat. The responses of the two smelt populations also reflect the fundamental ecological differences existing between shoal and channel habitats, indicating that future climate change may differentially affect other populations or species that are segregated between these two habitats.

Résumé : Les débarquements commerciaux de deux populations d'éperlans (*Osmerus mordax*) arc-en-ciel sympatriques, distinctes du point de vue écologique et ségréguées le long des deux rives de l'estuaire moyen du Saint-Laurent, montrent des variations cycliques inverses et une périodicité de l'ordre de 30 ans. L'influence du niveau d'eau du fleuve et de la température de l'air, choisis dans l'étude pour refléter les variations du régime hydrologique et du climat, diffèrent de façon marquée pour les deux populations. Les analyses révèlent que le niveau de l'eau et la température sont généralement corrélés positivement aux débarquements de la rive nord et négativement à ceux de la rive sud. Quelques un des principaux facteurs climatiques contribuant pour une grande part aux variations des débarquements des deux rives étaient décalés dans le temps, indiquant que les facteurs climatiques influencent le recrutement des éperlans. L'effet contrasté des variables hydroclimatiques sur les cycles d'abondance est vraisemblablement liée à l'utilisation différentielle des habitats de l'estuaire; la population de la rive sud est associée à un habitat peu profond et celle de la rive nord est à un chenal profond. Les réponses de ces deux populations d'éperlans reflètent aussi des différences écologiques existant entre des habitats peu profonds et un chenal profond, indiquant que les changements climatiques futurs pourraient avoir des effets différents sur d'autres populations ou d'autres espèces, qui sont ségréguées entre ces deux types d'habitats.

Introduction

Many fish families contain morphologically, ecologically, and genetically distinct populations that are sympatric during at least some part of their life cycle (Taylor 1999). The persistence of sympatric populations is often associated with ecological isolation and the development of ecotypes occupying different habitats in response to disruptive selection (e.g., benthic vs. pelagic morphotypes; McPhail 1984). The development and maintenance of sympatric populations associated with the differential exploitation of a resource gradient may be strongly influenced by the relative abundance of each population (Bridle and Jiggins 2000). However, no evidence is presently available to illustrate either the existence or magnitude of differences in the abundance of ecologically differentiated sympatric populations mediated

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by environmental variation. Long-term variation in climate has been shown to exert considerable influence on the abundance cycles of various aquatic species (Summers et al. 1987; Lluch-Belda et al. 1993). It is well known that major commercial fisheries undergo long-term oscillations in abundance that are governed by climatic events (e.g., Austin and Schubel 1976; Klyashtorin 1998). Given the ecological divergence of sympatric populations, changes in environmental conditions caused by climate variation may be expected to influence differentially their respective life cycles and abundances.

The rainbow smelt (*Osmerus mordax*) is found throughout northeastern North America in both fresh- and salt-water habitats (Scott and Crossman 1974). In lakes, they often form sympatric pairs (Taylor and Bentzen 1993). In the St. Lawrence River, smelt forms an important component of the estuarine fish community where its commercial exploitation has been recorded since 1917. Average annual commercial landings between the 1920s and 1980s varied between 40 and 60 metric tons (t). However, by the 1980s, smelt captures declined in relation to destruction of spawning grounds, chemical pollution, and an abandonment of traditional commercial and recreational fishing activity.

Rainbow smelt occurring in the middle estuary of the St. Lawrence River have long been considered as belonging to one stock for management purposes (Guy Trencia, Société de la Faune et des Parcs du Québec, 8400, avenue Sous-le-Vent, Charny, QC G6X 3S9, personal communication). However, mitochondrial DNA analyses have clearly shown that two genetically distinct populations exploit the St. Lawrence middle estuary (Bernatchez and Martin 1996). Moreover, they are spatially segregated: one is associated with the north shore and the other is found along the south shore of the middle estuary. Limited exchanges of adult smelt between the two shores have been documented by various means since the middle of the 20th century. Mark and recapture experiments conducted in the 1940s and 1950s revealed less than 1% mixing of adult smelt between the two shores of the middle estuary (Vladykov and Michaud 1957; Magnin and Beaulieu 1965). Morphometric analyses of adults demonstrated that smelt caught along the north shore were morphologically distinct from smelt captured on south-shore spawning sites (Fréchet et al. 1983). Finally, morphometric and mitochondrial DNA analyses revealed that less than 3% of the smelt caught by the north-shore commercial fishery originate from the south-shore population (Lecomte et al. 1999).

The two populations show considerable ecological divergence and may thus be expected to respond differently to environmental variability. Smelt associated with the south shore spawn in small tributaries just above the limit of salt intrusion (Ouellet and Dodson 1985). Larvae are quickly transported to the middle estuary where they occupy the shallow shoal habitat that characterizes the south shore of the estuary (F. Lecomte and J.J. Dodson, unpublished). In contrast, smelt associated with the north shore spawn ~100 km upstream in the St. Lawrence River freshwater estuary, near Neuville (Fig. 1). Following hatching, larvae drift downstream to the middle estuary. They are retained in the estuarine turbidity maximum by a combination of active vertical tidal migrations and estuarine circulation (Laprise and Dodson 1989). Larvae, juveniles, and adults of this population are mainly associated with the deep waters of the channel habitat that characterize the north shore as well as much of the middle estuary.

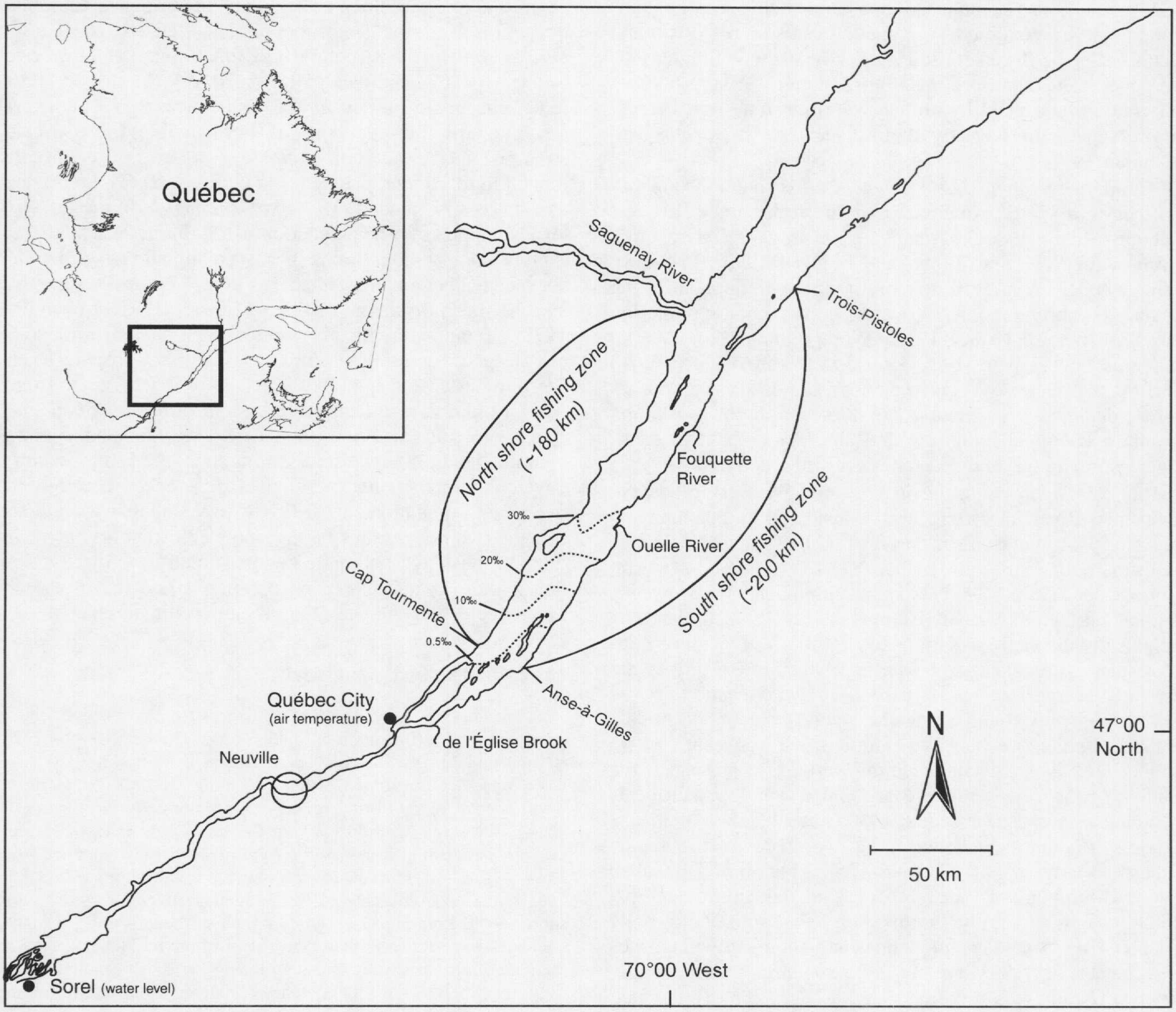
We focused on river discharge and temperature as the two environmental variables most likely to influence the abundance of estuarine smelt populations. Discharge plays a pivotal role in the structure and functioning of large river ecosystems (Vincent and Dodson 1999). In the St. Lawrence, discharge influences the abundance cycles of several commercially important species. For example, the year-class strength of lake sturgeon (*Acipenser fulvescens*) is strongly related to discharge in June (Nilo et al. 1997). The reproductive success of tomcod (*Microgadus tomcod*) during the winter also appears to be a function of discharge and tidal state (Fortin et al. 1990). Strong positive correlations were found between halibut and lobster catches in the Gulf of St. Lawrence and the mean discharge of the St. Lawrence River (Sutcliffe 1973). Temperature is also a dominant factor influencing most aspects of food-web processes at many trophic levels. We thus tested the hypothesis that river discharge and temperature play a significant role in controlling the abundance cycles of estuarine smelt populations, as indicated by commercial landings recorded throughout the 20th century. Given the fundamental ecological differences between the two smelt populations at all life history stages, we predicted that the two populations have responded differently to variations in these hydroclimatic factors. Finally, we discuss how these findings influence conservation strategies in the St. Lawrence estuary in the face of future climate change.

Materials and methods

Smelt landings were reported by fishers from 1917 to 1979 and compiled by the Bureau de la Statistique du Québec (Bérubé 1990; Bérubé and Yergeau 1992). These fishers have traditionally used large trap nets equipped with wings and leaders mounted on wooden posts in the littoral zone. They are normally installed every year at the same location early in the spring and removed during the fall. The fishing zones used for the present study extended from Anse-à-Gilles to Trois-Pistoles along the south shore (~200 km) and from Cap Tourmente to the Saguenay River along the north shore (~180 km; Fig. 1). There is no recorded fishing effort between the two shores in the open waters of the middle estuary. The traps are multi-specific, capturing other pelagic fish (including herring and capelin). Only the catches registered along the north and the south shores of the St. Lawrence middle estuary were used in this study and are expressed as total annual catches for each shore. Studies conducted since the middle of the 20th century have consistently shown that the two populations remain spatially segregated in commercial catches along the two shores throughout the ice-free season. We thus assumed that this spatial segregation has been maintained throughout the 20th century and that the landings recorded from trap nets located on either the north or south shore are a reliable indicator of the abundance of each population. Catch statistics from the south shore started in 1917 and from the north shore in 1922. Landings after 1979 are not taken into account due to large-scale abandonment of the smelt fishery related to habitat deterioration (Lecomte et al. 1999; see Discussion).

Aberrant values in the smelt catches, mainly registered during and shortly after World War II, were removed from the series. These outlying values were identified using the extreme studentized deviate method (also called Grubbs test; Grubbs 1969), recommended by the United States Environmental Protection Agency (USEPA 1992), and applied on segments of at least seven

Fig. 1. Study area, location of water level (Sorel) and temperature (Québec City) measurement stations, fishing zones, and average position of isohaline (‰) on the flood tide in the middle estuary of the St. Lawrence River, Canada. Spawning areas of the north-shore smelt population are located near Neuville and those of the south-shore smelt population are found in de l'Église Brook, Fouquette River, and Ouelle River.



values in the data series. The outliers correspond to the years 1941, 1942, 1944, 1947, 1950, and 1960 on the north shore, and to the year 1943 on the south shore. As the time series were relatively short (~60 data points), these missing data points were replaced with modelled values fitted to the raw data (simple exponential smoothing; SAS 1999). The cyclical patterns in both catches and climatic factors were characterized using a single spectrum Fourier analysis.

Because the smelt catches are expressed as annual landings and not as catch per unit effort, observed abundance cycles may partially reflect varying fishing effort or catchability. To test for this possibility, we verified whether the annual catches were correlated with the number of fishers (of smelt, herring, eel, others, and total) and (or) with the annual mean catches of other species captured in the same trap nets in the estuary (herring, capelin, and total catch). These additional variables were also available in the fisheries statistics (Bérubé 1990; Bérubé and Yergeau 1992).

Hydrological measurements came from Hydat, a CDROM updated by Environment Canada (HYDAT 1998). Water levels have been measured at the hydrographic station located at Sorel (Fig. 1) since 1912 and it was chosen as the reference station to represent the St. Lawrence River hydrological regime. Although we would have preferred to use flow rate in the St. Lawrence River, direct measurements are available only in the vicinity of Montréal, upstream of major affluents. Furthermore, flow reconstitution immediately upstream of the middle estuary (Québec City) requires a complex set of calculations and has only been completed for the years 1932 to 1998 (Jean Morin, Meteorological Service of Environment Canada, 1141 route de l'Église, Sainte-Foy, QC G1V 3W5, unpublished data). As the monthly average water levels at Sorel are strongly correlated with the reconstituted discharge data at Québec City ($r = 0.88$ and $p < 0.05$ for monthly means between 1932 and 1998), we used water level at Sorel as a surrogate measure of the river's flow into the middle estuary. Discharge is considered to have a far greater influence on smelt population dynamics than differences in water level because of the strong tidal regime in the middle estuary to which smelt populations are consistently exposed (mean tide range at Québec City is 4.1 m, but spring tide range can be as much as 6.9 m at the eastern tip of Île d'Orléans; SLC 1996). The Meteorological Service of Environment Canada also provided daily measurements of air temperature at Québec City in the vicinity of spawning and fishing areas. Water temperatures in the St. Lawrence River near Québec City are available only for the last decade, but are strongly correlated with air temperature (e.g., r = 0.95 and $p < 0.05$ for monthly means between 1986 and 1997). The daily measurements of water levels and temperature were used to calculate annual, semi-annual (between April and September to encompass the growing season), and monthly averages between 1917 and 1979. Water levels are expressed in metres according to the International Great Lakes Datum 1985. Two missing data points for water level (one in March and one in April) and one for temperature in August were replaced with the same implementation procedure used for annual smelt catches.

Climatic variables significantly correlated to smelt abundance were identified using univariate cross-correlation analyses (Pearson r; $p < 0.05$). Annual, semi-annual, and monthly averages of water level and air temperatures were computed to isolate specific moments of the year significantly related to annual smelt abundance. A lag of 0, –1, –2, and –3 years was introduced to detect any possible recruitment signal in the data series. Because smelt reproduce at 2–3 years of age and 2–3-year-old smelt dominate the commercial landings (Fournier and Landry 1990), changes in survival of young-of-the-year smelt related to temperature or discharge would not be evident in commercial catches for a period of 2–3 years.

Multiple regressions (forward stepwise; $p < 0.10$) were computed to quantify the relative contribution of significant climatic variables to variation in smelt landings and to rank them in order of importance. We used catches as dependent variables (north and south shores) and a set of significant climatic factors identified in univariate cross-correlation analyses as independent variables. Because the same data set was used in both univariate cross-correlation and multiple regression analyses, the latter cannot be used to reduce the probability of spurious correlations.

To explore the sensitivity of our findings to autocorrelation in the data series, we compared the results of the cross-correlation analyses using the uncorrected data series with that using a "prewhitened" data series. Prewhitening involved fitting the time-series model presented in Pyper and Peterman (1998, eq. 8) to each data set and using the residuals for computing correlations. Another multiple regression analysis was conducted as described above but using the time series of smelt landings and climatic variables corrected for autocorrelation. Except for the Grubbs test (available at www.graphpad.com/www/grubs.htm), the statistical analysis was carried out using Statistica™ edition 1998 (Statsoft Inc.; available at www.statsoft.com) and SAS (1999).

Results

Smelt landings

Low-frequency fluctuations were found in the landings. Smelt catches on the north shore varied with a periodicity of approximately 38 years (Fourier analysis; $p < 0.05$) (Fig. 2). The periodicity observed on the south shore is approximately 31 years (Fourier analysis; $p < 0.05$) (Fig. 2). The long-term patterns of smelt landings on the two shores are inverted resulting in a negative correlation between north- and south-shore landings ($r = -0.41$ and $p < 0.01$).

Smelt catches were not correlated with the number of smelt fishermen ($p > 0.05$). In addition, no significant correlations were observed between the annual catches of smelt and that of other pelagic fishes in the estuary including herring, capelin, and total fish landings ($p > 0.05$).

Hydroclimatic variables

Low-frequency fluctuations were also found in the climatic factors. Annual mean water levels measured at Sorel varied with a periodicity of approximately 34 years (Fourier analysis; $p < 0.05$) (Fig. 3). The annual mean air temperatures at Québec City varied with a periodicity of about 68 years (Fourier analysis; $p < 0.05$) (Fig. 3). Analyses of semi-annual and monthly means for both water levels and temperatures revealed periodicities similar to those of the annual means (data not shown).

Autocorrelation

The long-term data series of smelt landings contain positive autocorrelations only at lag-1 for the north and south shores. The annual, semi-annual, and monthly mean water levels had a significant autocorrelation at lag-1. No autocorrelation was found in the temperature series.

Univariate cross-correlation analyses

Time series uncorrected for autocorrelation

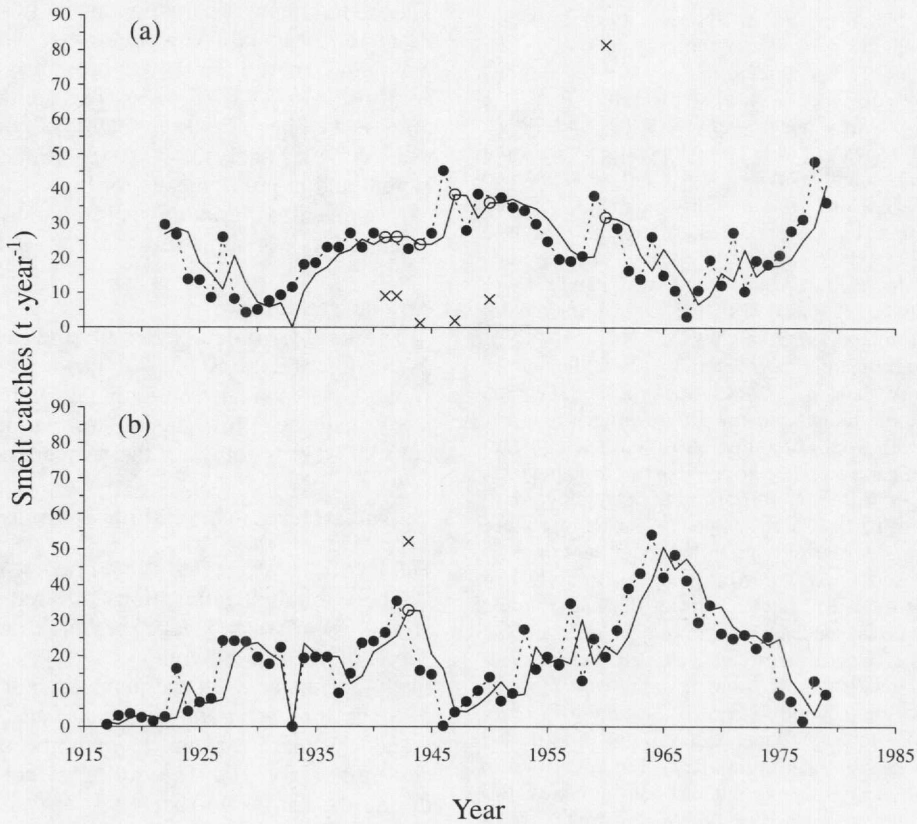
The two smelt populations differed in their responses to variations in water level. The smelt catches from the south shore of the St. Lawrence estuary are strongly and negatively correlated with the annual mean water levels at Sorel of year 0, to semi-annual mean water levels of year 0 and lagged by one year, and to monthly means between March and July (Table 1). The strongest correlations were found during the spring floods (April) of year 0, with a correlation coefficient $r_0 = -0.50$ and $p < 0.01$ (Table 1). The strength of the correlations tends to decrease but remains significant when introducing a lag of –1, –2, and –3 years in the analysis (Table 1). In contrast, the correlation coefficients between water level and smelt catches on the north shore are in general positively correlated with annual, semi-annual, and monthly averages. Significantly positive correlations between smelt landings and water levels were observed during March of year –2, April of year –1, and September of year –1. Significantly negative correlations occurred in December of years –2 and –3 (Table 2).

The two smelt populations also varied differently in their responses to variations in temperature. The correlation coefficients between temperature and smelt catches on the north shore are strong, significant, and positive for the annual and semi-annual means and in May of year 0, and tend toward null coefficients for the rest of the year and also when introducing a lag of –1, –2, and –3 years in the analysis (Table 2). In contrast, on the south shore, significant and negative correlations were found with the semi-annual mean temperatures of year 0 and year –1 as well as during August of year 0 and year –1 (Table 1).

Prewhitened time series

When the time series were corrected for autocorrelation (prewhitened), the relative importance of climatic variables on smelt landings along the two shores differed, whereas the sign of the correlations remained the same. On the south

Fig. 2. Total annual smelt landings in tonnes per year (t·year^{-1}) in the St. Lawrence middle estuary for (*a*) the north shore (1922–1979) and (*b*) the south shore (1917–1979); the symbol (●) and the broken line correspond to raw annual smelt catches, (×) to outliers removed from the series, and (○) to modelled values fitted to the raw data using a simple exponential smoothing (solid line). The cyclical patterns in both catches and climatic factors were characterized using a single-spectrum Fourier analysis (38 years for the north shore and 31 years for the south shore; $p < 0.05$).



shore, prewhitening reduced the number of significant correlations between water level and smelt landings from 15 to 3. However, the majority of correlations remained negative (37 in the prewhitened series vs. 32 in the uncorrected series of a total of 48 correlations). After prewhitening, smelt landings were significantly correlated to the March water level measured one year prior to landings and to those measured in October and December of the same year as the landings. (Table 1).

Following prewhitening, the four significant correlations observed between smelt landings on the south shore and temperature were no longer significant but remained negative. The majority of correlations were negative before and after prewhitening (38 before and 27 after prewhitening of 48 correlations). Smelt landings were significantly correlated to semi-annual temperature and mean October temperature (lagged by three years) and the December mean temperatures of the same year (Table 1).

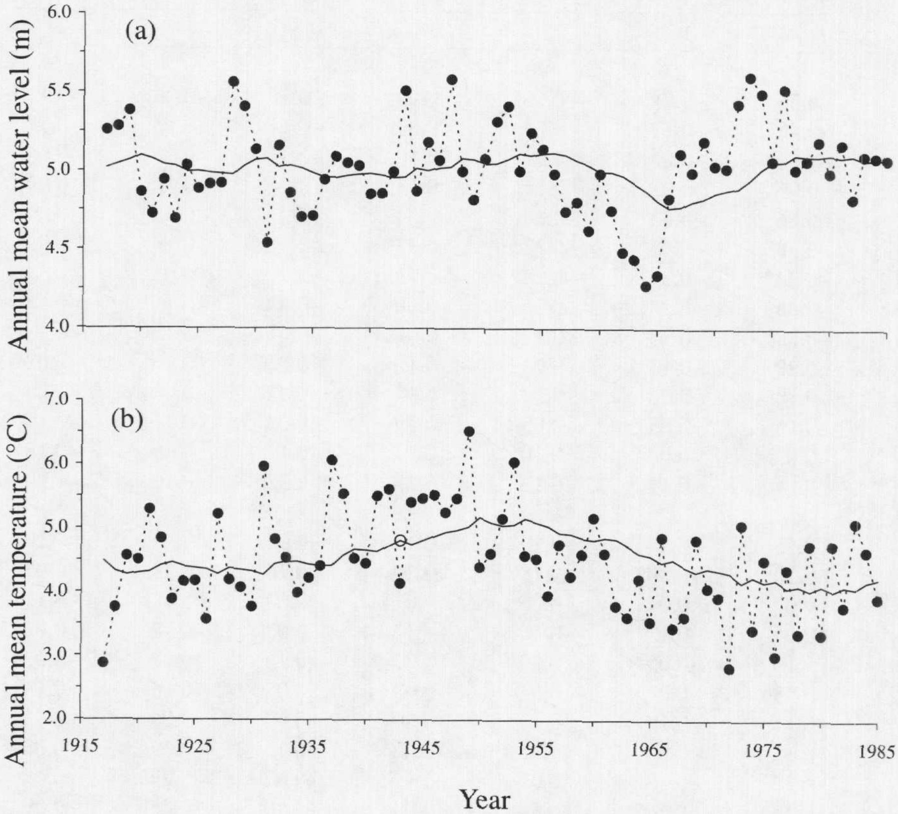
On the north shore, mean annual and semi-annual water levels and monthly means between May and October were all significant following prewhitening (except July). The significant correlations observed between landings and December water levels lagged by two and three years were reduced to nonsignificance following prewhitening (Table 2).

The correlation coefficients between temperature and smelt catches on the north shore before and after prewhitening remained essentially the same (Table 2). Following prewhitening, three new significant correlations were added: mean semi-annual temperature lagged by two years, April mean temperature of the same year, and October temperature lagged by three years.

Multiple regression analyses

The most significant climatic factors identified at $p < 0.05$ by the univariate cross-correlation analyses were combined as independent variables in multiple regression analyses, except when climatic variables were recorded after the fishing period in the same year as the landings (i.e., October and December water levels and temperatures, Tables 1 and 2). These were considered spurious correlations, since no plausible mechanisms can explain such relationships. The respective contributions to variance in smelt landings of the significant climatic variables retained for the analysis were quantified (Table 3). Uncorrected and prewhitened time series were analysed separately and compared. The multiple regression model for the south shore based on uncorrected time series combined four significant climatic factors explaining together up to 45% of the variance in smelt catches (Table 3). Mean April water level measured the same year as recorded landings explained 25% of the variance in smelt catches. Mean April water level two years prior to recorded landings explained an additional 10% but was removed at step 5 of the analysis. Mean April water level three years prior to recorded landings explained an additional 5% of the

Fig. 3. Annual mean (*a*) water levels measured at Sorel and (*b*) air temperatures at Québec City between 1917 and 1985. The broken line corresponds to raw annual smelt catches and the solid line to a simple exponential smoothing. The water level series shows a periodicity of approximately 34 years and the temperature series varies with a period of about 68 years (single-spectrum Fourier analyses; $p < 0.05$).



smelt catch. Mean March water level measured one year prior to recorded landings explained an additional 4% of the catch. Finally, the semi-annual temperatures averaged between April and September of the same year as recorded landings also explained 3% of the variance in smelt catches (Table 3).

Removing autocorrelation from the time series eliminated the significant negative correlations between spring water level and landings on the south shore (Table 3). For the prewhitened time series, mean October temperature three years before landings (explaining 9% of the landings) and mean March water level one year before landings (explaining 6%) were identified as the most significant climatic variables influencing smelt catches.

The multiple regression model based on the uncorrected time series for the north shore also combined four significant climatic factors explaining together 39% of the variance in smelt catches. Semi-annual temperatures averaged between April and September of the same year as recorded landings explained 15% of the variance in smelt catches (Table 3). Mean water level during March two years prior to recorded landings explained an additional 10% of the smelt catch (Table 3). Finally, mean December water levels measured two and three years prior to recorded landings explained an additional 9% and 5% of the catch (Table 3).

The multiple regression analysis of the prewhitened data series revealed some differences in the relative importance of climatic variables and the lag period. Semi-annual water level lagged by one year explained 14% of the variation in smelt landings. Mean semi-annual temperature lagged by two years explained 8% and mean October temperature lagged by three years explained 7% (Table 3).

Discussion

The time-series analysis of smelt landings and hydroclimatic factors in the St. Lawrence middle estuary revealed that the abundance of both smelt populations fluctuated significantly in relation to air temperature and water level with a periodicity of approximately 30 to 38 years. The periodicity of the cycles is difficult to assess with accuracy as only two cycles are represented in the landings and the water level series and only one cycle is represented in the temperature series. Nevertheless, comparable long-term cycles with periodicities of about 25 years have been reported in Great Lakes and St. Lawrence River water levels (Chanut et al. 1988 and references therein). Most importantly, the long-term patterns in smelt landings on the north and south shores are antiphase cycles. Water level and air temperature, chosen as two variables reflecting long-term changes in hydrology and climate, were significantly correlated with long-term patterns in smelt landings. However, the influence of these hydroclimatic variables differed markedly between the two sympatric populations. Univariate cross-correlation analysis using both uncorrected and prewhitened data series to remove autocorrelation revealed that both hydroclimatic vari-

Table 1. Pearson's correlation coefficient *r* for correlations between total annual smelt catches for the south shore (1917–1979) of the St. Lawrence middle estuary and annual, semi-annual, and monthly mean water levels at Sorel and air temperature at Québec City.

	South uncorrected				South prewhitened			
Parameter	0	–1	–2	–3	0	–1	–2	–3
Water level								
Annual	**–0.36***	–0.24	–0.16	0.00	–0.15	–0.05	–0.13	0.02
Semi-annual	**–0.40***	**–0.31***	–0.24	–0.09	–0.11	–0.12	–0.17	–0.04
January	–0.14	–0.06	–0.01	0.10	–0.14	–0.01	–0.06	0.00
February	–0.06	–0.02	0.11	0.13	–0.04	–0.13	0.09	–0.03
March	**–0.46***	**–0.43***	–0.24	–0.24	–0.09	**–0.30***	0.09	–0.12
April	**–0.50***	**–0.43***	**–0.37***	**–0.32***	–0.16	–0.15	–0.05	–0.12
May	**–0.34***	**–0.29***	**–0.28***	–0.11	–0.09	–0.06	–0.23	–0.05
June	**–0.36***	**–0.30***	–0.22	–0.08	–0.08	–0.16	–0.16	–0.10
July	**–0.28***	–0.23	–0.12	0.01	–0.01	–0.17	–0.11	–0.07
August	–0.20	–0.13	–0.01	0.12	–0.06	–0.19	–0.08	0.05
September	–0.18	–0.06	0.02	0.14	–0.22	–0.03	–0.08	0.02
October	–0.16	0.05	0.05	0.19	**–0.33**	0.16	–0.17	0.12
November	–0.03	0.08	0.10	0.24	–0.12	0.09	–0.12	0.15
December	–0.15	0.11	0.12	0.25	**–0.31**	0.10	–0.09	0.14
Temperature								
Annual	–0.15	–0.24	–0.20	–0.14	–0.02	–0.17	–0.10	–0.10
Semi-annual	**–0.28***	**–0.28***	–0.18	–0.20	–0.16	–0.24	0.03	**–0.26***
January	0.07	0.07	–0.06	0.07	0.00	0.18	–0.11	0.18
February	–0.04	–0.12	–0.12	–0.12	0.02	–0.12	0.02	0.06
March	–0.16	–0.05	–0.09	–0.02	–0.18	–0.07	–0.09	–0.04
April	0.03	–0.02	0.05	–0.08	0.05	–0.10	0.18	–0.02
May	–0.11	–0.18	–0.14	–0.20	–0.04	–0.09	0.03	–0.02
June	0.03	–0.06	–0.05	–0.02	0.13	–0.12	0.08	0.10
July	–0.20	–0.19	–0.07	–0.17	–0.07	–0.24	0.08	–0.21
August	**–0.28***	**–0.26***	–0.14	–0.08	–0.10	–0.25	–0.09	–0.07
September	–0.08	–0.01	0.01	–0.01	–0.13	–0.06	0.05	–0.15
October	–0.02	–0.06	–0.10	–0.07	0.04	0.06	–0.12	**–0.30***
November	0.05	–0.01	–0.06	0.02	0.06	0.07	–0.12	0.02
December	0.13	–0.16	–0.14	–0.13	**0.37**	–0.06	–0.13	–0.03

Note: Semi-annual corresponds to the averaged daily values recorded between April 1 and September 30. Correlations were performed with uncorrected and prewhitened time series and with lags of 0, –1, –2, and –3 years. Probability levels $p < 0.05$ are in bold; * corresponds to the variables used in the multiple regression analysis.

ables were generally positively related to north-shore smelt landings and negatively related to south-shore smelt landings.

Correcting the time series of smelt catches and water level for autocorrelation had a contrasting effect on our understanding of the dynamics of the two sympatric populations. For the north-shore population, three of the four significant climatic factors contributing to variance in smelt landings for both the uncorrected and prewhitened data series were lagged relative to the year of landings indicating that climatic variables influence recruitment. The positive influence of either temperature measured during the same year as captures or water level measured one year earlier was manifest at the semi-annual level (April–September), with monthly means of either water levels or temperatures being of secondary importance. For the south-shore population, two of the four significant climatic factors contributing to variance in smelt landings for the uncorrected data series were lagged relative to the year of landings indicating that climatic variables also influence recruitment of south-shore smelt. However, in contrast to the north-shore population, variance in the abundance of the south-shore population seems to be clearly related to water levels occurring in March or April either during the same year as landings or one to three years prior to the year of landings. Unfortunately, removing the effect of autocorrelation also eliminated this relationship. The significance of December temperatures and October water levels observed during the same year as the catches were recorded, thus after the annual closure of the fishery, cannot be interpreted. Although the removal of autocorrelation is statistically justified to compute correlations between two data series, removing autocorrelation also results in removing low-frequency variability from the data (Pyper and Peterman 1998). If the low-frequency components of variability in two time series are synchronous, then removing the autocorrelation may also remove much of this covariance (Thompson and Page 1989). It thus appears that prewhitening the data series eliminated an important relationship between long-term environmental processes and the dynamics of the south-shore smelt population.

Differing long-term fluctuations in abundance between sympatric smelt populations and the contrasting role of hydroclimatic variables in driving these cycles are likely re-

Table 2. Pearson coefficient *r* for correlations between total annual smelt catches for the north shore (1922–1979) of the St. Lawrence middle estuary and annual, semi-annual, and monthly mean water levels at Sorel and air temperature at Québec City.

	North uncorrected				North prewhitened			
Parameter	0	–1	–2	–3	0	–1	–2	–3
Water level								
Annual	0.07	0.19	0.06	–0.02	–0.16	**0.33***	–0.02	0.15
Semi-annual	0.09	0.24	0.04	–0.05	–0.14	**0.37***	–0.03	0.18
January	0.09	0.01	0.01	–0.02	0.11	–0.01	0.02	0.05
February	0.05	0.00	0.06	0.01	0.05	–0.06	0.07	0.05
March	0.22	0.12	**0.27***	0.13	0.15	–0.12	0.26	0.08
April	0.21	**0.28***	0.15	0.03	–0.01	0.22	0.09	0.12
May	0.02	0.19	–0.07	–0.18	–0.17	**0.37***	–0.04	0.15
June	0.08	0.19	–0.01	–0.05	–0.09	**0.32***	–0.06	0.18
July	0.03	0.13	–0.01	–0.02	–0.11	0.24	–0.06	0.20
August	0.08	0.23	0.08	0.01	–0.15	**0.35***	–0.01	0.17
September	0.12	**0.27***	0.16	0.04	–0.18	**0.37***	0.05	0.08
October	–0.01	0.21	0.07	0.01	**–0.27**	**0.36***	–0.01	0.08
November	–0.12	0.01	–0.12	–0.03	–0.20	0.24	–0.17	0.01
December	–0.22	–0.17	**–0.29***	**–0.29***	–0.19	0.10	–0.16	–0.10
Temperature								
Annual	**0.38***	0.18	0.23	0.08	**0.33***	–0.01	0.22	–0.09
Semi-annual	**0.39***	0.19	0.26	–0.03	**0.33***	–0.01	**0.36***	–0.06
January	–0.03	–0.08	–0.13	–0.10	0.04	0.00	–0.13	–0.07
February	0.13	0.05	0.17	0.19	0.13	–0.03	0.06	0.10
March	0.12	–0.02	0.10	–0.05	0.19	–0.03	0.14	–0.12
April	0.16	–0.02	0.21	0.10	**0.26***	–0.15	0.15	0.00
May	**0.34***	0.18	0.06	–0.04	**0.27***	0.15	0.13	–0.15
June	–0.08	–0.09	–0.04	–0.05	–0.06	–0.10	–0.03	0.18
July	0.14	0.05	0.02	–0.07	0.16	0.09	0.09	–0.03
August	0.07	0.15	0.08	–0.11	–0.02	0.15	0.18	0.07
September	0.07	–0.14	–0.09	–0.22	0.21	–0.19	0.14	–0.19
October	0.12	–0.02	0.04	–0.11	0.15	–0.10	0.15	**–0.27***
November	0.06	0.17	0.14	0.13	–0.10	0.08	0.09	–0.08
December	0.12	0.08	0.03	0.20	0.03	0.08	–0.10	0.13

Note: Semi-annual corresponds to the averaged daily values recorded between April 1 and September 30. Correlations were performed with uncorrected and prewhitened time series and with lags of 0, –1, –2, and –3 years. Probability levels $p < 0.05$ are in bold; * corresponds to the variables used in the multiple regression analysis.

lated to the differential exploitation of estuarine habitats. The two smelt populations exploit distinct physical habitats at all life stages. In the St. Lawrence middle estuary, the contrasted topography of the two shores drives the local hydrodynamics and influences water temperature. The south shore is characterized by large strands, a smooth slope, and shallow waters (<3 m), contrary to the north shore that corresponds to a deeper bed with a steep lateral slope (~20 m deep within 1 km of shore), high current speeds, and strong three-dimensional mixing processes (Laprise and Dodson 1989). As we have convincing evidence that these two populations are spatially segregated throughout their growing season (Fréchet et al. 1983; Bernatchez and Martin 1996; Lecomte et al. 1999), it is unlikely that the cause of variation in population abundance is the result of intraspecific competition for resources. Rather, it is likely that the south-shore population exploits a benthic feeding niche, whereas the north-shore population exploits a pelagic one. Exploitation of the benthic–pelagic resource gradient characterizes many species pairs (e.g., Smith and Skùlasson 1996).

High smelt landings on the south shore of the St. Lawrence estuary correspond to years of low spring water levels. Water level explains a significant fraction of the variance in the catches from the south shore and corresponds to the magnitude of the spring flood recorded either the same year as the catches, or one or three years before the year the catches were recorded. It is unlikely that water level itself directly influences the survival and recruitment of smelt in the macrotidal middle estuary. The shallow shoals along the south shore are exposed at low tide and flooded at high tide regardless of water level in the St. Lawrence River. It is more likely that discharge and associated current speeds have a greater impact on smelt population abundance. High discharge may influence larval survival in the shallow nursery areas, subsequent recruitment to the adult population, and survival of adults and their prey in the shallow feeding habitats. Newly hatched larvae leave their natal streams in mid-May shortly after hatching and are rapidly transported downstream (Ouellet and Dodson 1985). Young-of-the-year smelt appear to be passively retained in shallow bays along the south shore (F. Lecomte and J.J. Dodson, unpublished data). Because of Coriolis force and estuarine topography,

Table 3. Results of two multiple regression analyses (forward stepwise selection) between total annual smelt catches of the north and south shores in the St. Lawrence middle estuary and the most significant climatic factors identified by the univariate cross-correlation analyses. The analyses were performed for uncorrected and prewhitened time series.

Step	Variable	Variable removed	Partial R^2	Multiple R^2	F value	p
North shore						
Uncorrected time series						
1	**Semi-annual temperature –0**		**0.15**	**0.15**	**10.19**	**0.002**
3	**Water level March –2**		**0.10**	**0.25**	**8.11**	**0.006**
2	**Water level December –2**		**0.09**	**0.34**	**6.30**	**0.015**
4	**Water level December –3**		**0.05**	**0.39**	**4.24**	**0.045**
Prewhitened time series						
1	**Semi-annual water level –1**		**0.14**	**0.14**	**8.80**	**0.005**
3	**Seasonal temperature –2**		**0.08**	**0.22**	**5.63**	**0.022**
4	**Temperature October –3**		**0.07**	**0.29**	**5.34**	**0.025**
South shore						
Uncorrected time series						
1	**Water level April –0**		**0.25**	**0.25**	**19.77**	**0.000**
2	Water level April –2		0.10	0.35	9.49	0.003
3	**Water level April –3**		**0.05**	**0.40**	**5.10**	**0.028**
4	**Water level March –1**		**0.04**	**0.44**	**4.03**	**0.049**
5	(Water level April –2)	x	(0.03)	(0.42)	(2.61)	(0.112)
6	**Semi-annual temperature –0**		**0.03**	**0.45**	**3.44**	**0.069**
Prewhitened time series						
1	**Temperature October –3**		**0.09**	**0.09**	**6.07**	**0.017**
2	**Water level March –1**		**0.06**	**0.15**	**3.86**	**0.054**

Note: The respective contributions of climatic factors to variance in smelt landings correspond to the partial R^2, and the multiple R^2 corresponds to cumulative R^2 values. The climatic factors significant at $p < 0.10$ in the multiple regression are in bold and the global R^2 of each multiple regression is underlined.

the main route for freshwater outflow is directed along the south shore of the estuary (Laprise and Dodson 1989 and references therein). Thus, high discharge may reduce the efficiency of passive retention, resulting in an increase in downstream transport out of the St. Lawrence middle estuary of larvae and juveniles. This hypothesis may also apply to the major prey items of smelt, thus reducing survival at all life-history stages. Significant correlations between water level and smelt landings that occur without lag suggest that hydrological conditions prevailing during the summer of capture directly influence the survival of adult fish or catchability (see below). Although the assertion is speculative, strong flows in shoal habitat may be considered generally detrimental to all life-history stages of the south-shore smelt population that spends its entire life cycle in shallow waters (F. Lecomte and J.J. Dodson, unpublished data).

In contrast to the south-shore population, both temperature and water level appear to be equally important in influencing the abundance of the north-shore population. Average temperature measured over the entire growing season during the same year as the landings (uncorrected data) or two years prior to landings (prewhitened data series) influenced the abundance of the north-shore population. Higher temperatures will favour growth, which in turn favours survival, particularly for young-of-the-year fish exploiting the estuarine turbidity maximum (Sirois and Dodson 2000). The growth of smelt prior to reproduction is extremely variable and depends on temperature (McKenzie 1964; Fournier and Landry 1990), which in turn influences recruitment and the size or the age at which smelt enter the fishery. Temperature also influences production cycles of prey and trophic structure. The positive effect of high discharge on the abundance of this population may also act through the trophic dynamics and the physical extent of the estuarine turbidity maximum, which is exploited by the north-shore smelt throughout most of their life cycle. However, the biological mechanisms linking observed trends in temperature, discharge, and smelt population abundance in the estuarine turbidity maximum are complex and in the absence of more complete information, we may only speculate about their nature.

The fact that many of the correlations between catches and environmental variables were strongest during the year of the capture may suggest that temperatures and water levels affect the catchability of the smelt. We cannot completely refute this possibility. To a certain extent, catchability and abundance are positively related. Trap nets will be more efficient in catching fish when there are high densities of fish in the vicinity. However, several lines of evidence suggest that catchability is not a significant factor affecting landings. If catchability were a function of climatic variables, we would expect the varying catchability of trap nets to be reflected in the landings of all species of fish caught in the nets. Yet there was no relationship between smelt catches and the abundance of other fish species caught in the same nets. Furthermore, the absence of a relationship between the number of fisherman and smelt landings suggests that fluctuations in abundance dominate the variation in smelt catches. The annual smelt landings used in this study represent the integration of catches over a period of eight months and over a distance exceeding 100 km on both shores, thus decreasing the effects of short-term events such as wind, tides, and temperature variations on catchability. If variation in landings were significantly influenced by catchability, then years of low landings measured over hundreds of kilometres and during periods of months would imply major movements of fish outside fishing zones either across or along the estuary. This is not consistent with the important degree of genetic segregation that is observed between adjacent populations of smelt (Bernatchez and Martin 1996; Lecomte et al. 1999).

Regardless of the biological mechanisms responsible for the differential response of the two sympatric smelt populations to water level and temperature, it is evident that they are responding as two independent biological entities and as such should be considered as Evolutionary Significant Units (ESU; Waples 1995) for conservation and management purposes. An ESU is a population or group of populations that is substantially reproductively isolated from other conspecific population units and represents an important component in the evolutionary legacy of the species (Waples 1995). This definition provides criteria for the identification of ESUs, which are based on genetic isolation and the ESU's contribution to the ecological and genetic diversity of the species. This is particularly appropriate in the present case, as the persistence of the sympatric smelt populations will depend greatly on future climate change. The climate changes expected in the Great Lakes – St. Lawrence River basin might result in significant changes in water supply and temperature. Some authors expect a 40% decrease in water discharge in the St. Lawrence River in future years (Mortsch and Quinn 1996). Such extremely low water discharge was previously observed in the 1930s and 1960s, and according to the present data series, corresponded to high catches on the south shore and low catches on the north shore. However, the use of historical smelt abundance cycles described in the present study to predict future abundance cycles must be approached with caution. Apart from the uncertainties inherent in future climate change predictions, factors such as habitat deterioration must be considered in any attempt to predict future trends. Over the past 30 years, many spawning sites and smelt habitats have been disturbed or lost due to extensive fishing activities, agricultural pollution, and severe physical damages in the St. Lawrence River as well as in its affluents involving bank erosion and sedimentation. The Boyer River, located just downstream of de l'Église Brook, was traditionally one of the most important spawning sites on the south shore but was abandoned by spawners in the 1980s (Trencia et al. 1989). The south-shore population is presently the object of an enhancement program, the major objective of which is to restore the Boyer River spawning grounds (Trencia et al. 1989). Lower discharge should be advantageous for the south-shore smelt population and all efforts to enhance the south-shore population may have their greatest chance of success during periods of low discharge. In contrast, the north-shore population cannot be expected to respond in a similar fashion. High discharge and increased temperatures may favour the north-shore population. Finally, the differential response of the two smelt populations also serves to illustrate the fundamental ecological differences existing between shoal and channel habitats, suggesting that future climate changes may differentially effect other populations or species that are segregated between these two habitats. For example, populations of the copepod *Eurytemora affinis* sampled in the St. Lawrence middle estuary and adjacent salt marshes are genetically highly divergent (Lee 1999). Ecological and genetic segregation between channel and shoal habitat may be a common feature of the St. Lawrence estuarine ecosystem.

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