The impact of hydrological variation on the seasonal occurrence and migratory timing of freshwater fish species in the lower St. Lawrence River

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Abstract

Knowledge of the movement and seasonal distribution of local fish assemblages in the lower St. Lawrence River was incomplete and the importance of hydrological variability on fish distribution patterns was not fully understood. Given the variability in river level at both seasonal and interannual scales, the objective of this study was to test the hypothesis that variation in river level would affect the distribution dynamics of local fish assemblages in the lower St. Lawrence River. Using long-term data series (28 years) of both river level and fish catches at a fixed location, we examined the empirical relationships between attributes of the hydrological regime and the annual distribution patterns of 38 fish species. Results indicated that the annual timing and/or the duration of occurrence of 20 fish species components were significantly related to the river level. Correlation analysis indicated that an increase in the spring river level would delay the annual timing of occurrence of the spring fish components. In contrast, high autumn river level was associated with earlier timing of occurrence for fall fish components. Summer fish components appeared to be relatively unaffected by interannual variations in level. These results indicated that proposed scenarios for water level management in the St. Lawrence River should incorporate the temporal distribution and migratory patterns of fish in response to water level variations. These fish responses will inevitably have a direct influence on fishing activities and profitability of fisheries in the lower St. Lawrence River.

Introduction

The occurrence and distribution patterns of fish in rivers vary spatially and temporally as a result of specific habitat use and fluctuating environmental conditions (Northcote 1984). In large rivers, the diversity of habitats may lead to high spatial heterogeneity in local fish assemblages. Changes in environmental conditions may, however, incite fish to move among the different habitats in search of a better environment in order to optimize their well-being and complete their life cycles, because food resources tend to vary in quality and/or quantity over space and time (Townsend 1989). The most conspicuous evidence of fish movement is probably related to the annual reproductive imperative, when fish may travel long distances to spawn. Local fish assemblages will therefore change accordingly with these seasonal and/or annual fish movements within large river ecosystems (Wolter and Bischoff 2001). Many studies have documented fish movement and migration within small and large rivers, but the vast majority of these have dealt with diadromous fish species (Northcote 1978; Northcote 1997; Quinn *et al*. 1997; Wolter and Vilcinskas 1998). This led Northcote (1998) to conclude that the movements of many potamodromous species have not been studied in detail.

The environmental factors that can stimulate and control the timing of fish migration and the resulting local occurrence of fish in rivers include water discharge, water level, tidal current, water temperature, photoperiod, light intensity and variation in prey density and food resources (Leggett 1977; Northcote 1984; Jonsson 1991; Quinn and Adams 1996). These will affect both upstream and downstream movements and their relative influence will vary among habitats or fish species. The hydrological regime has often been reported as a major, if not the main cue for migration and movement in riverine fish (Jonsson 1991; Lucas and Baras 2001). Most of these migrations are related to the transition between life-history stages corresponding to different habitat needs (i.e. spawning, feeding and survival habitats). Thus, most environmental factors affecting the cue that triggers these transitions may also affect the timing of fish migration itself. By modifying migration timing and the relative distribution of the various fish species, the

fluctuation in the hydrological regime of large rivers, whether natural or human-induced by regulation, is the predominant variable that can disrupt the structure of local fish assemblages (Resh *et al.* 1988; Poff and Ward 1990; Stanley *et al.* 1997; Taylor and Warren 2001).

The dramatic effects of river flow alteration have been easiest to ascertain in the case of river damming and reservoir building because these works have resulted in radical and permanent changes in the occurrence and distribution of fish species and severely restricted fish movement along stretches of rivers (Bebars and Lasserre 1983; Kanehl *et al.* 1997; Chang *et al.* 1999; McKinney *et al.* 2001). In tropical waters, changes in fish movement and distribution patterns resulting from intense seasonal variations in environmental conditions, such as the rainy season and very large floods, have been easy to isolate because of their significant variability and cyclical periodicity (Jurajda *et al.* 1998; Reichard *et al.* 2002). In temperate waters, where variations in the seasonal hydrological regimes are less pronounced and often occur more gradually, impacts on fish movement and distribution patterns may be more difficult to detect than in tropical waters. In addition, water temperature and flow regime in large, temperate rivers may vary simultaneously and be closely linked, rendering the relative significance of each factor to fish distribution and migratory timing difficult to determine.

Nonetheless, empirical relationships linking variations in fish movement and distribution in large, temperate rivers to several environmental gradients, including water flow, water temperature, light and productivity, have been reported (Schlosser 1982; Schlosser 1987; Persson *et al.* 1991). These studies were, however, conducted on short time scales, between seasons or for periods of two to five years. The effects of long-term climatic changes or anthropogenic disturbance of the hydrological regime over many years on fish movement and migration timing has yet to be assessed. The impact of these effects on fish migration timing may be more difficult to detect because of fish longevity and the gradual interannual effect of these environmental changes over seasonal variations. To test the hypotheses linking anthropogenic disturbance and variations in fish movement and distribution patterns, a

continuous and relatively lengthy data series on fish movement and environmental conditions is required. However, there is no such assessment in the literature.

The objective of our study was to evaluate the level of interannual variability in the seasonal occurrence of fish and to examine the link between the hydrological regime and the seasonal distribution patterns of freshwater fish in a large river ecosystem. This was achieved by testing the empirical relationships between various hydrological variables and multi-species fish catch data recorded at a fixed station in the St. Lawrence River over a period of 28 years. The St. Lawrence River is a large, fluvial ecosystem supporting a rich diversity of fish, many of which migrate seasonally over a large section of the river (de Lafontaine *et al.* 2003). The availability of a long-term data series on daily catches of multi-species fish assemblages recorded at an experimental trap fishery operated by the Aquarium du Quebec in the lower part of the river since 1975 could provide a unique opportunity for testing our hypothesis. To our knowledge, studies investigating a fish community of more than 38 species over a long time period (i.e. more than 10 years) in a river as large and complex as the St. Lawrence River are virtually nonexistent in the literature. Our working hypothesis was that both the timing and the duration of seasonal occurrences of the different freshwater fish species at the experimental trap fishery will vary from year to year as a result of hydrological conditions in the river. Since it is posited that water temperature also influences migration timing and distribution of some fish species, its potential impact on the former will also be assessed if correlation with water level is observed. The availability of a significantly longer time series of fish abundance for many species and of environmental conditions (i.e. water level and temperature), relative to those commonly reported in previous studies, will allow us to better describe and assess the link between fluctuations in the hydrological regime and fish population distribution patterns in a large river ecosystem.

Materials and methods

Study area

The St. Lawrence River is the main outflow of the Laurentian Great Lakes and represents one of the largest temperate river ecosystems in the world. With a mean annual flow of 12, 600 m^3/sec, it is the 15th largest river system in the world (Environment Canada 1996). The freshwater stretch of the river extends over 500 km from the outflow of Lake Ontario to the St. Lawrence Estuary and consists of alternating sections of fluvial lacustrine widening and narrow, fast-flowing corridors, creating a rich diversity of corresponding habitats. At its downstream end, between Trois-Rivières and Quebec City, the river comes under the progressive influence of semidiurnal tides inducing high water-level variability (mean tidal range of up to 4 m at Quebec City) and current reversal, but its waters remain fresh (Godin 1978; El-Sabh and Silverberg 1990). The discharge at the river's outflow (Quebec City) varies seasonally from 8500 to 24, 000 m^3/sec, being maximal in spring and minimal in late summer. The river's water level and flow have been regulated at the outflow of Lake Ontario since 1960. A total of 88 freshwater and 18 diadromous fish species are found in the river, which supports important sport and commercial fisheries (Environment Canada 1996).

De Lafontaine *et al.* (2003) showed that many predominant fish species exhibit seasonal migratory behavior over a very large section of the lower St. Lawrence River. Several freshwater fish species, including walleye (*Stizostedion vitreum*), yellow perch (*Perca flavescens*), channel catfish (*Ictalurus punctatus*), longnose sucker (*Catostomus catostomus*), white sucker (*Catostomus commersoni*) and lake whitefish (*Coregonus clupeaformis*), move between the upstream fluvial lake (i.e. Lake Saint-Pierre) and the highly productive fluvial estuary downstream. These migratory movements result in both seasonal and interannual variability in local occurrence and distribution of fish along the river, which in turn affects fish availability to fishing gears. Factors controlling fish distribution and movement, however, are still

poorly understood in very large rivers, like the St. Lawrence. Given the relatively high seasonal variability in river flow and associated water levels, one can hypothesize that the distribution and local occurrence of fish in the lower St. Lawrence River could be largely influenced by the hydrological regime.

Empirical relationships linking fluctuations in the hydrological regime and fish population dynamics have been documented for some commercially exploited fish species in the St. Lawrence River using data collected over a relatively short time period (Fortin *et al.* 1990; Nilo *et al.* 1997; Mingelbier *et al.* 2001). These relationships provide additional evidence of the possible effect of hydrology on fish dynamics in large river systems.

Fish catch data

The experimental trap fishery is located in Saint-Nicolas on the south shore of the St. Lawrence River (71.2950° W, 46.7411° N), approximately 8 km upstream of the Quebec City port. This fish trap is a modified weir fishery similar to that traditionally used for catching American eel (*Anguilla rostrata*) by commercial fishermen in the lower St. Lawrence River. The fixed gear consists of a vertical net (leader line; 1¼-inch mesh) extending perpendicularly from the shoreline and attached to a box trap positioned at the low-tide line (~95 m from shore; 1¼-inch mesh). The trap is operational between May 15th and October 31st each year. Since 1975, twice a day at every low tide, fish of all species captured by the trap are identified, enumerated and then released back into the river by one knowledgeable fisherman, providing us with continuous daily records of adult fish abundance for 170 consecutive days every year (i.e. ~ 330 visits to the trap / year). A detailed description and a validation of the applicability of this experimental trap fishery to determine fish seasonal distribution is given in de Lafontaine *et al.* (2003). These authors showed that only a small proportion (< 5%) of fish are recaptured at the experimental trap and the vast majority (> 90% of < 5%) of them are recaptured within 48 hours of first capture.

Patterns in fish timing and duration of occurrence

Overall, 57 fish species have been reported at the experimental trap between 1975 and 2002. Following a preliminary inspection of the data, 38 species with years of capture exceeding 20 fish (i.e. >20 fish per year) were retained for subsequent statistical analysis. The remaining 19 species were considered rare and were excluded from the working data set (e.g. Round goby (*Neogobius melanostomus*), Striped bass (*Morone saxatilis*)). We visually classified the annual daily catch distributions of each of the 38 species into one of five different fish groups. These groups correspond to five general temporal patterns of fish occurrence during the course of a year. The resident group included eight species usually present during most of the fishing season, as in the case of smallmouth bass (*Micropterus dolomieui*). Spring, summer and fall species groups were characterized by species with unimodal peaks of occurrence in the respective season. The American eel typifies a fall species. Eleven species, including yellow perch, occur in spring and fall, corresponding to downstream and upstream seasonal movements (de Lafontaine *et al*. 2003). It was therefore decided to divide these 11 spring-fall species into their two seasonal components (i.e. Spring and fall) for which migratory timing and duration of occurrence were estimated. This increased our data set from 38 species to 48 different fish components each year (One component had insufficient number). To corroborate our visual classification, a statistical grouping analysis was done *post priori* using a cluster analysis of the annual timing and duration of occurrence of each of these 48 components as variables. The two techniques used to discriminate among fish groups produced the same results.

For each fish component and each year of occurrence, the cumulative frequency of abundance was plotted as a function of time and the dates corresponding to 25%, 50% and 75% of the cumulative catch were determined. The median date of total abundance (i.e. date at which 50% of the total seasonal catch was reached) was used as an index of seasonal timing of

occurrence for each fish component (Figure 1). In the case of migratory species, it corresponded to the annual migration timing, as reported in other studies (Leggett and Whitney 1972; Quinn and Adams 1996; Robards and Quinn 2002). The duration of fish occurrence at the experimental trap fishery in any given year was estimated by calculating the number of days between the dates at which 25% and 75% of catches were reached.

Hydrological and temperature regime

Because of tidal influences on the hydrological regime at Quebec City, daily flow or level cannot be directly measured at our study site. In ice-free conditions, the daily water level measured in the port of Montreal has been shown to be highly correlated (n = 34 years, r = + 0.93, $p < 0.0001$) to the daily flow discharge estimated in front of Quebec City using the method proposed by Carrier (1976). Therefore, we decided to use the water level data from the port of Montreal, since it is measured every day and not estimated, and a longer time series (i.e. 1975 to 2002) was available. Every year since 1975, water level attributes were calculated for the entire year (January through December) and for each of the four "hydrological seasons" corresponding approximately to winter, spring, summer and fall (Figure 2). The winter hydrological season starts on November 26 and lasts for 74 days; spring starts on February 9 and lasts for 135 days; summer begins on June 24 and terminates 70 days later, followed by fall, which starts on September 2 and lasts for 85 days. Every year for the entire year and for each of these four periods, 55 statistical attributes were calculated to describe various characteristics of the hydrological regime (Puckridge *et al.* 1998). Each of these 55 different attributes characterizes either the quantity of water, its variation within a season variation or its timing. The skewness of the level was calculated as the difference between mean and median divided by the median (Puckridge *et al*. 1998). Attributes quantifying the same characteristic of water level are to be correlated. This 28 years data set encompassed the entire period of fish catch data recorded at the experimental trap fishery.

Records of daily water temperatures in the St. Lawrence River were provided by the water pumping station and filtration plant of the John Labatt Brewery in Montreal, between May 3, 1977 and December 1, 2001 a period of nearly 25 years. This station is located on the north shore of the St. Lawrence River, in the western part of the island of Montreal, upstream of the Lachine Rapids. These temperature data were compared with a data set of 14 years, recorded a few kilometres upstream of the experimental trap fishery and they were significantly highly correlated ($n = 14$ years, $r = + 0.99$, $p < 0.0001$). We therefore considered these temperatures measured in Montreal to be representative of prevalent daily water conditions in the St. Lawrence River and at our study site. A total of 55 statistical parameters were calculated to describe annual and seasonal water temperature conditions. The seasonal periods were similar to those used for water level attributes.

Statistical analyses

For each of the 48 fish components analysed, the level of interannual variability of fish annual timing and duration of occurrence was first examined by calculating the descriptive statistics over the 28 years. Fish timing, duration, density and year were tested for collinearity to detect possible interactions in fish capture data. Collinearity between water level and temperature parameters was also tested to verify the degree of association between these two variables in each hydrological period. Temporal linear trends in physical and biological variables were assessed by Pearson correlation analysis of each parameter as a function of year and by visual inspection of the plots between the respective variables. Pearson correlations analyses were performed to detect possible interactions between fish timing, duration, and water level and temperature parameters. These analyses were performed only for years when 20 or more fish of a particular component were captured. To look for the possible indirect or combined effects of water level and temperature in seasons when correlation between them was observed and significant, stepwise multiple linear regression analyses were run using annual timing and

duration of occurrence as dependent variables. Collinearity between independent variables (i.e. water level and temperature parameters) was estimated by examination of the pairwise correlation coefficients. When collinearity occurred, each collinear variable was used to build a separate model, which was then compared with the other models. Residual scatterplots, normal probability plots (Tabachnick and Fidell 1983) and partial residual plots (Larsen and McCleary 1972) were used to determine if the assumptions of the multiple linear regression were satisfied (i.e. normality, linearity and homoscedasticity of residuals). All statistical analyses were performed using Statistica for Windows (Statsoft 1995).

Results

Variation in annual timing and duration of occurrence

The chronology of the annual timing of occurrence for each of the 48 species components captured at Saint-Nicolas clearly depicted the succession and seasonal changes in local fish assemblages in the lower St. Lawrence River (Figure 1). Species richness is high both in spring and fall, and the summer fish assemblage is usually characterised by a low number of fish species. The median date of occurrence of every fish component at the experimental trap has been very variable over the past 28 years. In general, spring and fall components exhibited smaller interannual variation in their annual timing of occurrence, relative to that noted for summer and resident species (Figure 2). The interannual variation in the timing of occurrence of the spring group (19 species components) averaged 30.2 days (SD 13.7 d) and the mean value for maximum variation between two consecutive years was 25.7 days (SD 10.4 d). The mean variation for the fall group, which included 19 species components, was 30.6 days (SD 16.7 d) and maximum variation between two consecutive years averaged 24.0 days (SD 11.5 d). The annual timing of the two summer species (i.e. alewife (*Alosa pseudoharengus*) and American shad (*Alosa sapidissima*)) was much more variable, averaging 99.5 days (SD 7.8 d) while their maximum variation between consecutive years was 57.5 days (SD 38.9 d). The eight resident species were also variable both in terms of timing of occurrence (mean = 78.2 days, SD = 49.9 d) and maximum variation for consecutive years (mean = 71.3 days; SD = 24.2 d). In terms of duration of fish occurrence, both spring and fall components tended to occur over shorter time periods during the year, as opposed to summer resident species, which were captured over a longer time period (spring and fall, μ = 23.7 days; summer, μ = 56.2 days; Figure 1). Interannual variability in duration was also more pronounced for summer and resident species.

Fourteen of the 48 fish components showed significant correlation between annual timing and duration of occurrence (Table 1). In most cases, the relationship was positive in the spring and negative in the fall. The annual timing of seven fish components was significantly correlated

with total catch, three being positive and four negative (Table 1). Correlations between duration of occurrence and total catch were significant for seven fish components, three of which were positive (Table 1).

Variation in water level and temperature

The mean annual water level at the port of Montreal ranged from 5.8 to 7.5 m between 1975 and 2002, and has decreased significantly since 1975 ($n = 28$, $r = - 0.64$, $p < 0.0001$). The mean estimates of spring, fall and winter water levels also decreased significantly during the same time period (i.e. spring, $r = - 0.50$, $p < 0.007$; fall, $r = - 0.69$, $p < 0.0001$; winter, $r = - 0.62$, $p < 0.001$), but this trend was not evident in the case of the summer level. Probably because it characterize by the lowest levels and less variable annually. The maximum spring level varied between 7.0 and 9.7 m, corresponding to a 37% difference in the peak level over 28 years (Figure 2a). The annual minimum level fluctuated between 5.2 and 7.2 m. The coefficient of variation in the daily level between years was minimal in September (6.5%) and maximal (11.5%) during spring (Figure 2b). This high variability was principally due to variation in the timing and the intensity of the spring freshet between the 40^{th} and 175^{th} day of the year. This 135-day interval encompassed all early and late spring freshet events over the past 28 years (1975-2002). The interannual water level variability decreased in summer and increased in autumn (Figure 2b).

Water temperature in the St. Lawrence River usually peaks in early August (Figure 2c), and over the past 25 years, the maximum temperature has ranged from 20.7 to 25.8 ^{o}C, a 25% difference. The coefficient of variation of daily water temperature (computed using Kelvin degrees to minimize the influence of zero values) indicated that interannual variability was most pronounced in late spring (May-June), at the time of annual warming (Figure 2d). Variability remained relatively high throughout summer and fall, but usually declined sharply during the winter, after ice formation in December. Mean annual water temperature ranged from 9.8 to

11.7 ^{o}C between 1978 and 2000, but without showing any significant trend. The statistically significant trend over this 25-year period was the increasing summer and fall temperatures (i.e. summer, r = + 0.53, $p < 0.007$; fall, r = + 0.62, $p < 0.001$).

Correlation between water level and temperature

Annual means of water level and temperature were significantly correlated (n = 23; r = - 0.54, $p < 0.008$). Results for spring, when both river flow and water temperature means varied most between years, water level and temperature were correlated (n = 24; r = - 0.56, $p < 0.005$). Summer level and temperature were also correlated (n = 25; r = - 0.70, $p < 0.0001$). As for the fall level and temperature means, no correlation was observed.

Correlations between fish occurrence and hydrological regime

The annual timing of occurrence at the experimental trap of five of the 19 spring fish components was positively correlated with attributes of the magnitude of water level (Table 2). The spring occurrence of yellow perch (*Perca flavescens*), channel catfish (*Ictalurus punctatus*), shorthead redhorse (*Moxostoma macrolepidotum*), walleye (*Stizostedion vitreum*) and lake whitefish (*Coregonus clupeaformis*) at Saint-Nicolas appeared to be delayed in years with a higher water level. The duration of occurrence of five spring fish components was positively and significantly correlated to water level (Table 2). In all cases, fish capture at the trap was spread over a longer time period in years of high seasonal water level (Table 2).

Black crappie (*Pomoxis nigromaculatus*) and alewife (*Alosa pseudoharengus*) were the only summer fish components whose annual timing of occurrence was significantly altered by the hydrological regime, both being negatively correlated with water level (Table 2). The duration of occurrence of three summer fish components, American shad (*Alosa sapidissima*), alewife, and pumpkinseed (*Lepomis gibbosus*), increased significantly in years with higher water levels (Table 2).

In general, the seasonal distribution patterns of several fall species components were particularly affected by fluctuations of the hydrological regime. The annual timing of six fish components was negatively correlated, and one component was positively correlated, with fall water levels (Table 2). Correlations between duration of fish occurrence and water levels were positive in all cases but one, for fall fish components (American eel, Atlantic tomcod [*Microgadus tomcod*], longnose sucker [*Catostomus catostomus*], yellow perch, walleye, white sucker and sauger [*Stizostedion canadense*] Table 2). In contrast to these seven fish components, the timing and duration of burbot (*Lota lota*) was negatively correlated with the hydrological regime (Table 2).

Correlations between fish occurrence and thermal regime

The annual timing of occurrence at the experimental trap of seven of the 19 spring fish components was correlated with water temperature (Table 2). Six were negatively correlated with an increase in spring temperature and one positively. The spring occurrence at Saint-Nicolas of yellow perch and lake whitefish among others, appeared to be delayed in years of lower temperature. The duration of occurrence of four spring fish components was negatively related to the temperature and one positively (Table 2). In these four cases, fish captures at the trap were spread over a shorter time period in years of high seasonal temperature (Table 2). As for channel catfish, its capture was spread over a larger time period in years of higher water temperature (Table 2).

Smallmouth bass and alewife were the only summer fish components whose annual timing of occurrence was significantly altered by the hydrological regime (Table 2). Smallmouth bass tend to arrive earlier, and alewife later, in years with higher water temperatures. The duration of occurrence of four summer fish components, alewife, black crappie, mooneye (*Hiodon tergisus*) and pumpkinseed, decreased significantly in years with higher water temperatures (Table 2). The timing and duration of occurrence of smallmouth bass was

inversely correlated with the hydrological regime compare with the other summer fish components (Table 2).

The seasonal distribution patterns of many fall species components were particularly affected by fluctuations of the thermal regime. The seasonal timing of eleven fish components was correlated with water temperature in the fall (Table 2). Eight fish components arrived at the experimental trap later (positive correlation) and three earlier (negative correlation) in years of higher temperature (Table 2). Correlations between duration of fish occurrence and temperature were negative for all fish components but one (American eel, Atlantic tomcod, longnose sucker, yellow perch, walleye, white sucker, and sauger; Table 2). In contrast to these seven fish components, the timing and duration of occurrence of lake sturgeon (*Acipenser fulvescens*) was positively correlated to the thermal regime (Table 2).

Relative influence of water level and temperature fluctuations

Because seasonal water temperatures and levels were significantly correlated in a number of cases, stepwise multiple regression models were used to isolate the most statistically important attributes influencing the seasonal timing and duration of the 48 fish components, with a reduced data set of 25 years. When temperature attributes were not selected in the models, the 28-year hydrological data set was used. Results of the multiple regression analyses yielded significant predictive models linking water level and/or temperature with the median date of capture of 12 spring, five summer and 14 fall fish components (Appendix 1 and 2). Results also yielded predictive models linking hydrological and thermal regime and the duration of capture of 10 spring, four summer and 13 fall fish components (Appendix 1 and 2).

Results showed that temperature came first in nine out of 12 models as the variable that explained the largest proportion of the variation in the timing of the spring fish component (Appendix 1). In summer, both level and temperature explained a similar proportion of the

variation in fish timing. However in the fall, water level came first in more models than temperature (Appendix 2).

Discussion

The results of the present study provided evidence that fluctuations in water levels can influence the seasonal occurrence and distribution patterns of several freshwater fish species in the lower St. Lawrence River. The seasonal distribution patterns of a total of 29 species components, out of 48 analysed, were shown to have varied from year to year in response to interannual variations in the hydrological and thermal regimes (Tables 2). This corresponded to 24 different fish species for which the annual timing and/or duration of occurrence was statistically correlated to water level and temperature (Table 2). This represented roughly 50% of the average number of fish species commonly captured at the experimental trap, as well as in commercial fisheries, in the lower St. Lawrence River each year. Although the scientific literature has accumulated evidence on the effect of water level fluctuations on the distribution of different fish species in various river systems (see Lucas and Baras 2001 for a review), to our knowledge, no previous study has attempted to make such an assessment for an entire fish assemblage. It is therefore difficult to ascertain whether half the species of a given fish assemblage responding to water level fluctuations, is relatively unique to the St. Lawrence River or whether it is typical of large, temperate river ecosystems.

The influence of hydrological characteristics on the temporal distribution of a large number of fish species would presumably be related to the migratory behavior exhibited by many freshwater fish species in the St. Lawrence River (de Lafontaine *et al*. 2003). A similar observation was made in the Murray-Darling River basin in Australia, where several migratory fish species required an appropriate flow regime to move upstream and spawn, while non-migratory species showed no response to river discharge/level fluctuations (Humphries and Lake 2000; Gehrke and Harris 2000). Agostinho *et al*. (2002) concluded that flow fluctuations had a strong impact on the dynamics of migratory species than on that of non-migratory species of the fish community of the High Parana River, in South America. The seasonal shift in species composition and abundance recorded at the experimental trap was clearly indicative of

extensive changes in local fish assemblage within a year at a given station in the lower St. Lawrence River (Figure 1). We interpreted the bimodal distribution in catches of some species, which peaked in spring and fall (e.g. yellow perch, walleye, rainbow smelt, lake whitefish) as evidence of upstream-downstream migratory patterns, as recently demonstrated by the results of a tagging experiment (de Lafontaine *et al*. 2003). Seasonality in fish abundance or catches at a fixed site in riverine or estuarine systems is normally taken as evidence of migratory behavior (Lucas and Baras 2001) rather than the result of local displacement of fish between nearby habitats (e.g. offshore versus inshore movement). Consequently, the median date of capture used here as an index of the timing of occurrence would indeed correspond to the migratory timing of many species. This therefore implies that the migration timing of many freshwater fish species in the lower St. Lawrence River differed widely from year to year, varying by more than 25 days in two successive years (Figure 1). Similarly, the duration of occurrence (and capture) at the experimental trap for many spring and fall fish components would correspond to the length of the migration time of each species when arriving in the vicinity of the experimental trap (Figure 1). This was altered by the water level in the St. Lawrence River as well (Table 2). Since many of these fish species are known to migrate over a relatively long distance between upstream Lake Saint-Pierre and Ile d'Orléans downstream, the impact of water levels on migration patterns would therefore influence fish distribution patterns at various localities along the lower St. Lawrence River. Ultimately, fish capture and fixed gear fisheries along the river ought to be directly affected by water level fluctuations.

The finding that approximately half of the species were apparently not influenced by water level fluctuations tends to support the view that fish assemblages are not necessarily composed of unit-discrete communities (Pusey *et al*. 2000) and that members of the assemblage may respond to environmental signals in a species-specific manner rather than as part of a strongly interacting guild (Grossman and Ratajczak 1998). Results of our study indicated that the potential link between water level and fish occurrence patterns varied between

seasons, not only as a result of different species assemblages, but also between seasons variability in the response of particular species. The proportion of fish components affected by water level fluctuations was higher for both spring and fall assemblages, but much lower for the summer assemblage in the lower St. Lawrence River.

Spring fish species components

Spring was the season with the highest degree of interannual variability, both in terms of water level and temperature conditions (Figure 2). Hudon *et al.* (2003) have recently demonstrated that these two variables are closely linked during this time of the year. Their analysis of long-term data series revealed that years with high water levels are generally associated with cooler water in May and June in the St. Lawrence River. This trend was most statistically significant for the month of May (r = + 0.81; Hudon *et al*. 2003). The interannual variability in environmental conditions appeared to influence the timing and duration of occurrence of nearly half of the spring fish species. Seventeen out of the 19 fish species captured during the spring at the experimental trap are spring spawners and were probably in spawning or post-spawning condition. It is generally admitted that water temperature rather than daily discharge, *per se*, would govern the beginning of fish spawning (Geen *et al*. 1966; Humphries and Lake 2000; Lucas and Baras 2001). The influence of water level on fish spawning movements is reportedly, however, more significant than temperature for some species, particularly for suckers (Catostomidae; Beamish 1974). It is worth noting that, in our study, shorthead redhorse, a catostomid, yielded the best predictive model linking water level fluctuations with its seasonal occurrence (Appendix 1). The migratory timing of this benthic species was delayed in years when water level was high and not very variable. Similarly, the spring median date of capture of yellow perch and walleye, two of the most economically important species, was also significantly delayed in years of high water levels. Since yellow perch is not usually considered a migratory species, studies investigating the influence of water

levels on its migration timing are virtually absent from the literature. Walleye are known to migrate long distance to spawn in the spring under certain conditions and to exhibit homing behaviour (Crowe 1962; Forney 1963). This migration behaviour has been observed in the St. Lawrence River, with walleye entering into tributaries to spawn (Desrochers 1953; Magnin and Beaulieu 1968; de Lafontaine *et al*. 2003). Although it has been reported that the spawning behaviour of yellow perch and walleye begins at a specific temperature (Scott and Crossman 1973), recent studies have linked the spawning time and spawning success of these species to water level fluctuations (Scott *et al*. 1995). Water levels have long been managed to meet objectives in stock management of Percidae (Willis 1986). Our results indicated that the downstream migration timing of these two fish components in the lower St. Lawrence River is related to the quantity of water and not solely to water temperature, in agreement with these practices. The downstream migration for these fish species components would correspond to the transition between spawning grounds and summer growth habitats, and would be directly influenced by the water level. This also seems to be the case for channel catfish, lake whitefish and shorthead redhorse, whose timing of occurrence in spring was delayed in years of high water level (Table 2). We believe that both temperature and level are probably equally important factors influencing the movement and distribution of spring fish species components in the St. Lawrence River, and that limitation in one of these factors will accentuate the relative influence of the other one on fish migration timing and duration of occurrence.

Summer fish species components

Alewife and black crappie were the only two summer fish components whose seasonal occurrence was partially explained by water level (Table 2). With the exception of American shad and alewife, all summer species can be considered resident, as indicated by their long period of capture at the experimental trap (Figure 1). The Centrarchidae, including smallmouth bass, black crappie and pumpkinseed, dominated the catch during the summer months. These

species are not very mobile and are generally considered sedentary or even cryptic, seeking slow-flowing environments and avoiding high flow magnitudes associated with high water levels (Gerking 1959; Knights *et al.* 1995; Richardson-Heft *et al.* 2000; Lucas and Baras 2001). Tagging results have shown that smallmouth bass was much less mobile that other fish species at the experimental trap, and tagged fish were always recaptured within a distance of 10 km from the tagging site in the lower St. Lawrence River (de Lafontaine *et al.* 2003). Correlation analysis showed that water level had no significant effect on timing or duration of occurrence of this species (Table 2), but multiple regression models suggested that water level fluctuations might delay their median date of capture (Appendix 1). Since the duration of occurrence was negatively correlated with the seasonal timing (Table 1), the presence of these species in the nearshore environment would be extended over a longer time period in years of higher level conditions during spring and summer. Presumably, high water levels may provide longer and more profitable nearshore habitats, contributing to increased residence time for warm-water species.

The migration timing of alewife, one of the two anadromous species that migrate in the summer, was related to water level, but much more significantly with temperature in the lower St. Lawrence River. This is somewhat expected, since the migration timing of Clupeidae varies with latitude, with northern populations spawning later. Interannual variations in the migration timing of American shad has been linked to water temperature, with cooler temperatures delaying their upstream migration (Bigelow and Schroeder 1953; Leggett and Whitney 1972; Quinn and Adams 1996). Similarly, the upstream movement of three cyprinid species within the River Ouse system in Yorkshire, England, was positively correlated with day length during the summer, but not significantly correlated with mean daily temperature or mean water level (Lucas 2000).

Overall, our results, and those of previous studies in other rivers, suggest that the timing and duration of occurrence of summer fish species in riverine systems are not strongly controlled by water level fluctuations. We can not dismiss the possibility that the lack of significant

relationships for summer fish components might be attributed, in part, to the fact that the summer was the season with the lowest interannual variability in water level (Figure 2), rendering the impact of a narrow range of variation more difficult to assess statistically. In addition, the longer duration of occurrence (~90 days) of summer species could introduce more variability in the estimate of the annual timing. We consider, however, that the analysis of long data series as used in our study should minimize these statistical constraints.

Fall fish species components

The fall fish assemblage had the highest proportion (60%) of species responding significantly to the interannual variability in water level. As indicated earlier for the spring group, fall species were essentially migratory fish, which are usually more sensitive to variations in river discharge (Lucas and Baras 2001). Except for the catadromous American eel, all other fall fish components migrated upstream. Since the majority of these species are late-winter or spring spawners, the displacement of these species in the fall would not correspond to a "pre-spawning" migration *per se*, but would be more analogous to "refuge-seeking" migration (Northcote 1984) or a "climatic" migration ("winter" migration, sensu Nikolsky 1963). Winter conditions prevailing in the downstream portion of the river are particularly harsh due to ice piling and scouring the nearshore shallow environments. This would force freshwater fish to leave the downstream sector and migrate further upstream, seeking better winter habitats. Although the "winter" migration described in other studies was often associated with the downstream displacement of fishes in rivers, migration from riverine to lacustrine environments also has been documented (Knights *et al*. 1995). This strategy seems to prevail in many fish species of the St. Lawrence River, where upstream Lake Saint-Pierre would represent the preferred winter habitat. As pointed out by Lucas and Baras (2001), this suggests that the direction and extent of fish movements is influenced by local geomorphological and physical conditions in a particular river and floodplain system.

Many fall species, like American eel, Atlantic tomcod, and walleye, tended to delay their migratory timing in years of low water levels. It is worth noting that low level conditions in the fall produced a similar effect on the migratory timing of both downstream (e.g. American eel) and upstream (e.g. walleye, white sucker, Atlantic tomcod) migratory fish species. Delayed downstream migration of catadromous eel in response to low water level has been reported for European eel (*Anguilla anguilla*) also (Vøllestad *et al*. 1986). In the case of fish that migrate upstream, Potter (1988) has observed that Atlantic salmon fall migrators stayed in the estuary for several weeks before entering fresh water because of unusually low water levels. Reduced freshwater levels could presumably shorten the transition habitat between fresh and salt water, so that fish would face a more pronounced and more rapid change in the salinity gradient. The migration timing of diadromous species might then vary according to the spatial variability of this transitional habitat. Increasing freshwater levels in the fall would therefore have a positive impact by facilitating both the upstream or downstream movements of diadromous fall fish species components. Mechanisms explaining the variability in the migration timing of potamodromous fish species remain, however, unknown for the St. Lawrence River, but might involve some rheotropic stimuli (Northcote 1984). Such behavior could well be modified by other stimuli, like temperature, as shown for the upstream spawning migration of shiners (*Notropis cornutus*; Dodson and Young 1977).

Impact of fish density

The migration timing of seven fish species components appeared to be significantly correlated with the total catch (Table 1). Except for Atlantic tomcod, which exhibited an exceptionally large and continuous decline in catches over time (from 2330 to < 20 individuals, CV in catch = 115%), multiple stepwise regression models did not select total fish catch as a significant variable explaining the interannual variation in the migration timing of these seven species. Fish density is not usually considered an important factor controlling the timing of fish

occurrence locally, and there is no convincing evidence or theoretical basis for density-dependent effects on fish migration timing (Lucas and Baras 2001). Our empirical results support this conclusion. It is plausible to argue that density might affect the duration of fish occurrence locally, assuming that no other environmental stimuli were influential. The positive relationships expected for such an effect were noted only in three specific cases in our study (Table 1). Again, except for Atlantic tomcod, none of these species duration was significantly related to water level, indicating that density was not an important confounding factor in our statistical analyses.

Impact of Fluctuating Water Levels

Although our results revealed that hydrological fluctuations significantly affected the seasonal distribution patterns of several freshwater fish in the St. Lawrence River, obviously other cues, such as temperature, light or food availability, can intervene and interact to trigger fish movement and migration (Jonsson, 1991). Consequently, all species of a given fish assemblage may not respond in a similar way to the same factors. Given that approximately half of the species were apparently not influenced by water level fluctuations and that the statistical significance of the predictive models was not always very high, it is suggested that water level was not necessarily the sole or even the main factor affecting the temporal dynamics of fish occurrence in the lower St. Lawrence River during the past 28 years. Although temperature is repeatedly cited as an important cue for migratory fish, the results of our multiple regression models revealed that water level was often the determining variable, even during seasons when both temperatures and levels were more closely related. That does not necessarily dismiss the potential importance of temperature, but it may indicate that our temperature attributes were not the ones influencing migration timing. As demonstrated by Leggett (1985), the time of occurrence may be either temperature specific or dependent on the rate of temperature change. Leggett (1985) further argued that the year-to-year variance in the

rate of temperature change might be more prevalent in fish populations in high latitudes. Such analysis using our results for the St. Lawrence River fish species was, however, beyond the scope of the present work and would require a much more detailed analysis of the association between water level and the rate of temperature change in the St. Lawrence River.

The present study aimed at developing predictive models of fish migration in response to water level fluctuations. This does not necessarily imply a causal link between water level and fish responses. However, the above analysis was based on fish catches from a fixed gear installed in the nearshore environment, for which accessibility by fish would be enhanced during periods of high water level. Consequently, the positive relationships between water level and fish duration at the trap may be not surprising and would give stronger support to the habitat-mediated influence of water levels and corresponding flows on annual occurrence patterns of freshwater fish in the lower St. Lawrence River. The significant relationships between water level and fish distribution response may indeed be the result of fish habitats availability. The response observed in long distance migrant and open water species is however most probably a result of water current preferendum by each of these species. Given that water levels and water flows were highly correlated in the St. Lawrence River as usually the case in large river systems, the relationship between water level and fish responses for these species may not be related to nearshore habitat availability, but rather to the water current regime and open water habitats conditions.

Conclusion

Fluctuating water levels may affect fish reproductive behaviour and recruitment. Regular and high flood pulses have been reported to enhance riverine fish productivity. Alabaster (1970) observed salmonid reproductive behaviour variations and demonstrated a strong correlation between the annual water flow and the total catch of upstream migratory fish in many rivers in England. It remains to be demonstrated that variation in migration timing, resulting from

fluctuating water levels, would have an impact on the reproductive success of St. Lawrence River fish populations. One could speculate that fish timing, which can be viewed as the first step of the reproductive process, could be out of phase with the optimised periods for undertaking different stages of the life cycle. Drastic modification of the St. Lawrence River water levels could limit the use of winter habitats, limit the ability of some fish species to spawn, or affect feeding and survival of recruits. The possible impact of interannual water level variability on fish population abundance and recruitment will be assessed in the near future in using the fish catch data from the Saint-Nicolas experimental trap fishery.

The variability of the seasonal occurrence of fish species has a direct impact on sport and commercial fisheries by changing fish accessibility to specific sites as well as catchability to migratory fish dependant fisheries. Understanding fish movement is important for cost-effective and sustainable exploitation of different fish stock in the St. Lawrence River and other large river ecosystems. On a short-term basis, changes in water level may eventually affect the fishing economy of the lower St. Lawrence, and a better knowledge of the processes involved would allow fisheries management to adapt. Since water level fluctuations affect individual species differently, we advise against focusing on individual stock management and rather taking a new perspective by considering the fish assemblage as a whole. Changes in predator-prey interactions and food web structures may cause irreversible collapse of specific fish stocks (Hutchings 2001; Pauly *et al.* 2002). That is why, water level management allowing the maintenance of high fish diversity should be foreseen. Our results indicate that hydrological regime is an important, if not crucial, factor controlling distribution processes for completion of life cycles of many fish species in the lower St. Lawrence River. In our view, the use of only one “keystone” fish species as an indicator of response to an anthropogenic influence, such as level alteration, would be unsuitable.

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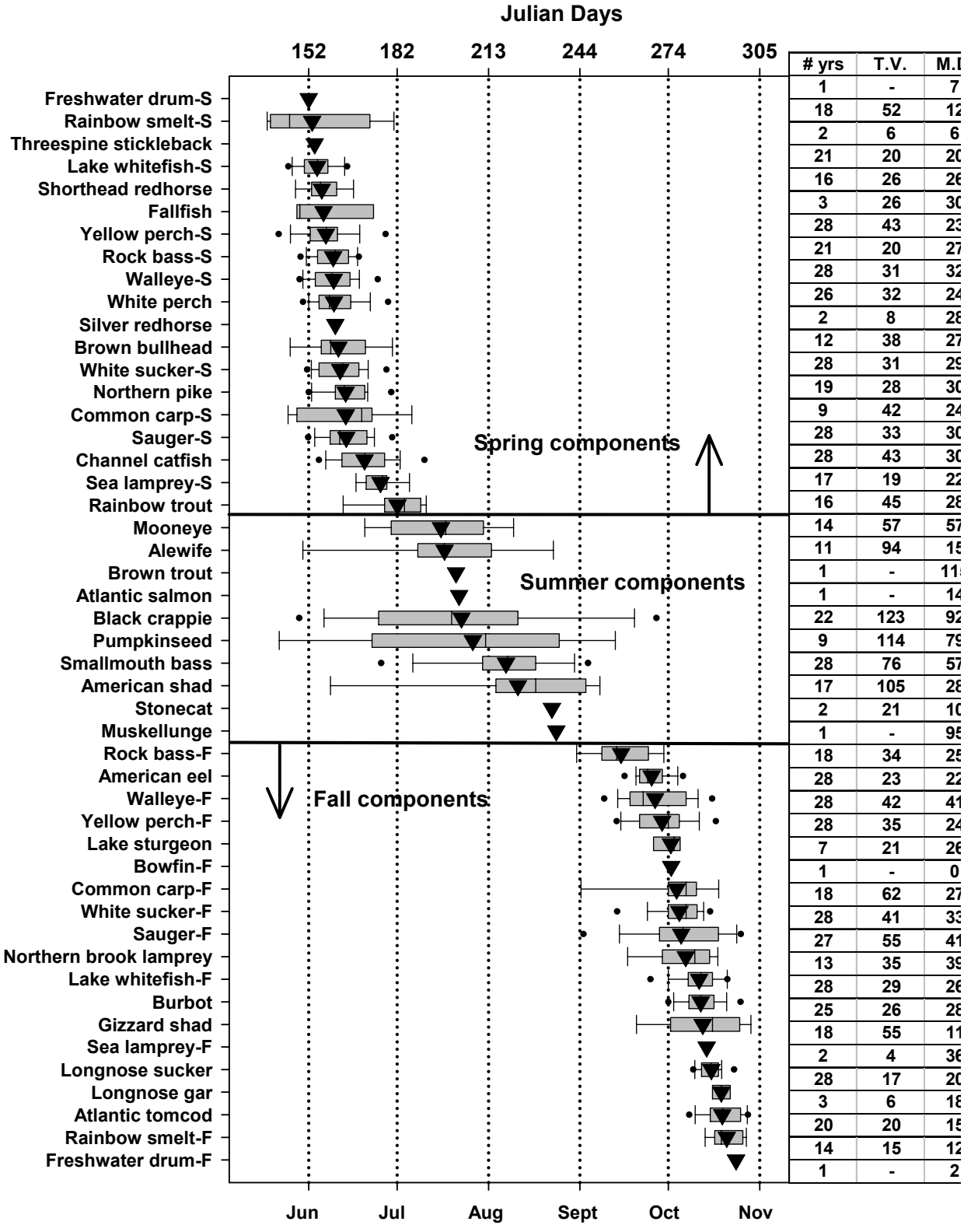

Figure 1 Calendar of fish species migratory timing at the experimental trap fishery in Saint-Nicolas, Quebec, Canada. (# yrs = number of years exceeding 20 fish, T.V. = timing

variation, M.D. = mean duration of occurrence. Species-S = spring component and species-F = fall component).

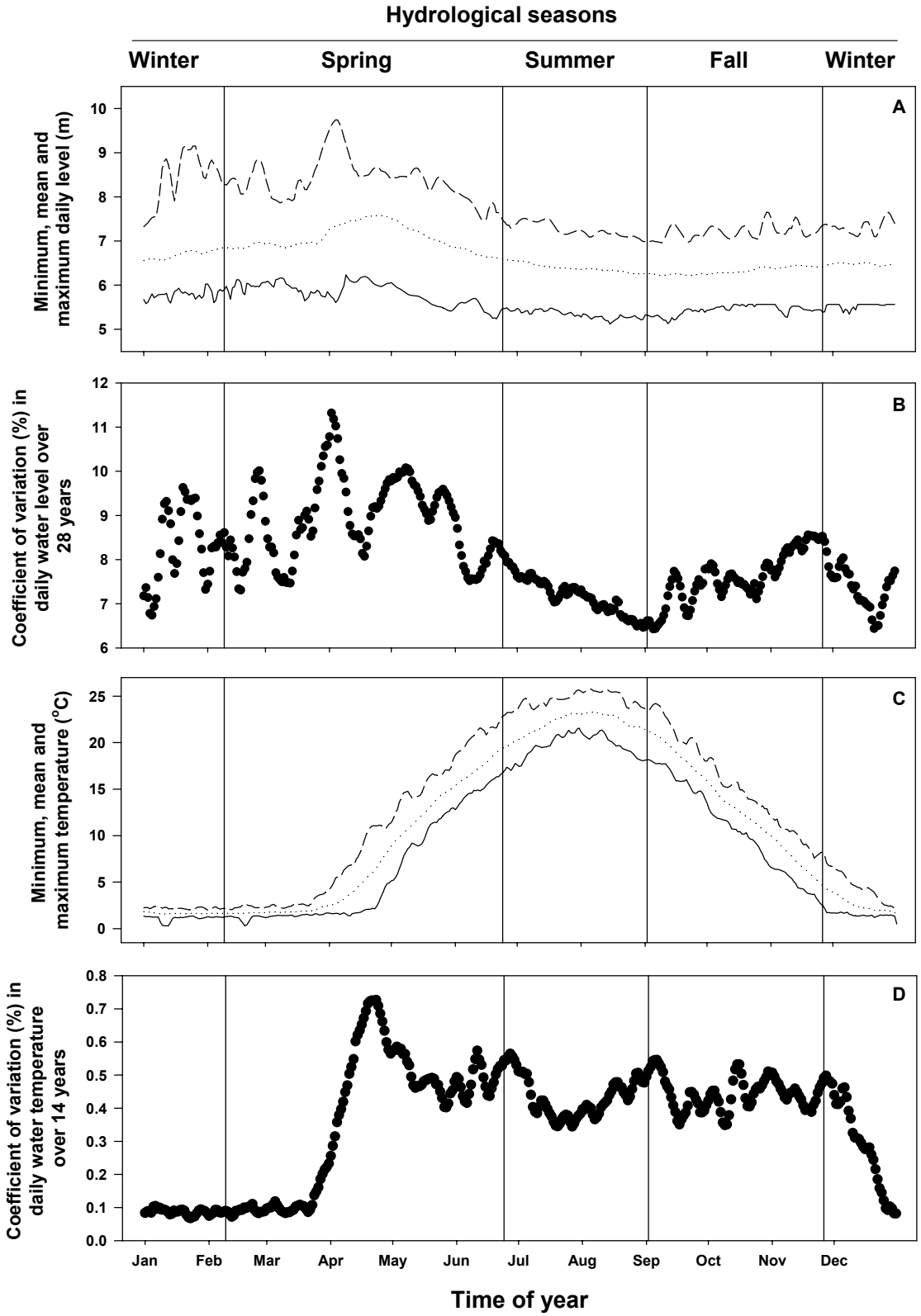

Figure 2 Average and range (A), and coefficient of variation (B) in daily level (m) at the port of Montreal between 1965 and 2002. Average and range (C), and coefficient of variation (D) in water temperature in the lower St. Lawrence River between 1986 and 2001.

Table 1 Pearson correlation coefficients between annual timing of occurrence, duration of occurrence, total catch and year for various fish components between 1975 and 2002 at the experimental trap fishery, Saint-Nicolas, Canada.

Season	Fish Component	N	Timing *vs* Duration	Abundance *vs* Timing	Abundance *vs* Duration	Year *vs* Abundance	Year *vs* Duration	Year *vs* Timing
Spring	Yellow perch-Spring	28	+ 0.44*	- 0.36*	- 0.36*		- 0.43*	
	Walleye-Spring	28	+ 0.58**	- 0.59***	- 0.62***	+ 0.46**	- 0.52**	- 0.69***
	White sucker-Spring	28	+ 0.48**			+ 0.82***		
	Sauger-Spring	28			- 0.37*			
	Rock bass-Spring	21	+ 0.49*					
	Lake whitefish-Spring	21				+ 0.61**		- 0.58**
	Rainbow smelt-Spring	18	+ 0.72***	+ 0.48*				
	Channel catfish	28				+ 0.79***		- 0.36*
	Northern pike	19				- 0.44*		
	Shorthead redhorse	16				+ 0.84***		
	Brown bullhead	11			+ 0.62*			
Summer	Smallmouth bass	28	- 0.52**	- 0.47**		+ 0.51**		
	Brown trout	14			+ 0.57**			
	Mooneye	14					- 0.61*	
	Alewife	11						+ 0.78**
Fall	American eel	28	- 0.66***				- 0.38*	+ 0.53**
	Longnose sucker	28	- 0.49*			- 0.62***		
	Burbot	25	- 0.61**			- 0.60**		
	Atlantic tomcod	20	- 0.89***	- 0.63**	+ 0.74***	- 0.83***	- 0.83***	+ 0.73**
	White sucker-Fall	28	- 0.36*	+ 0.48**	- 0.39*	+ 0.60***		
	Yellow perch-Fall	28	- 0.65**			- 0.49*		
	Lake whitefish-Fall	28	- 0.58**					
	Walleye-Fall	28				+ 0.40**		+ 0.83***
	Sauger-Fall	27		+ 0.39*				+ 0.51***
	Rainbow smelt-Fall	14	- 0.54*					

(*$p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

Table 2 Pearson correlation coefficients between annual timing of occurrence or duration of occurrence, and water level and temperature for various fish components between 1975 and 2002 at the experimental trap fishery, Saint-Nicolas, Canada.

Season	Fish Component	N	Timing *vs* Water Level	Duration *vs* Water Level	N	Timing vs Water Temperature	Duration vs Water Temperature
Spring	Walleye-Spring	28	+ 0.50**	+ 0.56**	24	- 0.57**	- 0.54**
	Yellow perch-Spring	28	+ 0.41*		24	- 0.41*	- 0.40*
	Rainbow smelt-Spring	17		+ 0.49*	14	- 0.61*	- 0.54*
	Lake whitefish-Spring	21	+ 0.56**		20	- 0.77***	
	Sauger-Spring	27		+ 0.40*	24	- 0.50*	
	Sea lamprey-Spring	17		+ 0.48*			
	Channel catfish	28	+ 0.55**		24	- 0.49*	+ 0.45*
	Shorthead redhorse	26	+ 0.55*	+ 0.54*			
	Rainbow trout				15	+ 0.65**	
	Northern pike				16		- 0.70**
Summer	Smallmouth bass				24	- 0.41*	+ 0.50*
	Black crappie	22	- 0.59**		19		- 0.46*
	American shad	17		+ 0.56*			
	Alewife	11	- 0.72*	+ 0.64*	7	+ 0.84*	- 0.82*
	Pumpkinseed	9		+ 0.85**	8		- 0.70*
	Mooneye				10		- 0.82**
Fall	Atlantic tomcod	20	- 0.61**	+ 0.70***	16	+ 0.54*	- 0.66**
	Longnose sucker	28		+ 0.48**	24		- 0.51**
	American eel	28	- 0.72***	+ 0.53**	24	+ 0.74***	- 0.41*
	Burbot	25	+ 0.45*	- 0.41*			
	Lake sturgeon				5	- 0.80*	+ 0.88*
	Northern brook lamprey				11	- 0.58*	
	Yellow perch-Fall	28	- 0.41*	+ 0.44*	24	+ 0.48*	- 0.59**
	Walleye-Fall	28	- 0.70***	+ 0.38*	24	+ 0.59**	- 0.40*
	White sucker-Fall	28	- 0.49**	+ 0.40*	24	+ 0.45*	- 0.58**
	Sauger-Fall	27	- 0.46*	+ 0.41*	23	+ 0.78***	- 0.57**
	Lake whitefish-Fall				24	+ 0.54**	
	Rainbow smelt-Fall				12	+ 0.61*	
	Common carp-Fall				14	- 0.61*	

(*$p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

Appendix 1 Best predictive models of migratory timing and duration of different fish components (i.e. fish species) for the spring and summer seasons. The regression parameters, the probability (*p*) associated with each independent factor, the standard error of slope coefficient (SE), the R^2 associated with the model, the adjusted R^2, and the standard error of the estimate (S_{xy}) are indicated.

Season	Dependent variable Sp timing and duration of occurrence		N years	Independent variables Level or temperature attributes	Regression parameters	*p* > *t*	SE	R^2	adj R^2	S_{xy}
Spring	Channel catfish	Timing	24	Intercept	+ 120.54			0.57	0.50	5.69
				May mean level	+ 5.53	0.01	1.95			
				March mean temperature	+ 12.06	0.005	3.91			
				Spring level rising rate	- 160.82	0.02	65.25			
		Duration	28	Intercept	+ 40.67			0.16	0.13	7.50
				Spring level rising rate	- 159.65	0.03	71.77			
	Northern pike	Timing	16	Intercept	+ 128.51			0.70	0.65	4.58
				Spring SD in temperature	- 21.02	0.0003	4.39			
				Spring level baseline	+ 183.88	0.02	71.39			
		Duration	16	Intercept	- 39.58			0.62	0.56	3.85
				Spring baseline temperature	+ 219.90	0.0009	51.95			
				Spring CV in level	+ 4.08	0.003	1.16			
	Shorthead redhorse	Timing	16	Intercept	+ 126.29			0.59	0.52	4.74
				June mean level	+ 17.39	0.001	4.16			
				Spring minimum level	- 13.68	0.01	4.57			
		Duration	16	Intercept	- 250.60			0.43	0.38	6.64
				Spring baseline level	+ 310.15	0.006	96.32			
	Lake whitefish	Timing	20	Intercept	+ 219.58			0.68	0.64	3.32
				Spring maximum temperature	- 3.03	0.00002	0.52			
				Spring level fall rate	+ 108.75	0.04	49.68			
		Duration	20	Intercept	- 165.91			0.42	0.35	7.28
				Spring baseline level	+ 228.96	0.01	80.58			
				Spring date of maximum level	- 0.19	0.03	0.08			
	White sucker	Timing	24	Intercept	+ 147.12			0.36	0.29	6.79
				February mean temperature	- 14.53	0.005	4.68			
				May mean level	+ 4.88	0.04	2.30			
	Brown bullhead	Timing	8	Intercept	+ 16.23			0.67	0.61	6.82
				May mean temperature	+ 12.31	0.01	3.46			
		Duration	8	Intercept	+ 52.73			0.66	0.61	5.43
				Spring date of maximum level	- 0.26	0.01	0.07			
	Yellow perch	Timing	24	Intercept	+ 393.39			0.43	0.34	7.74
				Spring SD in temperature	- 22.65	0.001	6.28			
				Summer maximum level	- 12.50	0.03	5.67			
				Spring level fall rate	+ 231.94	0.05	119.50			
		Duration	24	Intercept	+ 5.04			0.18	0.16	8.40
				Spring baseline in temperature	+ 104.46	0.03	47.16			
	Rainbow trout	Timing	15	Intercept	+ 149.98			0.45	0.41	8.62
				Spring baseline temperature	+ 175.52	0.005	53.39			
		Duration	15	Intercept	+ 43.25			0.49	0.41	7.24
				March mean temperature	- 18.94	0.01	6.23			
				Spring temperature fall rate	- 162.46	0.04	74.24			

Appendix 1 (*Continued*)

Season	Dependent variable Sp timing and duration of occurrence		N years	Independent variables Level or temperature attributes	Regression parameters	$p > t$	SE	R^2	adj R^2	S_{xy}
Spring	Walleye	Timing	24	Intercept	+ 216.10			0.68	0.63	4.68
				Spring maximum temperature	- 3.17	0.0001	0.66			
				Spring level fall rate	+ 250.78	0.001	68.49			
				March mean temperature	+11.11	0.001	3.09			
		Duration	28	Intercept	- 20.06			0.32	0.29	6.11
				April mean level	+ 6.98	0.001	2.01			
	Sauger	Timing	24	Intercept	+ 267.48			0.41	0.36	6.29
				Spring maximum temperature	- 2.95	0.003	0.89			
				Spring CV in temperature	- 0.55	0.02	0.23			
	Rainbow smelt	Timing	18	Intercept	+ 34.54			0.44	0.36	13.75
				Summer SD in level	+ 110.12	0.02	42.41			
				April mean level	+ 13.51	0.02	5.43			
		Duration	18	Intercept	- 72.71			0.24	0.20	12.89
				April mean level	+ 11.49	0.03	5.06			
	Common carp	Timing	6	Intercept	+ 91.70			0.75	0.69	9.67
				Spring temperature fall rate	- 768.70	0.02	222.62			
		Duration	9	Intercept	- 633.04			0.49	0.42	6.71
				Summer baseline level	+ 683.08	0.03	262.88			
Summer	Smallmouth bass	Timing	28	Intercept	+ 195.06			0.46	0.42	13.30
				Spring SD in level	+ 104.02	0.001	28.05			
				Spring level rising rate	- 438.76	0.002	128.99			
	Mooneye	Timing	10	Intercept	+ 327.68			0.68	0.64	10.14
				Spring temperature rising rate	- 566.30	0.003	136.42			
		Duration	10	Intercept	+ 89.71			0.67	0.63	8.04
				Spring median temperature	- 6.66	0.003	1.65			
	Pumpkinseed	Timing	9	Intercept	+ 1590.81			0.64	0.58	24.45
				Spring baseline level	- 1549.67	0.009	442.67			
		Duration	9	Intercept	- 226.48			0.72	0.68	15.18
				Spring maximum level	+ 37.48	0.003	8.77			
	Alewife	Timing	7	Intercept	+ 47.54			0.71	0.66	7.80
				Spring minimum temperature	+ 112.25	0.01	31.76			
		Duration	7	Intercept	+ 132.34			0.68	0.61	6.22
				Spring minimum temperature	- 81.95	0.02	25.34			
	Black crappie	Timing	22	Intercept	+ 594.81			0.35	0.32	28.34
				Summer maximum level	- 56.98	0.003	17.27			
		Duration	19	Intercept	- 72.73			0.49	0.42	14.06
				Spring CV in temperature	+ 1.58	0.01	0.58			
				Summer level fall rate	- 1762.64	0.03	749.35			

Appendix 2 Best predictive models of migratory timing and duration of different fish components (i.e. fish species) for the fall season. The regression parameters, the probability (*p*) associated with each independent factor, the standard error of slope coefficient (SE), the R^2 associated with the model, the adjusted R^2, and the standard error of the estimate (S_{xy}) are indicated.

Season	Dependent variable Sp timing and duration of occurrence		N years	Independent variables Level or temperature attributes	Regression parameters	*p* > *t*	SE	R^2	adj R^2	S_{xy}
Fall	Longnose sucker	Timing	28	Intercept	+287.08			0.47	0.43	2.86
				Fall level skewness	+ 173.32	0.0002	41.18			
				Summer level skewness	+ 213.71	0.03	94.39			
		Duration	28	Intercept	- 12.09			0.37	0.32	4.72
				September mean level	+ 5.33	0.02	2.17			
				Summer level skewness	- 372.81	0.02	158.75			
	Atlantic tomcod	Timing	17	Intercept	+ 241.86			0.65	0.60	3.42
				Fall level skewness	+ 210.55	0.002	55.73			
				Fall sum of degree days	+ 0.04	0.008	0.015			
		Duration	20	Intercept	- 51.02			0.49	0.47	4.91
				Fall median level	+ 10.29	0.0005	2.44			
	American eel	Timing	25	Intercept	+ 174.10			0.59	0.55	3.04
				Summer median temperature	+ 4.01	0.00002	0.76			
				Fall minimum temperature	+ 1.20	0.03	0.54			
		Timing	28	Intercept	+ 324.45			0.52	0.50	3.76
				September mean level	- 8.98	0.00001	1.69			
		Duration	28	Intercept	- 50.38			0.28	0.25	8.17
				September mean level	+ 11.65	0.003	3.67			
	Burbot	Timing	23	Intercept	+ 299.44			0.50	0.42	5.09
				Fall level skewness	+ 199.01	0.01	74.39			
				June mean temperature	- 3.29	0.01	1.15			
				Fall maximum temperature	+ 1.99	0.02	0.80			
		Duration	23	Intercept	+ 224.30			0.41	0.35	9.96
				Summer maximum level	- 18.23	0.002	5.21			
				Fall maximum temperature	- 3.44	0.04	1.58			
	Gizzard shad	Timing	17	Intercept	+ 61.63			0.54	0.47	11.12
				Fall level rising rate	+ 928.36	0.005	281.16			
				Summer maximum temperature	+ 7.92	0.03	3.50			
		Duration		Intercept	- 368.21			0.55	0.49	5.58
				Summer level baseline	+ 399.84	0.005	122.65			
				Fall CV in level	- 1.70	0.03	0.72			
	Sauger	Timing	24	Intercept	+ 68.11			0.71	0.66	7.75
				August mean temperature	+ 5.56	0.02	2.30			
				Fall maximum temperature	+ 3.97	0.01	1.41			
				Fall level skewness	+ 311.41	0.02	126.41			
		Duration	24	Intercept	+ 162.26			0.32	0.29	11.62
				Fall maximum temperature	- 5.57	0.003	1.71			
	Lake sturgeon	Timing	6	Intercept	+ 373.88			0.68	0.60	3.26
				Summer median temperature	- 4.61	0.04	1.58			
		Duration	6	Intercept	- 226.61			0.79	0.74	7.13
				Fall sum of degree days	+ 0.23	0.01	0.06			

Appendix 2 (*Continued*)

Seasons	Dependent variable - Occurrence timing or duration		N years	Independent variables Level or temperature attributes -	Regression parameters	$p > t$	SE	R^2	adj R^2	S_{xy}
Fall	Walleye	Timing	28	Intercept	+ 351.76			0.60	0.57	7.14
				Fall sum of level	- 0.17	0.00006	0.04			
				Fall level rising rate	+ 291.85	0.01	115.26			
		Duration	25	Intercept	+ 92.44			0.30	0.23	5.78
				Fall maximum temperature	- 2.65	0.008	0.92			
				Fall SD in level	+ 24.90	0.04	11.98			
	Yellow perch	Timing	25	Intercept	+ 118.53			0.35	0.30	7.87
				Fall mean temperature	+ 5.28	0.03	2.30			
				August mean temperature	+ 3.78	0.05	1.83			
		Duration	25	Intercept	+ 139.00			0.34	0.32	8.76
				Fall mean temperature	- 8.71	0.002	2.50			
	White sucker	Timing	25	Intercept	+ 325.31			0.36	0.30	7.24
				September mean level	- 11.04	0.004	3.53			
				Fall CV in temperature	+ 0.55	0.08	0.31			
		Duration	25	Intercept	+ 103.08			0.33	0.30	7.33
				Summer minimum temperature	- 3.59	0.002	1.06			
	Common carp	Timing	18	Intercept	+ 394.88			0.36	0.27	12.31
				Fall maximum level	- 15.56	0.02	6.47			
				Summer level rising rate	- 590.32	0.05	295.41			
	Lake whitefish	Timing	25	Intercept	+ 2.78			0.43	0.35	5.70
				Fall maximum temperature	+ 2.06	0.04	0.97			
				Summer baseline level	+ 184.97	0.05	90.87			
				Summer median temperature	+ 2.65	0.13	1.72			
		Duration	25	Intercept	+ 126.84			0.35	0.29	7.24
				August mean temperature	- 4.82	0.008	1.66			
				Summer level rising rate	+ 324.65	0.04	149.15			
	Northern brook lamprey	Timing	11	Intercept	+ 446.79			0.42	0.35	8.87
				June mean temperature	- 9.70	0.03	3.83			
		Duration	13	Intercept	+ 21.04			0.42	0.37	9.34
				Summer level rising rate	+ 941.64	0.01	331.48			
	Rainbow smelt	Timing	14	Intercept	+ 112.12			0.49	0.40	4.14
				Fall minimum level	- 8.14	0.02	3.06			
				Summer baseline level	+ 239.75	0.03	98.24			
		Duration	13	Intercept	+ 62.72			0.64	0.57	2.62
				Fall level rising rate	- 288.73	0.006	85.04			
				September mean temperature	- 2.31	0.01	0.80			