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Spawning migrations in landlocked Atlantic salmon: time series modelling of river discharge and water temperature effects

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River discharge and water temperature are frequently cited as controlling the upstream migration of adult salmonids to their spawning areas. The results of earlier studies on the effect of these environmental factors were examined. The statistical methods employed in some of these studies failed to consider the serial correlation often found in migration time series. To assess the effects of discharge and temperature on the migratory activity of the landlocked Atlantic salmon (ouananiche, *Salmo salar*), 12 years of data on spawning migrations in the Mistassini R., Quebec, Canada, were analysed and the results obtained by ordinary least squares regression and time series regression were compared. In six of the 12 years, upstream migratory movement was related negatively to changes in river flow, suggesting that fish favour falling water phases for ascent. Water temperature appeared to have little effect on migratory movement. The mean body size of migrating fish decreased significantly throughout the summer; early migrants were on average 11·4% larger (mean fork length 522 mm) than late migrants (469 mm). Larger, 3-lake-year salmon migrated 7·2 days earlier than 2-lake-year salmon. Because the residuals from ordinary regression exhibited strong autocorrelation, time series regression was more appropriate than ordinary regression for the analysis of migration time series.

Key words: *Salmo salar*; ouananiche; migratory response; body size; fish counter; Canada.

INTRODUCTION

Many studies have analysed the influence of river discharge and water temperature on the upstream migration of Atlantic salmon *Salmo salar* L., and other salmonids to spawning areas. An overview of earlier studies illustrates a lack of consensus on the effect of river flow and temperature on the upstream migration of adult salmonids (Table I). Although river discharge is the factor most frequently cited as controlling the rate of upstream migration, it is recognized that temperature and other environmental factors, such as turbidity, can modify the effect of discharge. As stated by Peters *et al.* (1973) ' the rate of flow of a river is important, if not the dominant stimulus to the upstream migration of fish '. Consequently, the migratory response varies widely from place to place and with season (Banks, 1969).

Factors associated with high flow levels seem to stimulate fish ascent, but it is unclear whether flow level *per se* affects or modifies the migratory response (Alabaster, 1970; Mills, 1993). The increases in migratory activity during

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TABLE I. Results from earlier studies of river discharge and temperature effects on upstream migration of salmonids

Study site	Species studied*	Method	Response variable	No. of years	Results†		Reference
					Entry‡	Within§	
Numerous sites reviewed	Several	Various	Movement, numbers	—	A	B, C, H	Banks (1969)
R. Coquet, U.K.	SS, ST	Trap	Numbers	6	—	B	Alabaster (1970)
R. Vefsna, Norway	SS, ST	Counter	Numbers	3	—	B, D	Jensen *et al.* (1986)
R. Spey, U.K.	SS	Telemetry	Movement	1	—	B	Laughton (1989)
R. Tay, U.K.	SS	Telemetry, counter	Movement, numbers	1	E	B	Webb (1989)
Girnock Burn, U.K.	SS	Telemetry	Movement	1	A	B	Webb & Hawkins (1989)
R. Spey, U.K.	SS	Telemetry	Movement	2	A	H	Laughton (1991)
R. Moser, Canada	SS	Angling data	Numbers	1	A	F	Huntsman (1948)
South Quiech, U.K.	ST	Trap	Numbers	1	—	F	Munro & Balmain (1956)
15 Rivers	SS	Angling data	Numbers	1 to 15	A	B	Baxter (1961)
R. Lune, U.K.	SS	Counter, trap	Numbers	3	—	F	Stewart (1969)
R. Axe, U.K.	SS, ST	Trap	Numbers	1	A	H, I	Allan (1966)
R. Axe, U.K.	SS, ST	Counter	Numbers	3	—	B, F	Swain & Champion (unpublished)
R. La Have, Canada	SS	Counting fences	Numbers	1	A	C, G	Hayes (1953)
R. Dee, U.K.	SS	Telemetry	Movement	1	E‖	J¶	Hawkins & Smith (1986)
R. Frome, U.K.	Several	Counter	Numbers	3	—	C, I	Hellawell *et al.* (1974)
St-Jean R., Canada	SF	Counting fence	Numbers	2	—	C, J	Castonguay *et al.* (1982)
Mistassini R. Canada	SS	Counter	Numbers	12	—	C, H	This study

*SS, *Salmo salar*; ST, *S. trutta*; SF, *Salvelinus fontinalis*.

†The results are coded as follows: A, increases in flow stimulated fish to enter the river; B, increases in flow stimulated fish to ascend the river; C, temperature had little effect on ascent; D, increase in water temperature favoured ascent; E, river entry occurred over a wide range of flows; F, major runs of fish occurred when a freshet was subsiding; G, major runs of fish occurred without freshets and were maintained by a steady waterflow; cuts in river level stimulated movement; H, fish favoured falling flows; I, fish tended to move at discharges lower than those generally available; J, no detectable effect of river flow.

‡Fish movement from estuary to river.

§Fish movement in the river.

‖River flow was unusually high during the study.

¶Several fish favoured falling flows.

freshets, and the fact that lower flow levels are used in summer than during spring and autumn (Alabaster, 1970), suggest that ascent depends more on relative change than on high absolute levels of flow. Although Jensen *et al.* (1986) found that the number of ascending salmon was positively correlated with increases in both river flow and water temperature, other studies have reported greater movements on falling river levels and less movement on steady flows (e.g. Huntsman, 1948; see also Discussion).

Two different analytical problems may bias the interpretation of factors responsible for upstream migration. First, because both number of migrants and river flow can change rapidly within a period of days, observations collected at a coarse level of temporal resolution (weekly, monthly) may be inappropriate for determining whether it is rising or falling water levels that influence migratory activity, especially in rivers where freshets are short-lived. Time series of quantitative data collected on consecutive days are well suited for this purpose (Alabaster, 1970). Second, the serial correlation, or temporal autocorrelation, that characterizes time series (e.g. fig. 4 in Greenstreet, 1992) must be considered in the statistical analysis (Ostrom, 1990). Failure to account for serial correlation in statistical tests may result in biased parameter estimates and misleading significance levels and thus in erroneous inferences concerning the magnitude and direction of effects (Norusis, 1990; Ostrom, 1990).

Here, the effects of river discharge and water temperature on the migratory activity of landlocked Atlantic salmon, or ouananiche, are assessed by means of multiple regression analyses of 12 years of daily data on spawning migrations in the Mistassini R., Quebec, Canada. To evaluate the influence of serial correlation on the analysis, results from ordinary least squares regression were compared with those from time series regression.

MATERIALS AND METHODS

In the study system, landlocked salmon spend the post-smolt growing phase in Lake Saint-Jean (surface area 1000 km^2) and ascend the Mistassini R. (total length 290 km; drainage basin area 21 900 km^2), as well as several other tributaries, to spawn. Most juveniles spend 2 or 3 years (mean 2·8 years) in the riverine environment before migrating downstream as smolts. Salmon in the lake are mostly 4, 5, or 6 years old (mean 5·1 years), with very few individuals aged beyond 7 years. Reproductive migrations in the Mistassini R. usually begin in mid-June and end in mid-August with spawning taking place in mid-October. The biology and fishery of Lake St-Jean ouananiche are described in Gouin & Hansen (1985) and Tremblay (1994); Havey & Warner (1970) provide a comprehensive treatment of landlocked salmon life history and management.

The data were collected during the summer at the fish ladder of the fifth falls (48°53′16″ N; 72°15′49″ W; 30·5 km upstream from the lake) of the Mistassini R. in 1976, from 1981 to 1984, and from 1986 to 1992. Although there are four minor falls downriver from the ladder, the fifth falls (height 6·1 m) is the first major obstacle for ascending adults. The fish ladder is built in concrete and comprises a series of 18 compartments (pools) each measuring 3·66 × 3·66 m. Fish movement through the ladder is facilitated by rectangular openings at the top of the dividing walls between pools. The Service de l’Aménagement et de l’Exploitation de la Faune (Ministère de l’Environnement et de la Faune, Quebec) kept daily records of the number of fish that passed the ladder, their mean fork length (mm), their river- and lake-age, the mean river discharge ($m^3 s^{-1}$; estimated from calibrated curves relating gauge level to discharge) and water temperature (° C). Fish were counted at the fifth pool from the top of the ladder between 07.00 and 18.00 hours, usually at 30-min intervals; length measurements and scales for ageing were taken from one in every three counted individuals. Over the 12 years included in this study, the dates on which the first migrant fish were observed ranged from 10 to 24 June and the last date of migratory activity ranged from 9 to 28 August. The number of consecutive days of data for any given year ranged from 55 to 66.

Ascending salmon often progress at average rates ranging from a few km day^{-1} to more than 20 km day^{-1} (Mills, 1991); ouananiche in the Mistassini R. ascend to their spawning sites at an average speed of 3·3 km day^{-1} but can sustain speeds of over 11 km day^{-1} over a period of several days (Lapointe, 1993). Spawners leaving Lake St-Jean may therefore take several days to reach the fish ladder. If fish movements triggered by environmental stimuli are initiated at some distance below the ladder, counts at the ladder may reflect a lagged or delayed response to such stimuli. To examine this possibility, for each year, the cross-correlation function (CCF command in the SPSS package; Norusis, 1990) between the fish count series and the river flow and water temperature series was evaluated with time lags of 0 to 14 days. The three time series were differenced once to render them stationary (Norusis, 1990). Because the introduction of lags did not significantly improve the cross-correlations relative to the unlagged series, only the latter were considered in the multiple regression analyses. The REGRESSION command in SPSS was used for ordinary least squares (OLS) multiple regression, and the AREG command (full maximum likelihood method) for generalized least squares multiple regression (GLS, time series). GLS regression takes into account the autocorrelation in data collected on successive days (Ostrom, 1990).

For each year, regressions were calculated of the form:

$$Y_t = \beta_0 + \beta_1 \Delta F + \beta_2 \Delta T \quad (1)$$

where Y_t is a dependent variable (number of migrants or mean body size), the βs are regression coefficients, and the independent variables are daily differences in river flow ($\Delta F = F_t - F_{t-1}$) and water temperature ($\Delta T = T_t - T_{t-1}$) (Jensen *et al.*, 1986). A GLS regression analysis of an augmented model including as independent variables river flow, F_t, water temperature, T_t, and an interaction term, $F_t \times T_t$, in addition to ΔF and ΔT indicated that the additional terms did not contribute significantly to the variation in Y_t (authors, unpublished data). Thus, the simpler model represented by equation (1) was retained for subsequent analysis. In addition, mean fork length was regressed on time (number of days since the onset of migratory activity) to determine whether there was a seasonal trend in body size. A $\ln(X+1)$ transformation was applied to the number of migrants to satisfy the assumption of normality.

RESULTS

There was considerable variability in the number of fish ascending through the fish ladder, river flow, and water temperature among the 12 years (Fig. 1). Examination of the autocorrelation (ACF) and partial autocorrelation functions (PACF) of the daily migration series indicated that the regression residuals were those of a first-order autoregressive process (Chatfield, 1989). The autocorrelation values estimated by GLS regression for the 12 years were high (Table II), indicating that for this data set results from time series regression should be more reliable than those from OLS regression.

For the time series regressions, the number of fish ascending the ladder was significantly ($P<0·05$) related to changes in water flow in six of the 12 years (Table II). The sign of the ΔF coefficient was negative in 10 of the 12 years (Table II), indicating that the number of migrants generally is higher in periods of decreasing flow than at rising water. This consistency in the sign of the ΔF coefficient is unlikely under the null hypothesis that positive and negative

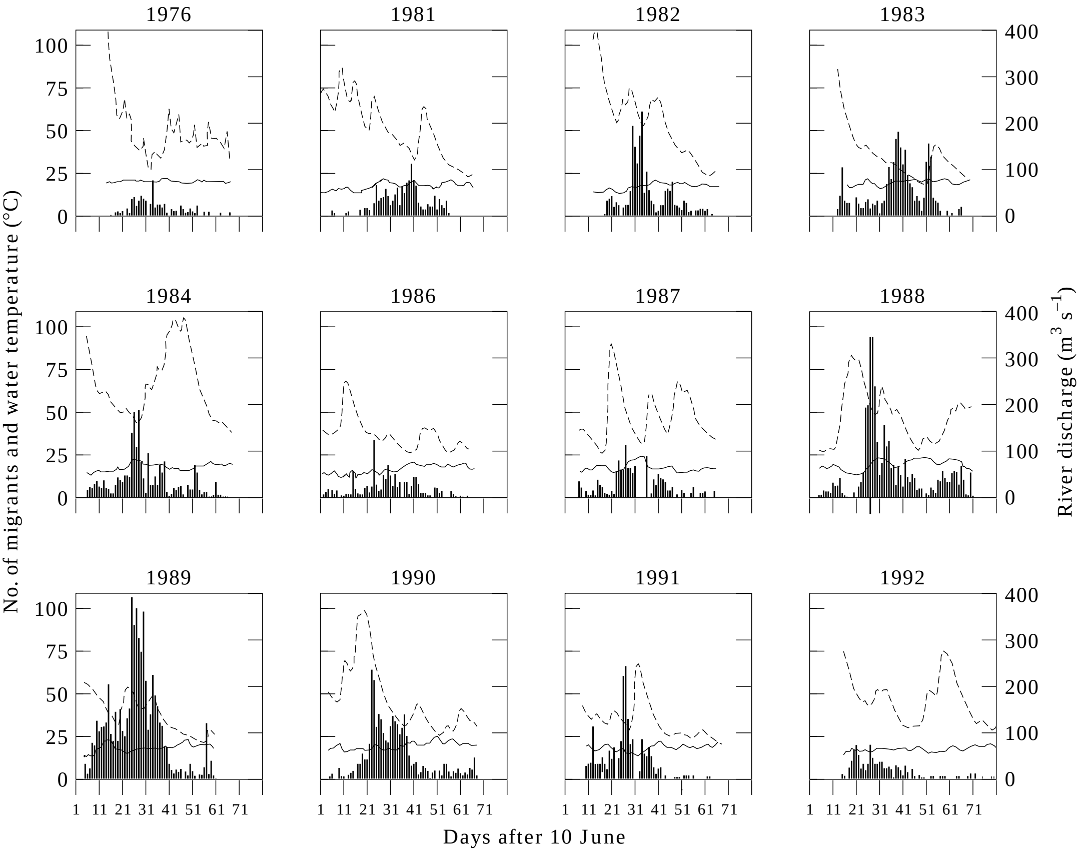

FIG. 1. Daily distribution of the number of upstream migrants (bars), river discharge (– – –) and water temperature (——) for years 1976, 1981 to 1984 and 1986 to 1992.

regression coefficients are equally likely to occur in any given year ($p=q=0{\cdot}5$): the binomial probability of having more than nine positive coefficients or more than nine negative coefficients in a sample of 12 years is 0·039 (two-tailed test). The 6 years showing a significant relationship between number of migrants and flow did not significantly differ (two-tailed *t*-test) from the other 6 years in terms of total run size, mean seasonal discharge, or seasonal discharge variability (standard deviation). There was no significant relationship (linear regression) between total run size or run timing (quantified as the mean day number after June 10) and mean seasonal discharge. Temperature appeared to influence ascent significantly ($P<0{\cdot}05$) in only 2 years, one with a decrease in temperature and one with an increase (Table II).

When OLS regression was used, which does not account for autocorrelation, 3 years showed a significant effect for river discharge (6 years for time series regression), and the sign of the ΔF coefficient was negative in nine of the 12 years (Table II), a result that would not be unexpected if the coefficient were equally likely to be positive or negative (the binomial probability is 0·146; two-tailed test). With OLS regression, one year yielded a significant temperature effect (2 years for time series regression; Table II).

TABLE II. Coefficients from ordinary least squares regression (REG) and time series regression (AREG) for the model $\ln(N) = \text{constant} + \Delta F + \Delta T$

Year	Constant		Δ Flow		Δ Temperature		Autocorrelation	
	REG	AREG	REG	AREG	REG	AREG	REG	AREG
1976	1·381	1·297	− 0·005	− 0·008**	0·285	0·304	—	0·562***
1981	1·418	1·260	− 0·012	− 0·012**	0·129	0·036	—	0·825***
1982	1·882	1·703	− 0·010	− 0·015*	0·184	− 0·109	—	0·806***
1983	2·275	2·142	0·034	0·009	0·130	0·045	—	0·791***
1984	1·971	1·835	0·001	− 0·008	0·088	− 0·086	—	0·794***
1986	1·433	1·413	− 0·009	− 0·001	− 0·055	− 0·079	—	0·552***
1987	1·625	1·637	− 0·005	− 0·004	0·111	− 0·036	—	0·475***
1988	2·344	2·212	− 0·027***	− 0·015*	0·275*	0·264**	—	0·752***
1989	2·805	2·264	0·001	− 0·008	0·163	0·067	—	0·819***
1990	2·104	2·014	− 0·029***	− 0·021**	− 0·075	− 0·019	—	0·706***
1991	1·688	1·620	− 0·023*	− 0·022**	− 0·271	− 0·193*	—	0·858***
1992	1·118	1·123	− 0·006	0·004	0·013	− 0·014	—	0·732***

*: $P<0·05$; **$P<0·01$; ***$P<0·001$.

No effects were found of discharge or temperature differences on the mean body size of migrating fish, but there was a significant decline in body size throughout the summer (Table III): early migrants were on average 11·4% larger (mean FL 522 mm) than late migrants (469 mm). In contrast with the regressions involving the number of migrants, the regressions with mean body size as the dependent variable showed significant autocorrelation in only two of the 12 years (Table III). The seasonal decline in body size was associated with a decline in the mean lake-age of migrants. Age determinations indicated that most returning adults had spent 2 years (71% of all migrants; mean SL 488 mm) or 3 years (25%; mean SL 535 mm) in the lake and 2 years (30% of all migrants) or 3 years (66%) in the river. Examination of the mean migration day (calculated for each year as the day number after 10 June, averaged over all fish in each age group) over the 12 years showed that 3-lake-year salmon (migration day 26·5; mean of yearly means) migrated on average 7·2 days (mean of yearly means; range 1·0 to 12·3 days) earlier than 2-lake-year salmon (mean migration day 33·7). No such difference in migration timing was found between river-age classes: adults that had spent 3 years in the river (migration day 31·9; mean of yearly means) migrated on average only 0·1 days (mean of yearly means; range −2·3 to 2·1 days) earlier than those that had spent 2 years in the river (mean migration day 32·0).

DISCUSSION

Telemetric studies of Atlantic salmon in Scottish rivers have shown that the riverine migration can be divided into three phases (Hawkins & Smith, 1986; Laughton, 1991). In the initial ascent phase, which involves sustained movement usually lasting about 1 day, the fish accomplish the transition from estuary to fresh water rapidly. A quiescent phase of variable duration follows in which there is little or no upstream progress. Ascent then resumes during the final phase when the fish move to their spawning sites. Telemetric data suggest that the migration pattern is simpler in the Mistassini R., where ouananiche skip the intermediate quiescent period and ascend directly to spawning grounds located approximately 130 km upriver from Lake Saint-Jean (Lapointe, 1993). At an average speed of 3·3 km day^{-1} (Lapointe, 1993) fish should require approximately 40 days to reach the spawning sites from the lake. Mating occurs on average 59 days after arrival at the spawning site (Lapointe, 1993).

Although it is generally believed that adult salmon show increased migratory activity in response to increases in river flow rate (Banks, 1969), this conclusion usually refers to the movement of fish entering the river from the estuary rather than to upstream movements within the river (Huntsman, 1948; Hayes, 1953; Webb & Hawkins, 1989; Laughton, 1991; Webb, 1992). The present results suggest that adult salmon in the Mistassini R. prefer decreasing water flow to rising water for upstream migration, in agreement with studies which have considered migratory movement after entry into the river (Huntsman, 1948; Hayes, 1953; Munro & Balmain, 1956; Stewart, 1969; Laughton, 1991). In the study of Huntsman (1948), salmon started to enter the river as a freshet developed, but the principal ascent came as the river was falling again. The author explained this result as a response to the opposition of effects between the

TABLE III. Reduction in mean fork length between the first day and the last day of migratory activity, by year

Year	First day (mm)	Last day (mm)	Difference (mm)	Reduction (%)	Intercept ± S.D.	Slope ± S.D.	r^2	Regression *P*
1976	527·4	476·4	51·0	9·7	6·29 ± 0·026	− 0·0019 ± 0·0007	0·16	0·01
1981	532·0	470·2	61·8	13·1	6·28 ± 0·012	− 0·0019 ± 0·0003	0·42	<0·001
1982	553·6	463·4	90·2	19·5	6·37 ± 0·033	− 0·0036 ± 0·0008	0·34	<0·001
1983	528·3	520·5	7·8	1·5	6·27 ± 0·024	− 0·0002 ± 0·0006	0·002	0·63
1984*	557·4	459·6	97·8	21·3	6·38 ± 0·032	− 0·0036 ± 0·0009	0·49	<0·001
1986	512·3	477·5	34·8	7·3	6·24 ± 0·027	− 0·0012 ± 0·0007	0·07	0·14
1987	526·1	459·6	66·5	14·5	6·28 ± 0·022	− 0·0023 ± 0·0006	0·26	<0·001
1988	500·6	445·2	55·4	12·4	6·22 ± 0·016	− 0·0018 ± 0·0004	0·29	<0·001
1989	499·3	460·9	38·4	8·3	6·22 ± 0·010	− 0·0014 ± 0·0003	0·30	<0·001
1990	504·0	481·0	23·0	4·8	6·22 ± 0·016	− 0·0007 ± 0·0004	0·06	0·07
1991	514·4	462·2	52·2	11·3	6·26 ± 0·027	− 0·0019 ± 0·0008	0·15	0·02
1992*	509·7	448·1	61·6	13·7	6·26 ± 0·052	− 0·0019 ± 0·0001	0·28	0·06
Mean	522·1	468·7	53·4	11·4				
S.D.	18·4	18·8	25·6	5·6				

For each year, the initial and final lengths were calculated with a regression model of the form ln(LENGTH) = intercept + slope (DAY NUMBER). OLS regression was used for years without significant autocorrelation.

*Estimated by GLS regression.

stimulation of a freshet to ascend a stream and the strength of its current tending to prevent ascent or carry fish downstream. Laughton (1991) reported that fish began progress at all stages of the spate event, although movements after the peak were the most common. Hawkins & Smith (1986) found that during the period of residence in the river, some fish appeared to move on falling flow rates, and suggested that fish that have spent a long time in the river may be unwilling or unable to stem the fastest flow rates.

In contrast with the present results, Jensen *et al.* (1986), using an OLS regression model similar to our equation (1), found that increases in both river temperature and flow were positively correlated with the number of ascending salmonids (74–85% Atlantic salmon and the remainder sea trout, *Salmo trutta* L.) in the R. Vefsna, Norway. The discrepancy may be due partly to differences in data handling and analytical technique in the two studies. Their statistical analysis included only periods when river flow and water temperature were favourable for fish ascent (flows between $70\,m^3\ s^{-1}$ and $300\,m^3\ s^{-1}$ and temperatures exceeding 8° C). They excluded the 3 days after each peak in ascent, stating that at that time, even though physical conditions for ascent may have been excellent, few fish remained below the fish counter. A reanalysis of their data (extracted from fig. 2 in Jensen *et al.*, 1986) revealed the presence of significant autocorrelation in the migration time series. Although their exclusion of the 3 days following a peak in ascent reduced the autocorrelation considerably and thus palliated the need for GLS regression, it also eliminated substantial portions of the data set; in the present analysis it was noticed that removal or addition of single points from the remaining data could lead to large changes in coefficient estimates. When no points were excluded from their data set, neither OLS nor GLS multiple regressions yielded significant relationships between the number of migrants and river temperature or flow. To avoid loss of information and of power in statistical tests, it is recommended that in future studies of migrant numbers, unless the absence of potential migrants in downstream areas is thoroughly documented, the full data set be analysed with statistical techniques that account for serial correlation. It should be noted that these techniques are appropriate for analysing movement data obtained by other means whenever autocorrelation is likely to occur, e.g. in telemetric studies relating the distances covered by individual fish over short time periods (hours, days) to environmental variables.

Two problems may arise when attempting to relate fish counts to flow over the whole of the migration season. First, it may prove difficult to disentangle the effects of short-term variations in flow from those of slower changes occurring over several weeks. When feasible, experimental manipulations of water discharge would help remedy this problem. Second, usually it is unknown how much the relationship between fish counts and flow has been influenced by the availability of fish downriver from the counter. If sometimes few or no fish are available when environmental conditions are favourable for migration, simple regression models will underestimate the effect of environmental stimuli on migrant numbers, which may explain partly why no statistically significant relationship was detected in 6 of the 12 study years. Telemetric tracking and direct observation of fish below the counter can enhance the interpretation of results in such cases.

As in many other studies (Hayes, 1953; Banks, 1969; Hellawell *et al.*, 1974), the water temperature appeared to have little effect on migratory behaviour. It is possible that temperature has an effect at very high or very low levels (Hellawell *et al.*, 1974; Mills, 1991) and that the temperature range in our study was too narrow to exert detectable effects (Beamish, 1978). Although summer temperatures in the Mistassini R. seem to be well within the range acceptable for movements of adult salmon (Hellawell *et al.*, 1974), the summer temperatures over the 12 study years (mean of seasonal means 18·6° C; range of seasonal means 16·6–20·2° C; also see Fig. 1), were often higher than the favoured range for migration (5·5–15·6° C) or the upper temperature limit for migration (16° C) cited by Mills (1993).

Early migration may allow larger adults to move further upstream and take over the best spawning areas (Hawkins & Smith, 1986; Laughton, 1989, 1991). In their study of Atlantic salmon, Hawkins & Smith (1986) proposed that, following the initial ascent phase, fish that arrive early reserve holding positions providing shelter and favourable current speeds immediately downstream of suitable spawning sites; thus, ' Larger, older fish, staying for several years in the sea [*or in the lake for landlocked salmon*], with greater capacity for storing food material, and lower maintenance requirements per unit weight (important if the fish is subsisting on stored food) may have an advantage ' (our italics). Larger individuals of anadromous brook charr *Salvelinus fontinalis* Mitchill also migrate upstream earlier in summer than smaller individuals in the St-Jean R., Quebec (Castonguay *et al.*, 1982). The present results, which indicate a decline of mean body size over the summer, support the findings of those earlier studies. This seasonal decline in mean size may be relevant to water management where the manipulation of flow rates could have a size-selective effect on reproductive success (Hellawell *et al.*, 1974). The decline in body size was associated with a reduction in the mean lake-age of migrants. In anadromous Atlantic salmon, the migration peaks of adjacent sea-year classes can overlap considerably in time (Saunders, 1967) or differ by several months (Jones, 1959; Shearer, 1990). It is presently unknown whether the 1-week difference in the timing of migration of the 2-lake-year and 3-lake-year classes, which represent the two main components of the spawning stock in the Mistassini R., is related to differences in genetic structure or spawning location within the river, as occurs in some anadromous populations (Saunders, 1967; Gardner, 1976; Laughton, 1991).

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