Short-term growth (RNA/DNA ratio) of yellow perch (*Perca flavescens*) in relation to environmental influences and spatio-temporal variation in a shallow fluvial lake

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Abstract: Shallow fluvial lakes are heterogeneous ecosystems in which marked spatio-temporal variation renders difficult the analysis of key ecological processes, such as growth. In this study, we used generalized additive modelling of the RNA/DNA ratio, an index of short-term growth, to investigate the influence of environmental variables and spatio-temporal variation on growth of yellow perch (*Perca flavescens*) in Lake St. Pierre, Quebec, Canada. Temperature and water level had seemingly stronger effects on short-term growth than seasonal change or spatial variation between and along the lakeshores. Consistent with previous studies, the maximum RNA/DNA ratio was found at 20.5 °C, suggesting that our approach provides a useful tool for estimating thermal optima for growth in the field. The RNA/DNA ratio showed a positive relationship with water level, as predicted by the flood pulse concept, a finding with implications for ecosystem productivity in fluvial lakes. The RNA/DNA ratio was more variable along the north than the south shore, possibly reflecting exposure to more differentiated water masses. The negative influence of both high temperatures and low water levels on growth points to potential impacts of climatic change on fish production in shallow fluvial lakes.

Résumé : Les lacs fluviaux peu profonds sont des écosystèmes hétérogènes dans lesquels l'importante variation spatio-temporelle rend difficile l'analyse des processus écologiques essentiels, tels que la croissance. Dans notre étude, nous utilisons des modèles additifs généralisés du rapport ARN/ADN, un indicateur de la croissance à court terme, pour examiner l'influence des variables environnementales et de la variation spatio-temporelle sur la croissance de la perchaude (*Perca flavescens*) au lac Saint-Pierre, Québec, Canada. La température et le niveau de l'eau ont vraisemblablement des effets plus importants sur la croissance à court terme que les changements saisonniers ou la variation spatiale, tant le long d'une même rive que d'une rive à l'autre. En accord avec des études antérieures, nous observons un rapport ARN/ADN maximal à 20,5 °C, ce qui laisse croire que notre méthodologie fournit un outil intéressant pour estimer les optimums thermiques pour la croissance en nature. Tel que prédit par le concept des poussées de crue, il y a une relation positive entre le rapport ARN/ADN et le niveau de l'eau, ce qui a des conséquences sur la productivité des écosystèmes dans les lacs fluviaux. Le rapport ARN/ADN est plus variable le long de la rive nord que de la rive sud, ce qui s'explique peut-être par une exposition à des masses d'eau plus distinctes. L'influence négative à la fois des températures élevées et des bas niveaux d'eau sur la croissance laisse présager les impacts possibles du changement climatique sur la production des poissons dans les lacs fluviaux peu profonds.

[Traduit par la Rédaction]

Introduction

Shallow fluvial lakes are spatially heterogeneous ecosystems. In these lakes, current velocities are low, water residence times are long, and light can travel through the entire water column, enhancing primary production of macrophytes and periphyton on the lake bottom. Littoral, rather than pelagic, zones are the most representative component (in area and volume) of shallow fluvial lakes. In northern temperate regions, fringing lake areas become flooded in spring following ice melt, vastly expanding the littoral zone and forming large floodplains that gradually become exposed as water levels progressively decline during the summer. Littoral zones are highly productive owing to terrestrial influxes of nutrients (Scheffer 1998) and can become dominated by submerged macrophytes during summer (Hudon 1997). Because of these characteristics, littoral habitats provide favourable feeding conditions, refuge from predators, and spawning sites for many fish species. In fluvial lakes with multiple inflows and large width/depth ratios, distinct water masses, each typified by their own unique physical and chemical characteristics, can form within the lake (Frenette et al.

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2003). These water masses remain relatively unmixed, conferring horizontal differentiation that accentuates spatial heterogeneity. Temporal gradients also arise from fluctuating environmental conditions and are particularly sensitive to water level fluctuations, which greatly affect shallow littoral systems (Frenette et al. 2006). Spatial and temporal environmental gradients associated with varying physical and chemical regimes in lotic ecosystems directly affect key ecological processes (Wiens 2002) and can thereby influence the growth of aquatic organisms.

Fish growth is influenced by biotic interactions, intrinsic factors such as physiological state and genetics, and a number of environmental factors, including temperature and food (Dutta 1994). Temperature is a potent environmental regulator of growth in fish. In nature, fish experience cyclic and episodic temperature changes and are generally able to seek out optimal thermal habitats for growth, for example, by means of forays between the littoral and deeper, colder waters. In shallow fluvial lakes, however, fish are particularly susceptible to the influence of temperature changes because the water column is shallow and rarely stratifies; meta- and hypo-limnetic thermal refugia are therefore unavailable. Food availability in fluvial floodplains depends on water level fluctuations, and consequently, fish growth is related to the extent and duration of flooding in these systems (Lowe-McConnell 1975; Welcomme 1979). In both tropical and temperate river–floodplain systems, the flood pulse concept predicts that the annual flood cycle is the primary determinant of productivity (Junk et al. 1989; Junk and Wantzen 2004). As water level rises, littoral areas expand into the floodplain, rendering available allochtonous food sources of terrestrial origin that enhance productivity and providing access for fish to suitable nursery grounds. Fish production should, therefore, be strongly related to the spatial extent of accessible floodplain and the duration of the flood.

Growth is a critical component of fisheries production and yield. In North America, yellow perch (*Perca flavescens*) is an economically important species because of its role in both commercial and sport fisheries. Recently, many yellow perch stocks appear to have been overfished, as revealed by declines in overall yield and mean body size (e.g., Marsden and Robillard 2004). This observation has promoted interest in uncovering the factors responsible for the reduction in growth and production of yellow perch. Although many studies have focused on the factors affecting age-0 recruitment (e.g., Staggs and Otis 1996), few have addressed how specific environmental variables, varying both spatially and temporally, may influence the growth rates of yellow perch in nature.

Growth rate in fish can be assessed by means of the RNA/DNA ratio, a sensitive biochemical measure of short-term growth (Bulow 1987). Use of the ratio as a growth index is based on the premise that the cell content of RNA is related to the amount of protein synthesis and thus reflects recent growth and nutritional condition (Buckley and Lough 1987). DNA cell content remains fairly constant and serves to normalize the measured RNA. Growth rate is correlated with the RNA/DNA ratio, and changes in this ratio reflect recent changes in growth rate (Bulow 1987). Although RNA/DNA ratios have often been examined in marine fish, few studies have measured RNA/DNA ratios in freshwater fish under natural conditions (Audet and Couture 2003; Tardif et al. 2005). Approximately 4 days are required for the RNA/DNA ratio to change significantly in response to changes in food availability for juvenile Atlantic salmon (*Salmo salar*) in the laboratory (Arndt et al. 1996), whereas responses to temperature fluctuations can span over a period of up to 1 week for larval yellow perch in the field (Tardif et al. 2005). RNA/DNA ratios measured in field-caught fish may be particularly useful for linking environmental effects to physiological processes because they provide accurate estimates of growth responses to short-term environmental fluctuations.

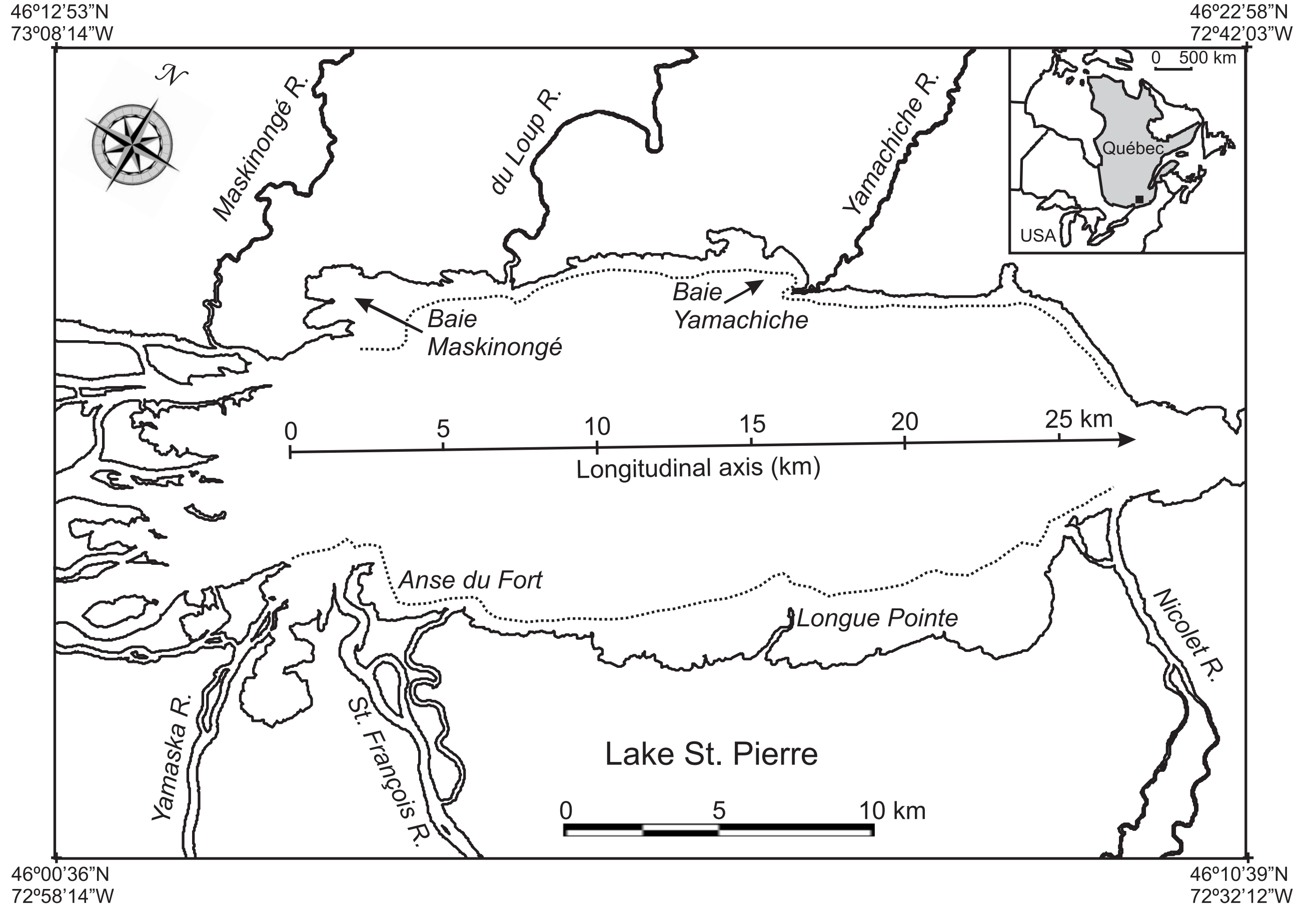
Here, our objective was to assess the dependence of short-term growth in yellow perch on temperature and water level in a shallow fluvial lake subject to marked environmental variation over the summer. We used generalized additive models (GAMs; Hastie and Tibshirani 1990) to allow for flexible, functional representation of partial, or conditional, relationships between the RNA/DNA ratio (short-term growth index, STGI) and environmental variables. Sampling date and spatial coordinates were included in the GAM as predictors to statistically adjust for spatial and temporal influences not directly quantified by the measured environmental variables. The use of RNA/DNA ratios, which respond rapidly to changes in food and temperature conditions, provides a more precise evaluation of short-term environmental influences than would be possible by means of more conventional methods for studying growth, such as analyses of annual increments on hard structures. Uncovering the impact of seasonal fluctuations in temperature and water level on fish growth should allow for better understanding of how biotic processes, such as growth rates, are regulated in shallow fluvial lakes. At a larger scale, knowledge about the effects of short-term environmental fluctuations on fish growth can yield insight into the potential impact of long-term climatic changes on fish production.

Materials and methods

Study area

Lake St. Pierre (LSP) (46°12′N, 72°49′W) is the largest fluvial lake in the St. Lawrence River system and the largest freshwater floodplain in Quebec, Canada. LSP is shallow (mean depth = 3.1 m at mean discharge), with the exception of a central navigation channel that reaches depths >13 m. The surface area of LSP fluctuates between 387 and 501 km^2 depending on water level (Hudon 1997). The annual range in water level, calculated as the difference between minimum (September) and maximum (April) monthly averages, is 1.38 m (Hudon 1997). Inflowing tributaries are found along both the north (du Loup and Yamachiche rivers) and the south (Yamaska, Saint-François, and Nicolet rivers) shores of LSP (Fig. 1). The north and south shores of LSP are associated with distinct water masses that are differentiated horizontally by optical and chemical properties corresponding to their watersheds of origin (Frenette et al. 2003). The shape and position of these water masses vary markedly in time (Frenette et al. 2006). LSP was designated as an ecological biosphere reserve by the United Nations Educational, Scientific, and Cultural Organization in 2001 and is presently protected under the Ramsar Convention. Yellow perch

Fig. 1. Map of Lake St. Pierre (Quebec, Canada) showing the sampling trajectories along which fish were collected on the north and south shores (broken lines) and the imaginary axis used to determine longitudinal position within the lake. The main tributaries along the north and south shores are also shown.



is the dominant fish species in LSP, which harbours >80 of the 116 freshwater fish species found in Quebec (La Violette et al. 2003). The lake supports both commercial and sports fisheries for yellow perch.

Fish sampling and environmental variables

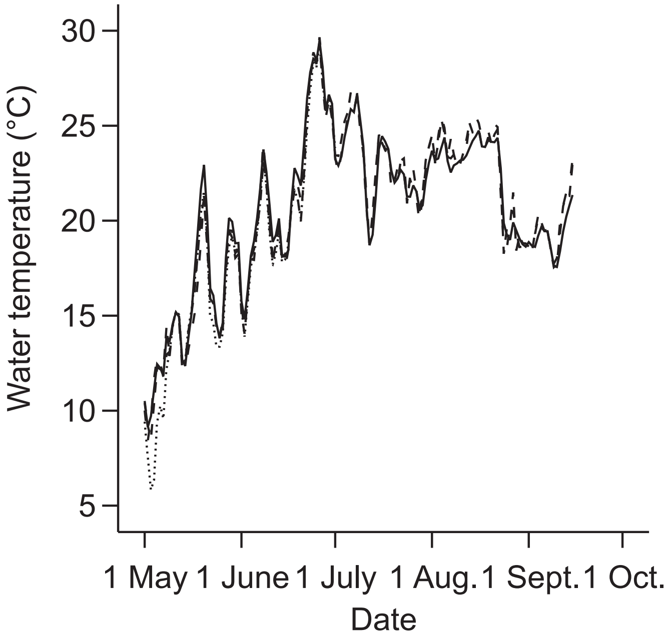
Fish were collected from the shallow littoral zone (<2.5 m depth) by electrofishing (Smith-Root CataRaft boat) along the north and south shores of LSP (Fig. 1) in the summer of 2003 (29 July – 14 September) and 2004 (9 June – 24 August). Fish were measured (total length), weighed, and kept on dry ice in the field and transferred several hours later to a freezer (–80 °C) in the laboratory. Variables coding for the number of days elapsed from 31 May until the day of capture (date) and the shore of capture (shore) were recorded for each fish. For fish from either shore, scores reflecting longitudinal position within the lake (axis) were created by projecting the geographic coordinates of the site of capture perpendicularly onto an imaginary linear axis spanning the length of the lake (Fig. 1).

Water temperature (daily mean) was derived from air temperature by means of a time-series regression model, calibrated as follows. Daily mean water temperatures were obtained from four recorders (Minilog, VEMCO, Shad Bay, Nova Scotia; ±0.1 °C) placed in the shallow littoral zone of LSP at depths <2 and 0.2 m from the bottom of the water column (Baie Yamachiche and Baie Maskinongé on the north shore; Anse du Fort and Longue Pointe on the south shore; Fig. 1) from 1 May to 15 September 2003. The mean values of readings from the four recorders differed little (Fig. 2) and were highly correlated (Pearson's r, mean of six pairwise values = 0.99); they were, therefore, averaged to obtain a daily mean water temperature for LSP. The calibrated model was obtained by regressing water temperature for day X (WaterT_X) against three predictors: the air temperatures (daily mean for the LSP station, Environment Canada) for that day, air temperature for day X (AirT_X), and the air temperature for the two preceding days (AirT_{X-1} and AirT_{X-2}). Errors were assumed to be first-order autoregressive based on an examination of autocorrelation and partial autocorrelation functions for the time series. The coefficient of determination of the multiple regression model (adjusted R^2 = 0.94) indicated that air temperatures were suitable predictors of water temperature in LSP (cf. Fig. 2 and water temperature for 2003 in Fig. 3*a*). Water level (stage height, daily mean for the LSP station) was obtained from HYMAP Hydrometric Data (Water Survey of Canada, Environment Canada) (Fig. 3*b*).

Short-term growth index: RNA/DNA ratio

The short-term growth index (RNA/DNA ratio) was determined for a total of 296 fish: 128 from the north shore and

Fig. 2. Water temperatures registered at four sites in the shallow littoral zone of Lake St. Pierre: Baie Yamachiche and Baie Maskinongé on the north shore; Anse du Fort and Longue Pointe on the south shore.

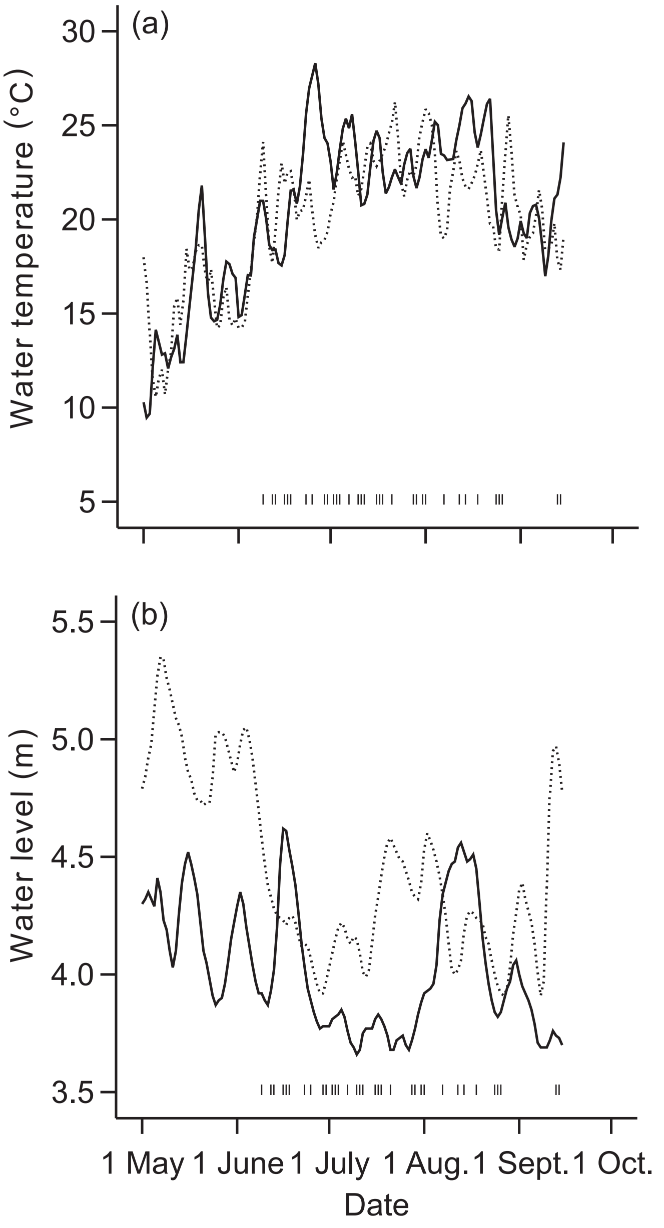


168 from the south shore (total length: median = 101 mm; min.–max. = 42–206 mm; age range = 0+ to 5+). White muscle tissue was dissected from the area posterior to the dorsal fin, well above the lateral line, on the left side of individual fish. Muscle tissue was homogenized in distilled water (1 g tissue·5 mL water^{-1}) and nucleic acids extracted following the method of Buckley and Bulow (1987). Nucleic acid concentrations were determined from absorbance readings at 260 nm taken on RNA and DNA fractions.

Quantitative analyses

GAMs are computer-intensive statistical tools that can be viewed as nonparametric extensions of multiple regression. GAMs retain several of the advantages of multiple regression, such as simultaneous inclusion of several explanatory variables and partialling out of effects to examine conditional relationships. Additionally, they allow for more flexible representation of the functional relationships between the response and explanatory variables, by means of smooth functions. Furthermore, because the shape of the smooths is undetermined a priori and can be data-driven, additive models can partial out trends arising from unspecified influences that are spatially or temporally structured but not directly measured in the study (Wood 2006). Thus, they allow for more precise estimation of the focal effects of main interest. GAM are a powerful tool for analyzing environmental influences because the smooth functions can adequately represent complex, possibly nonlinear trends in responses without strong assumptions about the functional form of the trends (Wood and Augustin 2002). GAMs have been used in fish ecology and fisheries to examine survey results (Swartzman et al. 1992), egg production (Borchers et al. 1997), recruitment (Cardinale and Arrhenius 2000), habitat relationships (Brosse and Lek 2000), and catch rates (Walsh and Kleiber 2001).

Fig. 3. (*a*) Water temperature and (*b*) water level (stage height) for Lake St. Pierre in 2003 (solid lines) and 2004 (broken lines). Sampling dates are indicated by rug plots (short vertical lines) along the horizontal axes.



A semiparametric additive model combining linear predictors and smooth functions was used to represent the relationship between the STGI and body mass, environmental features, and spatio-temporal variation:

$$\begin{aligned}\ln(\text{RNA/DNA ratio}_i) &= \beta_0 + \beta_1 \ln(\text{body mass}_i) \\ &+ f_1(\text{temperature}_i) + f_2(\text{water level}_i) + f_3(\text{date}_i) \\ &+ \beta_2(\text{shore}_i) + f_4(\text{axis, north shore}_i) \\ &+ f_5(\text{axis, south shore}_i) + \varepsilon_i\end{aligned}$$

Table 1. Summary statistics for fish characteristics and abiotic variables used in the semiparametric additive model.

	Median	Minimum	Maximum
Fish characteristics (N = 296 fish)			
RNA/DNA ratio	0.92	0.22	2.40
Body mass (g)	10.3	0.9	101.1
Abiotic variables (N = 34 sampling dates)			
Temperature (°C)	21.8	17.7	25.1
Water level (m)	4.13	3.73	4.58
Date of capture (days since 31 May)	48	9	106
Longitudinal axis (km)	17.7	0.3	26.7

where individual fish are indexed by i, β_0 is the intercept, β_1 and β_2 are coefficients quantifying the effects of body mass and shore, f_1 and f_2 are smooth functions of the environmental variables, f_3 is a smooth function representing a seasonal trend, shore is a binary variable coding for the north (shore = 0) and south (shore = 1) shores, f_4 and f_5 are shore-specific smooth functions for the spatial variable representing longitudinal variation (axis), and ε_i represents Gaussian error. Values for temperature and water level correspond to the date of capture of fish i. Summary statistics for fish characteristics and abiotic variables used in the model are given in Table 1. Body mass was log-transformed to avoid giving undue weight to extreme observations and was included as a linear term, because preliminary modelling showed that its relationship to growth was well represented by a straight line (smooth function with one degree of freedom). More complex models including differences between years, as well as interactions between body mass and temperature or water level, or between temperature and water level, were also examined. These models were rejected because the additional terms did not contribute significantly to explanatory power, as determined by the generalized cross-validation criterion (V_g) and graphical examination of the putative interactions.

Penalized thin-plate regression splines were used to represent the smooth terms (Wood 2006). All calculations were performed in the R software environment, version 2.4.0 (R Development Core Team 2006). Smoothing parameters for the model were chosen to minimize V_g as implemented in the mgcv package for R (Wood 2006), version 1.3–22:

$$V_g = nD/(n - \mathrm{df})^2$$

where n is the sample size, D is the deviance, and df are the effective degrees of freedom of the model. To avoid overfitting, and because the overall shape of growth responses to temperature and water level were expected to be monotonic or unimodal, the f_1 and f_2 terms were constrained to have at most 3 df (comparable with a cubic polynomial), the default level used in other programs such as the gam package for R. Model residuals were examined graphically to check for violation of assumptions. The effect size, a measure of the relative contribution of individual independent variables to variation in the STGI, was quantified for each independent variable as:

$$\text{effect size} = \left(\frac{\mathrm{STGI}_{\max} - \mathrm{STGI}_{\min}}{\mathrm{STGI}_{\min}}\right) \times 100$$

where $\mathrm{STGI}_{\max}$ and $\mathrm{STGI}_{\min}$ are the maximum and minimum predicted values, respectively, over the observed range of the independent variable. The effect size, therefore, reflects the maximum relative increase in STGI (%) associated with changes in each independent variable.

Results

The STGI had a near-parabolic relationship to temperature, as shown graphically (Fig. 4*a*) and by the smooth function (2.36 df; Table 2). The STGI attained a maximum at 20.5 °C, a value lower than the median water temperature over the study period (21.8 °C; Table 1). Among all independent variables in the study, temperature appeared to have the strongest influence on the STGI, as indicated by the effect size (Table 2); the predicted STGI was nearly 2.2 times greater at 20.5 °C than at the upper end of the temperature range (25.1 °C). The STGI had a curvilinear relationship to water level (2.54 df), with little discernable effect of water level at lower values up to ~4 m and a marked increase of the STGI (twofold) with water level thereafter (Fig. 4*b*). During the growing season, the greatest values of STGI were attained during periods when water level exceeded ~4 m. There was marked year-to-year variation in the duration and timing of those periods, which totalled 30 days in 2003 and 85 days in 2004 between 9 June and 14 September (Fig. 3*b*). Effect size for water level was nearly as large as that for temperature. Temporal and spatial effects on the STGI were smaller than those of temperature and water level. The STGI declined monotonically over the study period, as shown by the smooth function for sampling date (1.92 df) (Fig. 4*c*). The effect size associated with this seasonal decline reflected a 44% reduction in the STGI from early June to mid-September. Spatial differences in the STGI were also apparent; although the mean difference in the STGI between shores was small and marginally significant (as shown by effect size and P value for β_2; Table 2), the terms for longitudinal axis (f_4 and f_5) pointed to substantial differences in longitudinal variation between shores (Figs. 4*d*, 4*e*). No significant variation in the STGI was found along the south shore, whereas the STGI was markedly heterogeneous along the north shore. Accordingly, a fairly complex smooth function was needed to characterize longitudinal variation along the north shore (5.57 df). The STGI scaled positively with body mass as $M^{0.075}$, implying that the STGI for the largest fish in this study (101.1 g; Table 1) was 43% greater than that for the smallest fish (0.9 g; Table 1). Although growth

Fig. 4. Short-term growth of yellow perch (*Perca flavescens*) represented as smooth functions (solid lines) of (*a*) temperature, (*b*) water level, (*c*) date of capture, (*d*) longitudinal position along the north shore, and (*e*) longitudinal position along the south shore. The vertical axes represent predicted values of log(RNA/DNA ratio), centered so that function values add to zero. Approximate 95% confidence intervals (broken lines) are also shown. The distribution of observed values for the independent variables is indicated by rug plots (short vertical lines) along the horizontal axes.

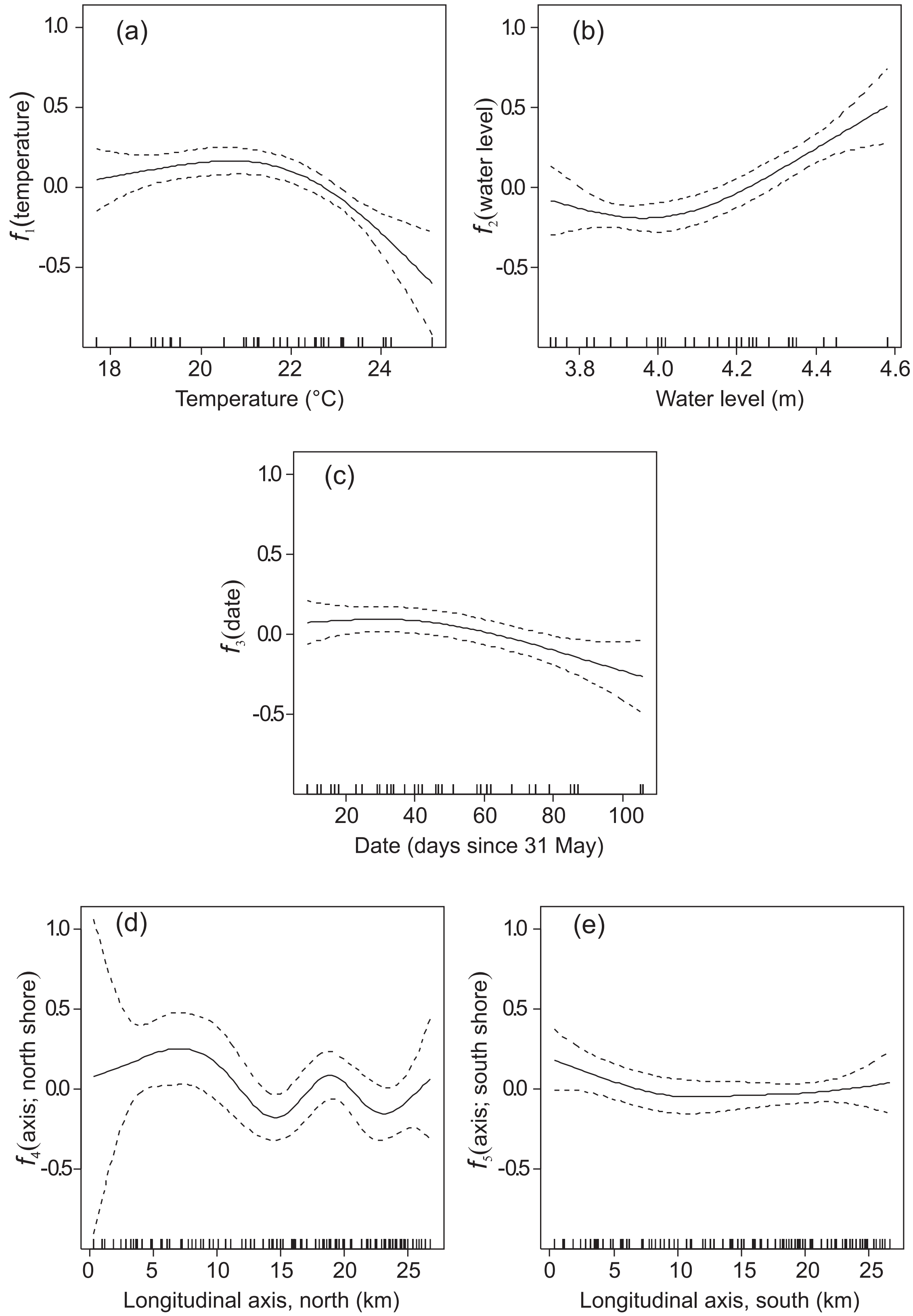


Table 2. (*a*) Estimated coefficients and standard error (SE) for the parametric terms and (*b*) estimated degrees of freedom (df) for the smooth (nonparametric) terms of the additive model (see Methods: Quantitative analyses).

(*a*) Parametric terms.

Variable	Coefficient	Estimate	SE	*P*	Effect size (%)
Intercept	β_0	–0.395	0.066	<0.001	—
Body mass	β_1	0.075	0.023	<0.001	43
Shore	β_2	0.104	0.051	0.045	11

(*b*) Nonparametric terms.

Variable	Smooth	Estimated df	*P*	Effect size (%)
Temperature	f_1	2.36	<0.001	115
Water level	f_2	2.54	<0.001	101
Date	f_3	1.92	0.020	44
Longitudinal axis, north	f_4	5.57	0.003	54
Longitudinal axis, south	f_5	2.32	0.221	NS

Note: *P* values and effect sizes for all terms are also provided. The model accounts for 41.2% of the deviance. $N = 296$ fish. NS, not significant.

in some fish species, including yellow perch, displays size- or age-dependent sensitivity to temperature (Boisclair and Leggett 1989), in the present study no size dependence was detected in GAM analyses that included a term for interaction between body mass and temperature.

Discussion

Temperature effect

Growth rate in fish generally increases with temperature to a maximum; above that optimal temperature, growth rate declines as the temperature approaches the lethal limit for the species (Dutta 1994). We obtained a similar response for the short-term growth of yellow perch in LSP, whereby RNA/DNA ratios increased with temperature up to a maximum followed by steady decline. Kitchell et al. (1977) found that growth rate of yellow perch attained a maximum at 23 °C and declined sharply at higher temperatures in the field. The STGI of yellow perch in LSP was greatest at 20.5 °C, near the optimal temperature (22 °C) for growth of yellow perch in Lake Monona, Wisconsin (Neill and Magnuson 1974). The temperature yielding the maximum STGI in LSP also corresponds well to reported values of the final temperature preferendum, the temperature eventually selected by fish exposed to an experimental thermal gradient along which they can move freely (20.1–24.2 °C for yellow perch: Coutant 1977; Jobling 1981). GAM analysis of RNA/DNA ratios therefore appears to be a useful tool to characterize the thermal response and estimate the optimum temperature for growth of fish in their natural environment. The STGI of yellow perch in LSP declined at temperatures greater than 22 °C, suggesting that short-term growth is reduced at those temperatures. Fish in shallow fluvial lakes are not able to respond to high surface temperatures by descending to thermally favourable habitats at greater depth; thus, any adverse affects of high temperatures on growth should be more apparent than in deeper, stratified lakes.

Water level effect

We detected a positive relationship between the STGI of yellow perch and water level in LSP. Among current models of ecological productivity in riverine systems (Thorp et al. 2006), the flood pulse concept appears to be the one most consistent with the observed growth response. Several studies of lotic and lentic systems subject to flooding events in more southern temperate regions also have reported a positive relationship between fish growth and water level. For example, in Lake Texoma, a large multipurpose reservoir on the Texas–Oklahoma border, growth rates of three fish species were significantly higher during a flood year than in previous years (Cone et al. 1986). In the Yolo Bypass, the seasonally inundated floodplain of the lower Sacramento River, juvenile Chinook salmon (*Oncorhynchus tshawytscha*) had higher growth rates than in adjacent river channels (Sommer et al. 2001). Another example stems from the lower Mississippi River, where the duration of floodplain inundation was directly related to growth of ictalurid catfishes (Schramm et al. 2000).

These results contrast with the effect of flooding on fish growth in some temperate streams. RNA/DNA ratios provided evidence that summer floods caused temporary reductions in growth rate (20%–30%) of juvenile Atlantic salmon in two streams in New Brunswick (Arndt et al. 2002). Flood conditions seemingly reduced growth rates through increased activity costs associated with the heavier discharge, coupled with reduced feeding efficiency in the more turbid waters. Our results indicate that LSP behaves more like a floodplain ecosystem than a fast-flowing river and that it may play an important role in the productivity of the St. Lawrence River system, as described by the flood pulse concept.

Not all studies have consistently found the growth response predicted by the flood pulse concept (Rutherford et al. 1995). The reasons invoked for this discrepancy are related to the degree to which particular species exploit the moving littoral zone, their trophic position, the amount and quality of flooded terrestrial areas, the water temperature during the flood, and the efficacy of the statistical analysis (Gutreuter et al. 1999). However, the ability to detect a response may also depend on the sensitivity of the growth estimate used. In most studies, growth estimates are obtained from analysis of hard structures, for example, from annual growth increments that integrate growth yearly and thus reflect the cumulative effect of environmental conditions encountered by fish over an extended time period. In comparison, the RNA/DNA ratio is a more sensitive growth index for assessing the effect of short-term environmental variations (Arndt et al. 1996; Tardif et al. 2005). Studies employing RNA/DNA ratios are likely better at detecting and quantifying growth responses to seasonal events such as flooding than those using hard structures, because of the rapid response time of the STGI.

The flood pulse concept posits that the mechanism by which flooding stimulates fish production is related to increases in primary and secondary production on the floodplain (Junk et al. 1989), and thus, to improved food supply for fish. The enhancement of biological production may be achieved through lateral exchange of nutrients between the floodplain and river channel and also through nutrient recycling within the floodplain (Junk et al. 1989). Several studies have found increased aquatic production in response to flooding events in temperate zones. Species able to exploit littoral resources in the Upper Mississippi River system displayed increased growth rates in response to an extreme flood (Gutreuter et al. 1999). An increase in allochtonous inputs as a consequence of flooding led to increased production in Lake Texoma (Cone et al. 1986), whereas availability of drift invertebrates for fish consumption increased following inundation in the Yolo Bypass (Sommer et al. 2001). Enhancement of biological production is presumably associated with nutrient enrichment during flooding and is therefore directly related to the increase in the surface area of the waterbody above baseline level (Bayley 1995). LSP contracts substantially (~30% decline relative to high water levels) and is surrounded by an extensive marshland at low water levels (Hudon 1997). Over the range of water level in our study, lake area underwent an expansion approaching 15% of the total surface area, which represents an even greater proportional increase relative to the highly productive littoral area.

The role of temperature has been a main consideration when extending the flood pulse concept beyond tropical systems (Humphries et al. 1999; Junk 1999; Tochner et al. 2000). The flood pulse concept may apply more strongly to temperate floodplain–river ecosystems when thermal aspects of flood pulses are considered. For example, the relationship between fish growth and floodplain inundation can become stronger when water temperature is integrated with the area and duration of floodplain inundation in the analysis (Schramm and Eggleton 2006). In the temperate zone, temperatures in the spring, the time of the year when peak flooding generally occurs, may be suboptimal for feeding and growth (Schramm et al. 2000). Likewise, optimum conditions for larval growth and fish recruitment in the inundated floodplain may be highly sensitive to the seasonal coupling of the thermal and hydrological regimes (King et al. 2003). Yellow perch do not grow in length at temperatures below 13.5 °C (Power and van den Heuvel 1999), a threshold that is generally not attained in LSP until mid- to late spring (Tardif et al. 2005). The annual peak flood in LSP usually occurs in April (Hudon 1997), previous to the onset of the growth season, and water level can be highly variable during the summer. This means that over the growth season, short-term growth in yellow perch appears to be stimulated mostly during periods when water level exceeds ~4 m, which may be relatively short-lived in some years. In our study, GAM analyses accounted for the additive effect of temperature on the STGI of yellow perch but revealed no interaction between temperature and water level, likely because temperatures over the study period always exceeded the lower thermal threshold for growth.

Temporal and spatial trends

The STGI of yellow perch in LSP displayed a seasonal decline over the period from June to September. Lower RNA/DNA ratios in maturing compared with immature Atlantic salmon parr in the wild have been observed in September, presumably because allocation of energy to somatic growth is reduced during maturation (Arndt 2000). However, seasonal decline in RNA/DNA ratios of nonmaturing parr in streams also has been related to adverse effects of flooding on growth (Arndt et al. 2002). RNA/DNA ratios of bluegill (*Lepomis macrochirus*) displayed a seasonal depression in growth during summer; however, this change was associated with the effects of thermal stratification and dissolved oxygen stress (Bulow et al. 1981), rather than sexual maturity. Contrary to these studies and to our results, the RNA/DNA ratio revealed a steady seasonal increase in growth of black crappie (*Pomoxis nigromaculatus*) from mid-May to mid-September, although a plateau or slight decline was observed during late July and early August (Haines 1980).

The cause of the seasonal decline in RNA/DNA ratio of yellow perch in LSP is not known but does not appear to be size-related, because the GAM accounted for additive effects of body mass. Audet and Couture (2003) noted a decline in RNA/DNA ratios for yellow perch in both pristine and mercury-contaminated lakes over the summer season but did not offer an explanation for it. It is unlikely that in LSP the observed decline in the STGI is related to sexual maturation, because yellow perch spawning has usually ended by early May in LSP. In female European perch, *Perca fluviatilis*, energy is diverted to perivisceral fat and the liver during the sexual resting period (June–August; Blanchard et al. 2005). Fat deposition in the months following spawning might similarly slow down the somatic growth of yellow perch over the summer. Seasonal changes in abiotic or biotic factors unrelated to water level and temperature may, therefore, be responsible for this decline in somatic growth and warrant further investigation. The seasonal trend in growth revealed by RNA/DNA ratios would not have been detectable by conventional methods that base growth estimates on annual increments, thereby masking the seasonal relationship.

The STGI of yellow perch displayed greater variability along the north shore than the south shore of LSP, as revealed by the GAM smooths for the two shores. LSP has distinct water masses along the two shores (Frenette et al. 2006). The northern water mass is more turbid and richer in suspended particles, dissolved organic carbon (DOC), and humic and fulvic acids. It includes waters emanating from three sources: the du Loup and Yamachiche rivers, several northwestern tributaries, and the Ottawa River. The southern water mass comprises a complex mixture of sources: tributaries draining surrounding farmlands and the St. François, Richelieu, and Yamaska rivers. The relative distribution of water masses along both shores changes seasonally in response to fluctuations in the discharge of the main tributaries and the St. Lawrence River (Frenette et al. 2006). Results from a hydrological model for LSP (Frenette et al. 2006) indicate that the composition of water masses traversed by our fishing trajectories was more variable along the north shore than along the south shore (cf. fig. 1 in Frenette et al. 2006). Because the physical and chemical properties of water masses can influence production and foraging success of fish, exposure to more differentiated water masses may explain the greater variability of the STGI of yellow perch on the north shore of LSP. The STGI was estimated to be on average 11% higher on the south shore than on the north shore. This result agrees with a previous study that compared growth rates of age-0 yellow perch from two littoral sites on each shore of LSP and found higher growth in the south shore (Tardif et al. 2005). Compared with studies based on examination of a handful of sites, the combination of GAM analysis with extensive sampling coverage of both lake shorelines enabled us to generate a more accurate and complete portrait of spatial variation in growth rates, including longitudinal variation and differences between shores.

In summary, short-term growth of yellow perch in LSP appears to be influenced by a combination of nonlinear effects. The environmental variables considered in this study, temperature and water level, had seemingly stronger effects on short-term growth than did spatio-temporal variation or body mass. The form of the smooth function for temperature hinted at a thermal optimum for short-term growth near 20.5 °C. The influence of water level on growth may have major implications on the productivity of LSP and other fluvial lakes of the St. Lawrence River system, as posited by the flood pulse concept. GAM analyses coupled with RNA/DNA ratios proved effective for revealing both temporal (seasonal) and spatial (along and between the shorelines of LSP) variations in growth rate, which may have otherwise remained veiled. Our results suggest that GAM analyses of RNA/DNA ratios can allow for accurate assessment of overall trends in growth of yellow perch in highly heterogeneous environments and provide insight into the ecological meaning of environmental variations. Future studies could test this approach on other fish species to corroborate its usefulness for determining thermal optima in the field and uncovering complex spatio-temporal patterns of variation in growth.

Changes in temperature and water level resulting from global warming may deliver a one–two punch to fish growth by shortening the duration of periods combining favourable temperature and water level. Our study revealed that both high temperatures and low water levels have a negative influence on growth of yellow perch. Jointly, these effects could have major long-term consequences on overall fish production and should thus be considered in management practices likely to alter either temperature or water level. The long-term fate of the yellow perch fishery in the St. Lawrence River system may depend on the maintenance of hydrological regimes that allow fish growth to attain levels required for self-renewal of stocks. Criteria for discharge regulation in the St. Lawrence River should, therefore, account for the effects of climatic change on temperature and flow regimes in the St. Lawrence – Great Lakes basin and the potential impacts on fish growth.

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