Additive modelling of fish growth in relation to environmental influences and spatio-temporal variation

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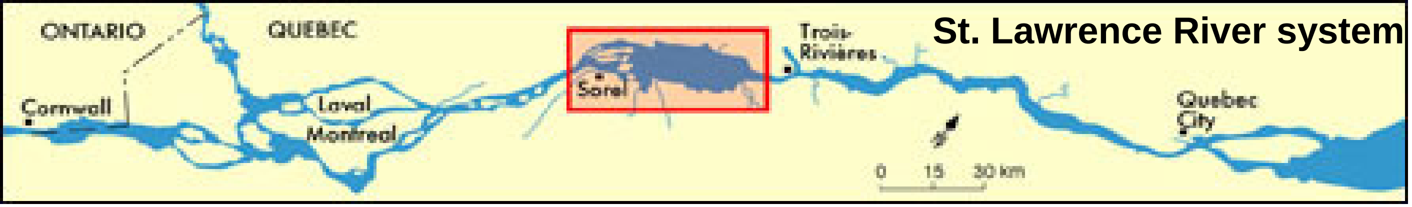
Background



Shallow, fluvial Lake Saint Pierre (LSP)

Water levels in the Saint Lawrence system

Determined primarily by:

- Natural fluctuations in precipitation (Great Lakes and Ottawa River Basin)
- Regulating structures (International St. Lawrence River Board of Control)
- Inputs from tributary rivers

Stable and above the historical average since the early 1960s

Amplitude of both seasonal and interannual fluctuations reduced by regulation

Regulation has limited effectiveness because total water inflow into the basin cannot be accurately controlled or predicted

Climate warming: Predictions from atmospheric general circulation models

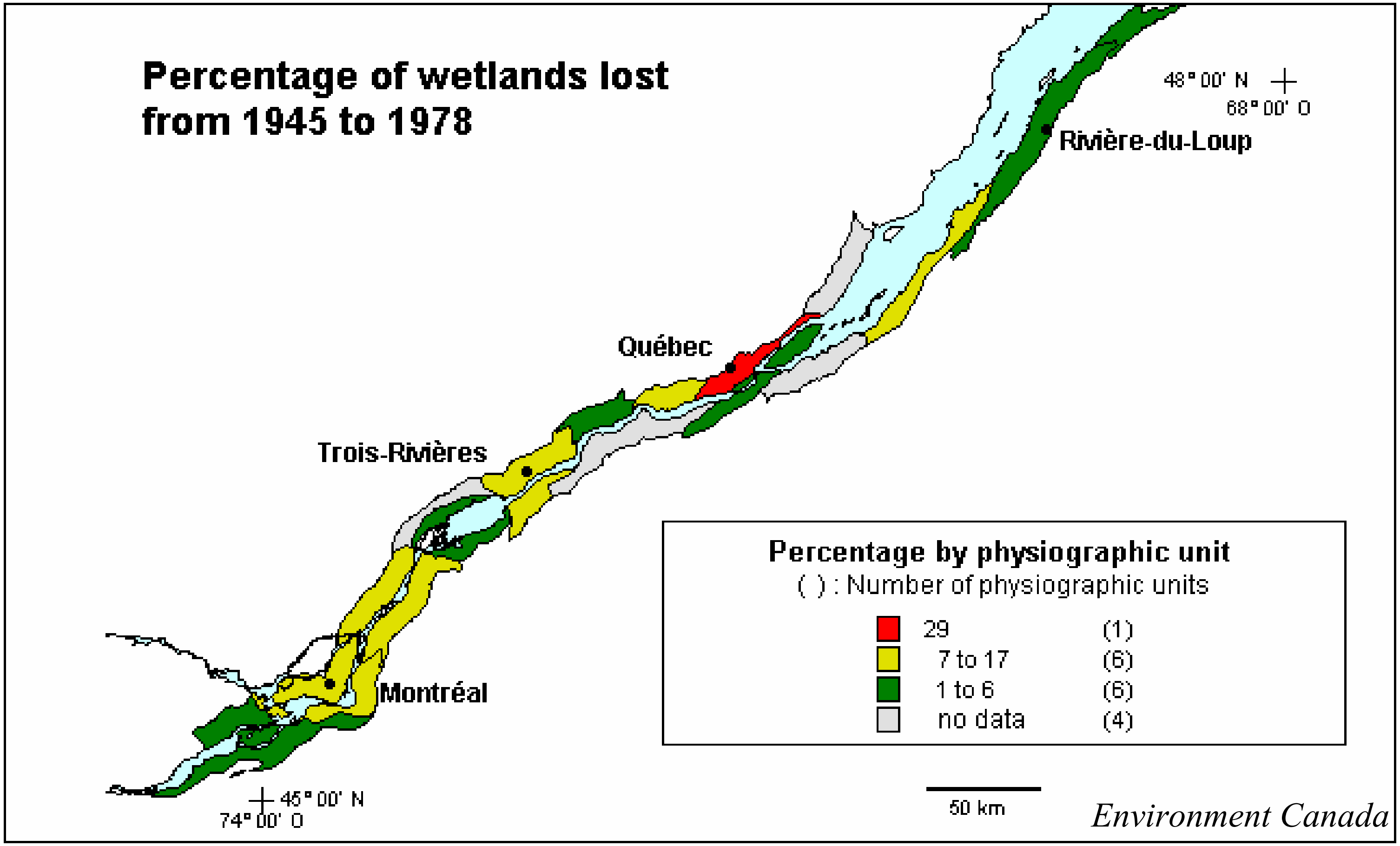
Warming of 0.7 °C and increase in climate variability in the Great Lakes and St. Lawrence Basin during the last century

Carbon dioxide concentration likely to double in this century if no steps are taken to reduce greenhouse gases

Predicted warming of 3 °C along the St. Lawrence within 50 years

- Increased precipitation in winter and spring
- Changes in timing of first frost and snow melt

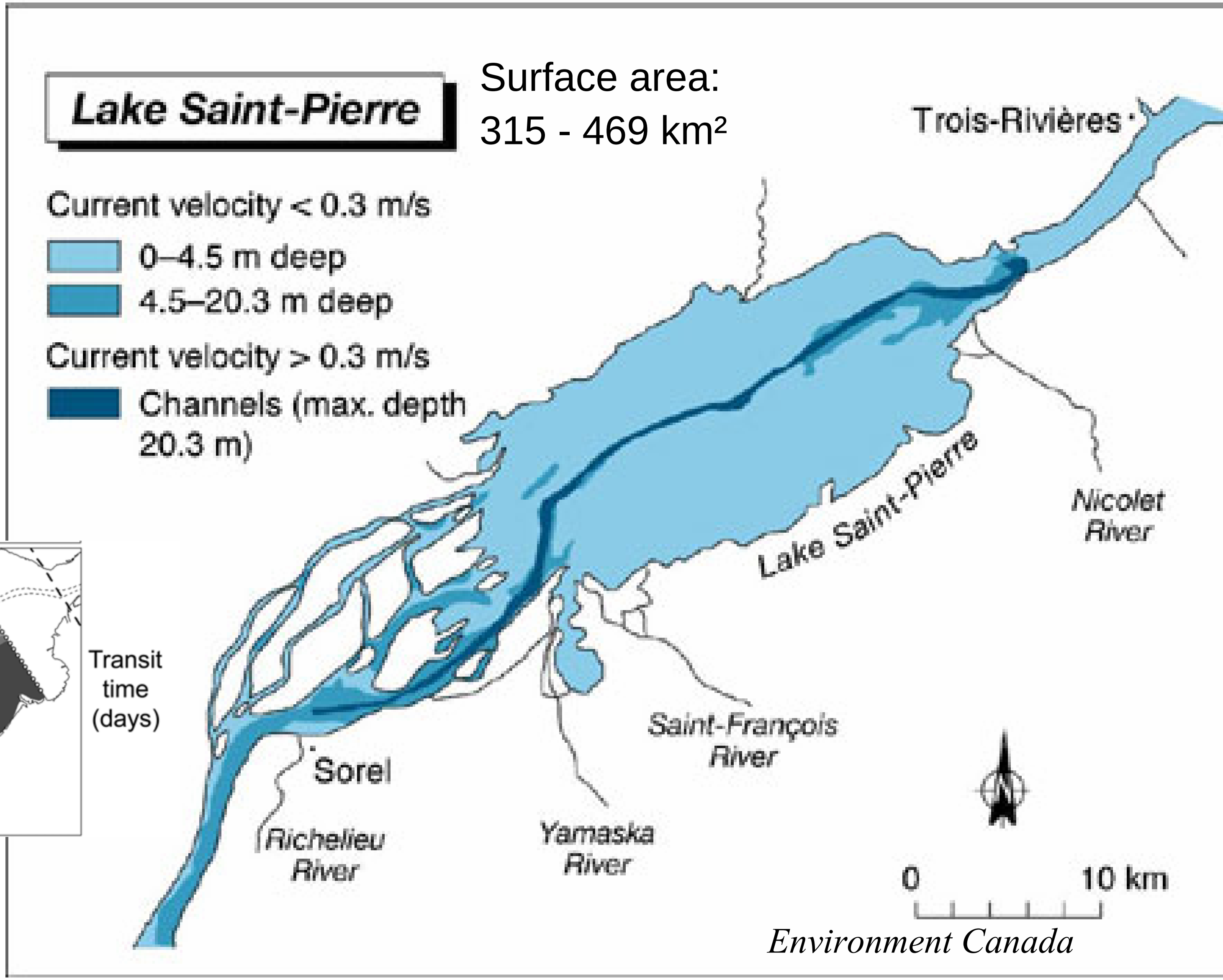
Reduced water flow from Lake Ontario could lead to decline in St. Lawrence River flow below lowest levels in nearly a century

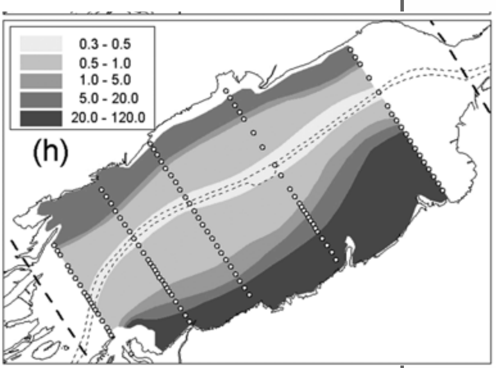


Variability of seasonal and interannual cycles in wetlands supports high diversity and productivity

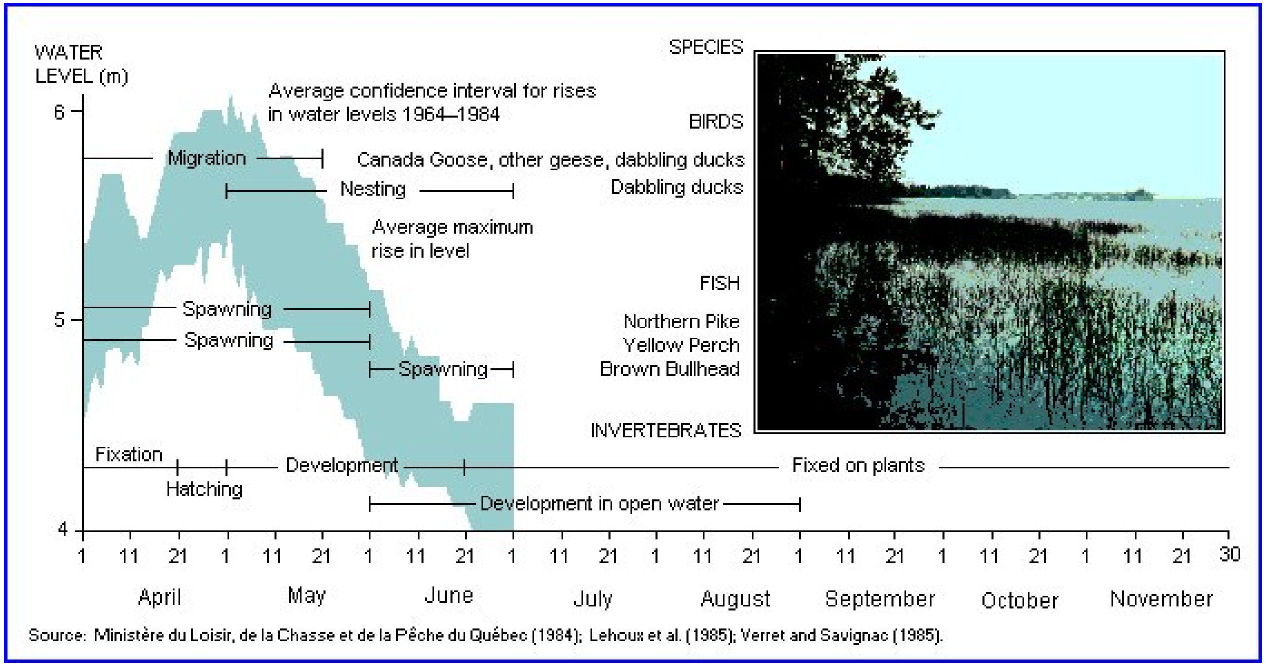
Modifications in the hydrologic regime and the regulation of water levels can disturb these cycles, causing shrinkage of wetlands and reductions in biological diversity

Predominance of shallow littoral zones in LSP





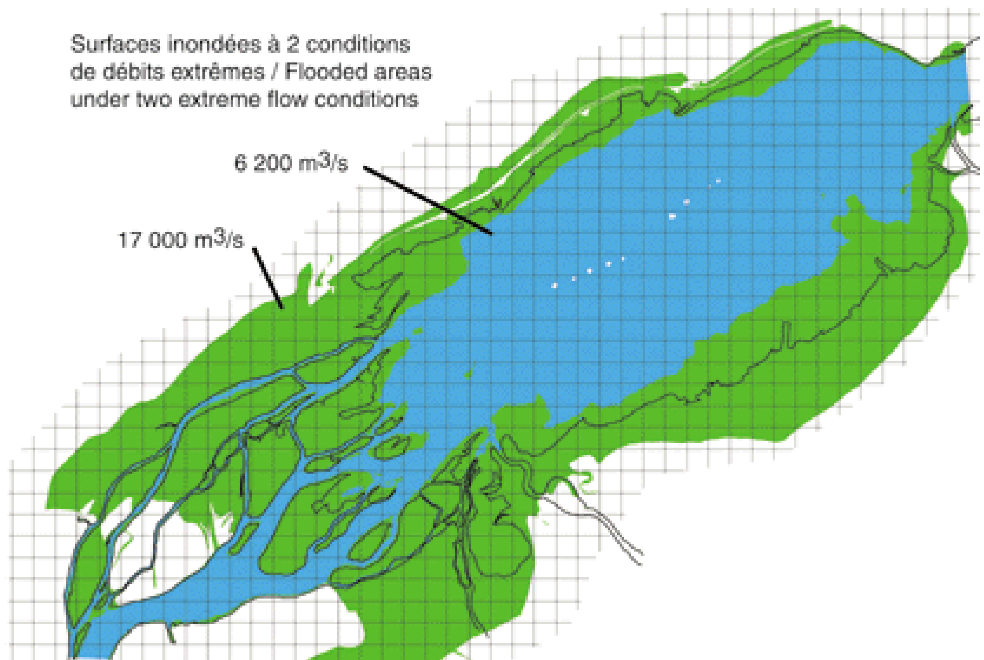
Transit time (days)



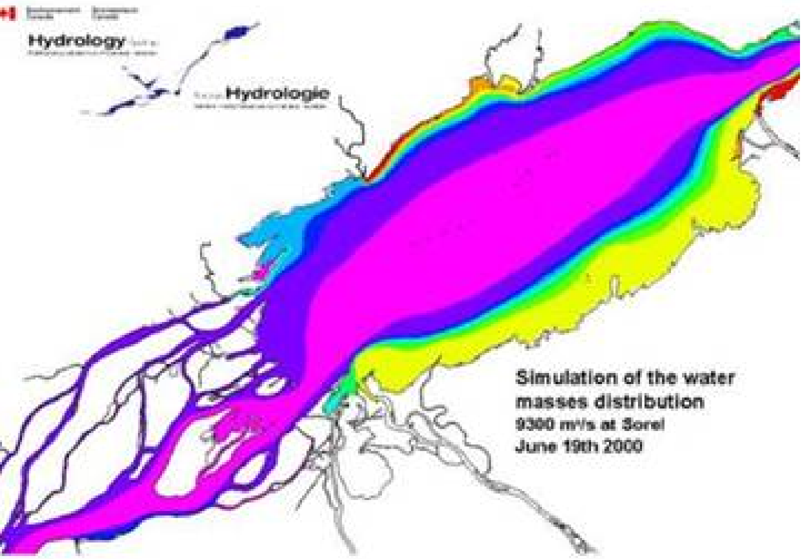
Marked variation in timing and magnitude of hydrological cycles

LSP contracts substantially (~30% decline in wetted area relative to high water levels) and is surrounded by an extensive marshland at low water levels

Areas flooded during annual cycle provide habitat and enhance productivity (“flood pulse” concept: *Junk et al. 1989*)



Environment Canada



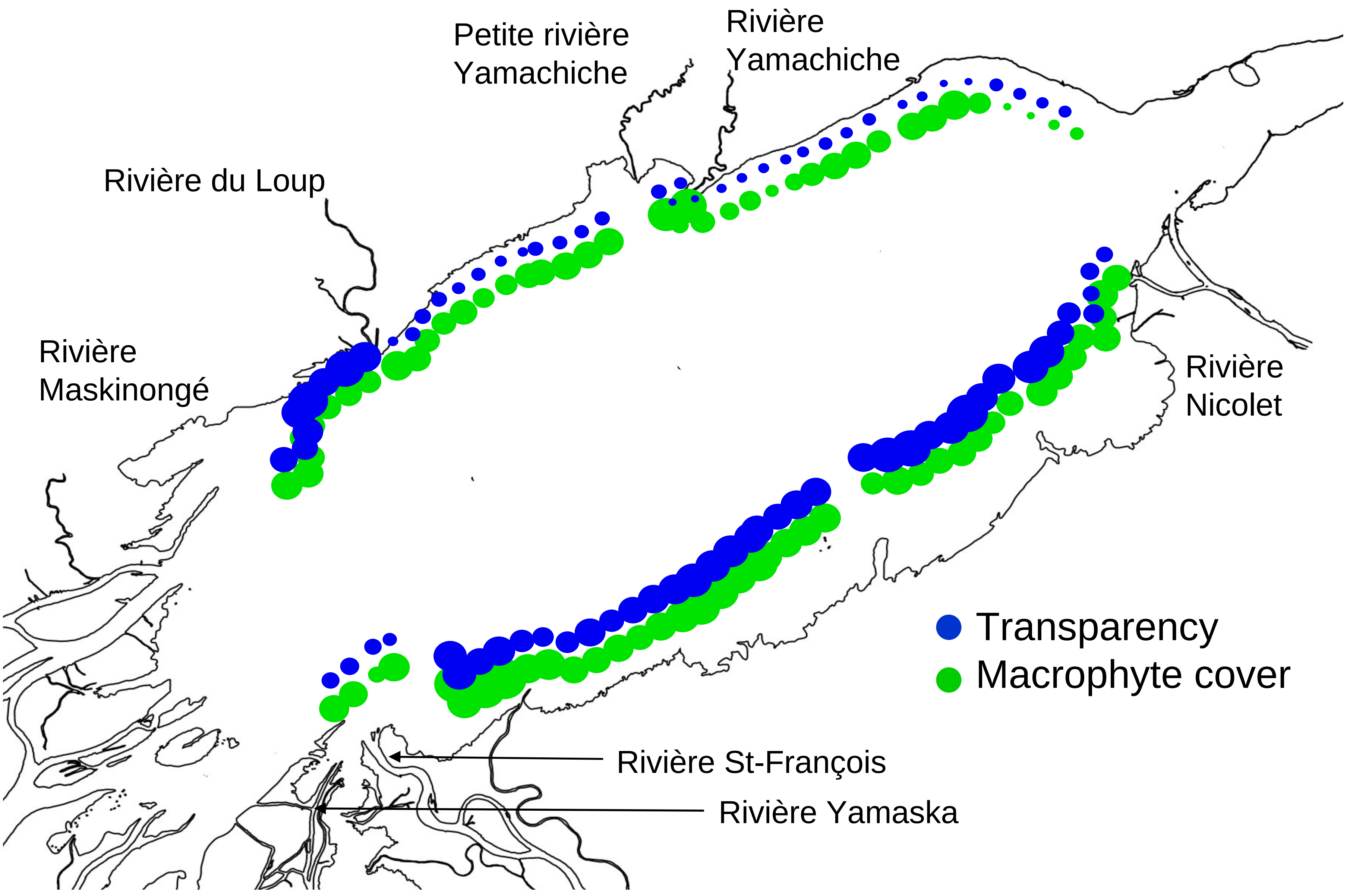
Water masses contrasting in transparency and color

North shore

Central navigation channel

South shore

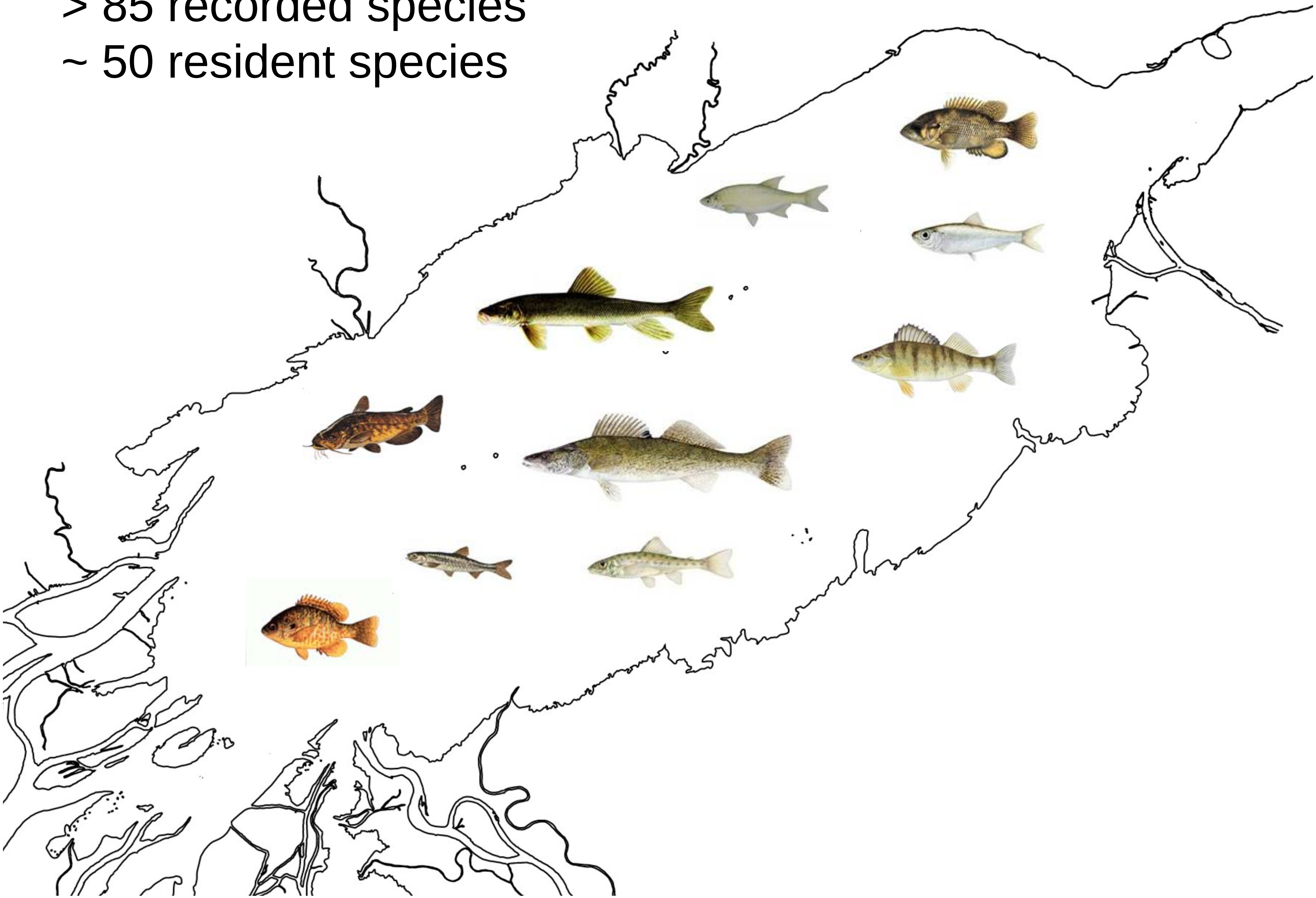
Spatial variation of transparency and macrophyte cover



Highly diverse fish community:

> 85 recorded species

~ 50 resident species

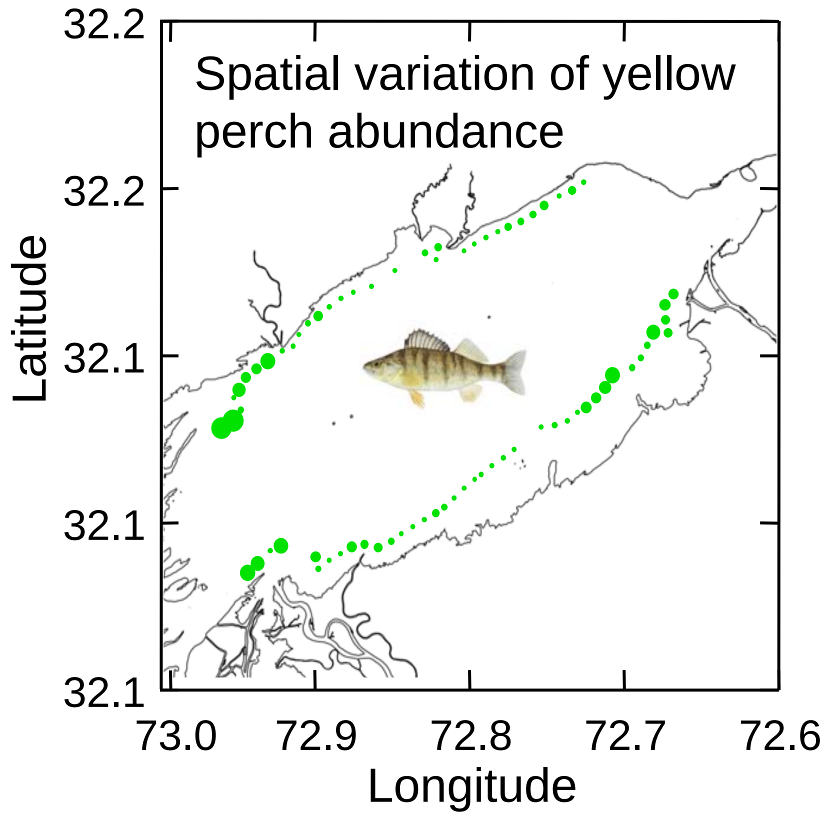


Why study yellow perch (*Perca fluviatilis*)?

Most abundant fish species in LSP

Major commercial and recreational fisheries in LSP and the Great Lakes/St Lawrence system

Shows marked spatial heterogeneity in LSP



Why study individual growth?

Critical component of fisheries production and yield

Influences mortality and fecundity

Quantifies ecological performance, thus providing a temporally-integrated measure of environmental quality as perceived by the organism

Links to theory: Do species distributions reflect spatial patterns in growth and mortality? (prediction: to maximize fitness, minimize the ratio mortality/growth; *Werner & Gilliam 1984*)

Main objective

Assess the influence of environmental variables and spatio-temporal variation on short-term growth of yellow perch in Lake St. Pierre

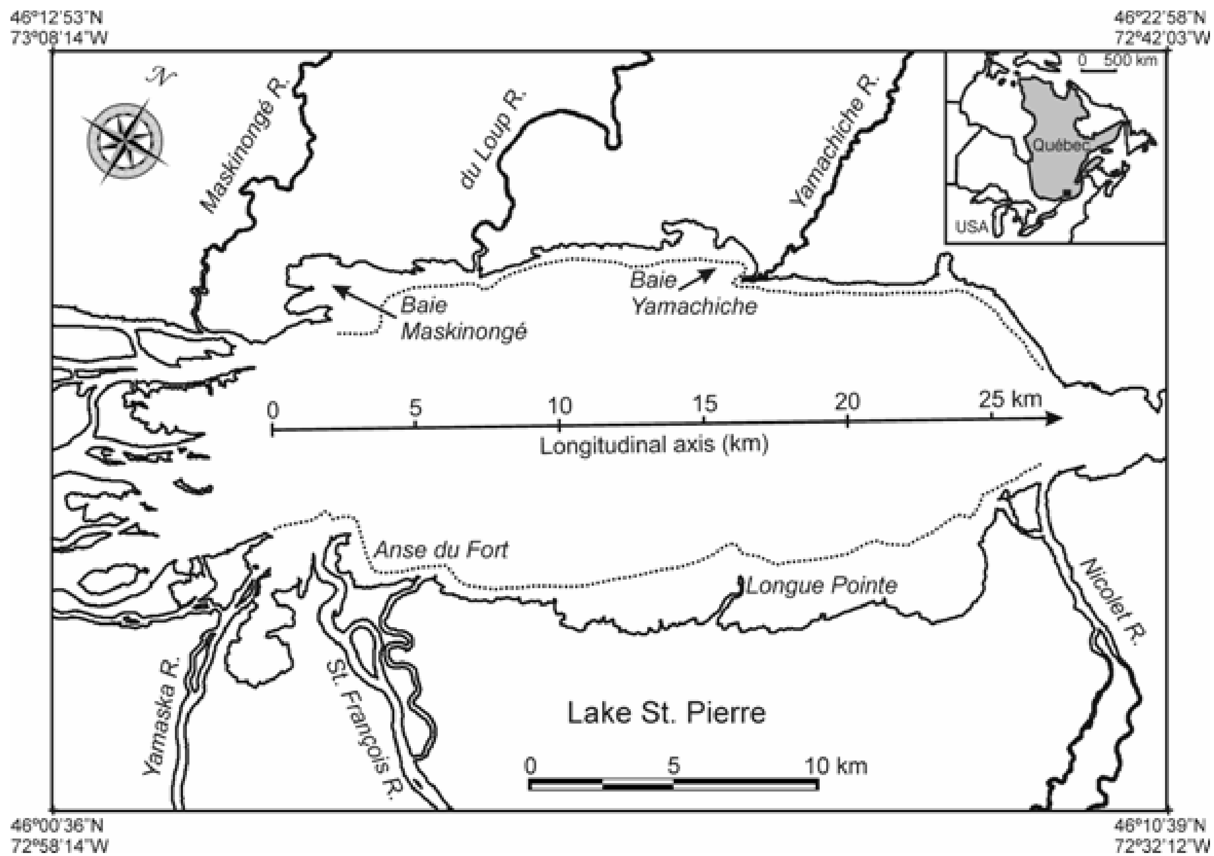
Methods

Electrofishing along littoral zone (<2.5 m depth) of northern and southern shorelines

Summer of 2003 and 2004

Date of capture coded as Julian day

Spatial position coded by reference to shore (north or south) and distance along a longitudinal axis

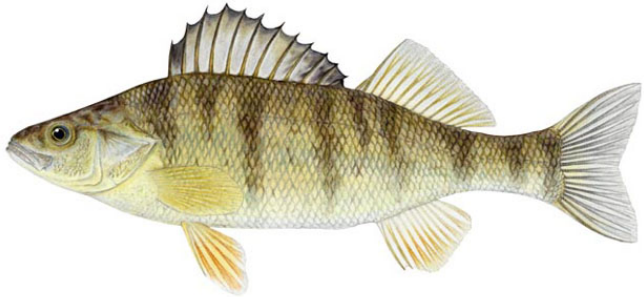


Local (capture site) measurement of habitat variables:

- Transparency
- Macrophyte cover
- Conductivity
- Substratum size

Lakewide measurement of environmental variables:

- Water level
- Water temperature



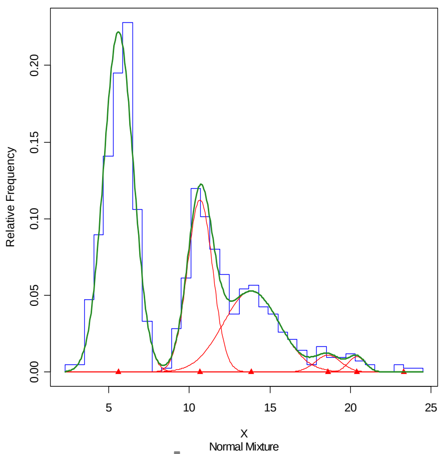
296 yellow perch
- 128 north shore
- 168 south shore

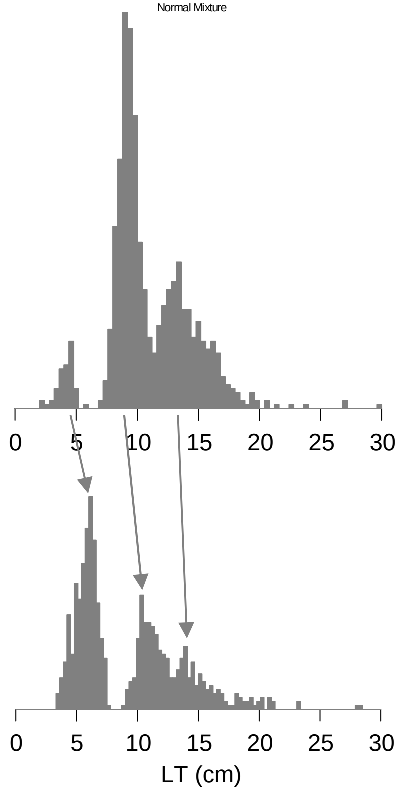
Measured and weighed
- Total length: 42 - 206 mm
- Age-class range: 0+ to 5+

Kept on dry ice and transferred to -80 ºC in laboratory

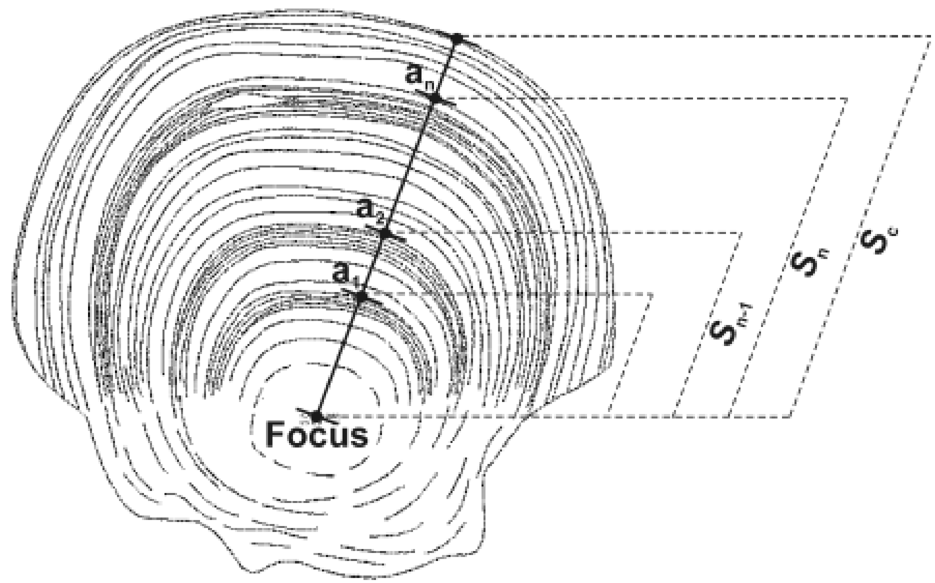
Nucleic acids extracted from white muscle tissue and quantified by spectrophotometry

Length-frequency distribution of cohorts





Annual growth increments from hard structures

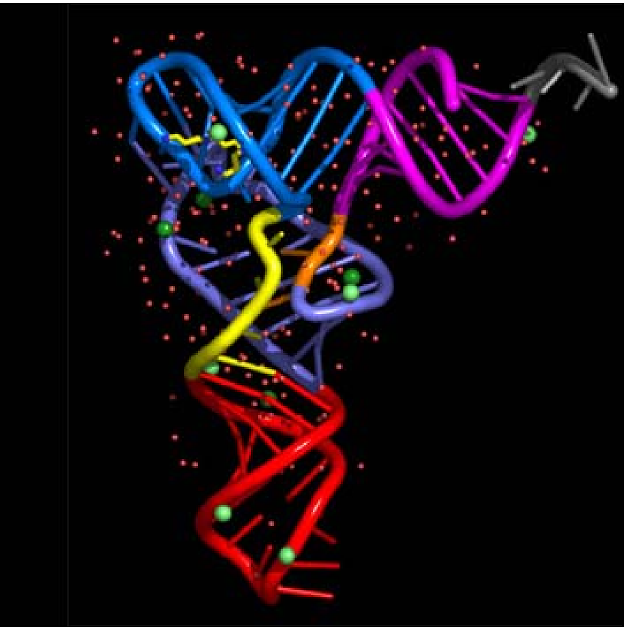


Conventional measures of growth

Integrate over extended time periods (months or years)

Do not reflect responses to short-term environmental fluctuations

Short-term growth index (STGI): RNA/DNA ratio



Cell content of RNA is related to the amount of protein synthesis and thus reflects recent growth and nutritional condition

DNA cell content remains fairly constant and serves to normalize the measured RNA

STGI responds rapidly to changes in food and temperature conditions

Provides an evaluation of short-term environmental influences on growth

Semi-parametric additive models

$$y_i = \beta_0 + \beta_1 x_{1i} + \ldots + \beta_p x_{pi} + f_1(z_{1i}) + \ldots + f_q(z_{qi}) + \varepsilon_i$$

Powerful tool for analyzing environmental influences

May include both parametric and non-parametric (smooth) terms in same model

Interactions between parametric and smooth terms are easily incorporated

Semi-parametric additive models

Retain advantages of multiple regression:

Simultaneous inclusion of several explanatory variables
Partialling out of effects to examine conditional relationships

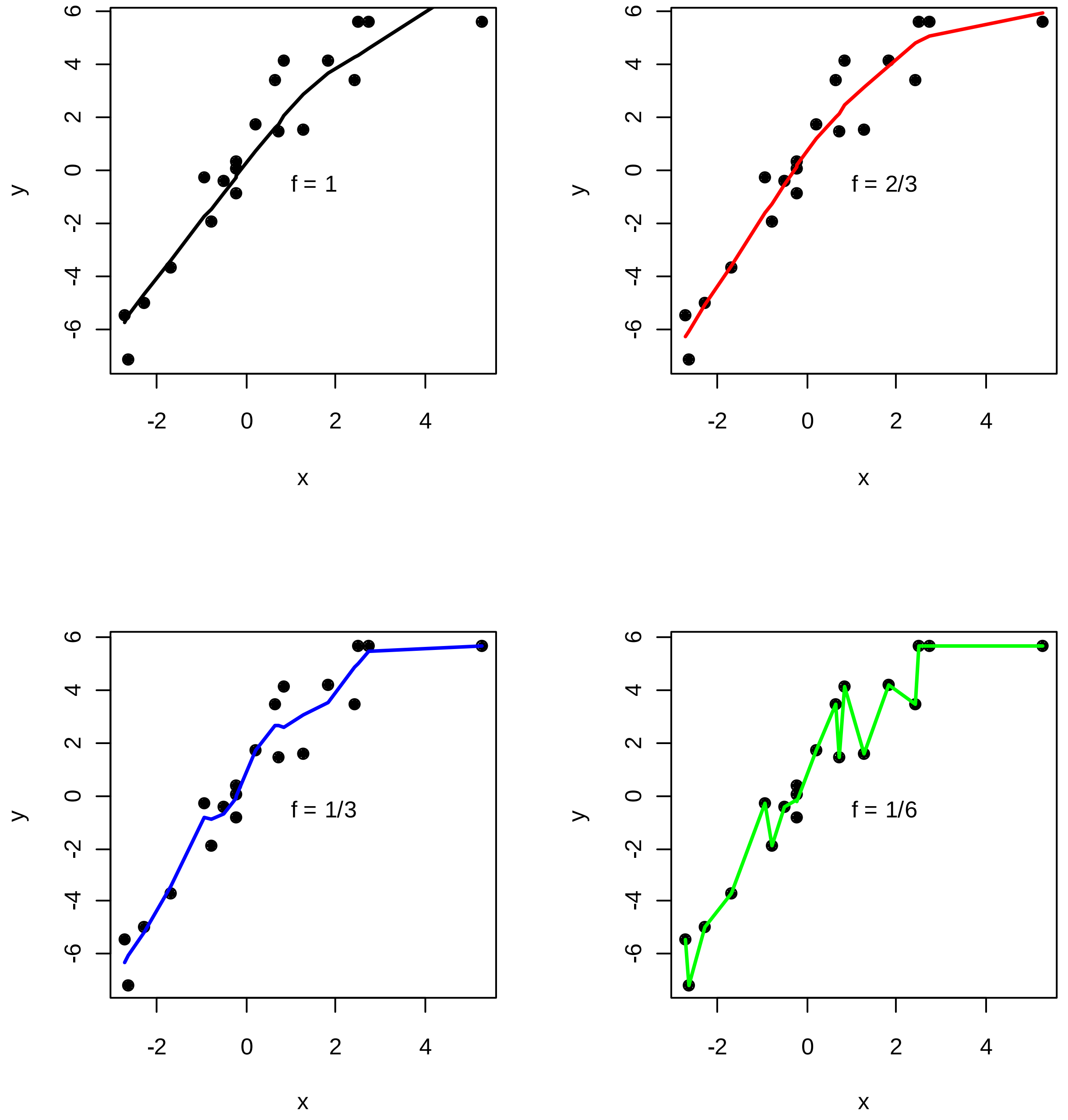
Additionally,

Allow for representation of complex functional relationships between response and explanatory variables by means of smooth functions, without strong assumptions about functional form

Shape of the smooths can be data-driven

Partial out unspecified influences that are spatially or temporally structured but not directly measured in the study, thus improving estimation of focal effects of main interest

How much smoothing is required?



Smoothing by generalized cross-validation

Penalized thin-plate regression splines used to represent the smooth terms

Smoothing parameters chosen to minimize the generalized cross-validation criterion, V_g (*mgcv* package for R; *Wood 2006*):

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

n = sample size
D = deviance
df = effective degrees of freedom of the model

Effect size for each independent variable quantified as:

$$effect\ size = \left(\frac{STGI_{\max} - STGI_{\min}}{STGI_{\min}} \right) 100$$

$STGI_{max}$, $STGI_{min}$: maximum and minimum predicted values of the short-term growth index over the observed range of the independent variable

Effect size reflects the maximum relative increase in $STGI$ (%) associated with changes in each independent variable

Results

Summary statistics for fish characteristics and abiotic variables used in the semi-parametric additive model

	Median	Minimum	Maximum
Fish characteristics (*N* = 296 fish)			
RNA/DNA ratio (STGI)	0.92	0.22	2.40
Body mass (g)	10.3	0.9	101.1
Abiotic variables (*N* = 34 sampling dates)			
Temperature (ºC)	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

Additive model with Gaussian errors

$$\ln(\textit{RNA/DNA ratio}_{\mathrm{i}}) = \beta_0 + \beta_1 \ln(\textit{body mass}_{\mathrm{i}}) + f_1(\textit{temperature}_{\mathrm{i}}) + f_2(\textit{water level}_{\mathrm{i}}) + f_3(\textit{date}_{\mathrm{i}}) + \beta_2\ (\textit{shore}_{\mathrm{i}}) + f_4(\textit{axis; north shore}_{\mathrm{i}}) + f_5(\textit{axis; south shore}_{\mathrm{i}}) + \varepsilon_{\mathrm{i}}$$

Sampling date and spatial coordinates included as predictors to adjust for temporal and spatial influences not directly quantified by the environmental variables

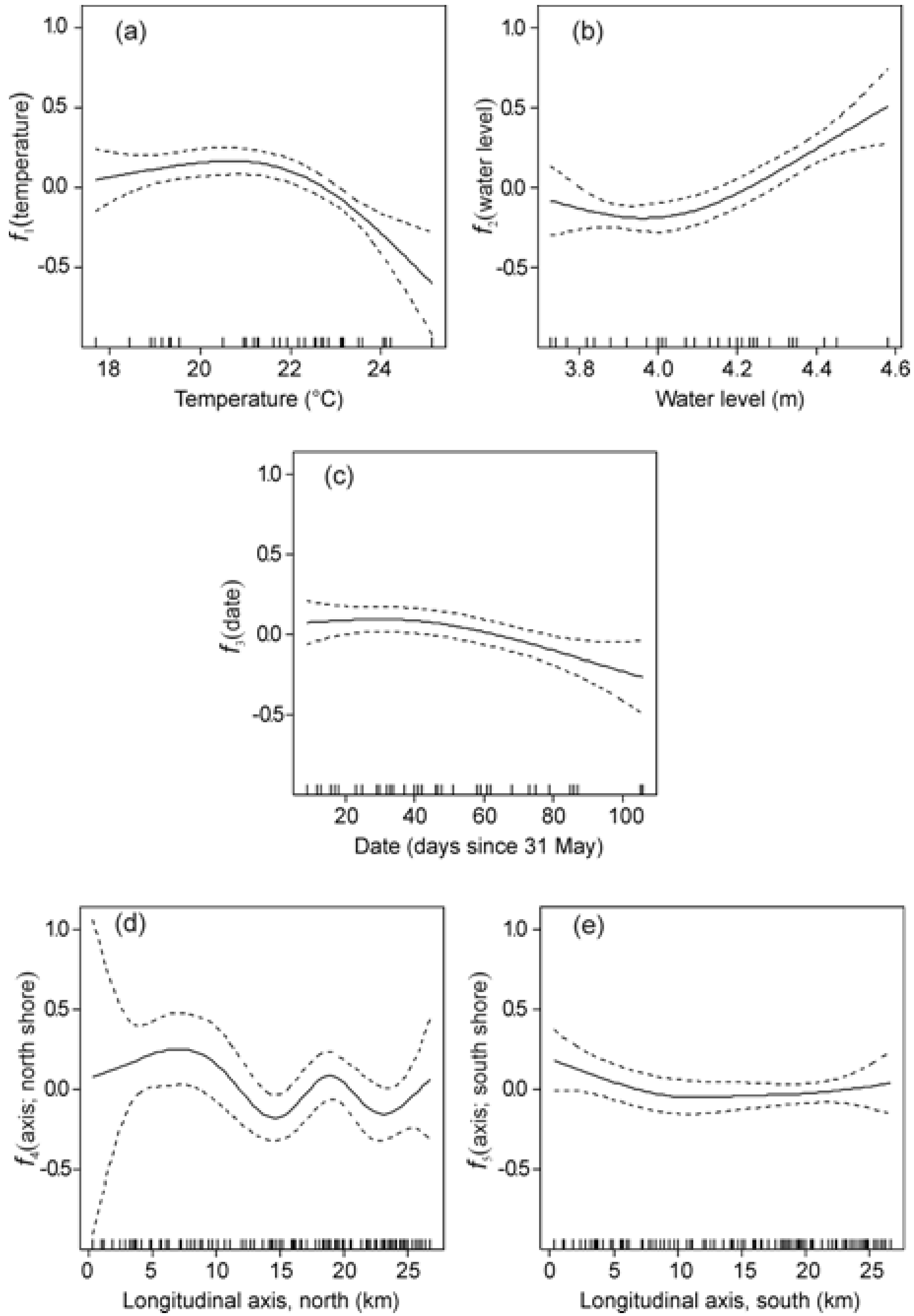
No influence of water transparency, macrophyte cover, or other local habitat variables on the STGI

No interaction between temperature and water level

No difference between years

Estimated coefficients and standard error for the parametric terms, and estimated degrees of freedom for the smooth (non-parametric) terms of the additive model. The model accounts for 41.2% of the deviance. $N = 296$ fish

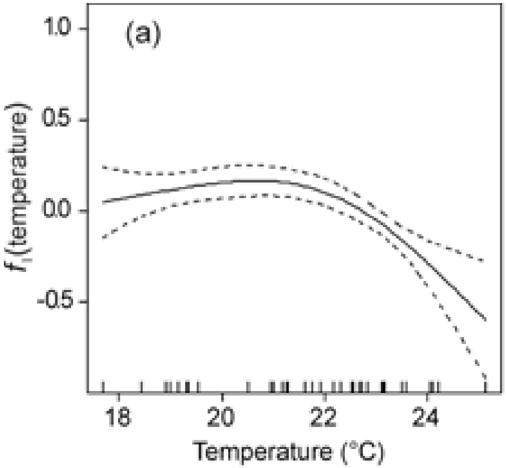
Variable	Parametric terms				
	Coefficient	Estimate	s.e.	P	Effect size (%)
Intercept	β_0	-0.395	0.066	<0.001	
Body mass	β_1	0.075	0.023	<0.001	43
Shore	β_2	0.104	0.051	0.045	11
	Non-parametric terms				
	Smooth	Estimated d.f.		P	Effect size (%)
Temperature	f_1	2.36		<0.001	115
Water level	f_2	2.54		<0.001	101
Date	f_3	1.92		0.020	44
Long. axis, north	f_4	5.57		0.003	54
Long. axis, south	f_5	2.32		0.221	n.s.



Environmental

Temporal

Spatial



Temperature

Observed maximum at 20.5 °C is consistent with thermal physiology of yellow perch

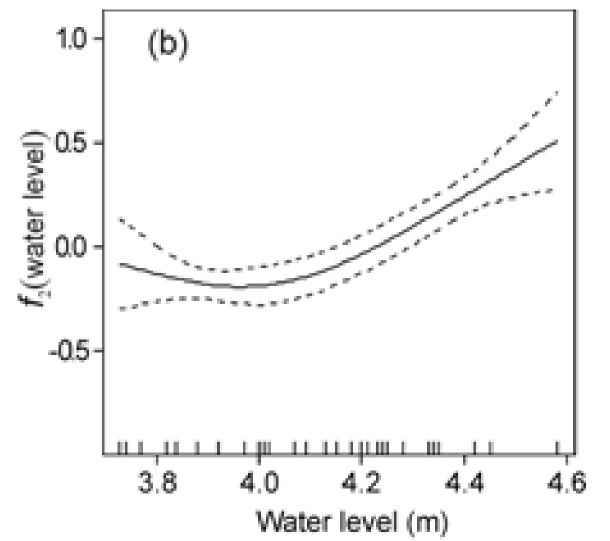
Optimal temperature (22 °C) for growth in Lake Monona, Wisconsin (*Neill and Magnuson 1974*)

Final temperature preferendum: 20.1-24.2 °C (*Coutant 1977; Jobling 1981*)

Maximum growth rate at 23 °C; sharp decline at higher temperatures in the field (*Kitchell et al. 1977*)

Fish in shallow fluvial lakes cannot avoid high surface temperatures by descending to thermally favourable habitats; thus, adverse temperature effects should be more apparent than in deeper lakes

Water level

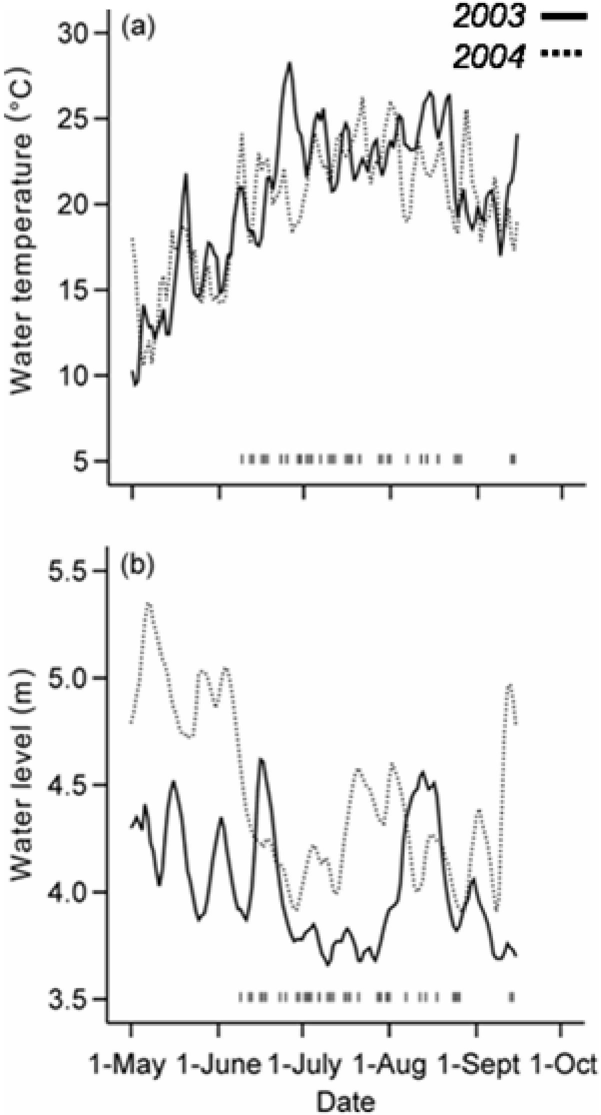


Lake area expansion ~15% of the total surface area; even greater proportional increase relative to the highly productive littoral area

As water level rises, littoral areas expand into the floodplain, rendering available food sources of terrestrial origin that enhance productivity (flood pulse concept)

Enhancement of biological production should be directly related to the increase in the surface area of the waterbody above baseline level

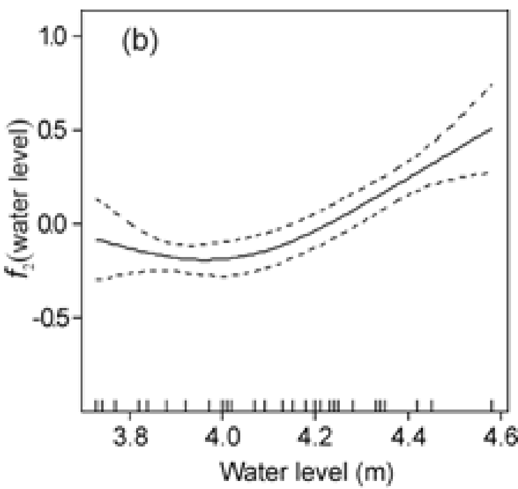
Variation in water temperature and water level

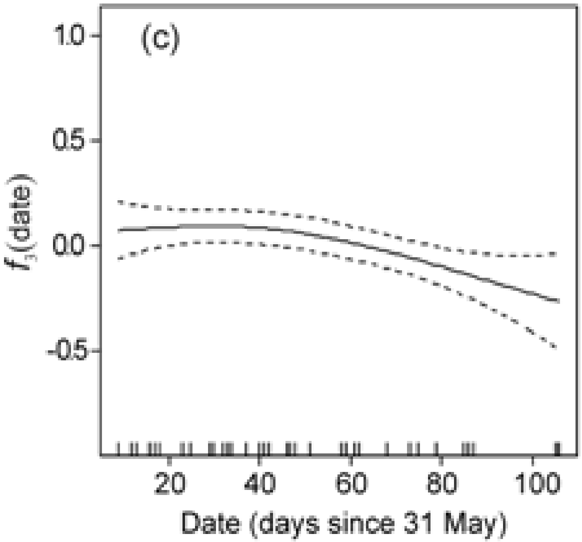


Yellow perch only grow at temperatures >13.5 °C

Temperatures over the study period always exceeded the lower thermal threshold for growth, possibly explaining the absence of interaction between temperature and water level

Periods of strong growth (water level >4 m) may be short-lived in some years





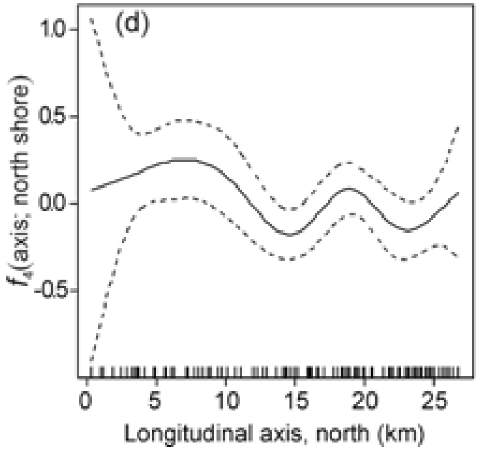
Temporal trend

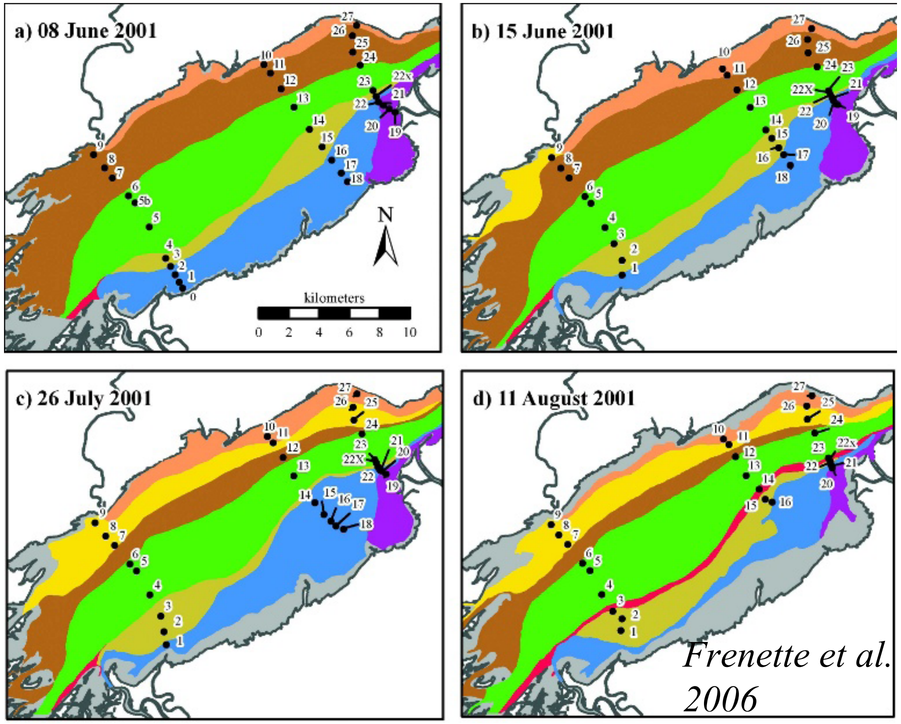
The observed decline in short-term growth is unrelated to sexual maturation

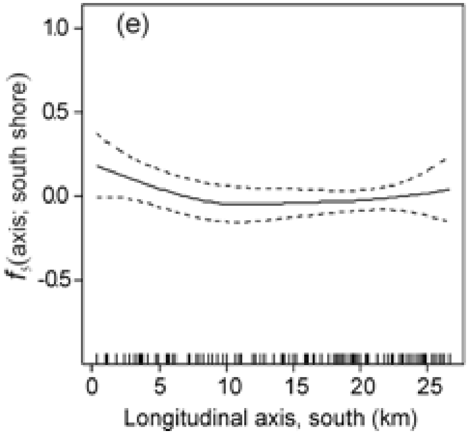
Seasonal changes in abiotic or biotic factors unrelated to water level and temperature may be responsible for decline in somatic growth

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

Spatial trends







The physical and chemical composition of water masses of LSP is more variable along the north shore than along the south shore

Properties of water masses can influence production and foraging success; exposure of fish to more differentiated water masses may therefore explain the greater variability of short-term growth on the north shore

Conclusions

Conclusions

Additive model analyses of RNA/DNA ratios (STGI) can provide:

Useful assessment of trends in fish growth in a dynamic, spatially heterogeneous environment

Insight into the ecological significance of environmental variation and the potential impact of long-term climatic changes on fish production

Short-term growth of yellow perch in LSP influenced by a combination of nonlinear effects

Effects of environmental variables (temperature and water level) greater than those of spatio-temporal variation or body mass

Conclusions

LSP behaves more like a floodplain ecosystem than a fast flowing river

The influence of water level on growth, as described by the flood pulse concept, has implications for the productivity of fluvial lakes similar to LSP

Effects of global warming can deliver a one-two punch to fish growth by shortening the periods combining favourable temperature and water level

Maintenance of hydrological regimes allowing sufficient growth for self-renewal of stocks may be critical to the long-term fate of the yellow perch fishery in the St. Lawrence River system