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The St. Lawrence River, Canada-USA : the Need for an Ecosystem-Level Understanding of Large Rivers*

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ABSTRACT

Although large rivers are important wildlife habitats and a valuable resource for potable water, transport, energy generation and waste disposal, they have received relatively little attention by limnologists. Successful management of these environments will require consideration of their unique properties as living systems. Using examples from the St. Lawrence River, we identify environmental pressures on large rivers that would greatly benefit from an integrated 'whole ecosystem' approach towards their understanding and management: hydraulic control, channel modification, contaminant discharge (industrial carrying capacity), eutrophication, climate change and community shifts, including the invasion of exotic species. The downstream reach of such environments, in particular the freshwater-saltwater transition zone (FSTZ), is a critical ecotone for the entire river system and is highly sensitive to each of these anthropogenic effects. The FSTZ integrates upstream and downstream processes, is one of the most biologically productive sections of the river, and is a prime site for monitoring fluvial and estuarine health.

Key words : estuary, fluvial ecosystem, production, river, St. Lawrence

INTRODUCTION

Throughout the course of civilization, large rivers have played a major role in transport, food and water supply, and human waste disposal. The pressure on these resources has greatly intensified over this century, but our ecological understanding of this most important class of freshwater environments remains poorly developed. In part this is because aquatic ecologists have traditionally been oriented towards lakes and have considered large rivers to be highly variable and difficult to study. It is also because large rivers have often been thought of more in engineering terms, as conduits for water and waste, rather than in terms of their true character as living systems. To meet the increasing demand for high quality in the water next century will require a more sophisticated, ecosystem-level understanding of

* This paper is dedicated to the memory of Professor R. Tsuda.

large river environments.

The development of the 'River Continuum Concept' some 20 years ago (VANNOTE *et al.,* 1980) provided a unifying whole-system perspective on flowing waters. By this concept, many of the biological characteristics of streams and rivers are seen to overlay the longitudinal gradients in their physical properties such as channel morphometry, discharge and temperature, and to change in a predictable fashion downstream ; for example, from detritus-based food-webs in the upper forested reaches grading into more autotrophic, periphyton-based systems where the river widens and becomes more exposed to light, culminating in the high-order lowermost reaches where planktonic processes become important. This concept has been modified in various ways over the last two decades. The 'Serial Discontinuity Concept' draws attention to the importance of dams and reservoirs along the river ecosystem (WARD and STANFORD, 1983) while the 'Flood Pulse Concept' emphasizes the critical role of seasonal flood events for riverine production and other community processes (JUNK *et al.,* 1989). More recently, THORP and DELONG (1994) have proposed an alternate 'Riverine Productivity Model' for large rivers, particularly those with constricted channels and limited floodplains, which places emphasis on local autochthonous production (phytoplankton, benthic algae, vascular plants and mosses) and on the direct inputs of carbon from the riparian zone (abscised leaves, particulate and dissolved organic carbon). Despite these many developments in ecological theory, flowing water research has tended to remain focused on low-order headwater streams. With only a few notable exceptions (*e.g.,* the Rhine Action Plan ; ADMIRAAL *et al.,* 1993), a holistic perspective has rarely been achieved in the management of the heavily impacted, downstream reaches of large river ecosystems.

The St. Lawrence River is one of North America's most important flowing water systems in terms of discharge as well as economic importance. In the 400 km section of the river that flows through southern Québec it supplies 3.2 million people in the province (46% of the population) with drinking water, provides a major transport artery into the interior of the continent, and is a key water source for much of the industry of the province. Yet in a recent review of river and stream ecosystems of Canada, the section on southern Québec is devoted exclusively to low order streams in the Laurentian mountain range to the north of the St. Lawrence River, affirming the author's conclusion that "there is still a tendency to seek small undisturbed streams for research sites rather than disturbed rivers that increasingly represent the 'normal' condition" (MACKAY, 1995).

The objective of this paper is to identify, by way of examples from the St. Lawrence River, environmental features that are central to an ecosystem-level understanding and long-term management of large river systems. A major synthesis document on the state of the St. Lawrence environment (SLC, 1996) collates much of the existing information on the river and is the most comprehensive attempt to date towards a whole-system perspective on the St. Lawrence environment. In the present paper we build on the SLC

(1996) document by focusing on key ecological processes and linkages that have previously received little attention. In particular, we present evidence that a specific downstream section, the freshwater-saltwater transition zone (FSTZ), is a critical ecotone for the entire river, is highly sensitive to upstream perturbation, and is a prime site for monitoring the long-term health of the St. Lawrence River and other large river ecosystems. We begin with an overview of the St. Lawrence ecosystem and a brief introduction to major features of the FSTZ. We then address a series of environmental issues for large rivers that would benefit from an ecosystem-level perspective, and conclude each section by considering potential impacts on the ecology of the St. Lawrence FSTZ.

SYSTEM OVERVIEW

The St. Lawrence River is one of the three largest rivers on the North American continent. It extends from the Laurentian Great Lakes to the Gulf of St. Lawrence (Fig. 1), draining a catchment of 1.6×10^6 km^2 that holds over 25% of the world's freshwater. The mean annual discharge at Québec City is 12,600 m^3 sec^{-1} (SLC 1996), with a total annual discharge of about 400 km^3 that constitutes the dominant input of freshwater into the Atlantic Ocean from the eastern seaboard of North America. The river system can be

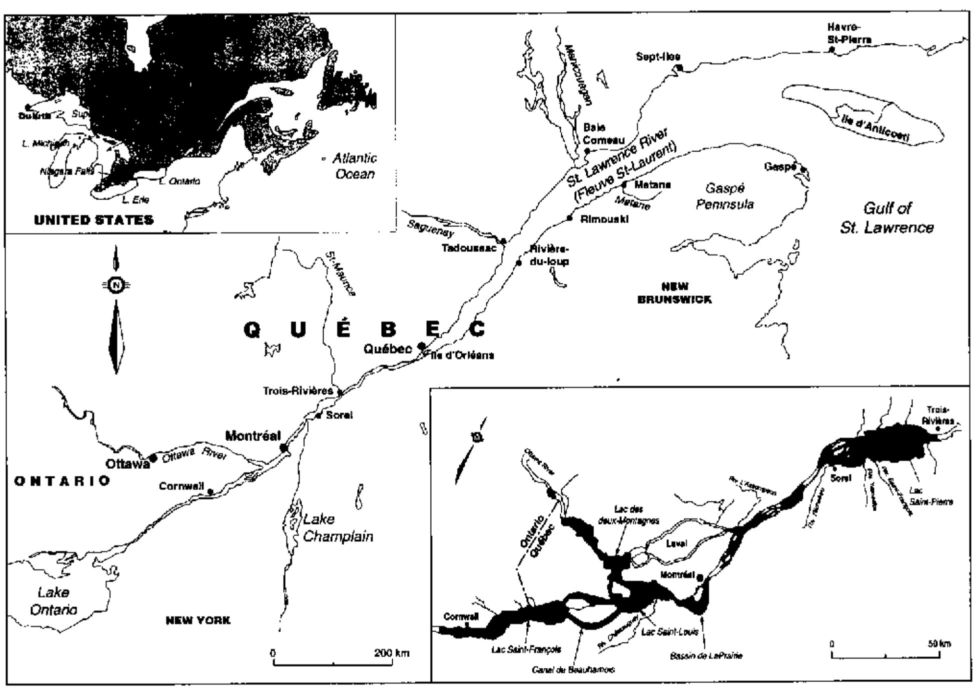

Fig. 1. Map of the St. Lawrence River ecosystem; the lower right panel shows the lakes of the fluvial section.

divided into four sections on the basis of its physical properties :
a) *Fluvial section.* This section flows 400 km through a highly industrialized corridor, from Kingston at the outlet of Lake Ontario to Pointe-du-Lac at the outlet of Lake Saint-Pierre. It passes through three shallow lakes : Lake Saint-Francois, Lake Saint-Louis (immediately upstream of Montréal) and Lake Saint-Pierre (immediately upstream of Trois-Rivières). Through much of this section there is a pronounced cross-channel zonation with brown, humic-stained water from the Ottawa River flowing beside the green, relatively clear water from the Great Lakes. The fluvial section has been extensively modified over the last 100 years for navigation and hydropower. There is a 68-m difference in height between Lake Ontario and Lake Saint-Pierre, but since the opening of the St. Lawrence Seaway in 1959 large ships have been able to traverse this reach via seven locks.
b) *Fluvial estuary (also referred to as the upper estuary).* This freshwater but tidal section runs 160 km from Lake Saint-Pierre to the eastern end of Île d'Orléans. The mean tidal amplitude near the end of this reach at Québec City is 4.1 m, rising to 5.8 m during spring tides. There is current reversal and strong mixing associated with the flooding tide, and this part of the river consequently lacks the distinct cross-channel gradients in water masses which are characteristic of the fluvial section. The combined ebb plus river currents can generate an instantaneous flow of 75,000 m^3 sec^{-1}.
c) *Upper estuary (also referred to as the middle estuary).* This highly turbid section extends 150 km from the eastern tip of Île d'Orléans to the mouth of the Saguenay River, with salinities in the range 0.5 to 25 psu. It has a complex bathymetry and strong tidal currents, and large amounts of sediment are exchanged with the marshes that border this section of the estuary (see below).
d) *Lower estuary (also referred to as the maritime estuary).* This 230-km stretch averages 42 km in width and ultimately discharges into the Gulf of St. Lawrence. The shoreline dynamics shift from tide-dominated to wave-dominated, with a resultant decreasing importance of tidal marshes and an increase in sand beaches.

FRESHWATER-SALTWATER TRANSITION ZONE (FSTZ)

The FSTZ is the dynamic frontal region where freshwater draining from the continent first mixes with saltwater (Table 1). In the Saint Lawrence River this region lies at the interface between the fluvial estuary and upper estuary sections (as described above) and is characterized by salinities in the range of 0.2–5 psu. As in other large river systems, the FSTZ has a number of distinct physical properties such as estuarine recirculation, semi-diurnal stratification and mixing associated with the tides, sediment entrapment and high turbidity. It is also a region with sharp gradients in biological properties (*e.g.*, the shift from planktonic to particle-based bacterial populations ; PAINCHAUD *et al.*, 1995) and food-web structure (*e.g.*, the localized importance of mysids in the herbivore community ; Table 1). It is a region

Table 1. Environmental characteristics of the St. Lawrence FSTZ and waters immediately upstream and downstream. The data are for the season of maximum fish larval development in the region (mid May), from VINCENT *et al.* (1996) and J. J. DODSON and W.F. VINCENT (unpublished).

Variable	Upstream	FSTZ	Downstream
Salinity (psu)	0.1	0.2-5	>2
Turbidity (NTU)	<10	30	<20
Bacteria (10^6 cells ml^{-1})	0.3	0.5	1.8
% attached bacteria	26	45	41
Chlorophyll *a*	High	Tidally variable	Low
(mg. m^{-3})	6	2-7	1
Mysids (per m^3)	0	6.6	3.1
Fish larvae (per m^3)			
Osmerus mordax	0.15	0.85	0.05
Microgadus tomcod	0	1.53	1.41

of elevated primary production and zooplankton biomass, and acts as a food-rich nursery site for fish populations, in particular Atlantic tomcod (*Microgadus tomcod*) and rainbow smelt (*Osmerus mordax*).

The FSTZ frontal system has been a major focus of biological research over the last 10 years, and information is now available on its larval fish ecology (DODSON *et al.,* 1989 ; DAUVIN and DODSON, 1990 ; LAPRISE and DODSON, 1990), zooplankton dynamics (LAPRISE and DODSON, 1994), bacterial and primary production (PAINCHAUD and THERRIAULT, 1989 ; VINCENT *et al.,* 1994, 1996), protozoan community structure (LOVEJOY *et al.,* 1993), heterotrophic and phototrophic picoplankton (PAINCHAUD and THERRIAULT, 1989 ; PAINCHAUD *et al.,* 1995 ; BERTRAND and VINCENT, 1994), and hydrodynamic effects on the microbial food-web (FRENETTE *et al.,* 1995).

An important supply of carbon, nutrients and energy for microbial processes in this region may be derived from the tidal marshes of the upper estuary, particularly during periods of peak grazing activity. During the autumn months each year, several hundred thousand snow geese stop over on their migration pathway from the Arctic to feed on plant roots in these marshes. This results in the disturbance and release of large amounts of organic-rich sediment. At Cape Tourmente, for example, the feeding activities of the migrating geese result in the export of 4,500 t of sediment per tidal cycle (LUCOTTE and D'ANGLEJAN, 1986 ; D'ANGLEJAN, 1990).

HYDRAULIC CONTROL

Discharge plays a pivotal role in the structure and functioning of large river ecosystems. According to an analysis by DYNESIUS and NILSSON (1994), the hydrological regime of 77% of the 139 largest rivers in North America and Eurasia has now been subject to modification by dams and other control structures with deleterious effects (including fragmentation) on habitat quality, land-water interactions and migration corridors for aquatic wildlife. Throughout the twentieth century, the St. Lawrence River has been extensively modified for navigation, flood control and hydroelectricity generation, but little consideration has been given to the ecological impacts of these changes.

Variability in discharge is an important feature that influences the productivity and biodiversity of flood plain environments. The Flood Pulse Concept draws attention to the dynamic character of the floodplain and the importance of periodic flooding for vegetation dynamics, nutrient exchange and access by fish and other animals to wetland habitats as well as to the main stem of the river (JUNK *et al.,* 1989). As with large rivers elsewhere throughout the developed world, the management regime of the St. Lawrence has striven towards reducing this variability. Since 1966 the discharge at the outlet of Lake Ontario has been controlled by Regulation Plan 1958-D to ensure safe navigation, a minimum water level at the port of Montréal, maximum hydroelectric capacity, and the elimination of extreme water levels that would affect human activities along the shores of Lake Ontario. The result is a modified annual discharge cycle which lacks certain features of the natural flow regime in rivers elsewhere in Québec, notably the pronounced winter low water and sudden massive flooding in the period late April-late May (SLC, 1996). This flooding is likely to have been especially important for ecological processes in the fluvial lakes, but is now substantially reduced ; for example, in Lake Saint-Francois over the period 1975-86 the monthly variations in mean water level were c. 0.04 m, with extreme deviations of only 0.2 m.

Further downstream in the fluvial section of the river there is less hydraulic control and greater seasonal variation in water level and flow (Fig. 2). At Lake Saint-Pierre during the spring flood, the water level rises by 1.3 m (in exceptional years by 3 m), and the lake increases in area by >40%, incorporating an additional 100 km^2 of floodplain. Although reduced in magnitude relative to the natural regime, this annual fluctuation is likely to be critical to the survival, productivity, zonation and species diversity of the rich biological communities which inhabit this lake and its surrounding environment. Lake Saint-Pierre is the most important section of the St. Lawrence River-Estuary-Gulf in terms of wetland area, and it is second only to Lac des Deux-Montagnes in terms of diversity of plant communities (GRATTON and DUBREUIL, 1990). These marshes in turn provide food and nesting sites for a diverse bird fauna, including a number of species that are rarely found elsewhere in Québec (SOCIETÉ ORNITHOLOGIQUE DU CENTRE DU QUÉBEC, 1988). Commercial fishing on the St. Lawrence fluvial section is centered on Lake Saint-Pierre (560-822 tonnes per annum over the period 1986-1992 ; SLC, 1996), and water level fluctuation is likely to be important in the food-web dynamics which sustain these harvested populations. Any future regulation of the St. Lawrence system must therefore take into account the central role of hydraulic variation in the ecology of this impor-

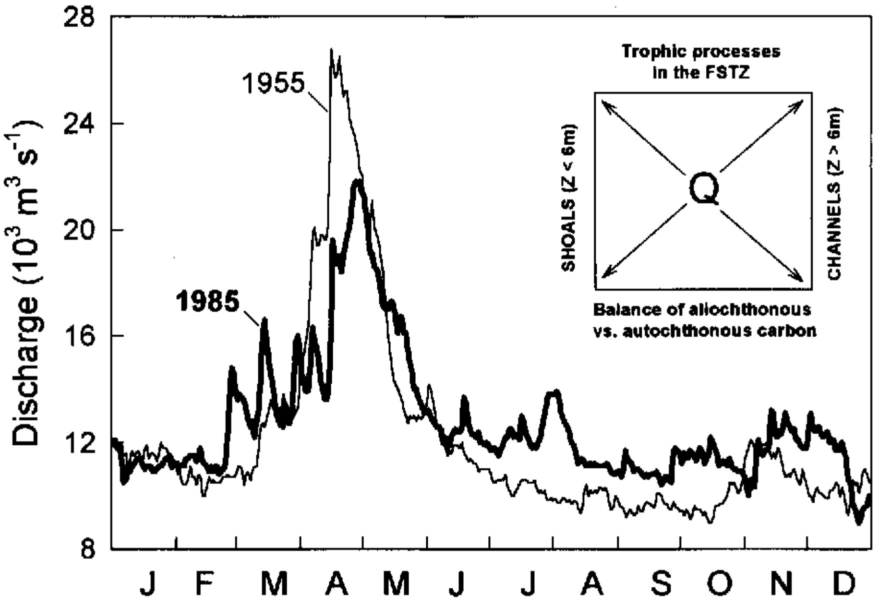

Fig. 2. Seasonal variation in discharge for two years in the St. Lawrence River at Québec City (unpublished data from the Ministère de l'environnement et de la faune du Québec). Insert : Discharge (Q) is a master variable affecting trophic processes in the FSTZ. For example, it affects the relative importance of autochthonous versus allochthonous production through its influence on DOC and POC transport into this frontal region, and it affects the balance of phytoplankton photosynthesis versus respiration in the water column by controlling the proportion of shallow (shoals) and deep (channel) environments. The euphotic depth in this region is typically < 1.5 m, and the average depth of mixing is 6 m (VINCENT *et al.,* 1996).

tant floodplain resource.

In the St. Lawrence River a number of key environmental variables are significantly correlated with discharge, including particulate organic matter (POM, positive relationship) and dissolved organic matter (DOM, negative relationship) (POCKLINGTON and TAN, 1987). These constituents are likely to play a major role in the heterotrophic microbial processes which contribute a large fraction of total metabolism in the St. Lawrence River (PAINCHAUD and THERRIAULT, 1989 ; VINCENT *et al.,* 1996) and large river ecosystems elsewhere (HOWARTH *et al.,* 1996).

Certain freshwater fish species have life cycles that are intimately linked to the hydrological cycle and flow variations in the St. Lawrence. For example, the year class strength for lake sturgeon (*Acipenser fulvescens*) in the river appears to be strongly determined by hydrological conditions in June, the time of year when the larvae drift from their spawning grounds and begin exogenous feeding (NILO *et al.,* 1997).

Discharge also has a decisive influence on the estuarine environment into which a river discharges. In San Francisco Bay (California, USA), the position of the 2-psu isohaline within the upper estuary (*i.e.*, the FSTZ) is a correlate of discharge and a sensitive index of many biological variables including the annual phytoplankton production, benthic macroinvertebrate density, mysid population abundance, and larval fish survival (JASSBY *et al.*, 1995). Similar effects are likely to operate within the FSTZ of the St. Lawrence River. We surmise that discharge influences not only the flux of autochthonous and allochthonous production in the FSTZ, but also the proportion of shallow versus deep water environments and thus the average water column balance of photosynthesis and respiration in this turbid, optically deep system (Fig. 2).

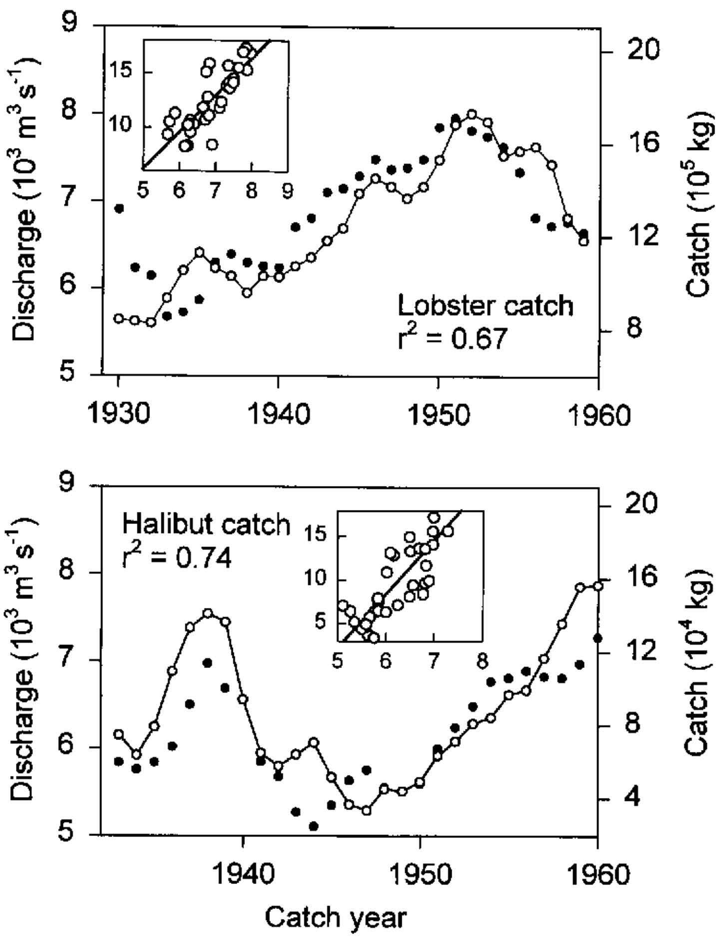

Fig. 3. Relationship between estuarine biota and discharge. The data for lobster or halibut are the reported catches from the Gulf of St. Lawrence (solid line with open circles). The discharge data (closed circles) are for the St. Lawrence River lagged by several years to account for growth from the larval stage to adult. The data have been replotted from SUTCLIFFE (1973) ; the inserts show the correlation between annual catches (in 10^5 kg, y-axis) and lagged discharge (in 10^3 m^3 sec^{-1}, x-axis).

There is evidence that discharge influences certain biological variables in the downstream, marine environments of the St. Lawrence ecosystem. SUTCLIFFE (1972) found a strong positive correlation between the lobster and halibut catch in Québec (mostly from the Gulf of St. Lawrence) and the mean annual discharge of the St. Lawrence which he attributed to the influence of freshwater flow on thermohaline circulation, upwelling and nutrient supply in the Gulf. He subsequently refined these observations by showing that the catch of halibut and lobster was highly correlated with the discharge during those months in which the larvae pass through critical life stages (Fig. 3). Peaks in freshwater discharge of the St. Lawrence River can also exert a strong influence on mesoscale circulation and the distribution of algal blooms in the lower St. Lawrence Estuary (SAVENKOV *et al.,* 1997).

CHANNEL REGULATION AND SEDIMENTS

Extensive dredging and other channel modifications have been a long-standing feature of human activities in the St. Lawrence and have been considered almost entirely in terms of the navigation requirements for the river. Some of the larger works include : a 25-km long ship canal (Canal de Beauharnois) built at the outlet of Lake Saint-Francois between 1930 and 1932 ; the creation of islands in the river at Montréal for Expo '67 ; and dredging throughout the system to maintain a 8–12 m deep ship channel from Lake Ontario to the sea. Dredging is also underway to remove contaminated sediments in some sections of the river.

Channel alignment and deepening is a typical feature of management strategies for large river ecosystems, but the trade-off is generally a substantial change in hydraulic gradients and unpredicted shifts in the pattern of bed erosion and deposition. Careful GIS mapping of sediments in the St. Lawrence River between Montréal and Sorel has revealed major changes over the period from 1848 to the present (LAPOINTE, 1994). In particular the concentration of flow in the main ship channel appears to have led to deposition of between 0.5 and 1 m of new sediment over wide areas, well away from the channel. In one part of the fluvial section of the river (the central channel west of Saint-Ours) this bed-aggradation rate has averaged 1.5 cm yr^{-1} between 1945 and 1988 (total accumulation of 0.6 m). These sediments contain the legacy of severe contamination earlier this century, and their subsequent mobilization is therefore of concern for the entire St. Lawrence ecosystem.

In certain parts of the world, considerable funds are now allocated towards the process of 'renaturalization' of heavily modified streams and rivers. For example, the Danube River in Europe has been subjected to large-scale hydraulic modification for more than 100 years. All the meanders have been cut off from certain reaches thereby shortening the channel by c. 20% and increasing the hydraulic gradient. This increase has led to more rapid erosion and a lowering of the river by 2.5 m in some places, with the concomitant results of a lowering of the water table and loss of wetland habitat. The German government has allocated 100 million DM for the rehabilitation of a 160-km stretch of the Danube involving re-adjustment of water levels, re-activation of old meanders and the retention of the straight-channel sections for flood control. This trend towards renaturalization has been strengthened by environmental laws in most of the German states (LARSEN, 1995). Although the St. Lawrence River system has not been subject to the severe level of modification experienced by some European rivers, this more advanced perspective in environmental engineering is now being directed towards certain tributaries; for example, the concrete embankments of Rivière Saint-Charles at Québec City are now being removed.

The effects of dredging and other channel modifications are likely to extend well downstream, ultimately to the receiving waters of the estuary. Sediment input into the FSTZ of the St. Lawrence River is a critical element of its ecology affecting underwater light and photosynthesis, the flux of allochthonous carbon, and the presence of physical substrates for bacterial attachment and growth (Table 1; PAINCHAUD *et al.*, 1995). Recent evidence also indicates that larval fish growth rates are positively correlated with sediment concentration in the transition zone, with effects beyond those simply associated with food availability (P. SIROIS and J. J. DODSON, unpublished). Changes in the timing, magnitude and quality of sediment input to this region may therefore have a strong influence on food-web processes at several trophic levels.

EUTROPHICATION

Excess nutrient input, algal blooms and oxygen depletion have created major water quality problems in many large European rivers and in some flowing water systems in North America. In the Seine River in France, respiration by the phytoplankton during algal blooms tips the precarious balance of oxygen gains and losses towards deoxygenation, and in some years has resulted in complete water column anoxia (GARNIER *et al.*, 1991). Deoxygenation is unlikely to be a problem in the fast-flowing St. Lawrence River, particularly in the downstream freshwater section where the river plus tidal currents ensure vigorous mixing of the water column. Furthermore, the background heterotrophic respiration by bacteria is also much less than in European rivers that are subjected to a much greater degree of habitation and organic pollution. Changes in phytoplankton biomass as well as species composition may be of concern in large rivers if they lead to blooms that create difficulties for water treatment or to shifts towards algal species such as cyanobacteria that cannot be readily utilized as a food source by zooplankton or benthic animals in the river. Although planktonic chlorophyll a levels are generally low throughout the St. Lawrence system, the development of noxious growths of periphyton may be a problem in some tributaries, for example, in response to nutrient-rich agricultural run-off.

For rivers fed by headwater lakes such as the St. Lawrence, consideration must also be given to changes in the water quality of the lacustrine environment. There is evidence of change in the nutrient concentrations (decreasing total phosphorus) of the source waters in Lake Ontario, but no long-term data sets appear to be available for the water column in downstream reaches of the river. Sediment analyses of the St. Lawrence fluvial lakes indicate higher algal deposition in the 1960s than before the mid 50s or after 1975 (CARIGNON *et al.*, 1994).

The advective input of phytoplankton into the FSTZ appears to be a major source of organic carbon for food-web processes in this region. For the period May-July, the export of phytoplankton carbon by the river into the FSTZ is estimated to be equivalent to 20–30% of the carbon flux associated with *in situ* photosynthesis and bacterial production (VINCENT *et al.*, 1996). The species composition of the river nanoplankton and its suitability as a food source for herbivores is therefore important for the FSTZ food-web, and is likely to be modified by changes in nutrient status of the upstream environment.

CONTAMINANTS AND FOOD WEB PROCESSES

There has been an increasing research effort towards measuring the level of contamination of biotic and abiotic components of the St. Lawrence River ecosystem. Up-to-date records are now available for trace metals and many organic contaminants in the water, sediments, plants and animal species ranging from molluscs to red-winged black birds, snapping turtles and whales (BISHOP *et al.*, 1995 ; BONIN *et al.*, 1995 ; MUIR *et al.*, 1996). These records have been important in identifying the pervasive nature of contamination throughout the entire river system, the sites of biological concentration (*e.g.*, macrophyte stands ; RICHARD *et al.*, 1997), the sites of discharge (*e.g.*, urban effluents from the City of Montreal ; PHAM and PROULX, 1997) and for defining temporal and spatial trends. These findings have in turn allowed specific management strategies to be defined or subsequently monitored ; for example, the analysis of sediments from Lake St. Louis shows a general reduction in contamination in response to improved management regimes, although the levels are still well above the pre-industrial background (Table 2). Such analyses also highlight the long-term legacy of pollution contained within the sediments which could be remobilized and transferred to other parts of the river ecosystem by inadvertent actions. At Cornwall, for example, contaminated sediment is being removed from the St. Lawrence River by dredging ; *in situ* assays with trout have shown an ecotoxicological response to sediment resuspension at that site (OTTO *et al.*, 1996), providing strong support for the use of containment walls that have been constructed to isolate the effects from other parts of the river.

Although the contaminant data from the St. Lawrence has obvious utility for management decisions, there is an insufficient functional understanding of what these measurements mean at an ecosystem level. For example, little is known about how the contaminants are taken up, processed and degraded,

Table 2. Contamination of sediments in Lac Saint-Louis, St. Lawrence River. The data are compiled from the text and Fig. 6 of CARIGNAN *et al.* (1994). Pre-industrial values are for the bottom 35–45 cm of a sediment core, dated at >130 years before present, containing 1.1% organic carbon. The values are in ppm (trace metals) or ppb (organic contaminants).

Contaminant	Pre-industrial	Max. during the 1960s	1990
Trace metals			
Cd	0.15	3.5	1
Cr	62	140	120
Cu	17	70	48
Ni	32	70	60
Pb	15	72	38
Zn	78	750	260
Organic contaminants			
PCB # 118	0	10	2
Mirex	0	0.8	0.1
DDD	0	8*	0.5

* Higher values of DDD (up to 13 ppb) were recorded in 1950s sediments.

or what their combined effects might be on the biota and food-web relations. Such information would help establish the limits of tolerance and the self-purification ability of the St. Lawrence, and thus its industrial carrying capacity.

A major impediment to a full understanding of the pathways and effects of contaminants in the St. Lawrence is the lack of information about food-web relationships and biogeochemical cycling processes in this system. Even for the base of the food-web, our understanding of *in situ* production processes is still rudimentary. Zooplankon populations are likely to be controlled by hydraulic residence time (PACE *et al.*, 1992), but little is known about the St. Lawrence in this regard. Large rivers are sometimes thought of as heterotrophic systems (HOWARTH *et al.*, 1996) but autotrophs achieve high biomass concentrations and are also likely to play a major role in riverine food-web processes (THORP and DELONG, 1994 ; VINCENT *et al.*, 1996). As emphasized by REYNOLDS (1995), the storage zones of rivers such as slow-flowing side-channels and lakes are likely to be important sites for maintaining the stocks and supporting the growth of river phytoplankton. The most detailed seasonal study of St. Lawrence River phytoplankton investigated a 250-km reach of the river at several times of the year and observed a gradual increase in algal biomass with distance downstream accompanied by changes in species composition and size structure (HUDON *et al.*, 1996). Further information of this sort is required throughout the St. Lawrence ecosystem, in combination with measurements of rate variables such as phytoplankton photosynthesis.

Our knowledge of microheterotrophic processes in large rivers is especially poor and will require a greatly improved level of understanding for ecosystem-level management of these environments. Microbial communities are likely to play a major role in the biological flux of materials and energy in the St. Lawrence ecosystem, but little is known about microbial food-web structure and dynamics in the freshwater sections of the river. In one of the few acknowledgments of the role of microbial processes in this system, VANIER *et al.* (1996) point to microbial dechlorination as one of the factors explaining the fate of PCB congeners in the sediments of the St. Lawrence River. This type of information is essential towards addressing the question of how well the microbiota can process and de-toxify these materials.

On the issue of riverine contamination, the FSTZ again provides a prime site for environmental monitoring, for several reasons. First, this section of the river lies downstream of the industrial and urban corridor and thus experiences the cumulative impact of the various effluents. Second, the FSTZ is characterized by a prolonged residence time of biota (DODSON *et al.*, 1989), thus increasing the probability of contaminant transfer and bioconcentration at higher trophic levels. Third, it is a biologically productive region for organisms from the estuarine as well as fluvial sections of the ecosystem, and is thus a critical ecotone to protect. PCBs may be concentrating within the food chain of this region; for example, GAGNON *et al.* (1990) observed PCB accumulation in the macrozooplankton and at all fish life-history stages. It is possible that the sediment exchange with the tidal marshes acts as a pumping mechanism for PCBs and other contaminants, prolonging their residence in the system, and increasing the likelihood of transfer to other biota such as the snow geese that aggregate and feed in large numbers in these marshes in spring and fall.

CHANGES IN COMMUNITY STRUCTURE

Partly as a result of physical and chemical modifications of their environment, large river ecosystems are also subject to major perturbations in biological community structure. Certain species are reduced to low population densities or even extinction by human activities in the river and its surrounding catchments. In addition, new species are introduced, for example though ship ballast water or by deliberate transfers from other parts of the world. The biota of the St-Lawrence River provides many examples of species declines as well as exotic invaders, changes that are likely to have far reaching impacts on ecosystem structure and dynamics.

The physical alterations occurring in the St. Lawrence River from the Lachine rapids to the middle estuary have strongly affected its fish community (ROBITAILLE *et al.*, 1987, 1988). Catches of the anadromous striped bass (*Morone saxatalis*) declined in both estuarine and freshwaters between 1954 and 1960. The last commercial captures of striped bass were recorded in 1966 and, apart from the occasional capture of one or two specimens from time to time, the species has been extirpated. American shad (*Alosa sapidissima*) also declined dramatically from 1971 to 1986 as revealed by an experimental fishery conducted by the Québec Aquarium on the south shore of the St. Lawrence River at St. Nicholas. The fishery has captured no more than a dozen shad annually since 1981 whereas, prior to this date, thousands were captured annually. Commercial catches of rainbow smelt (*Osmerus mordax*), whitefish (*Coregonus clupeaformis*) and Atlantic sturgeon (*Acipenser oxyrhynchus*) all collapsed in 1967. Although the Québec Aquarium's experimental fishery has indicated an increase in whitefish abundance beginning in 1976, and commercial catches of sturgeon have also been on the increase in recent years, there is no evidence of a parallel recovery in the rainbow smelt populations (Fig. 4). These several examples serve to illustrate the major changes occurring in fish community structure since the 1950s. Changes of similar importance are likely to have occurred

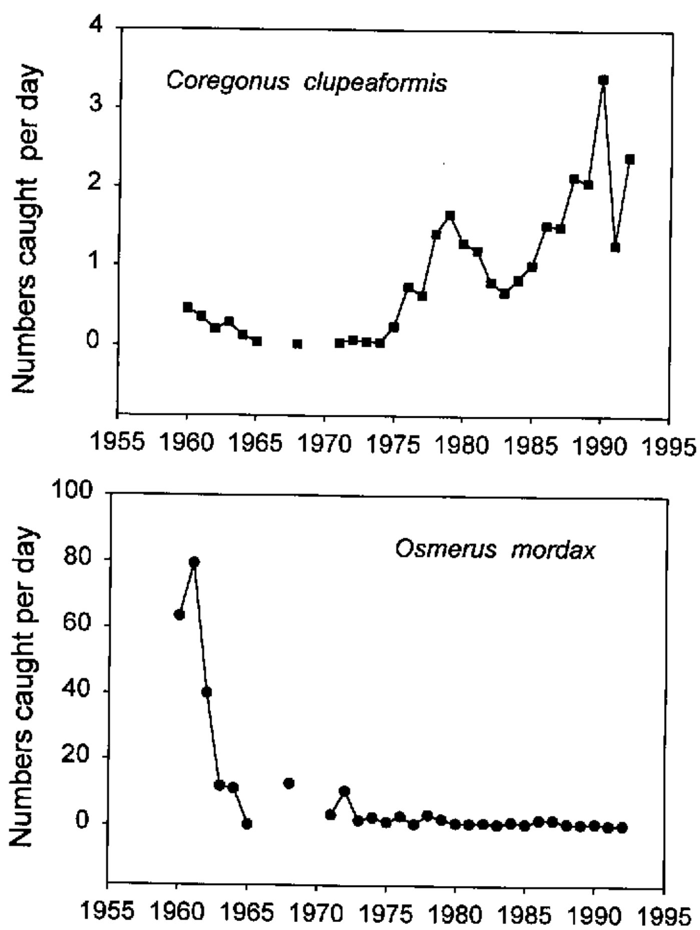

Fig. 4. Average daily catches of two fish species in an experimental fishery near Québec City for the period May-October each year. Unpublished data from the Québec Aquarium.

in the benthic and pelagic invertebrate communities of the region, with alterations of the flow of carbon and energy throughout the river's trophic network.

The St. Lawrence River has a long history of invasion by exotic plants and animals. Some 140 invading species have now been documented in the St. Lawrence-Great Lakes system, and they occupy every trophic level. The rate of invasion accelerated with construction of the St. Lawrence Seaway which allowed the transfer of biota by ship's ballast water as well as via improved migration pathways; about one third of the known invaders arrived after the opening of the Seaway (MILLS *et al.,* 1993).

The invasion of exotic weed species into large river ecosystems has the potential to radically alter their plant community structure, with effects on habitat quality for associated animal communities. For example, the invasion of purple loosestrife (*Lythrum salicaria*) last century has substantially influenced wetland plant communities in many parts of the St. Lawrence River system. This perennial weed species produces up to 3 million seeds per plant, also reproduces by way of new shoots from root buds, and can outcompete other wetland species (MAL *et al.,* 1997). As a result, purple loosestrife displaces the native flora, ultimately producing monospecific stands that have reduced habitat value for water fowl and other marsh animals. Its colonization and dominance is especially favoured by extremely low water levels (HUDON, 1997).

A recent animal invasion of particular concern is the arrival of the Eurasian mussels *Dreissena polymorpha* and *D. bugensis* into the St. Lawrence-Great Lakes system in the early 1990s. At some sites in the river, these organisms have caused up to 100% mortality of the native unionid mussels which they colonize and then overgrow (RICCIARDI *et al.,* 1996). This prolific growth can result in increased substrate heterogeneity and biodeposition, which in parts of the St. Lawrence River has led to a 2- to 8-fold increase in macroinvertebrate densities (RICCIARDI *et al.,* 1997). These efficient filter-feeding invertebrates are also having a major impact on seston concentrations in the St. Lawrence-Great Lakes system (MELLINA *et al.,* 1995). When zebra mussels became abundant in the Hudson River in 1992 they caused a 80-90% decline in phytoplankton biomass (CARACO *et al.,* 1997) and a >70% decline in zooplankton biomass (PACE *et al.,* 1998). The latter effect was mostly due to their predation on microzooplankton such as tintinnids, rotifers and nauplii, and there was no evidence of their impact on larger zooplankton (copepods) or planktivorous fish.

Zebra mussels are known to bio-accumulate contaminants, resulting in elevated concentrations of organic pesticides and PCBs that can be passed to consumers such as waterfowl (MACISAAC, 1996). Another exotic species, the round goby (*Neogobius melanostomus*), has been spreading rapidly in the St. Lawrence-Great Lakes system since the 1990s, and unlike most other fish in the system, this species feeds heavily on zebra mussels. These interacting effects of invasion increase the likelihood of enhanced bioaccumulation of contaminants up the food chain via goby predators (RICCIARDI, pers. comm.).

The mussel invasion may also be having a substantial influence on the food-web structure in the St. Lawrence FSTZ. *Dreissena* larvae were not recorded in our June cruises in 1991 and 1992, but in June 1995 they were among the dominants in the metazoan plankton, with concentrations peaking at 293,227 per m^3 in freshwater and declining by a factor of 10 at 5 psu salinity (DODSON and VINCENT, unpublished data). These species do not appear to be a prey item for the larval fish and could therefore deflect the flow of carbon and energy away from this consumer pathway. Changes in biotic particle export from the Great Lakes caused by Dreissena might also impact on downstream processes, including those in the FSTZ.

CLIMATE CHANGE

Large rivers are likely to be highly responsive to climate change, in particular through shifts in the water balance of their catchments and thus hydrology. As noted above, discharge is a pivotal variable that has a wide-ranging influence throughout the system, with an especially strong effect on FSTZ position and dynamics. Indirect effects may operate through changes in nutrient regeneration and export. For example, climate-related changes in temperature and water balance are likely to affect the export of DOC from catchment vegetation and soils to the river, thereby modifying the flow of organic carbon to the FSTZ.

The river margin is another ecotone that is also likely to respond strongly to climate change. Studies are currently underway at a series of floodplain sites in a north-south gradient through Scandinavia and Europe to identify the key ecological processes that will be affected in large river systems such as flooding regimes, decomposition and net primary production (TAYLOR and BLACK, 1995). In the St. Lawrence River ecosystem, climate-related variations in water level have an especially marked influence on the vegetation dynamics and primary productivity of Lake Saint-Pierre (HUDON, 1997). Under low water levels, the lake is an extensive marshland (387 km^2) with a large plant biomass, whereas under high water levels the lake becomes a vast body of open water (501 km^2) with much reduced vegetation stocks.

The shallow waters of the floodplain environment are critical to the survival of many species ; for example, fish such as northern pike (*Esox lucius*) which spawn in the warmer shallows of Lake Saint-Pierre (SLC, 1996). These species may be especially vulnerable to any shifts in temperature, flow regime, and habitat quality that result from climate change.

Climate change could also influence the distribution and abundance of migratory species via effects elsewhere within the species range, but well away from the riverine environment. For example, the St. Lawrence stocks of the American eel (*Anguilla rostrata*) have fallen precipitously over the last decade, with a 99% decrease between 1983 and 1992 in the number of juveniles migrating upstream. This population collapse may be a result of the weakening of the Gulf Stream Current which transports the eel larvae from spawning sites in the Sargasso Sea towards the entrance to the St.

Lawrence system (CASTONGUAY *et al.*, 1994).

It is likely that climate change will have major repercussions for the human use and regulation of waters in the St. Lawrence basin, which in turn will impact upon the downstream ecosystem. In a recent analysis of climate scenarios for Lake Ontario, LEE *et al.* (1997) note that their model output includes extreme water conditions where "none of the regulation criteria can be met simultaneously, priority of interests may change, and new interests may need to be considered, potentially requiring substantial revision to the Boundary Waters Treaty of 1909". These authors also draw attention to the need to improve the present day operational management of the lake, and the need to consider 'ecosystem health' as well as socioeconomic issues in any future revision of regulation criteria.

CONCLUSIONS

Large rivers are a vital resource for aquatic biota and for human society, yet they are still poorly understood as living systems. Long-term management of the St. Lawrence River and other fluvial ecosystems will require an improved definition of their trophic relationships, seasonal dynamics, microbial food-web processes and the physical linkages and coupling between different ecosystem components. This 'whole-system' approach acknowledges the interdependence of environmental issues (*e.g.*, the influence of climate change on the invasion and establishment of exotic species) and will ultimately lead to a more integrated management strategy for entire river ecosystems, from their headwaters to the sea.

Each of the environmental perturbations described in this review has some impact on the FSTZ (Fig. 5). This biologically productive reach is sensitive to upstream human activities, and it is the interface across which energy, materials and biota pass to the marine environment. The FSTZ of large river systems is an ecotone with a unique combination of upstream and downstream properties. It is therefore a key integrative site for monitoring the health of the St. Lawrence environment, and it may offer similar potential for monitoring strategies within large river-estuary ecosystems elsewhere.

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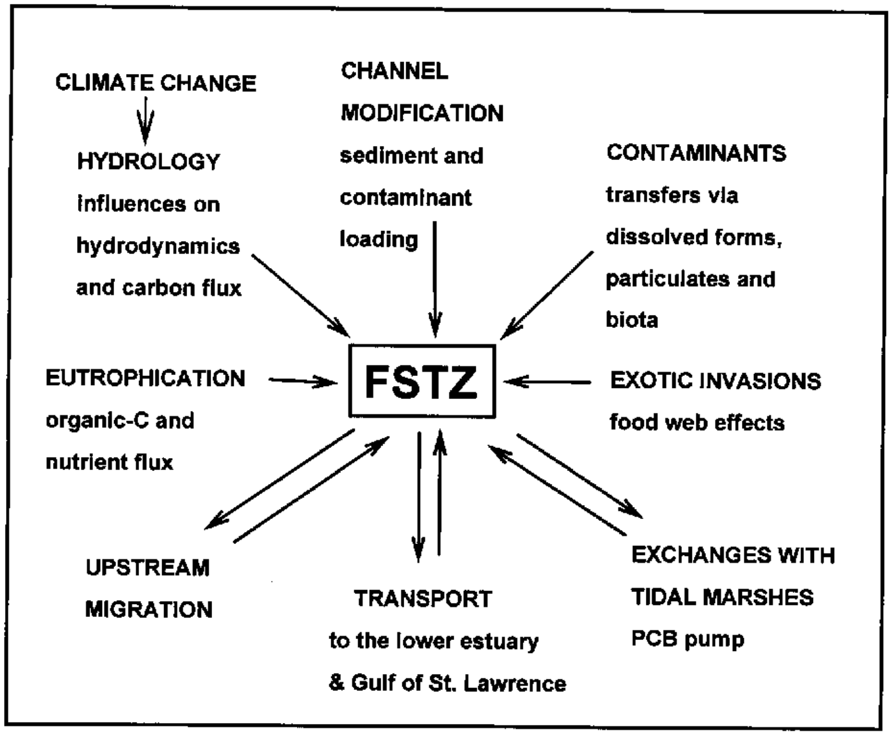

Fig. 5. The freshwater-saltwater transition zone (FSTZ) as a critical interface for large river ecosystems.

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