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Photosynthetic and bacterial production gradients in a larval fish nursery: the St. Lawrence River transition zone

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ABSTRACT: Phytoplankton biomass, primary production and bacterial abundance and production were measured across the freshwater-saltwater transition zone of the St. Lawrence River (Canada) during the seasonal period of maximum concentrations of fish larvae and macrozooplankton. The estuarine front was characterized by steep gradients in biological as well as physical properties. Maximum turbidity and high phytoplankton biomass occurred in the well-mixed, low salinity (0.2 to 4 psu) region immediately upstream of the salt wedge. Peak zooplankton and ichthyoplankton biomass occurred within and slightly downstream of this frontal region. The hypothesis that lower food chain processes were controlled exclusively by allochthonous carbon and bacterial heterotrophy was not supported. Photosynthetic rates per unit chlorophyll *a* (chl *a*) remained high across the freshwater-saltwater transition and the low light penetration was offset by a shallow mean depth of mixing. Bacterial concentrations and activity remained relatively constant across the transition, while chl *a* declined sharply downstream of the front, consistent with grazing losses. Photosynthesis contributed 34 to 66% of the total production (bacteria + phytoplankton). Freshwater phytoplankton advected from upstream contributed another 20 to 30%. These first-order estimates underscore the combined importance of photosynthesis plus bacterial processes within the downstream food web of large river ecosystems.

KEY WORDS: Bacteria · Estuary · Maximum turbidity zone · Phytoplankton · Production

INTRODUCTION

The estuarine transition zone is the dynamic frontal region where freshwater draining from the continent first mixes with the sea. It is characterized by sharp gradients in many environmental properties including salinity, nutrient concentrations, temperature and underwater light. This region has been variously referred to as the entrapment or retention zone, the tidal null zone and the maximum turbidity zone. It is often a region of prolonged hydraulic residence time where river discharge combined with estuarine recirculation (Kranck 1979) and turbulence supression (Geyer 1993) result in high concentrations of suspended sediment. The transition zone can also be a major site for secondary production, with dense populations of crustacean zooplankton (e.g. Barclay & Knight 1981) and fish larvae (e.g. Lardeux 1986).

The freshwater-saltwater transition is an important interface for the entire river-estuary system. Apart from acting as a nursery for certain fish species, it is a reprocessing region for upstream materials before they are exported into the marine environment. In contaminated river systems it may be a critical site of toxic waste bioaccumulation (Gagnon et al. 1990). However, the production ecology and food web structure of this frontal ecosystem remain poorly understood.

The larvae of 2 principal fish species in the St. Lawrence River and Estuary (Canada), rainbow smelt *Osmerus mordax* and Atlantic tomcod *Microgadus tomcod*, achieve high population densities in the transition zone immediately after the spring spawning season (Laprise & Dodson 1989, Dauvin & Dodson 1990). Their time of development corresponds to a period when prey species such as mysids and other

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crustacean zooplankton occur in high concentration (Dodson et al. 1989, Laprise & Dodson 1994). However the primary food chain processes which support these large standing stocks have not been evaluated. Studies to date have identified a diverse microbial assemblage in the St. Lawrence transition zone (Lovejoy et al. 1993); a photosynthetically active phytoplankton community (Bertrand & Vincent 1994, Vincent et al. 1994); and a shift towards larger celled microplankton that has been attributed to estuarine recirculation and entrapment (Frenette et al. 1995).

The downstream reaches of large rivers have been referred to as 'heterotrophic ecosystems' in which bacterial processes dominate the carbon and energy flux (Findlay et al. 1991, Vaqué et al. 1992). Previous authors have drawn attention to the broad range of organic substrates available for bacterial production in the St. Lawrence transition zone such as marsh-derived detritus, upstream dissolved and particulate organic carbon, and urban waste discharge (Painchaud & Therriault 1989). The rising salinities coupled with high turbidity have been identified as potentially limiting factors for the survival and growth of phytoplankton entering this region (Therriault et al. 1990). In combination, these observations implied that animal communities in the estuarine transition zone environment would ultimately depend on allochthonous inputs rather than autochthonous carbon produced *in situ* within the river-estuary, and that heterotrophic processes would dominate, even at the base of the food chain.

The aim of the present study was to evaluate the hypothesis that higher trophic levels in the St. Lawrence transition zone are supported by bacterial rather than photosynthetic production. We undertook 2 cruises to define the biological gradients across this region during spring-early summer. At this time of year the maintenance of high concentrations of zooplanktonic prey is of critical importance to the survival of smelt and tomcod which are passing through their vulnerable pre-metamorphic phase of development. Our measurements encompassed population estimates of planktonic bacteria, phytoplankton, zooplankton and fish larvae, and rate determinations of bacterial and photosynthetic activity. From this combination of measurements we make a first-order estimate of the relative importance of bacterial versus phototrophic production during the period of maximum larval fish abundance.

MATERIALS AND METHODS

Study site. The St. Lawrence estuarine transition zone is located between 50 and 90 km downstream of Québec City (Canada) and encompasses the salinity range 0.1 to 10 psu (practical salinity units). The river has a mean average discharge of 10 000 m^3 s^{-1}, with maximum values in the range 15 000 to 25 000 m^3 s^{-1} during spring snow melt (Pocklington & Tan 1987). The transition zone is a region of strong tidal currents, estuarine recirculation and sediment resuspension (Cardinal & Bérard-Therriault 1976, Kranck 1979) with turbidity values up to 115 NTU (nephelometric turbidity units) (Lucotte & d'Anglejan 1986).

Sampling. Two sampling cruises were undertaken, from 10 to 14 May 1991 and from 27 June to 1 July 1991. The mean daily river discharge at Québec City was 16 400 m^3 s^{-1} during the May sampling period; this cruise began 2 d after neap tide, and finished 2 d before spring tide. Discharge had fallen to a mean of 10 400 m^3 s^{-1} during the late June sampling period (Ministère de l'Environnement et de la Faune, Québec, unpubl. data); this second cruise began 6 d after neap tide and the final date of sampling (1 July) in Zone 2 corresponded to a spring tide.

During the first cruise, 12 stations were sampled in the upper St. Lawrence Estuary (Fig. 1): 4 stations in

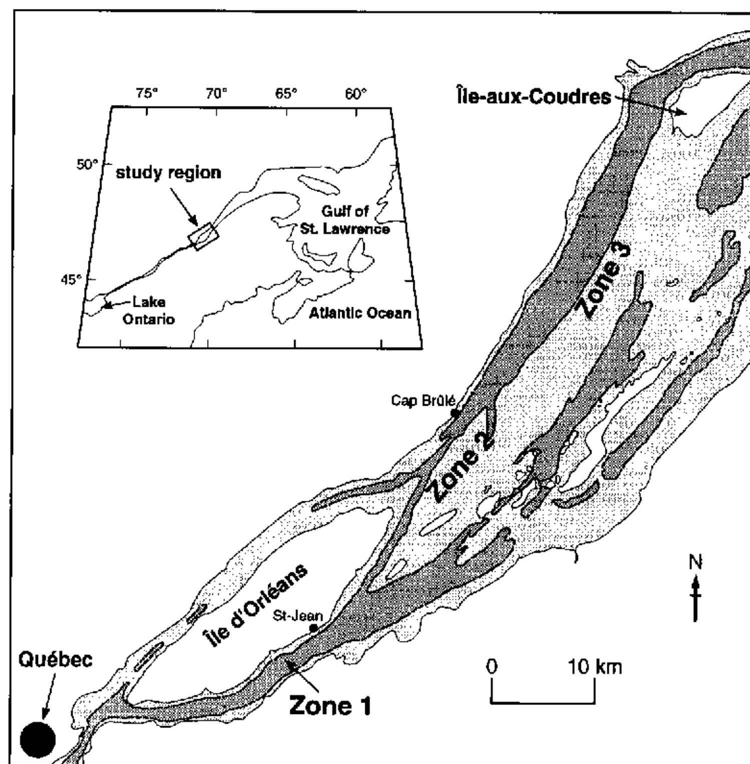

Fig. 1. Map of sites on the St. Lawrence River system (Canada)

the lower freshwater (but tidal) section ca 30 km downstream of Québec City (Zone 1); 4 stations in the frontal region of increased turbidity with surface salinities in the range 0.7 to 2 (Zone 2); and 4 stations 30 km further downstream with surface water salinites in the range 4 to 8 (Zone 3). Each zone was sampled over a 24 h period, twice at low tide and twice at high tide.

Zone 1 and the Zone 2 frontal region were more intensively studied in the second cruise to obtain better temporal resolution of the tidal water masses. A fixed station was occupied in each zone and sampled at 3 to 4 h intervals over 3 tidal cycles. The freshwater station was located ca 500 m off St. Jean (Île d'Orléans) and the transition zone station was located within 1 km of Cap Brulé (north shore).

In both cruises, the water column at each site was initially profiled with a Sea Bird conductivity-temperature-depth (CTD) probe model Sealogger SBE-19. Discrete samples were then obtained with 5 l Go-Flow bottles. The turbidity of each sample was measured immediately after collection with a model 2100A Hach turbidity meter. Samples were filtered onto GF/F glass fibre filters for seston dry weight analyses.

Underwater light. Underwater photosynthetically available radiation (PAR) was determined with a Biospherical Instrument Co. quantum irradiance probe (model QSP-160) connected to a QSP-170B integrating meter. Light attenuation was also measured with a 20 cm white Secchi disk. Mean water column irradiance (I_{av}) was calculated as in Vincent et al. (1994):

$$I_{av} = [100\%/(-Z_{av}K)][\exp(-KZ_{av}) - 1]$$

where K is the diffuse attenuation coefficient for underwater PAR and Z_{av} is the mean water column depth. The Z_{av} values were calculated from digitized estimates of the areas delimited by specific isobaths within 5 nautical mile (9 km) sections of the river using the 1:50 000 bathymetric charts produced by the Canadian Hydrographic Service.

Nutrient analysis. Samples for nutrient analysis were prefiltered through GF/F filters, stored frozen and later analysed on a Alpkem model RFA-300 autoanalyser. Nitrate was measured by diazotization after cadmium reduction to nitrate (American Public Health Association 1976), dissolved reactive phosphorus (DRP) by the method of Whitledge et al. (1981), and silicate after repolymerization at room temperature, by the method of Truesdale & Smith (1975). The limits of detection were 0.2 µmol P or Si l^{-1}, and 0.02 µmol N l^{-1}.

Chlorophyll analysis. Subsamples of water for chlorophyll *a* (chl *a*) fractionation were prefiltered through either a Nitex 200 µm screen (total fraction), a Nitex 20 µm screen (<20 µm fraction) or a Nuclepore 2 µm filter (picoplankton, <2 µm fraction), and then were filtered onto 25 mm Whatman GF/F filters. Care was taken to rinse each filter with GF/F-filtered sample water during and at the end of filtration to minimize filter blockage effects. These filters were stored frozen and subsequently ground in 90% acetone with a Teflon tissue grinder. The extract was cleared by centrifugation and assayed by fluorometry (Shimadzu spectrofluorometer model RF5000U) before and after acidification (Strickland & Parsons 1972).

Fish and zooplankton sampling. The fish larvae and mysid zooplankton samples were collected with a 1 m^2 Tucker trawl fitted with an opening-closing device and a 0.5 m standard plankton net (0.5 mm mesh). A General Oceanic flowmeter fitted at the mouth of the net measured filtration rate. At each station a 10 min tow was performed at 0.5 m and then a second at 17 m, at a towing speed of about 5 km h^{-1}. The catch was preserved immediately with buffered formaldehyde (1.5% final concentration) and later split and enumerated under a binocular microscope linked to a video camera and digitizing system.

Photosynthesis. Photosynthetic rates were measured by shipboard incubations with $^{14}C\text{-}HCO_3^-$. Each sample was dispensed immediately after collection into 70 ml Corning polycarbonate bottles and inoculated with 4.2 µCi of $NaH^{14}CO_3$. The bottles were incubated in a water bath set to surface water temperatures, and under a photon fluence rate of 180 µmol photons m^{-2} s^{-1} provided by a 250 W Optimarc high pressure lamp. At the end of a 2 h incubation the samples were fractionated as for chl *a*, and the filters then immediately frozen. The filters were subsequently acidified for 5 min in an atmosphere of HCl, and were each placed in a scintillation vial containing 10 ml of Cytoscint. The ^{14}C activity was measured in a LKB 1219 RackBeta liquid scintillation counter. The dissolved inorganic carbon (DIC) was measured by pH and potentiometric titration (Wetzel & Likens 1990) of 50 ml subsamples. These analyses were completed within 10 min of sample collection.

Bacterial enumeration. Samples for bacteria were immediately fixed with 1% glutaraldehyde (final concentration) and stored at 4°C. They were later stained with the fluorochrome 4',6-diamidino-2-phenylindole (DAPI) and filtered through 25 mm diameter, 0.22 µm pore-size, black-stained Anapore membranes (Jones et al. 1989). The samples were then examined by epifluorescence microscopy using a UV excitation filter block and 1000× oil immersion.

Bacterial production. Samples for the bacterial production assays were dispensed into 70 ml, acid-washed Pyrex bottles and injected with [methyl-^{3}H]-thymidine at a final concentration of 10 nmol l^{-1} (specific activity of 81 Ci $mmol^{-1}$). Tests with samples from the transition zone during the second cruise showed that incorporation rates were not significantly increased by adding the radiolabelled thymidine at 50% higher substrate

concentrations; this indicates that uptake was saturated at 10 nM as in other estuarine systems (e.g. Shiah & Ducklow 1994), and that it was not necessary to correct for dilution by natural substrate concentrations as in Findlay et al. (1991). The samples were incubated under dim light (ca 50 µmol photons $m^{-2} s^{-1}$) at ambient surface water temperatures. For each water sample a control bottle was run in which the cells were killed with 2% formaldehyde (final concentration) immediately before the addition of the thymidine. At the end of a 60 min incubation, 10 ml subsamples were removed and filtered onto 25 mm MSI 0.22 µm membranes with or without prefiltration through a 47 mm, 2.0 µm Nuclepore membrane. The filters were then incubated in place for 5 min with 5 ml of cold 5% trichloracetic acid (TCA), rinsed twice with TCA, and then stored frozen until counting by liquid scintillation spectrometry. This protocol did not include a lipid solvent rinse, nor DNA extraction, and is therefore likely to overestimate the incorporation of thymidine (TD) into bacterial DNA (Robarts & Zohary 1993).

As a further measure of bacterial activity, 30 ml samples were incubated with ^{3}H-leucine at a final concentration of 8 nmol l^{-1}. The samples were incubated for 60 min and then the uptake stopped by addition of 2 ml of 5% TCA. The samples were then stored in the dark at 2°C. They were later hydrolysed at 60°C and filtered onto MSI filters that were air dried and then counted by liquid scintillation spectrometry. Formaldehyde-treated blanks were also run, as for the TD.

Production estimates. Daily integral primary production rates were estimated by numerically integrating photosynthesis as a function of depth (0.1 m depth increments) and time (1 h time-steps). Photosynthesis was modelled as in Platt et al. (1980) using the *P* versus *I* parameters determined by shipboard incubations at each station. The *in situ* irradiance for these calculations was for clear sky conditions, with attenuation through the water column determined by the measured diffuse attenuation coefficients.

Bacterial productivity was estimated from the surface water (0.5 m) TD incorporation rates. These were converted into bacterial carbon production using the factor 2×10^{18} cells per mole of thymidine incorporated and an average cellular biomass of 25 fg C which is a value characteristic of bacteria in nutrient-rich waters (Bell 1993). These values were multiplied by 24 h and the average water column depth (Z_{av}) to provide estimates of the daily carbon flux. For the first cruise, Z_{av} was estimated as the mean tidal average for sections 1 and 2 (Zone 1), sections 4 and 5 (Zone 2) and sections 6 to 8 (Zone 3). The same Z_{av} was used for Zone 1 calculations for the second cruise; for Zone 2 the high tide (HT) and low tide (LT) mean depths were used for sections 4 and 5.

RESULTS

Morphometry and light

There are major changes in channel morphometry across the St. Lawrence estuarine transition zone (Fig. 2). In the freshwater section near Québec City (Zone 1) the river occupies a deep [maximum depth of 58 m, mean depth (Z_{av}) of 22 m], narrow (1 km) channel. Immediately downstream of Île d'Orléans the estuary widens out to >10 km and the water passes across a shallow (Z_{av} < 10 m) reach that extends for about 40 km until the beginning of the deep (>50 m) lower estuary. Zones 2 and 3 in our sampling program corresponded to the upstream and downstream ends of this extensive region of shallows. These morphometric changes result in major differences in freshwater residence time, which for a discharge of 10 000 $m^3 s^{-1}$ and discrete 10 nautical mile sections of the estuary is calculated as 1.5 d in Zone 1 (corresponding to sections 1 and 2 in Fig. 2), 4 d in Zone 2 (sections 4 and 5) and 8.8 d in Zone 3 (sections 6 to 8).

The morphometric variations across the freshwater-saltwater transition were accompanied by changes in turbidity and underwater light penetration, with a marked shallowing of the euphotic zone across the freshwater-saltwater transition (Fig. 2). The upstream riverwater was more turbid during the first cruise, as-

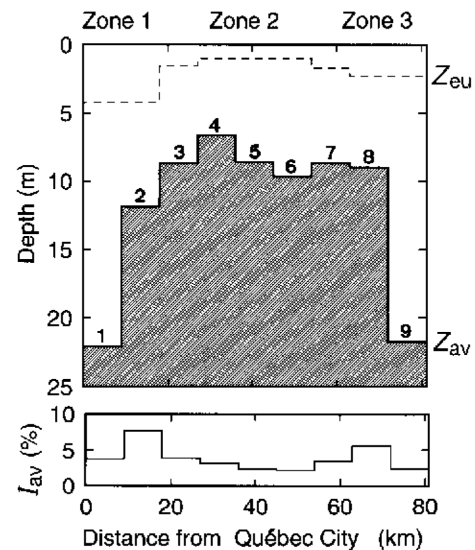

Fig. 2. Mean depth (Z_{av}) and underwater light availability in the downstream region of the St. Lawrence River. The *x*-axis refers to the distance north of Québec City (Canada) for the east-west lines of latitude at 5 nautical mile intervals that were used to demarcate each of the sections labelled 1 to 9 and referred to in the text. All *y*-axis values are for mid-tide. The euphotic depth (dashed line) and average water column irradiance (I_{av}, lower panel) have been calculated for the period of the second cruise

sociated with the spring discharge maximum. In both cruises there was an abrupt rise in the diffuse attenuation coefficient for PAR (k) across the Zone 1–2 transition, from 1.6 to 5.1 m^{-1} in May and from 1.1 to 4.8 m^{-1} in June. There was then a subsequent drop in k further downstream, to 1.2 m^{-1} in Zone 3 (first cruise) and to 2.3 m^{-1} in the high tide water in Zone 2 (second cruise).

The opposing effects of turbidity and average depth are seen by calculations of average irradiance for the water column (I_{av}, Fig. 2) and of the ratio Z_{eu} (depth of the euphotic zone) to Z_{av}. The mean I_{av} value was 2.6% of surface irradiance during the first cruise, rising to 3.8% during the second cruise, with little variation across the transition zone [SE = 0.2 (first cruise), 0.6 (second cruise)]. Similarly the Z_{eu} to Z_{av} ratio ranged from 0.12 (Zone 1) to 0.14 (Zones 2 and 3) in the first cruise; and from 0.18 (Zone 1) to 0.17 (LT) and 0.35 (HT) in Zone 2 in the second cruise. Underwater PAR availability was thus similar between zones because the steep optical gradient was offset by the large changes in mean depth.

Cruise 1, 10 to 14 May

The physical and chemical properties of the 3 zones sampled during the first cruise are given in Table 1. Zone 2 corresponded to the upstream end of the maximum turbidity zone. It was the region showing the onset of saline water conditions and contained the highest concentrations of suspended sediment. The Secchi disk depth changed from approximately 1 m in Zone 1 to 0.2–0.4 m in Zones 2 and 3. The CTD profiles showed that the water column was always completely mixed in Zone 1 and stratified in Zone 3, but in Zone 2 the water column structure was much more variable, from mixed to weakly stratified. Nitrate concentrations were similar across all 3 zones while silicate and to a much greater extent DRP rose between Zones 1 and 2 (Table 1).

Table 1. Distribution of environmental properties across the St. Lawrence transition zone (Canada). Each value is the mean (±SE) from the surface waters (0.5 m) at 4 stations within each zone, sampled during the first cruise, 10 to 14 May 1991. NTU: nephelometric turbidity units; DRP: dissolved reactive phosphorus

	Zone 1	Zone 2	Zone 3
Salinity (psu)	0.097 (0.002)	0.80 (0.26)	5.04 (0.39)
Temperature (°C)	10.29 (0.12)	10.14 (0.11)	9.21 (0.26)
Turbidity (NTU)	7.00 (1.38)	29.00 (1.08)	23.75 (3.19)
Seston (g m^{-3})	10.6 (2.4)	61.3 (4.4)	54.0 (3.3)
Nitrate (mmol m^{-3})	18.11 (0.10)	14.78 (0.83)	13.46 (0.59)
DRP (mmol m^{-3})	0.12 (0.00)	0.27 (0.02)	0.41 (0.01)
Silicate (mmol m^{-3})	74.7 (1.6)	91.0 (4.0)	80.9 (1.9)

Table 2. Distribution of fish larvae and macrozooplankton species during the first cruise. Each value is the mean number per m^3 for 4 surface and 4 bottom tows in each zone (±SE)

	Zone 1	Zone 2	Zone 3
Larval fish			
Osmerus mordax			
<7 mm length	1.52 (0.31)	0.44 (0.11)	0.03 (0.01)
>7 mm length	0.15 (0.05)	0.85 (0.19)	0.05 (0.01)
Microgadus tomcod	0.00 (0.00)	1.53 (0.72)	1.41 (0.61)
Amphipods			
Gammarus sp.	0.05 (0.01)	0.08 (0.02)	0.05 (0.01)
Mysids			
Mysis littoralis	0.00 (0.00)	2.43 (0.97)	1.39 (0.61)
Neomysis americana	0.00 (0.00)	4.21 (2.10)	1.68 (0.50)

The macrozooplankton and ichthyoplankton sampling showed that the highest concentrations of total fish larvae, amphipods and mysids occurred in the transitional Zone 2 region (Table 2). Slighter higher concentrations of *Osmerus mordax* larvae were recorded in Zone 1, but this freshwater population was composed almost entirely of small (<7 mm) individuals that had recently hatched upstream in the main stem of the river. This species hatches at 5.5 mm (Ouellet & Dodson 1985) and therefore these small larvae had only recently absorbed their yolk sacs. More than 50% of the individuals in Zone 2 were greater than 7 mm and dependent on exogenous food sources. *Microgadus tomcod* and the mysids were absent from the upstream freshwater reach. *M. tomcod* persisted at high concentrations in Zone 3, but the *O. mordax* population density dropped 16-fold and there was a 2-fold drop in mysid concentrations in this downstream section of the estuary.

The phytoplankton biomass (Table 3) showed little change between Zones 1 and 2, but dropped significantly in Zone 3 ($p < 0.05$). The photosynthetic characteristics of the phytoplankton population such as P^B_{max}

Table 3. Distribution of phytoplankton properties during the first cruise. Each value is the mean (±SE) of the surface waters (0.5 m) at 4 stations within each zone. The photoinhibition index (*PI* index) values are the photosynthetic rates at the maximum irradiance tested (900 to 1100 µmol photons m^{-2} s^{-1}) expressed as a percentage of P_{max}

	Zone 1	Zone 2	Zone 3
Chl *a* (mg m^{-3})	6.5 (0.4)	4.8 (0.5)	1.1 (0.5)
P^B_{max} [mg C (mg chl *a*)$^{-1}$ h^{-1}]	3.5 (0.3)	3.8 (0.3)	2.1 (0.1)
P_{max} (mg C m^{-3} h^{-1})	22.8	18.2	2.3
α [mg C (mg chl *a*)$^{-1}$ h^{-1} (µmol m^{-2} s^{-1})$^{-1}$]	0.018	0.017	0.013
I_k (µmol m^{-2} s^{-1})	194	223	161
PI index (%)	89	87	89

Table 4. Distribution of bacterial populations and bacterial activity as measured by thymidine or leucine incorporation (nmol m^{-3} h^{-1}) during the first cruise. Each value is the mean (±SE) for surface water samples (0.5 m) from 4 stations within each zone

	Zone 1	Zone 2	Zone 3
Bacteria (10^6 ml^{-1})			
Free-living	0.29 (0.06)	0.27 (0.02)	1.06 (0.50)
Attached	0.11 (0.04)	0.23 (0.04)	0.75 (0.42)
% attached	26 (6)	45 (4)	41 (7)
Thymidine uptake			
Total	21 (2)	27 (4)	17 (3)
<2 µm	17 (4)	15 (3)	10 (2)
% >2 µm	19	46	40
Leucine uptake	68 (9)	80 (10)	54 (13)

and also remained relatively constant across the Zone 1–2 transition, but there were substantial changes in Zone 3 indicative of an impaired photosynthetic ability. The photoinhibition index showed that the phytoplankton in all 3 communities were relatively insensitive to the inhibitory effects of bright light. In fact, the communities appeared to have a high light requirement for maximum photosynthesis; all the *P* versus *I* curves obtained during this cruise gave values for the photoadaptation parameter I_k that were at or above 150 µmol m^{-2} s^{-1}.

The total bacterial concentration did not change substantially across the Zone 1–2 transition (Table 4). However, there was a major shift in the proportional abundance of attached bacteria which made a small contribution to total counts in Zone 1, but accounted for 40 to 50% of the counts in Zones 2 and 3.

The bacterial production rates as measured by thymidine incorporation showed no significant shift in surface water activities between Zones 1 and 2, but a very large increase in the contribution of bacteria attached to particles >2 µm. This contribution was not significant in Zone 1 but accounted for 40 to 60% of the total activity in Zone 2. The bacterial activity as measured by ^{3}H-leucine similarly showed no significant variations between zones.

Cruise 2, 27 June to 1 July

As in the first cruise, there were 3 to 4 m tidal variations in water level at both stations. However, the freshwater zone maintained relatively constant physical, chemical and biological characteristics throughout the 36 h of sampling, while at the transition zone station there were strong tidal variations in salinity and temperature (Fig. 3). The Zone 1 CTD profiles were always isothermal and indicative of a well-mixed water column. At the Zone 2 station there were major differences between tidal states (Fig. 4) ranging from the well-mixed and low salinity (0.4 to 1.0 psu) at low tide (LT) to highly stratified with a 3 to 5 psu difference

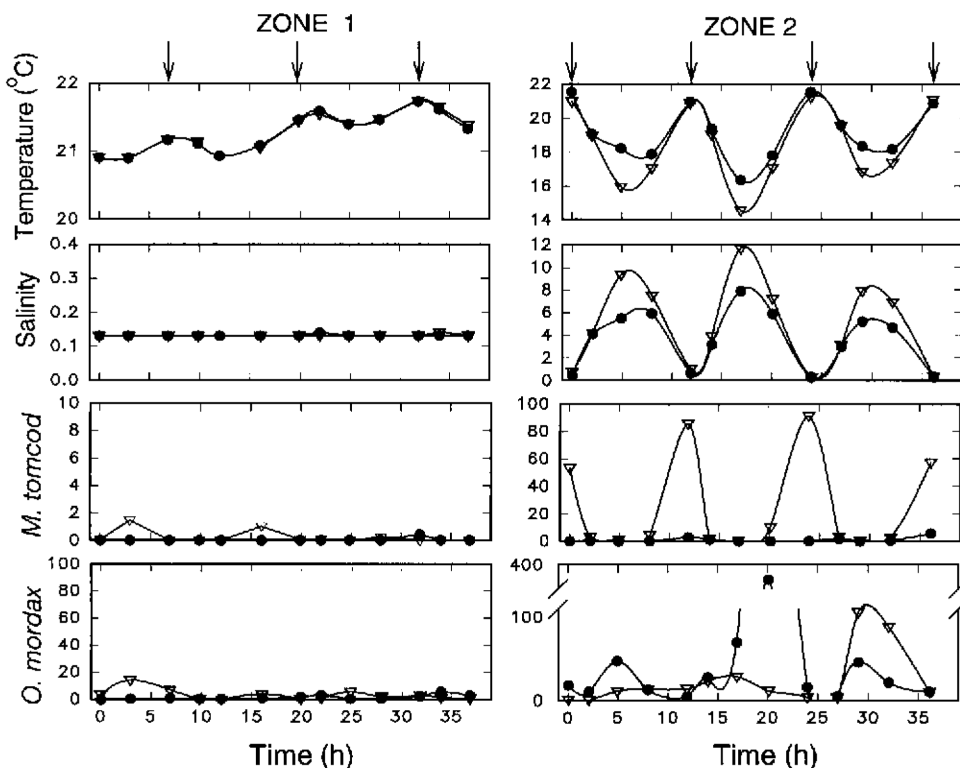

Fig. 3. Salinity, temperature and fish larvae in Zones 1 and 2 during the second cruise. (●) 0.5 m; (▽) 17 m; arrows: low tide

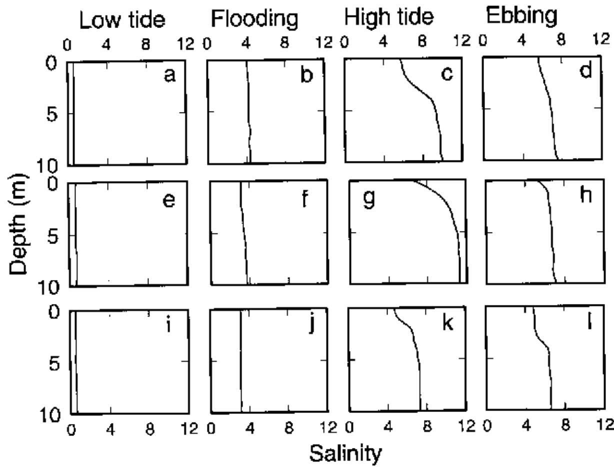

Fig. 4. Frontal structure as shown by salinity profiles in Zone 2 during the second cruise. Letters a to l denote the sequence of profiling at approximately 4 h intervals

between the top and bottom of the water column at high tide (HT). These semi-diurnal fluctuations in water column stability are further illustrated by the change in Brunt-Väisälä frequency through time (Fig. 5). Figs. 4 & 5 both illustrate the distinct tidal asymmetry with the persistence of unstable conditions (low N) during the flooding tide and the persistence of stratified conditions (higher N) during the ebbing tide.

The larval fish data confirmed that our Zone 2 sampling station was within the region of high ichthyoplankton biomass (Fig. 3). *Microgadus tomcod* was absent from Zone 1, but occurred in high biomass at the bottom of the water column at each LT sampling time. *Osmerus mordax* was present in Zone 1, but peak biomass occurred in Zone 2 at HT, completely out of phase with *M. tomcod*.

The temperature-salinity fluctuations in Zone 2 were accompanied by large tidal variations in other variables (Fig. 5, Table 5). Seston concentrations were higher at all Zone 2 tidal states relative to Zone 1, but achieved extreme maximal values during the flooding tide. Silica concentrations followed the the general pattern of water column stability with minimum concentrations at low tide that were well below those recorded in Zone 1. Chl *a* peaked during the period of maximum instability at low and flooding tide. It was inversely correlated with silica concentrations (r = −0.77 for the linear regression in Fig. 6a) and with water column stability as measured by Brunt-Väisälä frequency (r = −0.81 for the non-linear regression in Fig. 6b).

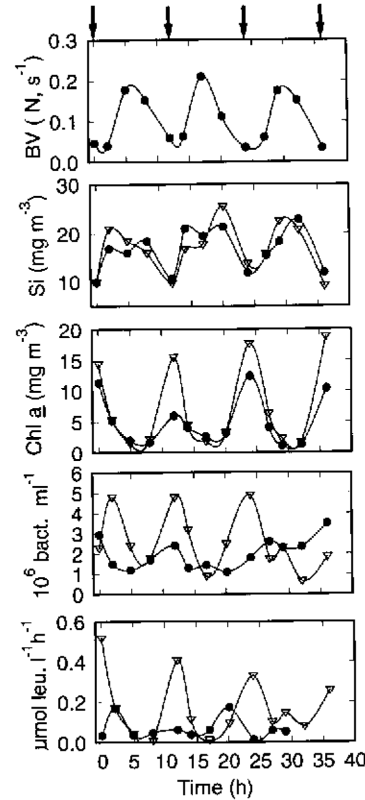

Fig. 5. Tidal variations in physical, chemical and biological properties of Zone 2 during the second cruise. BV: maximum Brunt-Väisälä frequency for the water column. (●) 0.5 m; (▽) 17 m; arrows: low tide

Surface and bottom water samples were similar in Zone 1 but there were often large differences between depths in Zone 2, particularly during low tide (Fig. 5, Table 6). Analysis of P_{max} values by ANOVA showed that there was no significant difference between zones or depths ($F = 2.57$, $p = 0.096$). However, analysis of the TD data by ANOVA showed highly significant effects ($F = 30.4$, $p < 0.001$), specifically between depths in Zone 1 (Student-Newman-Keuls test, $q = 3.99$, $p < 0.05$) and Zone 2 ($q = 11.65$, $p < 0.05$). There was a signifi-

Table 5. Seston, phytoplankton and bacterioplankton gradients in the surface waters (0.5 m) across the St. Lawrence River-Estuary during the second cruise, 27 June to 1 July 1991. Values for Zone 1 are the means (±SE) of 13 sampling times. Each value for Zone 2 is the mean (±SE) of 3 sampling times at each of the tidal states as shown in Fig. 4

	Zone 1	Zone 2			
	All tides	Low tide	Flooding	High tide	Ebbing
Silica (mg m^{-3})	19 (0.9)	11 (1.3)	18 (1.6)	19 (1.5)	21 (2.7)
Seston (g m^{-3})	5.9 (0.9)	52 (10)	128 (28)	28 (4)	33 (5)
Chl *a* (mg m^{-3})	11.9 (0.4)	9.9 (2.0)	4.4 (0.7)	1.9 (0.8)	2.2 (1.3)
Bacteria (10^6 cells ml^{-1})	2.4 (0.2)	2.4 (0.4)	1.8 (0.4)	1.7 (0.3)	1.7 (0.4)

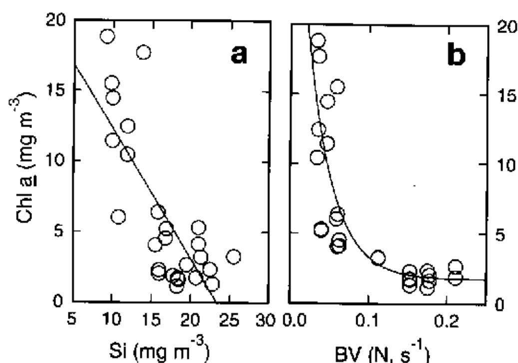

Fig. 6. Relationship between (a) chl *a* and silica, and (b) chl *a* and water column stability (as measured by the Brunt-Väisälä frequency, BV) in Zone 2 during the second cruise

cant drop in the surface water TD incorporation rates between low and high tides in Zone 2 ($q = 5.42$, $p < 0.05$), but not between Zones 1 and 2 (LT) ($q = 1.93$, $p > 0.05$). As in cruise 1, the >2 µm fraction contributed a major proportion (>30%) of the total TD uptake, with a significantly higher percent contribution in the bottom samples.

The leucine uptake data for Zone 2 showed similar trends as for the the TD assays, with a substantial drop between LT and HT, and much greater bacterial activity in the bottom samples, particularly at LT (Fig. 5). The highly variable leucine uptake rates at 17 m were significantly correlated with chl *a* ($r = +0.841$, $p < 0.001$) but not with bacterial cell concentrations ($r = +0.503$, $p = 0.080$).

Photosynthetic and bacterial production

The total water column estimates of production showed that maximum photosynthesis and bacterial production were in Zone 1 associated with the deeper

Table 6. Photosynthetic capacity [P^B_{max} in mg C (mg chl *a*)$^{-1}$ h^{-1}] and bacterial activity as measured by thymidine (TD) incorporation rates during the second cruise. Zone 1 values are the mean of 6 samplings (±SE); Zone 2 values are the mean for 2 to 3 values (±SE); –: single value only

	Zone 1	Zone 2	
	All tides	Low tide	High tide
Photosynthesis (P^B_{max})			
0.5 m	9.4 (0.8)	7.0 (0.8)	8.3 (0.3)
17 m	6.9 (0.7)	6.3 (1.3)	7.5 (0.5)
Bacterial production (nmol TD m^{-3} h^{-1})			
0.5 m	49 (5)	38 (3)	13 (1)
17 m	68 (4)	116 (10)	34 (–)
% TD uptake <2 µm			
0.5 m	0	31 (6)	44 (12)
17 m	0	67 (8)	54 (–)

Table 7. Comparison of photosynthetic and bacterial production rates across the St. Lawrence River transition, 10 to 14 May 1991. The value for each zone is the mean (±SE) from 4 sets of photosynthetic (*P* vs *I*) or bacterial (thymidine) incubations with surface (0.5 m) water samples

	Zone 1	Zone 2	Zone 3
Production (mg C m^{-2} d^{-1})			
Photosynthetic	522 (46)	124 (44)	19 (9)
Bacterial	431 (31)	242 (33)	180 (36)
Total	953	366	199
Photosynthesis as % total	55	34	9

mean water column depth, highest chl *a* concentrations and conditions of least turbidity (Tables 7 & 8). Total production dropped by a factor of 2.6 (first cruise) or 4.3 (second cruise) in Zone 2 (LT), and then by an additional factor of 2.6 or 1.8 in Zone 3 (cruise 1) and Zone 2 (HT, cruise 2). The initial drop was largely the result of decreased water column depth (bacterial production) and a shallowing of the euphotic zone (photosynthesis) while the subsequent decrease was primarily the result of decreased photosynthetic and bacterial activities per unit volume.

In the first cruise, photosynthesis contributed more than 30 to 50% of the total production in Zones 1 and 2. In the second cruise the contribution from photosynthesis rose to in excess of 2/3 of the total production. However, in Zone 3 the reduced chl *a* coupled with impaired photosynthetic rates per unit chl *a* and turbid water conditions resulted in very low integral photosynthetic rates, and production was almost exclusively dominated by the bacterial component.

DISCUSSION

This study confirmed that the freshwater-saltwater transition of the St. Lawrence River was a region of high standing stocks of fish larvae and macrozooplankton. Consistent with earlier studies in the region

Table 8. Comparison of photosynthetic and bacterial production rates across the St. Lawrence River transition, 27 June to 1 July 1991. Each value is the mean (±SE) from 4 sets (Zone 1) or 2 sets (Zone 2) of photosynthetic (*P* vs *I*) or bacterial (thymidine) incubations with surface (0.5 m) water samples

	Zone 1	Zone 2	
		Low tide	High tide
Production (mg C m^{-2} d^{-1})			
Photosynthetic	2671 (518)	611 (14)	213 (6)
Bacterial	1268 (117)	310 (15)	147 (13)
Total	3939	921	360
Photosynthesis as % total	72	66	59

(e.g. Dodson et al. 1989), these animal populations were distributed throughout the estuary, but achieved their peak total abundance in the frontal Zone 2 where turbidity was also maximal and where salinities were in the range 0.5 to 2.

Our TD estimates indicate that high bacterial productivity is maintained across the transition zone throughout the period of larval fish development. These values equate to bacterial production rates in Zones 1 and 2 of ca 20 to 60 µg C l^{-1} d^{-1}, which is towards the upper end of the range for other river-estuary systems (Chin-Leo & Benner 1992 and references therein). There was no evidence of inhibition of bacterial activity by rising salinities across the freshwater-saltwater transition. This observation is consistent with Painchaud et al. (1995) who found that freshwater bacteria in the St. Lawrence River were not affected by salinities up to at least 5 psu. The results contrast with findings from the Fraser River plume (Canada) (Valdés & Albright 1981) and the Tamar Estuary (UK) (Mantoura 1987) in which bacterial catabolism of glucose was severely inhibited by only small increases in salinity. We did, however, observe reduced bacterial activity in Zones 2 (HT) and 3 despite high bacterial numbers; this could reflect either inhibition at high salinities, or decreased availability of substrates for metabolism and growth.

The bacterial communities across the St. Lawrence saltwater transition differed from those in the freshwater zone by containing a high percentage of cells attached to suspended particulate material. This increased proportional abundance of attached bacteria in the maximum turbidity section of the river has been previously noted by Painchaud & Therriault (1989). Our thymidine assays confirm that attached bacteria also make a large contribution to total bacterial production (40 to 60%) in the transition zone. However, there was no evidence to suggest that organic carbon availability rose in this zone, for example by phytoplankton cell lysis as has been discussed for the Columbia River estuarine transition zone (Simenstad et al. 1990). The concentration of heterotrophic bacteria as measured by DAPI counts, and their activity as measured by thymidine and leucine incorporation, were high in Zone 2, but of a similar magnitude to values measured in Zone 1. It is possible, however, that the attached bacteria are more available than free-living cells as a food source to larger invertebrates that are incapable of filtering out submicron particles (cf. Wylie & Currie 1991).

The data from the first cruise indicate an almost complete shift away from phototrophy in the Zone 3 reach. However, our concurrent measurements of fish larvae and macrozooplankton show that the region of peak animal biomass occurred further upstream, in Zone 2. In this frontal region of the river, and contrary to our hypothesis, lower food chain production was not exclusively bacterial; phytoplankton made a substantial contribution in terms of biomass as well as productivity. P^B_{max} did not significantly differ between Zones 1 and 2 in either cruise, showing that there was no impairment of physiological activity caused by rising salt concentrations and turbidity. Our measurements and calculations show that because of the extensive shallows in Zone 2, average irradiance conditions are no worse than further upstream in the freshwater section. Photosynthetic studies on these populations indicate that the phytoplankton are well adapted to the intermittent exposure to bright light that they would experience within the turbid, well-mixed waters of the St. Lawrence River transition zone (Vincent et al. 1994). The decrease in dissolved silica combined with high concentrations of chl *a* in the frontal region indicates that this is a zone of active diatom growth rather than exclusively the result of passive accumulation of cells due to hydrodynamic entrapment. This physical process, however, will accelerate silica depletion by causing the recirculation of large, heavy diatom cells back into the frontal region (Frenette et al. 1995).

The estimates of total integral primary production and bacterial production (Tables 7 & 8) rest on many assumptions and can only be considered first order approximations. The photosynthesis calculations, for example, do not take into account depth-dependent changes in light quality, the effects of fluctuating light on integral photosynthesis, nor the effects of diurnal variations in photosynthetic parameters. The bacterial estimates rest on standard conversion factors for TD uptake which are known to vary widely and which have not been well evaluated for attached bacteria. They do not include values from the bottom samples which in Zone 2 contained elevated concentrations of suspended sediment, chl *a*, and bacteria, and which also showed the highest bacterial activity. Although these deep samples are likely to have been within the turbulent boundary current and thus unrepresentative of the overall water column, they indicate a rich additional source of carbon which may contribute to production at higher trophic levels. The bacterial and photosynthetic measurements were not corrected for daily respiration losses (a source of major uncertainty in turbid systems; see Kromkamp & Peene 1995) nor were they adjusted for spatial heterogeneity at right angles to the longitudinal axis of the estuary, which we suspect to be large (Bertrand & Vincent 1994). Despite these shortcomings, the estimates show that *in situ* bacterial as well as phototrophic production are both likely to be important sources of organic carbon at the base of the food web supporting animal populations across the estuarine front.

The advective transport of materials from upstream constitutes another major input of carbon into the transition zone. Much of the dissolved and particulate organic matter is likely to be of terrestrial origin, but its biological availability is at present unknown. Some of this material, for example dissolved and particulate humic substances, is only slowly metabolized, although such processes can be accelerated by photochemical reactions (Wetzel 1995). Howarth et al. (1992) estimated that more than 60% of all allochthonous inputs to a tidally influenced freshwater reach of the Hudson River (USA) are metabolized within the river. Within the transition zone of the St. Lawrence Estuary, phytoplankton carried in by the river from the upstream freshwater reach must be considered an additional carbon source for food web processes. Phytoplankton achieve high concentrations in the freshwater portion of the river, and once advected into the transition zone they are likely to be readily grazed by the zooplankton. A preliminary estimate of the daily contribution of this input (C_i) can be calculated as:

$$C_i = (\Delta \text{chl } a \times F \times Q)/\tau$$

where Δchl *a* is the chl *a* in the input (Zone 1 mean) minus chl *a* in the output (Zone 2 mean), F is the ratio of cellular C to Δchl *a* (taken as 50:1), Q is the daily discharge and τ is the hydraulic residence time in days. For the 10 nautical mile section downstream of Île d'Orléans this gives an advective input (and net loss) of 50 t algal C d^{-1} during the May cruise, and 86 t d^{-1} during the late June cruise. These values divided by the surface area of this section of the estuary give rates of 110 and 190 mg C m^{-2} d^{-1} which equate to 30% (May) or 21% (June) of the daily *in situ* production (bacteria plus photosynthesis).

The importance of phytoplankton in the overall carbon economy of the St. Lawrence transition zone is further suggested by stable isotope ratios in this section of the river-estuary. Gearing & Pocklington (1992) presented a compilation of data from several studies (their Fig. 2) showing that the ^{15}N and ^{13}C are as high in the reach 30 to 60 km downstream of Québec City (equivalent to our Zone 2) as in the Gulf of St. Lawrence (300 km further downstream), and indicative of a strong autochthonous contribution by phytoplankton. The intermediate section of the estuary between these 2 regions was characterised by low ^{15}N and ^{13}C ratios suggestive of a greater proportional importance of allochthonous materials. This is also consistent with our results showing a precipitous drop in chl *a* and photosynthesis, and the pre-eminence of bacterial production, in Zone 3.

The downstream gradient in phytoplankton biomass across the frontal zone is the net result of several gain and loss processes. Inputs to the water column of transitional Zone 2 include *in situ* primary production, the advection of phytoplankton from upstream (riverine transport) and downstream (tidal transport) reaches, and the resuspension of phytoplankton from the bottom sediments. The major net loss across this zone could be from cellular death and lysis, flocculation and/or zooplankton grazing. The first of these mechanisms is unlikely given the absence of evidence of physiological stress. Flocculation also seems less probable; the major drop in chl *a* during the second cruise was between low and flooding tides at which time water column mixing was at its most vigorous and unlikely to support major sedimentation losses. The high biomass of protozoa (Lovejoy et al. 1993, Frenette et al. 1995) and macrozooplankton (Laprise & Dodson 1994, this study) in Zone 2 strongly implies that grazing processes play a dominant role in cropping the phytoplankton as well as bacteria in this region, but quantitative estimates of these processes are still lacking throughout the St. Lawrence River and Estuary.

The combination of measurements undertaken here provides striking evidence of the sharp gradients in biological properties which accompany the physical changes across the estuarine front. Maximum turbidity as well as high phytoplankton biomass occur in the well-mixed, low salinity region immediately upstream of the salt wedge. Peak zooplankton and ichthyoplankton biomass occurs within or slightly below this phytoplankton-rich zone. Several features are likely to favour their large standing stocks in this region including the continuously renewed food supply of bacteria and phytoplankton, and the physical retention associated with prolonged hydraulic residence time, estuarine recirculation and tidal stream transport. Pace et al. (1992) underscored the importance of residence time as a major control on zooplankton abundance in advective environments. Further downstream of the front the chl *a* has been cropped down to low concentrations, and light limitation is severe, causing a shift towards bacterial dominance of production in Zone 3. Earlier studies in the St. Lawrence maximum turbidity zone (e.g. Therriault et al. 1990) have centered on this downstream reach, which fostered the view that this entire region is photosynthetically unproductive. Our observations provide evidence to the contrary, specifically in the freshwater-saltwater front where turbidity is maximal and where the larval fish populations are centered.

A general paradigm has begun to emerge that large rivers and the upper estuaries that they discharge into are bacteria-dominated ecosystems in which phototrophs play a relatively minor role (e.g. Painchaud & Therriault 1989, Findlay et al. 1991, Howarth et al. 1992). While allochthonous carbon sources are undoubtedly important in such systems, this view may

obscure the potential contribution of upper estuary phytoplankton as a direct carbon and energy source to the riverine and transition zone foodweb. Phytoplankton populations accumulate to high concentrations in many nutrient-rich rivers, for example up to 12 mg chl *a* m^{-3} in the St. Lawrence River (this study), and to 20 mg chl *a* m^{-3} in the Hudson River (Findlay et al. 1991). The biomass carbon from this source can be of proportional importance; for example phytoplankton contribute up to 55% of the total particulate organic matter in the Loire River (France) (Pocklington & Tan 1987). Phytoplankton carbon may also pass more directly to higher trophic levels, for example via copepods to fish larvae, rather than via the multi-step pathways of the microbial food web from bacteria to fish. Our results from the St. Lawrence show that autochthonous carbon generated at and above the frontal zone, as well as *in situ* bacterial growth, both contribute substantially to carbon flux within the highly productive food web of the estuarine transition zone.

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