Seasonal variation of the biological activity in the lower St. Lawrence Estuary

C. Savenkoff, L. Comeau, A.F. Vézina, and Y. Gratton

Marine Environmental Sciences Branch
Department of Fisheries and Oceans
Maurice Lamontagne Institute
P.O. Box 1000
Mont Joli (Québec)
Canada G5H 3Z4

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SEASONAL VARIATION OF THE BIOLOGICAL ACTIVITY IN THE LOWER ST. LAWRENCE ESTUARY

by

C. Savenkoff, L. Comeau, A.F. Vézina, and Y. Gratton[1]

Marine Environmental Sciences Branch
Department of Fisheries and Oceans
Maurice Lamontagne Institute
P.O. Box 1000
Mont-Joli (Quebec)
G5H 3Z4

1: INRS-Océanologie, Centre Océanographique, Université du Québec à Rimouski, Rimouski (Québec), Canada G5L 3A1

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Three to four stations located in the Laurentian Trough were investigated six times during four missions. Three missions were conducted during periods of expected maximal biological production according to the seasonal variation in the lower St. Lawrence Estuary. Two missions took place during the principal summer bloom (COUPPB90-1 in July 1990 and COUPPB91-2 in July 1991) and one was conducted during a secondary bloom in the fall (COUPPB90-2 in September 1990). The fourth mission occurred during a period of low surface production, following the melting of the ice cover (COUPPB91-1 in May 1991). The physico-chemical and biological characteristics present during all missions distinguished the upwelling region (stations 67 and 26) from the plume region (stations 23 and 95). We generally measured the highest salinities and lowest temperatures in the upwelling region whereas the lowest salinities and the highest temperatures were observed in the plume region. The significant relationships between phytoplankton biomass, surface production, and surface and deep respiration indicated that there was a coupling between the surface biological activity and the aphotic metabolism over a seasonal scale. Different explanations are presented to qualitatively and quantitatively describe the respiration/production budgets during these missions.

RÉSUMÉ

Savenkoff, C., L. Comeau, A.F. Vézina, and Y. Gratton. 1994. Seasonal variation of the biological activity in the lower St. Lawrence Estuary. Can. Tech. Rep. Fish. Aquat. Sci. 2006: v+22 p.

Trois à quatre stations localisées dans le chenal Laurentien ont été étudiées six fois en quatre campagnes océanographiques. Trois campagnes ont été effectuées pendant des périodes où la production biologique était supposée maximale suivant le cycle saisonnier dans l'estuaire maritime du Saint-Laurent. Deux parmi celles-ci ont été réalisées pendant le bloom estival principal (COUPPB90-1 en juillet 1990 et COUPPB91-2 en juillet 1991) et une pendant le bloom secondaire à l'automne (COUPPB90-2 en septembre 1990). La quatrième campagne a été accomplie pendant une période où la production de surface était faible, après la fonte des glaces (COUPPB91-1 en mai 1991). Quelque soit la campagne, les caractéristiques physico-chimiques et biologiques distinguent la région d'upwelling (stations 67 et 26) de la région de plume (stations 23 et 95). Nous avons mesuré généralement les plus fortes salinités et les plus faibles températures dans la région d'upwelling, tandis que les plus faibles salinités et les plus fortes températures ont été observées dans la région de plume. Les relations significatives entre la biomasse phytoplanctonique, la production de surface et la respiration en surface et en profondeur ont montré qu'il existait un couplage entre l'activité biologique de surface et le métabolisme profond sur une échelle saisonnière. Différentes explications sont présentées pour décrire qualitativement et quantitativement les rapports de respiration/production pendant ces campagnes.

PREFACE

This work is included in a multidisciplinary program known as COUPPB ("COUplage des Processus Physiques et Biogéochimiques"; Mesoscale Physical-Biogeochemical Coupling) that was carried out in the lower St. Lawrence Estuary from June 1989 to July 1991. The COUPPB project was a collaboration between Fisheries and Oceans Canada (A. Vézina, N. Silverberg, T. Packard, L. Godbout, C. Savenkoff), the University of Québec at Rimouski (J.-P. Chanut, G. Desrosiers, A. Mauviel, B. Vincent), the University of Québec at Montréal (K. Juniper), and IRNS-Oceanology at Rimouski (Y. Gratton, S. Roy). The present study was one of many different projects involved in modelling trophic and biogeochemical processes that regulate carbon flows in the Estuary and Gulf of St. Lawrence and was supported by grants from Fisheries and Oceans Canada. This report is a contribution to the program "Research on the carbon flux and climatic variations" of the Maurice Lamontagne Institute.

INTRODUCTION

Ocean biogenic cycles play a key role in controlling atmospheric CO_2 levels (Sundquist 1985; Jahnke 1990). The formation of organic carbon through photosynthesis (primary production) reduces the partial pressure of CO_2 in the surface waters. Some fraction of the biogenic material sinks or is actively transported out of the surface waters into deeper waters where it is decomposed and oxidized back to CO_2. This combination of processes is referred to as the "biological pump" (Longhurst and Harrison 1989). Virtually all of the organic carbon produced from CO_2 by photosynthesis is eventually remineralized to CO_2 by respiration. The flux of organic carbon leaving the photic layer is a major source of uncertainty in understanding the chain of events leading to the sequestration of atmospheric carbon by the biological pump. It is not clear where and when remineralization occurs relative to production: is organic matter mineralized close to where it is formed, or do advection and dispersion create important spatial separations between production and mineralization?

The margins of the world's oceans are important in the biogeochemical carbon cycle and are characterized by high and variable phytoplankton production relative to the open sea (Platt and Subba Rao 1975; Csanady *et al.* 1987; Walsh 1991). Althought it is widely accepted that coastal and marginal seas account for a significant portion of the global primary production, the rates and pathways by which this production is stored, metabolized, and exported to the deep-sea have not been fully described. A better understanding of the coupling of organic carbon production and degradation processes to short-term physical variability is needed to accurately determine carbon exchange between sources and sinks at ocean margins. Measurements of *in situ* respiratory activity can shed light on this question. Due to the normally low respiratory rate of microorganisms in the deeper layers of the ocean, there is no direct *in situ* procedure for its measurement; it is therefore necessary to resort to indirect methods. For this reason, an enzymatic approach was introduced by Packard (1971). Oxygen consumption by respiration is mostly due to oxidative phosphorylation driven by the respiratory electron transfer system (ETS). The measurement of the ETS activity (ETS assay) provides a method for determining the maximum potential respiration of the assayed respiratory systems.

The lower St. Lawrence Estuary (hereafter called the LSLE) is one of the most laterally stratified estuaries in the world (Larouche *et al.* 1987) and, because its width (20 to 30 km) is equal to several internal Rossby radii, complicated circulation patterns are generated that have a large influence on the zonation and processes of the marine planktonic organisms (Ingram and El-Sabh 1990; Mertz and Gratton 1990). We have undertaken a study of the physical-biological interactions regulating carbon flows in this large-scale estuarine system. Our project is included in a multidisciplinary program known as COUPPB ("COUplage des Processus Physiques et Biogéochimiques"; Mesoscale Physical-Biogeochemical Coupling), which was carried out in the LSLE from June 1989 to July 1991. This work is based on the investigation of four stations visited on four separate missions between June 1990 and July 1991 during different levels of surface production. We have already shown that surface biological activity and deep respiration were not correlated over a temporal scale of weeks and spatial scale of tens of kilometers during a neap-spring tidal cycle (Savenkoff *et al.* in press). Our objective here is to explore relationships between phytoplankton biomass, surface production, and surface and deep respiration during

periods that presents varying biological and physical conditions. We wanted to know how these variables were related to the stratification of the LSLE and to possible upstream-downstream gradients. We also attempted to balance various euphotic and aphotic measurements of new production in the LSLE.

MATERIALS AND METHODS

STUDY AREA

Our study concerns an area of the LSLE between Pointe à Cives - Sault au Mouton and Pointe au Naufrage - Baie Comeau (Fig. 1). The LSLE offers a wide range of hydrodynamic conditions, including seasonal ice cover, fronts, gyres, freshwater input and influence, and large seasonal variations in vertical stratification.

Using variations in phytoplankton production and biomass during the summer productivity period, Therriault and Levasseur (1985) distinguished four main regions: outflow, upwelling, plume, and near-Gulf regions from upstream to downstream, respectively. Each region corresponds to one of the major mesoscale features described by Ingram and El-Sabh (1990) and each has a characteristic food web (Therriault *et al.* 1990; De Lafontaine *et al.* 1991). During summer, the LSLE can be described as a three-layered system on the basis of its thermal properties: a warm surface layer with low salinity, an intermediate cold layer, and a warmer deep layer (Ingram 1979).

MISSIONS

Three missions were conducted during periods where biological production was expected to be maximal according to the seasonal cycle suggested by Bugden *et al.* (1982) and Levasseur *et al.* (1984). Two took place during the larger summer bloom (COUPPB90-1, surveys G2-G4; and COUPPB91-2, survey C2) and one was conducted during a secondary bloom in the fall (COUPPB90-2, survey G5) (Table 1). The fourth mission took place during a period of low surface production, after the melting of the ice cover (COUPPB91-1, survey C1) (Table 1).

This study is based on the investigation of four stations (67, 26, 23, and 95 from upstream to downstream) located in the Laurentian Trough (Fig. 1, Table 1). Station 95 was sampled only in 1991. The other three stations were investigated three times during COUPPB90-1, as the mission covered a full summer neap-spring tidal cycle. According to Therriault and Levasseur (1985), stations 67 and 26 were located in the upwelling region and stations 23 and 95 in the plume region.

SAMPLING PROTOCOL ON STATION

Underwater irradiance was measured at the stations in daytime with a Photosynthetically Active Radiation meter (PAR, LICOR). A quantum irradiance meter (LICOR) was used to take readings at specific surface incident radiations and to compute the vertical attenuation coefficient

of the PAR meter. Samples from depths where 50, 10, and 1% of the surface incident radiation remained were collected for biomass determinations (chlorophyll), ^{14}C and ^{15}N incubations (biological incorporation of carbon and nitrogen in the euphotic layer), inorganic nutrient content, dissolved oxygen content, and measurement of microorganism ETS activity to estimate water column respiration.

Below the photic zone, defined as extending to the depth where 1% of the surface incident radiation remains, sea water was collected from up to eight depths (from 25 m down to 20 m off-bottom) during daytime with 12 l Niskin bottles. The depths sampled were usually as follows: 25, 50, 70, 90, and 110 m (intermediate water), and 150, 200, 250, and, station depth permitting, 300 and 320 or 340 m (deep water). Subsamples drawn off each Niskin bottle were used for dissolved oxygen determination, ETS activity assay, and inorganic nutrient content.

PHYSICO-CHEMICAL PARAMETERS

At each station, temperature, salinity, density, oxygen, and turbidity profiles were determined down to 5-10 m off-bottom with an autonomous multiparametric Applied Microsystem STD-12. The dissolved oxygen concentration was determined according to the Winkler method as described by Aminot and Chaussepied (1983). Water samples for nutrient determinations (nitrates and silicates) were frozen and analysed ashore by standard automated methods on a Technicon Autoanalyser II (Parsons *et al.* 1984).

CHLOROPHYLL a AND SURFACE PRODUCTION

Duplicate samples for chlorophyll a determinations were collected on precombusted 25 mm Whatman GF/F filters, stored frozen, then analysed ashore by *in vitro* fluorometry (Parsons *et al.* 1984). Surface production was determined by the ^{14}C method outlined by Strickland and Parsons (1972). Measurements of NO_3^- and NH_4^+ uptake by ^{15}N methods were made as in Vézina (in press). The inoculated samples were incubated for 4 h on deck in acid-washed polycarbonate bottles placed in incubators cooled with running surface seawater and fitted with neutral density screening (Stork Veco International, Brookline, MA). These measurements were used to compute an index of regenerated production as [(1-f) PP], where PP is the primary production (surface production) and f is the ratio of NO_3^- uptake to total NO_3^- (new production) and NH_4^+ (regenerated production) uptake (Dugdale and Goering 1967).

ETS ACTIVITY MEASUREMENTS

Water samples were filtered through a 200 µm mesh net to remove large particles prior to the ETS measurements. The sample volumes were 4 and 11.5 l for the euphotic and aphotic layers respectively. Samples for the ETS activity measurements were vacuum filtered (30 KPa or 0.3 atm) onto 47 mm GF/F glass fiber filters. The filters were subsequently stored in liquid nitrogen to preserve the enzyme activity (Ahmed *et al.* 1976). The assay procedure was performed according to Savenkoff *et al.* (in press). After control for aerobiosis (measurement of

O_2 content in sampled water), data were expressed in terms of molecular oxygen uptake rate (µl O_2 l^{-1} h^{-1}). The ETS activity was corrected from the incubation temperature (18°C) to *in situ* temperature of the seawater samples using an Arrhenius activation energy of 15.8 kcal $mole^{-1}$ (Packard *et al.* 1975).

Depth-integrated ETS activities were then calculated by integration of single depth values according to the equation:

$$int(ETS) = \Sigma [(ETS_i + ETS_{i+1})/2] (Z_{i+1}-Z_i)$$

where ETS_i is the ETS activity at the depth Z_i. We estimated ETS activities between the sea surface and the shallowest sample by rectangular integration. The resulting values were then added to the ETS activity calculated by the trapezoidal integration of the measured profiles. We also applied this procedure to the other biological measurements (chlorophyll a and surface production).

ESTIMATION OF RESPIRATION

We used the R/ETS ratio of 0.34 measured by Packard and Williams (1981) on a mixed community of phytoplankton, bacteria, and microzooplankton in the Gulf of Maine to convert the ETS activity into rates of respiration (R) in the euphotic zone. To facilitate the comparison with surface production, we used a respiratory quotient of 1 to convert the moles of O_2 uptake (ETS activity and respiration) to the moles of CO_2 produced in the euphotic layer (Packard 1979). Multiplying by 12 achieves the conversion to mg C m^{-2} d^{-1}.

We converted ETS activity below the euphotic zone into rates of respiration (R) and rates of CO_2 production following the procedure described by Packard *et al.* (1988). We chose the same ratio (0.09) to facilitate comparisons with the literature (Christensen and Packard 1979; Christensen *et al.* 1980; Packard *et al.* 1988). We used an O/C molar ratio of 138/106 (Redfield *et al.* 1963) to convert the moles of O_2 uptake to the moles of CO_2 produced in the aphotic layer.

RESULTS

SURFACE PHYSICO-CHEMICAL CHARACTERISTICS

In all four missions, the physico-chemical characteristics distinguished the upwelling region (stations 67 and 26) from the plume region (stations 23 and 95). We generally measured the highest salinities and lowest temperatures in the upwelling region while the lowest salinities and the highest temperatures were observed in the plume region (Table 2). The changes in temperature and salinity between 25 m and the sea surface were used as indexes of stratification. These stratification indexes were lowest in the upwelling region, corresponding to a well-mixed surface layer, and highest in the plume region, indicating the presence of two layers of water (fresh water on saltier water). However, we did not regularly detect a physico-chemical gradient from upstream to downstream (Table 2).

During the 1990 missions, the physical features could be represented by two extremes (Table 2): (1) station 67, with the lowest temperatures and vertical stratification indexes and the highest salinities (upwelling); and (2) station 23, with the highest temperatures and vertical stratification indexes and the lowest salinities (plume). The plume end point (warmer and less saline water) could move and mix upstream at station 26 (S26G4), increasing the productivity in the surface layer over the whole study area.

During the 1991 missions, the extreme values of temperature and salinity were measured at stations 26 and 23. Station 26 had the most pronounced features of the upwelling region and station 23 those of the plume region (Table 2). We measured the highest salinity and the lowest temperature at station 26 related to the closeness of the upwelled water during the two missions in 1991. The processes (solar heating, freshwater runoff, winds, tides) that led to the migration of the front separating the physical extremes of stations 26 and 23 remain under study. These results indicate that there is interannual variability in physical parameters.

EUPHOTIC AND APHOTIC BIOLOGICAL CHARACTERISTICS

The horizontal and vertical patterns of the biological parameters were more complex. Table 3 summarizes the seasonal trend of the euphotic and aphotic biological parameters. The differences in biological parameters between a supposed period of low surface production (C1: after the melting of the ice cover) and periods of high surface production (G2-G4, C2: summer plankton bloom; G5: autumn plankton bloom) were especially pronounced in the surface waters, but could be detected in the deep waters as well. The increase in surface biological activity at each station from May to July 1991 was not related to an increase in deep-sea metabolism of the same magnitude. Nevertheless, the respiration in the aphotic zone increased 2 to 3 times from May to July 1991 (Table 3).

Because euphotic and aphotic respirations were estimated from ETS activity, we only considered relationships between ETS activity (potential respiration) and the other biological parameters (surface production, chlorophyll a). When we considered all the four missions, the relationships among the biological variables were significant (Table 4). However, these relationships showed mainly the opposition between low biological measurements made in May 1991 and high biological measurements made during the larger summer bloom (COUPPB90-1 and COUPPB91-2) and the secondary fall bloom (COUPPB90-2) (Fig. 2). We noted that the aphotic ETS activity increased as the surface production and the euphotic ETS activity increased during the season (Figs. 2c, d). Because the depth of the water column sampled at station 95 was different than that of the other stations, the aphotic ETS activity were divided by (Z max-25 m) to examine the relation with the euphotic biological parameters. The results were similar to those obtained for untransformed data (same relationships and same temporal pattern of the aphotic ETS activity).

Chlorophyll a concentration and surface production had the largest temporal variations during the missions carried out in July and September (COUPPB90-1, COUPPB90-2, and COUPPB91-2; Table 3). Euphotic and aphotic ETS activities were relatively stable in the upwelling region during the same periods: we measured a mean euphotic ETS activity of 236 ± 43 and 326 ± 63 mg C m^{-2} d^{-1} at stations 67 and 26 respectively, while the aphotic ETS activity

was 564 ± 137 and 572 ± 116 mg C m^{-2} d^{-1} at stations 67 and 26 respectively (Table 3). The temporal variations were stronger at station 23 (euphotic ETS activity: 518 ± 226 mg C m^{-2} d^{-1}; aphotic ETS activity: 630 ± 269 mg C m^{-2} d^{-1}). These differences once again separated the upwelling and the plume regions.

The correlation between surface production and temperature (or thermal stratification) is significant, while the correlation between surface production and salinity (or saline stratification) is not significant (Table 4). The level of significativity was better between the other biological parameters and temperature, than between the other biological parameters and salinity. The negative correlations between surface production and nutrient concentrations resulted from nutrient uptake by phytoplankton during increased surface production (Table 4).

RELATIONSHIP BETWEEN PRODUCTION AND EUPHOTIC ETS ACTIVITY

The linear relationship between surface production and euphotic ETS activity is highly significant ($n = 16$, $r = 0.83$, $p < 0.001$, slope: 3.99, intercept: -175.78; Fig. 2a) as is the corresponding non-parametric correlation coefficient (Table 4). The significant level of the linear relationship was higher with the log-transformed data ($n = 16$, $r = 0.87$, $p < 0.001$, slope: 1.04, intercept: +0.78). However, we noted that the euphotic ETS activity/surface production ratios (or euphotic respiration/surface production ratios) showed large variations (Fig. 2a and Table 3). In fact, a more detailed analysis of our results suggests that the slope of the regression between surface production and euphotic ETS activity vary with the level of surface production. The data showed two slopes: the first slope (1.51) was obtained with surface production values lower than 1000 mg C m^{-2} d^{-1} ($n = 9$, $r = 0.78$, $p < 0.05$, intercept: 66.12; Fig. 2a); the second slope was higher (4.00) and was calculated with surface production values larger than 1000 mg C m^{-2} d^{-1} ($n = 7$, $r = 0.80$, $p < 0.05$, intercept: 91.06; Fig. 2a). We could not find a better fit to describe this relationship between surface production and euphotic ETS activity.

During the COUPPB90-1 mission, we compared the euphotic ETS activity/surface production ratios with (1-f), which is proportional to regenerated production [RP = (1-f) SP]. Regenerated production is supported by nutrients recycled locally by heterotrophic activity (ammonia, urea; Dugdale and Goering 1967). The euphotic ETS activity/surface production ratio was significantly correlated with (1-f) ($n = 15$, $r = 0.67$, $0.001 < p < 0.01$). This positive relation was computed for the whole mission with the measurements made at depths where 50 and 10% of the surface incident radiation remained (Fig. 3). The regenerated production and euphotic ETS activity were of similar magnitude and followed the same trend.

FRACTION OF CARBON RESPIRED

We calculated the fraction of carbon respired (ER/SP: euphotic respiration/surface production), which represents the carbon lost as respired CO_2 in the euphotic zone. The remaining carbon could enter different food webs, be exported to the deeper layers through organic matter sedimentation, or be laterally advected by estuarine circulation. The ER/SP ratios

were generally high at station 67 during all missions and at stations 26 during periods of low surface productions (G2, C1; Table 3). As the biological activity increased, the ER/SP decreased (Table 3). The lowest ratios were found in the plume region.

The flux of organic matter exported from euphotic zone into deeper waters, where it is decomposed and oxidized back to CO_2, is assumed to be equivalent to the new production as defined by Eppley and Peterson (1979), when averaged over the appropriate time and space scales (Eppley 1989). Our respiration rate in the aphotic layer estimates thus the new production in the euphotic layer. In addition, we estimated primary production in the surface water using the ^{14}C method. In this way, we were able to determine a aphotic respiration/surface production ratio (AR/SP), analogous to the new/total production ratio at each station for each survey (f ratio, Table 3). The AR/SP ratios had roughly the same spatio-temporal trend as those of the ER/SP. This pattern is opposite that of the surface biological increase. The AR/SP ratios were generally higher in the upwelling region than in the plume region. We measured a decrease in the ratio from upstream to downstream with the exception of the ratios determined for the COUPPB91-2 mission (July 1991).

If we add the ER/SP and AR/SP ratios, we obtain the fraction of carbon lost by respiration in the entire water column (Table 3). It is thus obvious that a variable fraction (between 22 and 95%) of the surface production was not locally respired in the water column at stations 26 and 23. Moreover, the divergence between the surface production and the carbon lost by respiration increased during the onset of the plankton bloom, as shown during the COUPPB90-1 mission (G2-G4) and during periods of high biological activity (G4, C2; Table 3). These results lead us to assume that there may be a large amount of carbon exported either through the trophic web (e.g. to secondary production) or through horizontal advection.

DISCUSSION

From a two-year study of the LSLE, Therriault and Levasseur (1985) identified among four zones, two zones converging in our study area: one is an upwelling zone overlying the Laurentian Trough, with moderate productivity fed by nutrients advected from head region upwellings and limited by low vertical stability and low residence time; the second is a plume zone over the downstream part of the LSLE, with the highest production levels due to mixing of nutrient-rich upwelled waters with warmer and fresher waters flowing in from the north shore rivers and the southern Gulf of St. Lawrence. Our results broadly confirm this structure but indicate an interannual variability in physical attributes. The upwelling-plume gradient described by Therriault and Levasseur (1985), which we observed in 1990 (but not in 1991), seemed to undergo interannual variations. However, the surface production was generally largest in the plume region with the exception of the measurement made at station 26 during the July 1991 mission. Tidal mixing in the plume region is less intense (Forrester 1974; Therriault and Lacroix 1976), so the confined fresh water ensures the stabilization of the surface water over a large area. Our results could be influenced by the fact that it was difficult to know whether what we sampled resulted from a seasonal cycle or mesoscale spatio-temporal variability.

Our explanations ignore the semi-diurnal tides, which can be substantial in the LSLE. Furthermore, our sampling procedure was not designed to resolve tidal effects. However, because we focused the effort on stations located in the Laurentian Trough, where tidal mixing is too weak to periodically break the stratification (Sinclair *et al.* 1981), we minimized the chance that tides would significantly affect biological processes (Demers and Legendre 1981). Confirming this, the results indicated that the neap-spring tidal cycle did not have any influence on the patterns: production and stratification were both maximal during the spring tide (G4), when vertical mixing was presumably at its highest as shown by the measurements taken during the COUPPB90-1 missions (Table 3).

The surface production followed the same general trend as euphotic ETS activity and chlorophyll a concentration. Our estimate of 1250 mg m^{-2} d^{-1} averaged over the July missions (G2-G4 and C2) and including all the stations is comparable to the values measured by Levasseur *et al.* (1984; ≅ 1200 mg m^{-2} d^{-1}) and Therriault and Levasseur (1985; ≅ 1300 mg m^{-2} d^{-1}) during July in the same area. They also fall within the range expected for bloom periods in large estuaries and coastal system (≅ 1000-3000 mg m^{-2} d^{-1}; Holligan *et al.* 1984; Malone *et al.* 1986; Harrison *et al.* 1991). The large spatio-temporal variability in surface production is also not unexpected; Therriault and Levasseur (1985) observed high spatial heterogeneity in the LSLE, with mean production values that varied between 11 and 179 g C m^{-2} y^{-1} depending on the station considered. In a previous mission in the same area (COUPPB89), Vézina *et al.* (unpublished data) showed considerable variability and complexity in the physical-biological structure over a one-month period. The initiation of the summer phytoplankton bloom was apparently associated with eddy variability in the circulation pattern.

Surface production was correlated with chlorophyll a concentration. Primary productivity in nutrient-rich estuarine environments has been shown to be a function of phytoplankton biomass, biomass-specific carbon assimilation rate and light availability (Boyton *et al.* 1982; Cole and Cloern 1984). We obtained the highest Sperman correlation coefficient between surface production and euphotic ETS activity. The surface production represents autotrophic activity while the ETS activity represents the catalictic-autotrophic and anabolic-heterotrophic components of the population. A good correlation between these two variables is not surprising. Packard (1979) found in a study in the Northwest African upwelling area a high correlation between surface production and euphotic ETS activity (data recalculated in the same units than our study; $n = 16$, $r = 0.64$, $0.001 < p < 0.001$, slope: 2.00, intercept: 763.41).

Our results suggest that the slope of the regression between surface production and euphotic ETS activity vary with the level of surface production. A close coupling between surface production and plankton respiratory activity can be interpreted in two ways: either (1) autotrophic organisms are the major contributors to plankton community respiration rates; or (2) the growth and/or standing stock of phytoplankton populations significantly enhances the presence and/or activity of microheterotrophs, the latter being the most important contributors to overall respiration even under conditions of high surface production. As the slopes of both the relationships between surface production (autotrophic activity) and euphotic ETS activity (autotrophic and heterotrophic activities) were larger than 1, our results suggest that an important role was played by the autotrophic organisms in the biological activity. This finding is in agreement with other studies in phytoplankton-dominated zones such as upwelling systems,

ocean fronts, or chlorophyll maximum layers (Packard 1979; Packard and Williams 1981; Packard 1985; Martinez 1991; Iriarte *et al.* 1991; Estrada *et al.* 1992). A close qualitative association between surface production and ETS activity does not exclude the important role of microorganisms in the overall ETS activity, as microorganism biomass and activity are likely to be positively related to surface production (Fuhrman *et al.* 1980; Cole *et al.* 1988; White *et al.* 1991).

EUPHOTIC RESPIRATION/SURFACE PRODUCTION RATIOS

The ratio of productivity to respiration in an ecosystem has been used as an index of the ecosystem maturity (Margalef 1974). If the P/R ratio is close to 1, the ecosystem energy and carbon demands are met by its primary productivity and the ecosystem is said to be mature. In this state, there is no excess productivity to be exported to, or exploited by another ecosystem. If the P/R is less than 1, the ecosystem is a consumer system and must be coupled to an exploitable, immature ecosystem with a high P/R ratio. The euphotic respiration/surface production (ER/SP) ratios measured in this study are equivalent, but inverse to the P/R ratios. We measured the highest ER/SP ratios in the upwelling zone. This finding is in agreement with that of Sorokin and Kogelschatz (1979), who observed high bacterial activity in newly upwelled water. Similarly, McManus and Peterson (1988) showed in the near-shore off central Chile that bacterial production was much higher relative to primary production during active upwelling than during stratification; the temporal patterns of phytoplankton and bacterioplankton in the upwelling area were related to the upwelling cycle. The difference between the surface production and the euphotic respiration was largest during the periods when the highest biological measurements were taken (G4, C2), even in the plume region. This showed a larger contribution of the autotrophic organisms to the biological activity than the heterotrophic organism, while the euphotic ETS activity (consequently our euphotic estimated respiration) and the regenerated production were correlated. The regenerated production is supported by nutrients recycled locally by heterotrophic activity (ammonia, urea; Dugdale and Goering 1967).

APHOTIC RESPIRATION/SURFACE PRODUCTION RATIOS

Based on estimates of annual primary production for the upwelling and plume regions (94 and 134 g C m^{-2} y^{-1} respectively; Therriault and Levasseur 1985) and on estimates of the carbon flux to deep water (74 g C m^{-2} y^{-1}; Silverberg and Sundby 1990), the annual f ratio was calculated as 0.79 for the upwelling region and 0.55 for the plume region. Our AR/SP ratios (between 0.01 and 0.52) are substantially lower than these f ratios calculated from the literature. The high phytoplankton productivity in the estuary is expected to increase the importance of the pelagic community in oxidizing organic matter (Hargrave 1973; Hopkinson 1985). Carbon availability is generally considered to limit both the biomass and metabolic activity of heterotrophic bacteria in the aphotic zone. Consequently, habitats or environments having high fluxes of organic carbon would be expected to exhibit an increase in microorganism biomass, an elevated rate of community metabolism, or both (Karl and Knauer 1984).

Oxygen consumption during respiratory degradation of organic compounds in plankton communities occurs in conjunction with photosynthetic carbon assimilation. Photosynthetic and respiratory rates define the trophic status of pelagic environments and the difference between them describes the actual export or degradation of imported organic compounds. Even though Savenkoff *et al.* (in press) showed that spatio-temporal variability of biological activity was restricted to surface production and did not affect organic matter oxidation at depth over a temporal scale of weeks (surveys G2 to G4), our interannual results showed that deep-water metabolism and surface productivity were correlated over this temporal scale. However, our results showed that a variable fraction (between 22 and 95%) of the surface production was not locally respired in the water column. Different biological-physical hypotheses could explain the fate of the remaining carbon.

FATE OF REMAINING CARBON

The response time (organic matter oxidation) of the aphotic layer to oxidize sinking organic matter from the surface layer depends largely on the settling speed of the particulate matter, which also influences the timing and location of biodegradation in the water column. Other factors influencing biodegradation include duration of the diatom production cycle and the transfer of surface production to the metazoan food web. Phytoplankton has a normal doubling time of the order of 1 to 3 days and it generally takes less than a week for bloom conditions to develop (Takahashi *et al.* 1977; Levasseur *et al.* 1984). Within a few days, most of the photosynthetically-fixed carbon is transferred to herbivores, which are generally considered to be major contributors to the vertical carbon flux through the egestion of fast-sinking faecal pellets (Bishop *et al.* 1977; Knauer *et al.* 1979; Rainville and Marcotte 1985). Banse (1992) proposed that zooplankton grazing is instrumental in controlling primary production. His review covers major geographic areas of the world ocean and shows that grazing influences algal cell numbers, growth rates, and size. Longhurst and Harrison (1988, 1989) and Longhurst *et al.* (1990) stressed the importance of inter-zonal (vertically-migrating) zooplankton grazing in affecting both the vertical flux of dissolved nitrogen, by excretion of N-rich compounds in deeper layers, and the vertical flux of respiratory carbon, since animals that eat in the surface layer at night respire carbon away in the deep layers during the day.

Copepods usually constitute more than 75% of the total catch by plankton nets in the Gulf of St. Lawrence (De Lafontaine *et al.* 1991). With settling rates of about 100 m d^{-1}, leaving little time for degradation in the water column, faecal pellets produced by copepods reach bottom within a few days (Fowler and Knauer 1986). Furthermore, the shallowness of the estuary limits the magnitude of the pelagic respiration process and should enhance sedimentation rates. Silverberg *et al.* (1987) calculated the mineralization rate over the top 35 cm of the sediment to be 133 mg C m^{-2} d^{-1}. This value is 3 and 3.4 times larger than the mean aphotic respirations we calculated in the plume and upwelling regions respectively. Our calculations of metabolic CO_2 production based on microorganism ETS activity are minimum estimates because they do not include zooplankton respiration. If we consider the zooplankton metabolism, our rates would be higher. In the eastern tropical North Pacific, King *et al.* (1978) found that zooplankton (size > 200 μm) accounted for 57% of the total ETS-respiration in the euphotic zone and dropped to 9.1% of the total from 1% of the surface incident radiation to 200 m.

Plourde and Runge (1993) found that the spawning of *Calanus finmarchicus* was synchronised with the timing of the phytoplankton bloom and that the LSLE is a regionally important zone of *Calanus finmarchicus* reproduction. Moreover, a dominant feature of the surface circulation in the LSLE is the Gaspé Current, a coastal jet that rapidly moves the mass of the discharge from the St. Lawrence River out along the estuary's southern side to the Gulf of St. Lawrence (El-Sabh 1988). The transfer of the surface production through the metazoan food web and its horizontal advection could explain our unbalanced respiration/production budget. Thus, the results of Fortier *et al.* (1992) lead to the conclusion that the Lower Estuary and Gaspé current system acts as a *Calanus* pump, supplying fish larvae with abundant food and exporting zooplankton to the Gulf of St. Lawrence during the summer months.

CONCLUSION

The highly significant relationships between phytoplankton biomass, surface production, and surface and deep respiration throughout periods of varying biological and physical features indicated that there was a coupling between the surface biological activity and the aphotic metabolism over a seasonal scale. Considering the data from all missions, the physico-chemical and biological characteristics distinguished the upwelling region (stations 67 and 26) from the plume region (stations 23 and 95). These mesoscale hydrographic-production features seemed to undergo interannual variation.

A combination of various factors (horizontal advection, transfer through the metazoan food web) may explain the relatively low fraction of the surface production respired in the euphotic and aphotic layers during periods of high surface biological activity. Information on the relationships between surface production and surface and deep respiration over a seasonal scale and under varying biological and physical conditions is essential for modelling trophic and biogeochemical processes that regulate carbon flows in the Estuary and Gulf of St. Lawrence. Basic knowledge at the first trophic level is necessary for other long-term studies of trophic dynamics in this estuarine ecosystem.

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REFERENCES

Ahmed, S.I., R.A Kenner, and F.D. King. 1976. Preservation of enzymic activity in marine plankton by low-temperature freezing. Mar. Chem. 4: 133-139.

Aminot, A., and M. Chaussepied. 1983. Manuel des analyses chimiques en milieu marin, CNEXO, Brest, 395 p.

Banse, K. 1992. Grazing, temporal changes of phytoplankton concentrations, and the microbial loop in the open sea, p. 409-440. In P.G. Falkowski and A.D. Woodhead [eds.]. Primary productivity and biogeochemical cycles in the sea. Plenum Press, New York.

Bishop, J.K.B., J.M. Edmond, D.R. Ketten, M.P. Bacon, and W.B. Silker. 1977. The chemistry, biology, and vertical flux of particulate matter from the upper 400 m of the equatorial Atlantic Ocean. Deep-Sea Res. 24: 511-548.

Boyton, W.R., W.M. Kemp, and C.W. Keefe. 1982. A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production, p. 69-90. In V.S. Kennedy [ed.]. Estuarine comparison. Academic Press, New York.

Bugden, G.L., B.T. Hargrave, M.M. Sinclair, C.L. Tang, J.-C. Therriault, and P.A. Yeats. 1982. Freshwater runoff effects in the marine environment: the Gulf of St. Lawrence example. Can. Tech. Rep. Fish. Aquat. Sci. 1078: 1-89.

Christensen, J.P., T.G. Owens, A.H. Devol, and T.T. Packard. 1980. Respiration and physiological state in marine bacteria. Mar. Biol. 55: 267-276.

Christensen, J.P., and T.T. Packard. 1979. Respiratory electron transport activities in phytoplankton and bacteria: comparison of methods. Limnol. Oceanogr. 24: 576-583.

Cole, B.E., and E. Cloern. 1984. Significance of biomass and light availability to phytoplankton production in San Francisco Bay. Mar. Ecol. Prog. Ser. 17: 15-24.

Cole, J.J., S. Findlay, and M.L. Pace. 1988. Bacterial production in fresh and saltwater ecosystems: a cross-system overview. Mar. Ecol. Prog. Ser. 43: 1-10.

Csanady, G.T., K.H. Brink, E.E. Hofmann, and W. Sturges. 1987. Physical processes at continental margins: their role in the global biogeochemical cycle, p. 19-23. U.S. GOFS Planning Report 6, Ocean Margins, Report of the Workshop on: "the impact of ocean boundaries on the interior ocean", March 10-12, 1987, University of Southern Mississippi.

Demers, S., and L. Legendre. 1981. Mélange vertical et capacité photosynthétique du phytoplancton estuarien (estuaire du Saint-Laurent). Mar. Biol. 64: 243-250.

De Lafontaine, Y., S. Demers, and J. Runge. 1991. Pelagic food web interactions and productivity in the Gulf of St. Lawrence: a perspective, p. 99-123. In J.-C. Therriault [ed.]. Le Golfe du Saint-Laurent: petit océan ou grand estuaire ? Publ. Spéc. Can. Sci. Halieut. Aquat. 113.

Dugdale, R.C., and J.J. Goering. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. Limnol. Oceanogr. 12: 196-206.

El-Sabh, M.I. 1988. Physical oceanography of the St. Lawrence Estuary , p. 61-78. In B. Kjerfve [ed.]. Hydrodynamics of Estuaries, Vol. II. CRC Press Inc., Boca Raton, Florida, USA.

Eppley, R.W. 1989. New production: history, methods, problems, p. 85-97. In W.H. Berger, V.S. Smetacek, and G. Wefer [eds.]. Productivity of the ocean: present and past. J. Wiley and Sons Ltd., Chichester.

Eppley, R.W., and B.J. Peterson. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature 282: 677-680.

Estrada, M., R. Martinez, and S. Mathot. 1992. Respiratory electron transport activity in plankton of the Weddell and Scotia Seas during late spring-early summer: relationships with other biological parameters. Polar Biol. 12: 35-42.

Forrester, W.D. 1974. Internal tides in the St. Lawrence Estuary. J. Mar. Res. 32: 55-66.

Fortier, L., M. Levasseur, R. Drolet, and J.-C. Therriault. 1992. Export production and the distribution of fish larvae and their prey in a coastal jet frontal region. Mar. Ecol. Prog. Ser. 85: 203-218.

Fowler, S.W., and G.A. Knauer. 1986. Role of large particles in the transport of elements and organic compounds though the oceanic water column. Prog. Oceanogr. 16: 147-194.

Fuhrman, J.A., J.W. Ammerman, and F. Azam. 1980. Bacterioplankton in the coastal eutrophic zone: distribution, activity, and possible relationships with phytoplankton. Mar. Biol. 60: 201-207.

Hargrave, B.T. 1973. Coupling carbon flow through some pelagic and benthic communities. J. Fish. Res. Bd. Can. 30: 1317-1326.

Holligan, P.M., P.J. Leb. Williams, D. Purdie, and R.P. Harris. 1984. Photosynthesis, respiration and nitrogen supply of plankton population in stratified, frontal and tidally mixed shelf waters. Mar. Ecol. Prog. Ser. 17: 201-213.

Hopkinson, C.S. Jr. 1985. Shallow water benthic and pelagic metabolism: evidence of heterotrophy in the nearshore Georgia Bight. Mar. Biol. 87: 19-32.

Ingram, R.G. 1979. Water mass modification in the St. Lawrence Estuary. Naturaliste Can. 106: 45-54.

Ingram, R.G., and M.I. El-Sabh. 1990. Fronts and mesoscale features in the St. Lawrence Estuary, p. 71-93. In M.I. El-Sabh and N. Silverberg [eds.]. Coastal and Estuarine Studies, Vol. 39, Oceanography of a Large-Scale Estuarine System, the St. Lawrence. Springer-Verlag, Inc., New York.

Iriarte, A., G. Daneri, V.M.T. Garcia, D.A. Purdie, and D.W. Crawford. 1991. Plankton community respiration and its relationship to chlorophyll a concentration in marine coastal waters. Oceanol. Acta 14: 379-388.

Jahnke, R.A. 1990. Ocean flux studies : A status report. Rev. Geophys. 28: 381-398.

Karl, D.M., and G.A. Knauer. 1984. Vertical distribution, transport, and exchange of carbon in the northeast Pacific Ocean: evidence of multiple zones of biological activity. Deep-Sea Res. 31: 221-242.

King, F.D., A.H. Devol, and T.T. Packard. 1978. Plankton metabolic activity in the eastern tropical north Pacific. Deep-Sea Res. 25: 689-704.

Knauer, G.A., J.H. Martin, and K.W. Bruland. 1979. Fluxes of particulate carbon, nitrogen, and phosphorus in the upper water column of the northeast Pacific. Deep-Sea Res. 26: 97-108.

Larouche, P., V.G. Koutikonsky, J.-P. Chanut, and M.I. El-Sabh. 1987. Lateral stratification and dynamic balance at the Matane transect in the lower St. Lawrence Estuary. Estuarine Coastal Shelf Sci. 24: 859-871.

Levasseur, M., J.-C. Therriault, and L. Legendre. 1984. Hierarchical control of phytoplankton succession by physical factors. Mar. Ecol. Prog. Ser. 19: 211-222.

Longhurst, A.R., A.W. Bedo, W.G. Harrison, E.J.H. Head, and D.D. Sameoto. 1990. Vertical flux of respiratory carbon by oceanic diel migrant biota. Deep-Sea Res. 37: 685-694.

Longhurst, A.R., and W.G. Harrison. 1988. Vertical nitrogen flux from the oceanic photic zone by diel migrant zooplankton and nekton. Deep-Sea Res. 35: 881-889.

Longhurst, A.R., and W.B. Harrison. 1989. The biological pump: profiles of plankton production and consumption in the upper ocean. Prog. Oceanogr. 22: 47-122.

McManus, G.B., and W.T. Peterson. 1988. Bacterioplankton production in the nearshore zone during upwelling off central Chile. Mar. Ecol. Prog. Ser. 43: 11-17.

Malone, T.C., W.M. Kemp, H.W. Ducklow, W.R. Boynton, J.H. Tuttle, and R.B. Jonas. 1986. Lateral variation in the production and fate of phytoplankton in a partially stratified estuary. Mar. Ecol. Prog. Ser. 32: 149-160.

Margalef, R. 1974. Ecologia, Ediciones Omega, Barcelona, Spain, 951 p.

Martinez, R. 1991. Biomass and respiratory ETS activity of microplankton in the Barents Sea, p. 193-200. In E. Sakshaug, C.E.E. Hopkins, and N.A. Oritsland [eds.]. Proccedings of the Pro Mare Symposium on Polar Marine Ecology. Trondheim, 12-16 May 1990, Polar Res. 10.

Mertz, G., and Y. Gratton. 1990. Topographic waves and topographically induced motions in the St. Lawrence Estuary, p. 94-108. In M.I. El-Sabh, and N. Silverberg [eds.]. Coastal and Estuarine Studies, Vol. 39, Oceanography of a Large-Scale Estuarine System, the St. Lawrence. Springer-Verlag, Inc., New York.

Packard, T.T. 1971. The measurement of respiratory electron-transport activity in marine phytoplankton. J. Mar. Res. 29: 235-244.

Packard, T.T. 1979. Respiration and respiratory electron transport activity in plankton from the Northwest African upwelling area. J. Mar. Res. 37: 711-742.

Packard, T.T. 1985. Measurement of electron transport activity of microplankton, p. 207-261. In H. Jannasch and P.J. Leb. Williams [eds.]. Advances in aquatic microbiology, Vol. 3. Academic Press, New York.

Packard, T.T., M. Denis, M. Rodier, and P. Garfield. 1988. Deep-ocean metabolic CO_2 production: calculations from ETS activity. Deep-Sea Res. 35: 371-382.

Packard, T.T., A.H. Devol, and F.D. King. 1975. The effect of temperature on the respiratory electron transport system in marine plankton. Deep-Sea Res. 22: 237-249.

Packard, T.T., and P.J. Leb. Williams. 1981. Rates of respiratory oxygen consumption and electron transport in surface seawater from the northwest Atlantic. Oceanol. Acta 4: 351-358.

Parsons, T.R., Y. Maita, and C.M. Lalli. 1984. A manual of chemical and biological methods for seawater analysis. Pergamon Press, 173 p.

Platt, T., and D.V. Subba Rao. 1975. Primary production of marine microphytes, p. 249-280. In J.P. Cooper [ed.]. Photosynthesis and Productivity in different environments. IBP 3, Cambridge University Press.

Plourde, S., and J.A. Runge. 1993. Reproduction of the planktonic copepod *Calanus finmarchicus* in the lower St. Lawrence Estuary: relation to the cycle of phytoplankton production and evidence for a *Calanus* pump. Mar. Ecol. Prog. Ser. 102: 217-227.

Rainville, L.A., and B.M. Marcotte. 1985. Abundance, energy and diversity of zooplankton in the three water layers over slope depths in the Lower St. Lawrence Estuary. Naturaliste Can. 112: 97-103.

Redfield, A.C., B.H. Ketchum, and F.A. Richards. 1963. The influence of organisms on the composition of seawater, p. 26-77. In M.N. Hill [ed.]. The Sea, Vol. 2. Interscience, New York.

Savenkoff, C., A.F. Vézina, J.-P. Chanut, and Y. Gratton. In press. Respiratory activity and CO_2 production rates of microorganisms in the lower St. Lawrence Estuary. Cont. Shelf Res. (accepted April 15, 1994).

Silverberg, N., J. Bakker, H.M. Edenborn, and B. Sundby. 1987. Oxygen profiles and organic carbon fluxes in Laurentian Trough sediments. Netherlands J. Sea Res. 21: 95-105.

Silverberg, N., and B. Sundby. 1990. Sediment-water interaction and early diagenesis in the Laurentian Trough, p. 202-238. In M.I. El-Sabh and N. Silverberg [eds.]. Coastal and Estuarine Studies, Vol. 39, Oceanography of a Large-Scale Estuarine System, the St. Lawrence. Springer-Verlag, Inc., New York.

Sinclair, M., D.V. Subba Rao, and R. Couture. 1981. Phytoplankton temporal distributions in the estuaries. Oceanol. Acta 4: 239-246.

Sorokin, Y.I., and J.E. Kogelschatz. 1979. Analysis of heterotrophic microplankton in an upwelling area. Hydrobiologia 66: 195-208.

Strickland, J.D.H., and T.R. Parsons. 1972. A pratical handbook of sea water analysis. Bull. Fish. Res. Bd. Can. 167: 311 p.

Sundquist, E.T. 1985. Geological perspectives on carbon dioxide and the carbon cycle, p. 5-59. In E.T. Sundquist and W.S. Broecker [eds.], The carbon cycle and atmospheric CO_2: natural variations archean to present, American Geophysical Union, Geophysical Monograph 32, Washington, D. C.

Takahashi, M., D.L. Seibert, and W.H. Thomas. 1977. Occasional blooms of phytoplankton during summer in Saanish Inlet, B. C., Canada. Deep-Sea Res. 24: 775-780.

Therriault, J.-C., and G. Lacroix. 1976. Nutrients, chlorophyll and internal tides in the St. Lawrence Estuary. J. Fish. Res. Bd. Can. 33: 2747-2757.

Therriault, J.-C., L. Legendre, and S. Demers. 1990. Oceanography and ecology of phytoplankton in the St. Lawrence Estuary, p. 269-295. In M.I. El-Sabh and N. Silverberg [eds.], Coastal and Estuarine Studies, Vol. 39, Oceanography of a Large-Scale Estuarine System, the St. Lawrence. Springer-Verlag, Inc., New York.

Therriault, J.-C., and M. Levasseur. 1985. Control of phytoplankton production in the lower St. Lawrence Estuary; light and freshwater runoff. Naturaliste Can. 112: 77-96.

Vézina, A.F. In press. Mesoscale variability in nitrogen uptake rates and the f ratio during a coastal phytoplankton bloom. Limnol. Oceanogr. (accepted October 11, 1993).

Walsh, J.J. 1991. Importance of continental margins in the marine biogeochemical cycling of carbon and nitrogen. Nature 350: 53-55.

White, P.A., J. Kalff, J.B. Rasmussen, and J.M. Gasol. 1991. The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. Microb. Ecol. 21: 99-118.

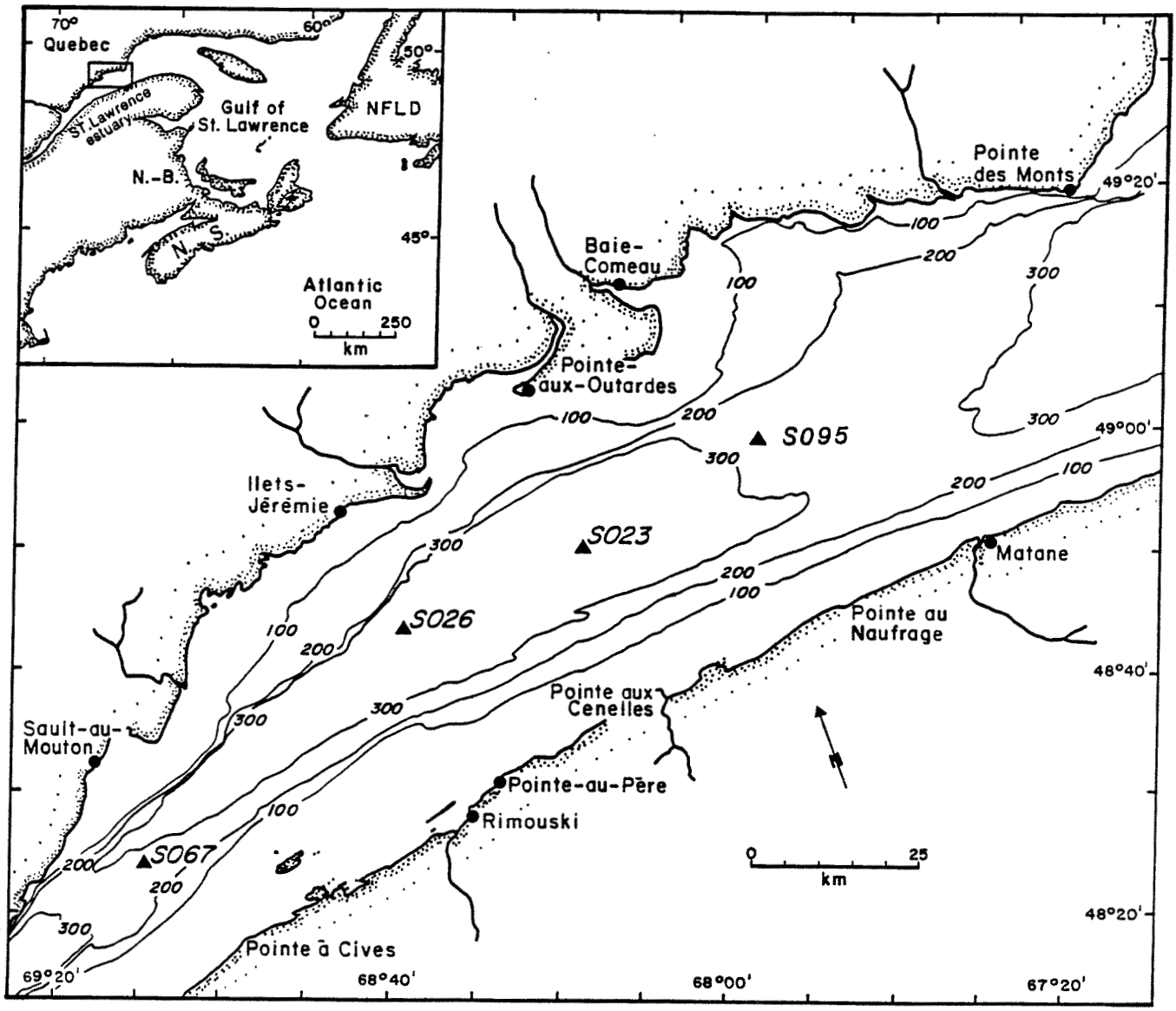

Figure 1. Bathymetric map of the lower St. Lawrence Estuary and station locations during the COUPPB cruises.

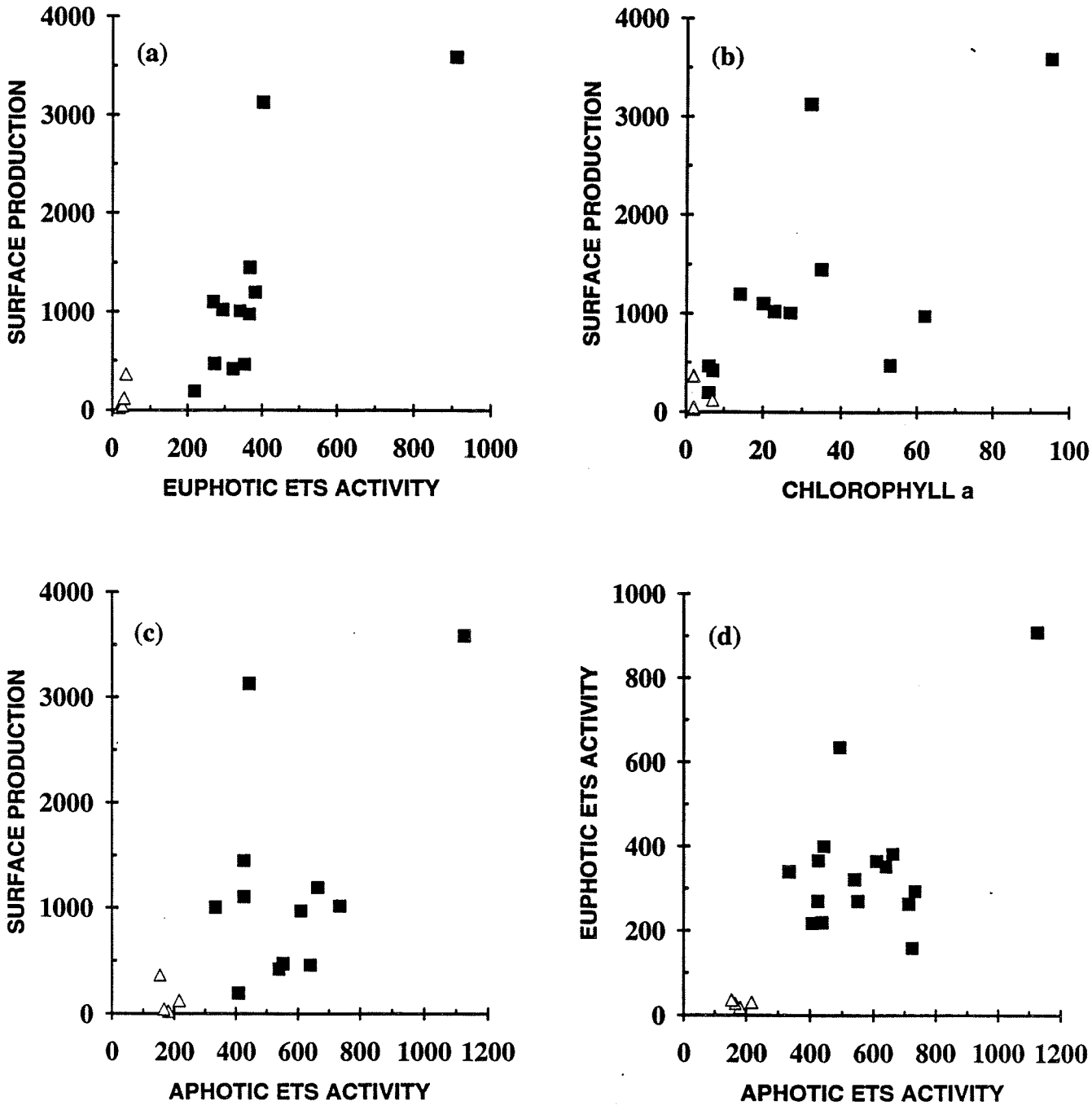

Figure 2. Relationships between the biological variables. Surface production: mg C m^{-2} d^{-1}; chlorophyll a: mg m^{-2}; euphotic ETS activity: mg C m^{-2} d^{-1}; aphotic ETS activity: mg C m^{-2} d^{-1}. The measurements made in May 1991 are represented in white triangle.

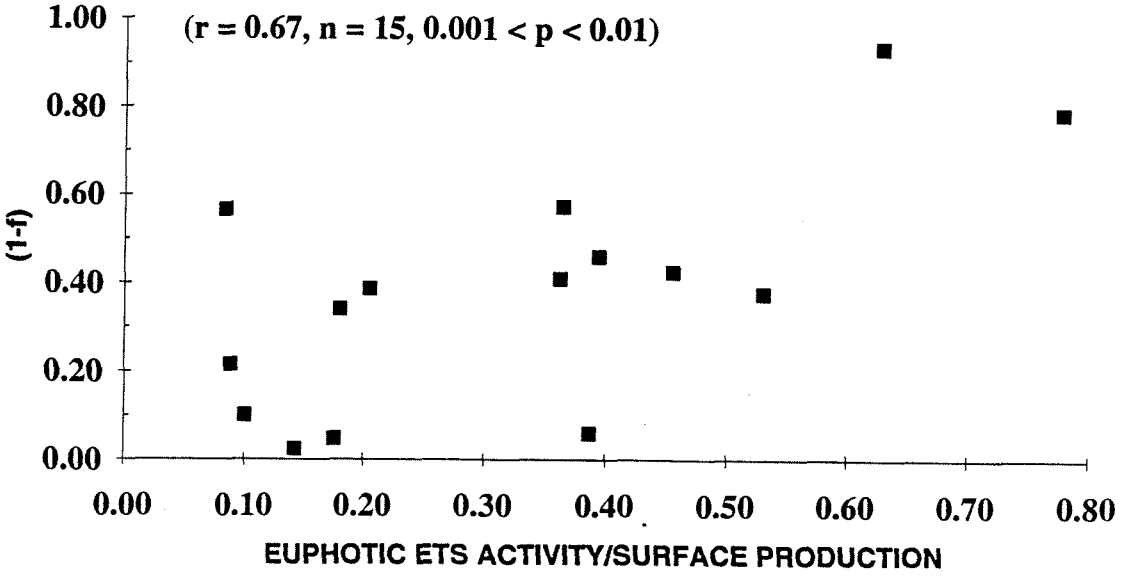

Figure 3. Relationship between euphotic ETS activity/surface production ratio and (1-f), which is proportional to regenerated production (RP = (1-f) SP). This positive relationship was computed with measurements made at depths where 50 and 10% of the surface incident radiation remained during the COUPPB90-1 cruise.

TABLE 1. Stations sampled, phase of the M_2 (semi-diurnal component), and fortnightly tidal cycles during the cruises. The phase of the tide (flood or ebb) was determined by consulting the Canadian Hydrographic Service tide tables at the Pointe-au-Père tidal observatory adjacent to Rimouski. The station coordinates are: (1) station 67 (300 m depth, upwelling region): 48° 24' 00" N, 69° 09' 20" W; (2) station 26 (350 m depth, upwelling region): 48° 43' 15" N, 68° 39' 50" W; (3) station 23 (350 m depth, plume region): 48° 50' 20" N, 68° 19' 30" W; (4) station 95 (280 m depth, plume region): 48° 59' 00" N, 67° 59' 00" W.

cruise	survey	station	date (d/m/y)	M_2 phase	neap-spring phase
COUPPB90-1	G2	67	30/06/90	mid to early flood	neap
		26	01/07/90	mid to late ebb	neap
		23	02/07/90	mid to late ebb	neap
	G3	67	04/07/90	mid to early ebb	mid-neap to spring
		26	05/07/90	mid to late ebb	mid-neap to spring
		23	06/07/90	mid to late flood	mid-neap to spring
	G4	67	07/07/90	mid to early ebb	spring
		26	08/07/90	mid to late flood	spring
		23	09/07/90	mid to late flood	spring
COUPPB90-2	G5	67	05/09/90	mid to late flood	spring
		26	07/09/90	mid to early ebb	spring
		23	06/09/90	mid to late flood	spring
COUPPB91-1	C1	67	18/05/91	mid to late flood	mid-spring to neap
		26	19/05/91	mid to late flood	mid-spring to neap
		23	20/05/91	mid to late ebb	mid-spring to neap
		95	21/05/91	mid to late ebb	mid-spring to neap
COUPPB91-2	C2	67	04/07/91	mid to late flood	neap
		26	05/07/91	mid to late ebb	neap
		23	06/07/91	late ebb to mid flood	neap
		95	07/07/91	early flood to mid neap	neap

TABLE 2. Physico-chemical parameters at each station during the different COUPPB cruises. The physical parameters were measured at the sea surface while the chemical data were from the shallowest depth. We show in parentheses the difference of physical values between 25 m and the sea surface, which was used as an index of stratification.

cruise	survey	station	temperature (°C)	salinity (psu)	nitrate (µM)	silicate (µM)	dissolved oxygen (%)
July 1990	G2	S67	5.5 (2.6)	28.1 (1.4)	12.2	15.8	82.9
		S26	7.5 (3.8)	26.0 (2.7)	11.5	14.1	101.6
		S23	7.4 (4.6)	25.8 (3.8)	11.3	15.2	105.1
	G3	S67	7.5 (4.3)	26.3 (3.0)	11.5	16.4	103.5
		S26	8.4 (4.9)	26.5 (2.5)	11.4	14.9	113.3
		S23	7.9 (4.7)	25.2 (4.2)	11.3	14.1	103.9
	G4	S67	8.0 (5.2)	26.0 (3.7)	11.0	15.3	102.0
		S26	9.6 (4.8)	23.9 (4.2)	12.1	13.4	108.9
		S23	9.9 (5.8)	23.0 (6.9)	1.5	4.8	130.0
September 1990	G5	S67	8.7 (5.4)	27.8 (3.0)	5.4	10.1	103.4
		S26	8.2 (4.2)	26.4 (3.9)	12.8	11.6	91.6
		S23	11.2 (8.0)	26.5 (4.6)	-	4.7	106.6
May 1991	C1	S67	3.2 (2.8)	27.3 (2.9)	10.6	19.2	132.6
		S26	3.0 (2.8)	28.0 (3.0)	12.7	17.2	115.2
		S23	4.2 (4.0)	26.2 (4.6)	13.5	19.6	112.2
		S95	1.9 (1.7)	27.9 (3.3)	9.4	16.8	105.8
July 1991	C2	S67	10.5 (9.0)	27.6 (3.0)	0.0	0.0	127.1
		S26	9.5 (8.0)	28.2 (2.3)	0.8	3.7	138.8
		S23	11.6 (9.6)	26.6 (4.0)	0.0	0.4	135.4
		S95	13.1 (9.5)	26.9 (4.1)	0.0	0.0	123.6

Table 3. Biological data from the microplankton at each station during the different COUPPB cruises. In the euphotic zone, each value represents an integration from 0 m to 1% of the surface incident radiation. Estimated respiration integrated (between the depth of 1% and 20 m off-bottom) in the aphotic zone are also shown. The ETS activity data (mg C m^{-2} d^{-1}) or ratios calculated from the ETS activity data are shown in parentheses. ER: euphotic respiration; AR: aphotic respiration; SP: surface production.

cruise	survey	station	1% depth (m)	chlorophyll a (mg m^{-2})	surface production (mg C m^{-2} d^{-1})	euphotic respiration (mg C m^{-2} d^{-1})	ER/SP	aphotic respiration (mg C m^{-2} d^{-1})	AR/SP	ER+AR/SP
July 1990	G2	S67	15	6	191	74 (218)	0.39 (1.14)	28 (406)	0.15 (1.86)	0.54 (3.00)
		S26	12	6	463	120 (352)	0.26 (0.76)	44 (640)	0.10 (1.38)	0.36 (2.14)
		S23	12	7	423	109 (322)	0.26 (0.76)	37 (538)	0.09 (1.27)	0.35 (2.03)
	G3	S67	10	9	-	54 (159)	-	50 (725)	-	-
		S26	12	23	1020	99 (293)	0.10 (0.29)	51 (734)	0.05 (0.72)	0.15 (1.01)
		S23	12	14	1196	130 (382)	0.11 (0.32)	46 (663)	0.04 (0.55)	0.15 (0.87)
	G4	S67	12	53	474	92 (271)	0.19 (0.57)	38 (550)	0.08 (1.16)	0.27 (1.73)
		S26	10	62	971	124 (364)	0.13 (0.37)	42 (609)	0.04 (0.63)	0.17 (1.00)
		S23	7	95	3587	309 (909)	0.09 (0.25)	78 (1124)	0.02 (0.31)	0.11 (0.56)
September 1990	G5	S67	12	33	-	90 (265)	-	49 (715)	-	-
		S26	12	28	-	74 (219)	-	30 (436)	-	-
		S23	14	356	-	216 (636)	-	34 (493)	-	-
May 1991	C1	S67	12	2	23	6 (19)	0.26 (0.83)	12 (180)	0.52 (7.83)	0.78 (8.66)
		S26	13	2	46	9 (28)	0.20 (0.61)	11 (166)	0.24 (3.61)	0.44 (4.22)
		S23	12	7	124	11 (32)	0.09 (0.26)	15 (216)	0.12 (1.74)	0.21 (2.00)
		S95	10	2	364	12 (36)	0.03 (0.10)	11 (153)	0.03 (0.42)	0.06 (0.52)
July 1991	C2	S67	12	20	1102	91 (269)	0.08 (0.24)	29 (424)	0.03 (0.38)	0.11 (0.62)
		S26	10	32	3129	136 (400)	0.04 (0.13)	31 (442)	0.01 (0.14)	0.05 (0.27)
		S23	18	27	1004	116 (340)	0.12 (0.34)	23 (333)	0.02 (0.33)	0.19 (0.45)
		S95	18	35	1450	125 (367)	0.09 (0.25)	29 (425)	0.02 (0.29)	0.11 (0.38)

Table 4. Matrix of Spearman correlation coefficients between physico-chemical and biological properties of the surface layer during the COUPPB cruises. The physical parameters were measured at the sea surface while the chemical data were from the shallowest depth. The difference in the physical values between 25 m and the sea surface was used as an index of stratification. Surface production (SP): mg C m^{-2} d^{-1}; chlorophyll a (CHL): mg m^{-2}; euphotic ETS activity (EETSA): mg C m^{-2} d^{-1}; aphotic ETS activity (AETSA): mg C m^{-2} d^{-1}; temperature (TEMP): °C; thermal stratification (ΔTEMP): °C; salinity (SAL): practical salinity unit; saline stratification (ΔSAL): psu; nitrate (NO_3): µM; silicate (SiO_4): µM; oxygen saturation (%OXY): %. Numbers in boldface indicate significance at $p < 0.05$.

	SP	CHL	EETSA	AETSA	TEMP	ΔTEMP	SAL	ΔSAL	NO_3	SiO_4	%OXY
SP	1.000										
CHL	**0.783**	1.000									
EETSA	**0.876**	**0.730**	1.000								
AETSA	**0.658**	**0.629**	**0.741**	1.000							
TEMP	**0.829**	**0.839**	**0.697**	**0.490**	1.000						
ΔTEMP	**0.796**	**0.810**	**0.611**	0.382	**0.940**	1.000					
SAL	-0.263	**-0.474**	**-0.459**	**-0.697**	-0.256	-0.187	1.000				
ΔSAL	0.244	**0.444**	0.315	0.181	0.271	0.288	**-0.702**	1.000			
NO_3	**-0.610**	-0.386	-0.379	-0.019	**-0.623**	**-0.678**	-0.140	-0.067	1.000		
SiO_4	**-0.860**	**-0.672**	**-0.754**	**-0.444**	**-0.923**	**-0.842**	0.127	-0.139	**0.695**	1.000	
%OXY	0.335	0.257	0.129	-0.202	0.412	**0.542**	0.266	0.069	**-0.595**	-0.378	1.000