

Lower Seine River and Estuary (France) Carbon and Oxygen Budgets During Low Flow

JOSETTE GARNIER^{1,*}, PIERRE SERVAIS², GILLES BILLEN¹, MAÏA AKOPIAN¹, and NATACHA BRION²

¹ *Unité Mixte de Recherche Sisyphe 7619 Centre National de Recherche Scientifique, BP 123, Tour 26, 5ème étage, 4 Place Jussieu, 75005 Paris, France*

² *Université Libre de Bruxelles, Ecologie des Systèmes Aquatiques, CP 221, Campus de la Plaine, 1050 Bruxelles, Belgium*

ABSTRACT: Ecological processes driving the oxygen budget were investigated in the downstream part of the Seine River and its estuary. Phytoplankton and bacterioplankton production were measured along longitudinal profiles (11 to 17 stations) in a range of low discharges from 300 m³ s⁻¹ in 1993 and 1995 to 140 m³ s⁻¹ in 1996. Values representative of the water column were based on investigations carried out during two tidal cycles. Net primary production was invariably greatest in the freshwater estuary, from Poses to Rouen (from 500 to 1,000 µg C l⁻¹ d⁻¹ between PK 202 and 240) and decreased sharply downstream (from 10 to 25 µg C l⁻¹ d⁻¹ between PK 250 and 310). This decrease was mainly due to the deterioration of the light conditions with the increase in depth and suspended matter concentrations. Heterotrophic activity was maximum in the reach where primary production declined. Judging by the production:respiration ratio (P:R), the system appeared clearly heterotrophic in the Seine River immediately downstream of the Paris region due to high allochthonous organic pollution by the incompletely treated Parisian effluents and in the part of the estuary characterized by intense degradation of autochthonous material. Because the effluents are not treated by a nitrification step, the oxygen consumption due to nitrification was much higher than expected from the P:R ratio. Oxidation of ammonium represented an oxygen consumption of between 1 and 14 g O₂ m⁻² d⁻¹, almost equalling the sum of heterotrophic respirations that were barely balanced by photosynthesis. The reaeration flux at the water-atmosphere interface was deduced from the calculations and a reaeration coefficient was estimated.

Introduction

The functioning of estuarine systems, which depends largely on inputs from rivers and coastal marine waters as well as on complex internal hydrodynamic sedimentological and microbial processes, is sometimes difficult to understand from field studies (Cloern and Nichols 1985; Nowicki and Oviat 1990). Estuaries have for too long been studied as separate entities of high primary production providing an abundant food supply, where nutrients are transformed and possibly trapped (Nixon and Pilson 1984; Nowicki and Oviatt 1990; Jordan et al. 1991). The awareness of the problems of coastal zone eutrophication has prompted development of a new approach which considers the entire river network and its estuarine zone as an interconnected whole including all systems from the headwaters to the coastal zone. Nutrient delivery to the marine system is seen as the result of transfers and transformations along the entire aquatic continuum. A hypothetical river was modeled in order to explore the chronological succession of human impacts on the basin, from pristine to present conditions, and to reproduce the main

trends of coastal eutrophication (Billen and Garnier 1997).

With these problems in mind, comprehensive programs were launched on the Seine River in 1989 (PIREN-Seine; see Meybeck et al. 1998) and on the Seine estuary in 1995 (Seine-Aval: this volume). In its downstream part, the Seine is greatly affected by the discharge of treated effluents by the Achères wastewater treatment plant (using the activated sludge process and treating 7.5 million inhabitants-equivalent from Paris and its suburbs). A typical feature of the ecological functioning of the Seine system is a strong summer deficit in oxygen immediately downstream of the Achères effluent outlet, due to degradation of organic matter (Garnier et al. 1992; Servais and Garnier 1993), and another deficit in its fluvial part due to nitrification of ammonium also contained in the effluents (Romana et al. 1992). The extensive knowledge gained on phytoplankton development and nutrient transfer (Garnier et al. 1995, 1998; Billen and Garnier 1999), as well as of heterotrophic organic matter degradation (Garnier et al. 1992; Servais and Garnier 1993) and nitrification (Brion 1997; Brion et al. 2000) was used to quantify all the major ecological processes involved in the oxygen budget in the Seine River and its estuary.

* Corresponding author; e-mail: jgarnier@biogeodis.jussieu.fr.

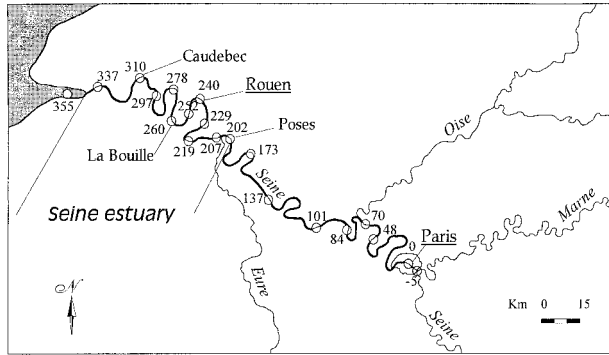


Fig. 1. Map of the investigated site in the Seine River. The sampled stations are indicated by their PK values.

The study was carried out in the summer mainly, along the course of the Seine River and its fluvial estuary from Paris to the coastal zone (Honfleur) to quantify the contribution of the different processes responsible for the oxygen deficit. Large-scale investigations of estuaries that include the river upstream are still scarce. Another objective was to improve our knowledge of the production versus respiration equilibrium in such human impacted ecosystems. Resulting data concerning the ecological processes and observations of the main variables of water quality were used in developing and validating a general ecological functioning model (Billen et al. 2001).

Study Site

The Seine estuary is the outlet of a drainage basin, characterized by high population density, heavy industrial activity, and intensive agriculture. This shallow estuary is rich in nutrients and organic matter. The weir at Poses, PK 202, 202 km from Paris (the Seine River is set at PK 0 in the center of Paris), represents the upstream limit of tidal propagation and of the estuary (Fig. 1). The freshwater part of the estuary extends down to Caudebec (PK 310), which represents the upstream limit of saline intrusion. From Caudebec to Honfleur (PK 350), the mouth of the estuary, there is a continuous salinity gradient influenced mainly by tides and river flow. In the oligohaline part (PK 310–320) salinity ranges from 0‰ to 10‰, in the polyhaline part (PK 320–337) salinity ranges from 5‰ to 20‰, and salinity reaches 33.2‰ in the euhaline part. Seasonally, the temperature rises to 20°C in summer with differences of less than 1°C along a longitudinal profile and with no vertical gradient. Oxygen conditions vary widely, from nearly full saturation to a state of strong depletion in summer (< 2 mg l⁻¹), mainly in the freshwater part of the estuary. The turbidity maximum (up to 2 g l⁻¹ of suspended matter) moves between Tan-

carville (PK 337) and the open sea, depending on the river discharge and the tide intensity.

Sampling

All sampling programs were carried out during stable meteorological periods. Both spatial and temporal variability of phytoplankton production and bacterial heterotrophic activity were investigated.

Vertical heterogeneity in the large meander of La Bouille (Fig. 1) was studied during two tidal cycles on April 3 and September 27, 1996 (river discharge of 260 and 180 m³ s⁻¹ in April and September and tide coefficient, i.e., relative tidal range in % of the mean spring equinox tidal range, 6.7 m, given for the Brest Harbor on the French Atlantic Coast, of 87 and 108, respectively for the two campaigns). In April, samples were pumped from a pier from three different depths on one bank. In September, samples were taken from a ship at three different depths, in the middle of the estuary and close to the two banks.

Sampling along longitudinal profiles was carried out at low water in the spring and the summer of 1993 (300 m³ s⁻¹) and in the summers of 1995 (300 m³ s⁻¹) and 1996 (140 m³ s⁻¹). Seventeen stations were sampled from Paris (PK 0) to the coastal zone at Honfleur (PK 350; Fig. 1). Each longitudinal profile was completed in 3 d. On days 1 and 2, samples of surface water were taken from bridges with a bucket in the river and in the upstream part of the estuary (from PK 0 to 229), going downstream; on day 3, samples were collected 1 m below the surface (with a peristaltic pump) from a ship, going upstream in the estuary from PK 350 to PK 260. Samples were taken during the flood, except at the three downstream stations where they were taken at the end of the ebb (Fig. 1). The residence time was about 10–15 d under these stationary conditions. Results therefore represent snapshots of the spatial variability of the water quality and metabolisms.

Methods

Oxygen was measured with a YSI probe in the river and with Winkler's method in the estuary during sampling. The fluxes were calculated as the product of river discharge and concentrations that were measured during the sampling. The oxygen budget, excluding the reaeration at the air-water interface, was calculated as the difference between oxygen inflowing into the considered reach and the flux at the outlet of the same reach. Oxygen inflow is represented by the sum of the fluxes at the inlet of the reach and the tributaries if any, those of the wastewater effluents discharging into the sector, and the reaeration at the weirs calcu-

lated according to Holler's empirical formula, as calibrated by Hervé and Falguière (1982):

$$\begin{aligned} & (\text{satO}_2 - \text{upstreamO}_2) / (\text{satO}_2 - \text{downstreamO}_2) \\ & = 1 + 0.21H \end{aligned}$$

where satO_2 is the oxygen concentration at saturation and H is the height (m) of the waterfall.

Phosphate, dissolved silica, and ammonium were determined spectrophotometrically on glass-fiber membrane (Whatman, GF/F) filtered water (Eberlein and Katter 1987; Rodier 1984; Slawyc and MacIsaac 1972, respectively). Nitrate was assessed spectrophotometrically on filtered water after cadmium-reduction to nitrite (Rodier 1984). Suspended matter was weighed on a GF/F (dried filter). Organic carbon concentrations were measured on water samples preserved with HgCl_2 . Particulate organic carbon determination was performed on suspended matter harvested on a 12 mm diameter filter GF/F (ignited at 550°C). Dissolved organic carbon (DOC) and particulate organic carbon (POC) concentrations were measured using a total organic carbon analyzer (Dohrmann DC-180, Belgium) which uses UV-promoted persulfate oxidation. Biodegradable DOC (BDOC) concentrations were estimated as the difference of DOC concentrations measured before and after a 30 d incubation at 20°C with indigenous bacteria (Servais et al. 1989).

Chlorophyll *a* (chl *a*) concentration was determined according to Lorenzen (1967). Photosynthesis parameters were measured with a method derived from Steemann-Nielsen (1952) in an incubator with controlled light intensity and temperature. About 10 samples of 20 ml of water inoculated with ^{14}C ($0.5 \mu\text{Ci ml}^{-1}$, Amersham 50–60 mCi mmol^{-1}) were incubated in a light gradient (from 10 to $1,000 \mu\text{Einst m}^{-2} \text{s}^{-1}$) at in situ temperature for 1 h. The initial slope in limiting light (α) and maximum rate of specific photosynthesis (P_{Bm}) were estimated by best fitting of Platt et al.'s equation (1980) to the data.

From these parameter values, in situ rates of photosynthesis, growth, and respiration were calculated according to the formulation by Lancelot et al. (1991), which distinguishes between photosynthesis controlled by light intensity and algal growth, controlled by nutrient availability (the Aquaphy model). The module was adapted to two groups of algae (diatoms and non-diatoms) and a formulation for losses by excretion and grazing was added (Garnier et al. 1995, 1998). Growth is regulated by the size of an intracellular pool of carbon precursors formed either directly by photosynthesis or by remobilization of reserves. The size of the

precursor pool is also controlled by excretion and respiration, the latter being represented by the sum of a term related to the energetic cost of growth (new macromolecules synthesis) and a term of maintenance of the biomass (Lancelot et al. 1991). The model calculates the daily values of these activities after integration over time and depth of the water column, assuming no stratification of phytoplankton biomass. Water temperature values, mean irradiance, and photoperiod are represented by sine functions (Billen et al. 1994) validated on a long-term series of data collected at the meteorological station of Trappes in the low Seine River watershed. The following relationship between the extinction coefficient (K , m^{-1}), inorganic suspended matter (SM, g m^{-3}), and chl *a* concentration (mg m^{-3}) was established empirically based on more than 50 observations in the estuary and the river and was taken constant over the water column.

$$K = 0.32 + 0.03 \text{ SM} + 0.03 \text{ chl } a$$

The mean value of suspended matter over the tidal cycle is considered for the integration over 24 h. Oxygen production by photosynthesis and consumption by respiration were estimated from these calculations, by means of a simple 1:1 molar stoichiometric coefficient between carbon and oxygen for both processes.

Bacterial production was estimated on the basis of leucine incorporation rates (Kirchman et al. 1985). Incorporation of ^3H -leucine (Amersham 165 Ci mmol^{-1}) was measured at four leucine concentrations which ranged from 2 to 77 nM (2 nM of tritiated leucine in each case with 0, 25, 50, and 75 nM non-radioactive leucine). Four 5-ml subsamples were incubated in the presence of the different concentrations of leucine for 30 min in the dark at in situ temperature. After incubation, cold trichloroacetic acid (TCA) was added (final concentration of 5%) and the samples were filtered through a $0.2 \mu\text{m}$ pore size cellulose acetate membrane (cold TCA procedure). Radioactivity associated with the filters was estimated by liquid scintillation. In some cases, duplicates were performed and heated to 85°C for 30 min after acidification following the procedure proposed by Kirchman et al. (1985) to specifically measure the incorporation into the proteins (hot-TCA procedure). The average ratio between the hot and the cold-TCA procedure was 0.93 ± 0.03 indicating that on average 7% of the radioactivity was not incorporated into proteins but into other macromolecules. This ratio is in agreement with other values mentioned in the literature for various aquatic systems (Servais 1995). When only the cold-TCA procedure was performed, incorporation rates were corrected ac-

cordingly. The maximum incorporation rates were estimated by best fitting of a hyperbolic function to the experimental data by means of a software based on the least squares criterion (Servais 1995). Bacterial production estimated from leucine incorporation (BPL) was calculated by multiplying the maximum incorporation rate into proteins by a conversion factor of 900 gC mol⁻¹ experimentally determined in the Seine River (Servais and Garnier 1993). Bacterial carbon demand was calculated by dividing bacterial production by the growth yield. A value of 0.3 was considered for the bacterial growth yield as previously determined for Seine River bacteria (Barillier and Garnier 1993). Oxygen consumption by heterotrophic activity was estimated with a carbon to oxygen molar ratio of 1. As the heterotrophic bacterial activity did not show any significant difference when measured in homogenized water samples and in the water after decanting of particulate matter, bacterial production was considered to be evenly distributed within the water column at any moment of the tidal cycle.

Bacterial abundance was determined by epifluorescence microscopy at 1,000× magnification, following the procedure proposed by Porter and Feig (1980). During the microscopic observations, bacteria were classified into 24 size classes by comparison to an eye-piece graticule, and the cell volume (V ; $\mu\text{m}^3 \text{ cell}^{-1}$) in each class was calculated (Garnier 1989). Biomass was estimated from abundance and biovolume distribution using the relationship determined from Simon and Azam's data (1989). A statistical study showed that the variation coefficient of the bacterial biomass estimates, following this protocol, was on average about 20%.

Nitrification was estimated by the difference between the ammonium flux entering in any reach and that at the outlet of the considered reach. These fluxes were all calculated as the product of the values of water discharge and concentrations. The N-NH₄ flux entering the reach has been calculated as a sum of the fluxes at the inlet of the reach, of the tributaries if any, and of those of the effluents located within the sector. The corresponding oxygen consumption rate was calculated by considering that 2 moles of oxygen are consumed for 1 mole of ammonium oxidized. The contribution of nitrification to the carbon budget was estimated on the basis of the growth yield (ratio of incorporated C to oxidized N) of 0.11 (mol mol⁻¹) found by Brion and Billen (1998) for pure cultures of nitrifying bacteria.

Results

HETEROGENEITY DURING TWO TIDAL CYCLES

Results of investigations carried out during two tidal cycles in April and September 1996 are shown

in Fig. 2. The two situations differed strongly regarding both the particulate and the dissolved phases, not only because hydrological conditions were different (260 and 180 m³ s⁻¹ in April and September, respectively), but also because September represented the end of the summer season during which suspended matter had accumulated in the estuary (Brion 1997; Brion et al. 2000).

The distribution of SM, POC, and chl *a* showed similar patterns, i.e., higher values in September than in April as well as greater heterogeneity within the water column (average values of SM of 26 and 200 mg l⁻¹, average values of POC of 5 and 8 mg C l⁻¹, in April and September, respectively; Fig. 2). Average concentrations of chl *a* within the water column were, however, quite similar at both times (70 and 80 $\mu\text{g chl } a \text{ l}^{-1}$ in April and September, respectively).

As the water column is well mixed, dissolved material was almost homogeneous over depth and time both in April and September (Fig. 2). Concentration of PO₄ was much lower in April, due to a dilution of point sources by higher discharge rates. Regarding silica, originating from rock weathering in the watershed, the lower April values were due to the development of spring diatoms.

LONGITUDINAL PROFILES OF WATER QUALITY

The longitudinal profiles, observed in similar summer conditions, all showed a similar pattern. Values were therefore averaged and are shown with error bars. The longitudinal variations of oxygen concentrations clearly showed two sectors of oxygen depletion. The first one, of limited extent, in the Seine River, is immediately downstream from the discharge point of the treated effluents of 7.5 million inhabitants-equivalent from Paris agglomeration, while the other one is in the freshwater part of the estuary, with much slower recovery (Fig. 3).

Phytoplankton biomass, given by chl *a* concentrations, was rather low (30 $\mu\text{g chl } a \text{ l}^{-1}$) compared to the value obtained in the spring of 1993 (180 $\mu\text{g chl } a \text{ l}^{-1}$; Fig. 4). The specific rate of maximum photosynthesis (P_{Bm} , $\mu\text{g C } \mu\text{g chl } a^{-1} \text{ h}^{-1}$) showed little variation along the longitudinal profile, although smaller values were observed in the estuarine part. Net depth integrated primary production, calculated by the model (expressed in $\mu\text{g C l}^{-1} \text{ d}^{-1}$ for the whole water column), showed a sharp decrease in the Rouen sector when depth, particulate organic matter as well as total SM concentration increased, light being the major limiting factor (Fig. 5).

Heterotrophic bacterial biomass and production in the water column increased according to effluent discharges, coinciding with the sectors of oxy-

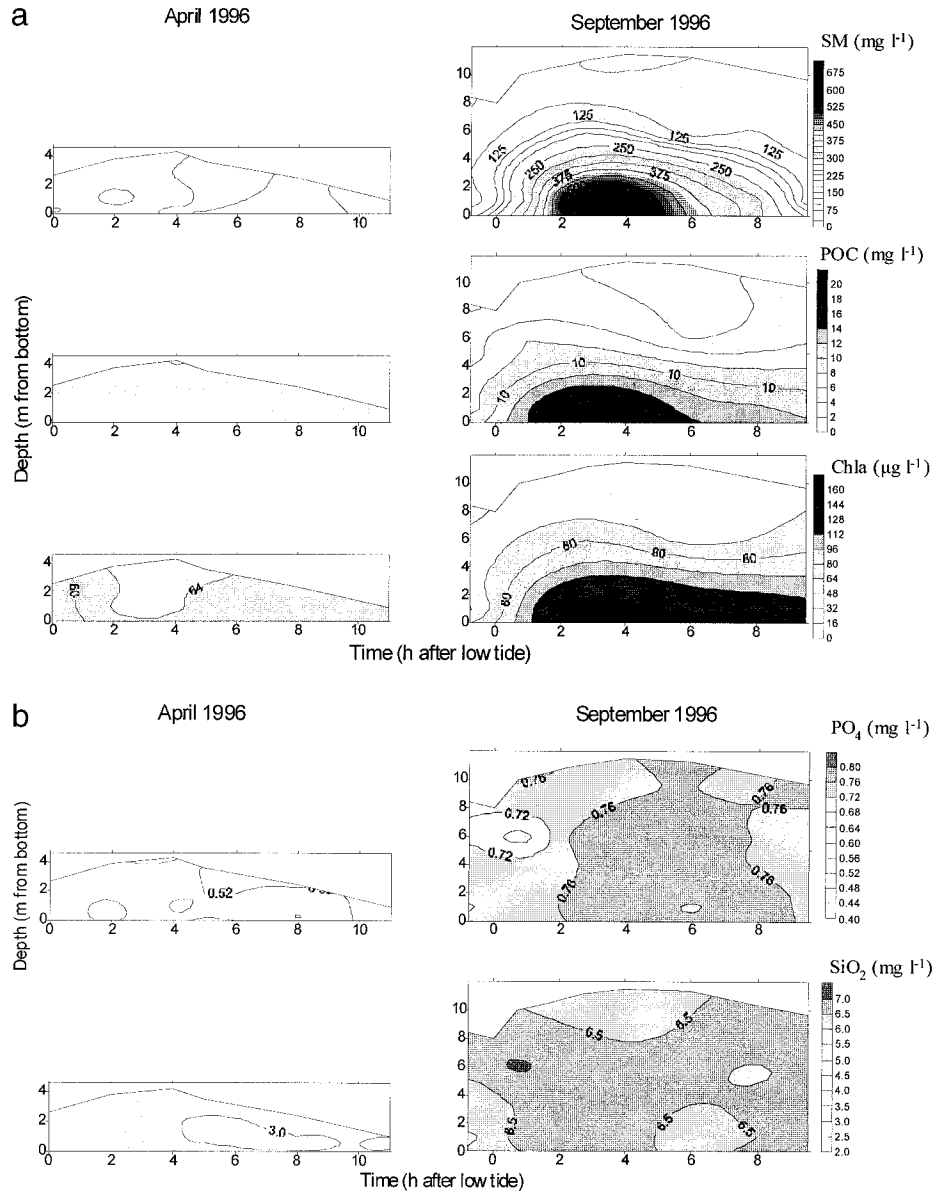


Fig. 2. Variations of suspended matter (SM; mg l^{-1}), particulate organic matter (POC; mg C l^{-1}), chlorophyll *a* ($\mu\text{g chl } a \text{ l}^{-1}$), phosphate (mg P l^{-1}), and dissolved silica ($\text{mg SiO}_2 \text{ l}^{-1}$) concentrations during two tidal cycles (Val-des-Leux (VL) and Moulineaux (M) in April and September 1996, respectively (see location in Fig. 1). Representation as isocurves by the SURFER software. The reference time (0 h means low tide) on x-axis, depth (m) on y-axis.

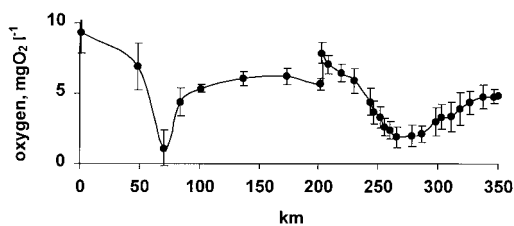


Fig. 3. Longitudinal variations of oxygen concentrations from Paris (PK 0) to Honfleur, the mouth of the estuary (PK 350).

gen depletion: the first increase occurred downstream of the Parisian zone and the second, smaller one, in the estuary (Fig. 6). Comparisons with data gathered from 1989 to 1991 (Garnier et al. 1992; Servais and Garnier 1993), showed that the impact of the Achères treatment plant appeared much stronger when samples were taken at shorter distance intervals in this organically polluted sector. The impact of the plant was greatly attenuated below the confluence with the Oise River (PK 72). The increase of bacterial production and biomass

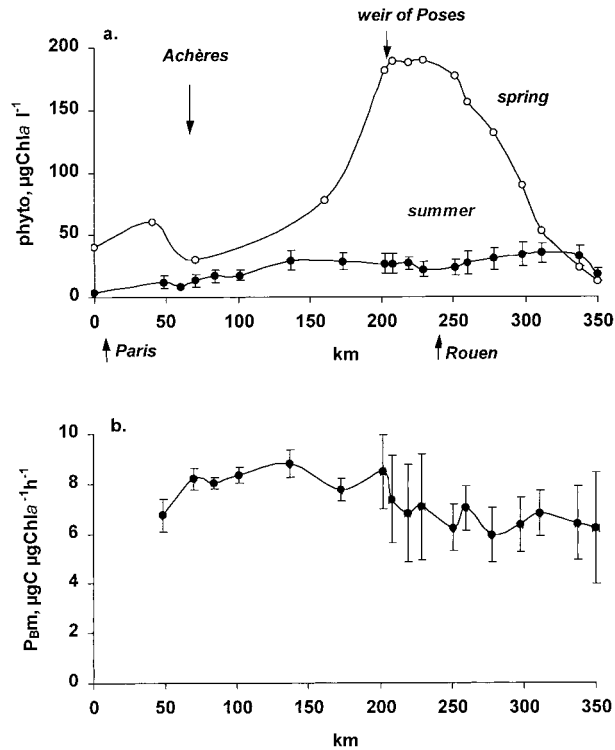


Fig. 4. a) Longitudinal variations of chlorophyll *a* concentrations ($\mu\text{g chl } a \text{ l}^{-1}$) and b) specific maximum photosynthetic rate (P_{Bm} , $\mu\text{g C } \mu\text{g chl } a^{-1} \text{ h}^{-1}$) from Paris (PK 0) to Honfleur, the mouth of the estuary (PK 350).

previously observed just downstream the Achères treatment plant effluent outfall was much more important (Servais and Garnier 1993). Regarding DOC, a general decrease was observed from the Parisian effluent discharge point to the mouth of the estuary, its biodegradable fraction representing about 40% of the total (Fig. 6).

CARBON BUDGET IN THE WATER COLUMN: ORGANIC MATTER PRODUCTION AND DEGRADATION

The balance of the carbon budget of any ecosystem can be characterized by the ratio between autotrophic production (P) and gross respiration (R) of organic matter. In a closed system at equilibrium, the P:R ratio equals 1; autotrophy is regulated by the supply of nutrients from the mineralization of autochthonous organic matter. When the system is supplied by external sources of nutrients, autotrophic metabolism can exceed respiration ($P:R > 1$); conversely with an input of allochthonous organic matter, heterotrophic processes can dominate ($P:R < 1$).

In the Seine River and estuary, we calculated autotrophic production as the sum of phytoplankton net primary production and the autotrophic production of nitrifying bacteria. Heterotrophic activ-

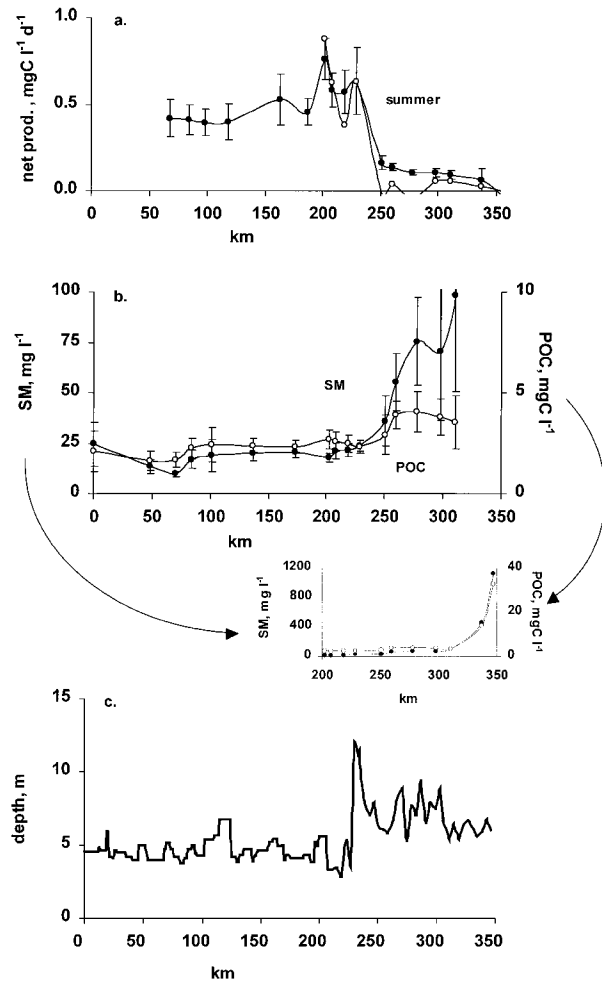


Fig. 5. a) Longitudinal variations of net primary production (net PP, $\mu\text{g C l}^{-1} \text{ h}^{-1}$) from Paris (PK 0) to Honfleur, the mouth of the estuary (PK 350). b) Suspended matter (mg C l^{-1}), particulate organic matter (mg C l^{-1}), and c) mean depth (m) of the water column are shown in comparison. Note that suspended matter and particulate organic matter are represented according to two scales (0–100 and 0–1,200 mg l^{-1} and 0–10 and 0–40 mg C l^{-1} , respectively).

ity is calculated from net production of bacterial biomass divided by growth yield, thus assuming that heterotrophic production is completely consumed and respired by predators (protozoa, zooplankton). Benthic heterotrophic activity, not measured in this study, was evaluated from oxygen consumption in bell jars deposited on bottom sediments in 1991 and 1992 at PK 65 and 202 (Garban et al. 1995; Garban and Ollivon personal communication). A mean sediment oxygen consumption of $117 \text{ mg O}_2 \text{ m}^{-2} \text{ h}^{-1}$ (from 60 to $300 \text{ mg O}_2 \text{ m}^{-2} \text{ h}^{-1}$) was calculated on the basis of 9 experiments (Garban et al. 1995; Garban and Ollivon personal communication). Assuming a respiration quotient of 1, this value corresponds to a respiration of

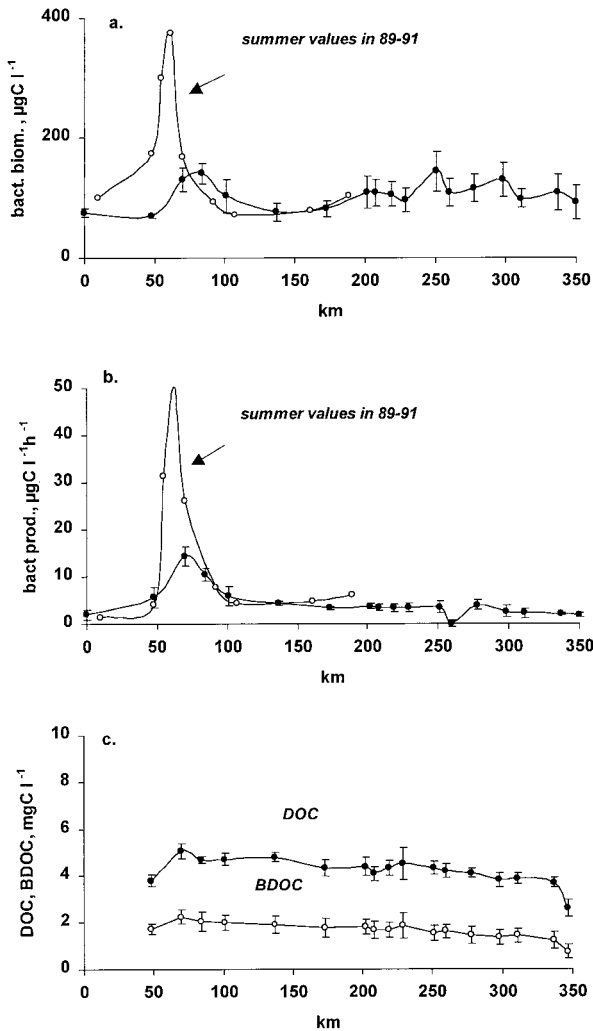


Fig. 6. a) Longitudinal variations of bacterial biomass ($\mu\text{g C l}^{-1}$) and b) net production ($\mu\text{g C l}^{-1} \text{h}^{-1}$) from Paris (PK 0) to Honfleur, the mouth of the estuary (PK 350). c) Dissolved organic carbon and biodegradable dissolved organic carbon concentrations (DOC and BDOC respectively, mg C l^{-1}) are shown in comparison.

about $1 \text{ g C m}^{-2} \text{ d}^{-1}$. The same value was assumed for the whole investigated sector and was included in the calculation of R.

In the Seine River, the sector downstream from the Achères wastewater treatment plant was highly heterotrophic, judging from its P:R ratio (Fig. 7). Balanced conditions were restored below the confluence of the Oise River, and became autotrophic around Poses. Along all the sectors of the lower Seine and upstream estuary, nitrification represent less than 6% of the total autotrophic metabolism. Downstream, the increase in depth (and decrease in net primary production) together with the mineralization of organic matter from domestic and industrial effluents and the nitrification of ammo-

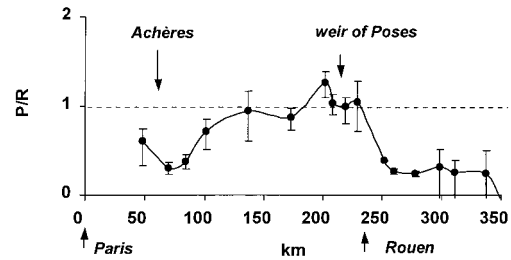


Fig. 7. Longitudinal variations of the P:R ratio, from Paris (PK 0) to Honfleur (km 350), the mouth of the estuary.

nia rendered the system heterotrophic as far as the mouth of the estuary. In this sector, nitrification amounted to 30–70% of the total autotrophic metabolism.

The total uptake of organic carbon by bacteria in the fluvial part of the estuary (PK 202 to 297) can be compared to the total amount of biodegradable organic matter originating from the same sector (net local production of biomass by phytoplankton, inputs of effluents and upstream river inputs such as phytoplankton biomass, biodegradable dissolved and particulate organic matter, Table 1). Bacterial uptake (demand) of organic matter was generally far lower than the amount available from these inputs, implying that a significant amount of carbon was exported downstream from this sector (Table 1).

TABLE 1. Organic carbon uptake by bacteria in the fluvial estuary (Poses-Heurtauville, PK 202–297). Comparison with the sources of biodegradable carbon in this sector and with the upstream river inputs. Units are given in t C d^{-1} . C uptake: mean bacterial production measured for the sector ($\mu\text{g C l}^{-1} \text{h}^{-1}$) \times 24 h/bacterial growth yield taken at 0.3 (Barillier and Garnier 1993) multiplied by the volume of the sector ($154.637 \times 10^6 \text{ m}^3$). C effluents: daily carbon flux brought by the wastewater treatment plant (data from the Service de Navigation de la Seine). Net PP: mean net primary production for the sector, calculated with the Aquaphy model from ^{14}C measurements multiplied by the volume of the sector ($154.637 \times 10^6 \text{ m}^3$). Phyto: phytoplanktonic carbon calculated from chl *a* ($\mu\text{g l}^{-1}$) values and a C:chl *a* ratio = 40 multiplied by the water discharge at Poses ($\text{m}^3 \text{ d}^{-1}$). BDOC: Biodegradable organic matter (mg C l^{-1}) multiplied by the water discharge at Poses ($\text{m}^3 \text{ d}^{-1}$). Detrit BPOC: difference between POC and phytoplanktonic carbon, calculated from chl *a* ($\mu\text{g l}^{-1}$) values and a C:chl *a* ratio = 40, taking the biodegradable fraction at 25% (i.e., detrital fraction at 75%). nd = not determined.

	Poses-Heurtauville			Upstream River Inputs		
	C Uptake	C Effluents	Net PP	Phyto	BDOC	Detrit BPOC
March 1993	31	13	22	187	44	nd
May 1993	48	13	17	21	52	nd
July 1995	81	13	31	41	35	9
Sept. 1995	35	13	16	29	71	5
July 1996	51	13	25	13	15	4

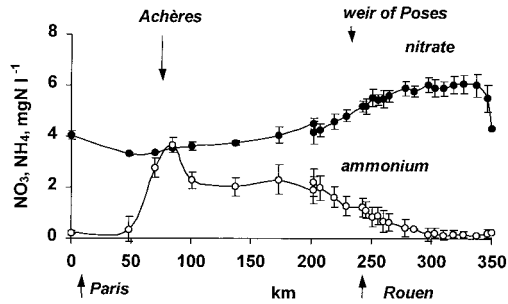


Fig. 8. Longitudinal variations of ammonium and nitrate concentrations (mg N l^{-1}) from Paris (PK 0) to Honfleur (PK 350), the mouth of the estuary.

OXYGEN BUDGET IN THE SEINE ESTUARY

Whereas primary production and heterotrophic bacterial degradation can be considered as the main processes involved in the carbon budget, the oxygen budget is much more influenced by the nitrification of ammonium. As shown in Fig. 8, ammonium brought in by the Achères wastewater treatment plant is nitrified downstream. A regular decrease in ammonium and increase in nitrate appeared from PK 202. Nitrification was completed at Caudebec (PK 310), the limit of the freshwater part of the estuary.

The median value of benthic oxygen consumption was $117 \text{ mg O}_2 \text{ m}^{-2} \text{ h}^{-1}$, a value that was used for the whole of the investigated longitudinal profile.

The values of the processes along the longitudinal profiles were converted into oxygen fluxes within 6 reaches (Tables 2 and 3): Maison Laffitte PK 48–Conflans PK 70, Conflans PK 70–Porcheville PK 101, Porcheville PK 101–Poses PK 202, Poses PK 202–Oissel PK 229, Oissel PK 229–Docks PK 251, and Docks PK 251–Heurteville PK 297.

TABLE 3. Comparison between the oxygen budget of the microbial processes and the in-out oxygen budget for each of the reaches. Standard deviation are given in parentheses. Proc budget: budget of the microbial processes ($\text{t O}_2 \text{ d}^{-1}$) expressed from Table 2 for each entire sector. In-out budget: budget calculated by the difference between oxygen inflow and outflow ($\text{t O}_2 \text{ d}^{-1}$) for the considered reach (see the text). Reaeration: calculated by the difference between the in-out and process budgets, divided by the surface area (in Table 2) of the considered reach, average value from 1993 to 1996 ($\text{mg O}_2 \text{ m}^{-2} \text{ d}^{-1}$). Csat-O₂: average deficit of oxygen saturation ($\text{mg O}_2 \text{ l}^{-1}$), i.e., difference between the oxygen concentration at saturation and the mean oxygen value for each reach.

Reaches	Proc budget	In-out budget	Reaeration	Csat-O ₂
Mais L–Conflans PK 48–70	–37 (22)	–26 (18)	127	5.4
Conf–Porch PK 70–101	–141 (5)	–7 (10)	195	4.7
Porch–Poses PK 101–202	–96 (19)	–46 (33)	98	4.2
Poses–Oissel PK 202–229	–69 (63)	–34 (17)	217	3.1
Oissel–Dock PK 229–251	–68 (48)	–49 (16)	149	4.7
Dock–Heurt. PK 251–297	–150 (35)	–51 (43)	252	6.9

In order to compare the intensity of the processes within each of the reaches, values are first given in $\text{g O}_2 \text{ m}^{-2} \text{ h}^{-1}$ in Table 2, that quantify the trends shown in the longitudinal profile figures (note that the trends are the same whether the values are given as $\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ or as $\text{g O}_2 \text{ km}^{-1} \text{ d}^{-1}$). The oxygen balance of the processes was invariably negative within all the investigated reaches (consumption terms exceeding the production term). Consumption is high in the first reach downstream of the Achères treatment plant (about $10 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) and mainly due to planktonic heterotrophic activity; it is maximum in the up-

TABLE 2. Average oxygen budget calculated from microbial processes within the six reaches of the downstream Seine River and fluvial estuary along longitudinal summer profiles from 1993 to 1996. Units are given in $\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ for a comparison between the different reaches. Photosynth: photosynthesis or gross primary production. Phyto resp: phytoplankton respiration as calculated by the Aquaphy model (see Methods). Bac min: bacterial oxygen mineralization, considering that the biomass produced is also mineralized by bacterial predators. Benth resp: benthic respiration (see the text). Nitrif: oxygen consumption by nitrification (see the text). Proc budget: budget of the microbial processes, i.e., sum of oxygen production and the respirations.

Reaches	Length (km)	Volume (10^3 m^3)	Surface (10^3 m^2)	Photosynth	Phyto resp	Bac min	Benth res	Nitrif	Proc budget
Mais L–Conflans PK 48–70	22	16,188	3,745	6.8	–1.9	–10.8	–2.8	–1.2	–9.9
Conf–Porch PK 70–101	31	28,558	28,658	1.5	–0.4	–2.1	–2.8	–1.1	–4.9
Porch–Poses PK 101–202	101	101,883	21,451	9.6	–2.7	–4.0	–2.8	–4.6	–4.5
Poses–Oissel PK 202–229	27	26,247	5,708	11.9	–3.6	–3.4	–2.8	–14.3	–12.2
Oissel–Dock PK 229–251	22	37,770	4,773	13.1	–3.9	–6.8	–2.8	–13.7	–14.2
Dock–Huert. PK 251–297	46	90,620	12,694	4.9	–2.0	–6.2	–2.8	–5.7	–11.8

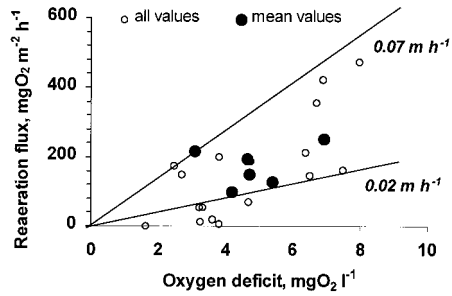


Fig. 9. Estimates of the reaeration coefficient in different reaches of the downstream Seine River (from Paris to the mouth of the estuary).

stream part of the estuary due to nitrification, where oxygen consumption by respiration is almost balanced by oxygen production through photosynthesis (Table 2).

In Table 3, the oxygen budget of the microbial processes in all reaches, in metric tons $O_2 d^{-1}$, is compared to the difference between the oxygen fluxes coming in and out each reach. The oxygen influxes accompanying the $25 m^3 s^{-1}$ of treated effluents from Achères and the other wastewater treatment plants along the downstream course of the river and estuary, the discharge of the tributaries (Oise River in the reach Conflans-Porcheville and Eure River in the reach Poses-Oissel), and the reaeration at weirs calculated by the Holler's formula (see Methods) are also taken into account.

If we consider that the budget of all processes and influxes discussed above is balanced by reaeration through the air-water interface, the latter can be estimated for each reach and each documented situation. These estimates, converted into $mg O_2 m^{-2} h^{-1}$ are plotted against the average deficit in oxygen concentration with respect to saturation for each reach (Fig. 9). These data indicate a reaeration coefficient in the range of 0.02 to 0.06 $m h^{-1}$, in good agreement with the estimates made by Thibodeaux et al. (1994) for the fluvial part of the Seine River (0.02 to 0.07 $m h^{-1}$).

Discussion

ECOLOGICAL PROCESSES

Phytoplankton determines a major part of primary production in estuaries and is fundamental to the ecosystem functioning and the local economy. Besides oxygen production, phytoplankton is at the root of energy flow through the food web. Primary production in the Seine freshwater tidal estuary, reaching $3.4 g C m^2 d^{-1}$ ($2.3 g C m^2 d^{-1}$ as a summer average in the more productive reaches) was in the upper range of the many values found in literature (see Flint 1984 and Pennock and Sharp 1986 for selected estuaries in the

world). In the lower deeper estuary, where turbidity is higher, net primary production may be negative, with phytoplankton respiration exceeding net production. In such cases, phytoplankton stock would be fed by inputs at the boundaries (Cole et al. 1992). Light is therefore a critical variable controlling phytoplankton production and distribution, especially in the nutrient-rich waters of the Seine River and estuary. Whereas integral productivity throughout the water column strongly decreased with increasing depth and turbidity in the lower reaches, a concomitant overall decrease in the specific rate of photosynthesis ($P_{b,m}$: from 8 to 6 $mg C \mu g chl a^{-1} h^{-1}$ and higher variability) was also observed. Algal respiration, representing up to 50% of the net production, became a real sink for photosynthetically assimilated carbon, important to take into account in primary production studies (Joint and Pomroy 1981; Cloern et al. 1985; Jensen et al. 1990; Cole et al. 1992). Phytoplankton in estuaries may, however, be controlled by many other factors such as physical-chemical ones (mixed currents, tide and wind, salinity, nutrients) or biological ones (parasitism, grazing). Concentrations of dissolved inorganic nutrients (nitrogen, phosphorous, silicon) generally exceeded the rate-limiting level, except during spring phytoplankton bloom when silica may be depleted in the drainage network (Garnier et al. 1995). Similar to the situation in the San Francisco Bay, invaded by *Potamocorbula amurensis* (Alpine and Cloern 1992), the biological control by the invasive *Dreissena polymorpha* was shown to be strong in the upper Seine estuary, as estimated through the flux of the larvae (Akopian et al. 2001).

Within the Seine estuary, high autochthonous production supplemented by discharge of wastewater together with large riverine input of organic matter supported a bacterial production of 3 to 5 $\mu g C l^{-1} h^{-1}$ and 2 to 3 $\mu g C l^{-1} h^{-1}$, respectively, in the upper autotrophic and lower heterotrophic estuary, which is in the upper range of values found in other systems (Painchaud and Theriault 1989; Ducklow and Carlson 1992; Pomeroy et al. 1995; Murrel et al. 1999). Bacterial production did not increase in the turbidity maximum zone but decreased along with BDOC concentrations. Regarding the values of bacterial production where treated effluents are discharged into the river (about 15 and up to 50 $\mu g C l^{-1} h^{-1}$, see Servais and Garnier 1993), labile organic molecules might be a limiting factor in the turbidity maximum. In the turbidity maximum, organic carbon accounted for 3 $mg C l^{-1}$ of DOC (30% of BDOC) and about 30 $mg C l^{-1}$ of POC (representing quite a high fraction, 4% in average but up to 10%, of suspended particulate material). Most of our results are

based on summer investigations and since particulate organic matter ages as the season progresses, it might become unavailable for bacteria (Murrell et al. 1999). This explanation is supported by the large fraction of bacterial biomass (70%) and an even larger fraction of bacterial production (98%) that were not decantable (i.e., not attached to particles). Alternatively adsorbed micropollutants may become toxic to bacteria in such a polluted system (Guézennec et al. 1999).

Besides being a source of organic matter, the treated effluents discharged into the Seine River are rich in ammonia. After having been diluted by the Oise River, ammonia was transported 100 km down to the estuary without any noticeable change in concentration. Transformation of ammonium into nitrate was accelerated in the freshwater section of the estuary as soon as the population of nitrifiers, present in low quantities (they originate from both effluent waters [Servais et al. 1999] and the upstream network), can build up a large biomass. These conditions were mostly met in the summer, when temperature was high, hydraulic residence time is sufficiently long, and SM concentrations are relatively high. The attachment of nitrifying bacteria to particles is well documented (Owens 1986; Admiral and Bottermans 1989; Brion 1997). The fact that the residence time of the particles is longer than that of the water (Guézennec et al. 1999) amplifies the nitrification process. In order to estimate the oxygen consumption from ammonium disappearance within each of the reaches, we assumed that the mineralization of organic nitrogen along the established longitudinal profiles was balanced by biological uptake, and we calculated that these fluxes were low compared to nitrification.

OXYGEN BUDGET

Summer oxygen depletion in the fluvial estuary of the Seine River is a constant feature of the ecological functioning of the system and represents a major disturbance for aquatic life. Hypoxia (below 2–3 mg O₂ l⁻¹) is a common estuarine phenomenon (see references in Ritter and Montagna 1999). As opposed to many situations where low summer oxygen levels are, besides flushing time, related to stratification (temperature, salinity), or decomposition of organic matter in the turbidity maximum, the oxygen budget in the Seine estuary revealed a large contribution of both nitrification and respirations (planktonic bacterial, benthic, as well as phytoplanktonic). Oxygen depletion dominated by nitrification could be a constant feature in large systems strongly impacted by domestic/industrial effluents not treated through a nitrification step, as is still often the case in Europe.

The calculation of the oxygen budget appears to be a very useful way of checking the coherence of separate measurements. Unfortunately, whereas the values of the ecological processes and fluxes at the boundaries of the reaches can be given with small variations, other components of the budget, such as point sources along the reaches and reaeration at the navigation weirs, introduce uncertainties so that cumulative errors may become large when all values are combined. If such budgets were not estimated, a general view of the system could not be obtained. We produced an average oxygen budget representative of summer situations, with standard deviations. The values found by difference for the reaeration at the water-atmosphere interface seem to be realistic (Thibodeaux et al. 1994) and to validate our approach. Although several earlier attempts have been made, with a variety of approaches, to measure major metabolisms in estuaries (Nixon and Pilson 1984 and cited references; Relexans et al. 1988; Kemp et al. 1997; Caffrey et al. 1998), examples are still too scarce and net ecosystem metabolism only refers to primary production and total system respiration. They do not consider the river-estuary as one connected system. Compared to the cases mentioned above, the Seine system has the specificity to receive the effluents of a huge sewage treatment plant in the lower part of its course, strongly influencing the estuary functioning through the nitrification of ammonia.

CARBON BUDGET

Vannote et al. (1980), in their river continuum concept, proposed a general scheme of an upstream-downstream succession of P:R status (production versus respiration) of undisturbed rivers. Large rivers are particularly affected by human impacts (organic pollution, hydraulic management) to the extent that the P:R sequences may be strongly modified (Garnier et al. 1999). A previous study of the upstream part of the Seine River showed that eutrophication led to heterotrophic conditions in the main branch of the major sub-basins (the Marne, upstream Seine, the Oise), when phytoplankton declined sharply and consumed more oxygen than it produced (Garnier et al. 1998). Many studies related to autotrophic versus heterotrophic metabolisms are reported in the literature but most of them concern phytoplankton and bacterial production coupling in oceans or lakes, analyzed on the basis of the microbial loop concept. In the Seine River and estuary, P:R represented the ratio between the sum of autotrophic metabolisms (net primary production and nitrification) and the sum of benthic and planktonic respirations. Planktonic respirations were estimated by total uptake by bacteria, which was supported by small varia-

tions in bacterial biomass between the investigated situations. Benthic sediment was considered as an oxygen sink over the whole sector, which is supported by the results of Rizzo et al. (1992) and Caffrey et al. (1998), showing enhanced benthic metabolism at summer temperature, for deep and organic carbon-rich water column. Regarding net ecosystem metabolism, we can identify three zones in the lower Seine River and estuary. The system shifts towards heterotrophy due to the input of organic matter by the Achères wastewater effluents. Autotrophy recovered again in the downstream branch of the river, due to phytoplankton development in nutrient-rich waters, light availability, and low grazing pressure (Akopian 1999). Downstream, in the deepest reach of the estuary, where the photic zone was considerably reduced, respiration once more exceeded autotrophic production by a factor of between 3 and 6. Due to the downstream position of the turbidity maximum, the estuary remained heterotrophic as far as its mouth. Like the Seine estuary, the Hudson estuary (Finlay et al. 1991), the Loire estuary (Relexans et al. 1988), the Scheldt estuary (Hermann personal communication), and many others affected by anthropogenic sources of carbon and by high phytoplankton biomass imported to deeper and more turbid areas have all been shown to be heterotrophic.

Riverine carbon inputs to coastal zones can be quantitatively very large and may contribute to sustaining the trophic chain depending on the quality of the inputs. Among the studied systems, the dominant contribution to the organic load has been shown to vary qualitatively between rapidly usable phytoplankton exudates, phytoplankton lysates, sewage effluents, and more refractory soil leachates (Aminot et al. 1990; Zweifel et al. 1995; Relexans et al. 1998).

We can compare the carbon uptake by planktonic heterotrophic bacteria in the estuary with the sources of biodegradable organic matter in the same sector (Table 1). The sources are those originated within the considered sector from local phytoplankton production and biodegradable organic carbon brought by effluent point discharges, and from the river upstream in the form of phytoplankton biomass and dissolved and particulate biodegradable organic matter. Table 1 shows that bacterial uptake could be entirely sustained by local carbon sources only. A large amount of biodegradable organic matter, equivalent to that originating from upstream sources, is exported downstream.

Conclusions

Oxygen and carbon balances in the lower Seine River and estuary are the result of a dense popu-

lation density ($195 \text{ inhab km}^{-2}$), with wastewater effluents being treated incompletely. In the absence of nitrogen limitation due to intensive agriculture in the watershed, phosphorus is at the origin of eutrophication responsible for large autochthonous production of organic matter which, paradoxically, consumes more oxygen than it produces in the estuary. Besides algal respiration, bacteria also represent an important component in the oxygen consumption. The secondary treatment of wastewater leads to large input of inorganic nutrients, especially ammonium which leads to oxygen consumption in the estuary. While waste management efforts have mainly focused on organic pollution, the main purpose mandated by the European Community Directive is now the removal of inorganic nutrients. In 2005, the wastewater treatment plant of Achères will be equipped with a nitrification treatment step, but no denitrification step will be implemented before 2015.

ACKNOWLEDGMENTS

This work was undertaken in the framework of the program Seine-Aval funded by the Région Haute-Normandie and the Agence de l'Eau Seine-Normandie. We are grateful to Dr. L. A. Romana, director of the program, for his helpful questions and suggestions during the study. Many thanks are due to Adriana Anzil, Bruno Leporcq, and Xavier Philippon for their precious help in the field and laboratory studies. We are also indebted for the facilities offered by André Ficht from the Service de la Navigation de la Seine and for his wide knowledge on the Seine estuary for more than 30 years.

LITERATURE CITED

- ADMIRAL, W. AND Y. J. H. BOTERMANS. 1989. Comparison of nitrification rates in three branches of the lower river Rhine. *Biogeochemistry* 8:135-151.
- AKOPIAN, M. 1999. Cinétique et rôle du zooplancton dans les flux de matière particulaire: Du lac de Der-Chnatecoq (réservoir de la Marne) à l'estuaire de la Seine. Ph.D. Thesis, Université Paris, Paris.
- AKOPIAN, M., J. GARNIER, P. TESTARD, AND A. FICHT. 2001. Estimating the benthic population of *Dreissena polymorpha* and its impact in the lower Seine River, France. *Estuaries* 24:1003-1014.
- ALPINE, A. E. AND J. E. CLOERN. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnology and Oceanography* 37:946-955.
- AMINOT, A., M. EL-SAYED, AND R. KEROUÉL. 1990. Fate of natural and anthropogenic dissolved organic carbon in the macrotidal Elorn estuary (France). *Marine Chemistry* 29:255-275.
- BARILLIER, A. AND J. GARNIER. 1993. Influence of temperature and substrate concentration on bacterial growth yield in Seine River water batch cultures. *Applied and Environmental Microbiology* 59:1678-1682.
- BILLEN, G. AND J. GARNIER. 1997. The Phison River plume: Coastal eutrophication in response to changes in land use and water management in the watershed. *Aquatic Microbial Ecology* 13:3-17.
- BILLEN, G. AND J. GARNIER. 1999. Nitrogen transfers through the Seine drainage network: A budget based on the application of the Riverstrahler model. *Hydrobiologia* 410:139-150.
- BILLEN, G., J. GARNIER, A. FICHT, AND C. CUN. 2001. Modelling

- the response of water quality in the Seine River estuary to human activity in its watershed over the last 50 years. *Estuaries* 24:977–993.
- BILLEN, G., J. GARNIER, AND P. HANSET. 1994. Modelling phytoplankton development in whole drainage networks: The RIVERSTRAHLER model applied to the Seine River system. *Hydrobiologia* 289:119–137.
- BRION, N. 1997. Etude du processus de nitrification à l'échelle de grands réseaux hydrographiques anthropisés. Thèse Européenne, Dr. Sciences Agronomiques, Université Libre de Bruxelles, France.
- BRION, N. AND G. BILLEN. 1998. Une réévaluation de la méthode d'incorporation de ¹⁴HCO₃⁻ pour mesurer la nitrification autotrophe et son application pour estimer des biomasses de bactéries nitrifiantes. *Revue des Sciences de l'Eau* 11:283–302.
- BRION, N. AND G. BILLEN. 2000. Wastewater as a source of nitrifying bacteria in river systems: The case of river Seine downstream from Paris. *Water Research* 34:3213–3221.
- BRION, N., G. BILLEN, L. GUEZENNEC, AND A. FICHT. 2000. Distribution of nitrifying activity in the Seine River (France) and its estuary. *Estuaries* 23:669–682.
- CAFFREY, J. M., J. E. CLOERN, AND C. GRENZ. 1998. Changes in production and respiration during a spring phytoplankton bloom in San Francisco Bay, California, USA: Implication for net ecosystem metabolisms. *Marine Ecology Progress Series* 172: 1–12.
- CLOERN, J. E., B. E. COLE, R. L. J. WONG, AND A. E. ALPINE. 1985. Temporal dynamics of estuarine phytoplankton: A case study of San Francisco Bay. *Hydrobiologia* 129:153–176.
- CLOERN, J. E. AND F. H. NICHOLS. 1985. Times scales and mechanisms of estuarine variability, a synthesis from studies of San Francisco Bay. *Hydrobiologia* 129:229–237.
- COLE, J. L., N. F. CARACO, AND B. PEIERLS. 1992. Can phytoplankton maintain a positive carbon balance in a turbid, freshwater, tidal estuary? *Limnology and Oceanography* 37:1608–1617.
- DUCKLOW, H. W. AND C. A. CARLSON. 1992. Oceanic bacterial production, p. 113–181. In C. Marshall (ed.), *Advance in Microbial Ecology*, Vol. 12. Plenum Press, New York.
- EBERLEIN, K. AND G. KATTNER. 1987. Automatic method for the determination of orthophosphate and dissolved phosphorus in the marine environment. *Frezenius Zeitung für Analytische Chemie* 326:354–357.
- FINDLAY, S., M. L. PACE, D. LINTS, J. J. COLE, N. F. CARACO, AND B. PEIERLS. 1991. Weak coupling of bacterial and algal production in a heterotrophic ecosystem: The Hudson River estuary. *Limnology and Oceanography* 36:268–278.
- FLINT, R. W. 1984. Phytoplankton production in the Corpus Christi Bay estuary. *Contributions in Marine Science* 27:65–85.
- GARBAN, B., D. OLIVON, M. POULIN, V. GAULTIER, AND A. CHESTERIKOFF. 1995. Exchanges at the sediment-water interface in the river Seine, downstream from Paris. *Water Research* 29:473–481.
- GARNIER, J. 1989. Peuplement phytoplanktonique et bactéries hétérotrophes d'un lac peu profond (lac de Créteil, région parisienne). Production, Fonctionnement, Evolution. Dr. ès Sci., Université de Paris 6, France.
- GARNIER, J., G. BILLEN, AND M. COSTE. 1995. Seasonal succession of diatoms and Chlorophyceae in the drainage network of the river Seine: Observations and modelling. *Limnology and Oceanography* 40:750–765.
- GARNIER, J., G. BILLEN, P. HANSET, P. TESTARD, AND M. COSTE. 1998. Développement algal et eutrophisation. Chapitre 14, p. 593–626. In M. Meybeck, G. De Marsily, and F. Fustec (eds.), *La Seine en son Bassin Fonctionnement Écologique d'un Système Fluvial Anthropisé*. Elsevier, Paris.
- GARNIER, J., G. BILLEN, AND L. PALFNER. 1999. Understanding the oxygen budget and related ecological processes in the river Mosel: The Riverstrahler approach. *Hydrobiologia* 410: 151–156.
- GARNIER, J., G. BILLEN, AND P. SERVAIS. 1992. Physiological characteristics and ecological role of small and large sized bacteria in a polluted river (Seine River, France). *Archiv für Hydrobiologie* 37:83–94.
- GUEZENNEC, L., R. LAFITE, J.-P. DUPONT, R. MEYER, AND D. BOUST. 1999. Hydrodynamics of suspended particulate matter in the tidal freshwater zone of a macrotidal estuary (the Seine estuary, France). *Estuaries* 22:717–727.
- HERVÉ, D. AND E. FALGIÈRE. 1982. Etude de la réoxygénation de l'eau aux barrages de navigation de la Seine à l'aval de Paris. Rapport Technique, Service de la Navigation de la Seine, Paris.
- JENSEN, L. M., K. SAND-JENSEN, S. MARCHER, AND M. HANSEN. 1990. Plankton community respiration along a nutrient gradient in a shallow Danish estuary. *Marine Ecology Progress Series* 61:75–85.
- JOINT, I. R. AND A. J. POMROY. 1981. Primary production in a turbid estuary. *Estuarine, Coastal and Shelf Science* 13:303–316.
- JORDAN, T. E., D. L. CORREL, J. MIKLAS, AND D. E. WELLER. 1991. Nutrients and chlorophyll at the interface of a watershed and an estuary. *Limnology and Oceanography* 36:251–267.
- KEMP, W. N., E. M. SMITH, M. MARVIN-DIPASQUALE, AND W. R. BOYNTON. 1997. Organic carbon balance and net ecosystem metabolism in Chesapeake Bay. *Marine Ecology Progress Series* 150:229–248.
- KIRCHMAN, D., F. K'NEES, AND R. HODSON. 1985. Leucine incorporation and its potential as a measure of protein synthesis by bacteria in natural systems. *Applied and Environmental Microbiology* 49:599–607.
- LANCELOT, C., C. VETH, AND S. MATHOT. 1991. Modeling ice-edge phytoplankton bloom in the Scotia-Weddel Sea sector of the Southern Ocean during spring 1988. *Journal of Marine System* 2:333–346.
- LORENZEN, C. J. 1967. Determination of chlorophyll and phaeopigments: Spectrophotometric equations. *Limnology and Oceanography* 12:343–346.
- MEYBECK, M., G. DE MARSILY, AND F. FUSTEC. 1998. *La Seine en son Bassin Fonctionnement Écologique d'un Système Fluvial Anthropisé*. Elsevier, Paris.
- MURRELL, M. C., J. T. HOLLIBAUGH, M. W. SILVER, AND P. S. WONG. 1999. Bacterioplankton dynamics in the northern San Francisco Bay: Role of particle association and seasonal freshwater flow. *Limnology and Oceanography* 44:295–308.
- NIXON, S. W. AND M. E. Q. PILSON. 1984. Estuarine total system metabolism and organic exchange calculated from nutrient ratios: An example from Narragansett Bay, p. 261–290. In V. S. Kenedy (ed.), *The Estuary as a Filter*. Academic Press, Inc., Orlando.
- NOWICKI, B. L. AND C. A. OVIAT. 1990. Are estuaries traps for anthropogenic nutrients? Evidence from estuarine mesocosms. *Marine Ecology Progress Series* 66:131–146.
- OWENS, N. J. P. 1986. Estuarine nitrification: A naturally occurring fluidized bed reaction? *Estuarine and Coastal Shelf Science* 22:31–34.
- PAINCHAUD, J. AND J.-C. THERRIAULT. 1989. Relation between bacteria, phytoplankton and particulate organic carbon in the upper St Lawrence Estuary. *Marine Ecology Progress Series* 56: 301–311.
- PENNOCK, J. R. AND J. H. SHARP. 1986. Phytoplankton production in the Delaware estuary: Temporal and spatial variability. *Marine Ecology Progress Series* 34:143–155.
- PLATT, T., C. L. GALLEGOS, AND W. G. HARRISON. 1980. Photo-inhibition of photosynthesis in natural assemblages of marine phytoplankton. *Journal of Marine Research* 38:687–701.
- POMEROY, L. R., J. E. SHELDON, W. M. SHELDON, JR., AND F. PETERS. 1995. Limits to growth and respiration of bacterioplankton in the Gulf of Mexico. *Marine Ecology Progress Series* 117: 259–268.
- PORTER, K. G. AND Y. S. FEIG. 1980. The use of DAPI for iden-

- tifying and counting aquatic microflora. *Limnology and Oceanography* 25:943–948.
- RELEXANS, J. C., M. MEYBECK, G. BILLEN, M. BRUGAILLE, H. ETCHEBER, AND M. SOMVILLE. 1988. Algal and microbial processes involved in particulate organic matter dynamics in the Loire estuary. *Estuarine, Coastal and Shelf Science* 27:625–644.
- RITTER, C. AND P. A. MONTAGNA. 1999. Seasonal hypoxia and models of benthic responses in a Texas Bay. *Estuaries* 22:7–20.
- RIZZO, W. M., G. L. LACKEY, AND R. R. CHRISTIAN. 1992. Significance of euphotic, subtidal sediments to oxygen and nutrient cycling in a temperate estuary. *Marine Ecology Progress Series* 86: 51–61.
- RODIER, J. 1984. L'Analyse de l'Eau. 7ème édition. Dunot, Paris.
- ROMANA, L. A., B. THOUVENIN, AND C. SAMMARI. 1992. Modèle mathématique sur la nitrification et le cycle de l'oxygène dissous en estuaire de la Seine. Rapport DEL/CCM/92-06, Agence de l'Eau Seine Normandie—IFREMER (Direction de l'Environnement et de l'Aménagement littoral—Laboratoire Chimie des Contaminants et Modélisation).
- SERVAIS, P. 1995. Measurement of the incorporation rates of four amino-acids into proteins for estimating bacterial production. *Microbial Ecology* 29:115–128.
- SERVAIS, P., A. ANZIL, AND C. VENTRESQUE. 1989. A simple method for the determination of biodegradable dissolved organic carbon in water. *Applied and Environmental Microbiology* 55: 2732–2734.
- SERVAIS, P. AND J. GARNIER. 1993. Contribution of heterotrophic bacterial production to the carbon budget of the river Seine (France). *Microbial Ecology* 25:19–33.
- SERVAIS, P., J. GARNIER, N. DEMARTEAU, N. BRION, AND G. BILLEN. 1999. Supply of organic matter and bacteria to aquatic ecosystems through wastewater effluents. *Water Research* 33:3521–3531.
- SIMON, M. AND F. AZAM. 1989. Protein content and protein synthesis of planktonic marine bacteria. *Marine Ecology Progress Series* 51:201–213.
- SLAVYCK, G. AND J. J. MCISAAC. 1972. Comparison of two automated ammonium methods in a region of coastal upwelling. *Deep-Sea Research* 19:1–4.
- STEEMANN-NIELSEN, E. 1952. The use of radioactive carbon (^{14}C) for measuring organic production in the sea. *Journal du Conseil International pour l'Exploration de la Mer* 18:117–140.
- THIBODEAUX, L., M. POULIN, AND S. EVEN. 1994. A model for enhanced aeration of streams by motor vessels with application to the river Seine. *Journal of Hazardous Materials* 37:459–473.
- VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Science* 37:130–137.
- ZWEIFEL, U. L., J. WICKNER, A. HAGSTRÖM, E. LUNDBERG, AND B. NORRMAN. 1995. Dynamics of dissolved organic carbon in a coastal ecosystem. *Limnology and Oceanography* 40:299–305.

SOURCES OF UNPUBLISHED MATERIALS

- GARBAN, B. Personal Communication. Laboratoire d'Hydrologie et d'Environnement, UMR Sisyphe 7619, Tour 26, étage 5, Boite 123, 4 Place Jussieu, 75005 Paris, France.
- HERMANN, P. M. J. Personal Communication. Netherlands Institute of Ecology, P.O. Box 140, 4400 AC Yerseke, The Netherlands.
- OLLIVON, D. Personal Communication. Laboratoire d'Hydrologie et d'Environnement, UMR Sisyphe 7619, Tour 26, étage 5, Boite 123, 4 Place Jussieu, 75005 Paris, France.

Received for consideration, May 30, 2000

Accepted for publication, July 19, 2001