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Biogeochemical mass-balances (C, N, P, Si) in three large reservoirs of the Seine Basin (France)

GARNIER JOSSETTE[1], BRUNO LEPORCQ[2], NATHALIE SANCHEZ[1] & PHILIPPON[1]

[1] *UMR 7619 Sisyphe CNRS, BP 123, Tour 26, 5ème étage, 4 place Jussieu, 75005 Paris, France;* [2] *Université de Bruxelles, Microbiologie Aquatique, CP 221, Campus de la Plaine, Bd du Triomphe, 1050 Bruxelles, Belgique*

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Abstract. Three major reservoirs (Marne, Seine and Aube), situated in the upstream basin of the river Seine represent a storage capacity of 800 10^6 m^3. In order to quantify the possible role of these reservoirs as a sink or source of nutrients and organic matter for the river system, an input/output mass-balance of suspended matter, organic carbon, inorganic nitrogen forms, phosphorus and reactive silica was established, providing reliable estimates of their retention/elimination and export. The study was carried out over 3 years (1993, 1994 and 1995) in differing hydrological conditions. The retention times varied from 0.3 to 0.8 year, depending on the reservoir and the year, but was longer in 1993 that was a drier year than 1994 and 1995, hydrologically quite similar.

Regarding retention (or elimination) and export, the behaviour of the three studied reservoirs was similar. A clear loss or retention of nitrogen, phosphorus and silica was observed in the reservoirs and represented about 40% of the incoming flux of nitrate, 50% of silica, and 60% of phosphate. The retention was lower for total phosphorus than for phosphate. The reservoirs are also sites of suspended matter deposition except during the decennial drawdown, when suspended matter is exported. For inorganic nitrogen, the average amount of nitrate retained in the Seine basin reservoirs upstream from Paris is 5000 tonnes y^{-1} that is almost equal to the estimated retention by deposition or denitrification in river channel sediments for the whole drainage network. The retention in the reservoirs represents about 12% of the total flux of nitrate at the outlet of the basin upstream from Paris, and 5% at the mouth of the Seine River.

We also calculated inlake C, N, P, Si budgets on the basis of direct process measurements. Measurements of planktonic primary and bacterial activity production led to annual net production of 4200 and 580 tonnes of carbon, respectively. A reasonable value (450 tonnes of carbon) of grazing was calculated. Corresponding N, P, Si fluxes were drawn from appropriate C:N:P:Si ratios. Benthic fluxes were measured with bell jars. The retention of P and Si represents a small fraction of important internal fluxes of phytoplanktonic uptake and recycling, while inorganic nitrogen retention depends mostly on benthic denitrification. The behaviour of P and Si differs in that P is mainly recycled in the water column, while Si dissolution occurs at the sediment interface. Nitrogen is recycled in both the planktonic and the benthic phase.

Introduction

The study of reservoirs has generally been approached in the same way as many lakes studies (Wetzel 1983; Gunnison 1985; Straskrabova et al. 1990; Thornton et al. 1990; Pourriot & Meybeck 1995). Ecological processes are similar in lakes and reservoirs and their manifestations at the scale of the ecosystem are, in both cases, driven by external constraints (meteorology, hydrology, morphology, nutrient input). Since Vollenweider (1968), limnological studies have focused on eutrophication problems under rising phosphorus loading resulting from increasing population density and sewage input in the watershed. The greater understanding of the ecological functioning, based on the concepts of top-down/bottom-up control, cascading effects, linear food chain versus microbial loop, etc. ... made possible successful restorations of many stagnant systems (Cooke et al. 1993).

Moreover, the problem of nitrogen pollution in surface- and groundwater, as well as in coastal marine waters, has become increasingly worrying as result of intensive use of nitrogen fertilisers and changes in agricultural practices (Jansson et al. 1994). Whereas phosphorus originates mainly from point-sources that can be reduced in sewage-treatment plants, the diffuse origins of nitrogen make it more difficult to handle. The ability to denitrify, of a variety of terrestrial, semi-aquatic or aquatic systems (Setzinger 1988, 1994), has focused attention on ponds, sand-pit lakes, lakes and reservoirs as possible sites of nitrate removal. Based on the ecotone concept, these stagnant systems must also be considered as a part of a river basin that may influence the biogeochemical transformation and circulation of biogenic elements (C, N, P, Si).

In the framework of a large programme on the Seine River, a study was undertaken to quantify the role of the reservoirs as sinks or sources of C, N, P, Si in the river system. Ultimately, by coupling models of the reservoirs (Garnier et al., submitted) with that of the Seine River (Billen et al. 1994; Garnier et al. 1995), we should be able to understand, but also to quantify their influence on the water quality of the river. Three major reservoirs (Marne, Seine and Aube) are situated in the upstream basin of the Seine River and represent a storage capacity of 800 10^6 m^3. This paper presents the results of a mass-balance study of the principal components of water quality, using flux measurements into and out of the reservoirs. The originality of the study lies in its wide scope. Besides taking into account the four major biogenic elements (C, N, P, Si), investigations were carried out simultaneously on these three majors reservoirs in the Seine basin through at least two hydrological cycles. All three reservoirs are off-channel and are supplied chiefly by the rivers of the same name. Thus, the approach is well suited to provide reliable estimates. In addition, the results of the process study (Garnier et

Table 1. Main characteristics of the Seine, Marne and Aube reservoirs.

	Marne	Aube	Seine
date of completed construction	1974	1990	1966
maximal storage capacity (10^6 m^3)	350	170	205
surface area (km^2) *at maximum capacity*	48	21	23
mean depth at the maximum level (m)	7.2 (4.5*)	7.6 (3.5*)	8.9
Extreme and mean values of the flow of the supplying rivers, m^3/s	20–300 *40 (Marne)* *6 (Blaise)*	5–100 *20 (Aube)*	1–150 *30 (Seine)*

*4.5 m and 3.5 m for the smaller lakes Champaubert and Amance, respectively.

al., submitted; Sanchez 1997) were used to establish a budget of internal C, N, P, Si fluxes that gives new insights into the ecological functioning of the reservoirs.

Study sites

The reservoirs are situated in the upper part of the drainage basin of the Seine River (France), in the temperate region of Champagne, east of the Paris Basin (Figure 1; Table 1). A severe flood in 1910 prompted the authorities to construct large reservoirs in order to reduce high water events during the winter. The reservoirs Marne, Aube and Seine, were completed in 1974, 1990 and 1966, respectively. They are located in a narrow zone where the clay substratum is totally impervious. The remaining part of the watershed consists of limestone and marl, used for mixed agriculture and cattle farming. The surface areas at maximum water level for the reservoirs Marne, Aube and Seine are respectively 48, 21 and 23 km^2. Whereas the Seine reservoir includes a single lake, with a diversion channel close to the release channel, the Marne and Aube reservoirs comprise two lakes each (Champaubert and Der Lakes and Amance and Temple–Auzon Lakes, respectively). In both cases, the smaller lake (about 0.5 km^2 for both reservoirs) receives the diverted river water, whereas water is released from the larger lake (Figure 1). The mean depths of the large lakes are about 7–10 m and 3.5–4.5 m for the smaller ones at the maximal level, with a maximum of 15–20 m. The water volume usually varies strongly throughout the hydrological cycle, reaching a maximum in late spring and a minimum in late autumn (Figure 2). Depending

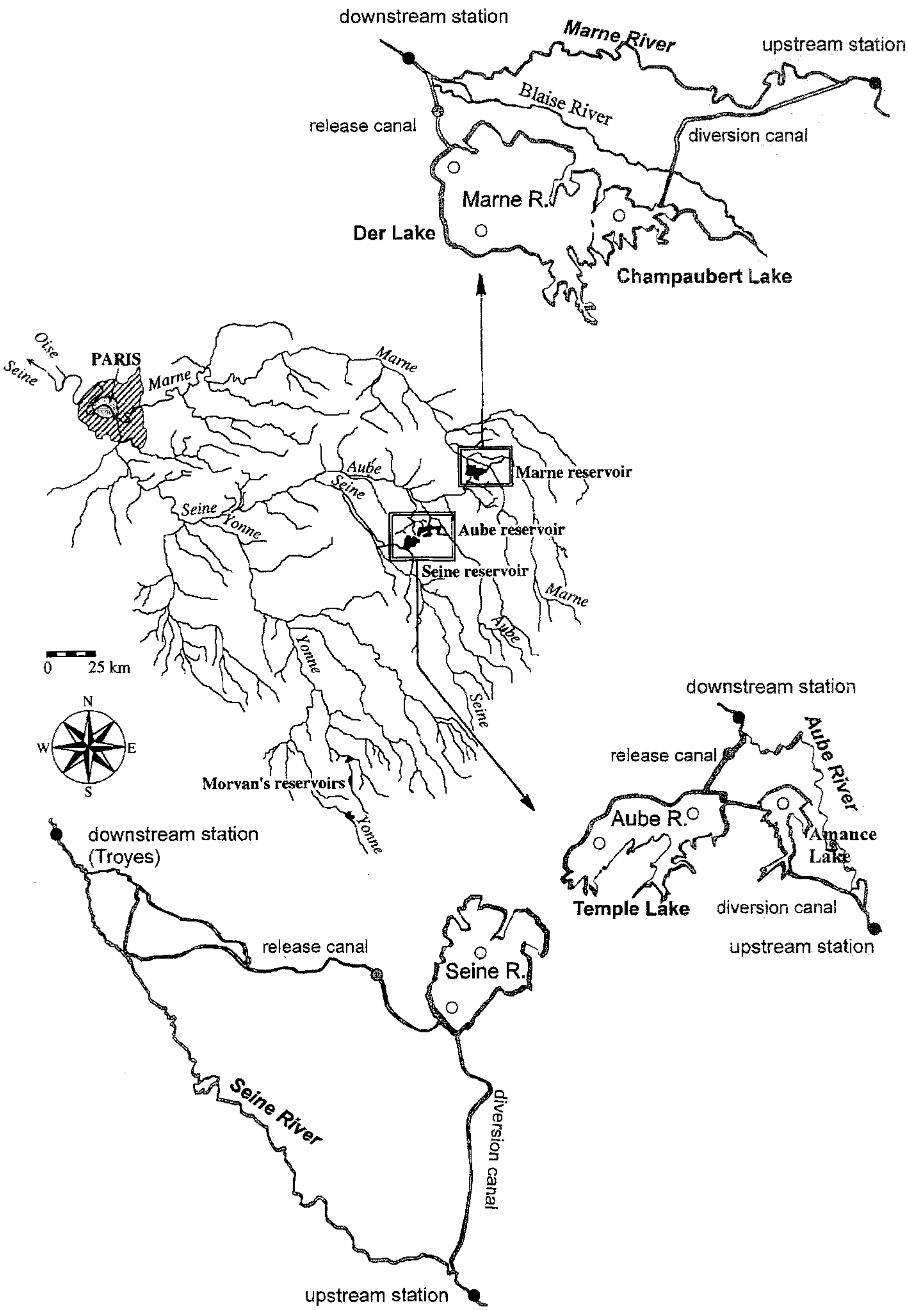

Figure 1. Map of the locations of the reservoirs in the Seine basin and presentation of the sampling stations. (Dark and open circles.)

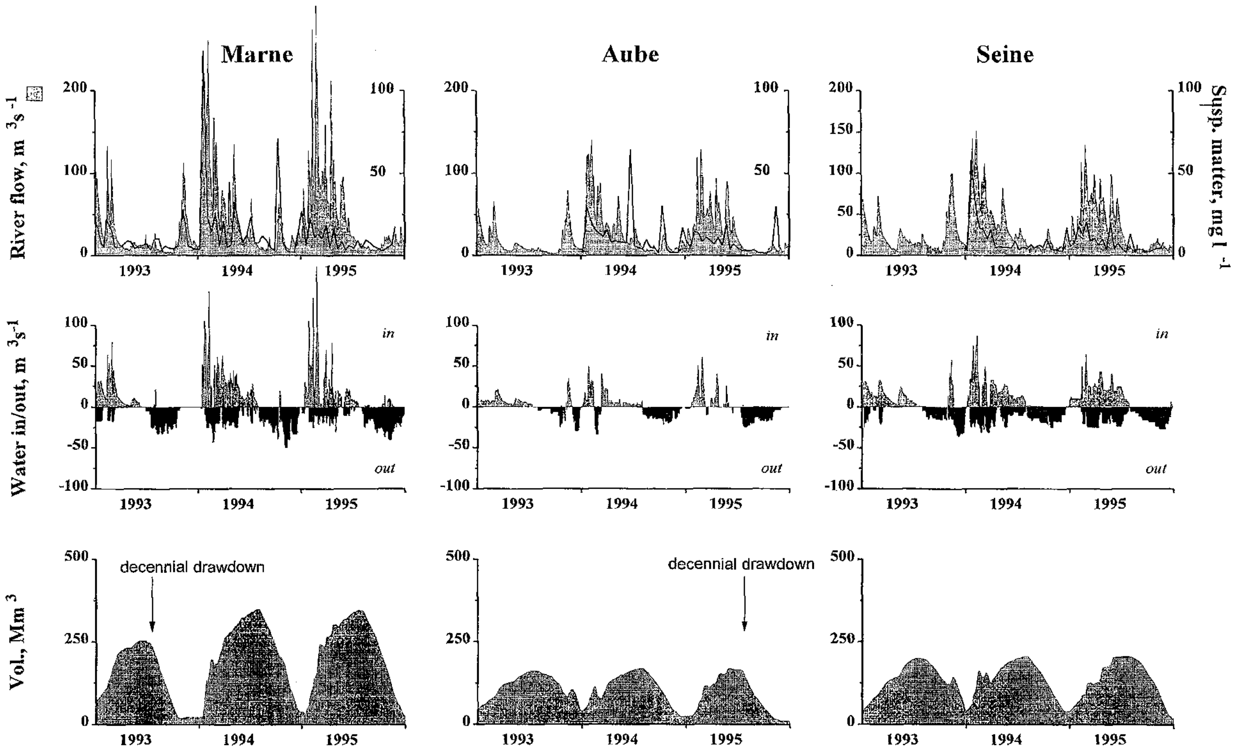

Figure 2. Seasonal variations of (a) the upstream river flow and suspended matter, (b) diverted flow (positive scale) and released flow (negative scale) and (c) of the volume of the Marne, Aube and Seine reservoirs for the years 1993, 1994, 1995.

on weather conditions (wind, temperature) and management strategies, the water columns stratify for a few weeks in the summer.

The hydrological cycles of the reservoirs are defined by rules of water management: they are filled from November 1 and emptied from July 1 in order to fit a theoretical filling-curve. They are emptied from the bottom. During flood events, the reservoirs are able to take 2/3 of the maximum discharge of the supplying rivers during a period defined by the management rules and the storage capacity of the reservoirs. However, as they are located upstream in the basin, their role in reducing flood intensity in Paris is limited. Their major role is mainly to sustain low summer flow in late summer. Together the three reservoirs are able to release about 60 $m^3\ s^{-1}$, which represents at least half of the total discharge through Paris in summer.

Sampling strategy

In order to establish biogeochemical C, N, P, Si budgets, samples were taken twice a month on the three sites at stations upstream (in the diverted rivers) and downstream from the reservoir (in the release channels and in the rivers) in 1994 and 1995 (Figure 1). One of the reservoirs (Marne) was studied for three years (1993, 1994 and 1995). The year 1993 was characterised by unusually low discharges. Note that to allow maintenance of the dams every ten years, special water management rules are applied: water release begins in June – one month earlier than usual –, and the reservoirs are emptied to a much lower level. This was the case for the Marne reservoir in 1993 and to the Aube reservoir in 1995.

Samples were also collected at others stations inside the reservoirs (Figure 1). In addition, process studies were carried out in the Marne reservoir in order to establish a budget of inlake processes. The process studies were used to develop an ecological model that has been published separately (Sanchez 1997; Garnier et al. 1998; Garnier et al., submitted).

Methods

Sampling and analytical methods

Water samples were taken from a bridge with a bucket in the rivers flowing into the reservoirs and in the outlet channel whereas samples from the reservoirs were pumped out at every meter depth throughout the water column, and then mixed.

The studied variables were those classically analysed when assessing water quality: suspended matter, total phosphorus and phosphate, reactive silica, ammonium and nitrate, chlorophyll *a* and particulate organic carbon. All samples were stored in disposable sterile polyethylene flasks.

Phosphate, silica and ammonium were determined spectrophotometrically on glass-fibre membrane filtered water, following respectively Eberlein and Katter (1984), Rodier (1984) and Slawyck and MacIsaac (1972). Total phosphorus was determined on non-filtered water after sodium persulfate digestion and mineralization at 110° in an acidic phase. Nitrate was assessed using ionic chromatography (Dionex). Chlorophyll *a* was analysed according to Lorenzen (1967). Particulate organic carbon analyses were performed on suspended matter harvested on a 12 mm diameter filter GF/F (ignited at 550 °C) using a DC-180 Carbon Analyser (Dohrman). DOC was analysed on filtered water (0.22 μm cellulose acetate membrane filter), all flasks being ignited at 550 °C. Suspended matter was weighed on a GF/F (filters dried at 40 °C).

In the conditions of our study, detection limits of the methods were 3 μgP l^{-1} for total phosphorus and phosphate, 2μgN l^{-1} for ammonium, 20 μgSiO2 l^{-1} and 20 μgN l^{-1} for nitrates with a precision better than 5%. Detection limits are about 1 μg chl*a* l^{-1}, 1μg l^{-1} of suspended matter and 0.2 μg C l^{-1} of organic carbon, with a precision of about 10%.

Hydrological data (discharges, volumes and water levels) were obtained from the authorities managing the reservoirs, the Agency 'Grands Lacs de Seine.'

Budget calculations

The biogeochemical mass-balances were calculated yearly from the beginning of water diversion to the end of water release, on the basis of the daily discharge and concentration values at the inlet and outlet of the reservoirs. Concentration values gathered twice-monthly were interpolated linearly.

Results

Typical and atypical features of water quality in the rivers and reservoirs

Seasonal variations of the biogeochemical variables show different patterns in the rivers and in the reservoirs. Results are shown for the years 1994 and 1995.

A marked decrease in seasonal concentrations of phosphate and silica is observed when the water transits through the reservoirs. Phosphate is taken up

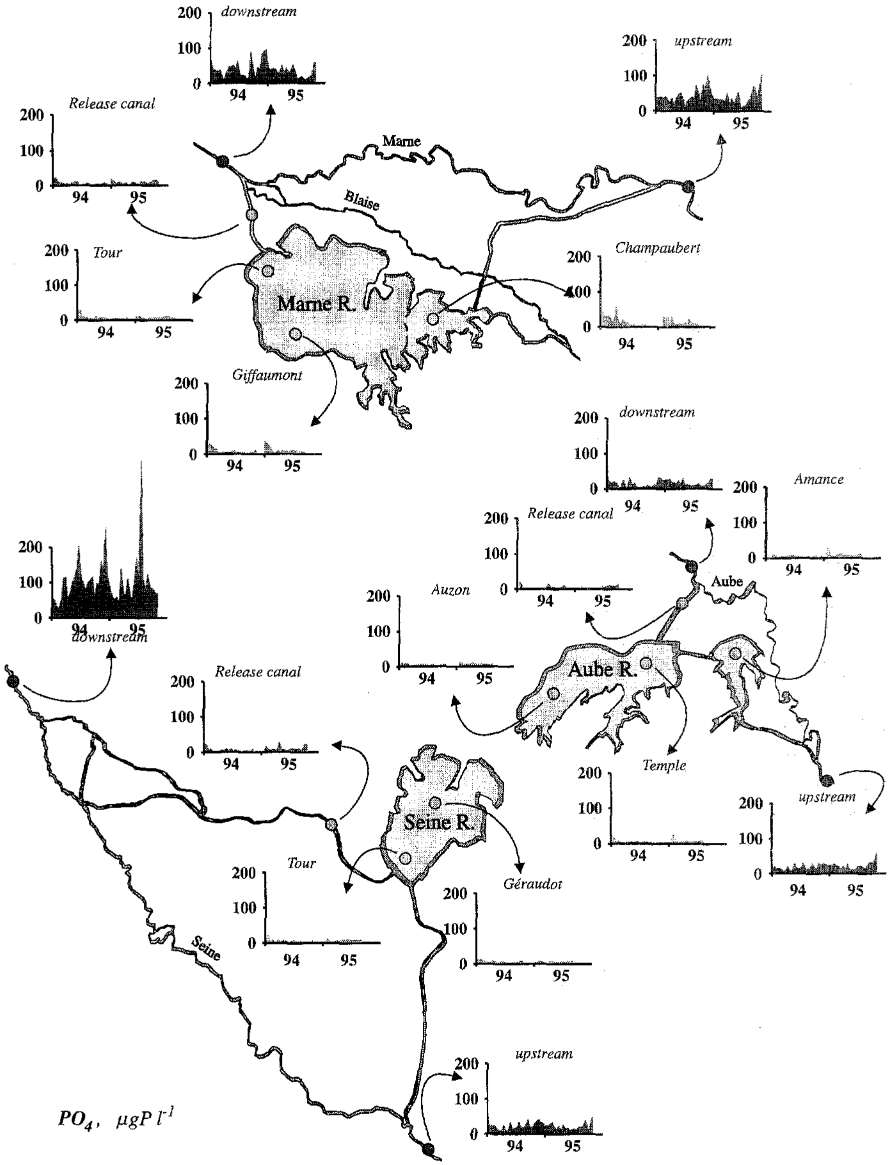

Figure 3. Seasonal variations in phosphate concentrations in the rivers upstream and downstream of the reservoirs, in the release canal and inside the reservoirs for the years 1994 and 1995.

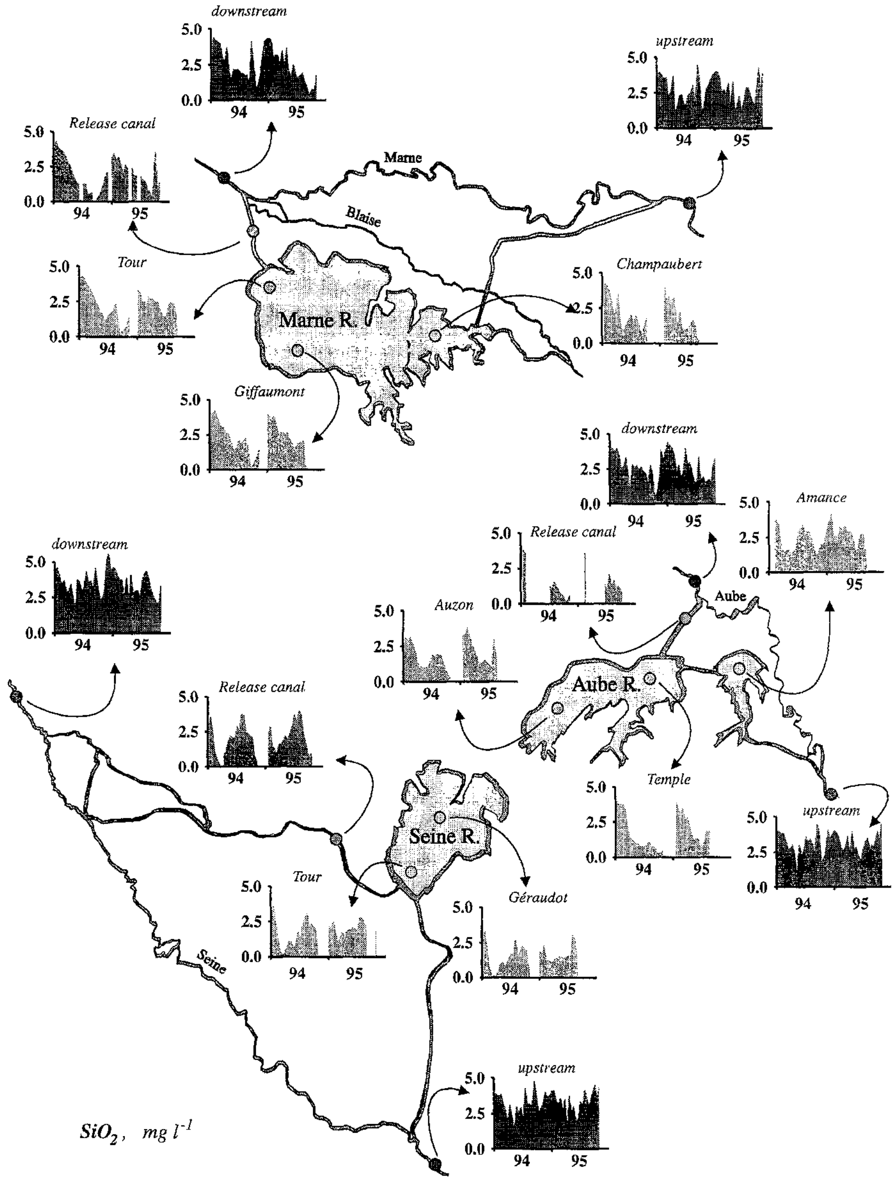

Figure 4. Seasonal variations in silica concentrations in the rivers upstream and downstream of the reservoir, in the release canal, and inside the reservoirs for the years 1994 and 1995.

by the phytoplankton and decreases very quickly. The concentration is very low ($< 5\ \mu$gP l^{-1}) from spring to late autumn (Figures 3 and 4). Dissolved silica is also taken up by phytoplankton during periods of diatom growth and decreases regularly during the spring bloom. It partly recovers in summer and then decreases again in late summer/early autumn, when there is a second development (Figure 5). Thus phytoplankton variations in the reservoirs show two main phases: an early spring bloom (February to April: 10 to 30 μg chl*a* l^{-1}) dominated by diatoms that take up silica and a late summer increase composed of mixed populations of Chlorophyceae and diatoms, which is indicated by a new decrease in silica (Figures 4 and 5).

For nitrate, a regular and important decrease occurred throughout the two years. As shown below, this decrease cannot be explained by algal uptake only, and is mainly due to benthic denitrification (Figure 6).

It seems clear that when the reservoir contains two lakes (Marne, Aube), the lakes receiving river water (Marne: Champaubert; Aube: Amance) can sustain a greater summer development of phytoplankton than observed in the downstream part of the reservoirs (Figure 5). However, the phytoplankton reaches higher biomass values in Champaubert Lake than in Amance Lake due to higher concentrations of phosphate in the river Marne than in the river Aube.

In the rivers, seasonal patterns of phosphate, silica and nitrate, i.e. a regular decrease throughout the year, are less pronounced due to continuous replenishment by headwaters (Figures 3, 4 and 6). When concentrations of phosphate and silica are lowered by phytoplankton uptake, they recover very quickly. In the upstream sector of the drainage network, seasonal phytoplankton variations are characterised by one major peak usually occurring as the flow decreases in late spring or summer. The intensity of the peak is clearly related to the phosphate level, that is much higher in the river Marne (Figure 3). Similar levels of silica and nitrate concentrations are found in all three rivers (Marne, Seine, Aube). A seasonal decrease of nitrate is also observed in the rivers but it is much less pronounced than in the reservoirs (Figure 6).

The seasonal pattern of the water quality is similar upstream and downstream of the reservoirs, except in the river Seine, which suffers phosphate contamination by effluents from the city of Troyes (200 000 inhabitants).

Water balance and residence time in the three reservoirs

The results of the hydrological budgets of the reservoirs Marne, Seine and Aube are shown in Table 2. Our water balance neglects direct precipitation inputs and evaporation losses, which represent relatively small and opposite contributions (Table 2). Because the flow of released water and the water

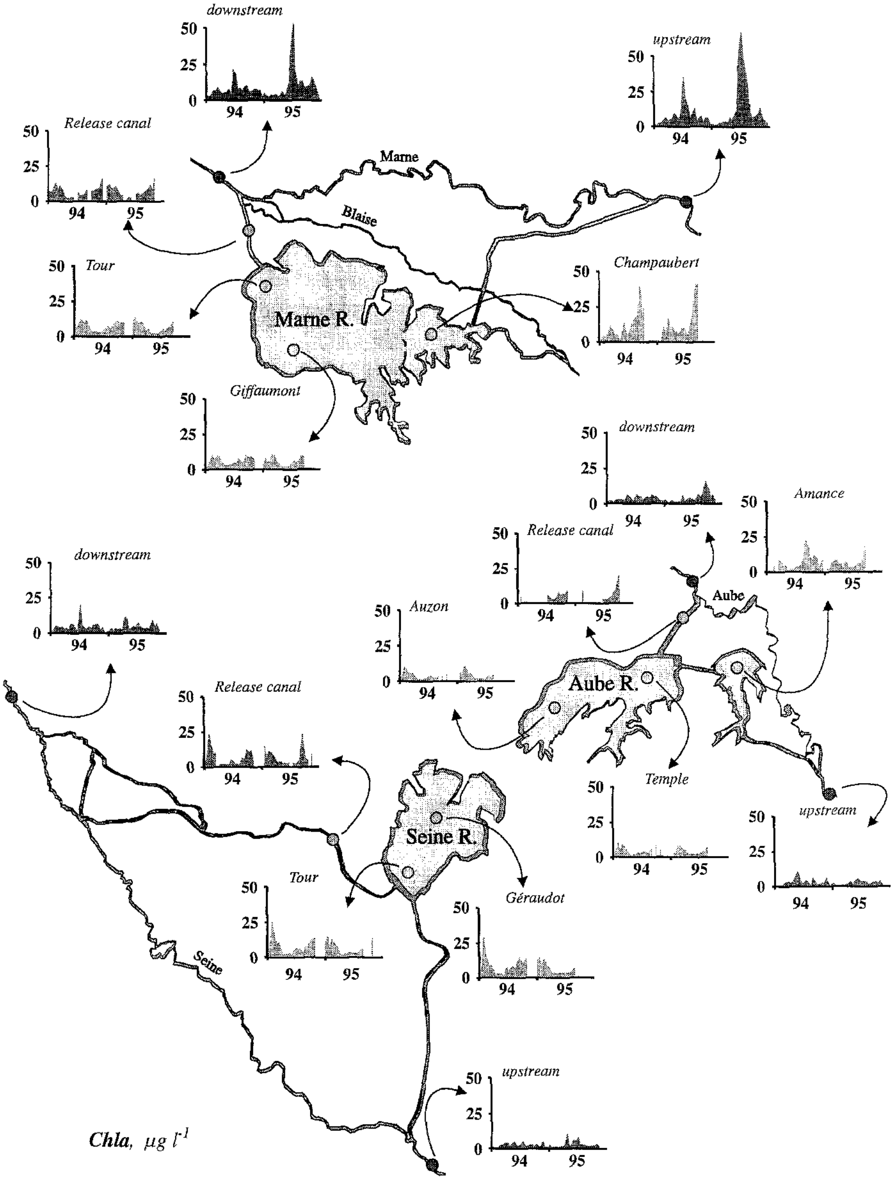

Figure 5. Seasonal variations in chlorophyll *a* concentrations in the rivers upstream and downstream the reservoirs, in the release canal, and inside the reservoirs for the years 1994 and 1995.

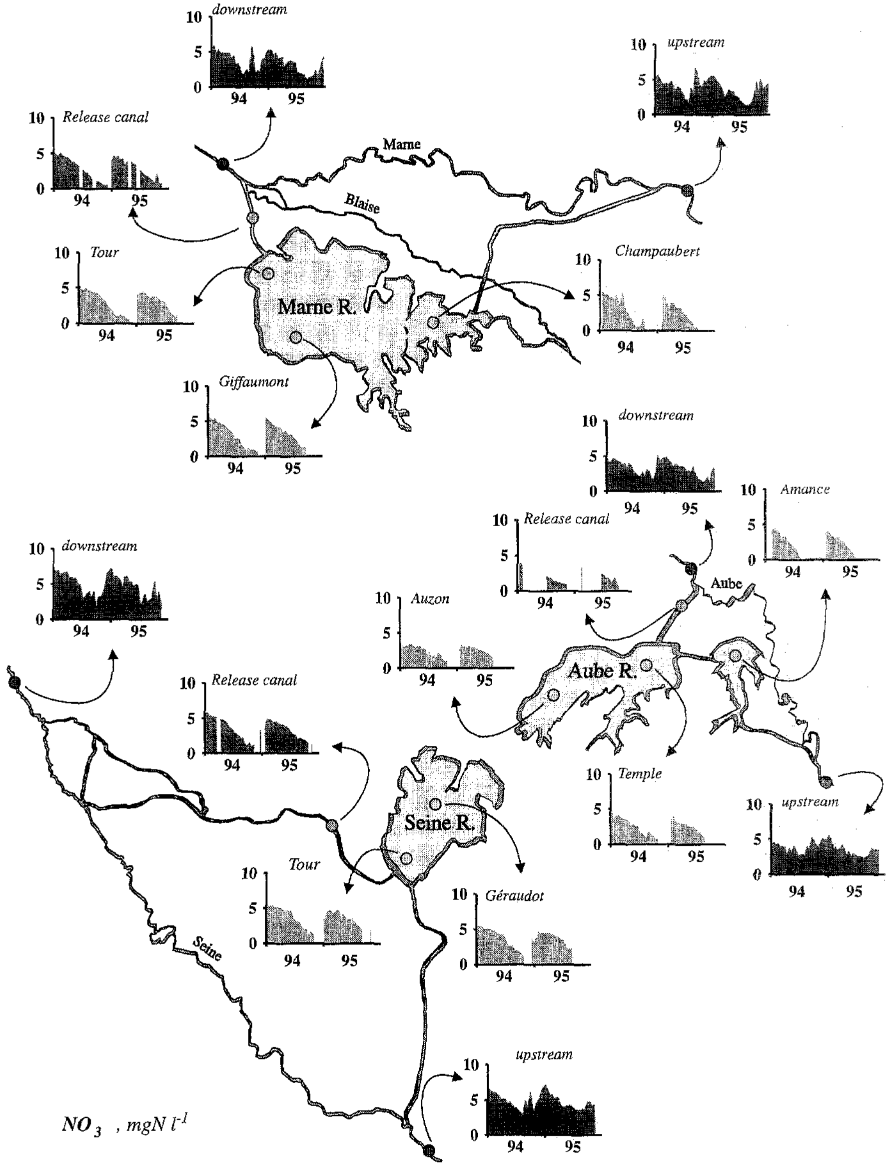

Figure 6. Seasonal variations in nitrate concentrations in the rivers upstream and downstream of the reservoirs, in the release canal, and inside the reservoirs for the years 1994 and 1995.

Table 2. Hydrological budget of the reservoirs Marne, Seine et Aube for 3 years. Mean rainfall values are given in italics for the whole Champagne region.

Water in/out, 10^6 m^3	1993		1994		1995	
	in	*out*	*in*	*out*	*in*	*out*
Marne	270	310	600	555	490	460
Aube	155	123	180	190	200	200
Seine	269	280	460	460	470	450
Water in/out, mm y^{-1}						
rainfall	*670*		*990*		*980*	
evaporation		*≈500*		*≈500*		*≈500*

Note that rainfall and evaporation expressed at the scale of the reservoirs are in the range of 0.1 to 0.5 10^6 m^3, 3 orders of magnitude lower than the volume of water flowing through the reservoirs. Evaporation has been estimated according to the Dalton law (Tassin, comm. pers.).

Table 3. Residence time of water in the reservoirs and in their two basins.

residence time, year		1993		1994		1995	
Marne		0.53		0.38		0.46	
	Der		0.49		0.35		0.43
	Champaubert		*0.03*		*0.02*		*0.03*
Aube		0.83		0.59		0.44	
	Auzon		0.69		0.49		0.35
	Amance		*0.13*		*0.10*		*0.10*
Seine		0.52		0.30		0.29	

level/volume of the reservoirs are better evaluated than the diverted flows (particularly during flood events), diverted flows were recalculated at daily intervals from corresponding figures of released water flow and total volume variations. These calculations yield a reasonably balanced water budget (Table 2). Small unbalances may be due either to our neglecting precipitation/evaporation, but more probably to the lack of precision in the data flow measurements and water levels in the reservoir.

The residence time of the water in the reservoirs was calculated as the ratio between a mean annual volume and the annual water influx (Table 3). Residence times vary from 0.3 to 0.8 year, depending on the reservoir and the year, but are much longer in the dry year of 1993 than in 1994 and 1995. Note that the water residence time in the small upper lakes (Champaubert and Amance) is very short (about 0.1 year).

Comparative C, N, P, Si mass balances in the three reservoirs in 1993, 1994 and 1995

Estimated inflow and outflow of suspended matter, nitrate, ammonium, phosphorus, dissolved silica, chlorophyll *a* and particulate organic carbon are summarised in Table 4. The mass balance of these substances is completely dominated by the flows. The direct inputs of domestic wastewater, related to the recreational role of the reservoirs were estimated from the visitor numbers at the camping sites and other tourist facilities around the lakes. The results show that they represent less than 0.1% of total N and P inflow from the river diversion. Direct atmospheric nitrogen deposition, amounting to about 300 kg km^{-2} in the upstream Seine basin (Thibert 1994), represents less than 1% of the nitrate received by the river.

Despite their different morphologies and hydrological conditions, the three reservoirs show a similar behaviour when retention/elimination and export, is expressed as percentage of the inflow. Retention/elimination of nitrate, phosphorus and dissolved silica is clearly observed in the three reservoirs, amounting to about 40% of the incoming flux of nitrate, 50% of silica, and 60% of phosphate. Note that ammonium represents a low proportion of the inorganic nitrogen input. The same is true for organic particulate nitrogen which represents less than 5% of incoming nitrogen (Martin & Romain 1998). A lower retention is observed for total phosphorus than for phosphate (Table 4). The reservoirs are also sites for suspended matter deposition, the amount retained depending on the incoming flux. Whereas from 36% to 73% of the suspended matter influx was retained in the reservoirs in 1994, the figure for 1995 was only 13% to 20%. Suspended matter appeared to have been exported when the reservoirs were emptied for the decennial drawdown (Marne in 1993 and Aube in 1995). The retention of particulate organic carbon is more variable (from 0% in the Aube reservoir to 30% and 50% in the Marne and Seine reservoirs). DOC, only measured in the Marne reservoir in 1993, was retained to only 15% (of 420 tonnes of carbon inflow). Generally, the reservoirs also export phytoplankton biomass.

As mentioned above, it was observed that, when the reservoirs comprise two lakes, the small upstream lake receiving river water can sustain a greater production of organic matter. In order to evaluate the respective roles of the two lakes in retention/elimination or export, the mass balances were calculated separately (Table 5). Whereas a small percentage of nitrate and silica were retained/eliminated from the upper lake, it retained both phosphate and

Table 4. Biogeochemical mass balances in the reservoirs Marne, Aube and Seine in 1993, 1994 and 1995. Retention/export is given in percentage (%). Export is indicated left in italics.

		Marne			Aube			Seine		
		Inflow	*Outflow*	*retention* *export*	*Inflow*	*Outflow*	*retention* *export*	*Inflow*	*Outflow*	*retention* *export*
		tons y^{-1}	tons y^{-1}	%	tons y^{-1}	tons y^{-1}	%	tons y^{-1}	tons y^{-1}	%
Suspended Matter	1993	3750	6300	*–68*						
	1994	28410	7750	73	3030	1930	36	8490	2380	72
	1995	7427	5945	20	1935	4998	*–158*	3399	2945	13
$N\text{-}NO_3$	1993	1320	590	55						
	1994	2900	1480	49	760	340	55	2630	1630	38
	1995	2129	1010	53	766	353	54	2124	1826	14
$N\text{-}NH_4$	1993	20	40	*–100*						
	1994	30	30	0	5	20	*–300*	20	50	*–150*
	1995	10	27	*–170*	2	9	*–350*	8	18	*–125*
$P\text{-}PO_4$	1993	9	2	78						
	1994	26	4	85	3.9	1.4	64	9.6	3.4	65
	1995	17.2	4.6	73	4.6	1.7	62	11.7	4.2	64

Table 4. Continued.

		Marne			Aube			Seine		
		Inflow	*Outflow*	*retention* / *export*	*Inflow*	*Outflow*	*retention* / *export*	*Inflow*	*Outflow*	*retention* / *export*
		tons y^{-1}	tons y^{-1}	%	tons y^{-1}	tons y^{-1}	%	tons y^{-1}	tons y^{-1}	%
P-tot	1993	27	13	52						
	1994	63	14	78	8	4	50	18	10	44
	1995	32	12	63	8	6	25	18	12	33
SiO_2	1993	890	520	42						
	1994	2010	1010	50	630	270	57	1500	890	41
	1995	1639	842	49	674	293	57	1559	861	45
C-Phytoplankton	1993	80	240	*–200*						
C:Chla = 40	1994	116	156	*–34*	16	40	*–150*	48	140	*–192*
	1995	64	160	*–150*	12	56	*–370*	48	124	*–158*
POC	1993	280	470	*–68*						
	1994	1090	550	50	160	160	0	560	390	30

Table 5. Biogeochemical mass balances of the upper lakes Champaubert and Amance of the reservoirs Marne and Aube respectively. Retention/export is given in percentage (%). Export is indicated left in italics.

		Champaubert			Amance		
		Inflow	*Outflow*	*retention* *export*	*Inflow*	*Outflow*	*retention* *export*
	1993	270	274		—	—	
hydro, $10^6 m^3$	1994	600	600		180	190	
	1995	490	488		200	207	
		tons y^{-1}	tons y^{-1}	%	tons y^{-1}	tons y^{-1}	%
Suspended Matter	1993	3750	2500	33	—	—	—
	1994	28410	6960	76	3030	810	73
	1995	7427	6477	13	1935	1390	28
$N\text{-}NO_3$	1993	1320	1100	17	—	—	—
	1994	2900	2700	7	760	630	17
	1995	2129	1922	10	766	527	31
$N\text{-}NH_4$	1993	20	0	100	—	—	—
	1994	30	30	0	5	10	*–100*
	1995	10	11	*–10*	2	9	*–350*
$P\text{-}PO_4$	1993	9	6	33	—	—	—
	1994	26	18	31	3.9	1.2	69
	1995	17.2	12.2	29	4.6	3.1	33
P-tot	1993	27	14	48	—	—	—
	1994	63	33	48	8	3	63
	1995	32	33	*–3*	8	7	13
SiO_2	1993	890	800	10	—	—	—
	1994	2010	1870	7	630	520	17
	1995	1639	1462	11	674	578	14
C-Phytoplankton	1993	80	120	*–50*	—	—	—
	1994	116	144	*–24*	16	32	*–100*
	1995	64	140	*–119*	11.6	52	*–348*
POC	1993	280	320	*–14*	—	—	—
	1994	1090	630	42	160	110	31
	1995	—	—	—	—	—	—

total phosphorus to a considerable extent. Although the retention of suspended matter is variable, retention in the upstream lake appears to be a constant feature, even during decennial drawdown when export is the general rule (Marne and Aube reservoirs in 1993 and 1995, respectively). Phytoplankton is also exported from the upper lakes.

C, N, P, Si mass balances in the Marne and Aube reservoirs for contrasting hydrological cycles and management rules

The amount of water entering the reservoir during the dry year of 1993 was much lower than in 1994 and 1995 (Table 2). Overall, the maximum flow of the rivers upstream of the reservoir in 1993 was half that found in 1994 and 1995 (Figure 2). Although the 1994 and 1995 flows were similar to each other, the flow increase was different: rapid at the end of 1993 and in early 1994, more progressive in 1995 with a maximum in February–March (Figure 2).

Accordingly, there were major differences in the behaviour and the budget of suspended matter in the course of the three years. The much higher influx of suspended matter in 1995 as compared to 1994 (by a factor of 4 in the Marne reservoir, 1.5 and 2 in those of the Aube and Seine), may be explained by the suddenness of the flood in 1994 which led to heavy erosion and solid transport. We have mentioned above the impact of decennial drawdown on suspended matter exportation.

Regarding the behaviour of the reservoirs with respect to the retention/elimination of nutrients, the percentages are rather similar in any conditions. Phytoplankton is generally exported and particulate organic matter retained.

Inlake C, N, P budget in the Marne reservoir in 1993

In order to better understand the ecological functioning of the reservoirs, we calculated inlake C, N, P, Si budgets on the basis of process measurements carried out in the Marne Reservoir (Sanchez 1997; Garnier et al. 1998; Garnier et al., submitted). Planktonic processes were measured in 1993. Annual net planktonic primary production was estimated (from twice-monthly ^{14}C-bicarbonate incorporation measurements, Steeman-Nielsen 1952) at 4200 tonnes C. Planktonic bacterial production was evaluated at 580 tonnes C (from twice-monthly ^{3}H-thymidine incorporation measurements, Fuhrman & Azam 1980, 1982). A bacterial growth yield of 33% (Barillier & Garnier 1993) gives an annual total uptake of 1725 tonnes C and a bacterial respiration of 1155 tonnes C. A reasonable value (450 tonnes C) of grazing has been estimated from preliminary analyses of the reservoir zooplankton (Akopian et al., in press) and filtration rates of lacustrine

Table 6. Nutrient fluxes measured in the Marne reservoir (at Champaubert station) with benthic bell jars. Negative fluxes represent a production, from the sediment to the water column, positive fluxes represent a consumption, from the water column to the sediment (Sanchez 1997).

	Oxygen	Nitrate	Ammonium	Reactive Silicate	Phosphate
	$mgO_2\ m^{-2}h^{-1}$	$mgN\ m^{-2}h^{-1}$	$mgN\ m^{-2}h^{-1}$	$mgSi\ m^{-2}h^{-1}$	$mgP\ m^{-2}h^{-1}$
12/04/94	+17.0	+19.0	−0.05		+0.17
04/07/94	+139		−20	−30.2	+0.39
22/06/95	+36.0	+10.2	−7.4		+0.05
	+43.5	+9.8	−6.6		0.00
01/08/95	+14.9	+2.9		−4.0	0.00
	+15.3	+4.7	−7.4	−4.6	0.00
10/06/96	+43.0	+24.0	−8.0	−8.1	−0.06
	+61.8	+24.8	−15.7	−13.3	−0.14
median value	*40*	*10*	*7*	*8*	*0*

zooplankton communities from the literature (Forsberg 1985; Garnier & Mourelatos 1991). Considering a zooplanktonic biomass of 70 μg C l^{-1} in the reservoir (average of 1994 and 1995), a reasonable estimate of the filtering rate for the whole community is 0.5 day^{-1} as an annual average. With a mean phytoplankton biomass of 6 μg chla l^{-1} in 1993, grazing can be estimated at 12 μg C l^{-1} day^{-1}. Planktonic fluxes expressed by unit volume were converted on the basis of the mean annual volume of 100 10^6 m^3 in 1993. Benthic processes were estimated from fluxes measured with benthic bell jars in 1994–1995 (Sanchez 1997, Table 6). Benthic degradation of organic matter in the sediment, was calculated from the sum of oxygen and nitrate fluxes to the sediment across the benthic interface. It was based on the assumption that oxygen and nitrate are the major electron acceptors for benthic organic matter respiration. (Although no sulfide accumulation was observed in the sediments, manganese and iron oxides could also play a role, which we neglected in our calculations, thus leading to underestimation of benthic activity). The ammonium flux to the water column was used to calculate organic nitrogen mineralisation. The nitrate flux to the sediment represents the benthic denitrification. Silica dissolution and phosphate release were directly estimated from the corresponding fluxes to the water column. All these results are summar-

Table 7. Inlake C, N, P, Si budget in the Marne Reservoir in 1993 calculated from mass-balances and measured microbial processes.

		C	$T\,y^{-1}$		N	$T\,y^{-1}$		P	$T\,y^{-1}$		Si	$T\,y^{-1}$
		inflow	outflow		inflow	outflow		inflow	outflow		inflow	outflow
inflow/outflow	phyto	80	240	phyto	*14*	*40*	phyto	2	6	phyto[7]	20	60
	zoo[1]	*<1*	*≅50*	zoo[1]	*<0.2*	*≅10*	zoo[1]	*<0.02*	*≅1*			
	DOC	420	780	N-NO3	1320	590	P-PO4	9	2	DSi	320	240
	POC[2]	200	230	N-NH4	20	40	Ppart	16	5			
				PON, DON	23	27						
processes	PP	4200		PP		740	PP		102	PP[7]		1050
	Zgraz[4]		450	Zgraz[4]	79		Zgraz[4]	11				
	BacResp[3]		1150	Bacupt	304		Bacupt	42				
	Bmin[5*]		2000	Bmin[5**]	640		Bmin[5]	0		Bmin[5*]	690	
				Denit[6]		860 *(605)*						
Internal budget		4900	*4900*		2400	2307 *(2052)*		80	115		1130	1350

phyto: phytoplanktonic biomass, C:Chla = 40; [1]zoo: *zooplankton biomass estimated from 1994 & 1995 values (Akopian et al., in press)*; [2]POC: nonphytoplanktonic particulate carbon , i.e., POC-phyto; PP: net primary production from ^{14}C measurement; [3]Bactresp: bacterial respiration (net B production/growth yield – net B production); Bactupt: bacterial uptake (net B production/growth yield); [4]Zgraz: zooplankton grazing estimated from grazing rates taken in from the literature – on the basis of average values of biomass in 1994 & 1995 – and average algal biomass in 1993; [5]Bmin C,N,P,Si: benthic mineralization, estimated from measured fluxes at the sediment interface (Sanchez 1997; Table 6). Measurements given in mg $m^{-2}h^{-1}$ are extrapolated at the scale of the whole reservoir and whole year as: median fluxes measured × annual average area (20 km^2) × 24h × 180 effective days; [5*]Bmin, in carbon unit: sum of the oxygen and nitrate fluxes considered as the major oxidants of organic matter; [5**]Bmin in N unit: N-NH_4 flux; [6]Denit: denitrification estimated from NO_3 fluxes and, in italics, by modelling (Garnier et al., submitted); [7]PP, [7]Phyto: diatoms account for 25% of the primary production and phytoplankton biomass, based on microscope counting in 1993.

Redfield ratio, w:w: C:N = 5.68, C:P = 41. C:Si, w:w ≅1 (Conley & Kilham 1989); C:N, w:w = 8.3 for detrical particulate organic matter (measured from sediment traps).

ised in Table 7. Benthic processes expressed by unit surface were converted into tonnes for the whole reservoir using the value of 20 km^2 for the mean annual surface of flooded bottom. A biologically active period of 180 days, from April to October, was taken arbitrarily into account for extrapolation to the whole hydrological cycle. As biological processes stronly depend on temperature with a maximum at about 30 °C and a minimum at less than 10 °C (Sanchez 1997), the estimation must be at a factor of less than 2.

Whereas C, P, Si budgets are dominated by internal recycling processes, the nitrogen budget is dominated both by the input of nitrate from the river and by an internal recycling of ammonium (Figure 7). Primary production represents the main input of carbon for the reservoir and is intensively recycled within the system (Figure 7(a)). Planktonic and benthic organic matter mineralization are of the same order of magnitude. The reservoir represents a sink for inflowing nitrate. Denitrification estimated from the benthic flux of nitrate explains most of the differences between reservoir input and output (Figure 7(b)). The nitrogen requirement by primary production may be largely supplied by planktonic and benthic ammonification. Planktonic and benthic nitrification was not evaluated. Although the reservoirs behave as sinks for phosphorus and reactive silica, there is intensive recycling of phosphorus in the planktonic phase and of silica and in the benthos (Figure 7(c, d)).

Discussion

The effect of reservoirs management practice is that the hydraulic residence time is about 0.5 year. The hydrological cycle, from November–December of one year to November–December of the following one, covers a classical seasonal cycle of biological activity. Water accumulation depends on meteorological conditions, but recharge to the reservoir is the strongest in winter so that the seasonal pattern of nutrient input can be compared to that in true lakes where it is due to winter overturn. Seasonal variations of nutrients and chlorophyll in the reservoirs therefore follow a well-known lake pattern (Sommer et al. 1986): as soon as light radiation and temperature increase in early spring phytoplankton develops and takes up phosphate and silica. Whereas the replacement of diatoms by others groups of algae allows some silica regeneration, phosphorus is maintained at a very low concentration until late autumn.

The amount of suspended matter entering the Marne reservoir (ratio between annual influx of suspended solids to total water influx) is relatively greater than for the two other reservoirs, due to the land use in the upstream basin, arable land being more important in the Marne Basin. Except during

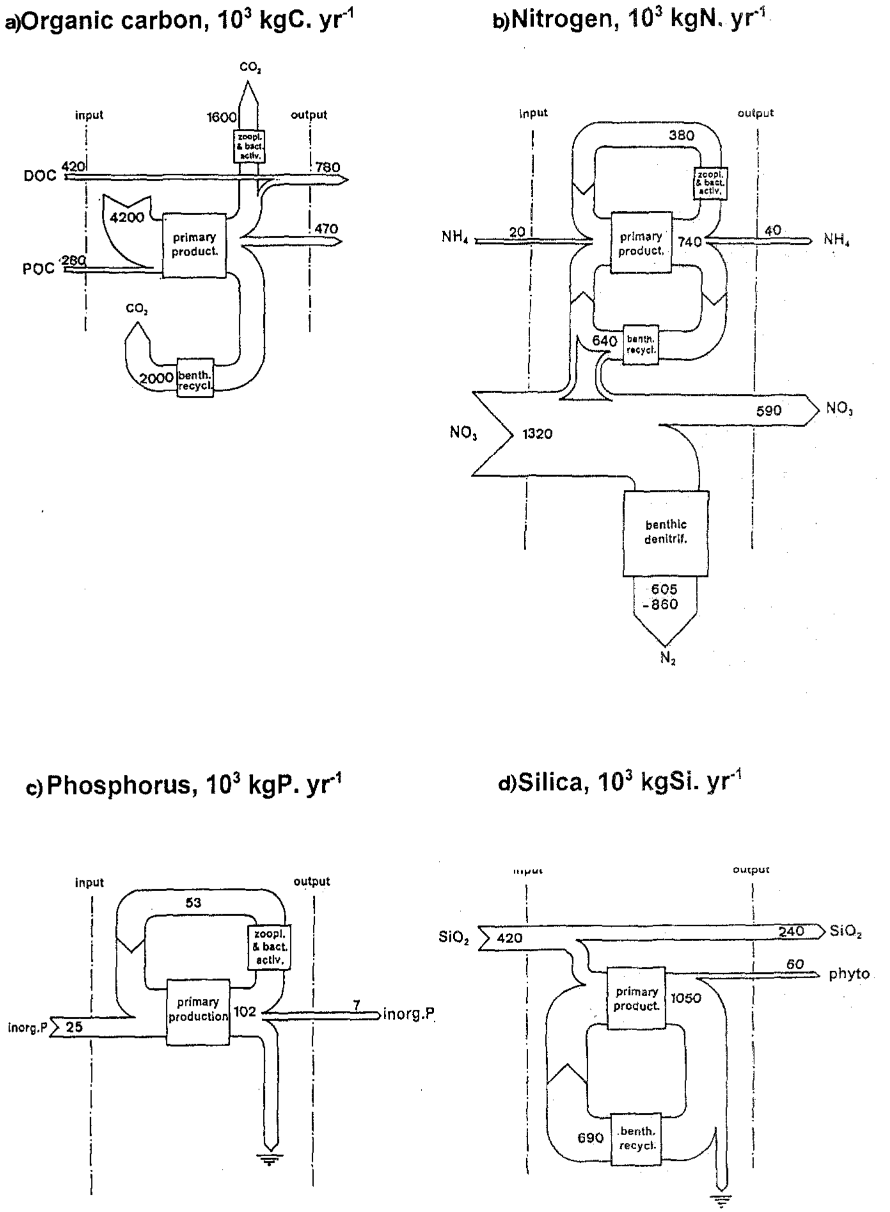

Figure 7. Schematic representation of inlake budgets. (a) Organic carbon, (b) Nitrogen, (c) Phosphorus, (d) Silica.

decennial drawdown, all three reservoirs of the Seine Basin are sites for sedimentation of suspended matter. Invariably, a decennial drawdown leads to overall export of suspended matter. When the water level is lowered, the bottom sediment is resuspended, the exposed shores are eroded, and suspended matter is exported. However, whatever the hydrological conditions, the case is different in the upper lakes. The area around the water inlet acts as a brake on incoming river water and creates a typical site for sedimentation. Besides the variability in suspended matter retention (from 13% to 73%) related to hydrological conditions, disparities between years might also be due to inappropriate frequency of sampling during high flow. However, sediment trapping by reservoirs seems to be seen a constant feature that has also been observed in larger reservoirs at the global scale (Vörösmarty et al. 1997).

For the river system, the reservoirs are a source of phytoplankton, but a sink of particulate organic carbon, except during decennial drawdowns. Autochtonous organic carbon, originating from algal production during the vernal period is parly exported while or allochtonous detrital particulate carbon brought in by high winter flow mostly sediments. The annual primary production of the Marne reservoir was evaluated at 4200 tonnes C, a much higher value than phytoplankton inflow and outflow which are 80 and 240 tonnes C, respectively. Preliminary estimates of zooplankton grazing show that a large part of the primary production is harvested by grazers which leads to intensive recycling of organic matter within the water column. A consequence of intense zooplankton grazing might that dissolved organic matter is produced through sloppy feeding (Lampert 1978; Jumars et al. 1989). Data collected in 1993 on the Marne Reservoir show such a high production of dissolved organic matter: besides the amount mineralised by bacterial activity, a large part was exported (see Table 7). The primary production is apparently in equal measure subject to planktonic and benthic degradation. As indicated above, our benthic mineralization figures may however be underestimated. Moreover, the deposition of refractory particulate organic matter is not taken into account in our study. In spite of these uncertainties, carbon circulation within the reservoir is largely dominated by the inlake primary production recycling.

Nutrient mass-balances show similar patterns for all years and reservoirs. Whereas uptake by primary production followed by sedimentation are the major processes by which phosphorus and silica are retained in the reservoir, it is well known that nitrogen is eliminated by denitrification in many other aquatic systems (Seitzinger 1988; Billen et al. 1991).

Under a particulate form, phosphorus is usually efficiently trapped in stagnant systems: values reaching 90% of P-trapped are reported by Serruya (1975) and Likens and Loucks (1978) for a range of lakes and reservoirs.

In the reservoirs studied here, about 60% of the phosphorus, is lost by sedimentation either retained by algal uptake or adsorbed on suspended matter. Although trapped, phosphorus appears to be rapidly recycled within the water column, as shown by the high primary production that it supports, which represent 3 to 4 times the flux of phosphorus coming into the reservoirs. Half of this incoming flux is in the form of phosphate, i.e. readily available. The phosphorus content in the sediment is relatively low (0.05% of the dry weight) due to a P-loading of about 0.5–1 g Pm-^{2} year^{-1}, rather moderate when compared to other systems influenced by human activity (reaching 10 g Pm-^{2} year^{-1}, Andersen 1974). Note however that the phosphorus content of the sediment depends in a complex way on P-loading but also on temperature, pH and redox conditions.

Silica is known to play a major role in regulating the composition of phytoplankton (Tilman et al. 1982) and to represent an important factor in eutrophication processes (Officer & Ryther 1980; Schelske 1985). The loss of silica in rivers due to trapping in reservoirs has been called the 'artificial-lake effect' (Van Bennekom & Salomons 1981). It results a shift in phytoplankton composition in downstream waters which has recently been shown by field data from the Iron Gate-Danube-Black Sea system (Humborg et al. 1997). The reservoirs in the upstream Seine Basin retain about 50% of the incoming silica. This could influence the seasonal pattern of phytoplankton development in the river downstream from the reservoirs, as shown by hypothetical scenarios of silica input – from 10% to 150% of the actual load –, tested by modelling (Garnier et al. 1995). Depletion of silica in the reservoirs is observed in April and May concomitantly with the spring diatom growth. A subsequent dissolution of diatom frustules is indicated by the rapid recovery of the concentration in the summer, when the reservoir is not supplied by river water. The inlake budget clearly shows the importance of redissolution for primary production in the reservoir.

Ammonium represents a small proportion of the inorganic nitrogen input but it is able to support a high primary production that is recycled by planktonic (bacterial and zooplanktonic activity) and benthic (degradation of organic matter) processes. Nitrate, the dominant form of nitrogen entering the reservoir, is eliminated to 40%, mostly by denitrification (Sanchez 1997; Garnier et al., submitted). This appears to be common in a variety of stagnant systems (Serruya 1975; Likens & Loucks 1978; Seitzinger 1988; Galicka & Penczak 1989; Molot & Dillon 1993). Extensive denitrification would explain the low N concentration in the sediment (0.2 to 0.3% (dry weight) Kjeldhal Nitrogen in the Marne reservoir). Several empirical or modelling studies (Lijklema et al. 1989; Molot & Dillon 1993; Kelly et al. 1987; Windolf et al. 1996; Garnier et al., submitted) have shown that the percentage of retention by denitrification is inversely proportional to the water residence time. A retention of 40% for a residence time of half a year is consistent with these studies.

The Riverstrahler Model applied to the Seine river system (Billen et al. 1994; Garnier et al. 1995) made it possible to calculate a comprehensive budget of nitrogen transfer and retention in the main sub-basins (Billen & Garnier 1998). According to the results, the retention in the reservoirs (about 5000 tonnes N yr^{-1}) represents 12% of the total nitrogen load of the Marne, Seine and Aube sub-basins and 5% of the flux at the mouth of the Seine river itself. Retention by denitrification and storage in river channel sediments represents about 4000 tonnes N yr^{-1}, a value similar to that of total retention in the reservoirs. Reservoirs may therefore be considered as sinks for nitrogen, although the effect of retention is only significant at the scale of the sub-basins, because of their upstream location in the watershed. The reservoirs are also sinks for other nutrients. While incoming nitrogen is mostly eliminated by benthic denitrification, the retention of P and Si amounts to as much as 60% and 50% of the respective incoming fluxes. This retention is due to sedimentation and benthic storage, which in fact represents limited 'leaks' in active internal cycling processes involving phytoplankton uptake and biomass mineralisation.

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References

Akopian M, Garnier J & Pourriot R (in press) A large reservoir as a source of zooplankton for the river: structure of the populations and influence of fish predation. J. Plankton Res.

Andersen VJM (1974) Nitrogen and phosphorus budgets and the role of sediments in six shallow Danish Lakes. Arch. Hydrobiol. 74: 528–550

Barillier A & Garnier J (1993) Influence of temperature and substrate concentration on bacterial growth yield in Seine River water batch cultures. Applied Environ. Microb. 59: 1678–1682

Van Bennekom AJ & Salomons W (1981) Pathways of nutrients and organic matter from land to ocean through rivers. In: Martin J-M, Burton JD & Eisma (Eds) River Inputs to Ocean Systems (pp 33–51). UNEP, IOC, SCOR, United Nations, New York

Billen G, Garnier J & Hanset Ph (1994) Modelling phytoplankton development in the entire drainage network: The RIVERSTRAHLER model applied to the Seine River system. Hydrobiologia 289: 119–137

Billen G & Garnier J (1998) Chapitre 10. Les sels nutritifs: l'ouverture des cycles. In: Meybeck M, de Marsily G & Fustec E (Eds) La Seine en son Bassin. Elsevier, Paris, in press

Billen G, Lancelot C & Meybeck M (1991) N, P, Si retention along the aquatic continuum from land to sea. In: Mantoura RFC, Martin JM & Wollast R (Eds) Ocean Margin Process in Global Change. John Wiley & Sons Ltd

Conley D & Kilham SS (1989) Differences in silica content between marine and freshwater diatoms. Limnol. Oceanogr. 34: 205–213

Cooke GD, Welch EB, Peterson SA & Newroth PR (1993) Restoration and Management of Lakes and Reservoirs. Lewis Publishers, U.S.A.

Eberlein K & Katter G (1984) Automatic method for the determination of orthophosphate and dissolved phosphorus in the marine environment. Fresenius Z. Anal. Chem. 326: 354–357

Forsberg RB (1985) The fate of planktonic primary production. Limnol. Oceanogr. 30: 807–819

Fuhrman JA & Azam F (1980) Bacterioplankton secondary production estimates for coastal waters of British Columbia, Antartica, and California. Appl. Envir. Microb. 39: 1085–1095

Fuhrman JA & Azam F (1982) Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters: evaluation and field results. Mar. Biol. 66: 109–120

Galicka W & Penczak T (1989) Total nitrogen and phosphorus budgets in the lowland Sulejow Reservoir. Arch. Hydrobiol. 117: 177–190

Garnier J. & Mourelatos S. (1991) Contribution of grazing in phytoplankton overall losses in a shallow lake (Créteil Lake, France). Freshwater Biology 25: 515–523

Garnier J, Billen G & Coste M (1995) Seasonal succession of diatoms and Chlorophyceae in the drainage network of the river Seine: Observations and modelling. Limnol. Oceanogr. 40: 750–765

Garnier J, Billen G & Levassor A (1998) Chapitre 5. Fonctionnement et impacts écologiques des réservoirs de Champagne. In: Meybeck M, de Marsily G, Fustec E. (Eds) La Seine en son Bassin. Elsevier, Paris, pp 263–300

Garnier J, Billen G, Sanchez N & Leporcq B (submitted) Ecological functioning of a large reservoir in the upstream basin of the Seine River (Marne reservoir, france): a modelling approach. Arch. Hydrobiol.

Gunnison D (1985) Microbial processes in reservoirs. Development in Hydrobiologia, 27, Dumont H (series Ed)

Jansson M, Andersson R, Berggren H & Leonardson L (1994) Wetlands and lakes as nitrogen traps. Ambio 23(6): 320–325

Jumars PA, Penry DL, Baroos JA, Perry M-J & Frost BW (1989) Closing the microbial loop: dissolved organic carbon pathway to heterotrophic bacteria from imcomplete ingestion, digestion and adsorption in animals. Deep Sea Research 4: 483–495

Humborg C, Ittekot V, Cosiascu A & Bodungen BV (1997) Effect of Danube River dam on Black sea biogeochemistry and ecosystem structure. Nature 386: 385–388

Kelly CA, Rudd JWM, Hesslein RH, Schindler DW, Dillon PJ, Driscoll CT, Gherini SA & Hecky RE (1987) Prediction of biological acid neutralisation in acid-sensitive lakes. Biogeochemistry 3: 129–140

Lampert W (1978) Release of dissolved organic carbon by grazing zooplankton. Limnol. Oceanogr. 3: 831–834

Likens GE & Loucks OL (1978) Analysis of five North American lake ecosystems. III. Sources, loading and fate of nitrogen and phosphorus. Verh. Internat. Verein. Limnol. 20: 568–573

Lijklema L, Jansen H & Roijackers RMM (1989) Eutrophication in the Netherlands. Wat. Sci. Tech. 21: 1899–1902

Lorenzen CJ (1967) Determination of chlorophyll and phaeopigments: spectrophotometric equations. Limnol. Oceanogr. 12: 343–346

Martin C & Romain A (1998) Temporal variability of particulate input, output and retention in the three reservoirs of the 'Grands Lacs de Seine' (1993–1996). Hydrobiologia, in press

Molot LA & Dillon PJ (1993) Nitrogen mass-balances and denitrification rates in Central Ontario Lakes. Biogeochemistry 20: 195–212

Officer CB & Ryther JH (1980) The possible importance of silicon in marine eutrophication. Mar. ecol. Prog. Ser. 3: 83–91

Pourriot R & Meybeck M (1995) Limnologie générale. Masson, Paris

Rodier J (1984) L'analyse de l'eau. 7ème édition. Dunot

Sanchez N (1997) Le processus de dénitrification dans les sédiments du barrage-réservoir de la Marne. Etude de sa cinétique et modélisation. Thèse Doct. Sci. Eau, Université. P. & M. Curie, Paris 6

Schelske CL (1985) Biogeochemical silica mass balances in Lake Michigan and Lake Superior. Biogeochemistry. 1: 197–218

Serruya C (1975) Nitrogen and phosphorus balances and load-biomass relationship in Lake Kinneret (Israel). Verh. Internat. Verein. Limnol. 19: 1357–1369

Seitzinger SP (1988) Denitrification in freshwater and coastal marine ecosystem. Limnol. Oceanogr. 29: 73–83

Seitzinger SP (1994) Linkage between organic matter mineralization and denitrification in eight riparian wetlands. Biogeochem. 25: 19–39

Slavyck G & McIsaac JJ (1972) Comparison of two automated ammonium methods in a region of coastal upwelling. Deep-Sea Res. 19: 1–4

Sommer U, Gliwicz ZM, Lampert W & Duncan A (1986) The PEG-model of seasonal succession of planktonic events in fresh waters. Arch. Hydrobiol. 106(4): 433–471

Steemann Nielsen E (1952) The use of radioactive carbon (14C) for measuring organic production in the sea J. Cons. Perm. Int. Expl. Mer. 18: 117–140

Straskrabova V, Brandl Z, Henderson-Sellers B, Lind OT, Sladecek V & Talling JF (1990) Proceedings of the International Conference on Reservoir Limnology and Water quality. Arch. Hydrobiol. Ergebn. Limnol. Vol. 33

Tilman D, Kilham SS & Kilham P (1982) Phytoplankton community ecology: the role of limiting nutrients. Annu. Rev. Ecol. Syst. 13: 349–372

Thibert S (1994) Exportations naturelles et anthropiques des ions majeurs et des éléments nutritifs dans le bassin de la Seine. Approches méthodologiques. Thèse Doct. Sci. Eau, Université. P. & M. Curie, Paris 6

Thornton KW, Kimmel BL & Payne FE (1990) Reservoir Limnology. Ecological Perspectives. John Wiley & Sons, Inc

Vollenweider RA (1968) Scientific fundamentals of the eutrophication of lakes and flowing waters with particular references to nitrogen and phosphorus as factors of eutrophication. O.C.D.E. Paris, Technical Report, DA 5/SCI/68.27

Vörösmarty CJ, Meybeck M, Fekene B & Sharma K (1997) The potential impact of neo-Castorization on sediment transport by the global network of rivers. In: Human Impact on Erosion and Sedimentation (Proceedings of the Rabat Symposium, April 1997), IAHS Publ, n° 245

Wetzel RG (1983) Limnology, 2nd edn. Saunders College Publishing, New York

Windolf J, Jeppensen E, Jensen JP & Kristensen P (1996) Modelling of seasonal variations in nitrogen retention and in-lake concentration: a four-year mass balance study in 16 shallow Danish lakes. Biogeochemistry 33: 25–44