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Wetland effects on water quality: input-output studies of suspended particulate matter, nitrogen (N) and phosphorus (P) in Grand-Lieu, a natural plain lake

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Abstract

The role of wetland on water quality of rivers was estimated in a natural lake, Grand-Lieu (5600 ha), discharging to the Loire estuary. Inputs of its two tributaries, budgets and retention within the lake for particulate matter (PM), nitrogen (N) and phosphorus (P) were compared during the inflow period (Oct–May), by an input-output study, in two hydrologically contrasted years, 1993–94 with high inflow (292 10^6 m^3), and 1995–96 with low inflow (76 10^6 m^3). Globally the loads per ha were similar for the two tributaries for the same year, with higher values at the beginning of the flows, and total inputs markedly higher in 1993–94. During this year, average loads for the main tributary were 154 kg ha^{-1} PM, 40 kg ha^{-1} total N and 1.35 kg ha^{-1} total P. In the two tributaries, NO_3 represented 80% of total N for the two years, and PO_4 65% and 44% of total P. Total inputs, total outputs and storages are highly related to annual inflow, with large differences between elements. The highest change of inputs occur for NO_2, PO_4 and PM, and the lowest for NH_4. Storage and outputs of the lake were also much higher in 1993–94, the most important annual differences concerning P storage, and outputs of PM and all forms of nitrogen except NH_4. However, only the retention rate of total P doubled with the high outflow of 1993–94 (40% against 18%), while those of PO_4 and NH_4 were equivalent (79–72% and 72–66% respectively). In contrast the retention rate of all the other elements was lower with the large flow of 1993–94: 61 against 86% for NO_3, 85–90% for NO_2, 32–60% for total N, and 14–20% for PM. Globally, this wetland received important discharge of inorganic nitrogen from its catchment area, trapping or converting most of it (62–85%) into organic matter, while it exported a large amount of dissolved and particulate organic nitrogen (16 g m^{-2} y^{-1} in 1993–94 and 4.5 in 1995–96), 2.6 and 1.9 times more than it received. The exportation of organic N per m^2 and retention of total N (9.9–14.5 g m^{-2} y^{-1}) represent record values. This seems mainly due to the importance of water flow, juxtaposition of habitats with different degree of closure, plant biomass and resuspended endogenous, organic sediments in exportation. The lake is not able to counterbalance the dramatic increase of agricultural and sewage inputs, that induce its eutrophication and silting up.

Introduction

Wetlands, including shallow lakes, play an important role in water quality of rivers by storing sediments and nutrients, even if this action is often controversial (Lee et al., 1975; Jones et al., 1976; Gersberg et al., 1986; Johnston et al., 1990; Johnston, 1991). Numerous studies on wetlands give concentrations of nutrients in water or standing stocks, but according to Johnston (1991) and Hopkinson (1992), studies on fluxes in wetlands are less common, in comparison with rivers (Dolan et al., 1981; Meybeck, 1982, 1993; Golterman et al., 1983; Probst, 1985; Seux et al., 1985; Walling, 1988; Dorioz et al., 1989; Kronvang, 1992). We measured input and output fluxes of particulate matter, nitrogen and phosphorus on the major

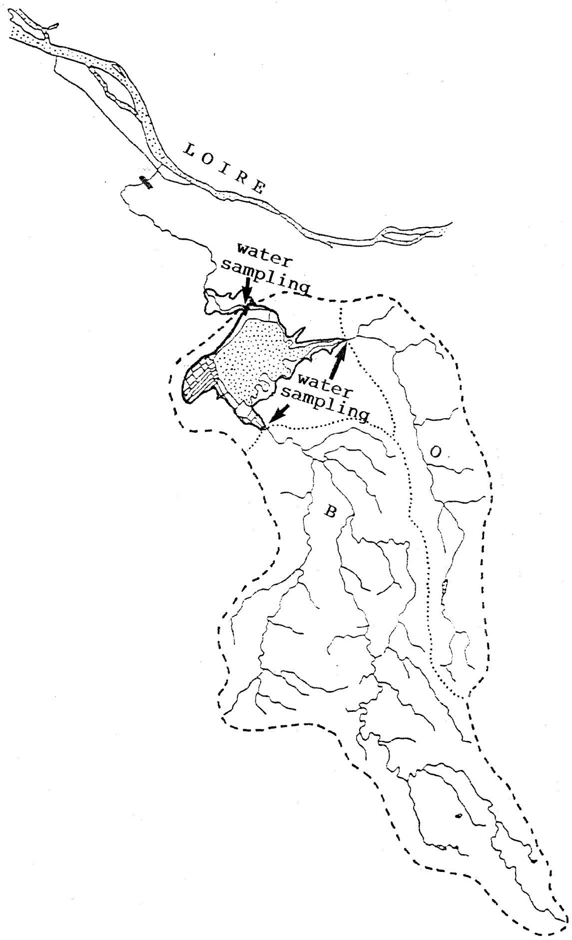

Figure 1. Map of the watershed of the lake (B = Boulogne, O = Ognon), with water samples points.

and oldest natural French floodplain lake, Grand-Lieu (5600 ha), that flows into the Loire estuary. Although most of the discharge in and out of the lake occurs in winter, its small catchment area (670 km^2) and its important biomass of algae, macrophytes and trees suggested that it could play an important role in water quality, in agreement with Odum's theory (1969) on higher retention in old succession stages' systems. We tested this role by a triple approach: comparisons between the two tributaries, between inputs and outputs of the lake, and between two hydrologically opposite winters, 1993–94 with one of the highest annual inflows since 1946 and 1995–96 with one of the lowest annual inflows. This paper focuses on the retention in the lake rather than on the watershed fluxes.

Description of site studied

The lake of Grand-Lieu is situated 23 km from the Atlantic Ocean, 25 km upstream of the Loire estuary (Figure 1). It is a natural lake formed by subsidence between the Tertiary and Pliocene periods. Several sea transgressions and regressions occurred until the Flandrian, the sea and an Ypresian river (50 million years) depositing sand in parts of the lake and of the catchment area. The lake covers about 4000 ha during summer, and 6300 ha during winter, by flooding adjacent peaty marsh grasslands used as pastures (Figure 2). Within the summer wet area, about 2000 ha of peat bog, that has progressively appeared in the last 7000 y, border a 20 km long shore, with *Phragmites*, *Salix* and *Alnus*. Parts of this peat bog are floating, while others are flooded from October to July. Most of the permanently flooded area of the lake is covered from April to October or November by about 1400 ha of floating macrophytes (mainly *Nymphea alba*, *Nuphar lutea*, *Trapa natans*, *Nymphoides peltata*), and more scarcely *Scirpus lacustris*. This macrophyte area has a muddy bottom, and its water depth is about 0.7 m in July. Other 600 ha, with rocky, sandy and/or clay bottom, has no floating macrophytes and extends to the eastern shore, bordered by a narrow vegetation belt of emerging macrophytes (*Scirpus lacustris*, *Typha angustifolia*, *Phragmites communis*). In July, depth varies from 1.2–1.7 m in the central part to 0.1 m on the edge. The rocky and sandy bottom subsides toward the West, to reach a pit, originally 15–20 m deep and now entirely full of muddy sediments. Organic sediment and peat (without marsh grass lands) represent about 160 10^6 m^3. For more details see Marion & Marion (1975).

Two rivers flow into the lake: the Boulogne (88 km long, average slope 0.01%) and the Ognon (45 km long, average slope 0.1%), with catchment areas of 485 and 185 km^2 respectively (Figure 1). These catchments are mainly under cultivation (cereals, maize, vine, grasslands with hedgerows, small woods). Soils are mainly sandy and clayey. The outlet, the Acheneau (25 km long), flows to the Loire estuary. The hydroperiod of the wetland with contrasted high and low water levels, is regulated by a sluicegate. This closes the outlet canal from the end of the flooding of the adjacent pastures (April) until the following winter, when a new flood must be evacuated (generally from December onwards). This sluicegate is situated on a ditch created in the 19th century, that separates the lake in two parts (5600 ha above, including 4000 ha of

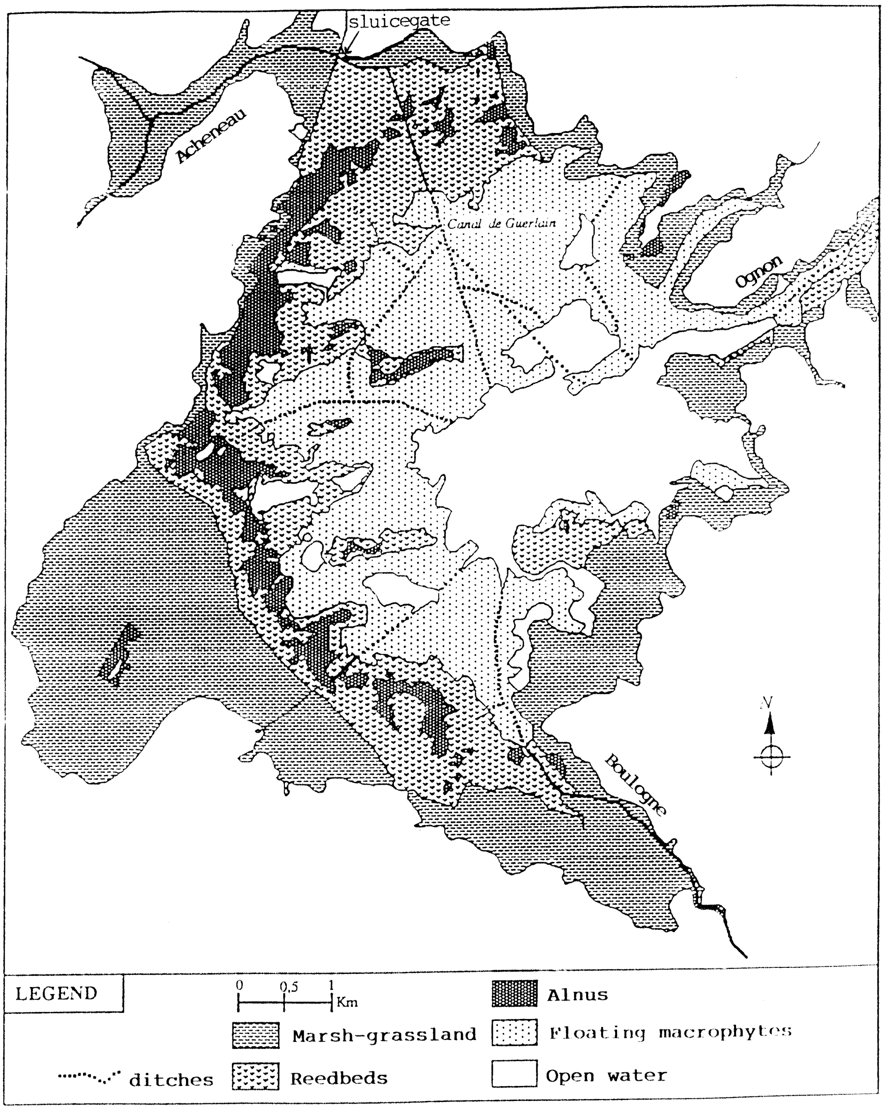

Figure 2. Map of the lake of Grand-Lieu with the different vegetation areas. The summer limit of water excludes the marsh grass land, that is seasonally flooded (Nov./Dec.–April/May). The reedbeds with Alnus are intermittently exposed (August–Sept.), and macrophytes with open water (central area) are permanently flooded.

permanent lake area with the peat bog and 1600 ha of adjacent marsh flooding grasslands, and 700 ha below, with only marsh flooding grasslands, see Figure 2). During the closing of the sluicegate, inflow from the catchment is generally nil, and rainfall on the lake (5600 ha = 16 10^6 m^3) does not counterbalance evapotranspiration (Penman method: 29 10^6 m^3) and pumping (3 10^6 m^3). So a 0.4 m decrease of the lake level is noted from May to September. Accordingly to these two hydraulic periods, the volume of water in the lake (before the sluicegate) varies during the year from 25 to 120 10^6 m^3. Most of the annual mean inflow of 168 10^6 m^3 (N = 45 y: 1946–90) occurs from December or January to March, with few peaks floods. During winter (October to April), mean direct input by rain represents only 24 10^6 m^3 and direct loss by evapotranspiration 12 10^6 m^3. Average net input from the atmosphere represents only 7% of total flow entering the lake during this period. There is no exchange with groundwater. Nutrient inputs from rivers are mainly due to agriculture, secondary to sewage. The lake was increasingly eutrophied since the 1970's (Marion et al., 1994). Water is saturated with oxygen during winter and oversaturared in the central area during the day in summer, while O_2 concentration in the macrophytes is about 4–5 mg l^{-1} at the surface of water and about 1 mg l^{-1} at -50 cm (Marion et al., 1986). The redox potential is high in water (rH = about 32 MV) and from 12.5 to 17 MV in sediments in September (Rofès, 1992). pH is about 6 in the peat bog, about 7 in the macrophyte area and in the central area in winter, but can increase to 11 in summer (Marion et al., 1992). The Alkalinity (about 0.8 meq l^{-1}) and carbonates ($< 1\%$) are low, and the conductivity increased from about 250 μS cm^{-1} in 1982 (Marion et al., 1986) to about 500 μS cm^{-1} in 1991 (Rofès, 1992).

Materials and methods

Flows and input – output concentrations of PM, N and P measurement

For simplicity, we name the 1993–94 and 1995–96 winters 1994 and 1996, respectively. During the inflow periods, water samples were taken once a week at the junction of the two tributaries with the lake, manually from early January to the end of May 1994, and by using automatic refrigerated sampling pumps every two hours (samples cumulated per day) in 1996 from December 24 to May 31. This last method was also used in the outlet draining channel during the two whole outflow periods (from December to May). Daily inflows were automatically measured every day in the two tributaries during the two years. Daily outflows of the draining channel were estimated for 1994 from the inputs (including net rain input) and daily variations of water level in the lake, and automatically measured in 1996. The water samples were analyzed in the laboratory for a range of variables including: particulate matter (PM), NO_2-N, NO_3-N, NH_4-N and PO_4-P after filtration on GF/C, and total N and total P on crude water. Data for ouputs give concentrations of water samples taken just before the sluicegate, even when the latter was closed (in this case output is nil although positive concentrations). PM was measured by filtering 250-750 ml water through precombusted and preweighted 0.7 m glass-fibre filters. Filters were dried for at least 1 h at 103 to 105°C, cooled in a dessicator and weighed. At the exit of the lake a turbidimeter (Ponselle Mesure) collected data every 15 mn when water output occurred. Concentrations of orthophosphate P were determined using the colorimetric technique with ascorbic acid reduction according to Murphy & Riley (1962). According to Golterman et al. (1978), total P and total N were determined using persulphate as oxidizing agent at 120°C during 1/2 h, NO_3 by the reduction cadmium method, NH_4 by the phenate method and NO_2 by diazoting with sulfamide and coupling with N-(1 BNnaphtyl)-ethylediamine to form a colored azodye.

Modelling of PM, N and P budgets and retention in the lake

Fluxes from January to May for each element were calculated by multiplying concentrations by water flow. To approach annual fluxes, we simulated fluxes from October to December, using daily inflows effectively measured in each tributary during each year, and average concentrations obtained during the January–May periods, increased by 7% for N and 14% for P and PM. These corrective factors are based on data obtained on a yearly basis in 1981–82 and 1990–91 (Marion et al., 1994). This estimate for October–December represents 34% of the global water inflow of the 1994 winter (October-May), and only 11% for 1996. Input from June to September was ignored, because it represented only 0.02% of the annual input of nitrogen and 0.1% of phosphorus in the 1990-91 study (Marion et al., 1994). Also, precipitation during the winter period was ignored, because it only contained 0.1 mg l^{-1} of NO_3-N, 0.04 mg l^{-1} of NH_4-N and no P (1996 data), due to the proximity of the sea from which most of wind and clouds come. For the whole winter, precipitation only countains about 2.4 tons of NO_3-N and 0.96 ton of NH_4-N. We also do not take into account inputs by birds, which represented 0.4% of total N and 6.6% of total P in the 1990–91 study (Marion et al., 1994).

Losses of PM and nutrients from the catchment area of the two rivers were obtained by dividing inputs arriving to the lake by the surface of each catchment. Real losses per ha are higher because only part reaches the lake. Retention rates for PM and nutrients within the lake were obtained by the difference of the input and the output, without supposing that output concerns the same particles. Also, retention per m^2 was obtained by dividing the total retention by 5 600 ha (= the area situated before the sluicegate), without supposing that real accumulation is regular in this area (see Discussion). We did not take into account dredging at the exit of the lake during the 1994 and 1996 winters (Marion, 1997).

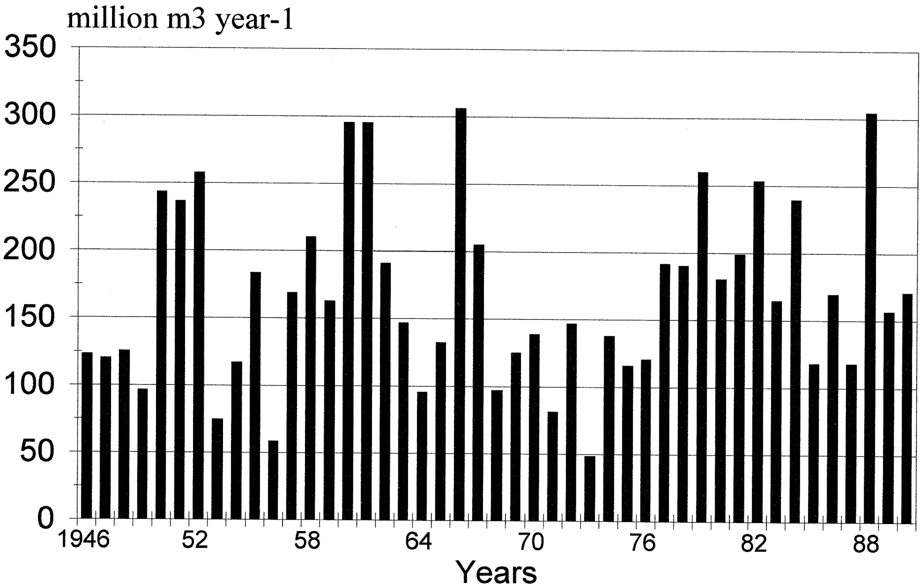

Figure 3. Annual inflow from adjacent streams entering the lake of Grand-Lieu from 1946 to 1990.

We shall take into condideration the summer period in the discussion about retention because each new winter input is first diluted in the volume of the lake, whose quality is influenced by processes occurring within the lake during its closing stage (spring-autumn).

Results

Inflow and outflow of water

1994 winter

During winter 1994, rivers discharge was the third highest since 1946: 292 10^6 m^3 against 306 in 1966 and 304 in 1988 (Figure 3). After a limited flow in October, the inflow really began on December 5 and practically stopped mid April. Most of the flow occurred between mid December and mid February. The Boulogne contributed 74% of the inflow, with 9 flood peaks (Figure 4A). The most important flows occurred during the first week of January (up to 8 10^6 m^3 during 24 h) and the first week of February (up to 10 10^6 m^3). Run-off varied during the winter from 0.90 to 119 m^3 s^{-1} ($\bar{x} = 10.26$ m^3 s^{-1}). The Ognon displayed simultaneous peak flows but at a lower level (< 3 10^6 m^3 per day). During the winter, its run-off varied from 0.25 to 36 m^3 s^{-1} ($\bar{x} = 3.66$ m^3 s^{-1}).

The outflow of the lake represented 288 10^6 m^3. It started on December 13 but was important only at the end of December, then decreased regularly until the beginning of May (Figure 4B). The outflow varied from 1.24 to 59.78 m^3 s^{-1} ($\bar{x} = 19.05$ m^3 s^{-1}). By reference to the minimum volume of the lake (in September), the residence time of water was 0.09 y.

1996 winter

During winter 1996 the discharge was only 75.5 10^6 m^3. Only two years have had a lower discharge since 1946 (48 10^6 of m^3 in 1973, 58 in 1956). The discharge began at the end of December and practically stopped at the end of March, most of it occurring before the end of February, with seven small flow peaks (all with about 1 10^6 m^3 for the Boulogne except the last one with 2 10^6 m^3, Figure 5A). This river contributed 68% of the winter inflow with a run-off varying from 0.10 to 29 m^3 s^{-1} ($\bar{x} = 2.79$ m^3 s^{-1}). Run-off of the Ognon varied from 0.10 to 16.60 m^3 s^{-1} ($\bar{x} = 1.31$ m^3 s^{-1}).

The outflow of the lake was lower than the inflow by only 58 10^6 m^3 (Figure 5B). It started on January 17, stopped temporarily the three last days of February, from March 30 to April 27, and from April 28 to May 3, and stopped definitely on May 30. When the sluicegate was open, the outflow varied from 0.32 to 12.44 m^3 s^{-1} ($\bar{x} = 4.88$ m^3 s^{-1}). The residence time of water was 0.33 y.

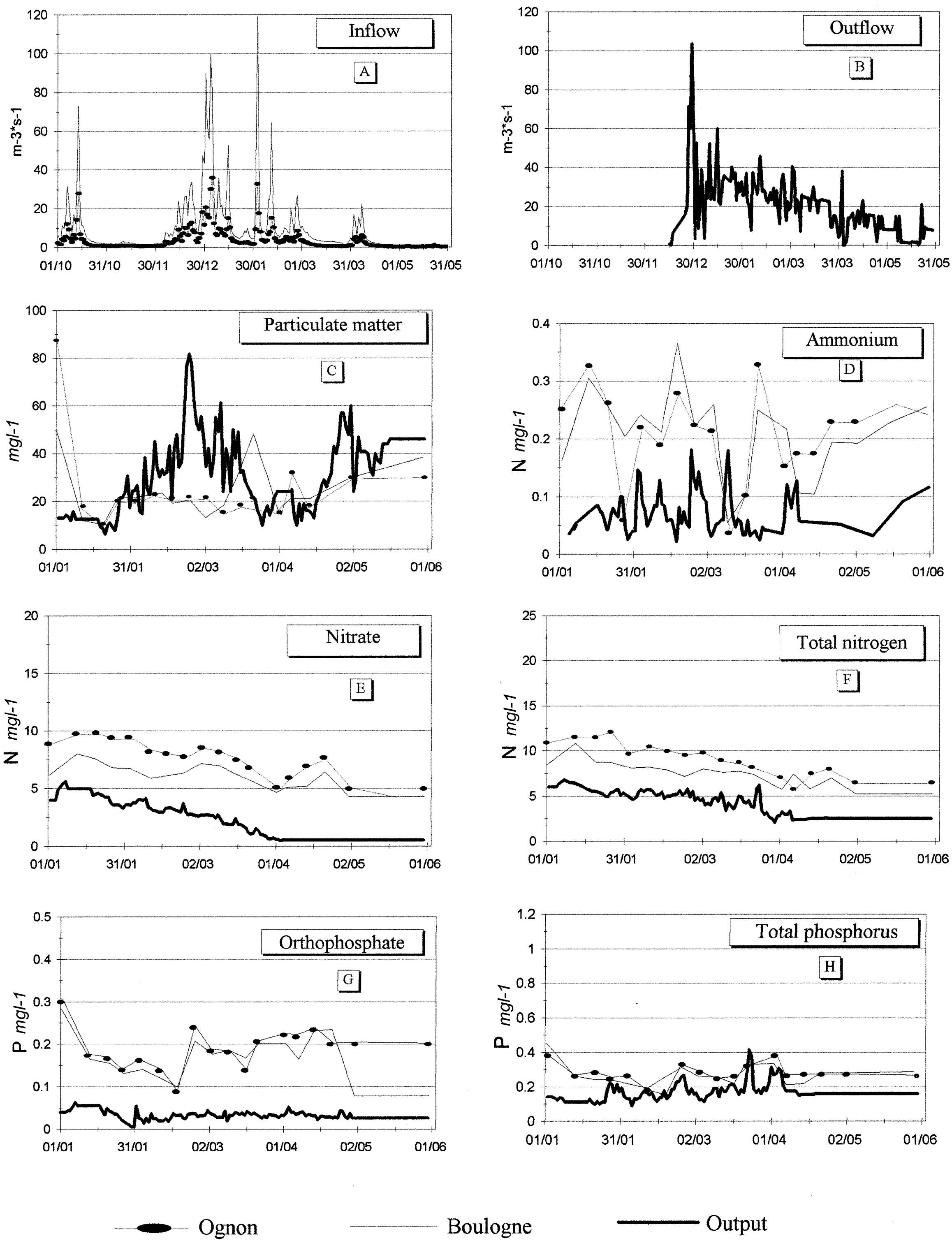

Figure 4. Comparison between inflow from the two tributaries (Boulogne and Ognon), outflow and concentrations of PM and nutrients in 1994.

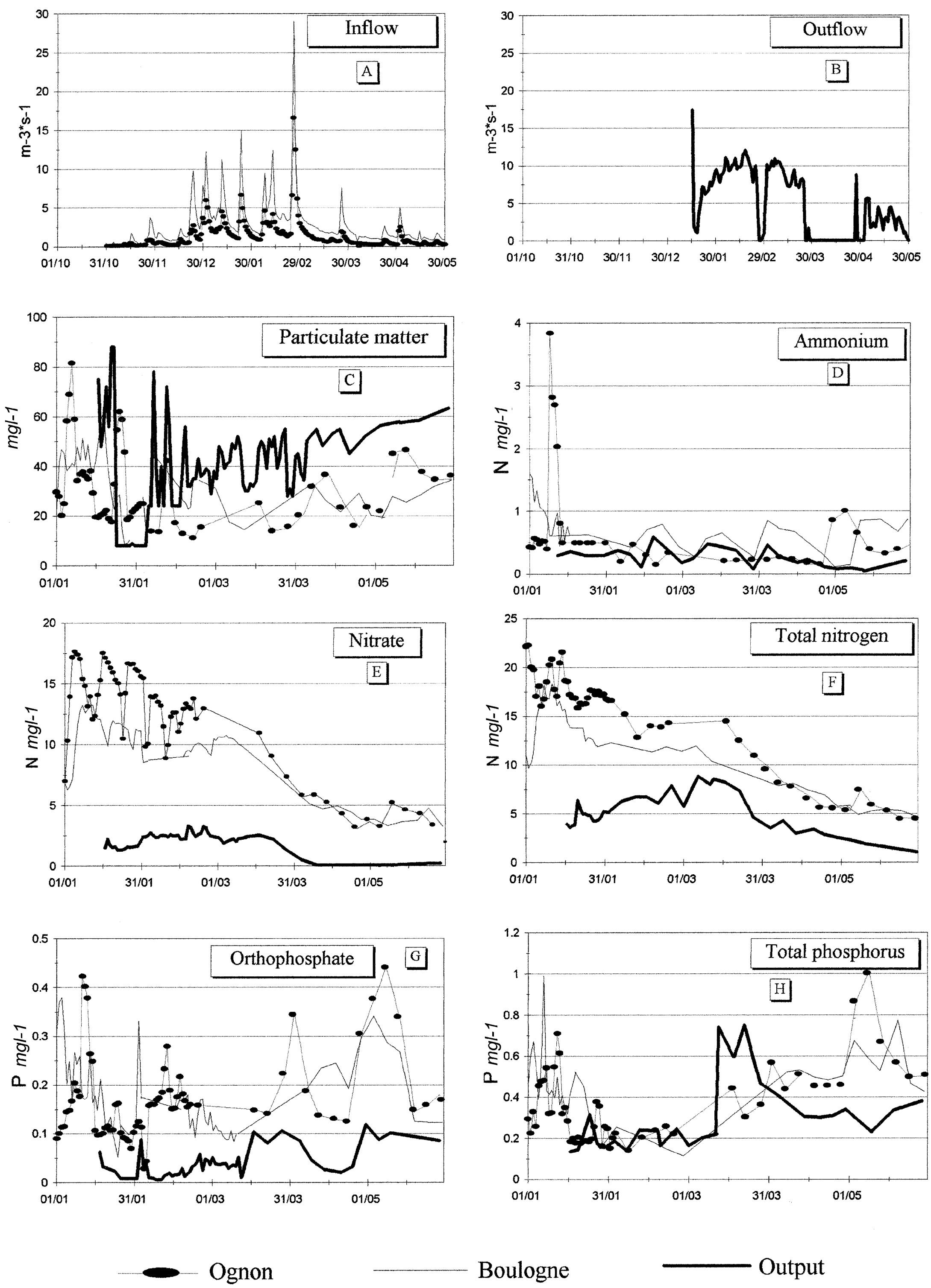

Figure 5. Comparison between inflow from the two tributaries (Boulogne and Ognon), outflow and concentrations of PM and nutrients in 1996.

Particulate matter (PM)

PM is largely represented by sediments during the winter inflow and outflow, whereas algae become more important in April and May (Marion et al., 1992).

1994 winter

PM concentration varied from 5 to 87 mg l^{-1} ($\bar{x} = 24.44 \pm$ SD 5.08 mg l^{-1}) in the Boulogne and from 5 to 49 mg l^{-1} ($\bar{x} = 25.22 \pm 7.81$ mg l^{-1}) in the Ognon (Figure 4C). The highest values for both were observed during the first flow of January, whereas the main flow peak (February 3) did not cause a peak of PM (21 mg l^{-1} in the Boulogne and 12 mg l^{-1} in the Ognon). Estimation of the PM input to the lake for the whole period October–May was about 9153 tons (69% from the Boulogne), and represented losses of 154 and 130 kg ha^{-1} for the catchment of the Boulogne and Ognon.

The PM output of the lake varied from 6 to 82 mg l^{-1} ($\bar{x} = 30.95 \pm 3.23$ mg l^{-1}, Figure 4C). During the whole winter, it totaled 7 913 tons, representing a retention rate of 14% within the lake (22 g m^{-2} y^{-1}).

1996 winter

PM concentrations varied from 9 to 62 mg l^{-1} ($\bar{x} = 32.58 \pm 3.10$ mg l^{-1}) in the Boulogne and from 11 to 82 mg l^{-1} ($\bar{x} = 31.03 \pm 4.02$ mg l^{-1}) in the Ognon (Figure 5C). As in 1994, the highest values occurred during the first flow of the rivers, for example 45 mg l^{-1} on January 2 in the Boulogne when entered 1 10^6 m^3 of water, against only 15 mg l^{-1} with 1.4 10^6 m^3 on January 24 or 34 mg l^{-1} during the major flow peak of 2.5 10^6 m^3 on February 26. The Ognon showed 82 mg l^{-1} on January 5 and only 37 mg l^{-1} on February 26. The estimate for the whole winter was 2526 tons (71% from the Boulogne), and represented only 40 and 37 kg ha^{-1} for each catchment.

The output of the lake varied from 8 to 88 mg l^{-1} ($\bar{x} = 36.51 \pm 3.83$ mg l^{-1}). During winter, it totaled 2019 tons, representing a retention rate of 20% (9 g m^{-2} y^{-1}).

Comparison between the two winters

In 1994, the PM input of the lake was 3.6 times and the output 3.9 times higher than in 1996, mainly due to the difference of inflow (3.9 times) and outflow (5 times), and consequently to the difference of speed of current in the rivers. However, the difference in total retention in the lake is less important (2.5 times), and the retention rate was higher in 1996, in relation with the longer highest residence time of water.

Nitrogen

1994 winter

Total N concentrations varied from 5.50 to 10.82 mg l^{-1} ($\bar{x} = 7.61 \pm 0.64$ mg l^{-1}) in the Boulogne and from 5.80 to 12.10 mg l^{-1} ($\bar{x} = 9.06 \pm 0.90$ mg l^{-1}) in the Ognon. In the two rivers concentrations decreased by about 50% from January to April, with comparatively higher values in the Ognon most of the time (Figure 4F). The estimate for the whole winter was about 2543 tons (70% from the Boulogne), representing losses of 41 and 37 kg ha^{-1} for the Boulogne and Ognon.

The output from the lake varied from 2.1 to 6.8 mg l^{-1} ($\bar{x} = 4.61 \pm 0.26$ mg l^{-1}) and decreased during winter by about 65% (Figure 4F). It totaled 1731 tons for the winter, resulting in a total N retention in the lake of 32% of the input (14.50 g m^{-2} y^{-1}).

Most nitrogen fluxed concerned nitrate, at concentrations from 4.50 to 7.76 mg l^{-1} of NO_3-N ($\bar{x} = 6.18 \pm 0.49$ mg l^{-1}) in the Boulogne and from 5.00 to 9.47 mg l^{-1} ($\bar{x} = 7.67 \pm 0.75$ mg l^{-1}) in the Ognon (Figure 4E). During winter, input to the lake was estimated to about 2040 tons (68% from the Boulogne), representing losses of 29 and 35 kg ha^{-1} from the river catchments.

The output from the lake varied from 0.53 to 5.63 mg l^{-1} ($\bar{x} = 2.71 \pm 0.33$ mg l^{-1}), with a steeper decrease during winter than for total N. During winter, 804 tons of nitrate were exported, or a retention rate of 61% (22.08 g m^{-2} y^{-1}).

Nitrite concentrations were not important and varied from 0.02 to 0.80 mg l^{-1} of NO_2-N ($\bar{x} = 0.33 \pm 0.13$ mg l^{-1}) in the Boulogne, and from 0.03 to 0.67 mg l^{-1} ($\bar{x} = 0.32 \pm 0.12$ mg l^{-1}) in the Ognon, with similar evolution in both rivers: increase in January, relatively low values until the major peak in March, and decrease thereafter. Input to the lake for the whole winter was about 94 tons (74% from the Boulogne). Output from the lake was lower and varied from 0.009 to 0.37 mg l^{-1} ($\bar{x} = 0.048 \pm 0.009$ mg l^{-1}). It totaled 14 tons, representing a retention rate of 85% (1.44 g m^{-2} y^{-1}).

Ammonium concentrations were generally similar in both rivers and fluctuated from 0.06 to 0.37 mg l^{-1} of NH_4-N in the Boulogne ($\bar{x} = 0.20 \pm 0.04$ mg l^{-1}) and 0.04 to 0.33 mg l^{-1} ($\bar{x} = 0.20 \pm 0.04$ mg l^{-1}) in the Ognon (Figure 4D). They were lower in the outputs from the lake ($\bar{x} = 0.07$ mg $l^{-1} \pm 0.02$) and largely fluctuating. The total input to the lake was only 63 tons (72% from the Boulogne), with an output of 18 tons (retention in the lake: 72% = 0.80 g m^{-2} y^{-1}).

1996 winter

During winter 1996, total N concentrations varied from 5.7 to 18.3 mg l^{-1} ($\bar{x} = 11.81 \pm 1.00$ mg l^{-1}) in the Boulogne and from 4.5 to 22.8 mg l^{-1} ($\bar{x} = 14.74 \pm 1.40$ mg l^{-1}) in the Ognon. They increased strongly with flow at the beginning of January in the Boulogne (from 9.9 mg l^{-1} on December 24 to 18.34 on January 9), and more quickly and strongly in the Ognon (Figure 5F). They decreased by about 75% from mid January to April, when concentrations began to be similar in both rivers. During the whole winter, the estimated input to the lake only reached about 930 tons (61% from the Boulogne), representing losses of 12 and 20 kg ha^{-1} from the catchment areas.

The output from the lake varied from 2.00 to 8.82 mg l^{-1} ($\bar{x} = 5.12 \pm 0.56$ mg l^{-1}), with increasing values until mid March and decreasing values after (Figure 5F). During winter, output totaled 376 tons (retention: 60% = 9.88 g m^{-2} y^{-1}).

Nitrate concentrations varied from 2.75 to 13.27 mg l^{-1} NO_3-N ($\bar{x} = 9.22 \pm 0.62$ mg l^{-1}) in the Boulogne and from 2.92 to 17.65 mg l^{-1} ($\bar{x} = 11.79 \pm 1.03$ mg l^{-1}) in the Ognon. Concentrations also largely increased from only 6.32 mg l^{-1} in the Boulogne and 6.43 in the Ognon on December 29 to reach the highest values in the flow of January (Figure 5E). They fluctuated until mid February in relation with flow, with highest values in the Ognon. Concentrations began to be similar in both rivers during the second period of the decrease. During winter, total input was estimated to 742 tons (60% from the Boulogne), representing losses of 9 and 16 kg ha^{-1} respectively for the two catchment areas.

The output from the lake varied from 0.06 to 3.29 mg l^{-1} ($\bar{x} = 1.98 \pm 0.19$ mg l^{-1}). In contrast to 1994, it increased during the first half period before decreasing to reach virtually nil in April (Figure 5E). For the whole winter, the output was only 105 tons (retention: 86% = 11.39 g m^{-2} y^{-1}).

Nitrites were negligible in 1996, varying from 0.01 to 0.11 mg l^{-1} NO_2-N ($\bar{x} = 0.06 \pm 0.01$ mg l^{-1}) in the Boulogne, and from 0.003 to 0.18 mg l^{-1} ($\bar{x} = 0.09 + 0.01$ mg l^{-1}) in the Ognon. The input of the lake for the winter is estimated to only 5 tons (59% from the Boulogne). The output from the lake was virtually nil and varied from 0.005 to 0.06 mg l^{-1} ($\bar{x} = 0.009 \pm 0.004$ mg l^{-1}). It totaled 0.52 tons, representing a retention rate of 90% (0.08 g m^{-2} y^{-1}).

Ammonium concentrations were much higher than in 1994 and fluctuated from 0.12 to 1.76 mg l^{-1} in the Boulogne ($\bar{x} = 0.87 \pm 0.14$ mg l^{-1}) and 0.15 to 3.84 mg l^{-1} ($\bar{x} = 0.62 \pm 0.18$ mg l^{-1}) in the Ognon (Figure 4D). Peaks of concentrations occurred in the Boulogne during the first flow on December 24 (out of Figure), and on January 9 in the Ognon, also with the first storm run-off, while following concentrations were always relatively low even during storms. Total input was estimated at 51 tons (76% from the Boulogne). Concentrations were lower in the outputs from the lake but higher than in 1996 ($\bar{x} = 0.28 \pm 0.04$), involving a similar total output of 17 tons (retention: 66% = 0.60 g m^{-2} y^{-1}).

Comparison between the two winters

On the one hand, the total N and nitrate inputs appeared relatively similar during both years. However, the decrease in 1996 was half as important as in 1994. On the other hand, the outputs differed largely, with a regular decrease in 1994 against an increase followed by a decrease in 1996.

Differences in fluxes between years (Figure 6) were less important for total N input ($\times$ 2.8 times in 1994) than for inflow of water ($\times$ 3.9), but the output basically fitted the outflow ($\times$ 4.6 and 5). However, the difference of global retention in the lake (Figure 7) was not very important ($\times$ 1.5), and the retention rate was almost twice higher in 1996 (Figure 8). Nitrates displayed a similar trend with a difference of 2.8 times for inputs and only 1.9 for retention, although the difference between outputs was important ($\times$ 7.7). So, the retention rate was also more important in 1996 (86% against 61%). Effectively, while nitrates represented the same proportion of total N in inputs for the two years (80%), they represented for outputs 46% of total N in 1994 and only 28% in 1996. Like for PM, the long residence time of water in 1996 probably favoured loss of nitrates. The annual difference of nitrites was the highest of all the studied elements: the input of 1994 was 18 times more important than in 1996, the output 27 times and the global retention 17 times. Thus the retention rate was also more important in 1996 (Figure 8). Inversely, ammonium was the least sensitive to run-off (Figure 6), the difference between years being only 1.2 times for inputs, while outputs and retention rates were similar, in spite of the large difference of flows.

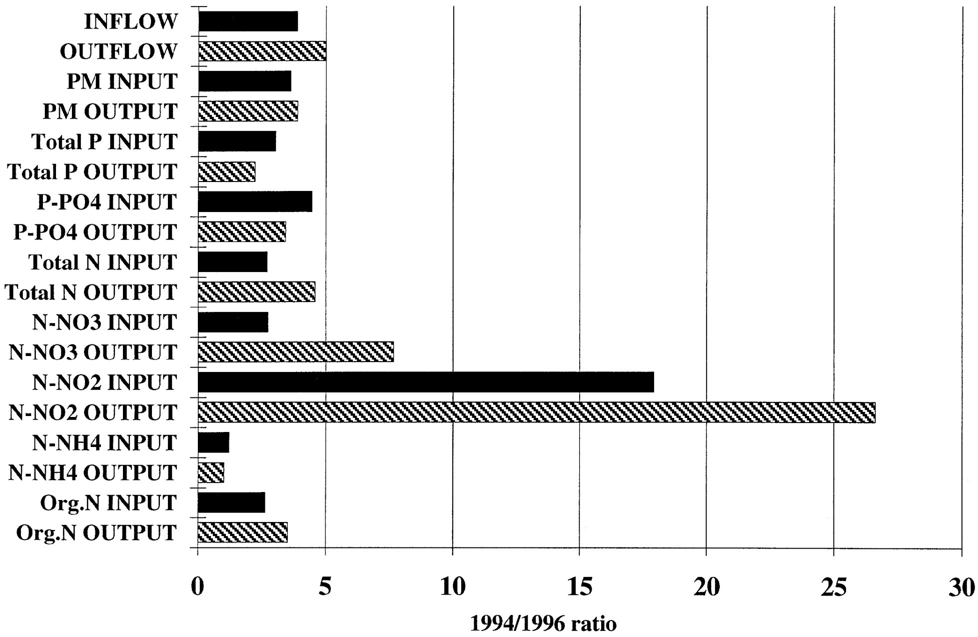

Figure 6. Annual differences of input and output of flow, PM, phosphorus and nitrogen (ratio of fluxes 1994/1996).

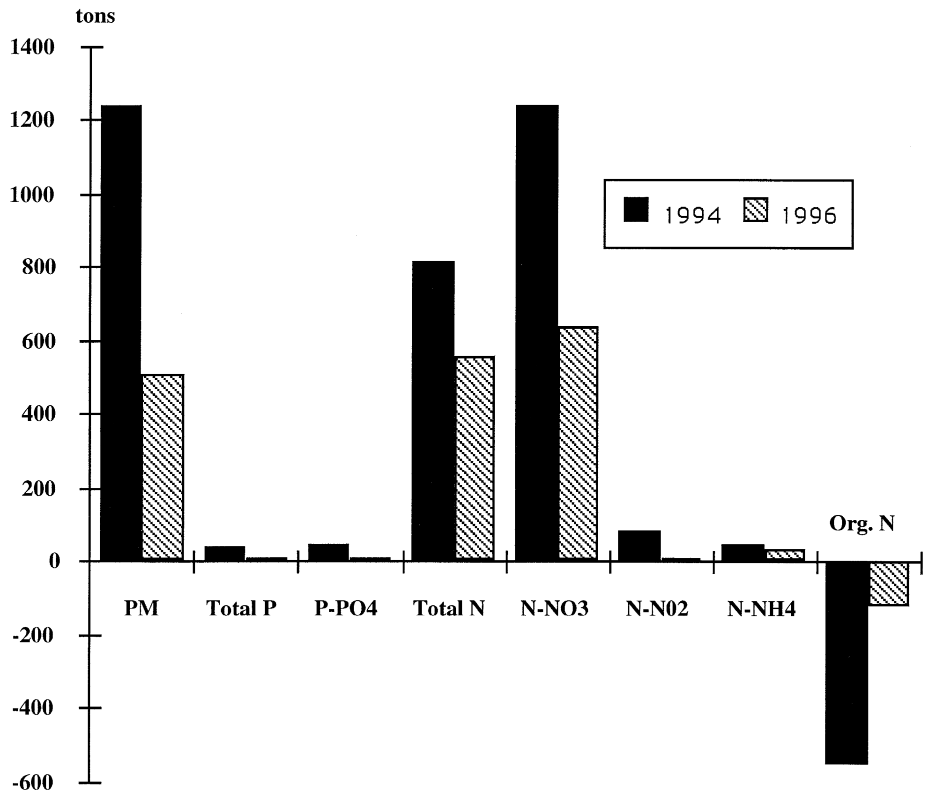

Figure 7. Annual differences of total retention (input–output in tons) between 1994 and 1996 for PM, P and N.

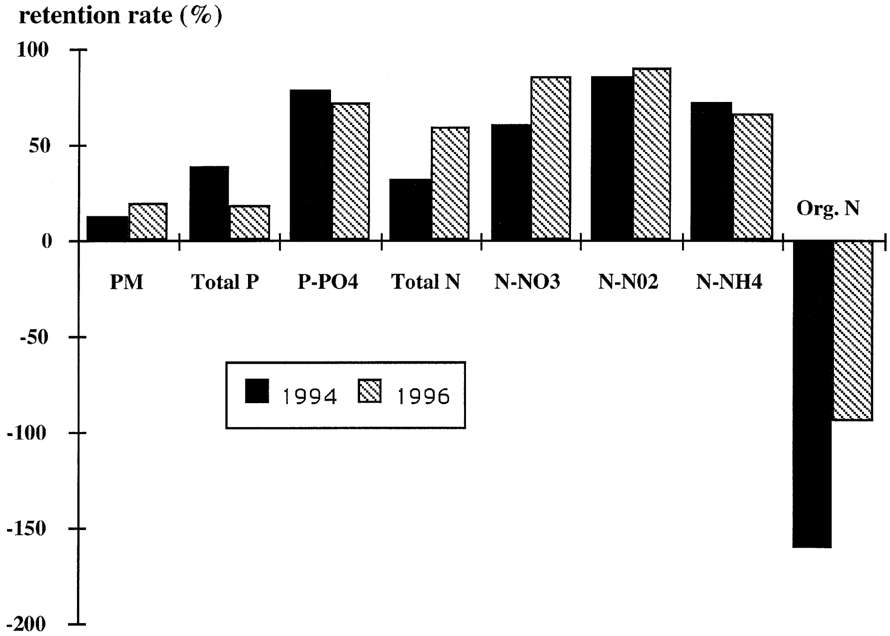

Figure 8. Annual differences of net retention rates (input–output/input) between 1994 and 1996 for PM, P and N.

Phosphorus

1994 winter

Total P concentrations varied from 143 to 450 mg m^{-3} ($\bar{x}$ = 260 ± 33 mg m^{-3}) in the Boulogne and from 153 to 380 mg m^{-3} ($\bar{x}$ = 275 ± 28 mg m^{-3}) in the Ognon. They largely fluctuated during the study, similarly for both rivers, with highest values at the beginning of January and April (Figure 4H). During the whole period, the input of the lake was estimated to about 88 tons (74% from the Boulogne), representing losses of 1.35 and 1.24 kg ha^{-1} for the catchment areas of each river.

The output from the lake varied from 89 to 415 mg m^{-3} ($\bar{x}$ = 170 ± 12 mg m^{-3}). During the whole period, it represented 53 tons, resulting in total P retention in the lake of 40% (0.63 g m^{-2} y^{-1}).

Concentrations of orthophosphate varied from 75 to 278 mg m^{-3} PO_4-P ($\bar{x}$ = 160 ± 23) in the Boulogne and from 88 to 300 mg m^{-3} ($\bar{x}$ = 190+ 23) in the Ognon, with similar evolution during the studied period for both rivers, with a decrease until mid February and higher concentrations after (Figure 4G). The estimated input of the lake reached about 57 tons (72% from the Boulogne), corresponding to losses of 0.84 and 0.88 g m^{-2} y^{-1} for the two catchments.

The output from the lake was low and varied from 5 to 63 mg m^{-3} ($\bar{x}$ = 30 ± 2 mg m^{-3}), with unimportant changes during the season. During the winter, it totaled only 12 tons (retention in the lake: 79% = 0.80 g m^{-2} y^{-1}).

1996 winter

Total P concentrations varied from 109 to 776 mg m^{-3} ($\bar{x}$ = 460 ± 52 mg m^{-3}) in the Boulogne and from 143 to 1010 mg m^{-3} ($\bar{x}$ = 370 ± 50 mg m^{-3}) in the Ognon. They showed several peaks corresponding to the storm run-off of the beginning of January, but less important than for nitrogen (Figure 5H). They then decreased to reach the lowest values of the studied period (about 200 mg m^{-3}) from end of January to mid March, in spite of a major flow peak of February 26 (2.5 10^{6} m^{3} and only 170 mg m^{-3} P in the Boulogne). Then concentrations increased again to reach the highest values ever for the Ognon (up to 1010 mg m^{-3} on May 8), but the flow was at this time low. Globally the curve of total P was inverse to that of nitrogen, except during the first storm flows. For the whole winter, the estimated input reached 29 tons (67% from the Boulogne), representing 0.40 and 0.51 kg ha^{-1} for the catchment of each river.

The output varied from 140 to 741 mg m^{-3} ($\bar{x}$ = 300 ± 63 mg m^{-3}). Concentrations were relatively low (about 200 mg m^{-3}) until mid March, similar to the inputs, then increased during one weak and regularly decreased after (Figure 5H). For the

Table 1. Comparison of N and P inputs in the Lake of Grand-Lieu for 4 y (concentrations averaged on fluxes).

	1980–81	1990–91	1993–94	1995–96
Inflow million m^3	270	135	292	76
N input in tons	780	2184	2543	930
Average concentration mg l^{-1}	2.89	16.18	8.69	12.24
P input in tons	82	36	88	29
Average concentration mg l^{-1}	0.30	0.27	0.30	0.38

whole winter, the output reached 24 tons, resulting in total P retention of 18% (0.09 g m^{-2} y^{-1}).

Orthophosphate was relatively similar in both rivers, with concentrations varying from 52 mg to 390 mg m^{-3} in the Boulogne ($\bar{x} = 180 \pm 20$) and from 83 to 440 mg m^{-3} ($\bar{x} = 170 \pm 20$) in the Ognon. Trend was globally similar to that for total P (Figure 5G). Estimate of the input to the lake was about 13 tons (66% from the Boulogne), and represented losses of 0.17 and 0.24 kg ha^{-1} for the two catchments.

The output varied irregularly during the period from 5 to 122 mg m^{-3} ($\bar{x} = 40 \pm 7$ mg m^{-3}). For the whole winter, it was only 3.6 tons (retention in the lake: 72% = 0.16 g m^{-2} y^{-1}).

Comparison between winters

Like for nitrogen, differences in fluxes (Figure 6) between years were less important for total P inputs (3 times) and output ($\times$ 2.3) than for inflow and outflow of water ($\times$ 3.9 and 5) or PM ($\times$ 3.6 and 3.9), but the annual differences in retention ($\times$ 6.6) and in retention rate ($\times$ 2.2) were the highest of all elements studied, except nitrites (Figure 7 and 8). The input of orthophosphate was 4.5 times more important in 1994, representing 65% of total P against 44% in 1996. Even if its proportion in total P outputs was also higher in 1994 (23% against 15%), the difference was lower and global retention was 4.9 times more important in 1994, despite a relatively similar retention rate (79% against 72%).

Discussion

Even though the flows of the two years (292 and 76 10^6 m^3) were at the extremes side of the known range of this lake, the nutrient inputs observed in the present study were largely higher than normal, due to the dramatic increase in nutrients inputs from sewage and agricultural run-off since the 1960's (Marion et al., 1994). In 1980–81 total P concentrations were already as high as in the 1990's, but the situation for N has degraded since this period (Table 1). Annual total N losses from the watershed (14 kg ha^{-1} for 1996, 39 for 1994) are within the range of values given in literature for agricultural watersheds. The same is true for total P loss for 1996 (0.43 kg ha^{-1}), but the 1994 P value was higher (1.32 kg ha^{-1} instead of a range of 0.18–1.0 reported by Jones et al., 1976).

The four annual budgets (Table 1) like in other lakes (Meybeck, 1995), show that total inputs are highly related to inflow, but considerable differences occur between elements. A comparison between 1994 and 1996 (Figure 6) shows that the largest annual differences were in nitrites, orthophosphate and PM, and the lowest in ammonium. Also, large inflow involved a dilution of most elements (by about 30–70% for PM, total N, NO_3 and total P, and 3–4 times for NH_4), except for orthophosphate (same average concentrations), and above all nitrites, average concentrations of which were 4.3 times lower in 1996. Such higher concentration with flow may be due to overflowing sewage storage tanks (of towns and cattle farms). Respective fluxes from both tributaries were also highly related to annual flow, but less in 1996. In 1994, the part of the Boulogne flux in total input to the lake was relatively similar, for all elements (68 to 74%), to its inflow (74%) and to the surface of its catchment (72%), the lowest proportions concerning nitrate and PM. In 1996, values were more heterogeneous, part of total N, nitrate and nitrites fluxes provided by the Boulogne being lower (61 to 59%) than its inflow (68%), those of ammonium and PM being higher to 1994, and only total P and PO_4 being similar to the contribution of its discharge flow.

As for inputs, the outputs from the lake of elements were higher during the larger flow of 1994, confirming Mitsch & Gosselink (1986) and Hopkinson (1992), who found that increased water inputs generally reflect increased nutrients loading. For Johnston (1991), fluxes are more involved than storage compartments in the control of the net effect of a wetland on water quality. Here again there are important differences between elements (Figure 6), the higher annual differences between outputs concerning PM and all forms of nitrogen except ammonium. Global retention in the lake also reflects the importance of inflow for all elements, but mainly for nitrites, total

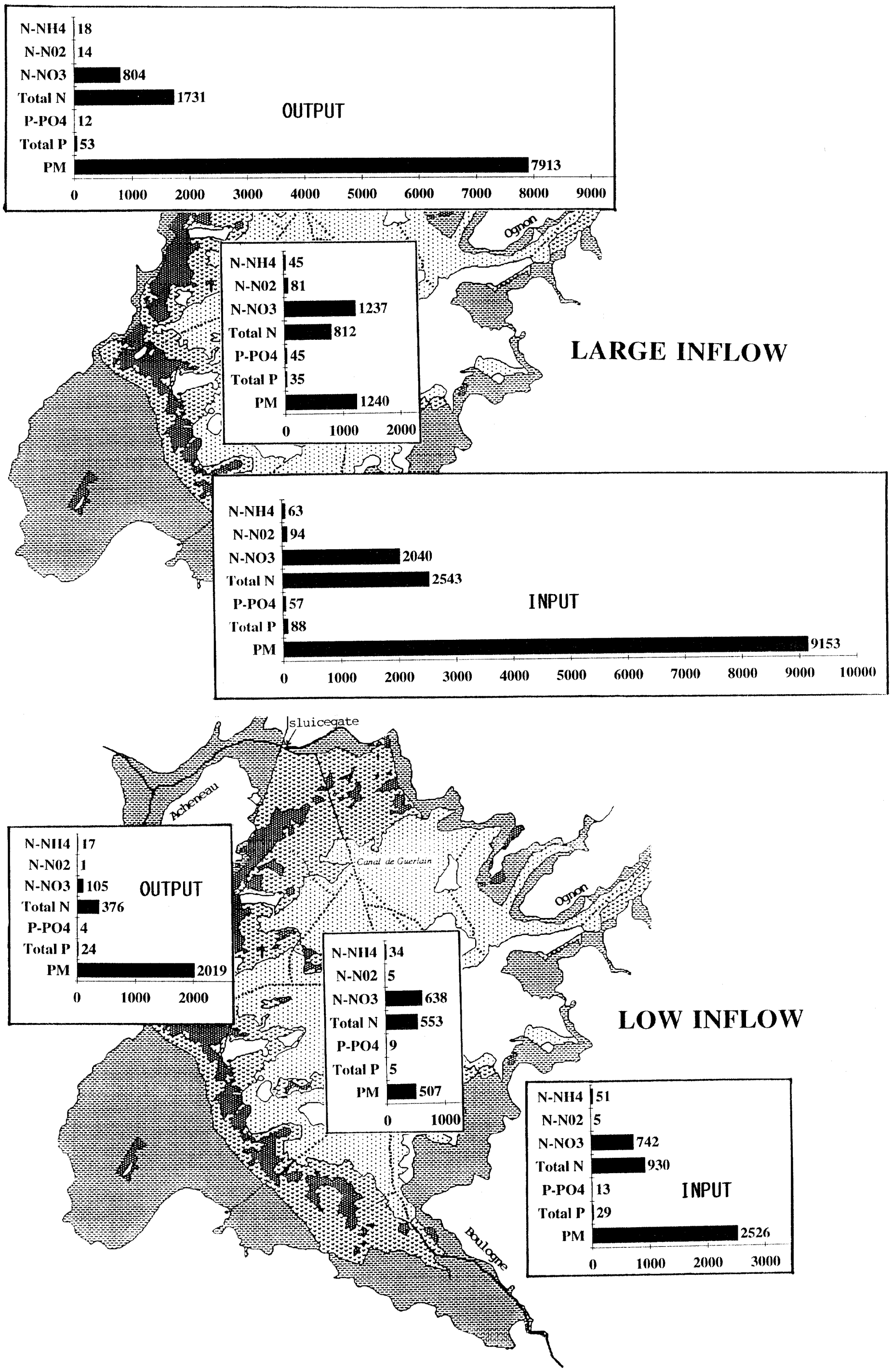

Figure 9. Overview of global retention (in tons) of PM and nutrients within the lake (central box), compared to inputs and outputs during the two opposite inflows in 1994 (large) and 1996 (low).

P, and orthophosphate (Figure 7). Retention rates do not respect this rule (except for total P), 1996 showing higher values for PM and all forms of nitrogen except ammonium (Figure 8). Globally, retention in the lake was less influenced by flow than input and output (Figure 9).

Particulate Matter

The small difference between retention rates of PM during the two years (14-20%), in spite of the different flows and amounts of sediments transported and deposited (from 2.5 to 5 times more important in 1994), could suggest that this retention rate is usual for this lake. It is lower than reported in literature from input-output studies, varying from 23 to 93% for 18 wetlands, with a mean of 44% (Johnston, 1991, after Phillips, 1989). The accumulation rate of allochthonous PM in Grand-Lieu (9–22 g m^{-2} y^{-1}) is naturally much lower than that of Alpine lakes (650–16 000 g m^{-2} y^{-1}, Campy & Meybeck, 1995), and Grand-Lieu should be compared to shallow lakes with a low residence time, that limits sedimentation (Meybeck, 1995). Other factors explain this relatively low retention. Although recent agricultural practices increase erosion (maize crop and vineyards without protecting vegetation during winter, drainage, destruction of hedgerows), such erosion is not important because the watershed is situated in an old, eroded basin (Tertiary), with a smooth relief. Only the PM yields of the two rivers observed during the major flow of 1994 (130 and 154 kg ha^{-1} y^{-1}) are of the same magnitude as shown by Kronwang (1992) for two Danish rivers (143 and 284 kg ha^{-1}), by Ongley (1973) for Canadian tributaries to Lake Ontario, or by Walling (1978) and Foster et al. (1985) for two British rivers. The PM yields that we observed in 1996 were much lower (37 and 40 kg ha^{-1}); Webb & Walling (1984) reported similar values during a nine-year study of a British river. Jigorel (1992) showed that erosion input into the Lake of Grand-Lieu was mainly clay and limon particles (average particle size: 3.6 μ for the Boulogne, 8.8 μ for the Ognon), with relatively little particulate organic matter (17% for the Boulogne, 23% for the Ognon), and many mineral (quartz) and Diatoms skeletal. This input would represent about 32% in 1994 and only 9% in 1996 of the estimated annual production of sediments within the lake, obtained by a model and sedimentation traps in 1990–91 (28 800 tons, Marion et al., 1992). Net retention (input minus output) would only represent 4.3% and 1.8% of this internal production, respectively.

The dynamics of PM inputs conforms to those of other lakes, particularly shallow lakes such as Balaton where wind plays a major role (Sebestyen, 1950; Campy & Meybeck, 1995). Sediments rapidly deposit in the proximate eastern parts of the lake, and small particles are partly resuspended by wind, transported to the center, and finally the western part of the lake (Jigorel, 1992). During winter, when the sluicegate is opened, outputs of sediments mainly concern autochthonous production of the lake, with a mean size of 2.0 μ and much of particulate organic matter (26-39%). Most of this output is sediment resuspended by wind in the western part of the lake, i.e. the macrophyte area, where organic matter represents from 23 to 40% of D.W. (Rofès, 1992). Thus, even if the global retention of sediments in the lake is small, the real sedimentation of PM input is probably higher that it appears here, partly due to its higher density (168 g l^{-1}) than autochthonous sediments (110 g l^{-1} at the surface of sediment), and because concentrations in inflows are higher at the beginning of inflow, when the exit is still closed.

Preliminary results from a recent study based on ^{210}Pb profiles indicate an annual accumulation of about 0.4 cm y^{-1} in the macrophyte area (Creach & Marion, in prep.). A first model concluded that the accretion rate was 1.4 cm y^{-1}, assuming that accumulation occurred on about 1100 ha (Marion et al., 1992), a probable underestimate. Both values confirm that net retention in the lake from inputs from the watershed (input minus output) is considerably lower than internal production. Total accumulation obtained with ^{210}Pb method is similar to that of Lac des Allemands in Louisiana (0.44-0.81 cm y^{-1}, Stow et al., 1985), but lower than that in other American lakes: 1.7 cm y^{-1} in Big Lake (Eckblad et al., 1977), 2.00 in lake Ellyn (Striegl, 1987) and even 2.6 for Capitol Lake (DeLaune et al., 1989). These are the highest values reported for wetlands, after Johnston (1991) who cited a mean of 0.69 cm y^{-1} ($N = 29$ wetlands with mineral sediments). Sedimentation can be even higher in ditches in freshwater marshes in Western France (2-6 cm y^{-1}, Giraud, 1992; Feunteun, 1992). Grand-Lieu represents a record of sedimentation if we only consider wetlands with organic soils (Johnston, 1991), with a mean of 0.12 cm y^{-1} ($N = 13$).

It is important to consider here, for PM and for nutrient retention (see below), the degree of closure of systems (related to the velocity of flow through wetlands), that increases along the four succession stages of the lake. The retentions mentioned in the present study are assumed to be an average at the scale of the lake, since effective retentions are certainly different in each area. The central area, directly connected to tributaries and sensitive to wind, is the most open and the most permanent in aspect throughout year. Its water quality follows that of tributaries (Marion et al., 1986). The floating macrophyte area has the same characteristics as the latter in winter, but becomes increasingly closed during spring. Due to decreasing water level, the peat bog is completely closed from the end of spring to autumn, being partially opened with winter flooding (Marion et al., 1994). The fourth area, the marsh grassland, is a man-created area from the peat bog by cutting all the trees. It is entirely disconnected from the lake when water level is low from spring to autumn, and even during floodings its water is filtered by the peat bog. There is no wind-resuspension in this area. Accumulation of sediment is important in the macrophyte area and in the adjacent peat bog, but nil in the centre (despite high turbidity) and in the grassland areas (no turbidity). Parts of peat bog that are close to the macrophytes probably receive most sediment, because reedbeds and trees suppress waves and currents (Prentki et al., 1979). This sedimentation decreases from the central area to the grassland area.

The water level was lower in 1996, decreasing both level and time of flooding and thus linkage of central water and the peat bog. These conditions may explain part of the differences in global retention between years, and the differences in nutrient retention.

Nitrogen

There are few studies about input-output of nitrogen in large wetlands crossed by streams, for which total N retention is comparable to Grand-Lieu: for example 39% and 50% in two swamps, and about 50% in a bog in the USA, although with only 0.68, 1.33 and 0.66 g m^{-2} y^{-1}, respectively (Johnston, 1991), much lower than in Grand-Lieu (about 10–15 g). This result is surprising because swamps and bogs are more closed than Grand-Lieu, and the percentage of nutrient inputs retained by a system is strongly related to its degree of closure (Hopkinson, 1992).

In contrast to the retention rate of sediments, the retention rate of total N in 1996 was twice more important than in 1994 (60–32%), related to the large difference in inputs, while loss was less variable. We consider than Grand-Lieu was a more closed system in 1996 than in 1994, due to a longer water residence time. Even though flow occurs in this lake during winter, retention of nitrates is important (61% in 1994, 86% in 1996), although retention per m^2 was higher in 1994 (22 g against 11). In 1996, higher retention rate gave lower concentrations in outputs in spite of higher concentrations in inputs.

Apart from the role of the flow and of residence time of water on nutrient retention, it is difficult to interpret all these ‘black-box’ input-output differences with internal lake processes because of the complexity of the N cycle in wetlands, for which Johnston (1991, adapted from Nixon & Lee, 1986) give seven kinds of standing stocks and 28 ways of fluxes. However, nitrogen fluxes seem essentially concerned at lake Grand-Lieu by inputs and outputs by rivers, consumption by vegetation, storage in sediments and denitrification, because of absence of exchanges with groundwater, negligible flux with precipitation (0.14 mg l^{-1}), and probably low fixation. Even though asymbiotic fixation, mainly from Cyanobacteria, can be important in eutrophic lakes (Labroue et al., 1995), it could partly be inhibited in the center of this lake by several factors (high levels of inorganic N, O^2, pH and turbididy). Symbiotic fixation by the very localized *Alnus* in the peatbog does not occur in winter and is moreover incorporated in wood and only released with decay. Before direct accumulation in sediments, the main retention factor during winter seems consumption by algae and denitrification, that could explain the strong decrease of nitrates from January to the end of March (Figure 4E and 5E), even if algae density is much lower (about 36 mg l^{-1} chlorophyll a in March) than during spring and summer (about 380 mg l^{-1} in June). From April onwards, concentration of nitrate in the water of the lake is very low, partly due to adding consumption by growing macrophytes and their periphyton. Between April and August, the *Nymphea alba-Nuphar lutea* area is the most depleted in total N (47 mg l^{-1}), followed by the less nitrophilous *Trapa natans* (110 mg l^{-1}), while proximate areas without macrophytes have the highest concentrations (137 mg l^{-1}, Marion et al., 1986). By adding *Limnanthemum peltata*, the standing stock of these floating macrophytes reached 105 tons of N (12 g m^{-2}) in summer 1996, representing about 19% of the net input of the lake during the preceding winter, a high level if we consider that these plants only represent about 25% of the total macrophytes biomass in this lake (Marion et al., 1989). Nevertheless, if we refer to literature, important part of this stock is directly taken in sediments and, except for annual *Trapa*, by retranslocation from roots, before partly returning in them by translocation before decay (Wetzel, 1990; Pieczynska, 1993). The total N stock in the first 10 cm of sediments represents in September at Grand-Lieu about 155 g m^{-2} in the macrophytes area and about 227 g m^{-2} in the sandy open water without macrophytes (after Rofès, 1992), totaling about 3 500 tons for the lake (without the peatbog area). While important, this stock only represents 4 to 6 times the annual net input of the lake, and the lower level in the macrophytes area could illustrate plant consumption, because these organic soils generally average twice as much N as mineral soil (Johnston, 1991). Macrophytes are supposed to pump nutrients from sediment, increasing nutrients concentration in water (Wetzel & Manny, 1972; Testard, 1995), but this opinion is controversial (Labroue et al., 1995) and seems to apply to submerged macrophytes. We consider here that the part of nutrients directly taken from the water by floating macrophytes and associated periphyton is probably not negligible and may contribute to decrease the nitrogen stock in water, even after decay of leaves. Jigorel (1992) showed that accumulation of total N in the deposited sediment in this lake was higher under the macrophytes during all the spring and summer, and reached 1.2% of total deposition. Yet, part of the latter is exported during winter by wind resuspension.

Denitrification was not measured and could occur mainly in the macrophyte area, at the water-sediment interface, and within the peatbog, where alternating aerobic and anaerobic conditions exist in space and time, a favourable situation for denitrification (Smith & Patrick, 1983). However, all muddy sediments under macrophytes are anoxic even at the surface, while the water column is generally aerobic even in summer (except in hot shallow areas, Marion, 1995), and always in winter (Marion, 1992), conditions that can limit denitrification (Reddy et al., 1980). Also, nitrates required for denitrification are provided by rivers only during winter, and their strong decrease before May could limit denitrification in such a lake. Labroue et al. (1995) reported a similar case of an eutrophic gravel pit lake (St-Caprais) where a strong decrease of nitrate occurs from March to June, when water has about 50 mg l^{-1} chlorophyll a before increasing up to 150 mg l^{-1} in summer. In this lake denitrification only occurs from December to May. At Grand-Lieu, the part of nitrates due to nitrification of ammonium from the inputs is probably relatively low during winter, because of its low level (ammonium only represented 2.5% and 5.5% of total N input in 1994 and 1996), and its low retention by the lake (16-18 times less than nitrates in flux). Nitrification is probably mainly supported by direct upward diffusion of NH_4 from sediments.

Finally, all these processes of N cycling during the closing watergate period involve low concentrations of total N in water of the lake (0.95 mg l^{-1} from April to September, Marion et al., 1994), before the beginning of new input from catchment area. This depletion in concentrations corresponds to a higher decrease in N stock of the water column because the simultaneous decrease in water level by 40 cm (about 33% of the volume of April), due to evapotranspiration, concentrates nutrients. Globally, this wetland receives an important discharge of inorganic nitrogen from its catchment area, and keeps most of it (62% in 1994 and 85% in 1996), but exports a large amount of dissolved and particulate organic nitrogen (254 tons = 4.54 g m^{-2} y^{-1} in 1996, 896 tons = 16 g m^{-2} y^{-1} in 1994), 1.9 to 2.6 times more than it receives (Figure 7 and 8). These characteristics are mainly related to the importance of vegetation in this hypereutrophic lake, and of wind resuspended organic sediments in outputs. In his review of input-output studies, Johnston (1991) only reported one wetland (Okefenokee Swamp, Blood, 1981) with a negative retention of organic N, moreover with considerable lower value (only -9%) than for Grand-Lieu. More recently Hopkinson (1992) mentioned net exportation of organic N for the same wetland, with higher rates (- 22%). Grand Lieu is both an opened and a closed system, favourizing retention of nutrients. Thus, its peat bog is relatively similar to swamps, with all the characteristics of high closure of old succession stages: high vegetation density that increases physical deposition of sediments during flooding, high biomass and storage capacities for N (long term or definitely stocked in wood and peat). However because of its proximity of the central area of the lake and of periodic important floods, this area is also largely more opened than swamps which receives most of their water budget from rain (77%, Hopkinson, 1992). The importance of vegetation on nutrient budgets of Lake Grand-Lieu is confirmed by organic C concentrations of outputs, higher than inputs (about 25 mg against 10), as for other bog lakes for which dissolved organic C can reach 40 mg l^{-1} in flooded areas (Gorham et al., 1985). In the sediments within the lake, all C is organic (Rofès, 1992). Grand-Lieu is mainly an autotrophic system, converting most of inorganic nutrients inputs to organic matter, which is only partly exported.

Phosphorus

Most considerations on nitrogen also apply to phosphorus. The review by Johnston (1991) about retention in wetlands mentioned similar retention rates for N and P in three studies in which both nutrients were studied, and a P retention varying from 4% to 80% (average 45%) for 11 wetlands where input-output studies were done. Only one lake was concerned, for which retention was only 10%, however with similar retention per m^2 than at Grand-Lieu in 1994 (0.56). The retention per m^2 at Grand-Lieu in 1996 (0.09 g) was the minimum cited by Johnston (1991), but it was higher than those observed in 7 major lakes on Iowa streams (0.03 g after Jones et al., 1976). Only one study (Kuenzler et al., 1980) compared two years with different flows, with a retention rate twice as high during large flow (57%) as during low flow (30%), due to increased sedimentation and uptake by algae. It is the same magnitude than that we observed at Grand-Lieu (40–18%), with also large difference in PM input, sedimentation (22 g m^{-2} against 9) and algae production (Le Rouzic et al., in prep.). This is not surprising, because this relationship of phosphorus with PM is known (Walling & Kane, 1982; Probst, 1985). However, Kronwang (1992) showed that there was no difference in transport of total P between two Danish rivers although a strong difference (twice more) in PM transport. In our study, even inputs of orthophosphate, although known to be related to storm run-off, had a lower difference between years than nitrites and total N. As for these elements, difference must be done between global relation concerning water flow and fluxes of nutrients, related to increase of loading from land, and on the other hand the punctual increase of P with first flow in rivers, partly due to storage of sewage P during low flow, that can reach 70% according to Dorioz et al. (1989).

In the present paper, we do not take into account net inputs by bird droppings, retention rates being only calculated from inputs-outputs of rivers. In fact, real total P retention rates of this lake would increase by about 1.7% in 1994 and 6.5% (total retention rate = 25% instead of 18%) in 1996, according to the study made on this site in 1990–91 (about 2.5 tons P, Marion et al., 1994). Birds do not really change the N input.

The lake's retention of P is obviously more important for orthophosphate (79–72%) than for total P. However, contrary to N, total P concentrations do not really decrease in spring and summer in the lake (see Marion et al., 1994). These similar concentrations correspond in fact to a decrease of the P stock because of the simultaneously decrease of water volume (by 33%, see above for N). This limited loss compared to N may be partly due to release of phosphorus by sediments under anaerobic conditions on the water-sediment interface (Boström et al., 1982, Wetzel, 1983). The total P stock in the first 10 cm represents in September at Grand-Lieu about 12 g m^{-2} in the macrophyte area and about 20 g m^{-2} in the sandy open water (mainly non apatitic inorganic phorphorus, the more easily used by plants), that represents without the peatbog area about 284 tons, 8 (1994) to 53 (1996) times the annual net input into the lake. Such a concentration in sediment exceeds the range cited by Labroue et al. (1995) for lakes (2–10 g m^{-2}). Like for nitrogen, the lower sediment concentration in the macrophytes area could illustrate plant uptake, because P concentrations are generally compararable for both organic and mineral soils (Johnston, 1991). The standing stock of the floating macrophytes mentioned above for N reached 13.5 tons of P (1.6 g m^{-2}) in summer 1996, representing about 2.5 times the net input of the lake that year but 39% in 1994. Probably algae play a major role in P retention from the water, rather than macrophytes that take most of their P in sediment. In contrast to N, there is effectively no difference from April to August in P water concentrations between *Trapa* area, *Nymphea-Nuphar* area and open water without microphytes. This can also be due to release from sediments and from regular decay of leaves, like in other lakes (Wetzel, 1990; Pieczinska, 1993; Labroue et al., 1995). The final and important decay of whole macrophytes in autumn is not noticeable in water P compared to autumnal inputs from the watershed.

Contrary to N, there is no loss of P by atmospheric exchange, so its stock increases continually in the system due to increasingly net input. In the 1960's, before the tremendous increase of sewage and agriculture run-off, inputs of P was very low and the lake was oligotrophic, probably receiving up to 95% of its P input from birds (Marion et al., 1994). Retention is probably lower now, because the actual input exceeds its retention capacities and makes the lake endangered. Such a decrease of retention rate with eutrophication has been demonstrated for lac Léman between the 1960's and the 1980's (Jacquet, 1985). The very low nutrients input occurring in 1996 involved a low turbidity in spring and summer due to low density of algae, and a return of submerged macrophytes, that disappeared after 1984. Water was also better oxygenated, due to higher water level because botulism also disappeared this year, after a dramatic outbreak in 1995 that killed 30 000 to 50 000 birds (Marion, 1995). This spectacular change illustrates the sensibility of this system to winter nutrient input and water level, and the multiplying effect of additional nutrients on the eutrophication processes when oxygen concentration drops in the water and favours mobilization of nutrients stocked in the sediment.

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References

Blood, E. R., 1981. Environmental impact of upland streams on the Okefenokee Swamp. University of Georgia Institute of Ecology Rep. N^o ERC 06-81, Athens, GA.

Boström, B., M. Jansson & C. Forsberg, 1982. Phosphorus release from lake sediments. Arch. Hydrobiol. Ergebn. Limnol. 18: 5–59.

Campy, M. & M. Meybeck, 1995. Les sédiments lacustres. In Pourriot, R. & M. Meybeck (eds), Limnologie générale. Masson, Paris: 185–226.

DeLaune, R. D., J. H. Whitcomb, W. H. Patrick, J. H. Pardue & S. R. Pezeshki, 1989. Accretion and canal impacts in a rapidly subsiding wetland. I. ^{137}Cs and ^{210}Pb techniques. Estuaries 12: 247.

Dolan, D. M., A. K. Yui & R. D. Geist, 1981. Evaluation of river load estimation methods for total phosphorus. J. Grt Lakes Res. 7: 207–214.

Dorioz, J. M., E. Pilleboue & A. Ferhi, 1989. Phosphorus dynamics in watersheds: role of trapping processes in sediments. Wat. Res. 23: 147–158.

Eckblad, J. W., L. L. Peterson, K. Ostlie & A. Temte, 1977. The morphometry, benthos and sedimentation rates of a floodplain lake in Pool 9 of the upper Mississippi River. Am. Midl. Nat. 97: 433–443.

Feunteun, E., 1994. Le peuplement piscicole du marais littoral endigué de Bougneuf-Machecoul (France, Loire Atlantique). Thèse Univ. Rennes, 256 pp.

Foster, I. D. L., J. A. Dearing, A. Simpson, A. D. Carter & P.G. Appleby, 1985. Lake catchment based studies of erosion and denudation in the Merevale catchment, Warwickshire, UK. Eth Surf. Proc. Land Forms 10: 45–68.

Gersberg, R. M., B. V. Elkins, S. R. Lyon & C. R. Goldman, 1986. Role of aquatic plants in wastewater treatment by artificial wetlands. Water Res. 20: 363–388.

Giraud, F., 1992. Modélisation hydrologique d'une zone humide agricole: perspective pour l'étude du transport d'azote et de phosphore dans le réseau hydraulique. Cas du marais de Moëze. Thèse Univ. Rennes, 224 pp.

Golterman, H. L., R. S. Clymo & M. A. N. Ohnstad, 1978. Methods for physical and chemical analysis of fresh waters. I.B.P. Handbook n^o 8, Blackwell Scientific Publications.

Golterman, H. L., P. G. Sly & R. L. Thomas, 1983. Study of the relationship between water quality and sediment transport. A guide for the collection and interpretation of sediment quality data. UNESCO, Paris, 231 pp.

Gorham, E., S. J. Eisenreich, J. Ford & M. V. Santelman, 1985. The chemistry of bog waters. In W. Stumm (ed.), Chemical Processes in Lakes: 339–363.

Hopkinson, C. S., 1992. A Comparison of Ecosystem Dynamics in Freshwater Wetlands. Estuaries 15: 549–562.

Jacquet, J. M., 1985. Bilan et modèle d'entrées-sorties du phosphore total dans le Léman. Annls Limnol. 21: 177–189.

Jigorel, A., 1992. Etude sédimentologique du lac de Grand-Lieu. Rapport de l'Institut National des Sciences Appliquées de Rennes, 83 pp.

Johnston, C. A., 1991. Sediment and nutrient retention by freshwater wetlands: effects on surface water quality. Crit. Rev. Envir. Contr. 21: 491–565.

Johnston, C. A., N. E. Detenbeck & G. J. Niemi, 1990. The cumulative effect of wetlands on stream water quality and quantity. A landscape approach. Biogeochemistry 10: 105–141.

Jones, J. R., B. P. Borofka & R. W. Bachmann, 1976. Factors affecting nutrient loads in some Iowa streams. Wat. Res. 10: 117–122.

Kronwang, B., 1992. The export of particulate matter, particulate phosphorus and dissolved phosphorus from two agricultural river basins: implications on estimating the non-point phosphorus load. Wat. Res. 26: 1347–1358.

Kuenzler, E. J., P. J. Mulholland, L. A. Yarbro & L. A. Smock, 1980. Distributions and budgets of carbon, phosphorus, iron and manganese in a floodplain swamp ecosystem. Water Resources Research Institute. University of North Carolina, Raleigh, Report n^o 157.

Labroue, L., J. Capblancq & A. Dauta, 1995. Cycle des nutriments: l'azote et le phosphore. In Pourriot, R. & M. Meybeck (eds), Limnologie générale. Masson, Paris: 727–764.

Lee, G. F., E. Bentley & R. Amundson, 1975. Effects of marshes on water quality. In Halser, A. D. (ed.), Coupling of Land and Water Systems. Ecol. Stud. 10, Springer-Verlag, Berlin: 105-127.

Marion, L. 1992. Productivité des macrophytes et du phytoplancton du lac de Grand-Lieu. SESLG-Univ. Rennes, 57 pp.

Marion, L., 1995. La catastrophe écologique du lac de Grand-Lieu: des dizaines de milliers d'oiseaux meurent de botulisme. La Recherche 283: 28–29.

Marion, L., 1997. Désenvasement: une expérience de génie écologique à grande échelle sur le lac de Grand-Lieu. In Forum des Gestionnaires 'la gestion de l'eau pour les zones humides', Ministère de l'Environnement, RNF, ENF, Paris (in press).

Marion, L., P. Marion, A. Bocquenet, L. Brient, 1986. L'eutrophisation des eaux du lac de Grand-Lieu. Ministère de l'Environnement-SESLG-LESNM-Univ. Rennes, 109 pp.

Marion, L., G. Bertru, L. Brient, M. Danais, A. Desgrée, A. Durbec, A. Dutartre, G. Galea, A. Jigorel, G. Rofès & P. Marion, 1992. Causes de l'envasement du lac de Grand-Lieu et mesures de sauvetage. Rapport de synthèse. Ministère Environnement, 72 pp.

Marion, L. , P. Clergeau, L. Brient & G. Bertru, 1994. The importance of avian-contributed nitrogen (N) and phosphorus (P) to Lake Grand-Lieu, France. Hydrobiologia 279/280: 133–147.

Marion, L. & P. Marion, 1975. Contribution à l'étude écologique du lac de Grand-Lieu. Bull. H.S. Soc. Sc. Nat. Ouest France, 611 pp.

Marion, L., P. Marion & Ph. Clergeau, 1989. Causes and consequences of accelerated eutrophic evolution of the lake of Grand-Lieu, France. Proc. Third Intern. Conf. Wetland, Rennes September 1988: 219–220.

Meybeck, M., 1982. Carbon, nitrogen and phosphorus transport by world rivers. Am. J. Sci. 282: 401–450.

Meybeck, M., 1993. C, N, P and S in rivers: from sources to global inputs. In: Wollast, R., F. T. Machenzie & L. Chou (eds), Interaction of C, N, P and S Biogeochemical Cycles and Global Change. Springer Verlag, Berlin: 163–193.

Meybeck, M., 1995. Les lacs et leurs bassins. In R.Pourriot & M. Meybeck (eds), Limnologie générale. Masson, Paris: 6–59.

Mitsch, W. J. & J. G. Gosselink, 1986. Wetlands. Van Nostrand Reinhold, New York, 534 pp.

Murphy, J. & J. P. Riley, 1962. A modified single-solution method for the determination of phosphate in natural waters. Analyt. Chim. Acta 27: 31–36.

Nixon, S. W. & V. Lee, 1986. Wetlands and water quality, Wetlands Research program. Tech. Rep. Y-86-2, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Odum, E. P., 1969. The strategy of ecosystem development. Science 164: 262–270.

Ongley, E. D., 1973. Sediment discharge from Canadian basins into lake Ontario. Can. J. Eth. Sci. 10: 146–156.

Phillips, J. D., 1989. Fluvial sediment storage in wetlands. Water Resour. Bull. 25: 867.

Pieczynska, E., 1993. Detritus and nutrient dynamics in the shore zone of lakes: a review. Hydrobiologia 251: 49–58.

Prentki, R. T., M. S. Adams, S. R. Carpenter, A. Gasith, C. S. Smith & P. R. Weiler, 1979. The role of submersed weedbeds in internal loading and interception of allochthonous materials in Lake Wingra, Wisconsin, USA. Arch. Hydrobiol. Suppl. 57: 221–250.

Probst, J. L., 1985. Nitrogen and phosphorus exportation in the Garonne Basin (France). J. Hydrol. 76: 281–305.

Reddy, K. R., P. D. Sacco & D. A. Graetz, 1980. Nitrate reduction in an organic soil-water system. J. Envir. Qual. 9: 283–288.

Rofès, G., 1992. Lac de Grand-Lieu: étude sédimentologique. Rapport du CEMAGREF de Lyon, 64 pp.

Seux, R., B. Sorelard, P. Boutin & J. P. Bechac, 1985. Azote et phosphore dans un cours d'eau du nord de la Bretagne: origine des apports, estimation des flux. Trib. Cebedeau 38: 11–24.

Smith, C. J. & W. H. Patrick, 1983. Nitrous oxide emission as affected by alternate anaerobic and aerobic conditions from soil suspensions enriched with ammonium sulfate. Soil Biol. Biochem. 15: 683.

Stow, C. A., R. D. DeLaune & W. H. Patrick, 1985. Nutrient fluxes in a eutrophic coastal Louisiana freshwater lake. Envir. Mgmt 9: 243.

Striegl, R. G., 1987. Suspended sediment and metals removal from urban runoff by a small lake. Wat. Res. Bull. 23: 985.

Testard, P. 1995. Rôle des macrophytes littoraux dans le fonctionnement des écosystèmes lacustres. In Pourriot, R. & M. Meybeck (eds), Limnologie générale. Masson, Paris: 296–326.

Walling, D. E., 1978. Suspended sediment and solute response characteristics of the the River Exe, Devon, England. In Research in Fluvial Geomorphology, Geo-Abstracts, Norwich: 169–197.

Walling, D. E., 1988. Erosion and sediment yield research – some recent perspectives. J. Hydrol. 100: 113–141.

Walling, D. E. & P. Kane, 1982. Temperal variation of suspended sediment properties. In Recent Developments in the Explanation and Prediction of Erosion and Sediment Yields, Proceedings of the Exeter Symposium. IAHS, Publ. n^{o} 137: 409–419.

Webb, B. W. & D. E. Walling, 1984. Magnitude and frequency characteristics of suspended sediment transport in Devon Rivers. In Catchement Experiments in fluvial Geomorphology, Geobookds, Norwich: 399–415.

Wetzel, R. G. 1983. Limnology. Saunders College Publ., Philadelphia, 760 pp.

Wetzel, R. G. 1990. Land-water interfaces: Metabolic and limnological regulators. Verh. int. Ver. Limnol. 24: 6–24.

Wetzel, R. G. & B. A. Manny, 1972. Secretion of dissolved organic carbon and nitrogen by aquatic macrophytes. Verh. int. Ver. Limnol. 18: 162–170.