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A mass balance assessment of the contribution of floating-leaved macrophytes in nutrient stocks in an eutrophic macrophyte-dominated lake

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Abstract

In this study we examine the contribution of three floating-leaved macrophyte species, *Nymphaea alba*, *Trapa natans* and *Nymphoides peltata* (covering about 700–750 ha), in the N and P stocks in a shallow eutrophic lake (4000–6300 ha) during a 3-year period (1995–1997). The monthly nutrient standing stocks in the above-ground structures of the plants were derived from biomass, nutrient content and area covered by each plant species during the growth period. These N and P quantities were compared to the net nutrient inputs of the lake waters from the catchment area recorded in the winter (water discharging phase), preceding the vegetation period. N and P contents reached high values for the three species (2.16–3.23% N and 0.29–0.68% P) showing the ability of the plants to accumulate large nutrient contents. Despite significant annual fluctuations in nutrient contents and biomass, not always in the same way for each floating-leaved macrophyte, and changes in the area they covered, the maximum monthly P stocks in the plants were globally uniform between the 3 years (7.10–8.85 tonnes). Maximum values for N ranged from 40.85 to 54.55 tonnes in summer. The vast beds of *N. alba* (until 75% of the total area in 1997), contributed largely to these annual nutrient stocks (50–72% and 46–70%, respectively, for N and P). Whereas the nutrient stocks estimated in the plants during the biomass peak represented little proportions of the annual net flux of N in the lake waters (3.35–5.00%), they reached high proportions for P sometimes exceeding the annual net loading of P in the lake according to years (16.80–156.25%). These results suggest that the nutrient-enriched sediments of the lake (6–53 and 2–6 times the net annual P and N inputs) probably compensate for annual variations in the external nutrient loading, notably for P, and floating-leaved macrophytes are likely not limited when the inputs from the catchment area are small.

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1. Introduction

In many aquatic ecosystems a large proportion of metabolism occurs in the littoral zone, with macrophyte beds and their associated epiphytes as major primary producers (Pieczyńska, 1993; Kairesalo and Matilainen, 1994; Gessner, 2000). The high productivity of macrophytes (Smart, 1980; Twilley et al., 1985; Kunii and Aramaki, 1992) contributes to high rates of nutrient mobilisation mainly from the sediment directly via root systems (e.g. Best and Mantai, 1978; Howard-Williams and Allanson, 1981; Barko and James, 1997) but also from the overlying water by foliage (Madsen and Cedergreen, 2002). In small shallow lakes dominated by macrophytes (e.g. Lake Zwemlust in The Netherlands), deficiency of some nutrients may even occur (Ozimek et al., 1993). Moreover macrophytes are important in nutrient related processes not only as nutrient uptake by roots and/or shoots, but also by translocation, release by healthy plants and from decaying plants and exchange of elements within the macrophyte/periphyton complex (Pieczyńska, 1993; Killingbeck, 1996).

Thus, in the frame of management measures to improve the water quality of aquatic ecosystems, macrophytes are often taken into consideration. Some restoration programs focus not only on a reduction of external nutrient loadings, but on additional measures concerning macrophytes: biomanipulation to reinstate submerged macrophytes and clearwater conditions (van Liere and Janse, 1992; van Donk and Gulati, 1995; Jeppesen et al., 1997), or plant harvesting to remove nutrients (Cooke et al., 1993; Asaeda et al., 2000).

Some models have been developed to assess the role played by submerged macrophytes in the nutrient cycle of both coastal marine (Oshima et al. (1999); Sfriso and Marcomini (1999) on seagrass) and freshwater systems (Asaeda et al. (2000) on *Potamogeton pectinatus*). However, compared to submerged macrophytes, there is little detailed information on the estimation of nutrient stocks used by floating-leaved macrophytes in aquatic systems (Twilley et al., 1985 on *Nuphar lutea*, Brock et al., 1983b on *Nymphoides peltata*) which often represent the dominant vegetation in shallow water, particularly *Nymphaeid* species, with emergent macrophytes (Brock et al., 1983a; van der Velde and van der Heijden, 1985; Wallsten and Forsgren, 1989).

The present study was designed to evaluate, by a mass balance procedure, the contribution of the floating-leaved macrophyte species on the nutrient loading of a shallow, turbid, eutrophic and macrophyte-dominated lake. The N and P stocks used by the above-ground organs of the plants in the ecosystem were determined monthly over a 3-year period (1995–1997) from nutrient contents, biomass and the area covered by the plants. The comparison between these stocks and the external nutrient loadings on the lake waters (Marion and Briant, 1998, 2000) is discussed in the context of the water quality restoration program.

2. Study area and methods

2.1. Study area

Lake Grand-Lieu is a large natural floodplain system located in Western France (47°05'N, 1°39'W). The lake covers 4000 ha during summer and 6300 ha during winter, by flooding adjacent peaty marsh grasslands. Half of the summer area is composed of a peat fen with *Phrag-*

mites, *Salix* and *Alnus*, which becomes progressively exposed in early summer (for more details see Marion et al., 1994) and thus isolated from the water area. Most of the permanently flooded area of the lake is covered from April to October by extensive beds of floating-leaved macrophytes (about 1000 ha of *Nymphaeae alba*, *N. lutea*, *Trapa natans* and *N. peltata*).

Water level fluctuations of the lake follow the seasonal cycle of rainfall in the catchment. High inflows occur from November to May, when the daily discharges from the two rivers entering the lake are highest (from 336 to 401 m³ s⁻¹). The water depth then reaches up to 2.2 m in the floating macrophyte area. A drainage channel flows from the lake to the Loire estuary 25 km away and a sluice gate regulates the water level of the lake, notably during spring and summer to keep sufficient water levels. Water inputs from the watershed (670 km²) are insignificant from June to September (from 2 to 42 m³ s⁻¹) when the sluice gate is closed. During these months, rainfall on the lake does not counterbalance evapotranspiration and pumping, and the water level of the lake generally falls by 0.40 m (Marion and Briant, 1998). The summer depth is reduced then to 0.70 m in the floating macrophyte area.

2.2. Nitrogen (N) and phosphorus (P) content in floating-leaved macrophytes

In the present study, we focus on the above-ground parts of floating-leaved macrophytes, although the permanent below-ground organs can constitute a large fraction of the total biomass in *Nymphaeoid* species (Brock et al., 1987; Malthus et al., 1990; Tsuchiya et al., 1990). Our aim is to compare the role of nutrient stocking by the annual above-ground parts of the plants to the net input nutrient stocks from the catchment area. So we did not take into account the complex exchanges of elements between the plant, the sediment and the water column (Frodge et al., 1990; Kok et al., 1990; Aerts, 1997).

Samples of the above-ground parts of *N. alba*, *T. natans* and *N. peltata* were harvested using the standing crop method (Brock et al., 1987), once a month from April to October according to species (see result section) on a sampling area of 1 m². *N. lutea* was investigated only in 1997 and no data was presented here in order to compare the contribution of the same species to nutrient stocks in the lake waters for the 3-year period. From 3 to 6 stations were defined each year in monospecific stands of each macrophyte species, according to a gradient from the shore to the centre of the lake. The above-ground organs were dried at 80 °C for 6 days and weighed. The N and P contents were determined from monthly samples of plant material crushed to a powder. The number of samples analysed each year varied from 17 to 42 for N and from 24 to 34 for P, totalling 455 nutrient contents during the 3 years. The phosphorus content (%P) was determined using the method of Murphy and Riley (1962) and a spectrophotometer ($\lambda = 720$ nm), and the nitrogen content (%N) was measured with an automatic chemical analysis system (Carlo-Erba 1500). Patterns of biomass and nutrient contents in the plants were analysed for the 3 years by one-way ANOVA—year factor—with differences located by a Tukey HSD test (SYSTAT software, SPSS Inc., 1998, version 8.0). Mean values presented were defined with a 95% confidence interval.

2.3. Evaluation of the N and P standing stock in the floating-leaved macrophytes

We determined the monthly stock of N and P from biomass and nutrient contents in the above-ground organs of each macrophyte species (expressed in grams of nutrient per

square metre). Then the quantities of N and P used by the three species at the lake scale were derived from monthly nutrient stocks and area covered by macrophytes. Field observations indicated that the area covered by each species was constant during the growing season and we used data from aerial photography realised annually in August. The areas were measured with a Geographic Information System (Idrisi software, Eastman, 1995, version 1.0), using the method of Nohara (1991).

2.4. Evaluation of the N and P input and output stocks of the lake

The method used for evaluating N and P stocks on the lake was described by Marion and Brient (1998). Daily inflows and outflows of water were automatically measured in the two rivers entering the lake and in the drainage channel at the outlet of the lake. Concentrations of N and P in the three rivers were analysed from samples of water collected by automatic refrigerated sampling pumps every 2 h (cumulated per day). Annual inputs and outputs of N and P were determined from nutrient concentrations and water discharges (Marion and Brient, 2000). Finally, the net input during each annual inflow period (October–May) was obtained from nutrient inputs and outputs. We compared these net inputs of nutrients in the lake waters with the monthly standing stocks of nutrients in the beds of floating-leaved macrophytes during the following growth season (April–October).

3. Results

3.1. Total nutrient contents and biomass in the floating-leaved macrophytes

The results of the series of one-way ANOVA showed that the N and P contents varied between years for the three floating-leaved species, except for *N. peltata* with no data of P content in 1995 and 1996 (Table 1). Both N and P contents were significantly higher in 1997 in all plants and also in 1996 for N in *N. peltata*. For N, values were either different or similar in 1996 and 1997 according to species but no difference was found for P. Nutrient contents

Table 1
One-way ANOVA of mean annual N and P contents (with 95% confidence interval in brackets) in the floating-leaved macrophytes over the 3 years

	1995	1996	1997	F	P	n
N content (%)						
<i>N. alba</i>	2.16 ^a (0.07)	2.34 ^b (0.08)	2.32 ^c (0.07)	7.26	0.001	109
<i>T. natans</i>	2.41 ^a (0.29)	2.17 ^a (0.14)	3.10 ^b (0.28)	25.56	<0.001	120
<i>N. peltata</i>	3.20 ^a (0.10)	2.73 ^b (0.32)	3.23 ^a (0.28)	3.34	0.04	60
P content (%)						
<i>N. alba</i>	0.317 ^a (0.030)	0.296 ^a (0.016)	0.417 ^b (0.019)	35.03	<0.001	88
<i>T. natans</i>	0.330 ^a (0.030)	0.347 ^a (0.018)	0.580 ^b (0.076)	27.96	<0.001	78
<i>N. peltata</i>	–	–	0.684 (0.052)	–	–	29

For each mean annual nutrient content, values with a common letter are not significantly different at $P = 0.05$ from pairwise comparisons in Tukey HSD tests. P was measured only in 1997 in *N. peltata*.

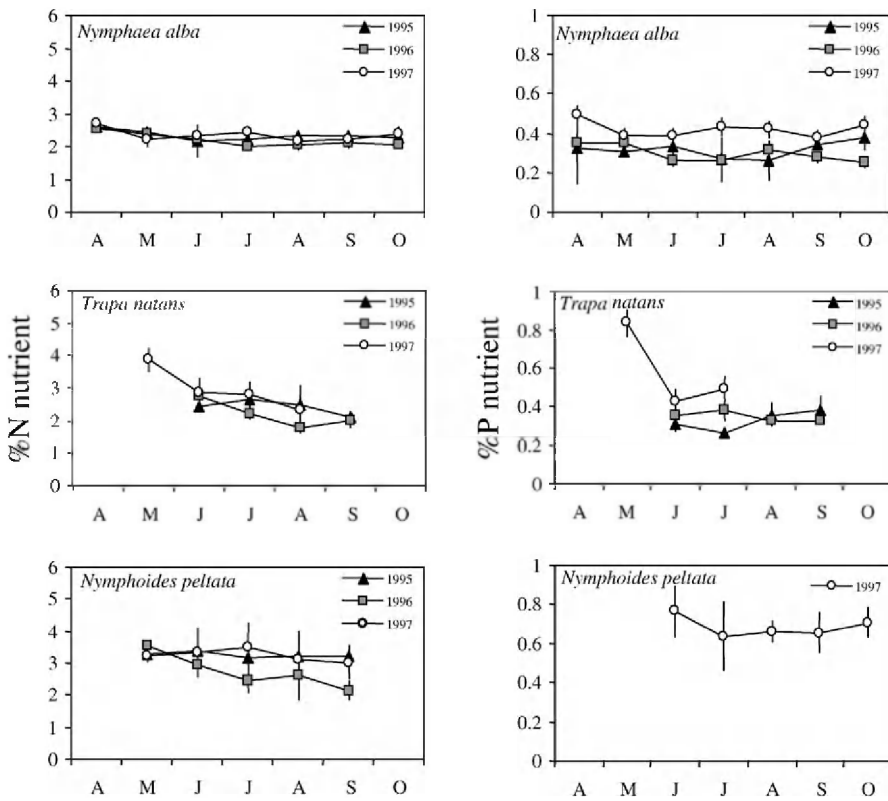


Fig. 1. Seasonal patterns of N and P contents (mean with 95% confidence interval) in the floating-leaved macrophytes in 1995–1997.

tend to be higher at the start of the growing season for *T. natans* and to lesser extent in the two *Nymphaeid* species whereas they were relatively stable during the following months (Fig. 1).

At the same time, one-way ANOVA tested on the biomass of the three macrophyte species, also showed a year effect but not in the same way for each species (Table 2). The biomass

Table 2

One-way ANOVA of mean annual biomass (with 95% confidence interval in brackets) in the floating-leaved macrophytes over the 3 years

	1995	1996	1997	<i>F</i>	<i>P</i>	<i>n</i>
<i>N. alba</i>	283.4 ^a (35.6)	172.8 ^b (38.9)	167.5 ^b (33.4)	13.68	<0.001	168
<i>T. natans</i>	211.1 ^a (41.5)	453.7 ^b (93.3)	96.5 ^c (59.5)	32.69	<0.001	88
<i>N. peltata</i>	109.7 ^a (14.8)	156.5 ^b (34.6)	160.9 ^b (38.4)	4.78	0.01	85

For each mean annual biomass, values with a common letter are not significantly different at $P = 0.05$ from pairwise comparisons in Tukey HSD tests.

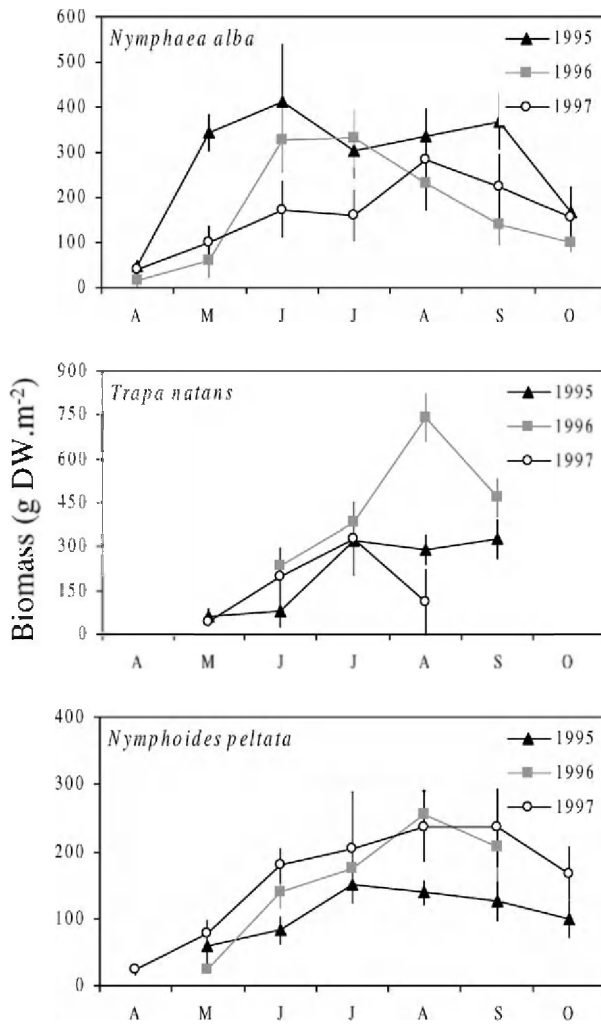


Fig. 2. Seasonal patterns of biomass (mean with 95% confidence interval) in the floating-leaved macrophytes in 1995–1997.

of *N. alba* was the highest in 1995 whereas similar biomass were recorded in 1996 and 1997. Conversely the biomass was low in 1995 for *T. natans* and for *N. peltata* and the highest in 1996, especially for *T. natans* with a substantial biomass peak (738.40 ± 80.25 g DW m⁻², Fig. 2). The beds of *T. natans* early disappeared in 1997 leading to a very low annual biomass.

Some delays in the phenology of *N. alba* were recorded according to years, from a peak in June in 1995 (412.20 ± 129.60 g DW m⁻²) to a peak in August in 1997 (284.40 ± 129.60 g DW m⁻², Fig. 2). The phenology of *N. peltata* was globally similar over the 3 years.

Table 3

Area covered by the floating-leaved macrophytes (expressed in ha)

Species	1995	1996	1997
<i>N. alba</i>	472.0	523.5	554.0
<i>T. natans</i>	205.5	184.5	163.5 ^a
<i>N. peltata</i>	— ^b	17.5	29.5

^a This year *T. natans* disappeared before seed production (see Paillisson and Marion, 2001a) and the area covered by the plant was deducted from data of surrounding years (Paillisson and Marion, 2001b).

^b No area was determined for *N. peltata*.

3.2. Estimation of the monthly nutrient standing stock in the plants

Some changes in the area covered by the floating-leaved macrophytes occurred during the 3-year period (Table 3). The size of the beds of *N. alba* increased from 472 to 554 ha, whereas in the same time the area of *T. natans* decreased. The area covered by *N. peltata*

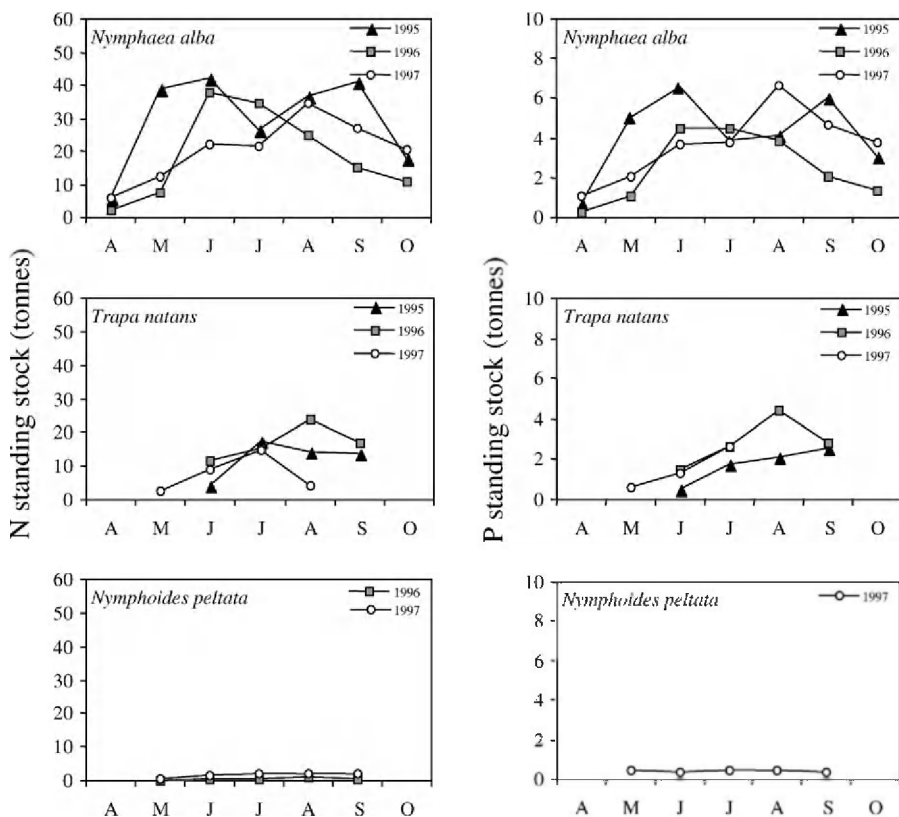


Fig. 3. Seasonal patterns of N and P standing stocks in the floating-leaved macrophytes at the lake scale in 1995–1997.

was not determined in 1995, but reached low values in 1996 and 1997. The dominance of *N. alba* thus increased to about 75% of the total area covered by the three species in 1997.

As shown in Fig. 3, the contribution of *N. alba* in the quantity of nutrient used in the beds of floating-leaved macrophytes of the lake was large ($65.45 \pm 9.45\%$ and $51.50 \pm 8.25\%$ of monthly data with the three species, respectively, for N and P). When standing stocks of the three species were grouped, maximum values occurred in August, except in 1995 due to a high biomass of *N. alba* in September (Fig. 2). The maximum standing stock of N was low in 1997 (40.85 tonnes) compared to 1995 (54.55 tonnes) and 1996 (50.95 tonnes) mainly in relation to the depletion of the biomass of *T. natans*. The maximum standing stock of P in the plants was globally uniform over the 3 years (7.10–8.85 tonnes) despite of annual fluctuations of P contents, biomass and area covered by the plants.

The importance of the plants in the nutrient stock of the lake waters was obtained by comparing the maximum standing stocks of N and P in the plants, to the net annual input of nutrients into the lake. The net N input into the lake varied from 553 tonnes in 1996 to 1628 tonnes in 1995, with an intermediate value in 1997 (853 tonnes), corresponding to a mean retention rate of 55.75% (Fig. 4). The maximum N monthly standing stock in the plants only represented from 3.35% of this net input in 1995 to 5.00% in 1996. The net P

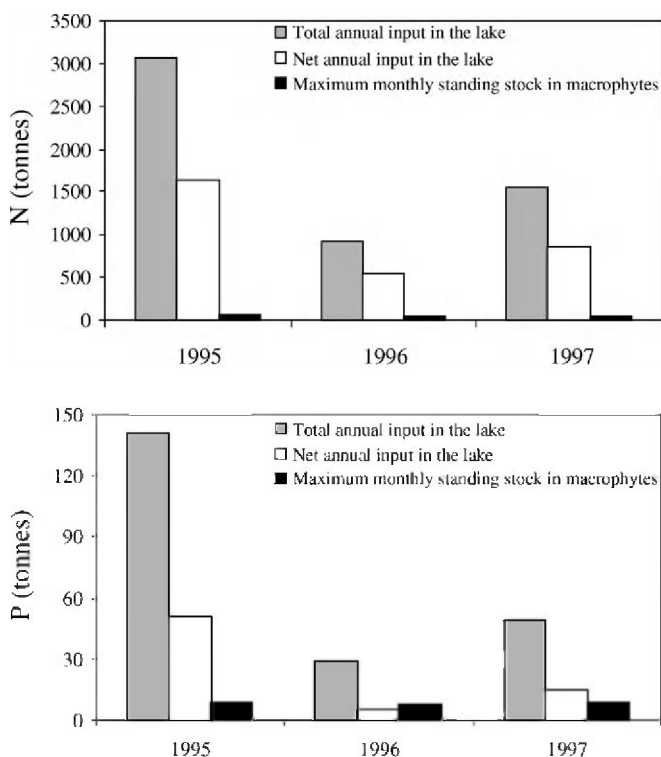


Fig. 4. Comparison of total and net N and P inputs into Lake Grand-Lieu and maximum monthly nutrient stocks in the plants over the 3 years (1995–1997).

input into the lake fluctuated much more than for N during the 3 years (10 times compared to less than 3 times for N), from about 51 tonnes in 1995 to 5 tonnes in 1996 and 15 tonnes in 1997, corresponding to a mean retention rate of 28.50%. The quantity of P used by the floating-leaved macrophytes was high. The maximum monthly standing stock reached 16.80% of the net P input into the lake in 1995, 58.45% in 1997 but exceeded the net P input into the lake in 1996 (156.25%).

4. Discussion

With a mean annual content (1995–1997) ranging from 2.16–3.23% N to 0.29–0.68% P for the above-ground organs, the three floating-leaved species showed much higher nutrient values in Lake Grand-Lieu than the growth limiting levels (1.3 and 0.13% DW, respectively) observed by Gerloff and Kromholz (1966). However these nutrient levels were similar to those recorded in previous studies for N but higher for P (Smart, 1980; Brock et al., 1983b; Malthus et al., 1990). The high values observed in Lake Grand-Lieu show the ability of the plants to accumulate large concentrations of N and P in a nutrient-rich ecosystem.

Little information is available on estimates of the contribution of floating-leaved macrophytes to N and P fluxes at the scale of an aquatic ecosystem. Brock et al. (1983b) studied the seasonal changes in nutrient concentrations of various parts of *N. peltata* with aspects of N and P cycling during each month of the growing period, but no comparison was made with nutrient quantities in the lake. Malthus et al. (1990) showed the importance of dominant macrophytes species including *N. alba* in P dynamics in the Loosdrecht lakes system using species cover data at the time of maximum biomass. In this last paper the P standing stock of the six major emergent and floating-leaved macrophytes represented 15% ($45 \text{ mg m}^{-2} \text{ year}^{-1}$) of the external P inputs whereas macrophytes covered only 1.8% (17.2 ha) of the area. This was lower than in the present study, except in 1995 (6.10%), in which the P standing stock of the plants at the maximum monthly biomass represented between 18.15 (1997) and 28.55% (1996) of the annual (external) P input of the lake. At the extreme, James et al. (1996) found that, together, tissue P release of the submerged macrophyte community of Lake Delavon plus release from sediments resulting from its metabolic activities, in summer, were equivalent to twice the external P loading of the catchment area.

Given the demonstrated ability of macrophytes to use nutrients from sediments via root uptake (e.g. Carignan and Kalff, 1980; Barko and Smart, 1980), it is obvious that nutrient-enriched sediments compensate for annual variations in the external loading into lake systems. For instance, Søndergaard et al. (1993) demonstrated that phosphorus release from sediments mainly occurred from April to October coinciding with biological activity. In the present study, the most critical year was 1996, when small net annual P input occurred and the maximum P standing stock during the plant growing period, alone, exceeded this P input from the catchment area (156.25%). The floating-leaved macrophytes are probably not limited (similar maximum P standing stock compared to 1995 and 1997), even when small annual inputs into the lake occur due to substantial nutrient quantities in sediments. Marion and Briant (1998) have estimated the total P stock in the top 10 cm of sediment to be about 284 tonnes (without the fen), 6–53 times the net annual input to the lake. Such a concentration (12 g m^{-2} in the macrophyte area) exceeds the range cited by Labroue et al.

(1995) for lakes ($2\text{--}10\text{ g m}^{-2}$). Conversely, N could be a more limiting nutrient than P for the plants according to net annual inputs into Lake Grand-Lieu, although, the mean retention rate was large (55.75%) and ranged in the top of the compilation of Windolf et al. (1993) on retention rates of some shallow Danish lakes. N has a relatively low sediment stock (about 3500 tonnes), that is 2–6 times the net annual input of the lake (Marion and Brient, 1998) but N stocks in the plants only represented 3.35–5.00% of the net N input into the lake.

From a water quality point of view, the role played by rooted macrophytes is ambiguous and needs to be considered within the specific context of each lake system (e. g. Barko and James, 1997; Scheffer, 1998). In some nutrient-enriched shallow systems where the major threat is silting-up related to high productions of organic matter coming from plants, harvesting is an effective way to remove nutrients (e.g. Cooke et al., 1993; Moss et al., 1997; Asaeda et al., 2000). In Lake Grand-Lieu, the present accumulation of organic matter on the bottom of the lake reached 7.6 mm per year in the macrophyte area (Creach and Marion, 1998). But harvesting cannot be used here due to strong conservation constraints and some less destructive management measures have been implemented since few years to improve water quality, such as limitation of macrophyte production through water regime changes and dredging to favour natural sediment exportations. So the present preliminary results constitute a first step in the understanding of the role played by the vast beds of floating-leaved macrophytes in terms of nutrient dynamics, and water quality in Lake Grand-Lieu and interactions with all components of the lake food web need to be studied.

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References

- Aerts, R., 1997. Nitrogen partitioning between resorption and decomposition pathways: a trade-off between nitrogen use efficiency and litter decomposability? *Oikos* 80, 603–606.
- Asaeda, T., Kien Trung, V., Manatunge, J., 2000. Modeling the effects of macrophyte growth and decomposition on the nutrient budget in shallow lakes. *Aquat. Bot.* 68, 217–237.
- Barko, J.W., Smart, R.M., 1980. Mobilization of sediment phosphorus by submerged freshwater macrophytes. *Freshwater Biol.* 10, 229–238.
- Barko, J.W., James, W.F., 1997. Effects of submerged aquatic macrophytes on nutrient dynamics, sedimentation and resuspension. In: Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), *The Structuring Role of Submerged Macrophytes in Lakes*. Springer, New York, pp. 197–214.
- Best, M.D., Mantai, K., 1978. Growth of *Myriophyllum*: sediment or lake water as the source of nitrogen and phosphorus. *Ecology* 59, 1075–1080.
- Brock, T.C., Arts, G.H., Goossen, I.L., Rutenfrans, A.H., 1983a. Structure and annual biomass production of *Nymphoides peltata*. *Aquat. Bot.* 17, 167–188.

- Brock, T.C., Bongaerts, M.C.M., Heijnen, G.J.M.A., Heijthuisen, J.H.F.G., 1983b. Nitrogen and phosphorus accumulation and cycling by *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). *Aquat. Bot.* 17, 189–214.
- Brock, T.C., van der Velde, G., van de Steeg, H.M., 1987. The effects of extreme water level fluctuations on the wetland vegetation of a nymphaeid-dominated Oxbow lake in The Netherlands. *Arch. Hydrobiol.* 27, 57–73.
- Carignan, R., Kalff, J., 1980. Phosphorus sources for aquatic weeds: water or sediments? *Science* 207, 987–989.
- Cooke, G.D., Welch, E.B., Peterson, S.A., Newroth, P.R., 1993. *Restoration and Management of Lakes and Reservoirs*, 2nd ed. Lewis, New York.
- Creach, V., Marion, L., 1998. Conditions of macrophyte and alga mineralization and their functions in silting-up of Lake Grand-Lieu, SNPN, Université de Rennes I (in French).
- Frodge, J.D., Thomas, G.L., Pauley, G.B., 1990. Effects of canopy formation by floating and submergent aquatic macrophytes on the water quality of two shallow Pacific Northwest lakes. *Aquat. Bot.* 38, 231–248.
- Gerloff, G.C., Kromholz, P.H., 1966. Tissue analysis as a measure of nutrient availability for the growth of angiosperm aquatic plants. *Limnol. Oceanogr.* 11, 529–537.
- Gessner, M.O., 2000. Breakdown and nutrient dynamics of submerged *Phragmites* shoots in the littoral zone of a temperate hardwater lake. *Aquat. Bot.* 66, 9–20.
- Howard-Williams, C., Allanson, B.R., 1981. Phosphorus cycling in a dense *Potamogeton pectinatus* L. bed. *Oecologia* 49, 56–66.
- James, W.F., Barko, J.W., Field, S.J., 1996. Phosphorus mobilization from littoral sediments of an inlet region in Lake Delavan. *Wisconsin Arch. Hydrobiol.* 138, 245–257.
- Jeppesen, E., Jensen, J.P., Søndergaard, M., Lauridsen, T., 1997. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia* 342/343, 151–164.
- Kairesalo, T., Matilainen, T., 1994. Phosphorus fluctuation in water and deposition emergent macrophyte stand. *Hydrobiologia* 275/276, 285–292.
- Killingbeck, K.T., 1996. Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. *Ecology* 77, 1716–1727.
- Kok, C.J., van der Velde, G., Landsbergen, K.M., 1990. Production, nutrient dynamics and initial decomposition of floating leaves of *Nymphaea alba* L. and *Nuphar lutea* L. (Nymphaeaceae) in alkaline and acid waters. *Biogeochemistry* 11, 225–250.
- Kunii, H., Aramaki, M., 1992. Annual net production and life span of floating leaves in *Nymphaea tetragona* Georgi: a comparison with other floating-leaved macrophytes. *Hydrobiologia* 242, 185–193.
- Labroue, L., Capblancq, J., Dauta, A., 1995. Nutrient cycling: nitrogen and phosphorus. In: Pourriot, R., Meybeck, M. (Eds.), *Limnology*. Masson, Paris, pp. 727–764 (in French).
- Madsen, T.V., Cedergreen, N., 2002. Sources of nutrients to rooted submerged macrophytes growing in a nutrient-rich stream. *Freshwater Biol.* 47, 283–291.
- Malthus, T.J., Best, E.P.H., Dekker, A.G., 1990. An assessment of the importance of emergent and floating-leaved macrophytes to trophic status in the Loosdrecht lakes (The Netherlands). *Hydrobiologia* 191, 257–263.
- Marion, L., Brient, L., 1998. Measures of a wetland's effect on water quality: input–output studies of suspended particulate matter, nitrogen (N) and phosphorus (P) in the main plain lake, Grand-Lieu. *Hydrobiologia* 373/374, 217–235.
- Marion, L., Brient, L., 2000. Effect of wetlands on water quality of rivers: the case of the important natural French plain lake, Grand-Lieu. *Verh. Int. Ver. Limnol.* 27, 368–371.
- Marion, L., Clergeau, P., Brient, L., Bertru, G., 1994. The importance of avian-contributed nitrogen (N) and phosphorus (P) to Lake Grand-Lieu, France. *Hydrobiologia* 279/280, 133–147.
- Moss, B., Madgwick, J., Phillips, G., 1997. *A Guide to the Restoration of Nutrient-Enriched Shallow Lakes*. Wetlands International Publications, Norfolk.
- Murphy, J., Riley, J.P., 1962. A modified single-solution method for the determination of phosphate in natural waters. *Anal. Chim. Acta* 27, 31–36.
- Nohara, S., 1991. A study on annual changes in surface cover of floating-leaved plants in a lake using aerial photography. *Vegetatio* 97, 125–136.
- Oshima, Y., Kishi, M.J., Sugimoto, T., 1999. Evaluation of the nutrient budget in a seagrass bed. *Ecol. Model.* 115, 19–33.
- Ozimek, T., van Donk, E., Gulati, R.D., 1993. Growth and nutrient uptake by two species of *Elodea* in experimental conditions and their role in nutrient accumulation in a macrophyte-dominated lake. *Hydrobiologia* 251, 13–18.

- Paillisson, J.M., Marion, L., 2001a. Interaction between coot (*Fulica atra*) and waterlily (*Nymphaea alba*) in a lake: the indirect impact of foraging. *Aquat. Bot.* 71, 209–216.
- Paillisson, J.M., Marion, L., 2001b. Floating-leaved macrophyte dynamics in Lake Grand-Lieu: relationships with water regime options. Rapport DIREN (in French).
- Pieczynska, E., 1993. Detritus and nutrient dynamics in the shore zone of lakes: a review. *Hydrobiologia* 251, 49–58.
- Scheffer, M., 1998. *Ecology of Shallow Lakes*. Chapman & Hall, London.
- Sfriso, A., Marcomini, A., 1999. Macrophyte production in a shallow coastal lagoon. Part II. Coupling with sediment, SPM and tissue carbon, nitrogen and phosphorus concentrations, nitrogen and phosphorus concentrations. *Mar. Environ. Res.* 47, 285–309.
- Smart, M.M., 1980. Annual changes of nitrogen and phosphorus in two aquatic macrophytes (*Nymphaea tuberosa* and *Ceratophyllum demersum*). *Hydrobiologia* 70, 31–35.
- Søndergaard, M., Kristensen, P., Jeppesen, E., 1993. Eight years of internal phosphorus loading and changes in the sediment phosphorus profile of Lake Søbygaard, Denmark. *Hydrobiologia* 253, 345–356.
- Tsuchiya, T., Nohara, S., Iwakuma, T., 1990. Net primary production of *Nymphoides peltata* (Gmel) O. Kuntze growing on sandy sediment at Edosaki-iri in Lake Kasumigaura. *Jpn. J. Limnol.* 51, 307–312.
- Twilley, R.R., Blanton, L.R., Brinson, M.M., Davis, G.J., 1985. Biomass production and nutrient cycling in aquatic macrophyte communities of the Chowan River, North Carolina. *Aquat. Bot.* 22, 231–252.
- van der Velde, G., van der Heijden, L.A., 1985. Initial decomposition of floating leaves of *Nymphoides peltata* in relation to their age, with special attention to the role of herbivores. *Verh. Int. Ver. Limnol.* 22, 2937–2941.
- van Donk, E., Gulati, R.D., 1995. Transition of a lake to turbid state six years after biomanipulation: mechanisms and pathways. *Water Sci. Technol.* 32, 197–206.
- van Liere, L., Janse, J.H., 1992. Restoration and resilience to recovery of the Lake Loosdrecht ecosystem in relation to its phosphorus flow. *Hydrobiologia* 233, 95–104.
- Wallsten, M., Forsgren, P.O., 1989. The effects of increased water level on aquatic macrophytes. *J. Aquat. Plant Manag.* 27, 32–37.
- Windolf, J., Jeppesen, E., Jensen, J.P., Kristensen, P., 1993. Modelling of seasonal variation in nitrogen retention and in-lake concentration: a four-year mass balance study in 16 shallow Danish lakes. *Biogeochemistry* 33, 25–44.