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Characterization of sediments in two Mauritian freshwater reservoirs

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2 Abstract

Tropical inland waters are different from temperate- and boreal systems in many respects. It has been brought forward that processes taking place within confinement of the lake/reservoir basin could be more important in determining water column nutrient dynamics in tropical inland waters than in their temperate- and boreal counterparts. The aim of this study was to characterize the sediments in two Mauritian freshwater reservoirs: tropical/subtropical lowland reservoirs Piton du Milieu (PdM) and La Nicoliere (LN). An assessment of if and how sediment nutrient remobilization could affect water column productivity was also pursued. Profundal sediments displayed very low total P concentrations in PdM and LN (< 0.25 µgP mg^{-1} of dry weight [DW]). Total nitrogen concentration (~0.7 % of DW) and organic content (> 20% of DW) could on the other hand be considered medium to high in both reservoirs (in comparison with other tropical inland waters). No correlation was observed between water O_2 concentration and water MRP (molybdate reactive phosphorus) concentration in performed laboratory experiments: O_2 decrease rate and MRP release was followed in air tight test tubes filled with superficial (top 3.4 cm) profundal reservoir sediment (~8.5 g) and unfiltered hypolimnetic water. Larger microcosms consisting of undisturbed sediment cores (inner diameter = 64 mm, length ≈ 40 cm) filled with ~50 % profundal reservoir sediment and ~50 % reservoir water were also set up. Sediment Fe / P ratios in PdM and LN were extremely high (> 400) indicating excess capacity for P retention. BPN ("bioproduction number") assessment confirms that LN is more productive than PdM. The high productivity of the reservoir might be explained by rapid internal nutrient cycling augmented by high resuspension. Resuspension of LN sediment caused an increase in water MRP concentration in test tube- and microcosm experiments. LN is shallow, highly wind exposed and has loosely arranged sediments, signs of wind induced erosion were furthermore observed along the western shore. External loading to oligotrophic PdM is probably reduced by the presence of a well developed buffer zone and by low catchment slope angle.

3 Introduction

Tropical regions hold a great diversity of inland waters (e.g. seasonal streams, huge rivers, temporary pools etc.). Interest in tropical limnology has increased in the past ~25 years but our understanding of these waters is still incomplete (e.g. Lewis 1996; Nascimento 2007). The study of limnology has historically been focused on temperate- and boreal systems in Europe and North America. Developed conceptual models are therefore often poorly adapted to tropical inland waters, while other concepts transfer well across latitudes (e.g. Lewis 1987; Roldán 1992; Cooke et al. 2005). Many physical parameters that directly and/or indirectly affect freshwater ecosystems differ between latitudes (e.g. Castagnino 1982; Lewis 1987; Torres-Orozco et al. 1996). Latitudinal trends can for example be seen in minimum and maximum daily irradiance, minimum and maximum water temperatures and in the strength of the Coriolis effect (e.g. Landsberg 1961; Lewis 1987). These physical parameters in turn affect the formation and stability of thermal stratification (e.g. Lewis 1973), primary production, secondary production and nutrient regeneration rates (e.g. Lewis 1978; Brylinsky 1980; Twombly 1983).

The economic growth and ever increasing need for potable freshwater in tropical countries around the world exact pressure on the freshwater supply (Salas & Martino 1989; Kelly & Whitton 1998). It is paramount that the biology and function of extant water resources is properly characterized and understood to enable the development of effective conservation designs and management policies (e.g. Tundisi & Barbosa 1995; Páez et al. 2001). Lake/reservoir eutrophication has become an increasing problem in several tropical regions (e.g. Infante et al. 1990; González et al. 2004). Associated water quality deterioration has completely undermined the very purpose of reservoir construction (potable- and/or industrial water supply) in some instances (Salas & Martino 1989). Water supply in Mauritius is highly dependent on reservoirs storing the water of seasonal streams (WRU 1999). Exploitation of surface- as well as ground water depots is constrained while the demand by public-, agricultural- and industrial sectors is increasing (Berg 2004; Proag 2006). The biology of Mauritian freshwater reservoirs has historically not received much attention. A water chemistry- and water biology survey carried out in two Mauritian reservoirs in 2003-2004 revealed a lack of correlation between productivity and catchment land use (Dumur 2005).

Dumur (2005) found no satisfactory explanation for this. A sediment characterization of these reservoirs would increase understanding of the water bodies and could provide an explanation to the findings of Dumur (2005) (e.g. Hutchinson 1973; Håkansson & Jansson 1983).

3.1 The lake/reservoir nutrient budget

Nutrients in the water column of a lake or reservoir can have many different origins. Elements that enter the water body from the catchment are referred to as the *external nutrient load.* External loading represents the major pathway of lake/reservoir nutrient loading. Losses of nutrients occur as water and suspended or dissolved material leave the water column through the lake/reservoir outlets (export) or through sedimentation processes (e.g. Talling 1992; Lal 1998). Nitrogen (N) can also be lost directly to the atmosphere through denitrification (e.g. Dudel & Kohl 1992). The level of external nutrient loading is primarily determined by the rainfall erosivity, soil erodibility, catchment slope angle and land use. This is in turn affected by the catchment geology, -topography, soil composition, agricultural activity, -practise and -locality, precipitation rate, precipitation-evaporation ratios etc. (e.g. Auerswald & Schmidt 1986; Jäger 1994). The effect of land use on erosion and nutrient export is usually strong (e.g. Jäger 1994; Morgan et al. 1998). A "buffer zone" of undisturbed natural growth can however halt the flow of inorganic- and organic nutrients from patches of agricultural land (or other diffuse sources) in the catchment. External nutrient loading may be greatly reduced by this (Kadlec & Knight 1996; Fennessy & Cronk 1997).

Nutrients that have settled to the bottom are made inaccessible for direct water column utilization, this process can however be reversed under certain conditions. *Resuspension* (section 3.4) physically carries sediment back into the water column. Phosphorus (P) may also be remobilized through a mechanism termed *internal loading* (section 3.2). The different facets of this complex chemical-, physical- and biological interaction has been studied for many years and accumulated knowledge is comprehensive (e.g. Mortimer 1941; Perkins & Underwood 2001; Søndergaard et al. 2003). The term "internal loading" is sometimes used referring to all forms of nutrient release taking place within lakes and reservoirs, other authors use it specifically to describe chemically induced release of P. The latter definition has been adopted in this thesis.

3.2 Phosphorus and internal loading

Production is most often limited by the availability of nutrients in the natural freshwater ecosystem (e.g. Cooke et al. 2005; Dejenie et al. 2008). Phosphorus is typically scarce in temperate and boreal systems whereas tropical inland waters more often display N limitation, P limitation is also common (e.g. Peters & MacIntyre 1976; Lewis 1996). P is vital for cell life. The element is a component in many biomolecules such as various proteins, nucleotides, phospholipids etc. and plays a central role in most endothermic biochemical reactions (ATP) (e.g. OECD 1982; Paes da Silva & Thomaz 1997). P exists in the sediments in particulate or dissolved form. Particulate P includes various forms of organic P, P incorporated into solid state molecules and minerals, P adsorbed to different metal oxides and hydroxides (especially those of Mn, Al and Fe), P adsorbed to clays, P adsorbed to or incorporated into carbonates etc. Dissolved P occurs in the interstitial water and consists mainly of phosphate (PO_4^{3-}) but also of small organic molecules and other species (e.g. Reynolds & Davies 2001; Wetzel 2001). The P concentration is typically several orders of magnitude higher in the sediments than in the ambient water (e.g. Holdren et al. 1977; Boström et al. 1982).

Under aerobic conditions oxygen penetrates the sediment surface a few centimetres down through diffusion. An oxidized micro-layer is created which acts as a trap for sediment P (e.g. Mortimer 1971; Carlton & Wetzel 1988). The hypolimnion is ceiled off from oxygen rich surface water during thermal stratification regimes, meanwhile the oxidative activity of aerobic micro-organisms and benthic meio-fauna consumes dissolved oxygen. This can render the hypolimnion and superficial sediment completely devoid of oxygen (e.g. Boström et al.1988; Leal et al. 2007). When this happens heterotrophic bacteria turn to other less electronegative electron acceptors such as nitrate or manganese. If the electron potential (E_h) drops below +200 mV (corresponds to an O_2 concentration of approximately 0.1 mg L^{-1}) ferric oxides and hydroxides starts being reduced (e.g. Håkansson & Jansson 1983; Caraco et al. 1993). Ferric iron (Fe (III)) has a high affinity for PO_4^{3-} whereas the product of the biochemical redox-reaction, ferrous iron (Fe (II)), has a low affinity PO_4^{3-}. The reduction of ferric oxides and hydroxides can therefore increase PO_4^{3-} (*aq*) concentrations in the interstitial water, this strengthens diffusional forces across the sediment-water interface and results in increased P loading to the water column (Einsele 1936; Mortimer 1941; Boström et al. 1982 and many others). Release of P by the aforementioned mechanism is referred to as the "Einsele and Mortimer model"- or the "classical model" of internal loading (e.g. Boström 1984; Jensen et al. 1992).

Flow of P across the sediment-water interface is however not only determined by hypolimnion electron potential and the size of the P pool associated with ferric oxides and hydroxides, as described in the previous section. Several other biological-, chemical- and/or physical factors may also affect flow rates and net flow direction:

If E_h drops well below +200 mV microbial *sulphate reduction* can occur. The produced sulphides combine with ferric- and ferrous iron forming exceedingly insoluble and chemically inert salts. The number of sorption sites for phosphate on Fe (III) oxides and hydroxides is thus permanently reduced. This can cause a greater "effective P release" than the direct microbial reduction of ferric compounds (e.g. Roden & Edmonds 1997; Søndergaard et al. 2003). The presence of *nitrate* (> 1 mg N L^{-1}) usually inhibits/delays Fe (III) reduction, and hence P release, since E_h remains high (e.g. Tirén & Pettersson 1985; Foy 1986). Rapid decomposition through denitrification can however in some instances counteract the inhibitory effect of NO_3^- so that P release is enhanced (Jansson 1987; Kleeberg & Schlungbaum 1993). The indirect effect of heterotrophic *microbial activity* may result in internal loading (previous section) but bacteria can also mobilize P directly through mineralization processes associated with their metabolism (Marsden 1989). An activation of lower sediment layers, the emergence of anoxic micro zones (locally enhanced microbial activity) and release of P from organic material can also cause limited P loading also during high E_h conditions (e.g. Rzepecki 1997; Gomez et al. 1999).

Ligand exchange-, dissolution/precipitation- and adsorption/desorption equilibria in the sediments between phosphate and various metal complexes and salts (equation 1) are affected by: *metal ion concentration*, phosphate concentration, *temperature*, *pH* and the concentration of "*competing ligands*" such as sulphate, carbonate and hydroxide.

$$PO_4^{3-}\ (aq) \leftrightarrow [Me(X)_Y]ZPO_4^{3-} \ /\ MeA_BPO_4\ (s) \qquad (1)$$

Me = Metal ion, e.g. of Fe, Al, Mn and Ca
X, Z and A = anions other than phosphate
$_Y$ and $_B$ = integer numbers

If metal ion concentration is high the equilibrium is shifted towards the "bound state" (equation 1). An increase in competing ligand concentration (X, Z and A) will on the other hand cause a shift towards dissolved phosphate (e.g. Golachowska 1971). High temperatures can result in decreased adsorption and may shift dissolution equlibria towards the dissolved state (e.g. Redshaw et al. 1990; Perkins & Underwood 2001). Increased pH shifts the ligand exchange equilibrium towards dissolved state P (OH^- is a competing ligand). Adsorption and re-precipitation to Fe (III) compounds is also reduced at pH values > 6.5 (e.g. Stumm & Morgan 1995; Koski-Vahala et al. 2001). pH driven P loading can be considerable in shallow productive lakes, the driving force is photosynthesis-induced pH changes in areas where the phototrophic zone coincides with the sediment surface (Håkansson & Jansson 1983). Co-precipitation of P on carbonates (mainly $MgCO_3$ and $CaCO_3$) is however increased when pH is increased, because of the imminent shift in the carbonate system equilibrium towards solid state molecules and lattices on/in which P can be adsorbed or incorporated. Carbonate P co-precipitation can cause significant drops in water P concentration in productive calcareous lakes (e.g. Andersen 1975a; Golterman 1988). P release is independent of both pH and E_h if the sediments are oversaturated with P (e.g. Clasen et al. 1982; Hoyer et al. 1982).

Internal nutrient release processes, such as internal loading or resuspension, can likely cause more production per unit nutrients released in tropical- than in temperate- or boreal systems (Kilham & Kilham 1990). The thickness of the epilimnion is highly variable in tropical lakes and reservoirs, this mediates a rapid return of nutrients from deeper water strata and high average epilimnion residence times for released nutrients (Lewis 1987). This is further augmented by rapid mineralization of organic material within the water column (Ruttner 1931b; Wetzel 2001). Twofold higher production per unit nutrients released is often used as a rule of thumb when tropical systems are compared with their temperate- and boreal counterparts, fast nutrient remobilization and high maximum photosynthesis rates are recognized as the main reasons for this (Lewis 1987, 1996; Kleeberg 2002). The sedimentation of nutrients is on the other hand counteracted by the aforementioned mechanisms. Sediments in tropical lakes/reservoirs are subsequently often comparatively nutrient poor (e.g. Tundisi et al. 1988; Uhlman et al. 1995). It could therefore be tempting to assume a more subordinate role of the sediments to the overall nutrient dynamics of tropical inland waters compared with temperate- and boreal systems. Oxygen depletion is more rapidly commenced in tropical systems however, BOD/COD (biological- and chemical oxygen demand) and temperature correlates positively and gas solubility and temperature correlates negatively (e.g. Lewis 1987). Sediment affinity for P is also reduced at high temperatures (previous sections). Payne (1986) hypothesized that the low E_h and low pH in many tropical lake hypolimnions could result in significant internal loading through the Einsele-Mortimer model. Internal nutrient cycling was suggested to have the potential of being more important to the overall nutrient dynamics of tropical lakes/reservoirs than in their temperate- and boreal counterparts by Kilham & Kilham (1990). Whether the process of internal loading displays distinct latitudinal differences remains to be eluciated, the subject is discussed in section 6.1.

3.3 Nitrogen

Nitrogen limitation of freshwater productivity is more widespread in tropical than in temperate or boreal water bodies (e.g. Kalff 1983; Fisher et al. 1988; Lewis 1996). Weathering of P is more efficient at high temperatures (Lewis 1996). Lake/reservoir P evapoconcentration and N loss through denitrification is also higher at low latitudes (e.g. Kalff 1983; Talling 1992). N-fixing cyanobacteria thrive under nitrogen deficient conditions and are often abundant in tropical lakes/reservoirs (Smith 1982; Mukankomeje et al.1993).

Dudel & Kohl (1992) found that the most important loss process for nitrogen in the aquatic ecosystem was denitrification, followed by sedimentation. Reduced inorganic N (NH_4^+) in the sediments can be mobilized under anoxic conditions, this can cause substantial internal N loading (Nielsen et al. 2004; Dumur 2005). Nitrification-denitrification processes and resuspension (next section) can also mobilize sediment N and cause internal N loading (e.g. Watts 2000b; Jorcin & Nogueira 2005). Approximately 90 % (or even more) of sediment N is typically present in organic form, covalently bound to organic molecules (Martinova 1993). Superficial sediment total N (tot-N) concentration can fluctuate a lot between years, this might be especially pronounced in tropical systems and could indicate that N cycling is more dynamic in these waters. Tropical sediment N dynamics are not well understood, there are still many question marks to be straightened (e.g. Lewis 1996; Tomaz et al. 2001).

3.4 Resuspension

The transport of released sediment P (and N) can be mediated and substantially enhanced by *resuspension*. Resuspension is caused by a physical disturbance of the sediments carrying sediment constituents back into the water, this can result from complete mixis, incomplete mixis, wave action and/or wind induced currents. These universal physical phenomena can alone or together inflict the shear stress needed to disrupt the sediment surface and for resuspension to occur (e.g. Evans 1994; Bloesch 1995). Wave height, effective lake fetch and disturbance duration determines how much kinetic energy is transferred into the water body by any given wind velocity. Basin orientation, wind protection (topography and vegetation), basin morphology, water depth, depth to volume relations, the “cohesitivity” of the sediments, sediment water content, sediment grain size, altitude, latitude etc. effects susceptibility for resuspension (e.g. Postma 1967; Wetzel 2001). Bioturbation by living organisms, such as benthic fauna, and the ebullition of microbially generated gases (e.g. CO_2 and CH_4) may also result in limited sediment resuspension regardless of basin morphology (e.g. Ohle 1978; Holdren & Armstrong 1980).

Resuspension will carry anything light and small enough into the water column. Not only interstitially dissolved phosphate is released (as in the case of internal loading, section 3.2) but other dissolved- or particle bound nutrients, POC (Particulate organic carbon), inorganic components, etc. are transferred back into the water column as well and made available for biological utilization (Håkansson & Jansson 1983). Water column P loading can be completely dominated by resuspension in shallow wind exposed lakes and reservoirs (e.g. Newman & Reddy 1992; Reddy et al. 1996). Frequent mixing and resuspension prevents the development of an oxygen-depleted hypolimnion however, and may thus also inhibit the classical model of internal loading (e.g. Håkansson & Jansson 1983; Kleeberg & Kozerski 1997).

The Coriolis effect is weak at low latitudes, wind induced currents can therefore reach higher maximum velocities. Mixing depth is directly proportional to surface current velocity, resuspension may subsequently affect deeper areas, dig deeper into the sediments and dispense heavier particles in tropical than in temperate or boreal water bodies. A two- to threefold difference in wind-induced water mixing depth has been theoretically conceived (Munk & Anderson 1948; Hutchinson 1957). The latitudinal difference is less pronounced for small lakes/reservoirs (< 1 km^2) since frictional forces against the basin boundaries restrict current development, the influence of decreased current deflection by the Coriolis effect is subsequently marginalized (Smith 1975).

The kinetic energy of currents and wave action do not transfer well across the thermocline boundary layer of a thermally stratified lake/reservoir, the epilimnion acts as a “protective layer” that absorbs energy inputs from weather and other external sources leaving the underlying hypolimnion relatively undisturbed. Thermally stratified lakes/reservoirs are thus rather resistant to mixis. If on the other hand thermal stability is low the physical restriction of downwards kinetic energy propagation is relived and the entire water mass may become to circulate (mixis). Sediments at all water depths can become subject to water turbulence and resuspension during mixis, mixis induced deep water sediment disturbance depths of several centimetres have sometimes been observed (e.g. Pennington 1974; White & Wetzel 1975).

The temperature difference between surface- and bottom water is often small in tropical lakes/reservoirs (the hypolimnion is warm). This makes developed thermal stratification regimes sensitive to heat loss. Strong winds accompanied by cloudy weather may over the course of a few days cause major thickening of the mixed layer or even complete mixis, and this in every season (e.g. Lewis 1987; Lehmusluoto et al. 1999).

3.5 Reservoirs

There are several important aspects, affecting ecology and function, that separates reservoirs from natural lakes. The geological history, basin morphology and water hydraulics of reservoirs is unique, flushing rates are typically high and water residence times short. Reservoirs are unfortunately often treated as functionally equal to natural lakes however, differences are ignored or insufficiently accounted for in many limnological texts. The unique features that set reservoirs apart should be recognized and properly addressed to assess these water bodies correctly (e.g. Kennedy 1999, 2001; Cooke et al. 2005).

Reservoir stratification is often disturbed by large and rapid changes in water level, irregular inflow- and outflow rates, turbidity and mixing (Wetzel 1990; Henry 1999). This translates into high susceptibility for sediment resuspension. The erosive energy of wave action can furthermore affect new sediment layers every time the water level is changed. Sediment constituents are effectively resuspended as the surge zone moves up and down the bottom. Water from the inlets may also dig into newly exposed areas eroding and resuspending sediment material, this mechanism has been termed *flushing* and is unique for reservoirs (e.g. Gibson & Guillot 1997; Vernieu 1997). Flushing can cause erosion, sediment export and sediment nutrient concentration reductions of unparalleled scale (Watts 2000a; Cooke et al. 2005). Export is favoured if the deepest part coincides with the reservoir outlet, the entire reservoir basin may then become drained and subject to river erosion. Other factors affecting flushing efficiency include water discharge, location of outlet in relation to inlets, the route of inlet water in relation to primary accumulation bottoms, steepness of banks, original stream gradient, sediment “cohesitivity” and grain size (Brown 1943; Brandt 2000). Export is reduced if a substantial water body persists in the emptied reservoir basin, this will act as a sediment trap capturing eroded material from upstream. Sediments above the water line can become dehydrated in partially- or completely emptied reservoir basins. *Sediment desiccation* can cause increased P mobilization in periodically exhausted tropical/subtropical reservoirs, export is favoured by rapid refilling of the reservoir (e.g. Twinch 1987; McComb & Qui 1998). Repeated desiccation and refilling has actually put internal loading to a complete halt in some eutrophic reservoir basins (De Groot & Van Wijck 1993). Despite all this the sediment still typically act as a sink for phosphorus and (to a lesser degree) nitrogen in tropical freshwater reservoirs (e.g. Uhlman et al. 1995; Tundisi et al. 1988; Agostinho et al. 1999).

3.6 Sediment analysis

The elemental composition of the sediments reflects the composition of the earths crust, sediments from calcareous regions are rich in calcium while silicon and aluminium dominate sediments in acidic bedrock areas (Jones & Browser 1978; Håkansson & Jansson 1983). Sediments can be characterized using either a genetic- or a descriptive approach. In a genetic approach interest is directed at the origin of the sediment constituents (e.g. Berner 1981; Seibold & Berger 1982). A descriptive approach is on the other hand only focused on the actual character of the sediment, colour, texture, structure, grain size, organic content or algal content can for example be used (e.g. Thomas et al. 1972; Bågander 1976). An important descriptive classification system was developed by Lundquist (1942). Organic sediments were divided into two main groups: dy and gyttja, based on a number of general characteristics.

Gyttja sediments are found in lakes/reservoirs with high autochthonous production and low humic inputs. Dy sediments are on the other hand common in small lakes with low autochthonous production, high littoral production and large allochtonous inputs of organic material (Hansen 1961; Wetzel 2001). “Deposition bottoms” are defined as bottoms where there is a continuous deposition of fine sediment particles (diameter < 0.006 mm) in another descriptive classification system. “Transport bottoms” display discontinuous deposition and “erosion bottoms” no deposition at all. Deposition bottoms can be found in deep areas that are protected from resuspension (section 3.4), desiccation and flushing (section 3.6). Deposition bottom sediments are typically “loose” and have high content of water- and organic substances. Erosion bottoms are found in shallow wind exposed areas, they have low organic contents and low water contents (< 50 %). Deposition bottom samples are preferred in comparative studies and whole lake approaches since they are more stable than erosion- and transport bottoms (Håkansson 1977; Håkansson 1981).

The nutrient- and organic content of the sediments is primarily determined by the rate of organic matter accumulation. This is in turn affected by the level of allochthonous import, water column productivity and sediment E_h conditions (Carter 1973; Rice et al. 2001). The nutrient content or “quality” of organic material is highly variable and sensitive to microbial degradation (e.g. Hansen 1961; Kaushik & Haynes 1971). Planktonic material (empirical formula: $C_{106}N_{16}P$) has an average C/N ratio of ~5.6 whereas humic substances range between 10 – 20 (e.g. Håkansson 1980; Golterman 1975). This means that the quality of autochthonous material is very different from the quality of allochthonous material. Autochthonous material basically consists of algal matter whereas allochtonous material is of terrestrial origin, has high humic content and is subject to terrestrial degradation before reaching the target lake/reservoir (e.g. Kaushik & Haynes 1971). The relationship between allochtonous- and autochthonous production and productivity of the water column can therefore be assessed solely through sediment analysis (e.g. Hutchinson 1973). Profundal sediment C/N ratio is employed in this genetic sediment characterization approach (Hansen 1961). Sediment C/N ratios < 10 indicates dominance of autochthonous production in temperate lakes/reservoirs, allochtonous inputs are on the other hand believed to be more important if C/N > 10 (e.g. Premazzi & Ravera 1977; Ravera & Parise 1978). The critical value could easily be > 10 in tropical lakes/reservoirs since degradation is faster at lower latitudes (e.g. Kaushik & Haynes 1971; Melillo et al. 1984).

Sediment tot-N concentration and a number of inter-relational sediment carbon (C)-, N- and P ratios have proved to correlate with lake/reservoir productivity (e.g. Horie 1969; Håkansson 1981). The BPN value (“bioproduction number”) represents the slope (k-value) of the sediment tot-N/sediment organic content regression line and has proved particularly useful for trophic status assessment. The BPN value is based on samples collected from all areas of the lake/reservoir and can therefore be considered a truly lake specific measure, basin morphology and areal spread is thus taken into account. Swedish oligotrophic lakes typically display BPN values < 0.33, mesotrophic lakes range between 0.33 - 0.45, eutrophic lakes range between 0.45 - 0.65 and hyper-eutrophic lakes display BPN values > 0.65 (Håkansson 1981). Tropical lake/reservoir BPN values should probably not be assessed according to Håkansson (1981) without adaptation of the grading system to tropical conditions (e.g. Salas & Martino 1991; Torres-Orozco et al. 1996).

The sediment Fe/P ratio provides an estimate of the P saturation level and correlates negatively with sediment P release rate and trophogenic zone total P (tot-P) concentration. The ratio can be used as an indicator of internal loading in shallow well oxygenated lakes/reservoirs (Jensen et al. 1992). Jensen et al. (1992) reported that sediment Fe/P ratios >15 indicates limited P release from well oxygenated sediments while Fe/P ratios >35 keep P release to a minimum. Cooke et al. (1993) and Gunkel (2002) instead suggest that Fe/P ratios > 10 are sufficient for the sediments to effectively retain P. Fe/P ratios < 7 indicate P over-saturation and thus P release independent of E_h- and pH conditions (Lennox 1984; Christophoridis & Fytianos 2006). Sediment tot-P concentration may indicate vulnerability for internal loading in deep stratified lakes/reservoirs but this is rather erroneous. Only certain fractions of the P pool are readily mobilized through internal loading (section 3.2) and P fractionation can differ a lot between lakes/reservoirs (e.g. Nürnberg 1988; Sas 1989).

3.7 Objectives

Dumur (2005) hypothesized that productivity would be high in Piton du Milieu Reservoir in Mauritius (PdM) because sugarcane- and tea plantations dominate the catchment. Water chemistry- and phytoplankton community analysis did however suggest oligotrophic productivity status in the reservoir (Dumur 2005). Another Mauritian reservoir, La Nicoliere (LN) has little agricultural activity in the catchment but was characterized as eutrophic by Dumur (2005). Productivity seems to be independent of catchment land use in these reservoirs. Studies of other tropical freshwater ecosystems have given the same result (e.g. Kilham & Kilham 1990; Tafangenyasha & Dube 2008). It has been put forward that internal nutrient remobilisation could be more important to the overall nutrient dynamics of tropical lakes/reservoirs than in their temperate- and boreal counterparts (Kilham & Kilham 1990; Lopes et al. 1997; Sampaio et al. 2002). This has not been empirically verified however, the total number of relevant studies is still insufficient. Lewis (1996) therefore highlights the need for future studies in this area.

Temperature gradients that suggest thermal stratification have been observed in PdM. Hypolimnion O_2 concentrations decreased during stratification and was followed by an increase in deep water PO_4^{3-} concentration (Dumur 2005). This suggests that the reservoir could be subject to the classical model of internal loading. Sedimentation in Mauritian reservoirs was surveyed 1996, sediment grain size and elemental composition was also analyzed but without limnological concern (e.g. WRU 1997a, 1997b). A characterization of the sediments in PdM and LN would provide valuable information about the sediment nutrient dynamics, water column nutrient dynamics, productivity and biology of these water bodies. Together with the work of Dumur (2005) and Liedholm (2007) a more complete picture of the function of Mauritian reservoirs is drawn.

The aims of this study were to: (I) physically- and chemically characterize the sediments in PdM and LN. (II) Assess susceptibility for internal loading and/or resuspension in PdM and LN. In addition attempts were made to: (III) from sediment analysis data assess productivity, nutrient- and carbon dynamics in PdM and LN and to revisit and reassess water chemistry data from Dumur (2005) in this new context.

4 Methods

4.1 Study area

Mauritius is a tropical volcanic island located ~900 km east of Madagascar in the Indian Ocean at 20 ˚S latitude and 57 ˚E longitude. The island has a surface area of ~1860 km^2 and is one of the most densely populated agricultural islands in the world. Tourism, light industry and agriculture are the corner stones of the economy (Berg 2005). Rainfall is plentiful in Mauritius (on average 1400 mm yr^{-1}) but unevenly distributed over the island. More than 70 % of total annual precipitation is received in the wet summer months of January – April, the central plateau receives most rain while the coastal regions, especially those in the north and west, receive less (e.g. Proag 1995; WRU 1999). The climate is tropical in summer (October – April), with diurnal temperature averages of 23 - 30 ˚C, but changes to subtropical in winter

(May - September), diurnal temperature averages of 17 - 23 ˚C (Proag 1995; Ng Kee Kwong et al. 2001). Predominantly south-easterly trade winds (usually 0.5 - 12.5 m s^{-1}) sweep over the island throughout the year. Mauritius is situated just outside the cyclone belt but is frequently affected, or directly hit by cyclones. This brings extreme winds and heavy rains (Berg 2004).

The 11 man-made reservoirs of Mauritius yield ~305 Mm^3 water yr^{-1} (WRU 1999). Inflow-, withdrawal- and evaporation rates vary over the year and water levels often plummet in the dry season. Water shortage arise when summer front systems fail to replenish withdrawn volumes (WRU 1997a, 1997b). Piton du Milieu (PdM, figure 4.1) was constructed in 1952 to store the water of seasonal streams River Vacoas and River Bateau for domestic purposes. The catchment of the reservoir is dominated by sugarcane- and tea plantations, these cover ~65 % of the catchment area (Dumur 2005). Mauritian sugarcane fields are turned on a regular basis and annually fertilized with P, N and potassium (K). Nutrient concentrations in effluent water often exceeds proposed guidelines (Sharpley et al. 1996; Ng Kee Kwong et al. 2002b). La Nicoliere (LN, Figure 4.2) was constructed in 1929 across the River Rempart, which is the major inflow. The La Pipe Feeder Canal, which diverts water from the Mid Land Dam, and a number of small temporary rain fed streams and channels also contribute considerable amounts of water to the reservoir. Water is stored for domestic purposes and irrigation (WRU 1999). The catchment of LN is mountainous and dominated by shrub land and dense forest, agricultural land occupy ~ 10 % of the catchment area. LN was characterized as eutrophic and hence more productive than PdM (oligotrophic) by Dumur (2005). Geometrical-, physical-, chemical-, biological-, geological- geographical- and meteorological information of PdM and LN is summarized in table 4.1.

Table 4.1 Some geometrical-, physical-, chemical-, biological-, geological- geographical- and meteorological characteristics of Piton du Milieu Reservoir and La Nicoliere Reservoir described or recorded by WRU (1997a, 1997b, 1999) or Dumur (2005).

	Piton du Milieu Reservoir	La Nicoliere Reservoir
Altitude (m.a.s.)	438	249
Latitude	20 17'S	20 09'S
Longitude	57 34'E	57 37'E
Maximum storage capacity (m^3)	$3.2E^6$	$5.8E^6$
Maximum Surface area (km^2)	0.76	1.02
Maximum depth (m)	~15	~10
Thermal stratification	Could occur in the wet season	Very weak or non existent
Trophic status	Oligotrophic - mesotrophic	Eutrophic
Turbidity	Moderate	Typically high
Mean annual water MRP concentration (1st row) and mean wet season water MRP concentration (2nd row). 2003 - 2004 survey ($\mu g\ L^{-1}$)	~4 ~3	~5 ~3.5
Mean annual water tot-P concentration (1st row) and mean wet season water tot-P concentration (2nd row). 2003 - 2004 survey ($\mu g\ L^{-1}$)	~15 ~18	~30 ~23
Shape	Elongated and dentritic	Triangular
Wind exposure	High protection from prevailing winds	Low protection from prevailing winds
Catchment area (km^2)	~6.4	~7.7
Catchment characteristics	High level of agricultural activity (sugarcane), flat landscape	Mostly forest, steep slopes
Agricultural land in catchment (km^2)	~4,2	~0,8
Soil of catchment	Humic ferruginous latosols	Lithosols and humic latosols
Geology of catchment	Pyroclasts and weathered basaltic flows, ancient basaltic flows and Scoria.	Pyroclasts and weathered basaltic flows, fresh basaltic flows and ancient basaltic flows.
Mean annual rainfall (mm)	3400 - 3600	2000 - 2400
Mean annual air temperature (°C)	20,5	24
Mean sunshine duration (h day^{-1})	6.5	8

4.2 Sampling procedure

Littoral wind shaded- (WS), littoral wind exposed- (WE) and profundal sediment samples were collected, figures 4.1 and 4.2 illustrate approximate sampling locations in PdM and LN respectively. The chronology and details of sampling and analysis are exhibited in figure 4.3. Littoral bottoms were sampled with a plexiglass Willner core (inner diameter = 64 mm, length ≈ 40 cm) that was forced by hand into the sediment. Profundal bottoms were sampled with a Willner core sampler until ~2008-03-20, when the sampler was lost in a boating accident. Profundal sampling was carried out with a sediment sampler of own design from this date on (Appendix A, figure 4.3).

The deepest area of PdM could not be sampled on April 16 because of the limited reach of the sediment sampler (Appendix A). Deposition bottoms at ~9 m depth were however successfully reached. Profundal bottoms in LN were very soft and loosely arranged and both the Willner core sampler and the purpose built sampler had to be upheld by hand to collect the uppermost sediment layer. Superficial sediment was transferred with a spoon from collected cores to plastic cups of known volume. Approximate sample collection depth (~3.4 cm) was backtracked and calculated from plastic cup volume (110 ± 1.3 ml) and Willner core inner surface area (32.15 cm^2). This approach was implemented because it was believed to exhibit better repeatability than the more straightforward approach of using a ruler and simple eye measure. Sediment samples were stored in a refrigerator at the university.

Undisturbed cores (~20 cm of sediment and ~20 cm of water in each core) were also brought to the university to be used in microcosm P release experiments (next section). The cores were closed with rubber corks and handled with care during transport to minimize sediment disruption. Cores and cups with sediment were covered with aluminium foil upon retrieval to prevent excessive heating and photosynthetic activity. Hypolimnetic water was collected from just above the sediment surface at all sampling occasions, a Ruttner sampler was used. In situ water temperature was measured in the sampler directly upon collection, the water was then tapped into plastic bottles that were covered with aluminium foil. Water samples were stored together with the microcosms in the lab at room temperature.

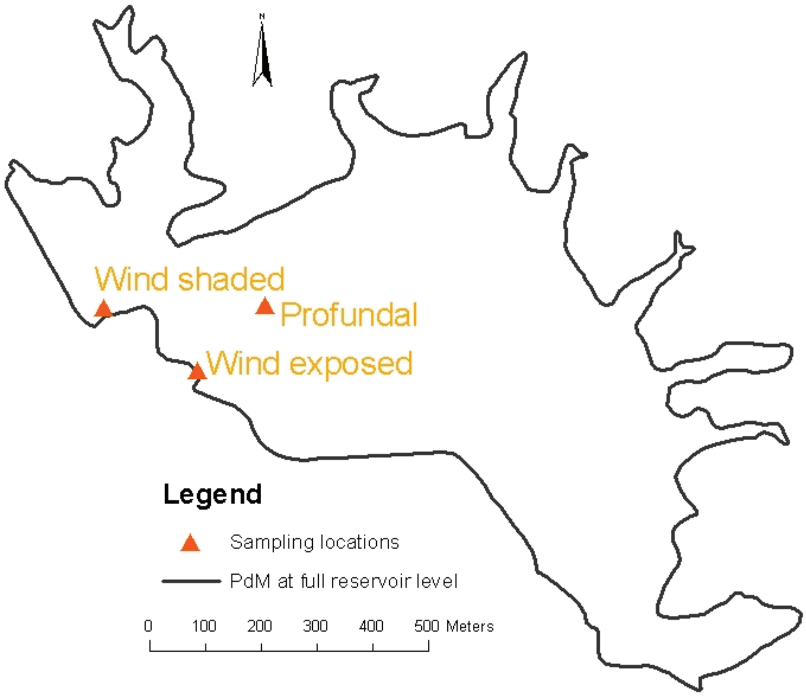

Figure 4.1 Approximate sampling locations in PdM. Sampling was carried out in 2008. PdM = Piton du Milieu Reservoir. Joel Segersten, Uppsala universitet 2009, digitized from depth chart data supplied by the Water Resources Unit of Mauritius (WRU 1997a).

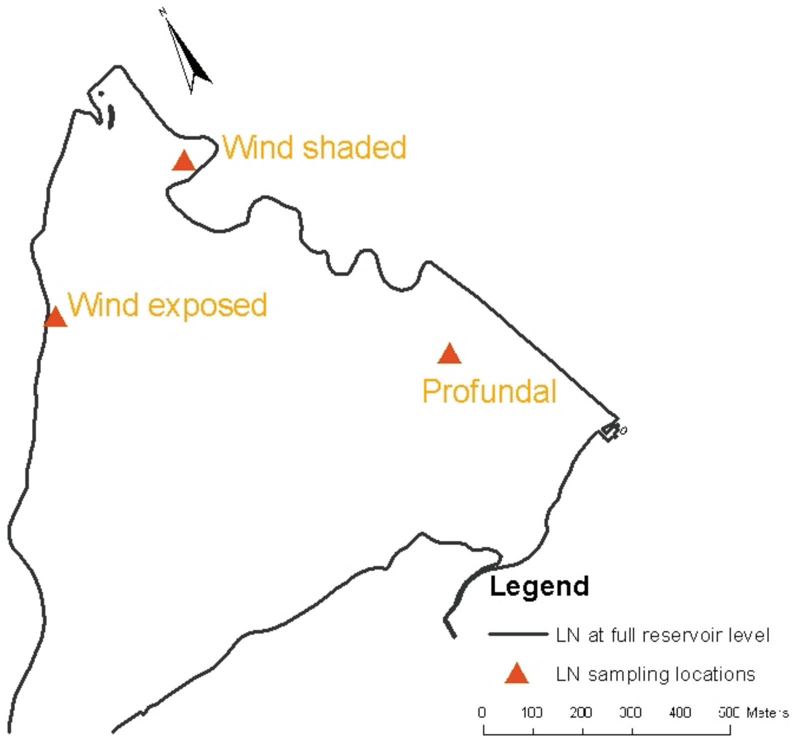

Figure 4.2 Approximate sampling locations in LN. Sampling was carried out in 2008. LN = La Nicoliere Reservoir. Joel Segersten, Uppsala universitet 2009, digitized from depth chart data supplied by the Water Resources Unit of Mauritius (WRU 1997b).

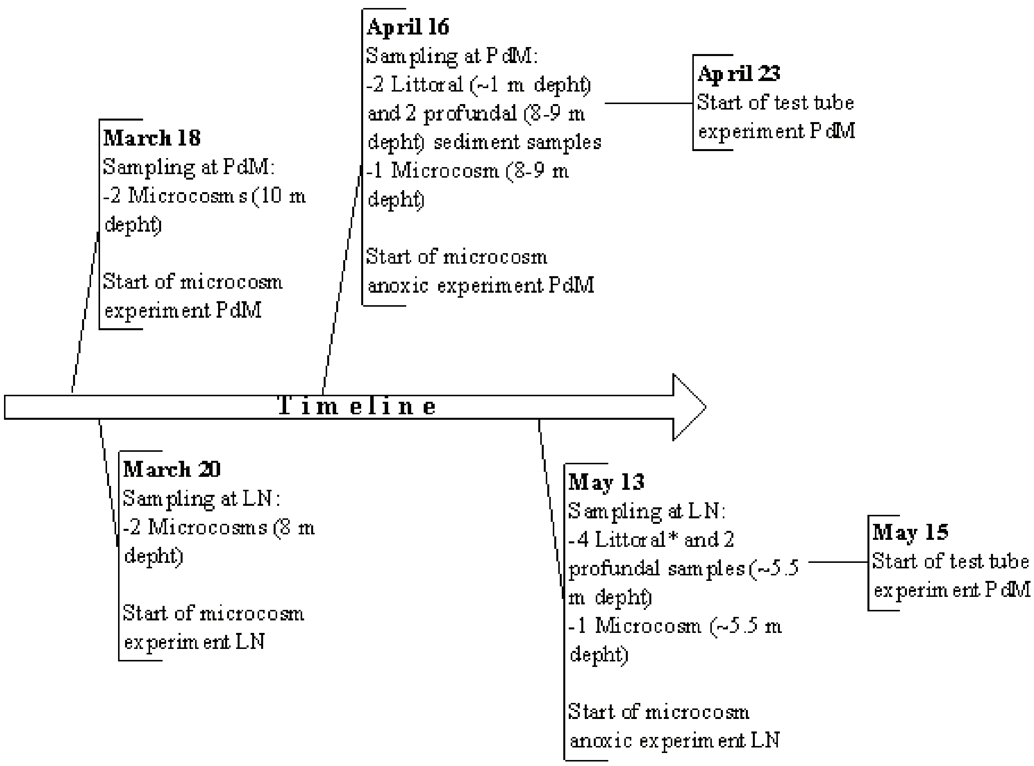

Figure 4.3 The chronology of sampling and analytical procedures. Sampling was carried out in 2008. Sampling depths are presented within brackets. PdM = Piton du Milieu Reservoir, LN = La Nicoliere Reservoir.

* Littoral samples in La Nicoliere Reservoir were collected both from ~1 m below maximum water level and from ~1 m below actual water level. The reservoir was ~3.2 m below maximum water level at the time of sampling.

4.3 Experimental setup

A *test tube experiment* was set up to investigate MRP release patterns from PdM and LN sediments under naturally decreasing O_2 conditions. 16 test tubes (~85 ml) were assembled, 8 for each reservoir. ~8.5 g ww (wet weight) of profundal sediment was added to each tube, they were then filled to the brim with unfiltered hypolimnetic water and sealed with airtight lids. When all test tubes had been assembled the complete set was shaken vigorously to suspend all sediment particles, this marked the beginning of the experiment (t_1). pH, MRP- and O_2 concentration was analyzed in the hypolimnetic water prior to experiment initiation, this was used as a reference value (t_0).The tubes were incubated at room temperature (~26˚C) under completely dark conditions. Deep water temperatures in PdM and LN regularly surpass 26˚C (Dumur 2005). Tube water was "homogenized" each weekday of experiment runtime to disrupt concentration gradient development, the tubes were revolved vigorously ten laps on a flat surface. Duplicates were analysed for pH, MRP- and O_2 concentration on an approximately weekly basis (figures 5.3 - 5.5). Test tube homogenization was carried out 15 minutes before each sampling, tube water was collected with a syringe from 4 cm above the sediment surface.

MRP release was also followed in larger microcosms in the *microcosm experiment*. Four sediment cores, two from each reservoir (figure 4.3), were incubated at room temperature (~26˚C) under completely dark conditions. pH and O_2 concentration was measured in water samples collected with a syringe from 5 cm above the sediment surface, precaution was taken to minimize turbulence. MRP concentration was measured in pooled samples covering all microcosm water dephts. Collected water was carefully replaced with unfiltered hypolimnetic water stored with the microcosms. This was done to reduce diffusional gas exchange with the atmosphere. Natural O_2 concentration decrease rate was slow and quite irregular and the experimental setup had to be modified to produce completely anoxic conditions. One microcosm from each reservoir was bubbled with N_2 gas for 30 min and then treated with Sodium sulphite (Na_2SO_3). 15 – 17 mg Na_2SO_3 was typically added, enough to decrease microcosm O_2 concentration with ~2.5 mg L^{-1} (Buecker 1997). "Anoxication" was repeated after each sampling to ensure continued oxygen deficient conditions and to keep the introduced error as constant as possible. Anoxication resulted in regular mixing (N_2 bubbling) and a stepwise increase in pH, as Na_2SO_3 acts as a weak base (Buecker 1997).

4.4 Physical and chemical analysis

pH was measured with a glass electrode pH-meter (pH Meter 3305, Jenway®). *Oxygen concentration* was determined with a modified Winkler titration (e.g. Carpenter 1965; Svensk standard 1987). The absorbance of the re-dissolved precipitate solution was measured at λ = 450 nm on a Spectronic 21D from Milton Roy. The concentration could be determined from a predetermined value (11.92) of the slope in the Lambert-Beer relationship (Broberg 2003). *Sediment density* was calculated from triplicate wet weight measurements in plexiglas dishes on a Denver Instrument Company® AA250 analytical balance. Samples were weighed in a purpose built plexiglas dish (Svensk standard 1981; Broberg 2003). *Water content* was determined by weighing 40 - 70 g ww of sediment prior to and after drying over night at 105°C (Broberg 2003). *Organic content* was assumed to correspond to the ash-free dry weight / sediment dry weight (dw) - 1 ratio. Ash-free dry weight was determined by combustion in a muffle furnace at 550 °C. Samples (~0.5 g finely grained dry sediment) were weighed on an electronic balance (ER-180A from AND®) before and after combustion (Svensk standard 1981). *Nitrogen-*, *sulphur-* and *carbon concentrations* were analyzed with a Nitrogen/Carbon/Sulphur analyzer from Carlo Erba instruments. *Acid dissolvable metal concentration* (Mn, Mg, Fe, Al and Ca) was analyzed according to the routines at the Swedish

University of Agricultural Sciences (SLU). ~1.5 g dry sample was digested with concentrated HNO_3 over night at room temperature, for 1 h at 60 ˚C, for 1 h at 100 ˚C and for 4 h at 125 ˚C. A supplementary 5 ml of concentrated nitric acid was added after two hours of boiling at 125 ˚C. Dissolved metal ion concentration was analyzed in diluted samples with inductively coupled plasma and atomic emission spectroscopy detection (ICP-AES). The ICP-AES was an Optima 3000 DV from PerkinElmer®. *Orthophosphate* (MRP) *concentration* was analyzed according to Murphy & Riley (1962). Absorbance was measured on a Spectronic 21D from Milton Roy. *Total phosphorous concentration* was analyzed with the ignition method (Andersen 1975b). Sediment samples (~0.2 g) were combusted in a muffle furnace (550°C) to break covalent P-C bonds. Remnant ash was boiled in 1 M HCl for ~15 min to transfer all P species to the fully oxidized state (PO_4^{3-}). Supernatant MRP concentration could be measured according to Murphy & Riley (1962) after dilution, volume adjustment (250 ml) and sedimentation over night. Weight measurements were made on an electronic balance (ER-180A from AND®) and absorbance measurements on a UV/VIS Spectrophotometer (Lambda 40, PerkinElmer®).

4.5 GIS analysis

Paper copies of depth charts supplied by the Water Resources Unit of Mauritius (WRU 1997a, 1997b) were scanned and rectified in ArcGIS®. Maximum- and sill level[1] water spread was digitized. LN sill level is 242.02 m.a.s. according to WRU (1997b). PdM sill level was assumed to approximately correspond to the depth at the conduit (~427 m.a.s.). Probable accumulation bottoms were identified from reservoir morphology. Field observations supported the results (Segersten, personal observations). Accumulation bottoms that might become exposed to running water at sill level were categorized as “accumulation bottoms susceptible for river erosion” (figure 5.7).

4.6 Statistical analysis

Only profundal sediment characteristics in PdM and LN were assessed statistically (section 3.4). A *Pearsons correlation coefficient* analysis was carried out on sediment characteristics (Appendix B). Data was assumed to be normally distributed (individually and jointly) and relationships between parameters linear. Microcosm water MRP concentration was evaluated with *multiple linear regression analysis* (Appendix C) in Microsoft Excel add-in software Analyze-it® (Analyze-it software Ltd.). pH, O_2 concentration, time from sampling at the reservoir and time from disturbance (mixing, bubbling or time from sampling at the reservoir) were chosen as independent variables. Inter-parametric relationships were assumed to be linear. The number of samples/number of terms ratio was low but 4 independent variables (terms) were none the less included. The “time from sampling at the reservoir”- and “time from latest disturbance” variables can furthermore not be considered truly independent. This could affect the value of the correlation coefficient (R). (Draper & Smith 1998)

5 Results

5.1 Sediment characterization

Profundal sediment *tot-P concentration* was significantly higher in LN than in PdM (p_{tot-P} = 0.0075). *Organic content, tot-C* and *tot-S concentration* were on the other hand higher in PdM than in LN ($p_{org. cont.}$= 0.0009, p_{tot-C} = 0.0009 and p_{tot-S} = 0.0045). There was no significant difference in sediment *tot-N concentration* between the reservoirs. The differences in tot-P concentration and organic content are visualized in figures 5.1 and 5.2 respectively. Sediment *Ca-, Mn-* and *Mg concentrations* were higher in LN than in PdM while *Fe-* and *Al*

[1] The water level when the dam structure is completely open.

concentrations displayed the opposite trend ($p_{Ca} = 0.0012$, $p_{Mn} = 5E^{-6}$, $p_{Mg} = 0.00013$, $p_{Fe} = 0.0008$ and $p_{Al} = 0.0006$). Neither PdM nor LN could be considered calcareous, Al and Fe dominated the sediments in both reservoirs. A summary of the sediment characterization is presented in table 5

It was concluded from colour, consistency and organic content (< 50 % of DW) that profundal sediments in both reservoirs should be characterized as gjyttja sediments. Profundal sediment *water contents* (> 80 %) indicate successful sampling of accumulation bottom areas in both reservoirs. There were no significant differences in sediment water content and *bulk density* between the reservoirs. Sediments in wind shaded littoral areas had higher water contents, organic contents, nutrient and carbon- concentrations than sediments in wind exposed littoral areas in both reservoirs (table 5.1).

Table 5.1 Physical- and chemical sediment characteristics in Piton du Milieu Reservoir and La Nicoliere Reservoir. WE = wind exposed littoral, WS = wind shaded littoral, a = sample collected ~1 m below maximum water level, b = sample collected ~1 m below water level at the time of sampling, PdM = Piton du Milieu Reservoir, LN = La Nicoliere Reservoir. Sampling April – May 2008.

	Density (g/cm^3)	Water content (%)	Organic content (% of DW)	Tot-C (% of DW)	Tot-N (% of DW)	Tot-S (% of DW)	Tot-P (mg g^{-1} of DW)	Ca (% of DW)	Fe (% of DW)	Al (% of DW)	Mn (% of DW)	Mg (% of DW)
PdM Littoral WS	1.581	48.5	24.1	3.97	0.32	0.1	0.06					
PdM Littoral WE	1.748	38.5	12.0	2.98	0.22	0.08	0.06					
PdM Profundal	1.010 (± 0.002)	82.8 (± 1.1)	29.1 (± 0.1)	9.00 (± 0.10)	0.70 (± 0.01)	0.26 (± 0.02)	0.08 (± 0.00)	0.13 (± 0.00)	13.99 (± 0.11)	13.14 (± 0.19)	0.04 (± 0.00)	0.04 (± 0.00)
LN Littoral WS	a:1.396, b:1.248	b:53.0	a:22.1, b:18.0	a:6.75, b:4.21	a:0.61, b:0.40	a:0.13, b:0.07	a:0.29, b:0.14					
LN Littoral WE	a:1.700, b:1.504	b:40.0	a:12.6, b:12.6	a:1.17, b:0.92	a:0.14, b:0.12	a:0.03, b:0.04	a:0.11, b:0.08					
LN Profundal	1.093 (± 0.007)	81.1 (± 1.3)	21.6 (± 0.4)	7.03 (± 0.06)	0.71 (± 0.00)	0.10 (± 0.00)	0.24 (± 0.03)	0.28 (± 0.01)	10.49 (± 0.17)	8.98 (± 0.09)	0.12 (± 0.00)	0.25 (± 0.00)

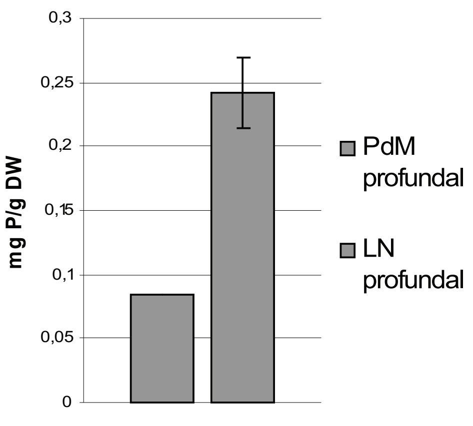

Figure 5.1 Tot-P concentration in profundal sediment samples from PdM and LN. Error bars are 2 σ. PdM = Piton du Milieu Reservoir, LN = La Nicoliere Reservoir. Sampling April – May 2008.

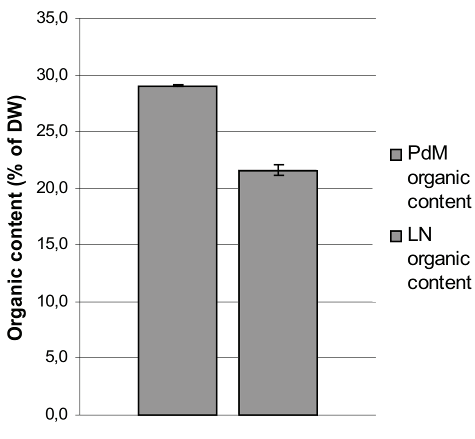

Figure 5.2 Organic content in profundal sediment samples from PdM and LN. Error bars are 2 σ. PdM = Piton du Milieu Reservoir, LN = La Nicoliere Reservoir. Sampling April – May 2008.

Pearsons correlation coefficient analysis (n = 4, two tailed analysis on 95 % significance level) showed that all analyzed profundal sediment parameters except PdM organic content correlated within the reservoirs (Appendix B). PdM organic did not correlate with any other sediment parameter. Sediment metal concentrations were excluded from the analysis.

The *BPN ratio* was low in PdM but very high in LN (table 5.2, section 3.4). *C/N ratio* (tot-C/tot-N) assessment indicates that allochtonous inputs are more important in PdM while LN displays higher autochthonous production (table 5.2). Profundal sediment *Fe/P ratio* (Acid extractable Fe concentration/tot-P concentration) was high in both reservoirs (table 5.2). Fe/P ratio and C/N ratio were significantly higher in PdM than in LN (n = 2, $p_{Fe/P} = 0.00004$, $p_{C/N} = 0.0004$, two tailed t-test analysis).

Table 5.2 Fe/P- and C/N ratio for profundal sediment samples from Piton du Milieu Reservoir and La Nicoliere Reservoir (n = 2). The BPN value is based both on littoral and profundal samples (n = 4). PdM = Piton du Milieu Reservoir, LN = La Nicoliere Reservoir. Sampling April – May 2008.

	Fe/P	C/N	BPN value
PdM	1670 (± 13)	12.8 (± 0.0)	0.3 (R^2 = 0.767)
LN	470 (± 8)	9.8 (± 0.1)	0.7 (R^2 = 0.980)

5.2 Test tube experiment

Oxygen decrease rate was higher in test tubes from LN than in test tubes from PdM. It took ~52 days for water in test tubes from PdM, and ~29 days for water in test tubes from LN to become completely free of oxygen (Figure 5.3).

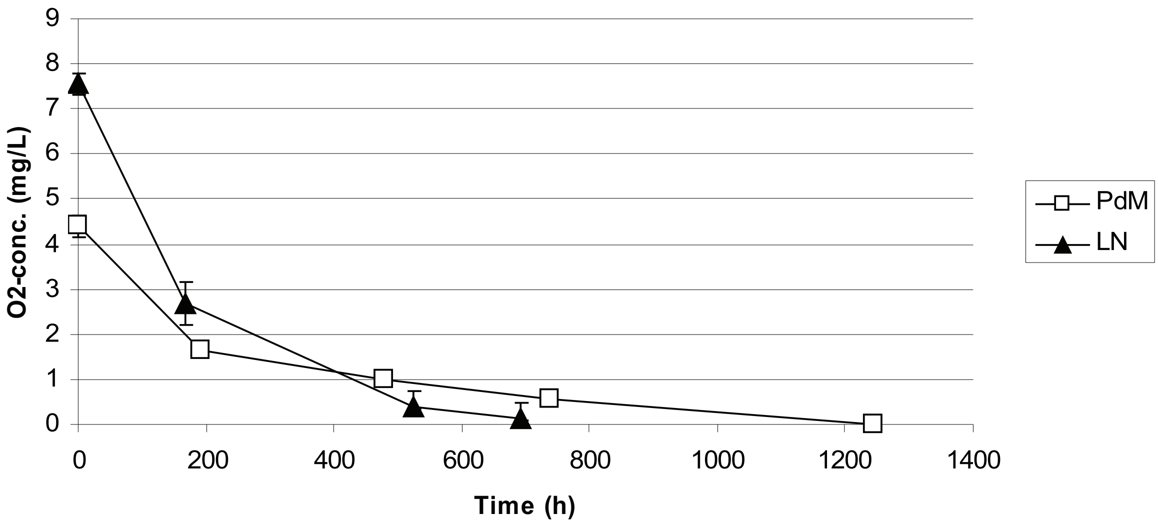

Figure 5.3 Decrease in O_2 concentration in the test tube experiment. Oxygen decrease was more rapid in test tubes from LN than in test tubes from PdM. PdM = Piton du Milieu Reservoir, LN = La Nicoliere Reservoir. Error bars are 2 σ. Sampling April – May 2008.

pH first decreased but began to increase after approximately one week in test tubes from both reservoirs (figure 5.4). pH increase was stable through the remainder of the experiment. LN test tubes had higher pH values than test tubes from PdM.

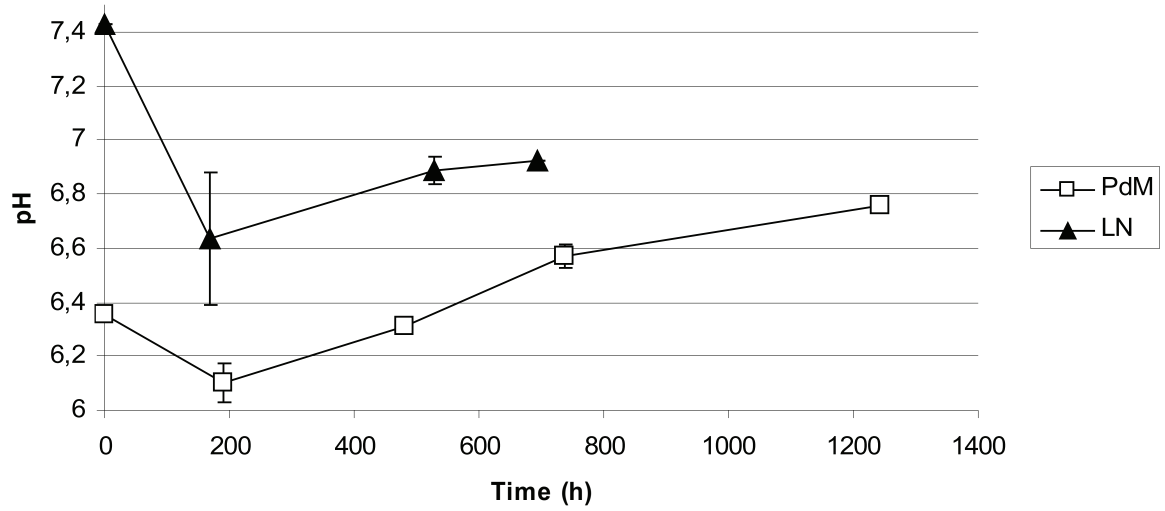

Figure 5.4 Trends in pH in the test tube experiment. There was an initial decrease followed by a gradual increase. PdM = Piton du Milieu Reservoir, LN = La Nicoliere Reservoir. Error bars are 2 σ. Sampling April – May 2008.

There were no significant differences in tube water MRP concentration between reference value (t_0, section 4.3) and the last sampling point (t_{end}). O_2 concentration was < 0.1 mg L^{-1} at t_{end} (figure 5.3). Notice the "hump" in figure 5.5 at the first measuring point (t_1) following complete sediment suspension (section 4.3). The difference in MRP concentration between t_0 and t_1 was significant in test tubes from both reservoirs (n = 2, p_{PdM} = 0,049 and p_{LN} = 0,006, two tailed t-test analysis).

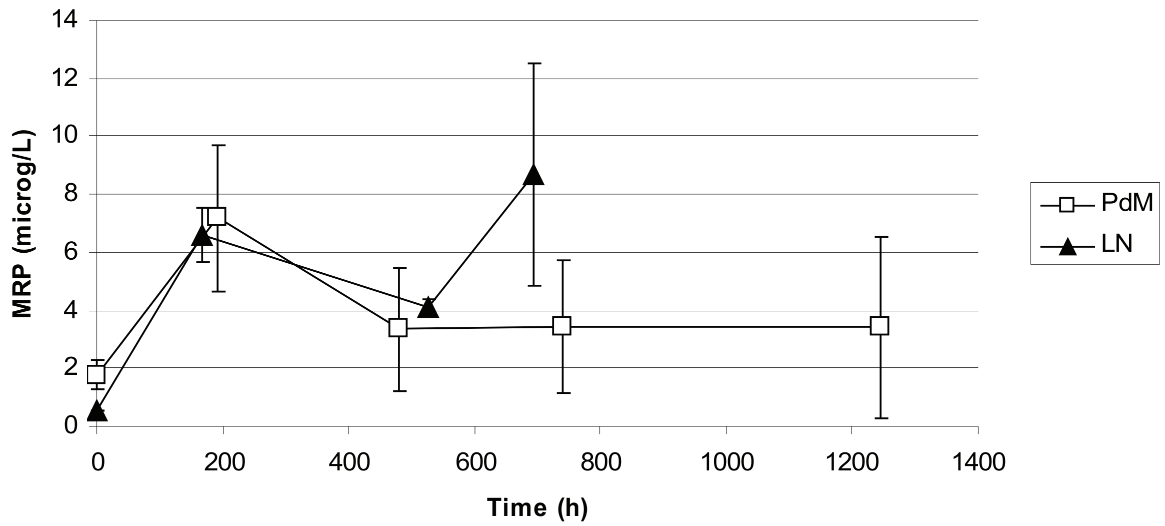

Figure 5.5 Change in MRP concentration in the test tube experiment. There was a significant difference between untreated hypolimnetic water (t_0) and the first measuring point (t_1, subsequent to complete sediment suspension) but not between t_0 and the last measuring point (anaerobic conditions) in test tubes from both reservoirs. PdM = Piton du Milieu Reservoir, LN = La Nicoliere Reservoir. Error bars are 2 σ. Sampling April – May 2008.

5.3 Microcosm experiment

The *multiple regression model* (n_{PdM} = 20, n_{LN} = 11) could account for 81 % of MRP concentration variability in microcosms from LN but only 13 % of MRP concentration variability in microcosms from PdM (Appendix C). Time from disturbance and time from sampling contributed significantly to the prediction of the dependant variable in LN microcosms (95 % confidence level, $p_{time\ fr.\ dist.} = 0.02$, $p_{time\ fr.\ sampl} = 0{,}04$).

5.4 GIS analysis

Flushing might affect PdM accumulation- and transport bottoms at reduced water levels, these could become subject to substantial river erosion (figure 5.6). The position of the inlets and the narrowness of the reservoir at sill level facilitate general movement of eroded and resuspended material towards the reservoir outlet (e.g. Brown 1943; White & Bettess 1984).

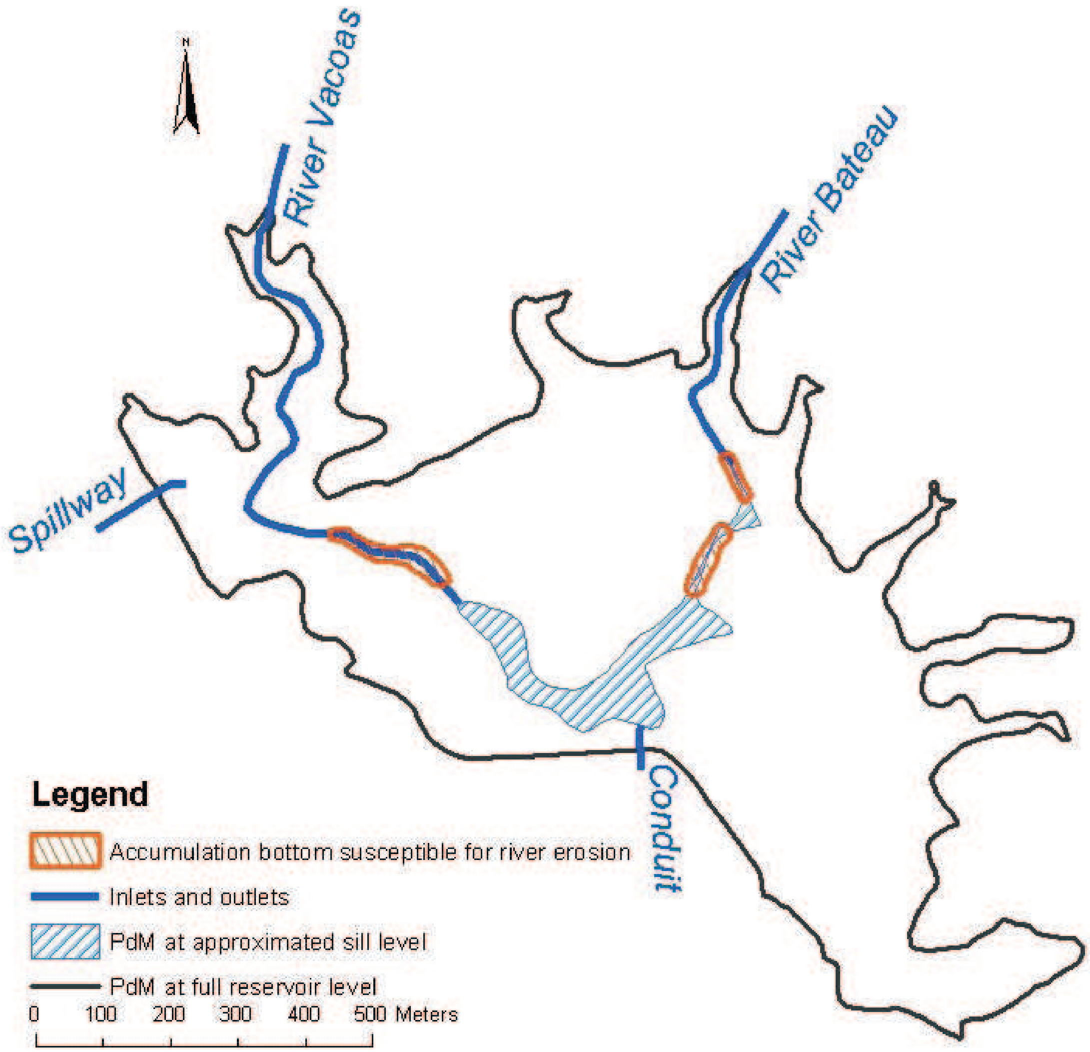

Figure 5.6 The route of inlet water through the PdM reservoir basin at sill level. Accumulation bottoms could become subject to river erosion and sediment flushing at reduced water levels. The River Vacoas and the River Bateau are the main inlets to the reservoir. PdM sill level was assumed to approximately correspond to reservoir depth at the conduit. PdM = Piton du Milieu Reservoir. Joel Segersten, Uppsala universitet 2009, digitized from depth chart data supplied by the Water Resources Unit of Mauritius (WRU 1997a).

LN accumulation bottoms are probably protected from flushing (figure 5.7). Deposition areas are not subject to river erosion at sill level and eroded/resuspended material is likely to settle within confinement of the reservoir basin (e.g. Brown 1943; White & Bettess 1984).

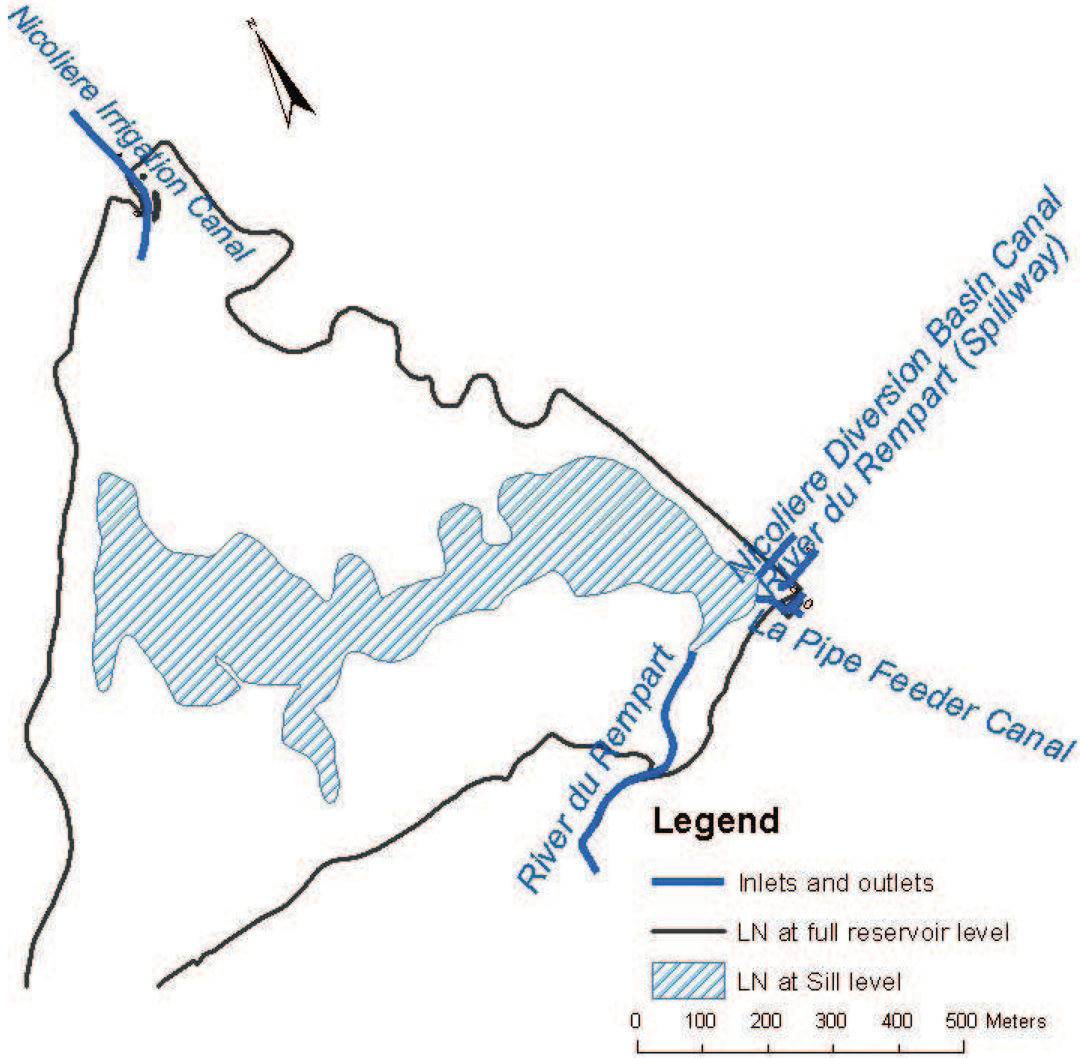

Figure 5.7 The route of inlet water through the LN reservoir basin at sill level. Accumulation bottoms in the reservoir are not exposed to river erosion at sill level. The River du Rempart and the La Pipe Feeder Canal are the main inlets to the reservoir. LN = La Nicoliere Reservoir. Joel Segersten, Uppsala universitet 2009, digitized from depth chart data supplied by the Water Resources Unit of Mauritius (WRU 1997b).

6 Discussion

The profundal sediment *tot-P concentration* was higher in LN than in PdM (tables 5.1 and figure 5.1) but the concentration could be considered low in both reservoirs. PdM and LN position themselves at the very lowest end of the spectrum compared to other tropical lakes/reservoirs (e.g. Engele & Sarnelle 1990; Thomaz et al. 2001; Jorcin & Nogueira 2005). The sediment tot-P concentration is basically a reflection of the sum of *external P loading* and *P export* (e.g. Talling 1992; Lal 1998). The level of external P loading is in turn determined by the catchment character (e.g. Lal 1998; Wetzel 2001). PdM and LN are in rather close proximity of each other. Both reservoirs have small, more or less mountainous, catchment areas dominated by volcanic rock and latosol soils (table 4.1). The bulk of investigated tropical lakes/reservoirs are on the other hand of continental floodplain origin and have large catchment areas. External P loading is typically somewhat related to catchment size (e.g. Cooke et al. 2005; Jorcin & Nogueira 2005). The small catchment areas of PdM and LN could subsequently help to explain the observed P poor conditions.

Another factor to consider is that the top 3.4 cm of superficial sediment was collected and analyzed instead of the standard top 1 cm, analyzed by e.g. Engele & Sarnelle (1990), Thomaz et al. (2001) and Jorcin & Nogueira (2005). The sediment nutrient content typically declines with increasing sediment depth (e.g. Håkansson & Jansson 1983). Higher tot-P concentrations would therefore probably have been attained had the standard top 1 cm been analyzed, the same applies to all sediment nutrient concentrations analyzed (e.g. Håkansson & Jansson 1983). Profundal sediment *tot-N concentration* was comparatively high (table 5.1) and profundal sediment *organic content* could be viewed as intermediate in both reservoirs (e.g. Håkansson 1983; Thomaz et al. 2001; Jorcin & Nogueira 2005).

The catchment of LN is dominated by tropical lowland forest and scrubland, agricultural activity is low. The catchment of PdM is on the other hand highly subject to modern agriculture (table 4.1). PdM is however secluded from direct contact with agricultural land by a buffer zone of natural forest growth. This zone is of variable width and thickness but strategic areas are rather well developed, e.g. the northern shore (Dumur 2005; Segersten personal observations, appendix D). Forest in the catchments of PdM and LN is of tropical lowland character, at least in the wet season (e.g. Berg 2005). Production in tropical lowland forest is typically P limited down to microbial level (e.g. Tanner et al. 1998; Cleveland et al. 2002). P might therefore be halted more effectively than the flow of other nutrients in woodland areas surrounding these reservoirs. This could perhaps explain the apparently small P loadings but relatively large C- and N loadings to the reservoirs (table 5.1, figures 5.1 and 5.2). Littoral N fixation in patches of rich epilittoral- and supralittoral growth established along the basin boundaries of both reservoirs (Segersten, personal observation) could also accentuate this pattern (e.g. Wetzel 2001; Nielsen et al. 2004).

Nutrients are predominantly exported/eroded from Mauritian sugarcane fields in particulate form during runoff events (Sharpley et al. 1996; Ng Kee Kwong et al. 2001). It has been suggested that the impact of runoff associated P on Mauritian freshwater ecosystems could be reduced by dilution (Ng Kee Kwong et al. 2001; Dumur 2005). Dilution should however not affect reservoir sediment nutrient accumulation unless outflow rates and water renewal times mediate significant sluicing of the nutrient load (Brandt 2000).

The catchment of PdM has relatively low slope angle (WRU 1997a). Export of runoff associated P from agricultural areas in the catchment could therefore be restricted. Soil P mobility is low in flat landscapes; also during runoff events (e.g. Quinton et. al 2001). The high profundal sediment organic content and *C/N ratio* in PdM (figure 5.2 and tables 5.1 and 5.3) indicate significant allochtonous inputs to the reservoir however (e.g.. Hansen 1961). This might be attributable to high DOC and POC import from partially degraded sugarcane leftovers in the catchment (Broberg, oral communication). The catchment of LN falls rather steeply towards the reservoir basin (1997b). Released inorganic nutrients and allochtonous organic material in the catchment may therefore display a high tendency towards being exported downstream/down slope (e.g. Auerswald & Schmidt 1986; Jäger 1994). LN and PdM are rather similar in terms of sediment organic content and C/N ratio but autochthonous production appears to be somewhat more important in LN (figure 5.2 and tables 5.1 and 5.3). Allochtonous material could also be of comparatively high quality in LN since short terrestrial residence times for organic material and nutrients translates into reduced terrestrial degradation and -nutrient absorption (e.g. Hansen 1961; Ravera & Parise 1978; Melillo et al. 1984). It can be assumed that external loading of organic- as well as inorganic P species is promoted by the step slope angel of the LN catchment. This could help to explain why sediment tot-P concentrations were higher in LN than in PdM (table 5.1 and figure 5.1). PdM accumulation bottoms might furthermore become subject to flushing in the dry season/wet season transition period (figure 5.6). Mauritian reservoirs are often low in water at this time and the first tropical front systems of the wet season can bring heavy rains and extreme water flows (WRU 1997a, 1997b; Berg 2004). Transport bottoms in PdM have become consolidated and hardened (WRU 1997a; Segersten personal observations). This is probably explained by repeated flushing and desiccation-inundation processes acting on the reservoir sediments since dam wall construction, over 50 years ago (e.g. WRU 1997a). The reservoir is not completely empty in figure 5.6. PdM sill level was however conservatively approximated and could easily be below 427 m.a.s. (section 4.5) susceptibility for flushing would in this case be increased (Brown 1943; Brandt 2000). LN is protected from substantial flushing by the proximity of outlets in relation to inlets, large surface area and reservoir width at sill level, etc. (figure 5.7).

The high agricultural development in the catchment of PdM made Dumur (2005) hypothesize that the reservoir should be more productive than LN. A 1 year water chemistry survey did however reveal the complete opposite result: LN appeared to be more productive than PdM. *BPN ratio* analysis supports the findings of Dumur (2005). The result confirms LN as being the more productive of the two reservoirs (table 5.2). Test tube experiment O_2 consumption rates also point in this direction (figure 5.3, e.g. Charlton 1980; Cross & Summerfelt 1987). The BPN ratio analysis is somewhat weakened by the lack of correlation between PdM sediment organic content and tot-N concentration (Appendix B). This inconsistency might be explained by some misconduct in the organic content analytical procedure. Qualitative assessment of the BPN numerical values according to Håkansson & Jansson (1983) is not attainable due to latitudinal differences manifested between temperate- and tropical systems (e.g. Salas & Martino 1991; Torres-Orozco et al. 1996).

External P loading to Mauritian reservoirs is likely higher in the wet season (when precipitation is high) than in the dry season (e.g. Morgan et al. 1998; Ng Kee Kwong et al. 2001). LN did none the less display higher water tot-P concentrations in the dry season (31.7 $\pm$ 9.9 $\mu g\ L^{-1}$) than in the wet season (23.4 $\pm$ 11.2 $\mu g\ L^{-1}$) in the water chemistry survey by Dumur (2005). The opposite trend was observed in PdM. This seems to suggest that "in reservoir" processes determine nutrient dynamics in LN while PdM nutrient dynamics could be more closely tied to external loading (Lewis 1996). *Resuspension* and/or wet season dilution coupled with dry season evapoconcentration could explain the observed pattern (e.g. Kalff 1983; Reddy et al. 1996; Ng Kee Kwong et al. 2001). Non-algal turbidity is negatively correlated to water residence time and typically decreases as you move along the length axis of an artificial reservoir (e.g. Cooke et al. 2005). Water turbidity was however higher in the LN main basin than in the reservoir inlets in the water chemistry survey by Dumur (2005). This can only be explained by high resuspension and/or shoreline erosion, or possibly also by high reservoir algal turbidity.

LN is located on the eastern side of Mauritius. There is virtually no wind protection to the east/south-east so wind exposure is extremely high (e.g. Berg 2004; Dumur 2005). Thermal stability was surveyed in 2003-2004 without any signs of thermal stratification (Dumur 2005). LN is ~ 10 m deep at full water capacity but < 3 m deep at sill level (WRU 1997b). The remaining water body is perfectly aligned with prevailing winds and reservoir fetch is substantial also at reduced water levels (figure 5.7). Accumulation bottoms in the reservoir are loosely arranged down to significant sediment depths (section 4.2) and the top ~3.4 cm sediment layer had a water content > 80 % (table 5.1). Water column nutrient loading can be completely dominated by resuspension in shallow wind exposed lakes/reservoirs (e.g. Newman & Reddy 1992; Reddy et al. 1996). This might be especially pronounced in low latitude water bodies (e.g. Lewis 1987; Kilham & Kilham 1990; Sampaio et al. 2002) especially since the utilization of particulate nutrients is so rapid within the water column (e.g. Engele & Sarnelle 1990; Shafer & Armstrong 1994). Water column productivity could probably be supported by resuspension also when sediment nutrient concentrations are very low (Nogueira et al. 2002a; Jorcin & Nogueira 2005; Santos et al. 2004). Resuspension of profundal LN sediment appears to cause an increase in water column MRP concentration: (I) There was a significant difference in water MRP concentration between the first (t_0) and the second (t_1) measuring point in the test tube experiment (figure 5.5, e.g. Jensen et al. 1992). (II) “Time from disturbance” and “time from sampling” displayed co-variability with water MRP concentration in the microcosm experiment (sections 4.3 and 5.3, Appendix C). The limited number of observations, possible interdependence between independent variables (section 4.6) and far from optimal experimental setup weakens the latter analysis. In vitro studies should furthermore only be related to the natural ecosystem and with great care and restriction (Kleeberg & Kozerski 1997). The western shore of LN appears highly subject to erosion: a bottom structure of large rocks and consolidated hardened clay prevailed down to at least 4 m depth (Segersten, personal observation). Sediment tot-C concentration and water content was low at the sampling location indicating erosion bottom status (figure 4.7 and table 5.1, e.g. Håkansson 1977). Shoreline erosion does not prove accumulation bottom resuspension in LN but it signals the high transference of wind energy into water movement in the reservoir. Wave erosivity can clearly be substantial also at reduced water levels. Eroded/resuspended material is likely to settle within confinement of the LN reservoir basin (figure 5.7, e.g. White & Bettess 1984). Nutrients may therefore become resuspended and biologically utilized over and over again and the ratio: production / unit nutrients that enter the water body could be very high. The eutrophic status of LN is probably explained by rapid and effective internal nutrient cycling supported by high resuspension.

PdM is a deeper reservoir than LN (table 4.1), it is well shaded from wind and has a limited lake fetch at reduced water levels (figure 5.6). Thermal stratification has been observed in the wet season (Dumur 2005). Resuspension is unlikely to have a substantial impact on PdM accumulation bottoms. The catchment of the reservoir receives more rain than the catchment of LN (table 4.1). Rain erosivity is subsequently higher in the catchment of PdM than in the catchment of LN. PdM nutrient dynamics could be closely linked to external nutrient loading but this has not been statistically evaluated (e.g. Morgan et al. 1998; Dumur 2005). Inefficient internal nutrient cycling and factors restricting external loading (the presence of a buffer zone, low catchment slope angel, see previous sections) might explain the oligotrophic status of the reservoir (Jordan & Escalante 1980; Kilham & Kilham 1990; Tafangenyasha & Dube 2008).

Sediment Fe/P ratios were extraordinary high in both reservoirs (table 5.2) even though acid dissolvable Fe/tot-P was calculated instead of the standard tot-Fe/tot-P ratio (e.g. Jensen et al. 1992; Cooke et al. 1993). Prolonged periods of high thermal stability are unlikely in LN but signs of thermal stratification have been observed in PdM (e.g. Lewis 1987; Dumur 2005). Anoxic conditions did not induce increased water MRP concentrations in test tubes from any of the reservoirs in the test tube experiment however (figure 5.5) nor did O_2 concentration display any co-variability with MRP concentration in the microcosm experiment for any of the reservoirs (section 5.3). Furthermore it took almost two months for PdM test tubes to become completely oxygen depleted, the time was about one month for LN test tubes (figure 5.3). P release can be somewhat related to sediment tot-P concentration under anoxic conditions (Nürnberg 1988). Tot-P concentrations were very low in the sediments of both reservoirs (table 5.1 figure 5.1). P release through chemical release mechanisms are probably of limited importance in PdM and LN. The affinity for inorganic P is high in the sediments and *internal loading* through the Einsele-Mortimer model appears insignificant (Håkansson & Jansson 1983; Schindler et al. 1977).

Decomposition and respiratory processes produce acidic CO_2 (aq), a decrease in hypolimnion *pH* is therefore typically concomitant to lake/reservoir stratification (e.g. González et al. 2004). A gradual decrease in pH was expected in the test tube experiment (figure 5.4). It is unclear why pH started to increase after ~1 week but a variety of H^+ consuming or OH^-

producing redox reactions could explain the observed pattern, including sulphate reduction of ferric iron (Caraco et al. 1993; Broberg, oral communication). Neither PdM nor LN can be characterised as calcareous (Jones & Browser 1978; Håkansson & Jansson 1983). Both reservoirs have sediments dominated by Fe and Al indicating acidic rock catchments (table 5.1). Co-variability was not observed between pH and MRP concentration in the microcosm experiment (section 5.3). Hence pH is probably not affecting nutrient dynamics in PdM and LN (e.g. Andersen 1975a; Håkansson & Jansson 1983).

6.1 Final thoughts

Water turbidity (Dumur 2005; Segersten, personal observations) and depth at the sampling locations (figures 4.1, 4.2 and 4.3) indicate that true profundal bottoms had been sampled in both reservoirs. Sediment water content analysis suggests these bottoms should be characterized as deposition bottoms (table 5.1) especially since the top ~3.4 cm sediment layer was analyzed (Håkansson & Jansson 1983). Transport bottom status would however be inferred if flushing (PdM) or resuspension (LN) has disturbed natural sediment accumulation. PdM water- and organic contents suggest no recent flushing (table 5.1). The top ~3.4 profundal sediment layer in the reservoir has probably accumulated continuously and should be viewed as a section of true deposition bottom (Håkansson & Jansson 1983). In LN however, resuspension might have affected physical- and chemical characteristics of profundal sediments (e.g. Watts 2000a). It is questionable if sampled profundal bottoms in the reservoir can be characterized as true depositions bottoms, this could affect the comparative relevance of some of the results (Håkansson 1977; Håkansson 1981). The evaluation of a larger data set collected from many different sampling locations in the reservoir would have strengthened the sediment characterization of LN (Cooke et al. 2005).

Sediment bulk density, organic-, C-, and water content are physically related and typically correlate (Håkansson & Jansson 1983). The result of the Pearson correlation coefficient analysis indicates that most sediment analyzes had been successfully performed and that the main mechanism of nutrient accumulation to PdM- and LN sediments was sedimentation of organic matter (Appendix B).

The multiple regression model could only explain 13 % of MRP variability in PdM microcosms (Appendix D). Microcosm MRP release patterns might have been affected by some unidentified variable that was left out of the model or maybe was the experimental setup too erroneous for (potentially minute) trends to be observed (section 4.3). More replicate measurements and an optimized experimental setup would have resulted in a higher adjusted R value for the analysis (Draper & Smith 1998). The multiple regression model could satisfactory account for MRP dynamics in LN microcosms however, 81 % of MRP variability was explained by the model (Appendix D).

Production is typically N limited in temperate forests while tropical lowland forests display P limitation in general (e.g. Tanner et al. 1998; Cleveland et al. 2002). Inorganic nutrients are conveyed from the ground litter into the standing stock of trees and plants outstandingly quickly and effectively in tropical forests. Although weathering of P is efficient at high temperatures (Lewis 1996) natural latosol soils typically display low leaching rates (Jordan & Escalante 1980; Jordan & Herrera 1981). Buffer zones could therefore be particularly effective in reducing external P loading to tropical lowland water bodies. This could be a realtively cheap, robust and effective conservation strategy for P limited systems that would ensure both water quality and biological diversity.

It has been suggested that internal nutrient release processes influence lake/reservoir nutrient dynamics more in tropical than in temperate- or boreal systems, attributable to rapid internal nutrient regeneration rates and dynamic thermal regimes (e.g. Kilham & Kilham 1990; Sampaio et al. 2002). These processes might however look very different from classical models of internal nutrient release (e.g. the classical model of internal loading, resuspension etc.) that have been built largely on studies of temperate systems (e.g. Lewis 1987; Roldán 1992; Cooke et al. 2005). Deep water temperatures are often high in tropical water bodies (Landsberg 1961; Lewis 1987) sediment nutrient dissolution equlibria may therefore display comparatively high K_s values (e.g. Perkins & Underwood 2001). Heterotrophic microbial activity is also increased at high temperatures (e.g. Lewis 1987). This may not only increase nutrient mobilization *per se* (Marsden 1989) but could also favour the development of anoxic micro zones and locally enhanced P release through the Einsele-Mortimer model (e.g. Gomez et al. 1999). Released nutrients are rapidly conveyed to the phototrophic zone and stay longer in the water column (e.g. Lewis 1996; Kleeberg 2002). Low sediment nutrient concentrations and the absence of distinct events of internal nutrient loading may therefore not necessarily infer that sediment nutrient release processes are not important in the tropical lake/reservoir. Chemical- and physical release mechanisms could instead cause a more or less continuous reflux of nutrients that would be difficult to detect, especially if assuming a temperate perspective. The internal nutrient dynamics of tropical systems is still not well characterized and understood. As pointed out by Lewis (1996) this is an area of research that should receive more attention in the future.

6.2 Conclusions

The sediments in PdM and LN are low in P in comparison with other tropical systems but rather high in N and organic content. BPN assessment confirms the finding of Dumur (2005) that LN is more productive than PdM, even though the latter has a catchment dominated by agricultural land. External loading to PdM is probably reduced by the presence of a well developed buffer zone and by low catchment slope angle. LN is very susceptible for resuspension and resuspended material is likely to settle within confinement of the reservoir basin. Internal nutrient cycling could therefore be very efficient in the reservoir and this might explain the reservoirs eutrophic status. P release through the Einsele-Mortimer model of internal loading could not be observed in any of the reservoirs.

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7 References

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Appendix A

The sediment sampler was built from three high pressure PVC tubes (~3 meters in length) on witch PVC joints and -fittings were glued. The tube sections could be screwed together forming a water tight ~9 meter composite tube. A plexiglas Willner core (inner diameter = 64 mm, length ≈ 40 cm) could be fitted to the bottom PVC section with a watertight seal (figure A1). Each tube section could be closed by a valve at the connection joint (figure A2). The composite tube could subsequently be closed at 3-, 6- and 9 meters. One or two sections could also be assembled and used separately. A rope was fitted to the lower end of the bottom PVC section and a floating device (a sleeping mat in closed-cell plastic) could be strapped to the uppermost tube (figure A3). The length of the sampler was marked from the tip of an attached Willner core and upwards. Sampling depth could hence be recorded.

Operation: A suitable number of sections were assembled on shore and the floating device strapped on. The sampler was towed behind the boat to the sampling location where a Willner core could be fitted to the connection module. By opening all valves water is allowed into the sampler and the lower end of the sampler starts to sink. The operator can control descent and "feel" when the bottom is reached with the rope. When the sampler has reached the bottom it is lifted and held vertically before it is pushed into the sediment. When sediment penetration to requested depth has been achieved the valve at the top of the sampler is closed. This relieves 1 atm of pressure and produces the "sucking power" needed. The top end of the sampler is now dropped into the water and allowed to float freely. The sediment core is retrieved by pulling the rope of the sampler and is eventually presented at the side of the boat. A "Willner cork" can now be pushed in and the Willner core detached from the sampler and brought into the boat. The superficial sediment strata was pushed to the top of the Willner core with a metal stand that fit the piston of the Willner cork (manufactured at the metal work shop of the University of Mauritius).

Maximum sampling depth was approximately 9.5 meters, any depth shallower than this was accessible for sampling. Depths < 6.5 meters were sampled with ease but greater depths were rather difficult to reach. The flexibility of the PVC tubes made the sampler difficult to operate when all three sections had to be used. Collected cores might have been disturbed by being held at an almost horizontal position at the end of the sampling procedure.

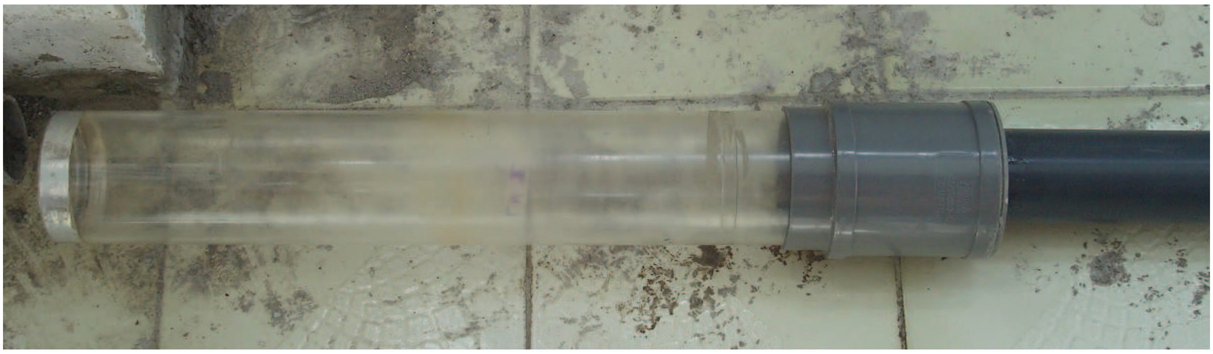

Figure A1 A Willner core attached to the connection module. The connection module was manufactured from a PVC reduction step and a number of other PVC fittings. Joel Segersten, Uppsala University 2008.

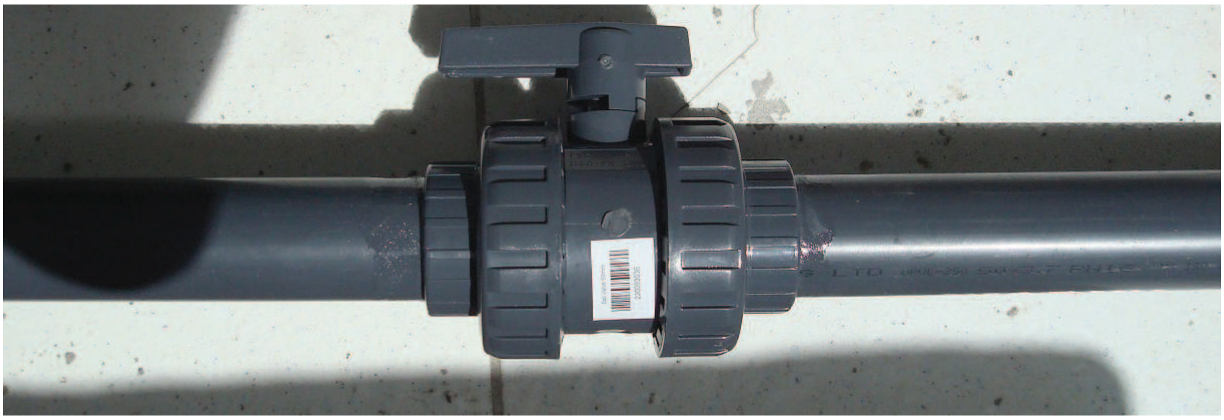

Figure A2. The joint between two PVC tube sections, notice the leaver of the valve on top. Joel Segersten, Uppsala University 2008.

Figure A3 The three sections of the dissembled sediment sampler. Each section measures ~3 meters, the module for Willner core attachment is visible in the lower right corner and the metal ring for fitting the rope can be seen just above the connection module. The floating device is visible to the left. Joel Segersten, Uppsala University 2008.

Appendix B

Table B The result of the Pearsons correlation coefficient analysis. Figures in bold indicate statistically significant correlation ($p_{crit.}$ 0.950). Sampling April – May 2008.

Piton du Milieu Reservoir	Bulk density	Water content	Organic content	Tot-C	Tot-N	Tot-S	Tot-P
Bulk density							
Water content	**0.993**						
Organic content	0.826	0.887					
Tot-C	**0.998**	**1.000**	0.861				
Tot-N	**0.995**	**0.998**	0.876	**0.999**			
Tot-S	**0.993**	**0.991**	0.833	**0.989**	**0.988**		
Tot-P	**0.996**	**0.998**	0.871	**1.000**	**1.000**	**0.987**	
La Nicoliere Reservoir							
Bulk density							
Water content	**0.983**						
Organic content	**0.992**	**0.956**					
Tot-C	**0.999**	**0.975**	**0.997**				
Tot-N	**1.000**	**0.987**	**0.99**	**0.998**			
Tot-S	**0.997**	**0.971**	**0.998**	**0.999**	**0.996**		
Tot-P	**0.971**	**0.972**	**0.966**	**0.971**	**0.976**	**0.979**	

Appendix C

Table C The result of the multiple linear regression analysis. Effects of pH, O_2 concentration, time from sampling and time from latest disturbance on MRP release were analyzed. Bold figures indicate statistically significant contribution to the prediction of the dependent variable ($n_{PdM} = 20$, $n_{LN} = 11$). Sampling April – May 2008.

	R^2	Adjusted R^2	Term	p-value
Piton du Milieu Reservoir	0.31	0.13	Intercept	0.47
			pH	0.33
			Time from disturbance	0.92
			O_2	0.17
			Time from sampling	0.29
La Nicoliere Reservoir	0.89	0.81	Intercept	0.27
			pH	0.20
			Time from disturbance	**0.02**
			O_2	0.28
			Time from sampling	**0.04**

Appendix D

Figure D The northern shore of PdM. Epilittoral- and supralittoral zones were well developed and natural forest growth is dense. Joel Segersten, Uppsala universitet 2008.