Phosphorus dynamics in coastal and inland lakes and reservoirs of British Columbia with special reference to water level fluctuation and climate variability

by

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Abstract

Conceptual models of lake epilimnetic phosphorus (P) cycling predict that, as total phosphorus (TP) concentration increases, the size of the various P pools and the movement of P within size fractions of the plankton community should change. It has bee further predicted that lakes with low TP should cycle P more efficiently (turn over at a higher rate) that lakes with high TP. These predictions were empirically tested in a set of lakes in British Columbia, Canada that ranged in TP. I further examined the relative importance of various P fluxes (plankton regeneration, zooplankton grazing and sedimentation) in lakes of varying P content. In general, I found limited support for the predictions of conceptual models and results indicate that further empirical examination of conceptual paradigms of P cycling in lakes is required. I also examined the impact of seasonal water level fluctuations on the physical and nutrient dynamics of an oligotrophic drinking water reservoir. I compared seasonal timing of stratification, and heat and nutrient fluxes to a nearby similar natural lake. Reservoir drawdown caused the timing and duration of stratification and thermal characteristics between the reservoir and the natural lake to differ. Further, seasonal trends in nutrient concentration and plankton nutrient deficiency were affected by reservoir drawdown. However, the magnitude of these impacts were less than those observed in more eutrophic reservoirs.

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Chapter 1: Introduction

The importance of phosphorus in lake ecosystems

Phosphorus (P) is a critically important element present in aquatic organisms (0.2-2% phytoplankton dry weight) required for a multitude of biological functions (Kalff 2002). At the ecosystem level, P concentration in lakes affects the biomass (Dillon and Rigler 1974; McCauley et al. 1988; Mazumder 1994a), productivity (Smith 1979) and composition (Watson et al. 1997) of plankton communities. Because of its central role in determining the biomass, abundance and composition of plankton communities, P has been a major focus of limnological research for decades, and has received relatively more research attention than other nutrients, such as nitrogen (N), silica (Si) and carbon (C). Ecologists and limnologists have also emphasized the importance of P in lakes because of research indicating P loading as a major factor causing lake eutrophication (Schindler 1977).

Because of the role of P in lake food webs and its critical position in eutrophication, a large number of studies since the 1970s have examined P cycling in whole lakes (Levine et al. 1986; Taylor and Lean 1991), lake enclosures (Mazumder et al. 1992) and in plankton cultures (Lean and Nalewajko 1976). These studies, and others, have revealed general models of P dynamics in lake ecosystems and have highlighted potential mechanisms regulating the flow of P through aquatic food webs. Based upon this large body of literature, ecologists have proposed that since P is often the limiting nutrient in aquatic food webs, the cycling of P should therefore be affected by the overall concentration of P. That is, as total P (TP) concentration increases, the relative importance of the various flux pathways in lakes should change predictably. Numerous ecologists have proposed conceptual models that predict trends in P cycling along a TP gradient (Reynolds 1984; Harris 1986; Capblancq 1990; Harris 1994). Ecologists have taken these predictions further and proposed that, as TP increases in lake ecosystems, P cycling should be cycled less "efficiently" (Harris 1986; Capblancq 1990; but see Baines and Pace 1994; Hudson et al. 1999). This is thought to be the case because at high TP concentrations, P is supplied to plankton in excess of demand, causing the plankton community to be less conservative in its P retention.

Placing the difficulties with defining the exact meaning of P cycling "efficiency" aside, very few studies have empirically assessed these predictions. A large part of the reason why there is a lack of studies which have empirically assessed these conceptual models has been a lack of effective and reliable methods for measuring parameters that are critically important for understanding P cycling, such as the concentration of dissolved inorganic phosphate (PO_4^{3-}) and the regeneration of P from plankton communities. Until recently, methods used for assessing these parameters had significant shortcomings, but the generation of newer methods (Karl and Tien 1992; Hudson and Taylor 1996; Hudson et al. 2000) have provided ecologists with the opportunity to assess conceptual models of P cycling along TP gradients.

In Chapter 2, I empirically assess three major predictions of the conceptual models of Harris (1986) and Capblancq (1990) of P cycling along a TP gradient. I examine patterns and trends in planktonic P uptake and regeneration in a set of British Columbia lakes that vary in TP concentration. Using recently published methods (Hudson and Taylor 1996), I examine the size-fractionated uptake and regeneration of plankton communities in these lakes. I also use a newly developed method for measuring PO_4^{3-} (Hudson et al. 2000) to examine PO_4^{3-} concentrations along the TP gradient. Further, I examine the turnover rate of the PO_4^{3-}, TP, and particulate P (PP) pools in this set of lakes to assess the hypothesis of declining cycling efficiency with increasing TP concentration.

In Chapter 3, I again examine the predictions of Reynolds (1984), Harris (1986) and Capblancq (1990) in a set of five coastal British Columbia basins of varying TP and productivity. I examine seasonal trends in PO_4^{3-} turnover, planktonic P regeneration, zooplankton grazing and P sedimentation over a 2 ½ -year period in the five basins. I also examine the prediction that as TP concentration increases, plankton communities will rely less upon internally recycled P sources and will rely more upon P from sources external to the epilimnion. I further assess the hypothesis that P losses from lake epilimnia through sedimentation will increase in importance as epilimnetic TP increases.

Together, Chapters 2 and 3 assess numerous hypotheses proposed by long-standing conceptual models of nutrient cycling that have been published in books (Reynolds 1984; Harris 1986) or as review papers (Capblancq 1990; Harris 1994). Hopefully, these chapters further our understanding of P cycling in lake ecosystems and provide a basis for future research of lake P cycling. In addition, Chapters 2 and 3 utilize and examine newer methods of measuring parameters that are important in our study of lake P dynamics.

Reservoir Ecosystems and the Importance of Drawdown

The impoundment of rivers, streams, lakes and ponds in order to form reservoirs is a common practice on the global scale and has been performed since 400 – 300 B.C. (Thornton et al. 1990). Most reservoirs in North America are relatively young, limnologically speaking (<60 years old), and serve a multitude of purposes (hydropower, drinking water, agricultural use, flood control, multipurpose). Despite their abundance in the landscape of many ecoregions, reservoirs have received relatively little attention from limnological researchers when compared to naturally formed lakes (Thornton 1990; Straškraba et al. 1993). The bias toward natural lakes in the limnological literature has led to a limited understanding of reservoir ecosystems and the factors that are important to their ecology. Due to the lack of interest in reservoirs and the abundance of natural lake studies, limnologists and ecologists have long assumed that reservoirs were identical to natural lakes (Hutchinson (1957) classified reservoirs as lake type 73) and that the relative importance of processes such as primary production, redox reactions, prey-predator interactions and internal mixing were the same between natural lakes and reservoirs (Thornton 1990). Obviously, the previously mentioned processes occur in reservoirs and are important to reservoir ecology, however, other processes are present in reservoirs that fundamentally impact their ecology and therefore make them distinct from natural lakes. In particular, dynamic hydrological movements of reservoirs can profoundly affect their ecology (Ford 1990; Straškraba et al. 1993).

Reservoirs are more hydrodynamically variable than natural lakes, and these large-scale water movements are closely tied to their ecology. The scale and magnitude of water movements are dependent upon the function of an individual reservoir. The relatively large water level fluctuations associated with water inflows and outflows are a characteristic that distinguishes reservoirs from natural lakes (Ryder 1978; Straškraba et al. 1993). Often in reservoirs, the movement of substantial volumes of water into and out of the reservoir at specific times of the year cause seasonally predictable water level fluctuations to occur. The effect of these relatively large annual water level fluctuations (referred to drawdown and recharge) have received some research attention (Barone et al. 1993; Effler and Bader 1998; Nowlin et al. 2003), but the phenomenon has been largely ignored by limnologists. Therefore, further study is obviously required to understand the ecological and water quality impacts of this common feature of reservoir ecosystems.

Chapter 4 examines the impacts of seasonal water level fluctuations (drawdown and recharge) on the physical limnology of an ultra-oligotrophic drinking water reservoir located on Vancouver Island during 2000 - 2001. Sooke Lake Reservoir supplies drinking water for the city of Victoria and annually experiences substantial drawdown during the summer and early fall. I compared the seasonal timing of thermal stratification and summer heat budgets of Sooke Lake Reservoir to nearby similar Shawnigan Lake. This comparison was performed in order to assess the impacts of summer drawdown on the stratification and thermal regimes of Sooke Lake Reservoir. The contrast of Sooke Lake Reservoir and Shawnigan Lake also allowed for the general comparison of reservoir and natural lake seasonal stratification and thermal regimes. In the second year of the study (2001), a 100-year drought prevented the reservoir from fully recharging prior to the summer 2001 drawdown period. Consequently, the drought allowed me to assess the sensitivity of an anthropogenically-manipulated reservoir and a relatively undisturbed natural lake to short-term climate variation.

In Chapter 5, I again examine the response of Sooke Lake Reservoir to summer drawdown over the 2 ½ year period. I determine the effect of summer drawdown on temporal trends of nutrient concentrations and phytoplankton biomass (chlorophyll *a*; Chl*a*). I also examine the impact of drawdown on seasonal trends of plankton community P-deficiency, measured as PO_4^{3-} turnover time. Similar to Chapter 4, I assess the impact of the 100-year drought in 2001 on nutrient concentrations, phytoplankton biomass and PO_4^{3-} turnover time. I also examine the seasonal fluxes of P into and out of Sooke Lake Reservoir through major water flows (drinking water outflow, dam spillway) and sedimentation. Within-epilimnion P fluxes were also examined (plankton regeneration and zooplankton grazing) to compare P fluxes within, into and out of the epilimnion of Sooke Lake Reservoir during the various seasonal phases of drawdown and recharge. For reference purposes, I also measured the same parameters in Shawnigan Lake over the same time period using the same sampling intervals.

Taken together, Chapters 4 and 5 provide a unique 2 ½ year study of an oligotrophic reservoir with fluctuating water levels. The two chapters examine the physical, nutrient and plankton impacts of drawdown on an oligotrophic drinking water reservoir. Further, these chapters provide insight into the potential water quality problems associated with the drawdown of oligotrophic reservoirs during the summer. Previous work examining drawdown in eutrophic reservoirs have concluded that there is a substantial water quality “cost” for reservoir operation (Effler and Bader 1998) and I assess whether an ultra-oligotrophic system is subject to the same “costs”.

Research Objectives

The objectives of this research are focused in two main directions. In the first portion of my dissertation, I wished to assess conceptual models of P cycling in the literature (Reynolds 1984; Harris 1986; Capblancq 1990; Harris 1994) using newer analytical methods. The objectives were to examine the plankton size-fractioned uptake and regeneration of P across a set of lakes that represent a range in TP. In this portion of my dissertation, I also wished to assess concepts of nutrient cycling efficiency in lakes of varying nutrient concentration. The second overall research objective in the latter portion of this dissertation was to determine the effects of summer reservoir drawdown on an ultra-oligotrophic drinking water reservoir. I wished to assess the effects of summer drawdown on stratification and thermal regimes of the reservoir, and further relate these impacts to the nutrient and plankton dynamics of the reservoir.

Chapters accepted, submitted and to be submitted to journals

Chapters 2, 3, 4 and 5 in this dissertation are written as individual manuscripts. It is my intention to submit each of these chapters to peer-reviewed journals for publication. Chapter 2 has been submitted and Chapter 4 is in press and should be published before the end of 2003. The manuscript titles, order of authorship and the journal the manuscript has been submitted to, yet to be submitted to, or accepted in is given below.

Chapter 2: Planktonic phosphorus pool sizes and cycling efficiency in lakes of varying phosphorus content: empirical examination of conceptual models. W.H. Nowlin, J.M. Davies, A. Mazumder. *In review* – Limnology and Oceanography.

Chapter 3: Relative importance of planktonic regeneration, zooplankton grazing and sedimentation in seasonal phosphorus dynamics of coastal British Columbia lakes. W.H. Nowlin, J.M. Davies, A. Mazumder. *To be submitted* – Journal of Plankton Research.

Chapter 4: Effects of water level fluctuation and short-term climate variation on thermal and stratification regimes of a British Columbia reservoir and lake. W.H. Nowlin, J.M. Davies, R.N. Nordin, A. Mazumder. *In press* – Lake and Reservoir Mangement.

Chapter 5: Effects of seasonal water level fluctuation on phosphorus cycling in an oligotrophic British Columbia drinking water reservoir. W.H. Nowlin, J.M. Davies, R.N. Nordin, A. Mazumder. *To be submitted* – Hydrobiologia or Lake and Reservoir Management.

During my dissertation research, I also collaborated with Marsha Spafard, John-Mark Davies and Asit Mazumder to produce a brief morphometric atlas of selected lakes in British Columbia. The lakes in the atlas served as the main study lakes of my dissertation, and the morphometric analyses that were performed as a part of that research were placed into the atlas. Hopefully, the atlas will be used by future students in the Drinking Water Ecology program at the University of Victoria and any interested parties that need morphometric information on lakes in the Kooteney region, Vancouver Island and Saltspring Island. Copies of the atlas are present in the University of Victoria and the University of British Columbia Libraries. It is also present at the National Library of Canada. The citation for the atlas is as follows

Spafard, M.A., W.H. Nowlin, J-M. Davies, A. Mazumder. 2002. A morphometric atlas of selected lakes in southern British Columbia: Vancouver Island, Saltspring Island, and the Kooteney region. University of Victoria, Industrial Research Chair Program, Environmental Management of Drinking Water, Victoria. http://gateway.uvic.ca

Chapter 2: Planktonic phosphorus pool sizes and cycling efficiency in lakes of varying phosphorus content: empirical examination of conceptual models

Introduction

The role of phosphorus (P) in lake ecosystems has received intensive study from limnologists and ecologists over the last 30+ years. Phosphorus has received much of this attention because it often limits the biomass and productivity of lake plankton communities (Dillon and Rigler 1974; Smith 1979; Mazumder 1994a) and excessive P inputs to lakes has been implicated as a major cause of eutrophication (e.g., Schindler 1977). The importance of P to freshwater plankton communities has led to the detailed examination of P cycling of individual lakes (Levine et al. 1986; Taylor and Lean 1991) and comparison of P fluxes in systems of contrasting productivity and plankton community structure (Mazumder et al. 1992). These studies and many others have identified factors controlling the structure and function of planktonic food webs and have provided valuable insight into nutrient cycling in general.

While the number of studies examining lake P cycling is extensive, limnologists have yet to resolve several fundamental issues related to P cycling (Tarapchak and Nalewajko 1986; Taylor and Lean 1991). A major challenge confronting limnologists is the lack of accurate methods for measuring the concentration of dissolved inorganic phosphorus (PO_4^{3-}) in lakes, especially lakes that are severely P-limited. The need for accurate PO_4^{3-} measurements is critical because PO_4^{3-} is considered the form of dissolved P most readily taken up by plankton. Limnologists have known for decades that traditional colorimetric methods used to measure PO_4^{3-} (soluble reactive phosphorus or

SRP) overestimate concentrations by orders of magnitude (Rigler 1964; Hudson et al. 2000) and even more sensitive methods, such the Rigler bioassay or column chromatography, may still greatly overestimate PO_4^{3-} concentrations (Taylor and Lean 1991; Hudson et al. 2000). The recently developed steady-state bioassay of Hudson et al. (2000) and the magnesium-induced co-precipitation (MAGIC) method of Karl and Tien (1992) have estimated phosphate concentrations in P-limited freshwater and marine systems in the pico- and low nanomolar range (Hudson et al. 2000; Wu et al. 2000), well below the detection limits of other methods. Despite the implications of such low PO_4^{3-} concentrations for P cycling in lakes (Karl 2000), few studies have utilized either of these methods to assess whether phosphate concentrations in other water bodies are within the same range and the potential impacts for our understanding of P dynamics in lake ecosystems.

The ability to measure P regeneration by planktonic organisms and the relative importance of different plankton groups as suppliers of regenerated P is an unresolved and critical issue in the study of lake P cycling. Recycled or regenerated nutrients from planktonic organisms can supply much of the nutrients for plankton communities, especially during summer stratification (Hudson et al. 1999; Vanni 2002). However, most methods used to estimate P regeneration from plankton communities have methodological limitations that may yield inaccurate or incomplete P regeneration rates. The more commonly used methods for estimating P regeneration rates may violate critical methodological assumptions (Harrison and Harris 1986), have ineffective or inconsistent treatments (Tremaine and Mills 1987; Dodds et al. 1991), or only measure regeneration from a select group, such as zooplankton (Lehman 1980). In addition, many of these methods rely upon colorimetric determination of SRP to calculate P regeneration rates, which, as previously discussed, greatly overestimate PO_4^{3-}concentrations. Regardless of methodological limitations, few studies have compared the absolute amounts and the relative contribution of different planktonic groups as recyclers of P (Fisher et al. 1988; Dodds et al. 1991; Taylor and Lean 1991; Hudson and Taylor 1996). Thus, in order to better understand P cycling in lake plankton communities, dissolved P regeneration rates and the relative importance of different planktonic groups requires further study.

Despite current uncertainties about lake P cycling, conceptual models have been proposed describing predicted P dynamics in lake epilimnetic waters of varying phosphorus content (Harris 1986; Capblancq 1990; Harris 1994). Accordingly, it is predicted that as total phosphorus (TP) concentration increases, the relative size of the various P pools, the movement of P within plankton community and the concentration of P within different planktonic groups should change in a predictable mannerr. Among the predictions made by these conceptual models of P cycling in lake surface waters, there are several predictions specifically related to PO_4^{3-} concentration, the size-fractionated uptake and regeneration of PO_4^{3-} by plankton, and the overall cycling efficiency of P within plankton communities. The predictions include:

(1) Smaller planktonic organisms, (pico- and nanoplankton <20μm) should dominate plankton biomass and production in oligotrophic waters and this dominance should decline as TP increases (Harris 1986; Capblancq 1990; Fig. 2.1a and b). The importance of pico- and nanoplankton in PO_4^{3-} uptake and regeneration

should decline with increasing system productivity (Harris 1986; Capblancq 1990).

(2) The concentration of PO_4^{3-} should increase with TP and become an increasing, if not dominant portion of TP (Harris 1986; Capblancq 1990; Fig. 2.1a and c). The ratio of PO_4^{3-} concentration to the concentration of P held within plankton biomass (particulate P or PP) should increase with TP (Capblancq 1990; Fig. 2.1a).

(3) The turnover of P pools will be more rapid in low TP waters than in higher TP systems (Fig. 2.1a). Therefore, P cycling efficiency, as indicated by P pool turnover rates, should decline with lake TP (Harris 1986). The turnover rate of the PO_4^{3-} pool should become slower as the size of the PO_4^{3-} pool increases and the PO_4^{3-}:PP ratio increases with TP. This indicates faster internal recycling of the PO_4^{3-} pool in more oligotrophic waters (Harris 1986; Capblancq 1990; Fig. 2.1d). Similarly, the turnover times of TP and PP pools should become slower as TP increases (Fig. 2.1a and d).

Studies have examined a number of these individual predictions and have found trends supporting some (Watson and Kalff 1981; White et al. 1982; Prepas 1983; Currie et al. 1986), however, more recent examination of nutrient turnover and cycling efficiency in lakes across productivity and nutrient gradients found no evidence supporting some these predictions (Currie 1990; Baines and Pace 1994; Hudson et al. 1999). Few studies have simultaneously examined a number of the above predictions to determine if these conceptual models accurately describe patterns and trends of P cycling across a gradient of TP concentration.

The goal of the current study is to test the above predictions of Harris (1986) and Capblancq (1990) in a group of lakes located in British Columbia, Canada. I examined trends in the concentration of P in the particulate and dissolved P pools in a set of lakes representing a range of TP concentration. I further examined trends in the size-fractionated PO_4^{3-} uptake and regeneration by the plankton community in lakes of varying TP concentration, and used estimates of PO_4^{3-} uptake and regeneration to assess the overall P cycling efficiency of epilimnetic plankton communities. I used recently developed methods of estimating PO_4^{3-} concentration (Hudson et al. 2000) and plankton P regeneration (Hudson and Taylor 1996). Therefore, this study is unique in that it utilized recent methods for examining epilimnetic P dynamics and to simultaneously test multiple predictions of P cycling in lake ecosystems.

Methods

Study sites and lake sampling - The eight lakes examined by this study are located in British Columbia, Canada on the south coast and in the southern interior of the province (Table 2.1; Spafard et al. 2002). In order to examine predictions regarding P cycling along a TP gradient (Predictions 1- 3 above), I selected lakes that varied in TP concentration (Table 2.1). Total nitrogen (TN) chlorophyll *a* (Chl*a*), zooplankton biomass, and bacteria abundance also varied between lakes, generally following the gradient in TP (Table 2.1). Based upon nutrient concentrations and organism densities and biomasses, the lakes represent a range in productivity from ultra-oligotrophic to meso-eutrophic (Wetzel 2001; Kalff 2002).

All lakes examined in this study had zooplankton communities dominated by large-bodied herbivorous zooplankton, according to the criteria of Mazumder (1994a). All lakes met at least two of the following criteria: (1) *Daphnia* density $\geq$5 individuals L^{-1}, (2) *Daphnia* mean length $\geq$1 mm, (3) cladoceran mean length $\geq$0.5 mm, or (4) *Daphnia* biomass $\geq$20% of total zooplankton biomass or $\geq$10% of total cladoceran biomass (Mazumder 1994a). Contrasting zooplankton community composition and size distribution (lakes dominated by small-bodied versus large-bodied zooplankton) can affect PO_4^{3-} turnover rates and the concentration of P in different size classes of the plankton community (Mazumder et al. 1988; Mazumder 1994b). Therefore, by having all lakes dominated by large herbivorous zooplankton, I likely avoided potential confounding effects of zooplankton community size and composition on lake P dynamics.

Lakes were sampled throughout the summers of 2000 and 2001, with each lake sampled a minimum of two times during the May – October stratification period (Table 2.1). Water temperature profiles were measured with a YSI Model 58, and the epilimnion was defined as the upper portion of the water column that did not exhibit temperature change $\geq$1°C m^{-1}. Epilimnetic water was collected with an integrated sampler made of a 5-cm diameter weighted Tygon tube. Integrated epilimnetic samples were collected from 0 - 5.5m, or to the bottom of the epilimnion if the bottom of the layer was shallower than 5.5 m. On each sampling date, triplicate water samples were collected to estimate TP, TN, Chl*a* and bacteria abundance. In addition, ~20L of epilimnetic water was collected in a large dark-colored plastic container that had been cleaned and thoroughly rinsed with distilled and deionized water prior to field collection.

Immediately prior to collection, all containers were rinsed a minimum of three times with epilimnetic water from the sampling site. Within 3-4 hours of collection, water was transported to the lab and water from the same 20-L sample was used for estimation of particulate phosphorus, $^{32}PO_4^{3-}$ uptake bioassays, and dissolved P regeneration rate estimates. Zooplankton were collected on each sampling date with triplicate vertical tows of a 80-µm Wisconsin plankton net and preserved in 4% sugar-formalin.

Plankton and nutrient analyses - Chl*a* was estimated by filtration onto Whatman GF/F filters and extracted in 95% ethanol at 4°C overnight in the dark. Absorption was measured on an Ultraspec® 2000 spectrophotometer with a 10-cm quartz cell and Chl*a* concentration (µg L^{-1}) was calculated according to Wintermans and DeMots (1965). Bacteria density was estimated by DAPI staining, filtration onto black Nuclepore 0.2-µm filters and counted under UV light (Kemp et al. 1993). To determine zooplankton density, crustacean zooplankton were counted under a dissecting microscope with the aid of software (Z-Count). Biomass was estimated by measuring at least 150 individuals or by measuring all individuals in at least 10% of the total sample volume. Length measurements were converted to biomass using published length-mass relationships (Bottrell et al. 1977; Rosen 1981; Culver et al. 1985; Yan and Mackie 1987).

TP was determined by potassium persulfate digestion in an autoclave and analyzed as phosphate on a Lachat autoanalyzer (Zellweger Analytics, QuickChem® 8000). Particulate phosphorus (PP) determination was performed by serial filtration (Mazumder et al. 1988; Taylor and Lean 1991). I measured concentration of PP in the following five size classes: >200 (mesoplankton), 200-41 (large microplankton), 41-20 (small microplantkon), 20-3 (nanoplankton), and 3-0.2 µm (picoplankton). Particulates were collected on 50x50 cm acid-rinsed squares of Nitex netting (200- and 41-µm) or 47-cm diameter Nuclepore polycarbonate filters (20-, 3- and 0.2-mm). I determined that brief acid rinsing did not change aperture size of Nitex by measuring apertures before and after rinsing pieces of Nitex with acid. A total of 2-6 L of lake water was used in the serial filtration process, depending upon the concentration of particles in the epilimnion at the time of sampling. After serial filtration, Nitex screens and Nuclepore filters were placed into acid-washed screw-cap test tubes and digested with potassium persulfate in an autoclave. P contained in each plankton size class was determined as in TP analyses and corrected for Nitex and Nuclepore blanks. The sum of concentrations in all size fractions was considered the concentration of total PP. Total dissolved phosphorus (TDP) was calculated by subtracting PP from simultaneously measured TP. TDP was composed of forms of P that can pass through a 0.2-µm filter, which generally includes very small particles (<0.2µm), colloidal P, small molecular weight organic P, and PO_4^{3-} (Lean 1973). TN was determined by autoclaving samples with alkaline potassium persulfate and measured as nitrate with the cadmium reduction method (APHA 1998).

PO_4^{3-} uptake and regeneration - PO_4^{3-} uptake experiments were conducted in a manner similar to Lean and White (1983) and Mazumder et al. (1988). Carrier-free $^{32}PO_4^{3-}$ was added to 100 ml of whole lake water (final activity 900 – 3200 Bq ml^{-1}) in an acid-washed high-density polyethylene (HDPE) beaker. 2-ml subsamples were removed at 0.5, 1, 2, 4, 6 and 10 minutes after addition of $^{32}PO_4^{3-}$ and passed through 25-mm diameter 0.2-µm Nuclepore filters and the filtrate was placed in scintillation vials. After 15 minutes, 5-ml subsamples were collected and passed through 0.2-, 3-, and 20-µm Nuclepore polycarbonate filters and filters were placed into scintillation vials and

dissolved with 100 µl of methylene chloride:ethanol amine (10:1). Scintillation flour (10 ml; Scintiverse II, Fisher Scientific) was added to vials containing filtrate and filters. ^{32}P activity of samples was determined using a Beckman LS6000IC or Wallac 1410 liquid scintillation counter. Uptake bioassays for each lake on each sampling date were conducted in duplicate or triplicate.

To estimate PO_4^{3-} turnover time, the natural log (ln) of the percent $^{32}PO_4^{3-}$ left in solution was plotted as a function of time (minutes) and ordinary least-squares regression was used to estimate the slope. The absolute value of the slope was the PO_4^{3-} uptake constant (k, min^{-1}) and the reciprocal ($1/k$) was the turnover time in minutes (Lean 1973). ^{32}P activities on the three different filters (0.2-, 3- and 20-µm) taken at the end of bioassays were used to estimate percent $^{32}PO_4^{3-}$ uptake by different size classes of plankton (0.2-3 µm, 3-20 µm and >20 µm). Assuming activity on the 0.2 µm filter represented the total assimilated $^{32}PO_4^{3-}$ by all size classes of the plankton community, the $^{32}PO_4^{3-}$ taken up by the 0.2-3 µm fraction was calculated by subtracting the activity of the 3 µm from the 0.2 µm filter, and the uptake of the 3-20 µm fraction was estimated by subtracting the activity of the 0.2-3 µm size class and the >20 µm size class (activity on the 20 µm filter).

To measure the dissolved P regeneration rate of the plankton community, I used the method of Hudson and Taylor (1996). Discussion of methodological and theoretical considerations of this method is outside the scope of this paper, but these topics are thoroughly discussed by Hudson and Taylor (1996). Briefly, immediately after bringing lake water into the lab, 4L was gently decanted into acid-washed HDPE square-sided bottles and carrier-free $^{32}PO_4^{3-}$ was added (final activity 225 – 800 Bq ml^{-1}). Bottles were incubated at approximately lake epilimnetic temperature for 28-36 h to label the plankton community. After the incubation period, 200-400 ml volumes were removed to determine the dissolved P release rates of the entire plankton community and of different plankton size fractions. I determined dissolved ^{32}P release rates from the unfractionated plankton community (whole water), plankton >200, 200-41, 41-20, and <20 μm. Size-fractionated samples were gently passed through 200-, 41- or 20-μm Nitex using gravity into acid-washed HDPE beakers. To determine the dissolved ^{32}P activity at time zero, 5-ml subsamples were immediately removed and passed through 25-mm diameter 0.2-μm syringe filters (Sarstedt Filtropur polyethersulfone filters) into scintillation vials. "Cold" $^{31}PO_4^{3-}$ was then added to each beaker to a final concentration of 24 μmol P L^{-1} (750 μg P L^{-1}) to act as a competitive inhibitor for ^{32}P (Hudson and Taylor 1996). Over the following 5-8 h, 4-7 subsamples (5 ml) were removed from each beaker and passed through 0.2-μm syringe filters into scintillation vials. Beakers containing the unfractionated plankton community and the various size fractions were performed in duplicate.

To estimate ^{32}P release rate of the various size fractions, dissolved ^{32}P activity (dpm L^{-1} in <0.2 μm filtrate) starting at time zero, was plotted as a function of time, and the slope was estimated using ordinary least-squares regression. The slope was considered the dissolved ^{32}P release rate. To estimate dissolved P release rate (ng P L^{-1} h^{-1}), the total ^{32}P added at the beginning of the initial incubation period and the P concentration in the specific size fraction were used in the following equation:

$$\text{P release rate} = (^{32}\text{P release rate x [P]}) / \text{total initial } ^{32}\text{P activity}$$

The P regeneration rate of each of the plankton size classes (unfractionated plankton community, >200, 200-41, 41-20 and <20 μm) was estimated by using the concentration of TP for the whole water regeneration rate or the sum of the concentration of particulate P in the specific size class (>200, 200-41, 41-20 and <20 μm) and TDP.

Estimation of PO_4^{3-} concentration - To estimate PO_4^{3-} concentration, I used the steady-state bioassay method of Hudson et al. (2000). Using the $^{32}PO_4^{3-}$ uptake constant (*k*) and the dissolved P regeneration rate, we estimated the steady state concentration of phosphate ($ssPO_4^{3-}$) concentration using

$$k \times [PO_4^{3-}] = \text{dissolved P regeneration rate}$$

This method assumes that, in systems with rapid PO_4^{3-} uptake and turnover (P is limiting), uptake and regeneration of dissolved inorganic P by the plankton community are tightly coupled and essentially equal in the short-term. In nutrient limited freshwater and marine systems, the uptake and regeneration of dissolved inorganic nutrients by plankton communities are approximately equal and the balance of uptake and regeneration control the short-term steady state concentrations of these inorganic nutrients (Dodds 1993; Harrison 1993). This method also assumes that dissolved P regenerated by the plankton community is mostly in the form of phosphate or low molecular weight organic compounds that are quickly hydrolyzed by phosphatases, an assumption supported by studies that have classified regeneration products (Peters and Lean 1973; Lean and Nalewajko 1976; Taylor and Lean 1981). Based upon the above assumptions, the method of using the plankton dissolved P regeneration rate and the PO_4^{3-} uptake constant to estimate the concentration of PO_4^{3-} can only be applied to systems that exhibit rapid uptake and turnover of the PO_4^{3-} pool (Hudson et al. 2000).

For comparative purposes, I also estimated PO_4^{3-} concentration with colorimetric SRP methods. For each sampling date, undigested filtered (<0.2 µm) lake water was analyzed for PO_4^{3-} using a Lachat autoanalyzer.

Statistical analyses - For nutrient concentrations, plankton biomass and densities, and rate measurements (TP, PP, TN, $ssPO_4^{3-}$, SRP, Chl*a*, zooplankton biomass, bacteria abundance, PO_4^{3-} turnover times, P regeneration rates) I calculated a mean of the summer stratified period for each lake in each year (8 lakes x 2 years; $n = 16$). I used summer means for each lake in each year instead of using individual time series measurements in analyses, because I wished to describe the average summer conditions and rate processes within each lake during the stratified period and to avoid issues of pseudoreplication (Hurlbert 1984). While use of summer means does not allow for examination of seasonal variability or seasonal trends in data, seasonal or annual means are commonly used in limnological research to describe lake conditions and processes (Fee et al. 1996; Mazumder 1994a; Knoll et al. 2003).

To evaluate hypotheses that P cycling should vary with TP concentration, I performed ordinary least-squares regression using TP to predict P concentrations of the various particulate and dissolved fractions (PP, PP of individual plankton size fractions, TDP, $ssPO_4^{3-}$, SRP). Rate processes, such as PO_4^{3-} turnover time (min) and the regeneration rates (nmol L^{-1} hr^{-1}) were also plotted as a function of TP. The percent $^{32}PO_4^{3-}$ taken up by different plankton size classes and the percent contribution of each plankton size class to the total regeneration rate were also regressed as a function of TP. Calculation of the percent of total PO_4^{3-} taken up or the percent contribution to the total community P regeneration rate of an individual plankton size fraction inherently makes that percentage dependent on the percentages of the other size classes. Therefore, I only regressed the percent uptake and regeneration of n-1 plankton size classes, where n is the total number of size classes examined. Data expressed as percentages were arcsine square root transformed prior to analyses (Zar 1999). Statistical analyses were performed with SPSS version 8.0. Significance for all analyses was set at $\alpha \leq 0.05$.

Results

Lake P concentrations and particulate phosphorus size distribution - Mean summer TP of lakes in 2000 and 2001 ranged from 0.09 – 0.59 μmol L^{-1} (2.7 – 18.2 μg L^{-1}). Several limnological variables exhibited significant relationships with TP (Table 2.2). Mean summer TN increased with TP, however, one lake (New Lake – NEL) had much higher TN concentrations than the other lakes (Table 2.1). When NEL was included in the TP-TN regression, TN significantly increased with TP, but the relationship was improved when NEL was excluded (Table 2.2). Bacteria abundance, Chl*a* and zooplankton biomass significantly increased with TP (Table 2.2).

Mean summer total PP ranged from 0.07 – 0.4 μmol L^{-1} (Table 2.3). The concentration of PP increased significantly with TP (Fig. 2.2) and on average, 74% (sd = ±21%) of TP in lakes was bound in particulates (Table 2.3). The ratio of PP to TP decreased with TP, as illustrated in Fig. 2.2 by the increasing deviation of the TP-PP regression line from a 1:1 line. Thus, as TP increased, the dissolved fraction (TDP) became an increasing portion of the TP pool. Five of the TDP seasonal averages (COL 2000 and 2001, SHL-S 2000, SOL-N) were extremely low (<0.0002 μmol L^{-1}) to undetectable (PP = TP; Table 2.3). It is important to note that all of these lakes had TP concentrations below 0.12 µmol L^{-1} (Table 2.3; Fig. 2.2).

Within the PP pool, the picoplankton (3 – 0.2µm) contained 35 – 57% ($\bar{x}$ = 50%) of the PP (Table 2.3). The proportion of PP in the picoplankton did not vary significantly with TP ($p = 0.305$). The proportion of the total particulate pool in the nanoplankton (20 – 3µm) was also not a significant function of TP ($p = 0.093$), and the nanoplankton, on average, contained 12% of PP. The combined pico- and nanoplankton (<20µm) contained >60% of PP. The small (41 – 20µm) and large (200 – 41µm) microplankton, on average contained 12 and 7% of PP, respectively. The mesoplankton (>200µm) contained the second largest proportion of the PP pool ($\bar{x}$ = 18%), and this proportion did not significantly vary with TP ($p = 0.105$). The only significant relationship between the proportion of particulate P in a plankton size class and TP was observed when the large microplankton and the mesoplankton were grouped together (plankton >41µm) and the proportion of PP held within plankton >41µm increased significantly with TP (arcsine $\sqrt{\text{proportion PP} > 41\mu m} = 0.49 + 0.34$ TP; $r^2 = 0.41$; $F_{1,14} = 9.8$; $p = 0.007$).

PO_4^{3-} uptake – $^{32}PO_4^{3-}$ uptake constants varied from 0.104 to 0.187 min^{-1} ($\bar{x}$ = 0.149 min^{-1}) (Table 2.4) and $^{32}PO_4^{3-}$ turnover times varied from 5.3 – 9.6 min ($\bar{x}$ = 6.7 min). These uptake constants and rapid PO_4^{3-} turnover times suggest that plankton in all lakes were strongly P-deficient.

The picoplankton size fraction overwhelmingly dominated the uptake of $^{32}PO_4^{3-}$, accounting for 74 – 91% of $^{32}PO_4^{3-}$ uptake (Table 2.4). The percent $^{32}PO_4^{3-}$ uptake by picoplankton (0.2 – 3µm) was not a function of TP ($p = 0.140$), but was a significant function of bacteria abundance, however, only 26% of the variance in percent uptake of $^{32}PO_4^{3-}$ by picoplankton was explained by the relationship (arcsine $\sqrt{\text{proportion} \; < 3\mu m}$ = 1.1 + 0.06 Bacteria abundance; $r^2 = 0.26$; $F_{1,\,14} = 4.8$; $p = 0.05$). Nanoplankton accounted for a smaller portion of the $^{32}PO_4^{3-}$ uptake (6 – 23%) and plankton >20μm only accounted for 1 – 9% of the $^{32}PO_4^{3-}$ uptake (Table 2.4). Lakes with the highest TP concentrations (ELL and CUL) exhibited the highest percent $^{32}PO_4^{3-}$ uptake values for plankton >20μm (Table 2.4), however, the relationship between lake TP and percent $^{32}PO_4^{3-}$ uptake by plankton >20μm was marginally non-significant ($p = 0.06$). The percent uptake of plankton >20μm was not a significant function of Chl*a* ($p = 0.08$) or bacteria abundance ($p = 0.604$).

PO_4^{3-} regeneration – Regeneration rates of unfractionated plankton communities ranged from 1.1 – 13.3 nmol P L^{-1} h^{-1} (34 – 413 ng P L^{-1} h^{-1}) and increased as a linear function of TP (Fig. 2.3a). In addition, the P regeneration rate of all plankton size classes had a significant positive relationship with TP (Fig. 2.3b-e). The relationship between TP and mesoplankton (Fig. 2.3b) and nanoplankton (Fig. 3e) regeneration rates was much stronger than the relationship between TP and the regeneration rates of large microplankton (Fig. 2.3c) and small microplankton (Fig. 2.3d).

The pico- and nanoplankton size fraction (<20μm) was typically the largest contributor to community regeneration rates (Table 2.5), accounting for 18 – 52% ($\bar{x}$ = 39%) of the community regeneration rate. Mesoplankton (>200μm) were also important contributors to community regeneration rates, accounting for 5 – 55% ($\bar{x}$ = 30%) of the community regeneration rate (Table 2.5). The percent contribution of large and small microplankton were more variable between lakes (large microplankton (200-41μm) = 0 -

34%, small microplankton (41-20μm) = 3 - 70%) compared to that of the <20μm and mesoplankton fractions. The percent contribution of nanoplankton to the community regeneration rate did not vary with TP ($p = 0.991$), but the percent contribution of the mesoplankton to the community regeneration rate did increase significantly with TP ($\text{arcsine}\sqrt{\text{proportion} > 200\mu\text{m}} = 0.41 + 0.60$ TP; $r^2 = 0.37$; $F_{1, 14} = 8.1$; $p = 0.013$), but the amount of variance explained by the relationship was relatively low.

PO_4^{3-} concentration – Steady state bioassay estimates of PO_4^{3-} concentrations ($ssPO_4^{3-}$) were 40 - 578 pmol L^{-1}, and the concentration significantly increased as a function of both TP (Fig. 2.4a) and TDP (Fig. 2.4b). When the $\log_{10}$ ($ssPO_4^{3-}$ - pmol L^{-1}) – $\log_{10}$ (TP – pmol L^{-1}) relationship is examined ($\log_{10} [ssPO_4^{3-}] = 1.1 (\log_{10} [TP]) - 3.7$, $r^2 = 0.77, p < 0.0001$), the slope of the relationship is close to 1, indicating $ssPO_4^{3-}$ did not did not increase as a proportion of TP with increasing TP, and that $ssPO_4^{3-}$ remained a consistent proportion of TP across lakes. Based upon steady-state bioassay estimates, PO_4^{3-} was always <0.004% of TP in all lakes. PO_4^{3-} concentrations measured as SRP were greater than $ssPO_4^{3-}$, ranging from 0 – 0.121 μmol L^{-1} (0 – 3.7 μg L^{-1}), with a mean of 0.048 μmol L^{-1} (Fig. 2.4c). One lake SRP seasonal mean (NEL in 2001) consistently had concentrations below detection limits, therefore SRP concentration was assumed to be zero. Lake SRP concentrations were 1.5 – 3.0 orders of magnitude greater than the simultaneously estimated $ssPO_4^{3-}$ concentrations (excluding NEL 2001) with an average difference of 2.5 orders of magnitude. Unlike $ssPO_4^{3-}$, SRP was not a significant function of TP ($p = 0.990$; Fig. 2.4c), or TDP ($p = 0.621$), nor were $ssPO_4^{3-}$ and SRP significantly correlated with one another (Pearson $r = 0.121$, $F_{1, 14} = 0.207$, $p = 0.656$).

The ratio of steady state phosphate to P held within plankton (PP) increased with TP (Fig. 2.5a), following the prediction of Capblancq (1990). Furthermore, the ratio of $ssPO_4^{3-}$ to P in nanoplankton (which account for 60% of PP, 90% of PO_4^{3-} uptake and 40% of PO_4^{3-} regeneration) also increased as a function of TP (Fig. 2.5b). However, the ratio of $ssPO_4^{3-}$ to PP and PP<20μm was always low in all lakes (<0.012).

PO_4^{3-} cycling – PO_4^{3-} turnover time in all lakes was rapid ($\leq$10 min) and did not vary significantly with TP ($p = 0.671$; Fig. 2.6a), $ssPO_4^{3-}$ ($p = 0.811$; Fig. 2.6b) or TDP ($p = 0.752$; Fig. 2.6c). PO_4^{3-} turnover time was not a function of the ratio of $ssPO_4^{3-}$ concentration to the concentration of P in all plankton (PP; $p = 0.239$) or the concentration of P in plankton responsible for the majority of PO_4^{3-} uptake (PP<20μm; $p = 0.567$). Additionally, PO_4^{3-} turnover time was not significantly related to SRP ($p = 0.319$), PP ($p = 0.667$), TN ($p = 0.437$), TN:TP ($p = 0.593$), particulate N (calculated as TN minus $NH_4^+ + NO_3^-$; $p = 0.488$), PP:PN ($p = 0.479$), PO_4^{3-}:NH_4^+ ($p = 0.148$), Chl*a* ($p = 0.366$) or bacteria abundance ($p = 0.620$).

TP and PP cycling efficiency - In order to examine the prediction that P cycling within plankton communities is efficient in lakes with lower TP, I estimated the cycling efficiency of TP and PP pools by calculating the turnover time (in days) of these pools. This was calculated as the TP or PP concentration divided by the plankton community daily regeneration rate (nmol L^{-1} day^{-1}). Regeneration rates were rapid enough to recycle TP pools every 1.5 – 6.1 days ($\bar{x}$ = 2.5 days) and there was no significant relationship between TP turnover time and the concentration of TP (Fig. 2.7a). The turnover times of the total PP in lakes (every 0.6 – 3.4 days) as expected was similar to that of TP, however, the PP pool turned over more rapidly at higher TP concentrations (Fig. 2.7b).

This relationship was probably driven by the turnover of the nanoplankton P pool (PP<20μm / PP<20μm daily regeneration rate), which ranged from 0.8 – 6.4 days and became more rapid with TP (Fig. 2.7c). The turnover time of the PP pool was not a significant function of TN:TP ($p = 0.703$) or estimated PN:PP ($p = 0.298$).

Discussion

The purpose of this study was to examine patterns and trends in P cycling across a TP gradient in order to further our understanding of P dynamics and to test the conceptual models of Harris (1986) and Capblancq (1990). In our study lakes, I found limited support for many of the predictions based upon these models. The pico- and nanoplankton size fractions (<20μm) of the plankton community contained the largest proportion of the PP, dominated PO_4^{3-} uptake, and contributed the largest proportion of the community P regeneration rate. These trends had little relationship with the size of the total P pool in lakes. Furthermore, the cycling efficiency of PO_4^{3-}, TP and PP, as defined by the as turnover times of these pools, was not faster in lower TP systems.

Prediction 1 (Role of pico- and nanoplankton in lakes of varying P content) – Smaller planktonic organisms (<20μm) were important in the cycling of P within the range of TP observed by this study, and this importance was little affected by the concentration of TP (Fig. 2.8a). In our study, the combined pico- and nanoplankton size fraction (<20μm) contained the largest portion (>60%) of PP. This is in agreement with findings that smaller plankton typically constitute a significant portion of the P in plankton communities (Mazumder et al. 1988; Vadstein et al. 1988; Taylor and Lean 1991). While the proportion of PP<20μm did not significantly vary with lake TP, there was a shift toward a higher proportion of PP occurring in larger size fractions (>41μm) with increasing TP. This latter trend may be associated with a shift toward larger algal species in more eutrophic lakes (Watson and Kalff 1981).

The combined pico- and nanoplankton size fraction dominated PO_4^{3-} uptake and the proportional uptake of this size fraction was little influenced by TP (Fig. 2.8a). The picoplankton, in particular, accounted for >80% of PO_4^{3-} uptake, and the proportional PO_4^{3-} uptake by did not vary with TP. Picoplankton <3μm are primarily responsible for the in situ uptake of PO_4^{3-} across a wide range of productivity, biomass and plankton community structure (Currie and Kalff 1984b; Mazumder et al. 1988; Suttle and Harrison 1988a). It has been hypothesized that PO_4^{3-} uptake partitioning among different plankton size fractions is primarily a function of the severity of plankton P-deficiency (Currie et al. 1986). All lakes in our study exhibited PO_4^{3-} turnover times ≤10 min, indicating strong P-deficiency. Under P-deficient conditions, smaller plankton (<3μm) with larger surface area to volume ratios are competitively superior to larger cells (>3μm) in PO_4^{3-} uptake. Furthermore, the rapid uptake of PO_4^{3-} by plankton <3μm may be a result of bacterioplankton P-limitation (Toolan et al. 1991; Coveney and Wetzel 1992) due to their relatively high P requirements (Vadstein et al. 1988). Therefore, it follows that the PO_4^{3-} uptake dominance of plankton <3μm over a wide range of systems should be influenced more by short-term nutrient deficiencies than by the size of TP or PP pools.

I observed little evidence of a shift in the relative importance different plankton size fractions in the regeneration of P across a range of TP examined by this study (Fig. 2.8a). The combined pico- and nanoplankton size fraction (<20μm) contributed, on average, 40% of the community regeneration rate, and this percentage did not significantly change with TP. The importance of smaller planktonic organisms in P recycling has received less attention than P recycled from zooplankton (Lehman 1980; Sterner 1986; Vanni 2002), but smaller plankton can contribute a significant portion of the recycled nutrients in pelagic environments (Harrison 1993). Hudson and Taylor (1996) found that plankton 0.8 – 40µm accounted for 58% of the community P regeneration rate, and that plankton <0.8 µm contributed an additional 19% of the community regeneration rate in two oligo-mesotrophic lakes. Dodds et al. (1991) determined that plankton <3µm accounted for 69% of the regenerated P in oligotrophic Flathead Lake. Harrison (1983) examined the relative importance of microplankton (defined as microzooplankton, phytoplankton and bacteria) in oceanic sites of varying productivity and found that the microplankton provided 50 – 100% of the SRP requirements required for planktonic production. The relatively large contribution of smaller planktonic organisms to community regeneration rates is not unexpected because smaller organisms are predicted to have more rapid mass-specific nutrient excretion rates than larger organisms (Peters 1983). However, my study also found that larger mesoplankton (>200µm) were important contributors to the community P regeneration rate (~30% of the community regeneration rate). The proportional contribution to the community regeneration rate by the mesoplankton size fraction, which typically contains zooplankton and large phytoplankton, slightly increased with TP. Again, this shift toward the importance of larger planktonic groups with increasing TP may reflect the size shift in phytoplankton communities associated with increasing TP (Watson and Kalff 1981).

Prediction 2 (PO_4^{3-} concentration in lakes of varying P content) – ssPO_4^{3-} concentrations were low in all lakes (40 – 578 pmol L^{-1}) and in the same range found by both Hudson et al. (2000) using the steady state bioassay method and Wu et al. (2000) using the MAGIC method. Colorimetric measurements of SRP were on average 2.5 orders of magnitude greater than ssPO_4^{3-}. This is approximately the same difference observed by Hudson et al. (2000) who compared historical SRP data in 14 lakes with ssPO_4^{3-} measurements. The lack of a significant correlation between simultaneously measured ssPO_4^{3-} and SRP indicates that, not only do SRP methods greatly overestimate PO_4^{3-} concentrations (Rigler 1966; Hudson et al. 2000), they do not consistently overestimate PO_4^{3-}. I further observed that the relationships between TP and ssPO_4^{3-} and TP and SRP were markedly different. ssPO_4^{3-} concentrations increased as a function of TP, whereas SRP did not. My data, and the data of others, strongly suggests that the use of SRP to examine P dynamics under P-deficient conditions is inappropriate and potentially misleading. My results emphasize that relationships, and thus conclusions generated regarding the concentration and cycling of PO_4^{3-} in lakes of varying P content is intimately dependent upon the method used to estimate PO_4^{3-} concentration.

Steady state PO_4^{3-} concentrations increased with TP, but in contrast to the prediction of Harris (1986) and Capblancq (1990), ssPO_4^{3-} constituted a relatively consistent proportion of the TP pool across the range of TP in this study (i.e. - the slope of $\log_{10}(PO_4^{3-}) - \log_{10}(TP)$ relationship is approximately 1). Hudson et al. (2000) also found that ssPO_4^{3-} concentrations increased with lake TP in a group of North American lakes, but contrary to my findings, the authors found that the proportion of PO_4^{3-} as TP declined with TP. Interestingly, in my study, the proportion of TP in the dissolved form

(TDP) increased with TP, making TDP more than 50% of the TP in some lakes. This follows the PO_4^{3-}:TP trend predicted by Harris (1986) and Capblancq (1990). Thus, the prediction that PO_4^{3-} will become an increasingly larger proportion of TP in more P-rich lakes may be based upon the use of colorimetric determinations of SRP to estimate PO_4^{3-} (Harris 1986; Capblancq 1990). However, in the present study, neither SRP nor $ssPO_4^{3-}$ increased as a proportion of TP with increasing lake TP, so this assertion cannot be verified.

Prediction 3 (PO_4^{3-}, TP and PP cycling efficiency in lakes of varying P content) - The turnover of the PO_4^{3-} pool in all lakes was rapid and not a function of TP, $ssPO_4^{3-}$or SRP (Fig. 2.8c). Currie (1990) examined PO_4^{3-} turnover in 36 north temperate lakes determined that TP explained relatively little variance in PO_4^{3-} uptake constants, and therefore PO_4^{3-} turnover times. However, White et al. (1982) and Prepas (1983) found that turnover of PO_4^{3-} in lakes was a function of the in situ concentration of PO_4^{3-} concentration. The results of White et al. (1982) and Prepas (1983) contrast with mine, but it is important to note that the authors estimated PO_4^{3-} with column chromatography and colorimetric SRP methods, respectively. At the greatest $ssPO_4^{3-}$ concentrations observed in my study (which are more than an order of magnitude lower than the smallest PO_4^{3-} concentrations of White et al. (1982) and Prepas (1983)) the uptake and turnover of the PO_4^{3-} pool was always rapid. Our TP range (0.09 – 0.59 μmol L^{-1}), and potentially PO_4^{3-}, was less than White et al. (1982) and Prepas (1983), and it is conceivable that my ranges were not great enough to include systems in which concentrations became large enough to influence PO_4^{3-} turnover time. However, Hudson et al. (2000) similarly observed rapid PO_4^{3-} turnover times ($\leq$10 min) in a set of lakes with TP and PO_4^{3-}

concentrations that encompassed a greater range than our study (TP = 0.06 – 4.5 µmol L^{-1}; $ssPO_4^{3-}$ = 27 – 16,800 pmol L^{-1}).

Plankton P-deficiency remained severe (PO_4^{3-} turnover time <10 min) in my study, even in lakes with the majority of the TP in the dissolved fraction. PO_4^{3-} is the most easily obtained form of dissolved P for plankton, however a large portion of TDP in lakes is in the form of organic compounds (Lean 1973). This dissolved organic P (DOP) is accessible with the aid of phosphomonoesterases (Feder 1973) and a significant portion of DOP pool may be usable by plankton (Chrost et al. 1986). Therefore, the size of the DOP (and potentially TDP) pool may affect the severity of P-deficiency of plankton communities (PO_4^{3-} turnover time).

The absence of a significant relationship between PO_4^{3-} turnover time and lake TDP concentration may derive from the rapid uptake and assimilation of PO_4^{3-} by picpoplankton (<3µm). It has been hypothesized that in severely P-limited plankton communities, larger phytoplankton (>3µm) will use DOP sources to meet P requirements, because picoplankton consistently out compete larger plankton for PO_4^{3-} under P-deficient conditions (Currie 1986; Currie et al. 1986). Evidence of the segregated uptake of dissolved P sources by different size fractions of the plankton community is not abundant and the limited available data does not entirely support this hypothesis. For example, Bentzen and Taylor (1991) found that bacteria dominated the uptake of organically bound P when plankton communities were P-deficient and the turnover of organic P was relatively rapid ($\leq$40 min). I did not examine the concentration of DOP sources in the TDP pool or the turnover and cycling of DOP compounds, therefore I am unable to address specific questions regarding the role of TDP and DOP in P cycling.

Currently, there is a paucity of data on lake DOP cycling and the availability of different DOP sources to plankton. Therefore, future studies should address links between the cycling and utilization of DOP and size fractionated plankton P-deficiency in lake ecosystems.

P cycling within the plankton community in oligotrophic lakes has been hypothesized to be more efficient than in eutrophic lakes. The turnover of P by plankton in lower TP systems has been likened to a "rapidly spinning wheel" (Harris 1986) that will slow down as TP increases. Results from my study do not support this prediction. TP pools turned over rapidly (every 1.5 – 6 days) and the turnover time was not a function of TP (Fig. 2.8c). The total PP and PP<20μm pool turnover times decrease slightly with TP which is opposite of the predicted trend (Fig. 2.8c). The turnover times of the TP, PP and the pico- and nanoplankton (<20μm) P pools were similar to the turnover times of these pools reported by others (Taylor and Lean 1991; Fisher and Lean 1992; Hudson and Taylor 1996; Hudson et al. 1999). Other studies that examining nutrient cycling efficiency in lakes have also failed to support the hypothesis that nutrient cycling efficiency should decrease in more nutrient-rich systems (Baines and Pace 1994; Hudson et al. 1999). Hudson et al. (1999) examined the turnover rate of the PP pool in a number of North American lakes of varying total P content and found that PP turnover did not vary with TP. Baines and Pace (1994) found the proportion of phytoplankton primary production lost to sedimentation declined with lake productivity, opposite to the predictions (Reynolds 1984; Harris 1986). The contradiction between nutrient cycling paradigms and recent empirical studies (including the present study) suggest that long-standing conceptual models of nutrient cycling need further empirical examination.

P dynamics in lakes are influenced by a multitude of biotic and abiotic factors. The cycling rate of both dissolved and particulate forms of P are dependent upon P concentration relative to other nutrients, such as carbon and nitrogen (Harris 1986). For example, PO_4^{3-} uptake rates by plankton communities are sensitive to the concentration of other dissolved nutrients, as observed by Suttle and Harrison (1988b) with changing PO_4^{3-}:NH_4^+ supply ratios. The turnover rates and regeneration of P from specific zooplankton taxa can be dependent upon the concentration of P in ingested algal food relative to the nutrient composition of the animal's body (ecological stoichiometric theory; Elser and Urabe 1999; Sterner and Elser 2002). The size distribution of grazer communities (small versus large bodied grazer communities) can also affect PO_4^{3-} turnover times and the concentration of P in different plankton size classes (Mazumder et al. 1988). In my study, all lakes were characterized as having large grazer communities. Under such conditions, it is probable that grazing pressure on phytoplankton is intense, but it is currently unknown what effect changes in the grazer size distribution would have on trends of TP and PP turnover observed by this study. In summary, contrary to the conceptual models examined by this study, the observed patterns in lake P turnover and cycling efficiency are most likely a result of the complex interaction between plankton biomass and composition, zooplankton grazing and the ratio of multiple nutrients(C:N:P), rather than a simple function of the size of the TP, PP or PO_4^{3-} pools.

Chapter 3: Relative importance of planktonic regeneration, zooplankton grazing and sedimentation in seasonal phosphorus dynamics of coastal British Columbia lakes

Introduction

Phosphorus (P) often limits the productivity and biomass of limnetic plankton communities, and ecologists and limnologists have emphasized the role of P in freshwater ecosystems since the 1970s (Dillon and Rigler 1974; Schindler et al. 1977; Smith 1979; Mazumder 1994). Due to the importance of P to the productivity of lake food webs and its role in eutrophication, limnologists have produced a large number of studies examining epilimnetic P cycling in lakes. This large body of literature has examined P dynamics in culture (Lean and Nalewajko 1976), lake enclosures (Mazumder et al. 1992; Mazumder and Lean 1994), and whole lakes (Levine et al. 1986; Taylor and Lean 1992).

Based upon the previously indicated studies and others, ecologists have predicted that as the total P (TP) concentration increases in lakes, the relative importance of the various epilimnetic P fluxes should change (Harris 1986; Capblancq 1990; Harris 1994). It is predicted that as epilimnetic TP concentration increases, plankton communities will rely less upon P that has been recycled within the epilimnion and more upon P sources from outside the epilimnion (Harris 1986, Capblancq 1990). Oceanographers have long distinguished between so-called “new” and “recycled” nutrient sources in the ocean (Harrison 1983; Harrison1993), however limnologists have only recently explored this concept (Hama 1990; Caraco et al. 1992; Hudson et al. 1999; Vanni 2002). This hypothesis states that as epilimnetic TP increases, P fluxes within the epilimnion, such as planktonic regeneration and zooplankton grazing will decline in importance and nutrient fluxes into the epilimnion, such as stream inflows and hypolimnetic mixing and will become increasingly important. For example, the impact of zooplankton grazing (and thus flux of P to zooplankton) should decline with increasing TP concentration (McQueen et al. 1986; Sager and Richman 1991). This hypothesized shift in importance from P fluxes within the epilimnion to externally-derived fluxes with increasing TP concentration has been used by ecologists to postulate that more oligotrophic systems should therefore cycle P more efficiently in the epilimnion than eutrophic systems (Harris 1986; Capblancq 1990).

Accompanying a decline in the importance of P sources from within the epilimnion with increasing TP concentration, it is predicted that eutrophic lakes should have a greater portion of epilimnetic nutrient pools lost to sedimentation (Reynolds 1984; Capblancq 1990). Because oligotrophic systems are hypothesized to recycle epilimnetic nutrient pools more efficiently, a smaller portion of the epilimnetic TP pool should be lost to sedimentation in relatively low TP systems. Therefore, as TP concentration increases, the proportion of the total P pool regenerated by the plankton community should decline and the proportional loss of the epilimnetic TP pool to sedimentation should increase. This prediction is commonly found in the limnological literature and has been included in several reviews of nutrient cycling in lake ecosystems (Reynolds 1984; Harris 1986; Capblancq 1990), but few studies have empirically assessed these patterns in a series of lakes that vary in TP concentration. Numerous studies have assessed P sedimentation rates (Levine et al. 1986; Wodka et al. 1985; Caraco et al. 1992; Kleeberg

2002) and P sedimentation responses to changes in factors such as fish predation (Wright and Shapiro 1984; Mazumder et al. 1989), but these studies have either focused exclusively on individual lakes or have not directly measured P regeneration rates from the plankton community. Similarly, there are an array of studies which examine P fluxes in epilimnetic plankton communities (including planktonic regeneration), but P sedimentation data are not provided in order to assess the relative importance of regeneration, grazing and sedimentation fluxes in systems of varying P content (Taylor and Lean 1991; Hudson et al. 1999).

The purpose of this study is to examine seasonal trends of P dynamics of three oligotrophic and two meso-eutrophic basins in British Columbia, Canada. I measured particulate P sedimentation rates, planktonic dissolved P regeneration rates, and P flux rates into zooplankton via grazing in these five basins over a two-and-one-half-year period (May 2000 – February 2002). I empirically assess the predictions of Reynolds (1984), Harris (1986) and Capblancq (1990) regarding trends in P sedimentation, P regeneration and P fluxes to zooplankton in lakes of varying P content. Specifically, I assess the hypotheses that as TP increases in a series of lakes, (1) planktonic regeneration of P will decline in importance, (2) the importance of P fluxes to zooplankton will decline, and (3) sedimentation losses of P will increase in importance. To test these hypotheses, I examined the mean summer regeneration, grazing and sedimentation rates as a function of the total P (TP) concentration of the five basins over the two-year study period.

Methods

Study sites and lake sampling - The five study sites are located in British Columbia, Canada on the southern coast (Table 3.1; Spafard et al. 2002). Council Lake (COL), Elk Lake (ELL), Shawnigan Lake North (SHL-N) and Shawnigan Lake South (SHL-S) are located on Vancouver Island and Cusheon Lake (CUL) is located on Saltspring Island. SHL-N and SHL-S are two basins within the same water body, however the basins are on opposite ends of the lake and experience largely independent mixing and thermal regimes through most of the summer (Nowlin et al. 2003). Based upon nutrient concentrations and plankton densities and biomasses, COL, SHL-N and SHL-S are oligotrophic, and CUL and ELL are meso-eutrophic (Table 3.1; Wetzel 2001; Kalff 2002). All lakes are considered warm monomictic water bodies that do not receive permanent winter ice cover due to the relatively mild winter climate in this region.

Sites were sampled from May 2000 until January - February 2002. All sites were sampled at least once a month from May – September 2000 and once in January or February 2001. In the summer 2001, COL, ELL, and CUL were again sampled once a month from May – October, but SHL-N and SHL-S were sampled every 2 weeks. All data and samples were collected from the deepest point at each site. Water temperature was measured with a YSI Model 58, and the epilimnion was defined as the upper portion of the water column that did not exhibit temperature change $\geq 1°C\ m^{-1}$. Epilimnetic water was collected with a 5-cm diameter integrated sampler made of a weighted Tygon tube. Integrated epilimnetic samples were collected from 0 - 5.5 m, or to the bottom of the epilimnion if the bottom of the layer was <5.5 m. On each sampling date, triplicate water samples from the epilimnion were collected for TP, TN, and Chl*a*. Triplicate water samples were collected from the hypolimnion with a Niskin bottle for TP and TN. In addition, ~20L of both epilimnetic and hypolimnetic water was collected in large dark-colored plastic containers that had been cleaned and thoroughly rinsed with distilled and deionized water prior to field collection. Water from the 20-L epilimnetic sample was used for measurement of particulate P (PP), $^{32}PO_4^{3-}$ uptake, planktonic dissolved P regeneration rates, and zooplankton grazing rates. The hypolimnetic sample was used for hypolimnetic PP. Immediately prior to collection, all containers were rinsed a minimum of three times with water from the sampling site. Within 3-4 hours of collection, water was taken to the lab for analysis.

Plankton and nutrient analyses - Chl*a* was determined by filtration through Whatman GF/F filters and extraction in 95% ethanol at 4°C overnight in the dark. Absorption was measured on an Ultraspec® 2000 spectrophotometer with a 10-cm quartz cell and Chl*a* concentration ($\mu g\ L^{-1}$) was calculated according to Wintermans and DeMots (1965). TP was determined by potassium persulfate digestion in an autoclave and analyzed as phosphate on a Lachat autoanalyzer (Zellweger Analytics, QuickChem® 8000). Particulate phosphorus (PP) determination was performed by serial filtration (Mazumder et al. 1988; Taylor and Lean 1991). I measured concentration of PP in the >41µm and <41µm particle size classes. Particulates were collected on 50x50 cm acid-rinsed squares of Nitex screen (41 µm) or 47-cm diameter Nuclepore polycarbonate filters (0.2 µm). I determined that brief acid rinsing did not change aperture size of Nitex by measuring apertures before and after rinsing pieces of Nitex with dilute acid. A total of 2-6 L of lake water was used in the process, depending upon the concentration of particles. After filtration, screens and filters were placed into acid-washed screw-cap test tubes and digested with potassium persulfate in an autoclave. P contained in each plankton size class was determined as in TP analyses and corrected for Nitex and Nuclepore blanks. TN was determined by autoclaving samples with alkaline potassium persulfate and measured as nitrate with the cadmium reduction method (APHA 1998).

Estimation of PO_4^{3-} turnover and dissolved P regeneration - PO_4^{3-} turnover and planktonic nutrient regeneration were measured at all sites once per month from May – September in 2000. In 2001, I again measured PO_4^{3-} turnover and P regeneration at all sites at least once per month, but SHL sites had these analyses performed every 2 weeks. These measurements were also taken in January and February 2002.

PO_4^{3-} uptake bioassays were conducted in a manner similar to Mazumder et al. (1988). Carrier-free $^{32}PO_4^{3-}$ was added to 100 ml of whole lake water (final activity 900 – 3200 Bq ml^{-1}) in an acid-washed high-density polyethylene (HDPE) beaker. 2-ml subsamples were removed at 0.5, 1, 2, 4, 6 and 10 minutes after addition of $^{32}PO_4^{3-}$ and passed through 25-mm diameter 0.2-μm Nuclepore filters and the filtrate was placed in scintillation vials. Scintillation flour (10 ml; Scintiverse II, Fisher Scientific) was added to vials and ^{32}P activity was determined on a Beckman LS6000IC or Wallac 1410 liquid scintillation counter. Uptake bioassays for each lake on each sampling date were conducted in duplicate or triplicate. To estimate PO_4^{3-} turnover time, the natural log (ln) of the percent $^{32}PO_4^{3-}$ left in solution was plotted as a function of time (minutes) and ordinary least-squares regression was used to estimate the slope. The absolute value of the slope was the PO_4^{3-} uptake constant (k, min^{-1}) and the reciprocal ($1/k$) was the turnover time in minutes (Lean 1973).

I used the method of Hudson and Taylor (1996) to measure the dissolved P regeneration rate of the plankton community. After returning to the lab from a field site, 4 liters were gently decanted into acid-washed HDPE square-sided bottles and carrier-free $^{32}PO_4^{3-}$ was added (final activity 225 – 800 Bq ml^{-1}). Bottles were incubated at approximately lake epilimnetic temperature for 28-36 h to label the plankton community. To determine the dissolved ^{32}P activity at time zero, 5-ml subsamples were immediately removed and passed through 25-mm diameter 0.2-μm syringe filters (Sarstedt Filtropur polyethersulfone filters) into scintillation vials. "Cold" $^{31}PO_4^{3-}$ was then added to a final concentration of 24 μmol P L^{-1} (750 μg P L^{-1}) to act as a competitive inhibitor for ^{32}P (Hudson and Taylor 1996). Over the following 5-8 h, 4-7 subsamples (5 ml) were removed and passed through 0.2-μm syringe filters into scintillation vials.

To estimate the ^{32}P release rate, dissolved ^{32}P activity (dpm L^{-1} in <0.2 μm filtrate) starting at time zero was plotted as a function of time, and the slope was calculated using ordinary least-squares regression. The slope was considered the dissolved ^{32}P release rate. To calculate the dissolved P release rate (ng P L^{-1} h^{-1}), the total ^{32}P added at the beginning of the initial incubation period and lake epilimnetic TP concentration were used in the equation

$$\text{P release rate} = (^{32}\text{P release rate x [TP]}) \,/\, \text{total initial } ^{32}\text{P activity}$$

Zooplankton grazing rates – Zooplankton grazing rates were measured on all dates that PO_4^{3-} turnover and P regeneration analyses were conducted. After returning to the lab from a field site, three to four 1.5-L alloquots of whole lake water were gently decanted into 2-L square sided HDPE bottles (grazing chambers) and incubated overnight in low light conditions at epilimnetic temperature. At the same time, 50 ml of lake water was passed through a 41-μm Nitex screen and into an acid-washed 100-ml HDPE beaker. "Cold" $^{31}PO_4^{3-}$ was added to the beaker at a final concentration of 0.32 μmol L^{-1} (10 μg P L^{-1}) and ~30 seconds later carrier-free $^{32}PO_4^{3-}$ was added to the beaker (final activity 900 - 3200 Bq ml^{-1}). The "cold" P was added prior to the ^{32}P to prevent the unequal distribution of the label into different size fractions of the <41μm plankton (Mazumder et al. 1990). After ~18 hours of incubation, 5 ml of the <41μm labeled "food' was added to a 1.5-L container of whole water. The zooplankton community was allowed to graze under low light conditions for 4-10 minutes before draining the container through 200-μm Nitex screen to remove zooplankton >200μm. Screening time (~45 seconds) was included in the feeding time. Nitex screens were rinsed with filtered lake water (passed through 0.2-μm Nuclepore filter) and placed into scintillation vials. 5 ml of deionized water was added to each vial followed by 10 ml of scintillation fluor, and vials were gently shaken. This was done to suspend zooplankton in the newly created translucent gel. 5 ml of the <200μm filtrate from the grazing chamber was collected and placed in a scintillation vial with 10 ml of fluor. Vials were read on the scintillation counter. Grazing rate (% d^{-1}) was calculated as Mazumder et al. (1990). All grazing rates were corrected by "blank" experiments in which the labeled food was added to 1.5 L of ordinary tap water. To calculate the flux of PP <41μm into zooplankton >200μm, the concentration of PP <41μm was multiplied by the grazing rate.

PP sedimentation rates – PP sedimentation rates were measured at all sites approximately once per month from May – September 2000 and once in the winter of 2001 (January and February). From May – October 2001, PP sedimentation data were again collected at least once per month in COL, CUL, and ELL. SHL-N and SHL-S had sedimentation rates measured every two weeks in the summer of 2001. Sedimentation rates were measured at all sites once during January – February 2002.

Sediment traps were constructed of PVC cylinders (10.2 cm diameter, 61 cm tall) and were of a 6:1 height:volume ratio to limit particle resuspension (Bloesch and Burns 1980). Each trap consisted of four cylinders bolted onto a piece of plexiglass attached to the end of a 1 m section of ABS pipe (2 cylinders per end). The collection cylinders were removable from the ABS cross piece to facilitate the collection of sedimentation trap material after the trap was retrieved and on board a boat. Ropes were attached to the center of the top and the bottom of the center ABS pipe with rust proof eye bolts. The bottom rope was attached to an anchor and the length of rope was long enough to position the top of the traps 1.5 m above the sediment surface when the rope was pulled taught. The top rope led to a buoy that was positioned approximately 1.5 m below the water's surface, in order to limit vertical movement of the trap suspended in the water column due to wave action on the lake's surface. Traps were deployed by slowly lowering the trap and anchor to the bottom of the lake. After 7 – 21 days ($\bar{x}$ = 14 d), traps were retrieved by slowly pulling the anchor and trap to the surface. This collection period interval was selected because it is often used in the literature (Wodka et al. 1985; Larocque et al. 1996) and this time period limits the amount of decomposition occurring in traps (Bloesch and Burns 1980). Most traps were left in lakes for 14 days, however, in 2001, traps in CUL were left for 21 days throughout the summer. On winter sampling dates (January and February of 2001 and 2002) the collection periods were allowed to proceed for longer (~28 days). After pulling the trap from the water, water was slowly decanted out of each of the four collection cylinders through a small hole in the side of each cylinder at the one-liter mark (Larocque et al. 1996). The decanting process did not appear to resuspend any of the material collected in the bottom of the cylinder. Material from the four cylinders was pooled and placed into a clean 4-L plastic container, and each cylinder was rinsed with deionized water to ensure all material was collected. Bottles containing sediment trap material were transported in a cooler to the lab. If the trap was immediately redeployed (SHL-N and SHL-S in 2001) cylinders were thoroughly rinsed with deionized water and slowly lowered into the lake ~10 m from the site it was previously located, in order to avoid trapping of material which may have been released into the water column when the trap was pulled to the surface.

PP sedimentation rates for each sampling date were estimated for PP >41μm and <41μm by using serial filtration of the sediment trap material. The absolute sedimentation rate (μmol m^{-2} d^{-1}) of PP >41μm and<41μm was calculated as Wodka et al. (1985). Concentration of both PP size classes in the sediment traps was corrected for hypolimnetic PP concentrations collected on the same day the trap was deployed.

Statistical analyses - In addition to examination of the seasonal trends of epilimnetic TP, TN, Chl*a*, and P fluxes (P regeneration, P flux to zooplankton and P sedimentation), I calculated mean summer concentrations and fluxes of each lake (May – September) in each year (5 sites x 2 years; $n = 10$). I used summer means for each lake in each year in statistical analyses instead of using individual time series measurements, because I wished to describe the average summer conditions and avoid pseudoreplication (Hurlbert 1984). Therefore, I examined both seasonal trends of P fluxes and the mean summer flux rates. Seasonal or annual means are commonly used in limnological research to describe lake conditions and processes (Fee et al. 1996; Mazumder 1994a;

Knoll et al. 2003). Mean summer P fluxes within the epilimnion (regeneration and zooplankton grazing P fluxes in moles l^{-1} d^{-1}) were converted to aerial rates (moles m^{-2} d^{-1}) in order to compare these fluxes to aerial sedimentation rates. For mean summer nutrient concentrations and plankton biomass (TP, PP, TN, Chl*a* in μg l^{-1}), I calculated the epilimnetic mass per unit area, (moles or μg m^{-2}) in order to facilitate the use of these measures into epilimnetic fluxes. Epilimnetic fluxes and concentrations were converted into per unit area measurements by multiplying the flux rate or concentration by the epilimnetic volume (in liters). Epilimnetic volume was estimated using the temperature profile on the sampling date and lake bathymetry (Spafard et al. 2002). If a site was not thermally stratified on a sampling date we considered the entire water column the mixed layer and the total basin volume was used in calculations. To evaluate hypotheses that P cycling should vary with TP, I performed ordinary least-squares regression (Zar 1999) using TP to predict P fluxes within (regeneration and grazing) and out of (sedimentation) the epilimnion. All statistical analyses were performed with SPSS version 8.0. Significance for all analyses was set at $\alpha \leq 0.05$.

Results

TP, TN and Chla concentrations - COL, SHL-N and SHL-S epilimnetic TP concentrations varied from 0.03 – 0.3 μmol L^{-1}, with COL concentrations often slightly lower than those of the SHL sites (Fig. 3.1a). All oligotrophic sites showed a trend of increasing TP concentration in the winter of both years. CUL TP ranged from 0.3 –1.2 μmol L^{-1} and ELL TP ranged from 0.3 – 2.5 μmol L^{-1} (Fig. 3.1b). Both meso-eutrophic lakes had increases in TP in the fall of both years. This increase may be due to the entrainment of anoxic P-rich hypolimnetic water above the thermocline later in the season (W. Nowlin, *unpubl. data*) and increased phytoplankton biomass (*See below*). Epilimnetic TN followed a similar seasonal pattern to TP at all sites (Fig. 3.1c and d). SHL-N and SHL-S had increases in TN in the winter in both years (Fig. 3.1c) and CUL and ELL TN concentrations, in general, increased in the fall and winter of both years (Fig. 3.1d).

In COL, SHL-N and SHL-S, epilimnetic Chl*a* concentrations were relatively low throughout both years (0.3 – 2.4 μg L^{-1}; Fig. 3.1e). Typically, COL Chl*a* concentrations were lower than the SHL sites. Chl*a* concentrations in all three oligotrophic sites remained consistent throughout the season in both years and did not vary by >2 μg L^{-1} from the annual average for each lake. In contrast, CUL and ELL Chl*a* remained low for most of the summer period (< 5 μg L^{-1}), but concentrations increased substantially in the fall or winter of both years (Fig. 3.1f). CUL Chl*a* concentrations increased by eleven-fold in September 2000 and by three-fold in September 2001. ELL Chl*a* remained <5 μg L^{-1} for all of 2000, but was ~18 μg L^{-1} in February 2001. Through most of the summer of 2001, ELL Chl*a* concentration remained <6 μg L^{-1} until a substantial increase in the fall of 2001. In addition, ELL and CUL experienced increased pelagic primary production in August and September of 2001 (Davies et al. *in review*). Unfortunately, primary productivity was not measured in 2000. The increases in Chl*a* in CUL and ELL in both years and primary productivity in 2001 were due to phytoplankton bloom events that contained significant numbers of nitrogen fixing bluegreen algae (J.M. Davies, *unpubl. data*).

Mean summer TP (μmol L^{-1}) and TN (μmol L^{-1}) of each site in each year were significantly correlated (Pearson $r = 0.97$, $F_{1,9} = 128.4$, $p < 0.000$). Mean summer epilimnetic Chl*a* concentration (μg L^{-1}) was a significant function of TP ($Chla = 7.3TP + 0.4$; $r^2 = 0.61$; $F_{1,9} = 12.4$; $p = 0.008$) and TN ($Chla = 0.2TN - 0.1$; $r^2 = 0.66$; $F_{1,9} = 15.5$; $p = 0.004$).

PO_4^{3-} turnover times and dissolved P regeneration – Turnover times of PO_4^{3-} pools in lakes were, in general rapid ($\leq$10 minutes) for most of the summer period, indicating strong P-deficiency of the plankton communities in all lakes (Fig. 3.2a and b). However, all sites exhibited seasonal variation in PO_4^{3-} turnover time. PO_4^{3-} turnover in COL varied seasonally in both years (Fig. 3.2a), but turnover time was always <20 minutes. SHL-N and SHL-S had rapid turnover times for most of the summer period (<10 minutes) and these times, in addition to PO_4^{3-} turnover times in COL, gradually increased as the season progressed in both years (up to 20 minutes in the fall and winter of both years). CUL and ELL exhibited greater seasonal variation than the three oligotrophic sites (Fig. 3.2b). Both CUL and ELL had rapid turnover times (<11 minutes) for most of the 2000 summer and, in August of that year, turnover times in both lakes increased to >20 minutes. The following month in both lakes, turnover times became rapid (<7 minutes). Similarly, in 2001, both lakes experienced large fluctuations in PO_4^{3-} turnover time. CUL PO_4^{3-} turnover time increased to 52 minutes in August 2001, but became rapid (4 minutes) the following month. By late October 2001 and February 2002, CUL exhibited PO_4^{3-} turnover times >35 minutes. In ELL, PO_4^{3-} turnover time was 66 minutes in May 2001, but became rapid (<10 minutes) and

remained so until late October (~239 minutes). From this point, ELL PO_4^{3-} turnover time remained >30 minutes through February 2002.

Examination of the seasonal patterns of phytoplankton biomass (Chl*a*) and PO_4^{3-} turnover time reveal that in CUL and ELL in both years, the late summer increases in PO_4^{3-} turnover times preceded (CUL 2000 and 2001, and ELL 2000) or coincided with (ELL 2001) seasonal Chl*a* maximums (Fig. 3.1f).

Planktonic dissolved P regeneration rates in COL, SHL-N and SHL-S were, on average, lower than in the two meso-eutrophic lakes (Fig. 3.2c and d). Regeneration rates from COL, SHL-N and SHL-S were relatively consistent throughout the year, but both SHL sites had high regeneration rates (0.14 and 0.24 μmol L^{-1} d^{-1}) in February 2002. In addition to having on average higher regeneration rates, ELL and CUL experienced greater seasonal variation in regeneration rates than the three oligotrophic sites (Fig. 3.2c and d).

Mean summer aerial dissolved P regeneration rates (Table 3.2) of each lake in each year increased with epilimnetic TP (Fig. 3.3a). Mean summer regeneration rates were sufficient to recycle 17 – 63% ($\bar{x}$ = 43%) of the epilimnetic TP pool per day. However, contrary to predictions (Harris 1986; Capblancq 1990), the percent of the TP pool recycled per day did not significantly vary with TP ($p = 0.14$; Fig 3.3b), indicating that the importance of planktonic regeneration did not decline with increasing TP.

Flux of PP <41µm to zooplankton – The grazing rates of COL, SHL-N and SHL-S ranged from 9.1 – 91% d^{-1}, however, on average across the summer period, grazing rates were approximately 30% d^{-1} at the three oligotrophic sites (Fig. 3.4a). SHL-S in January 2002 had a relatively high grazing rate (91%), which was much higher than any of the other systems at that time of year. The range of grazing rates in COL, SHL-N and SHL-S translated into flux rates for PP <41μm into zooplankton of 0.005 – 0.07 μmol P L^{-1} d^{-1} (Fig. 3.4c). CUL and ELL exhibited grazing rates similar to the oligotrophic sites, with a range of 11.6 – 99.2% d^{-1}, and zooplankton on average grazed ~33% d^{-1} in ELL and CUL (Fig. 3.4b). This range of grazing rates is translated into PP <41μm flux rates of 0.01 – 0.18 μmol P L^{-1} d^{-1} (Fig. 3.4d). Aerial PP <41μm zooplankton grazing flux rates were generally greater in ELL and CUL than in COL, SHL-N and SHL-S (Table 3.2), and the mean summer aerial flux rates of PP <41μm to zooplankton >200μm increased significantly with epilimnetic TP (Fig. 3.5a). The proportion of the PP <41μm pool grazed per day did not significantly vary with epilimnetic TP (Fig. 3.5b; $p = 0.144$); zooplankton >200μm grazed 21 – 41% ($\bar{x} = 32\%$) of the epilimnetic PP <41μm pool per day, regardless of epilimnetic TP.

PP sedimentation – PP sedimentation rates varied temporally in all lakes (Fig. 3.6). PP sedimentation rates into the hypolimnion of the three oligotrophic systems were on average lower than the two meso-eutrophic sites (Table 3.2; Fig. 3.6). COL, SHL-N and SHL-S sedimentation rates were always <17 μmol m^{-2} d^{-1} (Table 3.2; Fig. 3.6). COL had slightly higher PP sedimentation rates in the second year of the study, while SHL-N and SHL-S had similar average summer sedimentation rates in both years (Table 3.2). CUL and ELL sedimentation rates varied from 6.7 – 70.7 and 11.4 – 227.6 μmol m^{-2} d^{-1}, respectively. CUL and ELL exhibited higher summer PP sedimentation rates in 2000, when compared to 2001 (Table 3.2). Mean summer sedimentation rate increased with epilimnetic TP and this relationship was best fit by a non-linear function (Fig. 3.7a). The point in the relationship with the highest PP sedimentation rate (ELL in 2000) at first appears to dictate the non-linear function, however, if this point is removed, this relationship remains significant ($p = 0.002$) and is still best described by a non-linear function (r^2 of 2nd order polynomial function = 0.96; r^2 of linear function = 0.76). In agreement with the prediction of Reynolds (1986) and Capblancq (1990), the percent of the epilimnetic TP pool lost to sedimentation was a positive function of TP (Fig. 3.7b). Lakes lost 0.6 – 10.8% of their epilimnetic TP pools to sedimentation per day, and this relationship was non-linear (Fig. 3.7b).

PP >41μm accounted for 32 – 50% of the PP collected in traps in the May – September period in 2000 and 2001 (Table 3.3), and the mean proportion of PP >41μm collected in sediment traps from May – September was not significantly related to epilimnetic TP concentration ($p = 0.359$). In the winter of 2000, CUL, ELL, SHL-N and SHL-S all exhibited smaller proportions of PP >41μm in sediment traps, however, this trend was not present in winter 2001 (Table 3.3).

Comparison of P fluxes – Mean summer P fluxes within the epilimnion of all lakes (planktonic regeneration and zooplankton grazing) were always greater than the export of P through sedimentation (Table 3.2). Aerial regeneration fluxes within the epilimnion were 6 – 60 times greater ($\bar{x}$ = 28 times) than sedimentation export rates. The ratio of the mean summer regeneration flux rates to mean summer sedimentation rates was not significantly related to epilimnetic TP ($p = 0.296$). Similarly, the mean summer zooplankton grazing fluxes were 1.2 – 32 times ($\bar{x}$ = 11 times) greater than sedimentation losses (Table 3.2). The ratio of grazing P fluxes to sedimentation P fluxes was not significantly related to epilimnetic TP ($p = 0.179$).

Discussion

In summary, I observed that P fluxes in all sites exhibited seasonal variation over the 2.5-year study period, and oligotrophic systems typically had lower seasonal variation in P fluxes than the eutrophic systems. Mean summer P flux rates of planktonic regeneration, zooplankton grazing and P sedimentation increased with increasing epilimnetic TP, but the proportion of the TP pool recycled through regeneration and the proportion of PP <41μm grazed by zooplankton did not significantly vary with epilimnetic TP. However, the proportional sedimentation losses of epilimnetic TP increased with increasing epilimnetic TP. Regeneration and zooplankton fluxes rates were much greater than sedimentation losses, and the relationships between regeneration and sedimentation and grazing and sedimentation were not a significant function of epilimnetic TP.

Seasonal trends in P dynamics – In general, the meso-eutrophic sites exhibited larger seasonal fluctuations in PO_4^{3-} turnover time than the oligotrophic sites. In CUL and ELL, relatively long PO_4^{3-} turn over times (>20 minutes) preceded or coincided with Chl*a* peaks in the summer or fall of both years. Eutrophic ecosystems often exhibit greater seasonal variation and more defined periodicity in phytoplankton biomass than oligotrophic systems (Marshall and Peters 1989), and this trend was evident in my study sites. The late summer and early fall Chl*a* maxima in ELL and CUL in both years contained a large number of N-fixing cyanobacteria (J.M. Davies, *unpubl. data*), therefore, it is likely that variation in PO_4^{3-} turnover time was due to changes in P-deficiency associated with seasonal shifts in phytoplankton community composition.

All sites exhibited increases in PO_4^{3-} turnover times in the late-fall and winter period of both years. Most previous studies that have examined PO_4^{3-} turnover in lakes assessed mid-summer measurements or summer averages (Mazumder et al. 1988; Taylor and Lean 1991; Hudson et al. 2000), however, studies that have examined fall and winter PO_4^{3-} uptake and turnover have also noted similar increases in PO_4^{3-} turnover time (Halmann and Stiller 1975; Dodds et al. 1991; Millard et al. 1996). Halmann and Stiller (1975) hypothesized that increased winter PO_4^{3-} turnover time in Lake Kinneret may be associated with decreased water temperature or seasonal changes in lake hydrology. Millard et al. (1996) found that PO_4^{3-} turnover time ranged from 100 to more than 1000 minutes in Lake Ontario during the early spring and late fall. The authors concluded that the seasonal shifts in PO_4^{3-} turnover time were a complex function of lake stratification, light availability and phytoplankton composition.

Dissolved P regeneration rates and P fluxes to zooplankton also exhibited seasonal variation at all sites, however, these rates did not follow a clear temporal pattern. Interestingly, late fall and winter regeneration and grazing rates were often equal to or greater than summer rates in all sites. Few comparable data are available in the literature, however Dodds et al. (1991) found November and February planktonic P regeneration rates in oligotrophic Flathead Lake, Montana, USA, were equal to or higher than summer P regeneration rates.

Planktonic sedimentation rates often follow distinct seasonal variation related to shifts in plankton community composition (Sommer 1984). I observed large seasonal variation in PP sedimentation rates in all sites. Because I did not assess seasonal phytoplankton composition changes of study sites, I cannot comment on the role of seasonal plankton composition changes in affecting seasonal variation in PP sedimentation rates. Other studies have reported seasonal fluctuations in P sedimentation rates. For example, examination of PP sedimentation trends reported by Kleeberg (2002) in Lake Scharmützel reveals PP sedimentation rates varied as much as 6-fold within a single year. In my study, sedimentation rates within a single year (May – January or February) among all sites varied by an average of 9-fold (n = 10). The variation in PP sedimentation rates in lakes may be related to changes in the composition and size distribution of plankton communities (Sommer 1984; Mazumder et al. 1989; Larocque et al. 1996; Kleeberg 2002), however, further study is required to assess the relative strength of these and other factors in affecting seasonal trends in P sedimentation in lakes of varying TP concentration.

Mean summer P fluxes and implications for P cycling - Dissolved P regeneration rates of the plankton community increased with epilimnetic TP, however, the proportion of the epilimnetic P pool recycled per day did not exhibit a significant relationship with epilimnetic TP. According to the predictions of Harris (1986) and Capblancq (1990), as TP increases, plankton communities will recycle epilimnetic P less efficiently, therefore the proportion of the epilimnetic TP pool recycled per day should decline. My results do not support this prediction. Methodological problems are often associated with measuring planktonic P regeneration rates (Hudson and Taylor 1996), therefore the number of studies that have empirically evaluated this prediction are limited. Hudson et al. (1999) determined that in a large set North American lakes of varying TP concentration the turnover rate of the PP pool did not significantly vary with TP. In Chapter 2 of this dissertation, I determined that the turnover time of TP pools in eight

British Columbia lakes was independent from TP concentration. Based upon the results of this and other studies, further empirical assessment of this prediction is warranted in order to better understand the mechanisms controlling P regeneration in lake ecosystems of varying P concentration.

It has been hypothesized that the impact of zooplankton grazing should decrease with increasing nutrient concentration and productivity (McQueen et al. 1986; Sager and Richman 1991), however, there are data rejecting this hypothesis (Mazumder et al. 1992; Cyr and Pace 1993). The results of my study add further support to studies that have not found declines in grazing along increasing nutrient gradients. I observed that the flux of PP <41µm to zooplankton increased with epilimnetic TP, but the proportion of the PP <41µm pool grazed by zooplankton did not significantly vary with epilimnetic TP concentration (~30% d^{-1} on average for all systems). Cyr and Pace (1993) in a literature review of herbivore impact studies in terrestrial and aquatic ecosystems found that grazing rates increased with increasing annual net primary productivity and herbivores removed a similar proportion of annual net primary production in systems, regardless of productivity. My results agree with the findings of Cyr and Pace (1993) and further indicate that zooplankton appear to play a large role in the nutrient cycling of aquatic systems independently from the trophic status of the system. However, it is important to note that all of the systems included in this study were dominated by large zooplankton taxa (*Daphnia sp.* and calanoid copepods; W.H. Nowlin, *upubl. data*). Zooplankton communities dominated by small zooplankton taxa, such as *Bosmina sp.*, often do not exert the same grazing impacts as zooplankton communities dominated by large taxa (Carpenter et al. 1987; Mazumder et al. 1990). Therefore, it is unknown whether the inclusion of systems dominated by smaller zooplankton would affect the patterns observed by this study.

In the study presented here, PP sedimentation rates increased with epilimnetic TP and these rates were within the same range observed by other studies (Wodka et al. 1985; Mazumder et al. 1989; Caraco et al. 1992; Kleeberg 2002). In addition, the percent loss per day of the epilimnetic TP pool to sedimentation observed by this study (0.6 – 11%) was also within the same range observed by others. Mazumder et al. (1989) found that approximately 1 - 3% of the epilimnetic TP pool in lake enclosures was lost to sedimentation, however this percent loss was dependent upon the size distribution of the plankton community. Caraco et al. (1992) found that during the summer 3.4 – 6.7% of the epilimnetic TP from oligotrophic Mirror Lake was lost to sedimentation per day. Levine et al. (1986) in a whole lake ^{32}P addition experiment found that P was lost from the water column at a 2.1% d^{-1} rate during the late summer and early fall. In addition, I found that the percent of the epilimnetic TP pool lost to sedimentation increased significantly with epilimnetic TP, thus supporting the predictions of Reynolds (1984) and Capblancq (1990). This result is in contrast to other studies that have assessed this hypothesis. Mazumder et al. (1989) found that fertilization of lake enclosures did not have a significant effect on the proportion of TP lost to sedimentation per day. Baines and Pace (1994) reported that the proportion of planktonic primary production (as carbon) lost to sedimentation declined with increasing planktonic primary production (opposite of the predicted trend).

The continuous loss of epilimnetic P through sedimentation during the summer stratification period will presumably lead to the depletion of epilimnetic P. However, limnologists have long observed that the TP in many lakes does not significantly decline during summer (Juday et al. 1927, Caraco et al. 1992). Indeed, in the study presented here, epilimnetic TP concentration of all of the study sites remained consistent over the summer period, and in some cases periodically increased. Planktonic P regeneration on a daily basis recycled a large percentage ($\bar{x} = 43\%$) of the epilimnetic TP pools, however, this percentage did not significantly vary with epilimnetic TP. At the same time, the proportional sedimentation losses of epilimnetic TP increased as overall concentration of epilimnetic P (TP) increased. Obviously, in order to maintain consistent epilimnetic TP concentrations throughout the summer in light of 1 – 11% TP losses per day to sedimentation, all lakes regardless of TP concentration, must rely upon P inputs to the epilimnion throughout the summer. Yet, the increasing proportional loss of epilimnetic TP in the more eutrophic sites clearly indicates that these externally derived P inputs are of greater importance throughout the summer in more eutrophic systems. Therefore, the results from my study appear to support the prediction of Reynolds (1984), Harris (1986) and Capblancq (1990) that as epilimnetic nutrient concentrations increase, plankton communities will become increasingly dependent upon "new" nutrient sources during the summer stratification period. While this result does not necessarily mean that more oligotrophic systems cycle epilimnetic P more "efficiently", it indicates that more eutrophic systems must rely to a greater extent upon "new" P sources in order to maintain epilimnetic P concentrations throughout the summer. Among the numerous "new" sources of P to the epilimnion, hypolimnetic entrainment, surface runoff, atmospheric deposition and regeneration by fish have been indicated as important inputs in summer P budgets (Caraco 1992; Vanni 2002). I did not assess these potential sources, therefore I cannot comment on their relative importance of supplying P to epilimnetic plankton communities. Further study is required to assess whether the relative importance of these and other "new" sources of P in lakes have a significant relationship with TP concentration.

Results from my study indicate that planktonic nutrient fluxes within the epilimnion (P regeneration and zooplankton grazing) do not exhibit a significant relationship with epilimnetic TP, but both pathways cycle a substantial portion of a lake's TP pool per day, regardless of epilimnetic TP concentration. Further, I found that P sedimentation losses become increasingly important as epilimnetic TP increases. The trend of a consistent proportion of the epilimnetic P pool recycled by P regeneration accompanied by increasingly greater proportional P sedimentation losses across systems of varying TP indicates that the prediction that plankton will become increasingly reliant upon external nutrient sources and less upon recycled sources as TP increases is correct. Certainly, additional examination of these trends in lakes that represent a more extensive range of TP concentration is required, however, results from this study provide valuable insight to P cycling in lake ecosystems.

Chapter 4: Effects of Water Level Fluctuation and Short-Term Climate Variation on Thermal and Stratification Regimes of a British Columbia Reservoir and Lake

Introduction

Annual cycles of thermal stratification, water temperature and heat content fundamentally influence the ecology of lakes and reservoirs. Water column mixing and annual thermal regimes affect nutrient cycling (James 1990; Soranno et al. 1997), plankton species composition (Proulx et al. 1996) and organism growth rates (Edmundson and Mazumder 2001). Historically, limnologists have recognized the ecological importance of lake physical conditions and have examined these processes in individual lakes (Likens and Johnson 1969; Ambrosetti and Barbanti 2001) and at the regional scale (Benson et al. 2000; Edmundson and Mazumder 2002). However, most studies that have formed our current understanding of mixing and thermal regimes have been conducted in north temperate lakes of glacial origin (but see Kling 1988; Gellar 1992).

In contrast to natural lakes, reservoirs have received less intensive study from limnologists. Despite the dominance of natural lakes in the literature, limnologists have identified physical processes unique to reservoirs that influence their ecology and water quality (Ford 1990; Kennedy 2001). Reservoirs typically have more variable and complex hydrology than natural lakes, due to anthropogenic manipulation of inflows and outflows (Ford 1990). Reservoirs commonly experience relatively large water level fluctuations associated with operation (Ryder 1978; Straškraba et al. 1993). Annual water level fluctuations (hereafter known as drawdown and recharge) in north temperate reservoirs generally follow a pattern in which the reservoir is recharged in the winter or spring and drawn down over the summer or winter.

The continuous removal of reservoir volume over the summer (when inflows are low) can affect the length of summer stratification (Barone and Naselli-Flores 1994; Effler and Bader 1998) and be a significant term in heat budgets (Barone et al. 1993; Owens 1998c). In contrast, many natural lakes exhibit a period of hydraulic stagnation in summer characterized by low or absent inflows and outflows. Therefore, the management practice of removing substantial water volume over the course of the summer may cause a reservoir to significantly differ from seasonal stratification and thermal regimes of nearby natural lakes subject to the same meteorological conditions.

The magnitude of impacts from seasonal drawdown on reservoir physical processes is dependent upon factors including reservoir-specific hydrology and morphometry (Straškraba et al. 1993), and interannual climatic conditions (Owens et al. 1986). Interannual climatic variability can greatly influence stratification and thermal regimes of reservoirs and natural lakes (Effler et al. 1986; Fee et al. 1996; Snucins and Gunn 2000). Variation of meteorological parameters such as precipitation may be of concern for reservoirs, because reservoir ecology is closely coupled with their hydrology (Ford 1990). Reduced precipitation can affect regional hydrology, resulting in reduced stream inputs to lakes and reservoirs (Schindler et al. 1996). If sufficient water is not available to completely recharge a reservoir that experienced a relatively large summer drawdown, the influence of drawdown on physical processes during the following summer may be magnified due to lower reservoir water levels prior to the summer drawdown period. For example, a reservoir with relatively low water levels at the beginning of the summer drawdown period may will faster flushing rates and potentially shorter stratification period duration when compared to a summer in which the reservoir completely recharged prior to the drawdown season. Therefore, examining the effects of climatic variability on physical processes in reservoirs and natural lakes offers an opportunity to further understand the relative sensitivity of both systems to variation in climatic conditions.

In the study presented here, I examined the effects of summer drawdown over a two-year period in a reservoir and a natural lake in coastal British Columbia, Canada. I examined the effects of a relatively large percentage of volume removal over the summer and early fall on water column stratification, water temperatures and heat budgets of Sooke Lake Reservoir, and compared these seasonal regimes to Shawnigan Lake, a nearby natural lake of similar size, morphometry and trophic status. The comparison of Sooke Lake Reservoir and Shawnigan Lake allowed me to quantitatively assess the magnitude of the impacts of summer drawdown on the timing of reservoir thermal and stratification regimes in reference to conditions in a nearby similar natural lake (Straškraba et al. 1993; Kennedy 2001).

I further examined the relative magnitude of drawdown effects in relation to interannual variability in climatic conditions. During the second year of the study (2001), Sooke Lake Reservoir did not completely recharge prior to the summer drawdown period due to lower than average precipitation during the preceding recharge period (winter 2000 – spring 2001). Contrasting years of climatic conditions, in terms of precipitation, offered a unique opportunity to compare responses of an anthropogenically-manipulated reservoir and a natural lake to short-term changes in precipitation.

Methods

Study Sites - Sooke Lake Reservoir (Sooke) is located on Vancouver Island, British Columbia, Canada (Fig. 4.1). The reservoir was created in 1914 by damming the outlet of Sooke Lake, which discharges into the Sooke River. Sooke is classified as a lake-reservoir, which differs from a run-of-the-river reservoir (Straškraba et al. 1993). Sooke serves as the main drinking water supply for the city of Victoria (population ~ 300,000). Approximately 90% of annual inflow volume to the reservoir comes in October to April as rain-generated stream flow, and after the reservoir refills in winter and spring, a relatively large volume spills over the dam (1999-2000 recharge period total dam spill volume = 34 x 10^6 m^3 year $^{-1}$; mean flow rate = 0.34 x 10^6 m^3 day^{-1}). In late spring and early summer, stream inflow to the reservoir declines and drinking water consumption increases, causing the reservoir to decrease in volume until the late fall, when rainfall increases again. Both the drinking water intake and the dam allow for the outflow of epilimnetic water only.

Sooke has three main basins (Fig. 4.1). The largest basin at the north end of the reservoir (north basin) is relatively deep (Z_{max} = 70 m) and receives the majority of stream input, when compared to the south basin (Z_{max} = 22 m) (Fig. 4.1, Table 4.1). The north and south basins of Sooke represent physical environments that differ morphometrically and hydrologically (Table 4.1). Basins within the same water body that differ morphometrically (shallow versus deep) can create ecologically distinct environments (Frenette et al. 1996; Proulx et al. 1996). Therefore, we examined responses of the north and south basins of Sooke to seasonal drawdown in order to gain insight into the potential responses of relatively deep versus shallow systems to summer drawdown.

Shawnigan Lake (Shawnigan) is a lake of glacial origin located 4 km to the northeast of Sooke, primarily used for recreation, but a limited amount of water is withdrawn for local residents. Shawnigan has three main basins: a larger, deeper north basin ($Z_{max} = 53$ m) and a shallower south basin ($Z_{max} = 27$ m) separated by a middle basin (Fig. 4.1, Table 4.1). Inflows to Shawnigan follow the same seasonal pattern as Sooke (Nordin and McKean 1984). Shawnigan flows from the southern end to an outlet stream at the north end of the lake. We selected sampling sites in the north basin and south basin of the lake. While the direction of flow through Sooke and Shawnigan differs (Sooke flows north to south and Shawnigan flows south to north), the selection of morphologically similar sites within each water body allowed us to examine the seasonal mixing and thermal patterns in morphometrically similar basins in a reservoir and a natural lake under contrasting summer drawdown regimes.

Both water bodies are warm monomictic (Wetzel 2001), due to the mild climate in the North American coastal Pacific Northwest. In winter, minimum water temperatures typically reach ~5°C and permanent ice cover does not occur (W. Nowlin and Capital Regional District Water Department, *unpubl. data*). Both water bodies are oligotrophic, with Shawnigan having slightly higher Chl-*a* and nutrient concentrations than Sooke (Table 4.1), which may be due to development in the watershed. Sooke has a protected watershed with no public access and Shawnigan has ~600 houses within 1 km of its shoreline.

Meteorological and Hydrological Data - Meteorological data were obtained from a station on the Sooke Dam. Summer mean daily air temperature, solar irradiance and wind speed were calculated from hourly measurements taken at the meteorological station from 1 May - 30 September 2000 and 2001. Irradiance was measured on a Li-Cor LI-90SZ pyrheliometer and wind speed and direction were taken with an anemometer. Daily precipitation measurements have been taken at Sooke since 1895, and a 104-year average (excluding 2000 and 2001) of both total annual and total monthly precipitation were calculated.

Water surface elevations (meters above sea level – m.a.s.l.) of both water bodies were obtained from staff gauges. Daily measurements of water surface elevation were collected for Sooke and measurements were taken from Shawnigan every two to three weeks. Staff gauge measurements were used to calculate whole lake and basin water volumes using bathymetry (Spafard et al. 2002). The movement of water into and out of Sooke and Shawnigan was examined over the study period. I considered the only major inflows for both water bodies to be streams and the major water outputs to be lake surface evaporation, stream outflow (for Shawnigan) or the dam spillway and the drinking water intake (for Sooke). I did not estimate non-channelized surface runoff or subsurface inflows and outflows because estimates of these parameters are difficult to obtain (Winter 1985) and are likely small contributions to the water balance when compared to the fluxes examined by this study. I obtained inflow data for all major creeks discharging into Sooke from weir gauges maintained by the Capital Regional District (CRD) Water Department. Weirs recorded total daily flow volumes and monthly inflow rates ($x10^6$ m^3 day^{-1}) were calculated. Water inflow rates into the north and south basins were calculated separately, based upon location of inflowing creeks. Regular weir gauge measurements of inflowing creeks were not available for Shawnigan. However, the British Columbia Ministry of Environment, Lands and Parks (now BC Ministry of Water, Land and Air Protection) had previously conducted a long-term detailed study of Shawnigan Lake hydrology (Nordin and McKean 1984). I obtained a 15-year data set of monthly total creek discharge into the lake. Since creek flows in this region are tightly coupled with rainfall, I predicted total monthly inflow to Shawnigan from total monthly precipitation records from the Sooke Lake Reservoir dam meteorological station for the same 15-year time period. Total monthly rainfall (PCP_M in mm) predicted total monthly lake inflow (V_I in x10^6 m^3) reasonably well ($V_I = -166853.6 + 21134.5\ PCP_M + 79.12\ PCP_M^2$, $r^2 = 0.851$, $P = 0.0002$). I used this model to estimate total monthly inflow to the whole lake, the north basin and the south basin using monthly precipitation data.

Monthly estimates of surface evaporation from the entire water body and individual basins were obtained with the model of Morton (1979). Outflow data for Sooke were obtained from flow measurements taken from the dam and at the drinking water chloramination plant (downstream in the distribution system and gravity fed from the drinking water intake). Both outflows measured the total volume discharged over a 24-hour period. Shawnigan Lake total monthly outflow volume (V_O in x10^6 m^3) was from the difference of incoming and outgoing flows, according to

$$V_O = V_I - \Delta V_L - V_E \tag{4.1}$$

where V_I is the total monthly inflow, ΔV_L is the change in water volume of the entire lake over the month interval and V_E is the total monthly evaporation volume.

Longitudinal flow of water can be important in the transfer of heat and materials within a water body, potentially affecting physical dynamics (Owens 1998b), therefore I examined these water movements within the water bodies. Because Sooke flows north to south and Shawnigan flows south to north, the transfer of volume out of the north basin of Sooke (to the south basin) and out of the south basin of Shawnigan (to the north basin) was estimated with the following equation

$$V_{IBT} = \Delta V_B - (V_I - V_E) \tag{4.2}$$

where V_{IBT} is the monthly interbasin transfer volume (x10^6 m^3), ΔV_B is the change in basin volume over the interval, V_I is the inflow volume to the basin, and V_E is the evaporation loss volume. The interbasin transfer volumes into the south basin of Sooke (from the north) and into Shawnigan north basin (from the south) were calculated using Equation 2, but subtracting $(V_I - V_E - V_O)$ from ΔV_B, where V_O is the basin outflow volume (either the stream outflow for Shawnigan or the sum of the drinking water outflow and the dam spill for Sooke).

Stratification and Thermal Regimes - Sooke and Shawnigan were sampled from early May to late November at the north and south basin sites (Fig. 4.1) at least every three weeks in 2000 and at least every two weeks in 2001. Water temperature was measured with a YSI Model 58 every 1 m, except through the metalimnion, where I measured temperature every 0.5 m. At greater water depths when temperature changes with depth were minimal, I took measurements approximately every 5 m. I interpolated temperatures to every 0.5 m depth.

On each sampling date, I determined whether the water column was thermally stratified through inspection of the temperature profile. When there was a region in the water column where the rate of temperature change was ≥1°C m $^{-1}$, I considered the water column to be thermally stratified. The epilimnion was defined as starting at lake surface and down to, but not including, the depth where the rate of temperature change was ≥1°C m^{-1}, the metalimnion was the portion of the water column that exhibited temperature change of ≥1°C m^{-1}, and the hypolimnion was from the bottom of the metalimnion to the sediments. If the water column was not stratified, I considered the water column equivalent to the mixed layer (epilimnion). Thermocline depth was defined as the depth within the metalimnion that exhibited the greatest density change with depth. The relative thermocline depth (α of Gorham and Boyce 1989) was calculated as the ratio between thermocline depth and maximum water depth of the basin at the time of sampling.

I calculated Schmidt stability indices (*S*) of all basins on each sampling date. *S* is the quantity of energy (per unit surface area) required to instantaneously mix the entire water column to an isothermal temperature, without addition or subtraction of heat (Wetzel 2001). *S* (g-cm cm^{-2}) was calculated using

$$S = \frac{1}{A_0} \sum (z - z^*)(\rho - \rho^*) \mathrm{A_z dz} \qquad (4.3)$$

where A_0 is lake or reservoir surface area, z^* is the water column depth at which the mean water column density occurs, ρ^* is the water density at the depth of mean density (z^*), and A_z is the lake surface area at depth z. Calculations for all water depths (z) and water densities (ρ) were summed over a dz interval of 0.5 m.

On each sampling date, volume-weighted epilimnetic and hypolimnetic temperatures (T_E and T_H, respectively) was calculated using

$$T_E \text{ or } T_H = \frac{1}{V_W} \sum_{z=1}^{z=n} t_z V_z \tag{4.4}$$

where V_W the volume of the layer on a sampling date, t_z is the temperature of a depth interval in layer, V_z is the volume of the depth interval and n is the number of depth intervals. The summation was taken over all depths at 0.5 m increments from the initial depth of the layer to the bottom of the layer. I calculated the seasonal mean epilimnetic ($\overline{T}_E$) and hypolimnetic ($\overline{T}_H$) temperatures of each basin as the mean of all sampling dates in which the basin was thermally stratified.

I calculated Birgean summer heat budgets (θ_S) for each site within both water bodies. Most studies define θ_S as the amount of heat necessary (per unit surface area) to raise a lake from 4°C to the maximum summer heat content (Wetzel 2001). This definition is difficult to apply to Sooke and Shawnigan because both water bodies typically do not reach 4°C in the winter. Therefore, for the purposes of this study, I defined θ_S as the amount of heat required (per unit surface area) to raise water temperature in early May to the date of maximum summer heat content in summer. This definition shortens the effective heating season and leads to lower summer heat budget estimates than those calculated by other studies. However, this method allowed me to standardize the starting point of the heating season and estimate the date of maximum heat content of the basins (see below). To estimate θ_S for each basin (Wetzel and Likens 2000), I calculated the volume of 0.5 m depth intervals in each basin and multiplied the volume by the temperature of the interval to yield heat content (watts) (Edmundson and Mazumder 2001; Edmundson and Mazumder 2002). Heat content of all intervals was summed and divided by the surface area of the basin, yielding megawatt m^{-2}. I plotted basin heat content as a function of the day-of-year number (DOY) and fitted a 3rd or 4th order polynomial function. The date of maximum heat content (H_M) for the basin was estimated by taking the first derivative of the function, setting the solution to zero and solving for x. To calculate the predicted heat content on this date (θ_{HM}), I used the predicted date of maximum heat content in the fitted function and solved through substitution. To calculate θ_S of each basin, I subtracted the observed heat content of each basin in early May (from 2 - 10 May 2000 and 2001) from θ_{HM}.

To gain further insight into the relative importance of the different seasonal heat fluxes associated with water movement (Owens et al. 1998c; Wetzel and Likens 2000), I examined heat fluxes in each water body in relation to hydrological inputs and outputs. In Sooke, I calculated heat fluxes into the reservoir from hourly temperature measurements of all major inflowing streams. Mean monthly stream water temperature was multiplied to monthly flow volume, yielding monthly stream heat input (watts day^{-1}). Regular data on stream water temperature was not available for the inflowing creeks of Shawnigan. I obtained 5 years of hourly temperature data from a nearby stream (Rithet Creek) very similar to Shawnigan inflowing streams. I regressed mean monthly stream water temperature (T_I) as a function of mean monthly air temperature (T_A) and found that, on a monthly time scale, air temperature predicted stream water temperature very well ($T_I = 3.12 + 0.282\ T_A + 0.0263\ T_A^2$, $r^2 = 0.959$, $P < 0.0001$), and used this function to estimate mean monthly water temperature of streams discharging into Shawnigan. For both water bodies, I calculated monthly inflow heat fluxes (Φ_I) by dividing the total heat input by average water body or basin surface area for the time period. Monthly heat fluxes out of Sooke and Shawnigan were calculated by multiplication of outflow and evaporation volumes to mean monthly volume-weighted epilimnetic temperatures (T_E), because both Sooke and Shawnigan only discharge surface water. When Sooke and Shawnigan were not stratified, I used the mean monthly volume-weighted water column temperatures (T_W – calculated using Equation 4.4). These values were used to calculate heat fluxes out of Sooke through the drinking water inflow (Φ_{DW}), and the dam spillway and the Shawnigan outflow (Sooke dam spill and Shawnigan stream outflow both denoted Φ_S). I estimated the interbasin heat transfer (Φ_{IBT}) for each basin by multiplying interbasin transfer volume by T_E or T_W, depending upon whether the basin was stratified. All values were converted to fluxes by dividing the heat transfer by the surface area of the water body or basin.

Results

In 2000, Sooke water level decreased by 6.25 m from mid-April to late-November (Fig. 4.2). Reservoir total volume decreased by 30.3 x 10^6 m^3 over this period, a 70% loss of volume from the south basin and a 26% loss of volume from the north basin. During the same period, Shawnigan depth decreased 0.52 m (4.6% volume loss) (Fig. 4.2). Sooke did not completely recharge to full stage water depth and volume during the 2000-2001 recharge period (October 2000 – April 2001) and was 2.72 m below full stage prior to the start of the 2001 drawdown season (Fig. 4.2). At the point of maximum drawdown in 2001, the volumes of the south and north basin of Sooke were 0.94 x 10^6 m^3 (full stage = 3.81 x 10^6 m^3) and 70.2 x 10^6 m^3 (full stage = 98.65 x 10^6 m^3), respectively. Shawnigan completely refilled prior to the summer of 2001 and had a total water depth reduction of 0.52 m (4.4% volume loss) over the summer and fall of 2001 (Fig. 4.2).

Sooke did not completely recharge to full-stage prior to the summer 2001 drawdown season because of lower than average precipitation in the 2000-2001 recharge period. Monthly rainfall totals in the fall and winter of 2000 were equivalent to a 100-year drought, making the total annual 2000 rainfall 583 mm lower than the long-term annual average (1642 mm $year^{-1}$) (Fig 4.3a and 3b). This period of below-average rainfall persisted until the spring of 2001, but monthly totals were close to long-term monthly means by fall 2001 (Fig 4.3b). Mean summer air temperature, total daily irradiance and wind speed were remarkably similar between summers (Table 4.2), suggesting the principal meteorological difference between the two summers was the decrease in precipitation preceding the summer of 2001.

The drought in the 2000-2001 recharge period was associated with a 50% reduction in stream flow to Sooke and Shawnigan, compared to the 1999-2000 recharge period (Fig. 4.4). Both water bodies had similar seasonal stream inflow patterns and exhibited the same stream inflow reduction during the 2000-2001 winter drought. However, the relative importance of the various water exports from the two water bodies differed. In Sooke, over the two-year study period, drinking water consumption removed a total of 111×10^6 m^3 of water, a volume greater than the dam spillway (34×10^6 m^3) or evaporation (10.9×10^6 m^3). On a basin-specific basis in Sooke, evaporative losses were never greater than drinking water withdrawal losses (the drinking water intake in the south basin and the interbasin export out of the north basin). The greatest drinking water outflow rates in Sooke were observed from May - October ($0.13 - 0.26 \times 10^6$ m^3 day^{-1}), however, maximum drinking water outflow rates and total withdrawal volumes were lower in 2001 due to water use restrictions in response to the lower reservoir levels. In

Shawnigan, much smaller summer decreases in volume led to rapid lake volume recharge and a tighter coupling of lake inflows and outflow (Fig. 4.4). Evaporation was the dominant loss from Shawnigan during both summers (May-September 2000 and 2001 total evaporation loss = 8.58×10^6 m^3) and exceeded stream outflow (2000 and 2001 total stream outflow volume = 6.44×10^6 m^3).

Both basins of Sooke were stratified for shorter periods of time than both basins of Shawnigan in both summers (Table 4.3). Stratification of the south and north basins of Sooke was not observed until mid-June in 2000, approximately one month after stratification in both basins of Shawnigan, but all basins destratified during the same time period. In 2001, the south basin of Sooke had a stratification period approximately two weeks shorter than the previous year and ~1.5 months shorter than the stratification period of both basins of Shawnigan. Shawnigan had little variation in the duration of the stratification period between years.

Temperature profiles from all basins exhibited strong vertical temperature gradients through most of the summer period (Fig. 4.5). Surface temperatures in all basins did not exceed 24°C during the summer and hypolimnetic temperatures showed a gradual warming from May - September in both years (Fig. 4.5). Epilimnetic depth was generally greater in both basins of Sooke than in Shawnigan (Fig. 4.5, Table 4.4). In both water bodies, the larger north basins had deeper epilimnia when compared to their corresponding south basins (Table 4.4). The relative thermocline depth (α - proportion of the water column above the thermocline) also followed a similar trend, with the northern basins of both water bodies having a smaller proportion of the water column above the thermocline than in the shallower south basins (Table 4.4).

Longitudinal temperature gradients (north basin versus south basin) at specific depths (1, 5 and 10 m) within both water bodies were less than vertical temperature gradients (Fig. 4.6). Longitudinal temperature gradients in the surface waters (1 and 5 m) in both water bodies were small (on average $\leq 1^{\circ}$C difference between north and south basins of both water bodies) suggesting minimal impediment to mixing between surface waters between basins (Fig. 4.6a, b, d, e). At lower depths (10 m) temperature differences were greater than in the surface waters. In Sooke, water at 10 m in the south basin was consistently ≥ 3 °C cooler than in the north basin (Fig. 4.6c). Shawnigan also exhibited a similar longitudinal temperature gradient at 10 m (Fig. 4.6). Higher temperatures at 10 meters in the north basins of both water bodies reflect the relatively deeper epilimnia of the north basins than in the south basins (Fig. 4.5, Table 4.4). Longitudinal temperature gradients between basins at the same depths suggest that deeper waters between basins likely faced impediment to mixing and reflect basin-specific, rather than lake-wide, heating processes in both water bodies.

Average volume-weighted epilimnetic temperatures $(\overline{T}_E)$ were similar in all basins (Table 4.5). Sooke south basin had the highest volume-weighted hypolimnetic temperatures $(\overline{T}_H)$ of all basins in 2000 and 2001 (Table 4.5). Sooke south basin exhibited the smallest temperature differences between the epilimnion and hypolimnion (Table 4.5).

Maximum Schmidt stability (*S*) increased with basin volume (Fig. 4.7), but interannual differences in basin volume associated with the 2000-2001 drought affected maximum summer *S* of both basins of the reservoir. Maximum observed *S* of the south basin of Sooke was 408.77 g-cm cm^{-2} in 2000 and 185.8 g-cm cm^{-2} in 2001, a 55% reduction in 2001 (Fig. 4.7). Similarly, the north basin of Sooke experienced a 20% reduction in maximum S in 2001, when compared to 2000. The south basin of Shawnigan had no change in maximum S between years and the north basin had a greater maximum S in 2001 than in the summer of 2000 (Fig. 4.7).

Birgean summer heat budgets (θ_S) increased with basin size (Fig. 4.8). The smaller Sooke south basin volume in 2001 showed a 31% decrease in θ_S in 2001, when compared to the previous year (2000 = 2.6 megawatt m^{-2}, 2001 = 1.8 megawatt m^{-2}). θ_S of the north basin of Sooke and both basins of Shawnigan were not different between years. The timing of the date of maximum heat content (H_M) of the south basin of Sooke was affected by the relatively large volume reductions (Fig. 4.8). H_M of Sooke south basin was approximately 2 weeks earlier than all of the other basins in 2000. In 2001, during the period of low water levels, H_M was >5 weeks earlier than the other study basins. The north basin of Sooke and both basins of Shawnigan had H_M dates very close to one another in both summers.

The drinking water withdrawal out of Sooke was the largest heat flux out of the reservoir, especially during the summer and fall (Fig. 4.9). On a whole reservoir basis, the total flux out of the lake in the May – October period associated with the drinking water outflow (Φ_{DW}) was 7 – 10 times greater than evaporation losses (Φ_E). The magnitude of heat fluxes associated with the withdrawal of water from the two Sooke basins differed (Φ_{IBT} in the north basin and Φ_{DW} in the south basin). The maximum summer heat flux out of the north basin associated with the removal of water (Φ_{IBT}) was

2.78 and 2.91 megawatts m^{-2} day^{-1} in 2000 and 2001, respectively. The south basin exported heat at a maximum rate more than an order of magnitude greater than the north basin in both summers (2000 = 49 megawatts m^{-2} day^{-1}, 2001 = 30.2 megawatts m^{-2} day^{-1}). In contrast to Sooke, the dominant heat flux out of Shawnigan in the summer – fall period was evaporation (Φ_E) (Fig. 4.9). On average, from April – September of both years, total evaporative heat losses were 12 times greater than the heat flux out of the lake outflow stream.

Discussion

Lakes within the same region typically exhibit a high degree of temporal coherence in seasonal thermal conditions, and deviation of individual lakes from regional thermal regimes can be due to basin morphometry and water clarity (Fee et al. 1996; Benson et al. 2000). In the study presented here, despite similar morphometry and trophic states, seasonal stratification and thermal regimes differed between the morphometrically similar basins of Sooke Lake Reservoir and Shawnigan Lake. Contrasting drawdown regimes of the two water bodies caused the timing and duration of stratification, summer heat budgets and the relative importance of seasonal heat fluxes to differ, despite exposure to identical climatic conditions. Furthermore, the responses of the stratification and thermal regimes of the two water bodies to the drought of 2000-2001 differed because of human manipulation of the hydrology of Sooke Lake Reservoir. The magnitude of these impacts, however, were mediated by interbasin differences in morphometry, as observed by the greater interannual differences in stratification and thermal regimes in the south basin than in the north basin of Sooke.

Sooke Lake Reservoir was stratified for shorter periods of time than Shawnigan Lake in both years. Removal of reservoir volume over the summer and fall can shorten the stratification period (Effler and Bader 1998; Owens 1998c) or cause polymictic conditions (Barone and Naselli Flores 1994). Sooke experienced a later onset of summer stratification than Shawnigan (2 – 4 weeks later), which may be related to relatively higher flow rates out of the reservoir during the spring and early summer. Flow within reservoirs associated with inflows and discharge can create complex stratification patterns or prevent stratification if flow rates are great enough (Ford 1990; Townsend 1998). While the stream inflow rates into both water bodies were similar during May – June of 2000 and 2001 (Sooke May – June 2000 and 2001 mean inflow rate = 0.02×10^6 m^3 day^{-1}, Shawnigan mean inflow rate = 0.04×10^6 m^3 day^{-1}), the outflow rates were 8 times greater in Sooke (Sooke May – June 2000 and 2001 outflow rate = 0.16×10^6 m^3 day^{-1}, Shawnigan May – June 2000 and 2001 outflow rate = 0.02×10^6 m^3 day^{-1}). The timing of destratification in the fall of both years was similar between Sooke and Shawnigan, except for Sooke south basin in the second year of the study. In 2001, when reservoir water levels were lower, Sooke south basin destratified more than a month before the other basins. It is not unexpected that Sooke south basin had an earlier turnover date in 2001 because relatively shallow basins with warmer hypolimnetic temperatures are more likely to have earlier fall turnover dates than deeper lakes (Nürnberg 1988).

Lake heat budgets increase with lake depth, volume and surface area (Gorham 1964; Timms 1975) and in my study, Birgean summer heat budgets (θ_S) increased with basin size. θ_S values had little variation between years in the north basin of Sooke and both basins of Shawnigan, however, in 2001, Sooke south basin experienced a ~30% reduction in θ_S from the previous year. The reduction in θ_S in 2001 was due to the comparatively smaller basin volume and the removal of warmer epilimnetic water from the basin continuously through the summer. In addition, the relatively large volume of epilimnetic water removed from the south basin of Sooke affected the timing of the date of maximum heat content (H_M). H_M is often consistent at a regional scale, even among lakes representing a wide range of surface temperatures and optical properties (Edmundson and Mazumder 2002). H_M of the south basin of Sooke was two weeks earlier in 2000 and more than five weeks earlier in 2001 than H_M of the other study basins. I also observed a decoupling of the dates of maximum surface water temperature and H_M in the south basin of Sooke. Maximum epilimnetic temperatures occurred in all basins in late July to mid-August in both years, which coincided with H_M dates of the north basin of Sooke and both basins of Shawnigan. The assumption of synchrony in the dates of maximum heat content and the dates of maximum surface temperature made by previous studies (Edmundson and Mazumder 2001; Edmundson and Mazumder 2002) may not be applicable to reservoirs that experience relatively large summer epilimnetic withdrawals.

Removal of significant volumes of epilimnetic water from reservoirs will dissipate heat at high rates, creating large summer heat sinks from reservoirs (Martin and Arneson 1978; Kennedy 2001). In contrast, discharge of cooler, deeper waters of the meta- or hypolimnion may cause the reservoir to function as a seasonal heat trap, due to the retention of warmer epilimnetic waters. The discharge of epilimnetic water during the summer and early fall from Sooke was the largest heat export from the reservoir. In the south basin of Sooke the drinking water withdrawal removed up to 50 megawatts m^{-2} day^{-1}, while in the north basin the volume of water exported was similar, the per unit surface area heat flux was approximately 10 times less. In contrast to Sooke, evaporation dominated summer heat losses from Shawnigan, which corresponds with classical models of lake seasonal heat fluxes (Hutchinson 1957; Wetzel 2001). Shawnigan also discharges surface water, but total evaporative heat losses from April – September of both years were more than an order of magnitude greater than the total lake outflow heat losses.

Long- and short-term decreases in precipitation have been associated with changes in lake water clarity, ion and nutrient concentrations and mixing regimes (Schindler et al. 1996; Schindler et al. 1997; Webster et al. 2000). The effects of interannual changes in precipitation on reservoir ecosystems have received comparatively less attention (LaBounty and Sartoris 1981), and even less information is available on the comparison of responses of lakes and reservoirs to short-term changes in precipitation. The cumulative effect of climate and human activity on freshwater ecosystems has received recent emphasis and has underscored the lack of knowledge about the potential synergistic effects of climate and anthropogenic stressors (Schindler 2001). In the present study, reservoir stratification and thermal regimes were more sensitive to short-term changes in precipitation than the adjacent natural lake because the reservoir experienced large water level fluctuations associated with drinking water withdrawal. The shallower south basin had a much greater sensitivity to both stressors when compared to the north basin of the reservoir. The combined impacts of seasonal water level fluctuations and climate variability present ecological and management implications for reservoir systems. For example, the drawdown of a basin during the summer could lead to destratification and subsequent entrainment of nutrient-rich hypolimnetic water into the illuminated surface waters in the warmer portion of the growing season, rather than in the fall when water temperatures are considerably lower. In years where reservoir water levels are low due to decreased precipitation, the stratification period may be further shortened, leading to an even earlier turnover date. In addition, basin morphometry should also be considered when considering the impacts of water level fluctuations and climate variability. The stratification and thermal regimes of relatively shallow and less voluminous basins are likely to exhibit higher sensitivity to the combined impacts of water level fluctuations and short-term climate variation. Therefore, future research should focus on the interaction of reservoir hydrology and climate variability, and the implications for the ecology and management of reservoir systems.

Chapter 5: Effects of seasonal water level fluctuation on phosphorus cycling in an oligotrophic British Columbia drinking water reservoir

Introduction

Reservoirs are dynamic aquatic ecosystems that experience large-scale water movements associated with their operation (Ford 1990; Straškraba et al. 1993; Kennedy 2001). The temporal variation and magnitude of water movements within reservoirs are highly reservoir-specific and depend upon reservoir function (i.e. - hydroelectric power generation, drinking water, flood control or multi-purpose). Due to the relatively large variation in water inflows and discharges, many reservoirs experience large water level fluctuations. Typical north temperate reservoirs have a seasonal pattern of summer or winter drawdown followed by winter or spring recharge. Annual water level fluctuations in reservoirs are generally greater than those experienced by natural lakes, and are therefore a unique feature of reservoir ecology that distinguishes reservoirs from natural lakes (Ryder 1978; Straškraba et al. 1993; Nowlin et al. 2003).

Despite the cosmopolitan nature of seasonal water level fluctuations in reservoirs and the relatively numerous studies examining water movements in reservoirs (Wünderlich and Elder 1967; Owens 1998b), a comparatively small amount of research has addressed the direct impact of seasonal drawdown on reservoir ecology. Most of the research examining the effects of reservoir water level fluctuations has examined the effects of seasonal drawdown on stratification and thermal regimes of reservoirs. Reservoir drawdown during the summer and early fall can shorten the summer stratification period and water withdrawals associated with drawdown can be significant terms in seasonal heat budgets (Barone et al. 1993; Owens 1998c; Nowlin et al. 2003). Few studies have linked the impacts of seasonal drawdown on reservoir physical processes and the potential impacts of drawdown on the cycling of nutrients that limiting plankton productivity, such as phosphorus (P). Extreme summer reservoir drawdown can cause increased epilimnetic total P (TP) and chlorophyll *a* (Chl*a*) concentrations (Effler and Bader 1998), and the timing of drawdown events can be linked to the seasonal development of phytoplankton (Barone and Naselli-Flores 1994; Tundisi et al. 1993). Yet, little is known of the impacts of drawdown on the seasonal variation in P cycling and the P-deficiencies of plankton communities. Therefore, examination of P cycling and the timing of plankton P-deficiencies in reservoirs with fluctuating water levels would give both ecologists and water quality managers a better understanding of the impacts of reservoir operation and the sensitivity of reservoir plankton communities to potential nutrient perturbations.

In this study, I examined the impact of reservoir water level fluctuation on seasonal P dynamics in an oligotrophic coastal British Columbia reservoir. I examined temporal trends of nutrient concentrations in two morphometrically different basins in a drinking water reservoir which experiences pronounced annual water level fluctuations. I assessed temporal patterns of PO_4^{3-} turnover time (a measure of planktonic P deficiency) and the relative importance of numerous epilimnetic P fluxes in the reservoir. I further compared the temporal P dynamics of Sooke Lake Reservoir to the temporal trends of a nearby natural lake of similar morphometry and trophic status. The comparison of seasonal P dynamics of a reservoir with fluctuating water levels and a natural lake allowed me to determine the impact of reservoir drawdown on seasonal P dynamics.

Similar comparative approaches have been previously used to examine the effects of reservoir drawdown and ascertain differences between natural lake and reservoir ecosystems (Nowlin et al. 2003).

Methods

Site Description and Field Sampling

Study Sites - Sooke Lake Reservoir (Sooke) and Shawnigan Lake (Shawnigan) are located on Vancouver Island, British Columbia, Canada (Fig. 5.1). Sooke is a lake-reservoir that serves as the main drinking water reservoir for greater Victoria (population ~ 300,000). More than 90% of annual inflow to the reservoir comes from October to April generated as rain-generated stream water. After the reservoir refills in winter and spring, a relatively large volume is discharged over the dam spillway. In the late spring and early summer, inflows decline and drinking water consumption increases, causing reservoir volume to decrease until late fall, when inflows increase again. Both the drinking water intake and the dam spillway allow for the outflow of surface (epilimnetic) water. Shawnigan is a natural lake of glacial origin 4 km northeast of Sooke primarily used for recreation, but also has a small amount of water withdrawn by lakeside residences and two small water utilities. Shawnigan inflows follow the same seasonal pattern as Sooke (Nordin and McKean 1984; Nowlin et al. 2003). Sooke and Shawnigan are classified as warm monomictic water bodies that do not have permanent winter ice cover (Wetzel 2001). Both water bodies are considered to be ultra-oligotrophic (Wetzel 2001). Sooke's watershed is closed to public access and Shawnigan has houses and cottages along the shoreline (~600 residences within 1 km of shoreline) and some logging activity in the watershed.

Both water bodies have three main basins (Fig. 5.1). In Sooke, the larger north basin (SOL-N) is relatively deep ($Z_{max} = 70$ m) and receives the majority of stream input, when compared to the shallower south basin (SOL-S; $Z_{max} = 22$ m) (Fig.5.1, Table 5.1). Similarly, Shawnigan has a deeper north basin (SHL-N; $Z_{max} = 53$ m) and a shallower south basin (SHL-S; $Z_{max} = 27$ m) (Fig. 5.1, Table 5.1). I selected sampling sites in the north and south basins of both lakes because they represent physical environments that differ morphometrically and hydrologically within each water body (Table 5.1). Morphometrically contrasting basins (shallow versus deep) can represent ecologically distinct environments within the same water body (Frenette et al. 1996, Proulx et al. 1996). The use of morphologically similar sites within each water body allowed us to examine seasonal P dynamics in morphometrically similar basins in a reservoir and a natural lake.

Lake and Reservoir Hydrology – I obtained water surface elevations of both water bodies from staff gauges. Sooke water surface elevations were taken on a daily basis and Shawnigan measurements were taken every two to three weeks. Staff gauge readings were used to calculate water body and basin volumes using bathymetry (Spafard et al. 2002). Detailed hydrological information on both basins of Sooke and Shawnigan during the 2000 – 2001 period is described elsewhere (Nowlin et al. 2003) and this information was used to calculate the various flow rates into and out of the north and south basins of both water bodies over the study period. Water residence time (in days) of the mixed layer was calculated on a monthly basis in 2000 and on a bi-weekly basis in 2001 in order to assess temporal trends in the flushing of the mixed layer in all basins. In reservoirs, the ecology of plankton communities and nutrient cycling is often closely tied to the flushing rates of the water body (Søballe and Threlkeld 1985; Søballe and Kimmel 1987). Water residence time (τ_W, in days) of the mixed layer was calculated as

$$\tau_W = \frac{V}{Q}$$

where V is volume of the mixed layer over the time interval and Q is the basin outflow over the time period. The mixed layer was defined as the epilimnion (see below), but when a basin was not thermally stratified (see *Field Sampling* below, the entire basin volume was used.

Field Sampling - Sites were sampled from May 2000 until January - February 2002. In 2000, sites were sampled at least once a month from May – October 2000 and once in January or February 2001. In 2001, sites were sampled every 2 weeks from May – November and once in January of February 2002. Data and samples were collected from the deepest point in each site. Water temperature was measured with a YSI Model 58, and the epilimnion was defined as the upper portion of the water column that did not exhibit temperature change $\geq 1°C\ m^{-1}$. Epilimnetic water was collected with an integrated sampler made from a 5-cm diameter weighted Tygon tube. Integrated samples were collected from 0 - 5.5 m, or to the bottom of the epilimnion if the bottom of the layer was <5.5 m. On each sampling date, triplicate water samples were collected to assess TP, TN, and Chl*a*. Sooke and Shawnigan are ultra-oligotrophic lakes with relatively low epilimnetic dissolved organic carbon (DOC) concentrations (<4 mg L^{-1}), and many lakes of this type have metalimnetic Chl*a* maximums (Hutchinson 1957; Pilati and Wurtsbaugh 2003). Therefore, I collected triplicate water samples from the depth of maximum temperature change in the metalimnion with a Niskin bottle for Chl*a* analyses. Triplicate water samples were collected from the hypolimnion with a Niskin bottle for TP and TN. In addition, ~20 L of both epilimnetic and hypolimnetic water was collected in large dark-colored plastic containers that had been cleaned and rinsed with distilled and deionized water prior to field collection. The epilimnetic sample was used to measure particulate P (PP), $^{32}PO_4^{3-}$ turnover time, and planktonic dissolved P regeneration rates. The 20-L hypolimnetic sample was used to measure hypolimnetic PP. Immediately prior to sample collection, containers were rinsed at least three times with sampling site water. Water was taken to the lab for analysis within 3-4 hours of collection.

Laboratory Analyses

Plankton and nutrient analyses - Chl*a* was determined by filtration (Whatman GF/F filters) and cold extraction (4°C) for 24 hours in the dark with 95% ethanol. Absorption was measured on a spectrophotometer (Ultraspec® 2000) with a 10-cm quartz cell. Chl*a* concentration ($\mu g\ L^{-1}$) was calculated according to Wintermans and DeMots (1965). TP was determined by digestion with potassium persulfate in an autoclave and measured as phosphate on a Lachat autoanalyzer (Zellweger Analytics, QuickChem® 8000). Particulate phosphorus (PP) was measured by serial filtration (Mazumder et al. 1988; Taylor and Lean 1991). I measured concentration of PP in the >41µm and <41µm particle size classes. Particulates were collected on 50x50 mm acid-rinsed squares of Nitex screen (41 µm) or 47-mm diameter Nuclepore polycarbonate filters (0.2 µm). I determined that brief acid rinsing did not change aperture size of Nitex by measuring apertures before and after rinsing pieces of Nitex with dilute acid. A total of 2-6 L of lake water was used in the process, depending upon the concentration of particles. After filtration, screens and filters were placed into acid-washed screw-cap test tubes and digested with potassium persulfate in an autoclave. P contained in each plankton size class was digested as in TP analyses and corrected for Nitex and Nuclepore blanks. Total dissolved P (TDP) was determined by filtration through 0.2-µm Nuclepore filters and the filtrate was analyzed as TP. TN was determined by autoclaving samples with alkaline potassium persulfate and measured as nitrate with the cadmium reduction method (APHA 1998).

Calculation of PO_4^{3-} *turnover time* - PO_4^{3-} turnover time was used as a measure of the severity of P-deficiency of epilimnetic plankton communities. PO_4^{3-} turnover times <10 minutes are often cited as indicating strong plankton P-deficiency (Lean 1973; Hudson et al. 2000). PO_4^{3-} turnover time was measured at all sites once per month from May – September in 2000. From May – November 2001, I measured PO_4^{3-} turnover time every 2 weeks, and measured once in January or February 2002. PO_4^{3-} uptake bioassays were conducted as Mazumder et al. (1988). Carrier-free $^{32}PO_4^{3-}$ was added to 100 ml of whole lake water (final activity 900 – 3200 Bq ml^{-1}) in an acid-washed high-density polyethylene (HDPE) beaker. 2-ml subsamples were removed at 0.5, 1, 2, 4, 6 and 10 minutes after addition of $^{32}PO_4^{3-}$ and passed through 25-mm diameter 0.2-µm Nuclepore filters and the filtrate was placed in scintillation vials. Scintillation flour (10 ml; Scintiverse II, Fisher Scientific) was added to vials and ^{32}P activity was determined on a liquid scintillation counter (Beckman LS6000IC or Wallac 1410). Uptake bioassays were conducted in duplicate or triplicate. To estimate PO_4^{3-} turnover time, the natural log (ln) of the percent $^{32}PO_4^{3-}$ left in solution was plotted as a function of time (minutes) and ordinary least-squares regression was used to estimate the slope. The absolute value of the slope was the PO_4^{3-} uptake constant (k, min^{-1}) and the reciprocal ($1/k$) was the turnover time in minutes (Lean 1973).

Seasonal P dynamics of Sooke and Shawnigan basins

I examined seasonal P dynamics of the two basins in Sooke and Shawnigan using various P fluxes within and out of the epilimnion (planktonic dissolved P regeneration, P fluxes to zooplankton via grazing, and PP sedimentation). Volumetric P fluxes (μmol L^{-1} d^{-1}) were converted to aerial epilimnetic P flux rates (μmol m^{-2} d^{-1}) using lake bathymetry and temperature profiles. The calculation of aerial rates was done in order to facilitate the comparison of the various flux measurements.

Planktonic P regeneration - The method of Hudson and Taylor (1996) was used to measure dissolved P regeneration rates of the plankton community (P_R). After bringing water into the lab, 4 L were gently decanted into acid-washed HDPE square-sided bottles and carrier-free $^{32}PO_4^{3-}$ was added (final activity 225 – 800 Bq ml^{-1}). Bottles were incubated at epilimnetic temperature for 28-36 h to label the plankton community. To determine the dissolved ^{32}P activity at time zero, 5-ml subsamples were immediately removed and passed through 25-mm diameter 0.2-μm syringe filters (Sarstedt Filtropur polyethersulfone filters) into scintillation vials. Following this, "cold" $^{31}PO_4^{3-}$ was added to a final concentration of 24 μmol P L^{-1} (750 μg P L^{-1}) to act as a competitive inhibitor for the reuptake of $^{32}PO_4^{3-}$ (Hudson and Taylor 1996). Over the following 5-8 h, 4-7 subsamples (5 ml) were removed and passed through 0.2-μm syringe filters into scintillation vials. To estimate the ^{32}P release rate, dissolved ^{32}P activity (dpm L^{-1} in <0.2 μm filtrate) starting at time zero was plotted as a function of time, and the slope was calculated using ordinary least-squares regression. The slope was the dissolved ^{32}P release rate. To calculate the dissolved P release rate (ng P L^{-1} h^{-1}), the total ^{32}P added at the beginning of the initial incubation period and lake epilimnetic TP concentration were used in the equation

$$\text{P release rate} = (^{32}\text{P release rate x [TP]}) / \text{total initial } ^{32}\text{P activity}$$

Zooplankton grazing P fluxes - P fluxes to epilimnetic zooplankton communities (P_G) were measured on all dates that PO_4^{3-} turnover and P regeneration analyses were conducted. After returning to the lab from a field site, three to four 1.5-L alloquots of whole lake water were gently decanted into 2-L square sided HDPE bottles (grazing chambers) and incubated overnight in low light conditions at epilimnetic temperature. At the same time, 50 ml of lake water was passed through a 41-µm Nitex screen and into an acid-washed 100-ml HDPE beaker. "Cold" $^{31}PO_4^{3-}$ was added to the beaker at a final concentration of 0.32 µmol L^{-1} (10 µg P L^{-1}) and ~30 seconds later carrier-free $^{32}PO_4^{3-}$ was added to the beaker (final activity 900 - 3200 Bq ml^{-1}). The "cold" P was added prior to the ^{32}P to prevent the unequal distribution of the label into different size fractions of the <41µm plankton (Mazumder et al. 1990). After ~18 hours of incubation, 5 ml of the <41µm labeled "food' was added to a 1.5-L container of whole water. The zooplankton community was allowed to graze under low light conditions for 4-10 minutes before draining the container through 200-µm Nitex screen to remove zooplankton >200µm. Screening time (~45 seconds) was included in the total feeding time. Nitex screens were rinsed with filtered lake water (passed through 0.2-µm Nuclepore filter) and placed into scintillation vials. 5 ml of deionized water was added to each vial followed by 10 ml of scintillation fluor, and vials were gently shaken. This was done to suspend zooplankton in the newly created translucent gel. 5 ml of the <200µm filtrate from the grazing chamber was collected and placed in a scintillation vial with 10 ml of fluor. Vials were read on the scintillation counter. Grazing rate (% d^{-1}) was calculated as Mazumder et al. (1990). All grazing rates were corrected by "blank" experiments in which the labeled food was added to 1.5 L of tap water. To calculate the flux of PP <41μm into zooplankton, the concentration of PP <41μm was multiplied by the proportional grazing rate.

PP sedimentation - PP sedimentation rates were measured once per month from May – October 2000 and once in the winter of 2001 (January and February). PP sedimentation rates were measured every two weeks from May – November 2001, and once during January – February 2002. Sediment traps were constructed of PVC cylinders (10.2 cm diameter, 61 cm tall) of a 6:1 height:volume ratio to limit particle resuspension (Bloesch and Burns 1980). Each trap consisted of four cylinders bolted onto plexiglass that was attached to the end of a 1-meter ABS pipe (2 cylinders per end). Cylinders were removable from the plexiglass piece to facilitate collection of sediment trap material after it was retrieved and on board the boat. Ropes were attached to the center of the top and the bottom of the center ABS pipe with rust proof eye bolts. The bottom rope was attached to an anchor and the length of rope was long enough to position the top of the collection cylinders 1.5 m above the sediment surface when the rope was pulled taught. The top rope was attached to a buoy that was positioned approximately 1.5 m below the water's surface, in order to limit vertical movement of the trap suspended in the water column from surface wave action. Traps were deployed by slowly lowering the trap and anchor to the bottom of the lake. After 7 – 14 d, traps were retrieved by slowly pulling the anchor and trap to the surface. This collection period interval was selected because it is often used in the literature (Wodka et al. 1985; Larocque et al. 1996) and this time period limits the amount of decomposition in traps (Bloesch and Burns 1980). In January and February of 2001 and 2002, collection periods were allowed to proceed for longer (~28 days). After pulling the trap from the water, water was slowly decanted out of each of the four collection cylinders through a small hole in the side at the 1-L mark (Larocque et al. 1996). The decanting process did not appear to resuspend any of the material collected in the bottom of the cylinder. Material from the four cylinders was pooled and placed into a clean 4-L plastic container, and each cylinder was rinsed with deionized water. If the trap was immediately redeployed (summer 2001) cylinders were thoroughly rinsed with deionized water and slowly lowered into the lake ~10 m from the site it was previously located, in order to avoid trapping of material which may have been released into the water column when the trap was pulled to the surface. PP sedimentation rates (P_{SED}) for each sampling date were estimated by collecting sediment trap particulates on 0.2-μm Nuclepore filters. The absolute sedimentation rate (μmol m^{-2} d^{-1}) of PP was calculated as Wodka et al. (1985). Concentration of PP in sediment traps was corrected for hypolimnetic PP concentration collected on the same day the trap was deployed.

P fluxes associated with water movements - I also assessed P fluxes into and out of the study basins associated with major water movements. Flows into and out of basins ($x10^6$ m^3 d^{-1}) were used to calculate P fluxes. P fluxes were calculated as aerial rates (μmol m^{-2} d^{-1}) for the epilimnion. Fluxes were calculated by multiplication of epilimnetic TP concentration (μmol L^{-1}) to basin epilimnetic volume (in L), and division by basin surface area (m^2). When a basin was not stratified, the whole basin volume was used in flux calculations. Since Sooke flows north to south, I calculated the P flux (export) from SOL-N to the south end of the reservoir (interbasin transfer flux - P_{IBT}). In SOL-S, we calculated the input of P to the basin from the north (P_{IBT}) and the P export rate associated with the drinking water intake (P_{DW}) and the spillway over the dam (P_S). For SHL-S, we calculated the P flux out of the south basin to the north basin (P_{IBT}) and the P flux from the north basin to the outflow stream (P_S). All fluxes were calculated on monthly intervals in 2000 and two-week intervals in 2001, in order to coincide with TP concentration, P regeneration, zooplankton grazing and PP sedimentation measurements.

Results

Lake and reservoir hydrology - Shawnigan experienced little temporal variation in water level and both basins lost <5% of their total volume during both summers (2000 and 2001; Fig. 5.2). In contrast, from early May to late November 2000, Sooke was drawn down by 30.3 x10^6 m^3. In the SOL-N, this translated into a 26% loss of volume from full-stage conditions (Fig. 5.2). SOL-S lost a more substantial percentage of its full stage volume over the same period (70%). During the winter 2000-2001 recharge period, both Sooke basins only recharged to 2.72 m below full stage because of lower than average rainfall during the recharge period (equivalent to a 100-year drought event; Nowlin et al. 2003). This decline in rainfall greatly reduced the inflow to the reservoir, thus the reservoir did not receive adequate stream inputs to fully recharge prior to the 2001 summer drawdown period. Sooke was again drawn down in 2001, and at the point of maximum drawdown in the fall, SOL-N and SOL-S were 71% and 25% of full stage volume, respectively.

Thermal stratification of the water column in Shawnigan occurred from May until mid-October in both years (Table 5.2). Thermal stratification of SOL-N and SOL-S was not observed until mid-June in 2000, approximately one month after stratification in both basins of Shawnigan. In 2001, SOL-N had a shorter period of stratification than SHL-N and SHL-S, and SOL-S displayed a shorter stratification period than all basins.

In order to examine if drawdown and the earlier dates of basin turnover led to a faster rate of hypolimnetic water entrainment above the thermocline in Sooke, we calculated the entrainment rates of hypolimnetic water above the thermocline in all basins. To obtain this rate, we calculated the hypolimnetic volume on the date of maximum epilimnetic temperature (late July – mid-August in both years). Following the date of maximum epilimnetic temperature, the epilimnion progressively cools and the thermocline moves down in the water column. Therefore, we calculated the proportion of the hypolimnetic volume remaining on successive dates following the date of maximum epilimnetic water temperature (date of maximum epilimnetic temperature proportion = 1.0). Both SHL-N and SHL-S had larger proportions of the hypolimnion remaining prior to the date of fall turnover than both Sooke sites in 2000 and 2001 (Fig. 5.3a - d). We estimated the slope of the relationship between day of the year (day number) and the proportion of hypolimnetic volume left for each basin. In order to compare the rates of hypolimnetic disappearance among basins, we preformed an ANCOVA comparing the slopes of the four basins. Sooke hypolimnia disappeared at a significantly faster rate than Shawnigan ($F_{7,3} = 19.02$, $p < 0.001$), and the rates of hypolimnetic entrainment were not different between Shawnigan sites ($F_{3,1} = 0.225$, $p = 0.642$). On average, SHL basins lost ~0.68% of their hypolimnetic volume per day from the date of maximum epilimnetic temperature until the date preceding the date of fall turnover. When the rates of hypolimnetic entrainment of SOL-N and SOL-S were compared, the slopes were significantly different ($F_{3,1} = 8.9$, $p = 0.01$), indicating that the rate of hypolimnetic entrainment was significantly greater in SOL-S (1.8% d^{-1}) than in SOL-N (1.1% d^{-1}).

Residence time of the mixed layer (τ_W) varied seasonally in all basins (Fig. 5.4a - d). Due to the hydrologic stagnation of Shawnigan Lake during the summer period (little to no inflow and outflow out of both basins), τ_W of the mixed layer of SHL-N and SHL-S during the stratification period was relatively long (Fig. 5.4a and b). On average, SHL-N epilimnetic τ_W was 823 and 710 days in 2000 and 2001 during summer stratification. The epilimnion of SHL-S had more rapid flushing rates than SHL-N (548 and 156 days in 2000 and 2001, respectively), due to the smaller volume of SHL-S. Both Shawnigan basins had a decrease in epilimnetic τ_W in the fall of 2001, which caused the mean epilimnetic τ_W to be lower in 2001. In the fall of 2001, rainfall increased to pre-drought levels and stream inputs were relatively high to the lake (Nowlin et al. 2003). Mean epilimnetic τ_W during stratification in SOL-N during 2000 and 2001 685 and 433 days, respectively. SOL-S was rapidly flushed throughout the year in both years, due to its small basin volume and the large volumes removed by the drinking water outflow. In both summers, the mean epilimnetic τ_W was approximately 9 days.

Temporal nutrient and plankton dynamics – Epilimnetic TP concentrations in both basins of Shawnigan (0.09 – 0.30 μmol L^{-1}; Fig. 5.5a and b) were slightly higher than both basins of Sooke (0.04 – 0.24 μmol L^{-1}; Fig. 5.5c and d). In all basins in both summers, epilimnetic TP concentrations during the stratification period were not significantly correlated with day of year (day number; Table 5.3), indicating that epilimnetic TP concentrations did not significantly increase or decrease over the course of the summer. In the two shallower basins of both water bodies (SHL-S and SOL-S), hypolimnetic TP was often higher than in the epilimnion, especially in the late summer and early fall of both years (Fig. 5.5b and d). However, in both north basins, epilimnetic and hypolimnetic TP concentrations were often the equal and did not exhibit the pronounced differences present in the south basins (Fig. 5.5a and c). Mean summer stratification epilimnetic TP concentrations in Shawnigan were not significantly different between 2000 and 2001 (ANOVA comparing mean epilimnetic TP during stratification of SHL-N and SHL-S 2000 vs SHL-N and SHL-S 2001; $n = 4$, $F_{1,2} = 0.003$, $p = 0.96$). In Sooke, however, mean epilimnetic TP concentrations were slightly, though significantly lower in 2001 ($n = 4$, $F_{1,2} = 24.2$, $p = 0.04$), with decrease of approximately 0.03 μmol L^{-1} in 2001.

Epilimnetic dissolved P concentrations of Shawnigan during stratification were low (Fig. 5.6a and b). TDP concentrations in Shawnigan ranged from 0 – 0.16 μmol L^{-1} in both basins. Sooke epilimnetic TDP concentrations were similar to those in Shawnigan, but were slightly lower (Fig. 5.6 c and d). TDP concentrations in both Shawnigan and Sooke were notably higher in the second year of the study. In 2001, mean TDP concentrations in Shawnigan ($n = 4$, $F_{1,3} = 424.2$, $p = 0.002$) and Sooke ($n = 4$, $F_{1,3} = 747.9$, $p = 0.001$) during stratification were significantly higher than the previous year (Fig. 5.6 a – d).

Epilimnetic TN concentrations in Shawnigan were again slightly greater than in Sooke (Fig. 5.7a – d). Epilimnetic TN concentration in all basins during summer stratification was not significantly correlated with day of year (Table 5.3), indicating that epilimnetic TN did not significantly increase or decline during stratification. In SHL-N, SHL-S and SOL-S, hypolimnetic TN concentrations were consistently higher than in the epilimnion (Fig. 5.7a, b, d), but hypolimnetic TN in SOL-N was only greater than epilimnetic TN concentrations on 2 - 3 dates per summer (Fig. 5.7c). Shawnigan mean epilimnetic TN during stratification was not different between years ($n = 4$, $F_{1,2} = 0.001$, $p = 0.99$). Sooke mean epilimnetic TN concentrations were significantly higher in 2001 ($n = 4$, $F_{1,2} = 51.0$, $p = 0.02$), although this difference was ~1.4 µmol L^{-1}.

Epilimnetic Chl*a* concentrations in Shawnigan (0.3 – 2.4 µg L^{-1}) were slightly higher than Sooke (0.3 – 1.6 µg L^{-1}) during both summers (Fig. 5.8a – d). Mean summer Chl*a* concentrations in all basins were consistently higher in the metalimnion (Fig 5.8a – d) when compared to the epilimnion. In Shawnigan and Sooke, metalimnetic Chl*a* was 0.3 – 1.5 µg L^{-1} greater than epilimnetic concentrations, and typically declined and eventually converged with epilimnetic Chl*a* concentrations around the date of basin turnover (Fig. 5.8a – d). Shawnigan mean epilimnetic and metalimnetic concentrations during stratification did not significantly differ between years (Epilimnetic Chl*a* – $F_{1,2} = 23.69$, $p = 0.99$; Metalimnetic Chl*a* – $F_{1,2} = 7.0$, $p = 0.12$). Sooke mean epilimnetic Chl*a* concentration was slightly, although significantly, greater (~0.3 µg L^{-1} greater) in 2001 ($F_{1,2} = 50.97$, $p = 0.02$). Average metalimnetic Chl*a* concentrations did not differ between years in Sooke ($F_{1,2} = 2.74$, $p = 0.24$).

Seasonal trends in nutrient and Chl*a* concentrations were intensely studied in the summers of 2000 and 2001, however, TP, TN and Chl*a* samples were also periodically collected from SOL-S and SOL-N during the summer stratification period of 2002 and

2003. We examined if the magnitude of summer drawdown over this four-year period was correlated with nutrient concentration and phytoplankton biomass by regressing mean TP, TN and Chl*a* of the summer stratification period as a function of the percent of usable volume left in the reservoir at the point of maximum drawdown in the summer (from May – September). It is important to note that in the winter of 2002 – 2003, Sooke Lake Reservoir dam was raised to increase the storage capacity of the reservoir (~60% increase; Asit Mazumder, *upubl. data from 2003*), which limited the relative magnitude of the annual summer drawdown. Therefore, we performed all analyses both with 2003 and without 2003 data because of the potential nutrient release associated with the flooding of new areas in the winter of 2002 – 2003. TP was not a significant function of percent usable volume when all data were used (Fig. 5.9a, Table 5.4), however, when 2003 were excluded, contrary to predictions, TP increased in concentration as the percent usable volume increased (Fig. 5.9a, Table 5.4). TN did not significantly vary as a function of usable reservoir volume both with and without the 2003 data (Fig. 5.9b, Table 5.4). When using all data, Chl*a* concentration was a marginally non-significant function of percent water volume (Fig. 5.9c, Table 5.4), but when 2003 data were excluded, Chl*a* significantly declined as percent usable volume increased (Table 5.4).

PO_4^{3-} turnover times - PO_4^{3-} turnover times in Shawnigan varied from 4.7 – 13.3 minutes, indicating strong P-deficiency of the plankton communities throughout the study period (Fig 5.10a and b). In both years, PO_4^{3-} turnover time in both Shawnigan basins was rapid (<10 minutes) for most of the summer, but in the early and late fall as thermal stratification became less intense and epilimnetic water temperatures cooled, PO_4^{3-} turnover times gradually increased. Sooke followed a similar seasonal pattern in 2000 in

both basins (Fig. 5.10c and d), but SOL-N on 19 June 2000 had PO_4^{3-} turnover time increase to 30 minutes (Fig. 5.10c) and then return to <10 minutes until the late fall. In 2001, PO_4^{3-} turnover times in both Sooke basins were temporally more variable than the previous summer. SOL-N again had an increase in PO_4^{3-} turnover time in June, but PO_4^{3-} turnover time also became >20 minutes in mid-August and mid-October. SOL-S, contrary to the seasonal pattern of the previous year, had PO_4^{3-} turnover time vary from 6.6 on 21 June to 14.2 minutes on 5 July (Fig. 5.10d). Unlike the previous year, PO_4^{3-} turnover time in SOL-S did not increase to >10 minutes in the late fall. PO_4^{3-} turnover time in Sooke basins had significantly higher temporal variance during the stratification period than Shawnigan in 2000 (variance ratio test (Zar 1999) – $F_{11,\,11} = 9.23, p < 0.001$). Most of the seasonal variation in Sooke 2000 PO_4^{3-} turnover time is from the one date in SOL-N (19 June 2000; Fig. 5.10c). In 2001, Sooke seasonal PO_4^{3-} turnover time variation was again significantly greater than in Shawnigan ($F_{20,\,21} = 8.74, p < 0.001$). In 2001, both Sooke basins obviously exhibited different seasonal patterns than the previous year and Shawnigan basins did not.

Dissolved nutrient concentrations presumably affect the severity of plankton nutrient deficiency, therefore I performed Pearson correlations between PO_4^{3-} turnover time and epilimnetic TDP concentration of the four study basins during the stratification period of both summers (see Fig 5.6). TDP was measured on the same day that PO_4^{3-} turnover time was measured. TDP concentration and PO_4^{3-} turnover time were not significantly correlated in SHL-N ($n = 16$, Pearson $r = 0.15, p = 0.55$), SHL-S ($n = 17$, Pearson $r = 0.08, p = 0.71$), SOL-N ($n = 13$, Pearson $r = 0.15, p = 0.64$) and SOL-S ($n = 12$, Pearson $r = 0.02, p = 0.95$).

Seasonal P fluxes – In Shawnigan, planktonic P regeneration (P_R) was by far, the largest aerial flux of P within the epilimnion (Fig 5.11a and b; Table 5.5). P_R in Shawnigan, on average in both summers, recycled 241 μmol m^{-2} d^{-1} (Table 5.5). The flux of P into zooplankton (P_G) was also relatively large and was, on average, 106.5 μmol m^{-2} d^{-1}. In Shawnigan, the P fluxes associated with planktonic regeneration and zooplankton grazing were one to two orders of magnitude greater than fluxes associated with hydrological movements (Fig. 5.11a and b). P fluxes in both Shawnigan basins associated with hydrological movements exhibited pronounced seasonality. In SHL-N, the loss of P to the outlet stream (P_S) was only important in the fall and winter periods, when inflows and outflows to the lake were present. Similarly, the interbasin transfer of P out of SHL-S (P_{IBT}) to the north basin was greater in the winter when inflows to the lake were greatest. The loss of P through sedimentation (P_{SED}) was, on average, the largest summer loss of P in both Shawnigan basins (Fig. 5.11a and b; Table 5.5). In Sooke, P_R was also the greatest aerial P flux during summer stratification (Fig 5.11c and d; Table 5.5), however, P_R fluxes in winter 2002 were not as great as P_R fluxes in Shawnigan. P_G was also an important P flux within the epilimnion and was typically one of the larger P fluxes in the reservoir (Table 5.5). In SOL-N, loss rates to P_{SED} during the summer were approximately equal to losses to P_{IBT} (Table 5.5). In SOL-S, P_{DW} losses during summer stratification were 5 – 8 times greater than losses to P_{SED}. In the 2000 – 2001 winter period, there was no loss of water (and therefore P) over the dam spill way in Sooke (Table 5.5) because the reservoir did not completely recharge during the drought. In January 2002 after the reservoir had completely recharged after the drought, SOL-S exported 270.4 μmol m^{-2} d^{-1} over the dam spillway (Table 5.5).

Discussion

Effect of drawdown on nutrients, phytoplankton biomass and plankton P deficiency - In the present study, I observed a relatively small response of reservoir epilimnetic nutrient concentrations and phytoplankton biomass to seasonal drawdown, when compared to the nearby natural lake. Sooke TP, TN and Chl*a* did not significantly temporally increase or decrease during the summer drawdown period of both summers and generally followed the same seasonal trends observed in Shawnigan. In the second year of the study (2001), when reservoir water levels were lower due to the 100-year drought, epilimnetic TP was lower, and TN and Chl*a* were higher than in summer 2000. These differences, while relatively small, were significant. Shawnigan epilimnetic TP, TN and Chl*a* were not different between summers and, aside from the drought during the winter of 2000 – 2001, mean summer meteorological conditions (daily irradiance, wind speed and air temperature) were not different between years (Nowlin et al. 2003). Therefore, the differences in Sooke between summers were likely related to the lower reservoir water levels in the summer of 2001.

The magnitude of the responses of pelagic nutrient concentrations and phytoplankton biomass to reservoir drawdown in this study were less than those observed in other studies (Barone and Naselli-Flores 1994; Effler and Bader 1998). Barone and Naselli-Flores (1994) reported that seasonal shifts in phytoplankton community taxonomic composition and biomass in Lake Arancio, Sicily, were related to the timing of reservoir water level fluctuations. Effler and Bader (1998) found that over a 7-year period, TP and Chl*a* increased with the severity of summer drawdown of Cannonsville

Reservoir, New York, USA. In contrast, I observed a minor decline in epilimnetic TP and a slight increase in epilimnetic TN and Chl*a* in the second year of the study when reservoir water levels were lower. In addition, when summer TP of 2000, 2001 and 2002 (excluding the 2003 post-inundation year) were plotted as a function of the severity of summer drawdown, epilimnetic TP concentration declined with increasing drawdown. Chl*a* significantly increased with the extent of summer drawdown over the same period, however, this increase was slight. It is important to note that the water bodies of Barone and Naselli-Flores (1994) and Effler and Bader (1998) were eutrophic (20 – 240 μg TP L^{-1}). Differences in the directionality and magnitude of responses of nutrients and phytoplankton in oligotrophic Sooke and the more eutrophic reservoirs in the literature to drawdown suggests that more oligotrophic water bodies may experience relatively smaller nutrient and water quality problems associated with drawdown than eutrophic systems.

Previous studies have suggested that seasonal drawdown of reservoirs can impact the cycling of nutrients potentially limiting to phytoplankton and cause seasonal changes in phytoplankton nutrient deficiency (Barone and Naselli-Flores 1994, Effler and Bader 1998). In the second year of our study, I observed greater temporal variation in PO_4^{3-} turnover time in both Sooke basins during the summer stratification period. Increased seasonal variability in PO_4^{3-} turnover time in 2001 indicates increased variability in P-deficiency of the plankton community. Several potential mechanisms related to the physical impact of reservoir drawdown may have contributed, either individually or in combination to the increased seasonal variability in PO_4^{3-} turnover time in Sooke. First, entrainment of hypolimnetic water, and subsequently P into the epilimnion during stratification may have caused variability in plankton P-deficiency, because up to 90% of hypolimnetic P can be immediately bioavailable TP epilimnetic plankton communities (Nürnberg 1985). In natural lakes, the entrainment hypolimnetic P above the thermocline has been shown to affect epilimnetic P cycling and phytoplankton biomass (Kortmann et al. 1982; Stauffer 1987; Soranno et al. 1997), however, this process has received less attention in reservoirs (James et al. 1990). In my study, both the SOL-S and SOL-N exhibited higher hypolimnetic entrainment rates than Shawnigan. Because hypolimnetic entrainment is an episodic and not continuous process (Soranno et al. 1997), the observed irregularity of PO_4^{3-} turnover time in Sooke may be related to the relationship between the timing of sampling and the timing of entrainment events. However, it is unlikely that the entrainment of hypolimnetic P was related to the variability in PO_4^{3-} turnover time in SOL-N because epilimnetic and hypolimnetic TP concentration in SOL-N were approximately equal for most of the summer in both years. SOL-S hypolimnetic TP was higher than the epilimnion, therefore, we cannot omit the possibility that the higher hypolimnetic entrainment rates in SOL-S may have contributed to the increased temporal variability in 2001.

A second physical mechanism which may have contributed to the variability of PO_4^{3-} turnover time in the second year of the study may be related to the flushing rate of the mixed layer of the reservoir. Basin water residence time has been cited as a factor that affects the availability of nutrients to plankton communities (Søballe and Threlkeld 1985). Epilimnetic water residence time in SOL-S was more rapid than any of the other study basins (9 days), however, it is unlikely that epilimnetic residence time caused PO_4^{3-} turnover time to be more variable in the second year of the study. Mean summer epilimnetic water residence time in both Sooke basins was not different between summers (Fig. 5.4), and SOL-N water residence time during stratification was >400 days during both years of the study.

A third factor that may have contributed to the increased temporal variability of PO_4^{3-} turnover time in 2001 is the release of nutrients from lake sediments exposed during drawdown. Exposed sediments in the drawdown zone (area of reservoir sediments that is exposed and rewetted annually) can release significant amounts of dissolved nutrients into a reservoir (Perrin et al. 2000). If the greater exposure of sediments in summer 2001 led to a greater release of dissolved P into both basins of Sooke, then, presumably, the overall concentration of TP or TDP would therefore increase. However, Sooke TP concentrations were significantly lower in the summer of 2001. TDP concentrations were significantly higher in both Sooke and Shawnigan in 2001, and Shawnigan basins did not exhibit the same increased seasonal variation in PO_4^{3-} turnover time in 2001. It is possible that dissolved P release from exposed sediments was large enough to create greater temporal variability in PO_4^{3-} turnover time but not affect the overall concentration of epilimnetic TP or TDP. However, due to a lack of detailed data examining P release rates from exposed sediments, I cannot further assess the role of nutrient loading from exposed sediments in affecting temporal variability of plankton P-deficiency.

An alternate explanation to increased seasonal variation in PO_4^{3-} turnover time in Sooke in 2001 may derive from compositional differences in the phytoplankton community. Phytoplankton biomass (Chl*a*) in Sooke was slightly higher in summer 2001, but the taxonomic composition may have been significantly different from the previous summer. If Sooke phytoplankton taxonomic composition in summer 2001 was different from 2000, then the presence or absence of specific phytoplankton taxa in 2001 may have caused the observed differences in the seasonal pattern of PO_4^{3-} turnover time. Assessment of phytoplankton taxonomic composition was not preformed as a part of this study, so I cannot comment on whether phytoplankton composition was more variable or different in the summer of 2001. Therefore, the relationship between temporal trends in phytoplankton taxonomic composition and PO_4^{3-} turnover time in both Sooke and Shawnigan is unknown.

Seasonal P dynamics – Planktonic P regeneration (P_R) was the largest P flux in all basins. Regeneration of P by plankton maintains an important role in the internal cycling of P in the epilimnia of lakes and reservoirs (Hudson et al. 1999, Nowlin et al. *in review*), and our results indicate that this importance does not appear to be affected by reservoir drawdown. P exports associated with large-scale water movements (P_{DW}, P_{IBT}) were important in Sooke basins throughout the year, but the same fluxes (P_S, P_{IBT}) were only important in Shawnigan during specific times of the year. Hydraulic exports from reservoir ecosystems (dam spills, drinking water outflows) are often important fluxes of heat and energy (Barone et al. 1993, Owens 1998c, Nowlin et al. 2003). Not surprisingly, the same exports that are important heat fluxes are also important in exporting P. The magnitude of the importance of hydrological heat exports, however, is a function of the relationship between basin volume and the volume of water being exported from the basin (Nowlin et al. 2003). Similarly, P_{DW} fluxes were 5 –8 times greater than sedimentation losses in the summer, while sedimentation losses were greater than P_{IBT} in both summers in SOL-N.

In summary, the seasonal drawdown of Sooke Lake Reservoir in the summers of 2000 and 2001 had little impact on seasonal trends in TP, TN and Chl*a* concentration. In the second year of the study, when reservoir water levels were lower due to a 100-year drought, there was a small but significant difference in nutrient concentrations and phytoplankton biomass between years. We observed that P-deficiency of the plankton community, measured as PO_4^{3-} turnover time, was more variable in the second year of the study, but the specific mechanism or mechanisms behind this response is unknown. The strength of the impacts of drawdown appear to be dependent upon the trophic state of the waterbody, with oligotrophic systems such as Sooke Lake Reservoir experiencing relatively minor effects.

Chapter 6: Summary and Synthesis

Restatement of research objectives

The objectives of Chapters 2 and 3 of this dissertation were focused in the broad area of understanding trends and patterns of P cycling in lakes of varying P content. In this section of the dissertation, I had the following research objectives:

1. Test the predictions of Harris (1986), Capblancq (1990) and Harris (1994) in a set of lakes that ranged in TP concentration. Specifically, to examine trends in P concentration in the particulate and dissolved pools across a range of TP.

2. Examine the size-fractionated uptake and regeneration of the plankton community across a range of TP.

3. To assess trends in P cycling efficiency (measured as PO_4^{3-}, TP and PP turnover times) in lakes of varying TP concentration.

4. Assess the applicability of newer methods for measuring PO_4^{3-} and planktonic regeneration in lakes of varying TP.

5. Examine seasonal trends of P dynamics (P sedimentation, planktonic P regeneration and zooplankton grazing) in lakes of varying TP.

6. Empirically test the hypotheses of Reynolds (1984), Harris (1986) and Capblancq (1990) regarding trends in P sedimentation, P regeneration and P fluxes to zooplankton in lakes of varying P content.

7. Examine the prediction that more eutrophic systems should rely upon P sources from out side the epilimnion more than oligotrophic lakes.

The second portion of the dissertation (Chapters 4 and 5) focused on the impacts of reservoir water level fluctuations on the physical limnology, nutrients and plankton of an oligotrophic drinking water reservoir. The specific research objectives were:

1. Examine the effects of summer drawdown on the mixing patterns and thermal regimes of a reservoir experiencing summer drawdown.
2. Compare the responses of morphometrically differing basins within the reservoir in order to gain insight into the potential responses of relatively shallow and deep reservoirs to summer drawdown.
3. Compare seasonal trends in mixing and thermal regimes of a reservoir and a morphometrically and trophically similar natural lake.
4. Assess the response of lake and reservoir mixing and thermal regimes to short-term climate variation (drought).
5. Examine the impacts of reservoir drawdown on the concentration of nutrients and phytoplankton biomass in two morphometrically different basins of a reservoir.
6. Determine if temporal trends in plankton P-deficiency (measured as PO_4^{3-} turnover time) were affected by seasonal reservoir drawdown.

7. Examine if the severity of summer drawdown (extent of drawdown over a multi-year period) affects the water quality of oligotrophic reservoirs.

Summary of major findings and future directions

P cycling of lake ecosystems of varying P content – In Chapter 2, I examined conceptual models of lake epilimnetic P cycling predict that, as total phosphorus (TP) concentration increases, the relative size of various P pools (particulate and dissolved), the movement of P within size fractions of the plankton communities should change, and that lakes with low TP should cycle P more efficiently (turn over at a higher rate) than high TP lakes. I empirically tested these predictions in a set of 8 basins that ranged in TP. Contrary to predictions, the importance of nanoplankton (<20μm) did not decline with TP, as indicated by the lack of a significant relationship between TP and the proportion of particulate P (PP) in nanoplankton, the percent uptake of PO_4^{3-} and the percent contribution of nanoplankton to the community P regeneration rate. $ssPO_4^{3-}$ concentrations were low (<600 pmol L^{-1}) and increased with TP, but contrary to predictions, $ssPO_4^{3-}$ did not increase as a proportion of TP with increasing TP. Simultaneously obtained measurements of SRP were, on average, 2.5 orders of magnitude higher than $ssPO_4^{3-}$ measurements, and $ssPO_4^{3-}$ and SRP were not significantly correlated. TP turnover time was not a function of TP concentration, and PO_4^{3-} turnover time was not a function of $ssPO_4^{3-}$ or TP. PP and PP<20μm turned over more rapidly with TP, opposite from the predicted trend.

In my study basins, I found limited support for many of the predictions of the conceptual models of Harris (1986), Capblancq (1990) and Harris (1994), and these results indicate that further empirical examination of conceptual paradigms of P cycling in lakes is warranted. There are several areas for improvement of this study. The range in TP in our study lakes (0.09 – 0.59 μmol l^{-1}) is more limited than the ranges used in other studies that have examined P cycling paradigms (Prepas 1983; Currie et al. 1986; Currie 1990; Hudson et al. 1999). Therefore, the inclusion of lakes with TP >0.6 μmol l^{-1} into the data set would significantly improve the study. Further, the use of lakes dominated by large-bodied zooplankton may have limited the applicability of our study. Zooplankton size distribution can affect the intensity of grazing and therefore the turnover of the PO_4^{3-} pool (Mazumder et al. 1988). The inclusion of lakes dominated by small-bodied zooplankton in this study, such as *Bomina sp.*, may provide information on whether the turnover of TP and PP pools are dependent upon zooplankton community size and composition. Despite these limitations, results from this study provide the basis for several areas that might yield further fruitful research. The dominance of pico- and nanoplankton in PO_4^{3-} uptake suggests that larger plankton must obtain P from alternate sources in order to maintain production, such as the DOP pool (Currie et al. 1986) or through phagotrophy (Jansson et al. 1996; Rothhaupt 1996). Currently, our understanding of both of these phenomena in lakes is limited. Further, the extremely low PO_4^{3-} concentrations, as yielded by the steady state bioassay method, indicate the PO_4^{3-} can remain extremely low in lakes of varying TP and constitutes a small but relatively consistent proportion of the TP pool, regardless of TP. In addition to the many questions regarding competition between different planktonic groups for this limited pool, these data also provide a basis for addressing questions about the role of non-biological uptake of PO_4^{3-} in lakes. For example, in many reservoir ecosystems, clay minerals absorb significant amounts of PO_4^{3-} and are subsequently lost to sedimentation. However, many reservoirs remain productive, even in the presence of extremely high mineral turbidity. It has been shown that in lake epilimnia, bacteria can compete with iron for bioavailable P that has been entrained from the anoxic P-rich hypolimnion (Nürnberg 1985), therefore, it not unreasonable to assume that bacterio- or picoplankton in systems with high levels of mineral turbidity may also experience similar competition for PO_4^{3-} from non-biological sources (clays). Competition for PO_4^{3-} sources between picoplankton and clays under extremely low PO_4^{3-} concentrations is a potentially interesting area that may provide insight into the nutrient cycling of reservoir ecosystems.

In Chapter 3, I examined the seasonal trends in P dynamics in three oligotrophic and two meso-eutrophic basins. I addressed the hypothesis that, as TP concentration increases in a series of lakes, epilimnetic plankton communities should rely more heavily upon P sources that are derived externally from the epilimnion (hypolimnetic entrainment, stream inputs). That is, as TP increases, the relative importance of P fluxes within the epilimnion, such as planktonic regeneration and zooplankton grazing should decline. Accordingly, the proportional losses of epilimnetic P to sedimentation are also predicted to increase as TP increases. I observed that P fluxes in all sites exhibited temporal variation, but the oligotrophic systems typically had smaller seasonal variation. The mean summer flux rates of planktonic regeneration, zooplankton grazing and P sedimentation increased with mean summer epilimnetic TP. However, the proportion of the epilimnetic TP pool regenerated or grazed per day did not vary with epilimnetic TP.

Proportional P losses to sedimentation increased with epilimnetic TP. These results indicate that P cycling pathways within the epilimnion (regeneration, zooplankton grazing) are larger than sedimentation losses across a range of TP, and this importance does not vary with TP. Increased proportional loss of P to sedimentation in eutrophic systems, however, suggests that in order to maintain consistent TP epilimnetic concentrations throughout the summer stratification period, eutrophic systems must rely to a greater extent upon P inputs from outside the epilimnion.

The central importance of planktonic regeneration in maintaining plankton productivity has been questioned (Caraco et al. 1992), but other ecologists have emphasized planktonic regeneration as the P source that drives a large portion the productivity of surface waters during summer stratification (Hudson et al. 1999). The results from this study support the position that regeneration plays a central role in the P cycling of lakes, however, the data also indicate that sources external to the epilimnion must increase in importance as TP increases in order to offset losses to sedimentation. Future research directions should focus on coupling P regeneration measurements with detailed P budgets that include all possible inputs and outputs. Caraco et al. (1992) found that ~35% of the summer primary productivity in oligotrophic Mirror Lake, New Hampshire, USA was supported by so-called "new" nutrient sources. However, the authors did not directly measure P regeneration from plankton. Hudson et al. (1999) estimated the regeneration rates from a large set of lakes and found that regeneration rates increased with lake TP. The authors concluded that planktonic regeneration was of primary importance in lakes, yet the authors did not directly measure sedimentary losses or P inputs from sources external to the epilimnion. Therefore, it would be insightful and provide a definitive test of the hypothesis of a shift from "old" to "new" P sources by incorporating actual measured P regeneration rates with the type of detailed P budget presented by Caraco et al. (1992) in a series of lakes that vary in TP.

Effects of drawdown on reservoir ecology – In Chapter 4, stratification and thermal regimes of a reservoir with fluctuating water levels were compared to a natural lake of similar morphometry and trophic status over a two-year period (2000-2001). I compared the timing and duration of stratification, summer heat budgets and heat fluxes in two morphometrically contrasting basins of Sooke Lake Reservoir and Shawnigan Lake (one shallow and one deep basin per water body). In the second year of the study, a 100-year drought allowed me to compare responses of a reservoir and a lake to contrasting years of climatic conditions. Loss of volume from the reservoir during summer and fall caused stratification and thermal regimes to differ from Shawnigan Lake, but the magnitude of these differences was mediated by basin morphometry. Duration of summer stratification, timing of heat content, and the relative importance of seasonal heat fluxes in the shallow basin of Sooke Lake Reservoir were most different from Shawnigan Lake. While there were no major differences between years for Shawnigan Lake, contrasting years in precipitation and hydrology caused Sooke Lake Reservoir stratification and thermal regimes to differ between years. The magnitude of differences between years was mediated by basin size, with the shallower reservoir basin having greater differences between years. These results indicate that reservoir physical processes are sensitive to short-term changes in hydrology (2000 versus 2001), and that the combined impacts of short-term climate variation and anthropogenic manipulation of hydrology may be greater in shallow reservoir ecosystems.

In Chapter 5, I examined the effects of reservoir water level fluctuations on the temporal nutrient and plankton dynamics of Sooke Lake Reservoir during the period from May 2000 – February 2002. A drought prior to the second summer of the study (2001) prevented the reservoir from completely recharging, and thus allowed me to compare between-year responses of nutrients and Chl*a* to summer drawdown. Overall in both years, the progression of summer drawdown had little impact on the seasonal trends of TP, TN and Chla. In 2001, a significant but small decline in TP and increase in Chla occurred, suggesting the lower reservoir water levels in the second year of the study were associated with changes in nutrients and phytoplankton biomass. Planktonic P-deficiency, measured as PO_4^{3-} turnover time, was more temporally variable in 2001. However, I was unable to determine the reason for this difference between years.

Previous research on reservoir ecosystems has been criticized for being too "provincial" (reservoir-specific) and has not attempted to provide a general framework for numerous reservoir ecosystems (Thornton et al. 1990; but see Kennedy and Thornton 2001). Consequently, most studies that have examined reservoir dynamics have been largely descriptive in nature. In the studies presented here (Chapters 4 and 5), I attempted to not only examine the effects of seasonal water level fluctuations on the ecology of Sooke Lake Reservoir, but also to expand the discussion of drawdown impacts beyond Sooke to reservoir systems, in general.

In Chapters 4 and 5, it is not surprising that the ecology of Sooke was influenced by water movements within, into and out of the reservoir. The link between the ecology and hydrology of reservoirs is a paradigm in the field of reservoir limnology. However, unlike many studies that have examined the influence of seasonal water level fluctuations on stratification and thermal regimes (Barone et al. 1993; Owens 1998c), I distinguished between morphologically and hydrologically distinct portions of the study reservoir in an attempt to understand the relative importance of water level fluctuations under contrasting morphometry and hydrology. As expected, the strength of the effects of summer drawdown on stratification and thermal regimes was mediated by the relationship between basin size and the volume of water exported from the basin. Further, I found that the shallow basin of the reservoir was most sensitive to the combined impacts of drawdown and short-term climate variation. From a management perspective, the interaction between climate (precipitation and therefore local hydrology) and reservoir operation must be considered before creation of water management practices and application of water quality criteria to a water body. In addition, as scenarios of global climate change are applied at a local level, managers and ecologists must take into account the combined impacts and interaction between hypothetical changes in local hydrology and management practices.

In Chapter 5, the effects of drawdown on nutrient and phytoplankton biomass were relatively small when compared to eutrophic lakes in the literature. Effler and Bader (1998) in a detailed multi-year study of the impacts of drawdown on Cannonsville Reservoir, New York, concluded that there was a significant water quality "cost" for reservoir operation. In Sooke, I also observed a "cost" for operation, but the water quality costs were much less severe than those noted in eutrophic systems. Interestingly, the poorest water quality in Sooke was observed during summer 2003, the first summer after the raising of the dam. Undoubtedly, there was a water quality impact of raising the dam, however, the future limitation of the impacts of summer drawdown with the increased water level will likely outweigh the short-term water quality costs of inundation of new areas. The concept of water quality "costs" and "benefits" in Sooke before and after the raising of the dam is an area that requires future research attention.

The increased variability of plankton P-deficiency in Sooke in 2001 is an important finding, even though I could not conclusively determine the mechanism responsible for the differences in the temporal trends of 2000 and 2001. Fluctuation in P-deficiency in Sooke in 2001 may indicate that the plankton community oscillated between deficiencies of multiple nutrient sources (such as P and N) over the course of the summer. This potential alteration in deficiency of different nutrients would have implications for the sensitivity of the reservoir to nutrient perturbations. If management practices were structured to prevent potential water quality declines (phytoplankton blooms, decreased water clarity) based upon a so-called "typical" year's plankton P-deficiencies, then water quality managers would provide criteria to limit P inputs to the reservoir. In a more extreme drawdown year, however, the loading of other nutrients, such as N, at specific times of the summer might cause unforeseen water quality problems. Therefore, reservoir water quality managers should be aware of the potential interaction between interannual variability in reservoir water level and hydrology and the nutrient deficient status of plankton.

Summary

Conceptual models of lake epilimnetic phosphorus (P) cycling were examined in a set of 8 basins in British Columbia, Canada that ranged in TP. These models predict that, as total phosphorus (TP) concentration increases, the size of various P pools, the movement of P within size fractions of the plankton communities should change, and that lakes with low TP should cycle P more efficiently (turn over at a higher rate) than high TP lakes. In addition, I examined the relative importance of various P fluxes (plankton regeneration, zooplankton grazing and sedimentation) in lakes of varying TP content. In general, I found little support for many of the predictions and my results strongly suggest that further empirical examination of these conceptual paradigms is warranted. In the latter portion of this dissertation, I examined the impact of seasonal water level fluctuations on the physical and nutrient dynamics of an oligotrophic drinking water reservoir (Sooke Lake Reservoir). I compared temporal patterns of stratification, heating and nutrient fluxes to a nearby similar natural lake (Shawnigan Lake) that does not experience significant water level fluctuations. Summer drawdown caused the timing and duration of stratification and heat fluxes between the reservoir and the natural lake to differ. Seasonal trends in nutrient concentration and plankton nutrient deficiency were also affected by reservoir drawdown. However, the magnitude of these impacts were less than those observed in more eutrophic reservoirs, suggesting that the water quality "costs" of reservoir operation in oligotrophic systems are less than in eutrophic systems.

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Tables

Table 2.1. Site abbreviations, number of times sampled in 2000 and 2001, the location within British Columbia, and the morphometric and limnological characteristics of the eight lakes examined by this study. Values for nutrient concentrations and plankton biomasses and densities are the mean (±1 SD) of the May – October period in 2000 and 2001.

Site	Site Abbr.	*N* 2000, 2001	Location	Lat, Long (°N, °W)	Surface Area (ha)	Z_{Mean}, Z_{Max} (m)	TP (µmol L^{-1})	TN (µmol L^{-1})	Zooplankton (µg L^{-1})	Chl*a* (µg L^{-1})	Bacteria x10^6 cells mL^{-1}
Council Lake	COL	5, 5	Coastal	48.31, 123.40	16	5.2, 17	0.12 (±0.04)	6.9 (±2.0)	15.8 (±16.9)	0.9 (±.25)	0.83 (±0.45)
Cusheon Lake	CUL	5, 5	Coastal	48.48, 123, 28	31	4.4, 9.5	0.52 (±0.22)	29.8 (±10)	51.9 (±44.0)	5.9 (±8.8)	1.89 (±0.53)
Elk Lake	ELL	5, 5	Coastal	48.31, 123.23	246	7.7, 19.4	0.57 (±0.17)	28.7 (±3.9)	51.1 (±57.9)	3.0 (±1.0)	2.04 (±0.79)
New Lake	NEL	3, 2	Interior	49.30, 115.50	27	3.0, 10.4	0.33 (±0.13)	76.9 (±14.2)	19.7 (±8.2)	2.3 (±1.4)	2.40 (±0.53)
Phillips Reservoir	PHR	3, 2	Interior	49.27, 115.42	30	7.7, 17.4	0.24 (±0.11)	7.2 (±2.2)	24.9 (±12.1)	0.7 (±0.4)	1.27 (±0.95)
Shawnigan Lake North	SHL-N	5, 12	Coastal	48.37, 123.38	360	14.3, 53	0.16 (±0.06)	11.0 (±1.9)	10.7 (±15.9)	1.6 (±0.4)	0.70 (±0.31)
Shawnigan Lake South	SHL-S	5, 12	Coastal	48.37, 123.38	60	11.9, 27	0.15 (±0.06)	11.0 (±1.7)	12.2 (±11.3)	1.7 (±0.5)	0.82 (±0.32)
Sooke Lake Reservoir North	SOL-N	4, 8	Coastal	48.33, 123.41	430	23.2, 70	0.10 (±0.05)	5.6 (±0.9)	12.6 (±22.6)	0.8 (±0.4)	0.68 (±0.28)

Table 2.2. Relationship between lake TP (μmol L^{-1}) and total nitrogen (TN; μmol L^{-1}), bacteria abundance, chlorophyll *a* concentration (Chl*a*) and zooplankton biomass of the study lakes. Regression analyses are based upon the annual means of 2000 and 2001 for the eight study lakes.

Variable	Equation	r^2	*F*	*df*	*p*
TN (with NEL)	$y = 70.1x + 3.5$	0.28	5.35	1, 14	0.04
TN (without NEL)	$y = 49.6x + 1.5$	0.88	86.54	1, 12	<0.001
Bacteria (x10^6 cells mL^{-1})	$y = 3.3x + 0.5$	0.65	25.53	1, 14	<0.001
Chl*a* (μg L^{-1})	$y = 7.2x + 0.1$	0.56	17.97	1, 14	0.001
Zooplankton (μg L^{-1})	$y = 78.1x + 5.1$	0.34	7.1	1, 14	0.018

Table 2.3. Concentration of particulate phosphorus (PP), the percentage of the total TP pool in the particulate form (%TP) and the percentage of PP in the various plankton size fractions of the eight study lakes. Mean summer values for 2000 and 2001 are given for each lake.

Site	PP (μmol L^{-1})	% TP	% PP 0.2- 3 μm	% PP 3 - 20 μm	% PP 20 - 41 μm	% PP 41 - 200 μm	% PP >200 μm
	2000, 2001	2000, 2001	2000, 2001	2000, 2001	2000, 2001	2000, 2001	2000, 2001
COL	0.09, 0.11	100, 100	41, 51	17, 9	22, 12	7, 12	14, 15
CUL	0.34, 0.20	59, 43	37, 53	8, 10	5, 6	23, 19	27, 11
ELL	0.40, 0.27	79, 45	35, 49	15, 7	4, 3	8, 17	38, 24
NEL	0.19, 0.20	66, 49	54, 62	11, 10	7, 5	15, 8	13, 14
PHR	0.17, 0.20	77, 72	51, 56	11, 17	4, 4	8, 13	25, 10
SHL-N	0.09, 0.10	49, 74	52, 45	17, 10	7, 8	11, 12	13, 24
SHL-S	0.12, 0.11	100, 99	57, 45	13, 15	10, 9	10, 15	9, 17
SOL-N	0.07, 0.10	66, 100	57, 56	14, 9	4, 6	11, 9	15, 20
All Sites	-----	74 (±21)	50 (±8)	12 (±3)	7 (±4)	12 (±5)	18 (±8)

Table 2.4. $^{32}PO_4^{3-}$ uptake constants (*k*) and the percent uptake of PO_4^{3-} by plankton size fractions during $^{32}PO_4^{3-}$ uptake bioassays. Values presented for each lake are the summer means of 2000 and 2001.

	k (min^{-1})	% 0.2 - 3μm	% 3 - 20μm	% >20 μm
Site	2000, 2001	2000, 2001	2000, 2001	2000, 2001
COL	0.147, 0.103	81, 74	16, 22	3, 4
CUL	0.191, 0.164	87, 83	9, 12	4, 5
ELL	0.134, 0.104	87, 75	10, 17	3, 9
NEL	0.167, 0.161	90, 92	9, 6	1, 2
PHR	0.163, 0.187	91, 89	7, 9	2, 1
SHL-N	0.170, 0.141	84, 74	13, 23	3, 3
SHL-S	0.140, 0.151	79, 74	18, 23	2, 3
SOL-N	0.136, 0.122	80, 78	17, 9	3, 3
All Sites	0.149 (±0.03)	82 (±6)	14 (±6)	3 (±2)

Table 2.5. Percent contribution of plankton size fractions to the community dissolved P regeneration rate. Values presented for each lake are the summer means of 2000 and 2001.

Site	% <20μm	% 20 - 41μm	% 41 - 200μm	% >200μm
	2000, 2001	2000, 2001	2000, 2001	2000, 2001
COL	44, 38	21, 9	8, 34	27, 19
CUL	27, 36	17, 19	7,13	51, 32
ELL	50, 31	10, 14	2, 18	32, 38
NEL	49, 42	22, 3	5, 0	24, 55
PHR	36, 52	12, 4	5, 5	46, 39
SHL-N	47, 35	19, 17	22, 22	12, 26
SHL-S	26, 47	15, 10	27, 8	32, 35
SOL-N	18, 40	70, 26	7, 28	5, 5
All Sites	39 (±10)	18 (±15)	13 (±11)	30 (±15)

Table 3.1. Site abbreviations, location, morphometric and limnological characteristics of the five study. Values for nutrient concentrations and plankton biomasses and densities are the mean (±1 SD) of the May – October period in 2000 and 2001.

Site	Site Abbr.	Lat, Long (°N, °W)	Surface Area (ha)	Z_{Mean}, Z_{Max} (m)	TP (μM)	TN (μM)	Zooplankton ($\mu g\ l^{-1}$)	Chl*a* ($\mu g\ l^{-1}$)	Bacteria $x10^6$ cells ml^{-1}
Council Lake	COL	48.31, 123.40	16	5.2, 17	0.12 (±0.04)	6.9 (±2.0)	15.8 (±16.9)	0.9 (±.25)	0.83 (±0.45)
Cusheon Lake	CUL	48.48, 123, 28	31	4.4, 9.5	0.52 (±0.22)	29.8 (±10)	51.9 (±44.0)	5.9 (±8.8)	1.89 (±0.53)
Elk Lake	ELL	48.31, 123.23	246	7.7, 19.4	0.57 (±0.17)	28.7 (±3.9)	51.1 (±57.9)	3.0 (±1.0)	2.04 (±0.79)
Shawnigan Lake North	SHL-N	48.37, 123.38	360	14.3, 53	0.16 (±0.06)	11.0 (±1.9)	10.7 (±15.9)	1.6 (±0.4)	0.70 (±0.31)
Shawnigan Lake South	SHL-S	48.37, 123.38	60	11.9, 27	0.15 (±0.06)	11.0 (±1.7)	12.2 (±11.3)	1.7 (±0.5)	0.82 (±0.32)

Table 3.2. Mean summer (May – September) epilimnetic depth and P flux rates of study sites for 2000 and 2001. Values are means and the values in parentheses are the range of values.

Site	Epilinetic Depth (m)		Regeneration (μmol m^{-2} d^{-1})		Zooplankton grazing (μmol m^{-2} d^{-1})		Sedimentation (μmol m^{-2} d^{-1})	
	2000	2001	2000	2001	2000	2001	2000	2001
COL	5.4 (4 - 8.5)	6 (5 - 7.5)	87.4 (25.2 - 202.5)	207.4 (37.0 - 417.2)	55.4 (18.6 - 92.7)	99.8 (24.1 - 293.3)	5.4 (0.5 - 6.9)	10.0 (4.4 - 14.3)
CUL	3.4 (1.5 - 6.0)	3.9 (3.0 - 5.0)	1113.8 (666.4 - 1857.0)	721.2 (81.9 - 875.2)	155.9 (45.4 - 415 .9)	208.2 (46.1 - 618.5)	55.2 (8.3 - 70.7)	18.4 (6.7 - 32.9)
ELL	5.4 (3.5 - 7.0)	6.2 (5 .0 - 7.0)	1208.8 (475.1 - 1982.1)	1103.6 (161.8 -2109.5)	226.6 (80.8 - 455.3)	191.1 (73.1 - 402.3)	193.1 (167.6 - 227.6)	78.4 (11.4 - 166.6)
SHL-N	7.2 (4.0 -10.0)	7.3 (6.0 -9.0)	186.1 (50.7 - 303.1)	335.2 (76.5 - 1182.2)	100.8 (38.4 - 267.2)	180.4 (60.0 - 351.4)	6.7 (4.1 - 10.0)	5.6 (3.1 - 6.9)
SHL-S	6.1 (4.5 - 8.5)	6.4 (4.0 - 8.0)	306.7 (134.6 - 660.6)	235.1 (32.7 - 273.1)	65.1 (23.9 - 121.4)	123.3 (39.1 - 235.2)	8.2 (4.4 - 12.6)	6.2 (4.2 - 9.5)

Table 3.3. Proportion of PP >41μm in sediment traps for the summer periods of 2000 and 2001 and the winters (January – February) of 2001 and 2002. For the summers, mean proportions (±1SD) are presented for the May – September period. No standard deviations are presented for winter values because data was collected once in both winters.

Site	Proportion >41 μm Summer		Proportion >41 μm Winter	
	2000	2001	2001	2002
COL	0.43 (±0.34)	0.32 (±0.18)	0.33	0.58
CUL	0.34 (±0.21)	0.41 (±0.36)	0.05	0.38
ELL	0.50 (±0.27)	0.43 (±0.29)	0.05	0.54
SHL-N	0.41 (±0.30)	0.49 (±0.23)	0.17	0.51
SHL-S	0.33 (±0.22)	0.45 (±0.21)	0.17	0.6
All Sites	0.40 (±0.07)	0.42 (±0.06)	0.15 (±0.12)	0.52 (±0.09)

Table 4.1. Morphometry, hydrology, water clarity, nutrient concentrations and plankton biomass of the north and south basins of Sooke Lake Reservoir and Shawnigan Lake. Surface areas and volumes are full-stage values and water exchange rates are the mean of January – December 2000 and 2001. Values are summer (May – September) epilimnetic means of 2000 and 2001.

			Sooke Lake Reservoir			Shawnigan Lake	
		Whole Lake	North Basin	South Basin	Whole Lake	North Basin	South Basin
Lat, Long	N, W	48° 33', 123° 41'	----	----	48° 37', 123° 38'	----	----
Elevation	m	180	----	----	116	----	----
Max Length	km	7.0	----	----	6.9	----	----
Max Fetch	N-S, km	5.0	4.1	1.2	5.5	3.7	1.4
Catchment Area	km^2	87	----	----	69.4	----	----
Surface Area	$x\ 10^6\ m^2$	6.0	4.3	0.5	5.5	3.6	0.6
Max Depth	m	70	70	22	53	53	27
Mean Depth	m	19.5	23.2	8.6	13.0	14.3	11.9
Volume	$x\ 10^6\ m^3$	117.9	100.5	3.9	71.9	51.1	6.8
Water Exchange Rate	yr^{-1} (± 1 SD)	0.7 (± 0.27)	----	----	0.5 (± 0.14)	----	----
Secchi depth	m (± 1 SD)	----	8.5 (± 2.0)	7.4 (± 1.7)	----	5.9 (± 0.5)	5.9 (± 1.9)
Light Extinction Coefficient	m^{-1} (± 1 SD)	----	0.3 (± 0.05)	0.4 (± 0.05)	----	0.4 (± 0.08)	0.4 (± 0.06)
Chlorophyll *a*	μg/L (± 1 SD)	----	0.7 (± 0.4)	0.9 (± 0.3)	----	1.3 (± 0.64)	1.5 (± 0.74)
Total phosphorus	μg/L (± 1 SD)	----	3.1 (± 1.5)	3.3 (± 1.5)	----	4.9 (± 1.8)	4.4 (± 2.1)
Total nitrogen	μg/L (± 1 SD)	----	80.9 (± 13.3)	85.6 (± 20.4)	----	152.4 (± 26.5)	153.4 (± 24.2)
DOC	mg/L (± 1 SD)	----	2.0 (± 0.3)	2.0 (± 0.3)	----	3.1 (± 0.31)	3.1 (± 0.29)

Table 4.2. Mean summer (1 May – 30 September) daily meteorological conditions (air temperature, solar irradiance, and wind speed) at the Sooke Lake Reservoir Dam meteorological station in 2000 and 2001. Minimum and maximum daily values are also given.

	Air Temperature (± 1 SD) (°C)		Irradiance (± 1 SD) kwatt m^{-2} day^{-1}		Wind Speed (± 1 SD) m s^{-1}	
	Mean	Min, Max	Mean	Min, Max	Mean	Min, Max
2000	13.9 (± 3.3)	6.4, 20.9	4.8 (± 1.7)	0.8, 7.7	9.4 (± 1.9)	5.9, 18.2
2001	13.7 (± 3.1)	6.4, 20.0	4.9 (± 1.7)	0.08, 7.6	8.9 (± 2.1)	3.9, 14.4

Table 4.3. Observed duration of the stratification period in the north and south basins of Sooke Lake Reservoir and Shawnigan Lake. Duration of stratification (number of days) was determined from the date on which stratification was initially observed to the last date stratification was observed. Observed dates are the calendar dates of the stratification observed stratification period.

	2000		2001	
	Stratification Period (no. of days)	Observed Dates	Stratification Period (no. of days)	Observed Dates
Sooke Lake Reservoir				
South Basin	113	19 June - 10 Oct	98	21 June - 28 Sept
North Basin	113	19 June - 10 Oct	126	7 June - 11 Oct
Shawnigan Lake				
South Basin	153	11 May - 11 Oct	161	8 May - 16 Oct
North Basin	153	11 May - 11 Oct	147	22 May - 16 Oct

Table 4.4. Mean epilimnetic depth (m) and relative thermocline depth (α) during the summer stratification period for the north and south basins of Sooke Lake Reservoir and Shawnigan Lake. Values are calculated from all sampling dates during the stratification period for each basin. Values in parentheses are the range observed during stratification.

	2000		2001	
	Epilimnetic Depth (m)	α	Epilimnetic Depth (m)	α
Sooke Lake Reservoir				
South Basin	9.0 (7.0 - 10.0)	0.59 (0.49 - 0.69)	8.4 (7.5 - 9.5)	0.55 (0.51 - 0.60)
North Basin	10.6 (6.0 - 14.0)	0.18 (0.13 - 0.23)	10.9 (7.5 - 15.0)	0.19 (0.12 - 0.24)
Shawnigan Lake				
South Basin	6.7 (4.5 - 9.5)	0.31 (0.22 - 0.42)	6.6 (4.0 - 9.5)	0.32 (0.26 - 0.40)
North Basin	7.8 (4.0 -11.0)	0.17 (0.11 - 0.22)	7.6 (6.0 - 11.0)	0.16 (0.14 - 0.23)

Table 4.5. Mean (± 1SD) volume-weighted epilimnetic (T_E) and hypolimnetic (T_H) temperatures (°C) for the north and south basins of Sooke Lake Reservoir and Shawnigan Lake in 2000 and 2001. Means for T_E and T_H were calculated from all volume-weighted temperatures obtained on sampling dates in which a basin was thermally stratified.

	Sooke Lake Reservoir		Shawnigan Lake	
	South Basin		South Basin	
	T_E	T_H	T_E	T_H
2000	16.4 (± 3.0)	9.3 (± 0.5)	17.5 (± 4.0)	8.2 (± 0.6)
2001	17.5 (± 1.3)	10.5 (± 0.6)	17.5 (± 3.3)	8.2 (± 0.7)
	North Basin		North Basin	
	T_E	T_H	T_E	T_H
2000	17.0 (± 2.9)	7.5 (± 0.8)	17.2 (± 3.7)	7.6 (± 0.1)
2001	17.4 (± 2.2)	8.6 (± 0.4)	17.6 (± 2.6)	7.9 (± 0.5)

Table 5.1. Location, morphometry and water clarity of the north and south basins of Sooke Lake Reservoir and Shawnigan Lake. Surface areas and volumes are full-stage values and water exchange rates are the mean of January – December 2000 and 2001.

		Sooke Lake Reservoir			Shawnigan Lake		
		Whole Lake	North Basin	South Basin	Whole Lake	North Basin	South Basin
Lat, Long	N, W	48° 33', 123° 41'	----	----	48° 37', 123° 38'	----	----
Elevation	m	180.0	----	----	116.0	----	----
Max Length	km	7.0	----	----	6.9	----	----
Max Fetch	N-S, km	5.0	4.1	1.2	5.5	3.7	1.4
Catchment Area	km^2	87.0	----	----	69.4	----	----
Surface Area	x 10^6 m^2	6.0	4.3	0.5	5.5	3.6	0.6
Max Depth, Mean Depth	m	70.0, 19.5	70.0, 23.2	22.0, 8.6	53.0,13.0	53.0, 14.3	27.0, 11.9
Volume	x 10^6 m^3	117.9	100.5	3.9	71.9	51.1	6.8
Secchi depth	m (± 1 SD)	----	8.5 (± 2.0)	7.4 (± 1.7)	----	5.9 (± 0.5)	5.9 (± 1.9)

Table 5.2. Period of observed stratification in the north and south basins of Sooke Lake Reservoir and Shawnigan Lake during the summer and fall of 2000 and 2001.

		2000	2001
		Stratification Period	Stratification Period
Sooke Lake Reservoir			
	South Basin	19 June - 10 Oct	21 June - 28 Sept
	North Basin	19 June - 10 Oct	7 June - 11 Oct
Shawnigan Lake			
	South Basin	11 May - 11 Oct	8 May - 16 Oct
	North Basin	11 May - 11 Oct	22 May - 16 Oct

Table 5.3. Results of Pearson correlation analyses between day of year (day number) and the concentration of TP and TN in the four study basins during the stratification periods of 2000 and 2001. Numbers in the table are *p* values for the correlations. Presented for each basin are the *p* values of 2000, 2001.

	TP μmol L^{-1}	TN μmol L^{-1}
SHL-N	0.911, 0.483	0.264, 0.836
SHL-S	0.687, 0.245	0.506, 0.128
SOL-N	0.591, 0.817	0.129, 0.845
SOL-S	0.779, 0.096	0.149, 0.305

Table 5.4. Results of least-squares regression analyses of mean summer TP, TN and Chl*a* concentrations and the minimum summer percent usable reservoir volume in Sooke Lake Reservoir for the 2000 – 2003 time period (See Fig. 5.9 for data). Given are the results of analyses including 2003 and excluding 2003 data. r^2, F (with degrees of freedom) and p values are given for each variable for each analysis. Equations describing relationships are only given if the relationship was found to be significant.

	TP		TN		Chl*a*	
	Incl. 2003	Excl. 2003	Incl. 2003	Excl. 2003	Incl. 2003	Excl. 2003
r^2	0.01	0.87	0.41	0.41	0.48	0.84
F	$0.03_{(1,7)}$	$13.2_{(1,5)}$	$4.2_{(1,7)}$	$2.8_{(1,5)}$	$5.5_{(1,7)}$	$20.6_{(1,5)}$
p	0.87	0.02	0.09	0.17	0.06	0.01
Equation	-----	$y = 0.002x + 0.2$	-----	-----	-----	$y = -0.03x + 1.9$

Table 5.5. Mean seasonal aerial P fluxes ($\mu M\ m^{-2}\ d^{-1}$) within, into and out of the epilimnion of Shawnigan Lake and Sooke Lake Reservoir. Mean values are given for each basin during the summer stratification period (S) and in the winter (W) in 2000 and 2001. ND = no data collected during this period.

	SHL-N				SHL-S				SOL-N				SOL-S			
	2000		2001		2000		2001		2000		2001		2000		2001	
	S	W	S	W	S	W	S	W	S	W	S	W	S	W	S	W
Internal Cycling																
Regeneration	186.1	ND	230.3	1998.4	306.7	ND	241.7	2906.7	339.8	ND	548.537	196.775	334.6	ND	194.8	75.4
Grazing	100.8	ND	138.6	267.3	65.1	ND	121.6	1430.9	71.2	ND	291.0	420.5	71.5	ND	124.3	158.1
Inputs																
IBT	0.65	2.2	1.8	1.8	----	----	----	----	----	----	----	----	63.0	32.4	33.1	344.3
Outputs																
Sedimentation	-6.7	-2.7	-5.6	-9.3	-8.2	-1.5	-5.8	-10.9	-5.7	-2.4	-3.8	-3.1	-9.2	-1.3	-9.2	-22.3
IBT	----	----	----	----	-3.3	-8.5	-10.3	-56.6	-3.5	-1.2	-2.7	-6.8	----	----	----	----
Stream/Dam Spill	-0.9	-2.2	-2.5	-15.4	----	----	----	----	----	----	----	----	0	0	0	-270.4
Drinking Water	----	----	----	----	----	----	----	----	----	----	----	----	-72.3	-37.1	-45.5	-37.2

Figures

Figure 2.1. Conceptual diagram and predicted relationships of epilimnetic P cycling along a TP gradient. (a) Conceptual diagram depicting predicted shifts in the P content and fluxes along a gradient of total phosphorus (TP), similar to figures in Reynolds (1986) and Capblancq (1990). Sizes of circles and sections within circles represent the relative concentrations of particulate P pools within the plankton community (PP>20 and PP<20 μm) and the PO_4^{3-} pool. Arrows represent the uptake and regeneration of PO_4^{3-} by the two different plankton size fractions, with arrow size indicating importance (i.e. – larger arrows represent proportionally larger uptake or regeneration by a size fraction). (b) Predicted response of the percent of the particulate phosphorus pool (PP) contained by plankton <20 μm, and the percent uptake and regeneration of PO_4^{3-} by plankton <20 μm, compared to other plankton size fractions, along a TP gradient. (c) Predicted relationship between PO_4^{3-} concentration and TP, after Fig. 7.2 in Harris (1985). Note, that as TP increases, PO_4^{3-} becomes an increasing portion of TP (the predicted TP – PO_4^{3-} line converges with the 1:1 line). (d) Predicted relationship between PO_4^{3-}, TP and PP pool turnover rates and TP concentration.

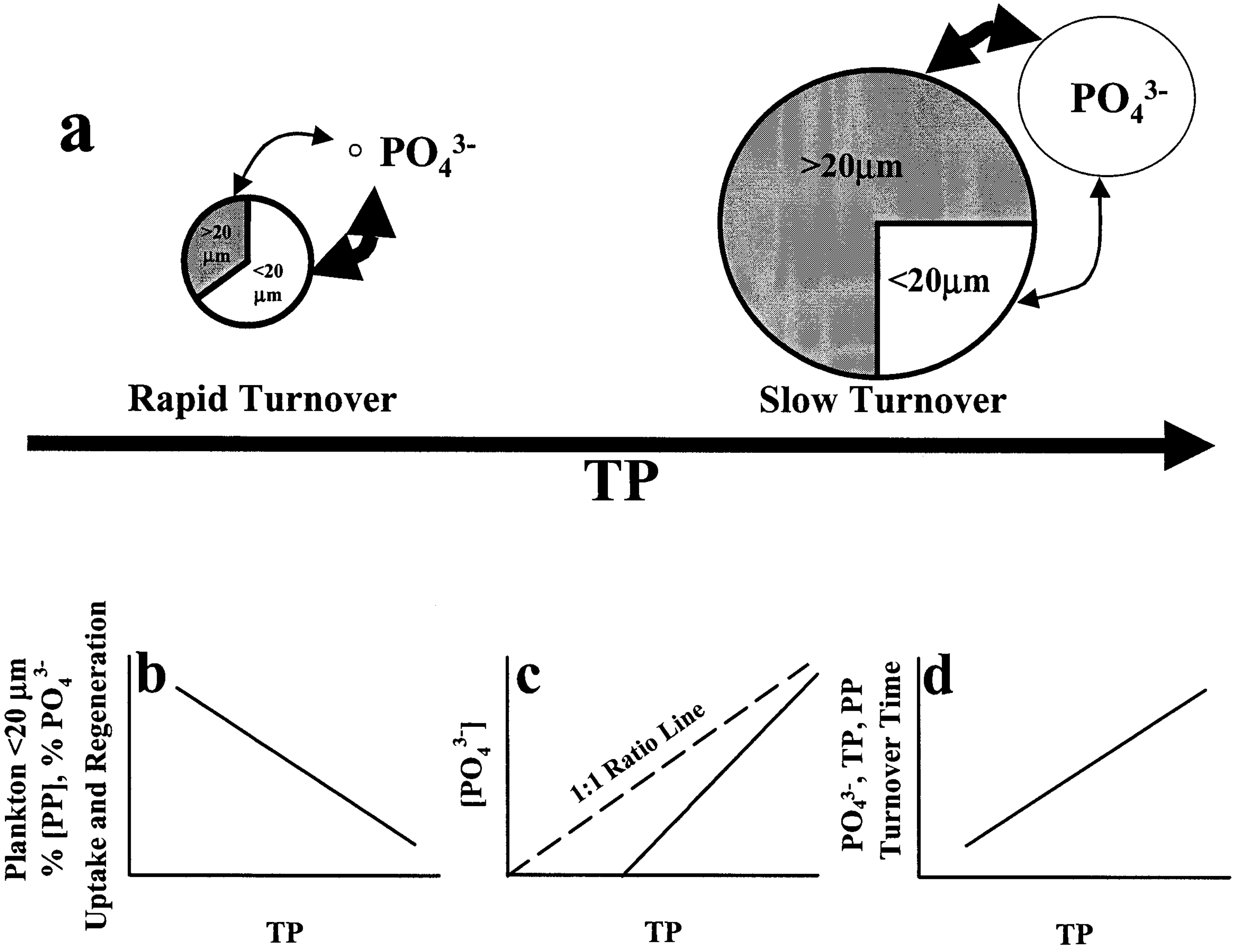

a
>20 µm
<20 µm
○ PO_4^{3-}
Rapid Turnover
>20µm
<20µm
PO_4^{3-}
Slow Turnover
TP
b
Plankton <20 µm % [PP], % PO_4^{3-} Uptake and Regeneration
TP
c
$[PO_4^{3-}]$
1:1 Ratio Line
TP
d
PO_4^{3-}, TP, PP Turnover Time
TP

Figure 2.2. Relationship between TP and the concentration of particulate phosphorus (PP) in the lakes examined by this study.

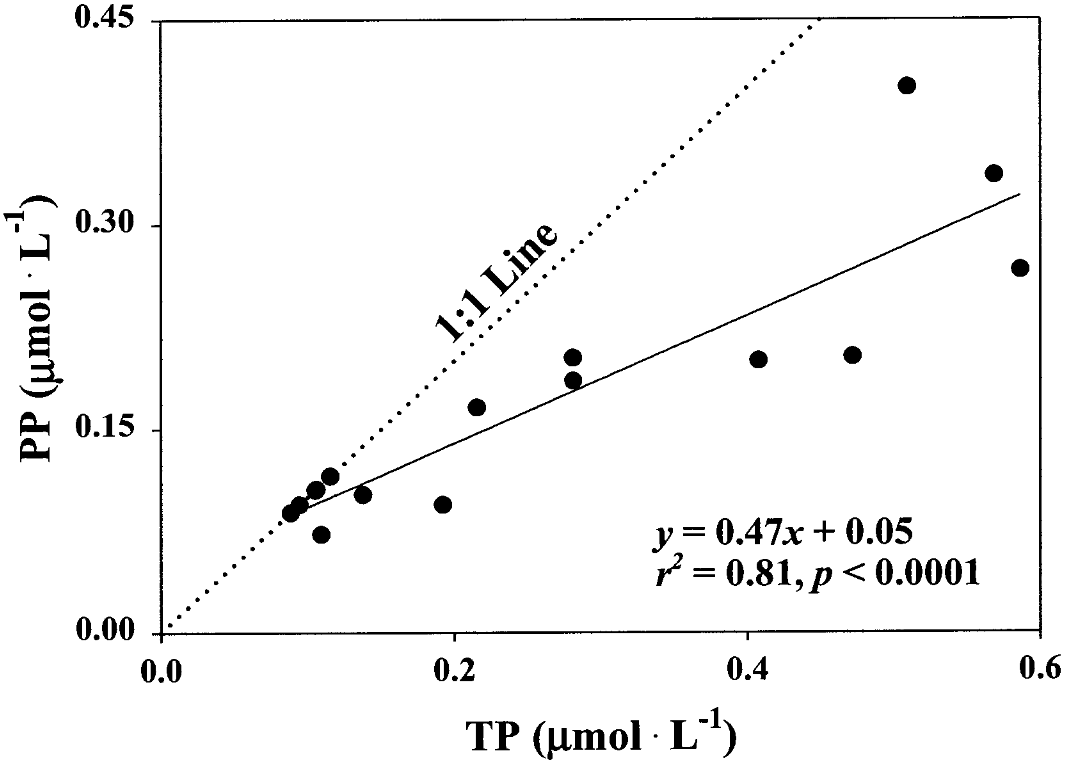

0.45
0.30
0.15
0.00
PP (μmol · L^{-1})
0.0
0.2
0.4
0.6
TP (μmol · L^{-1})
1:1 Line
$y = 0.47x + 0.05$
$r^2 = 0.81, p < 0.0001$

Figure 2.3. Dissolved phosphorus regeneration rates (nmol L^{-1} h^{-1}) of the various size fractions of the plankton community as a function of TP. (a) The whole water (WW) unfractionated plankton community, (b) the >200 µm mesoplankton, (c) the 200-41µm large microplankton,(d) the 41-20µm small microplankton, and (e) the <20µm pico- and nanoplankton.

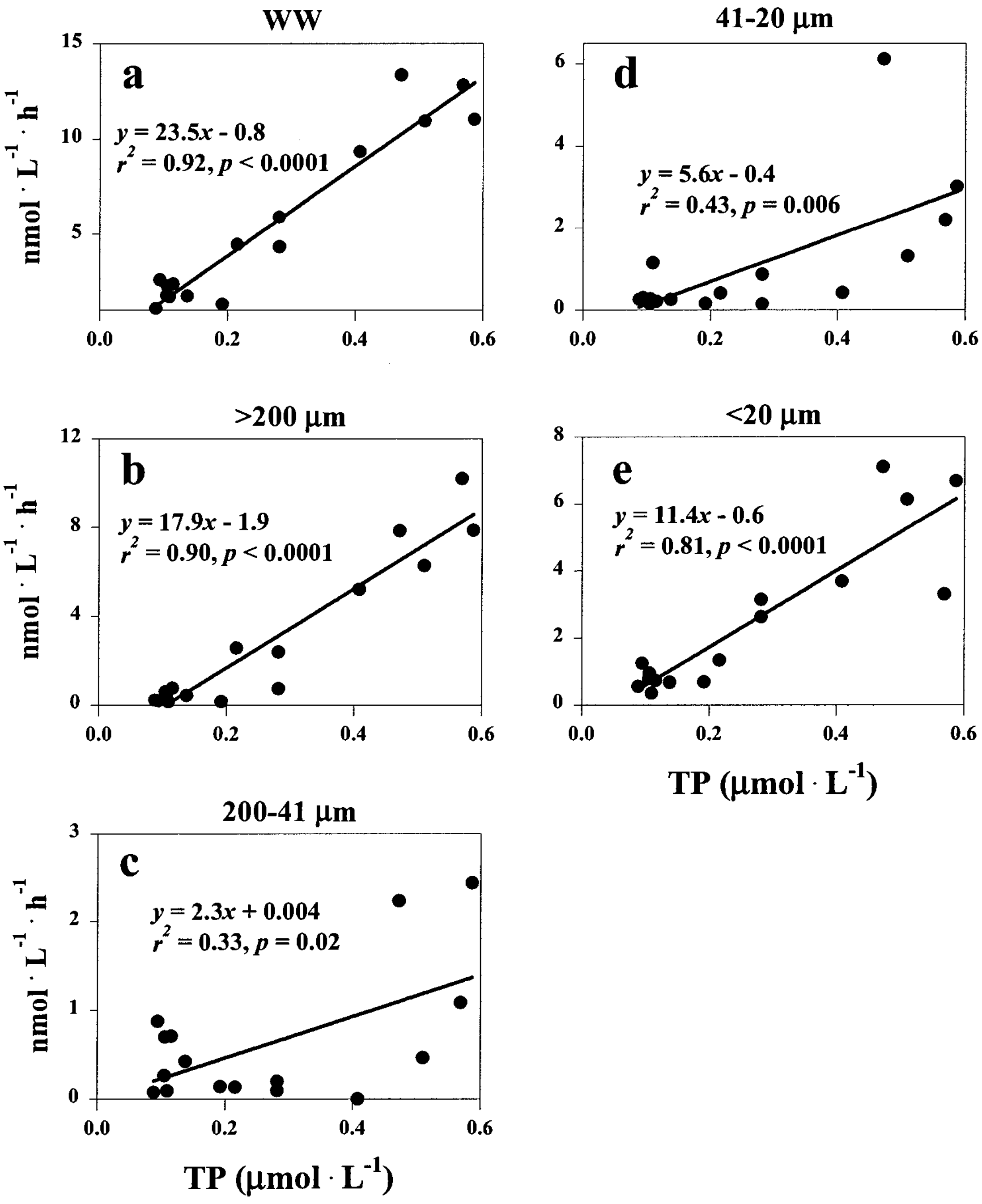

WW
a
y = 23.5x - 0.8
r² = 0.92, p < 0.0001
15
10
5
nmol · L⁻¹ · h⁻¹
0.0
0.2
0.4
0.6
41-20 µm
d
y = 5.6x - 0.4
r² = 0.43, p = 0.006
6
4
2
0
>200 µm
b
y = 17.9x - 1.9
r² = 0.90, p < 0.0001
12
8
4
0
<20 µm
e
y = 11.4x - 0.6
r² = 0.81, p < 0.0001
TP (µmol · L⁻¹)
200-41 µm
c
y = 2.3x + 0.004
r² = 0.33, p = 0.02
3
2
1
0
TP (µmol · L⁻¹)

Figure 2.4. Steady state bioassay estimates of PO_4^{3-} concentration ($ssPO_4^{3-}$) plotted as a function of (a) TP and (b) TDP. (c) SRP concentration plotted as a function of TP. The lack of a regression equation, r^2 value and p value in Fig. 4c indicates the relationship was not significant (p value in text).

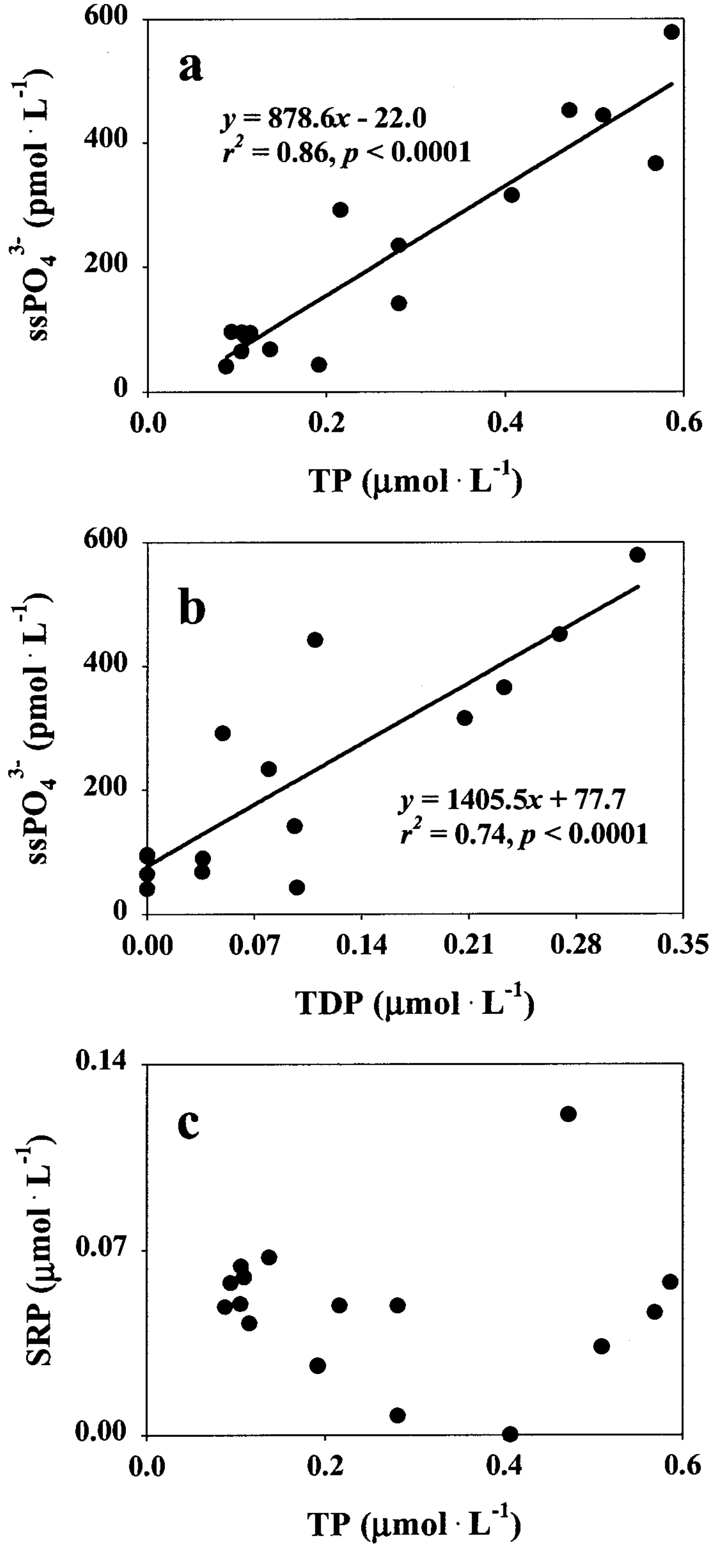

a
y = 878.6x - 22.0
r² = 0.86, p < 0.0001
ssPO4 3- (pmol · L-1)
600
400
200
0
0.0
0.2
0.4
0.6
TP (µmol · L-1)
b
y = 1405.5x + 77.7
r² = 0.74, p < 0.0001
ssPO4 3- (pmol · L-1)
600
400
200
0
0.00
0.07
0.14
0.21
0.28
0.35
TDP (µmol · L-1)
c
SRP (µmol · L-1)
0.14
0.07
0.00
0.0
0.2
0.4
0.6
TP (µmol · L-1)

Figure 2.5. Relationship between TP and the ratio of PO_4^{3-} to (a) PP, and (b) PP<20μm.

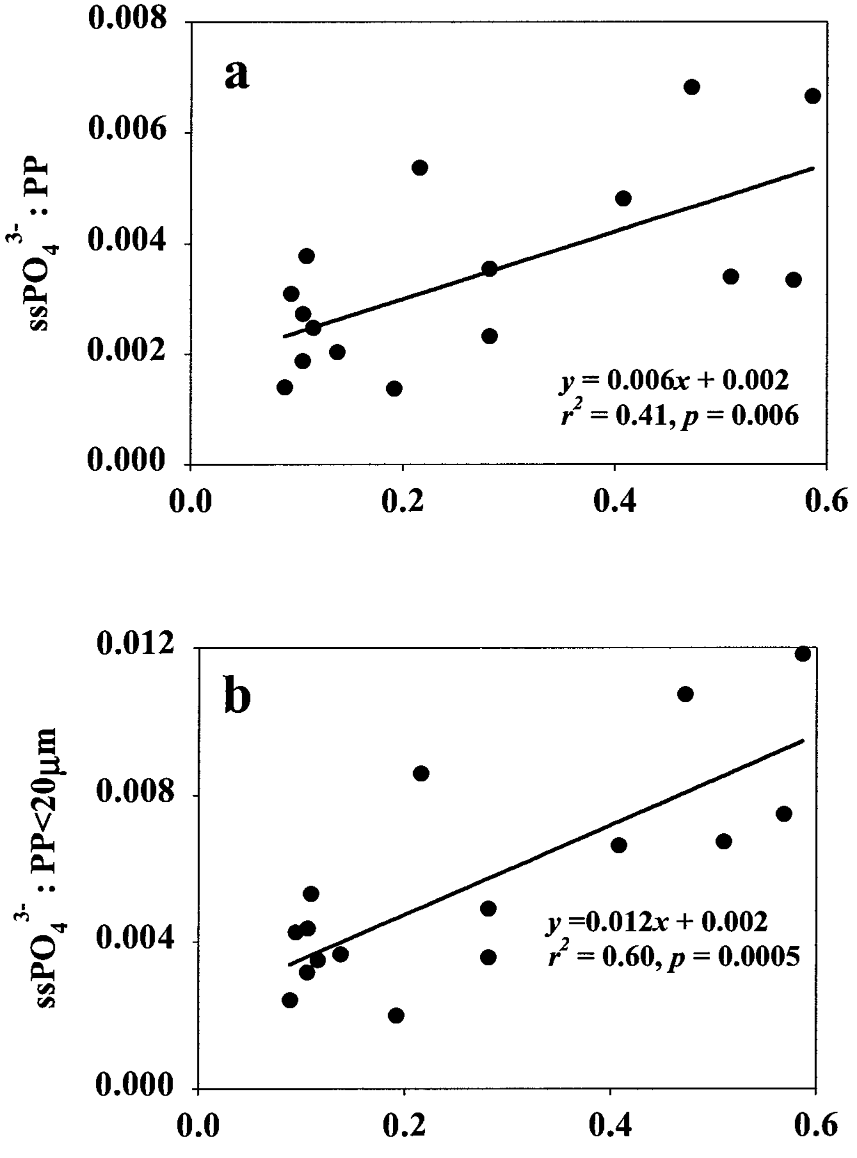

a
0.008
0.006
0.004
0.002
0.000
0.0
0.2
0.4
0.6
$ssPO_4^{3-}$: PP
$y = 0.006x + 0.002$
$r^2 = 0.41, p = 0.006$
b
0.012
0.008
0.004
0.000
0.0
0.2
0.4
0.6
$ssPO_4^{3-}$: PP<20μm
$y = 0.012x + 0.002$
$r^2 = 0.60, p = 0.0005$
TP (μmol · L^{-1})

Figure 2.6. PO_4^{3-} turnover time (minutes) plotted as a function of (a) TP concentration, (b) the concentration of $ssPO_4^{3-}$, and (c) TDP concentration. The lack of regression equations, r^2 values and p values indicate that relationships were not significant (p values are presented in text).

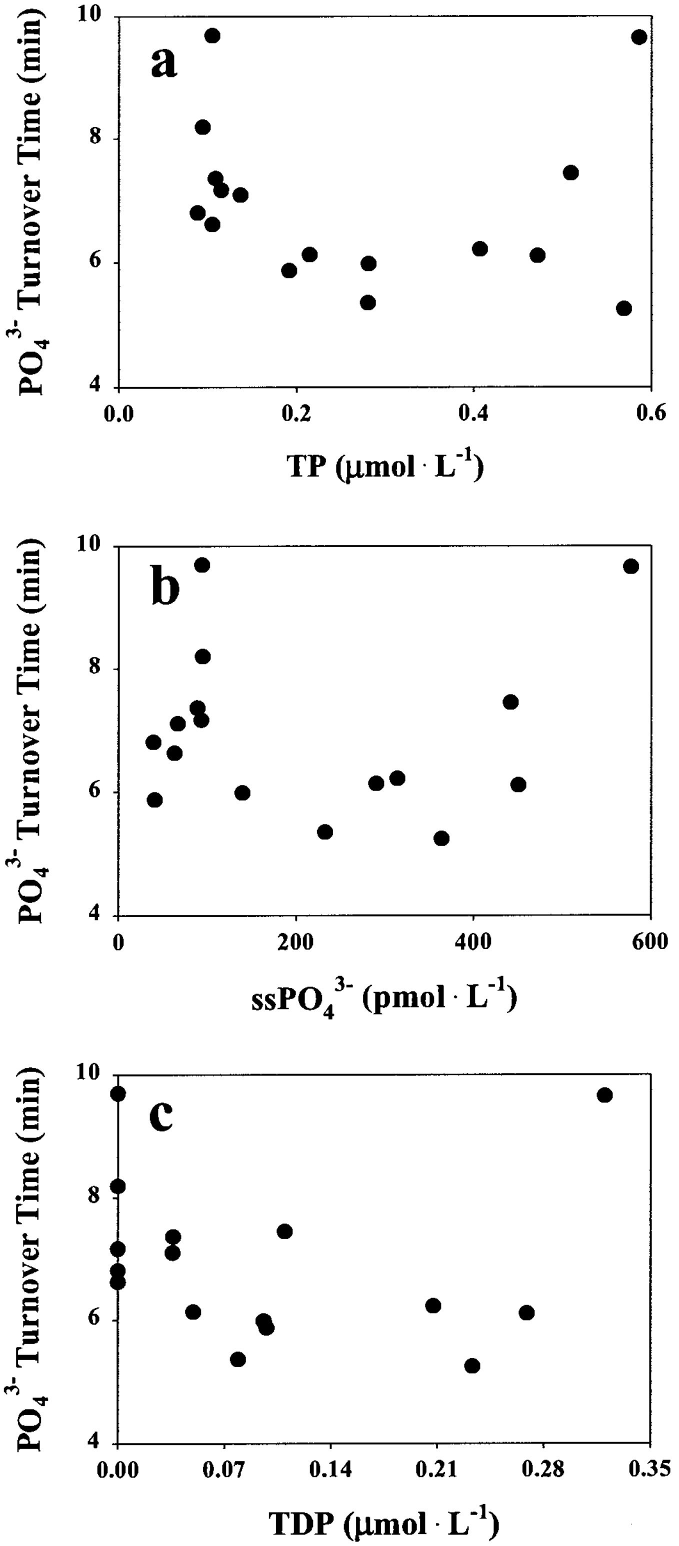

a
PO_4^{3-} Turnover Time (min)
10
8
6
4
0.0
0.2
0.4
0.6
TP (μmol · L^{-1})
b
PO_4^{3-} Turnover Time (min)
10
8
6
4
0
200
400
600
$ssPO_4^{3-}$ (pmol · L^{-1})
c
PO_4^{3-} Turnover Time (min)
10
8
6
4
0.00
0.07
0.14
0.21
0.28
0.35
TDP (μmol · L^{-1})

Figure 2.7. Relationship between TP and the turnover time (in days) of the (a) TP pool, (b) the TPP pool, and (c) the nanoplankton P (PP<20 μm).

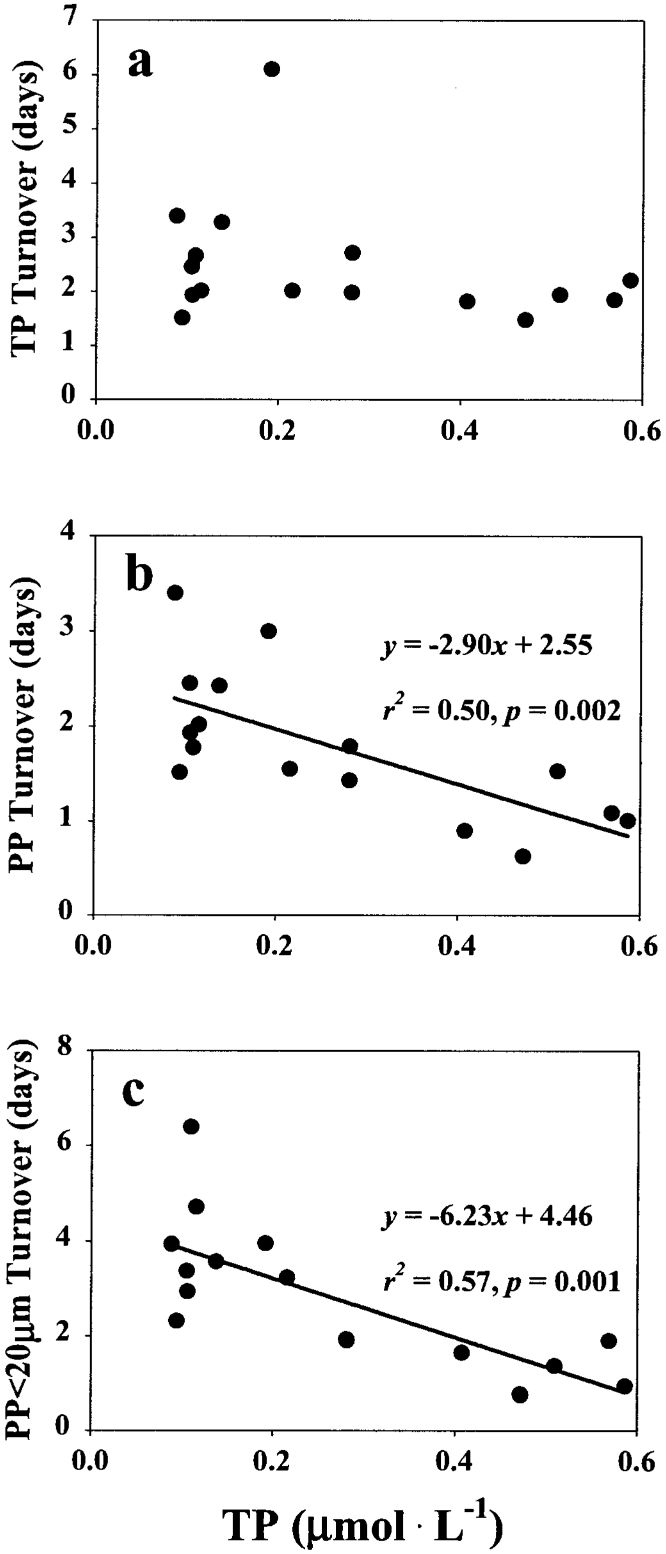

a
TP Turnover (days)
0
1
2
3
4
5
6
7
0.0
0.2
0.4
0.6
b
PP Turnover (days)
$y = -2.90x + 2.55$
$r^2 = 0.50, p = 0.002$
0
1
2
3
4
0.0
0.2
0.4
0.6
c
PP<20μm Turnover (days)
$y = -6.23x + 4.46$
$r^2 = 0.57, p = 0.001$
0
2
4
6
8
0.0
0.2
0.4
0.6
TP (μmol · L^{-1})

Figure 2.8. Figures representing the predicted (see Predictions 1 – 3 in Introduction and Fig. 1b, c and d) and observed trends in P cycling across the range of TP of this study. (a) Relationship between the percent of PP contained in plankton <20 μm, and the percent uptake and regeneration of PO_4^{3-} by plankton <20 μm, compared to other plankton size fractions, along the TP gradient. (c) Relationship between the concentration of $ssPO_4^{3-}$ and TP. (d) Relationship between TP and the turnover rates of PO_4^{3-}, TP, PP and PP<20 μm pools in lakes. It is important to note that the depicted relationships are not meant to portray actual slopes or *y*-intercepts. Rather, they depict general relationship between predicted and observed trends in the data.

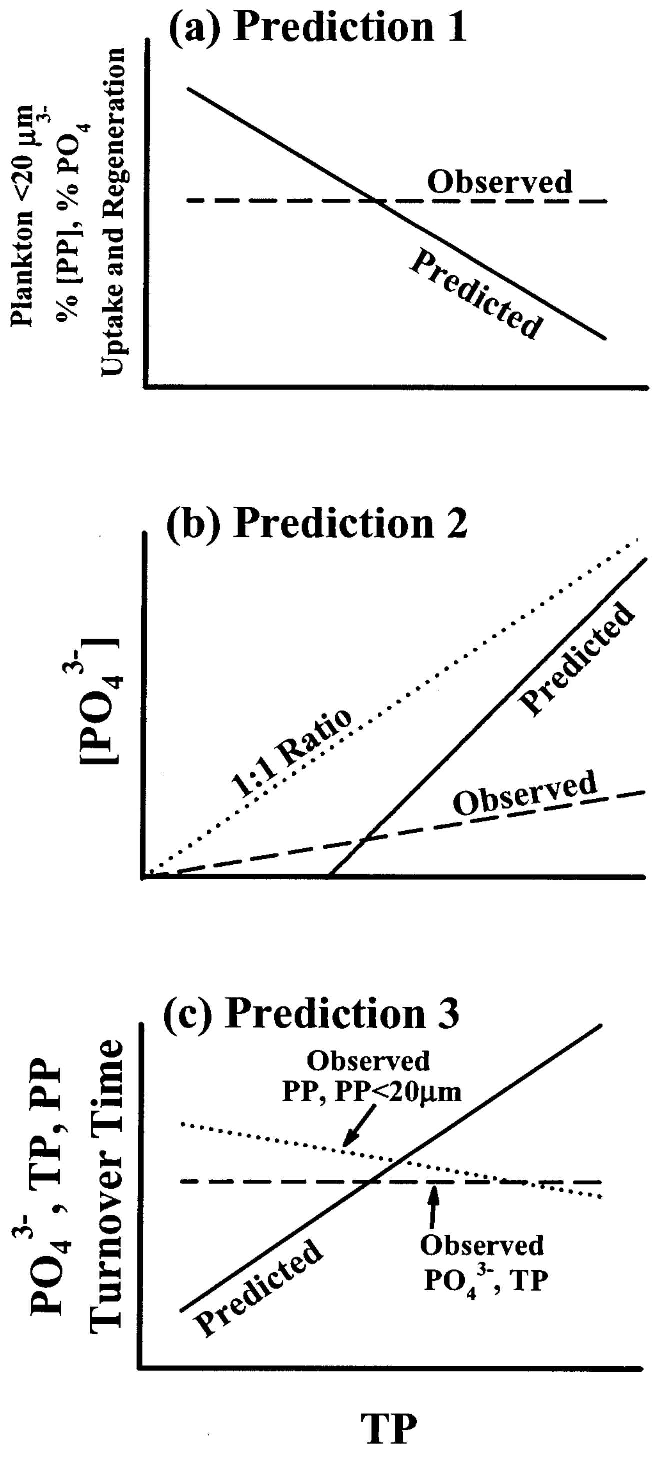

(a) Prediction 1
Plankton <20 µm
% [PP], % PO4 3-
Uptake and Regeneration
Observed
Predicted
(b) Prediction 2
[PO4 3-]
1:1 Ratio
Predicted
Observed
(c) Prediction 3
PO4 3-, TP, PP
Turnover Time
Observed
PP, PP<20µm
Observed
PO4 3-, TP
Predicted
TP

Figure 3.1. Temporal trends of TP (a - b), TN (c – d) and Chl*a* (d – e) in the five study basins from May 2000 – February 2002. Data for the three oligotrophic sites (COL, SHL-S and SHL-N) are presented on the left side of the figure and the data for the meso-eutrophic sites are presented on the right side of the figure.

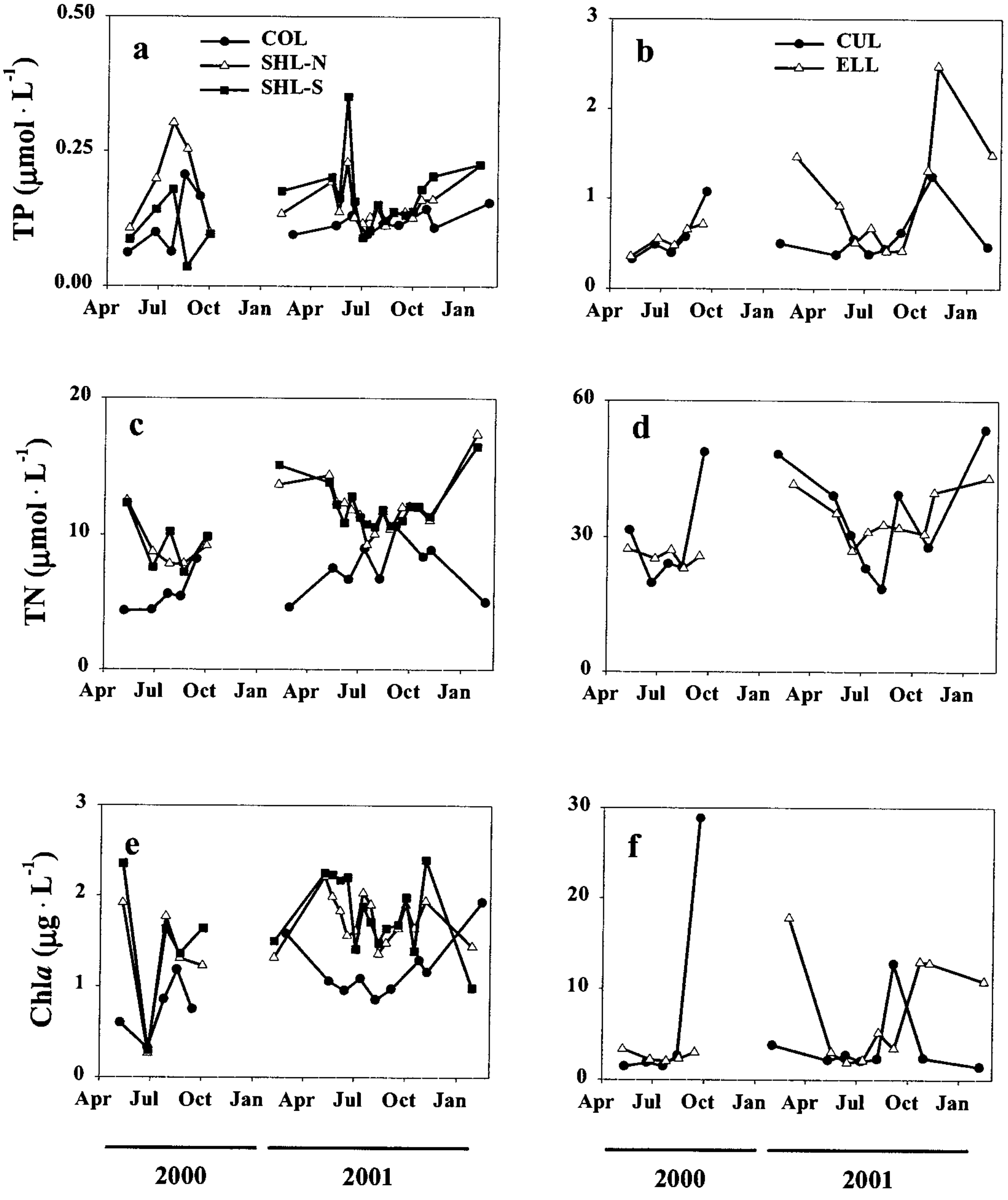
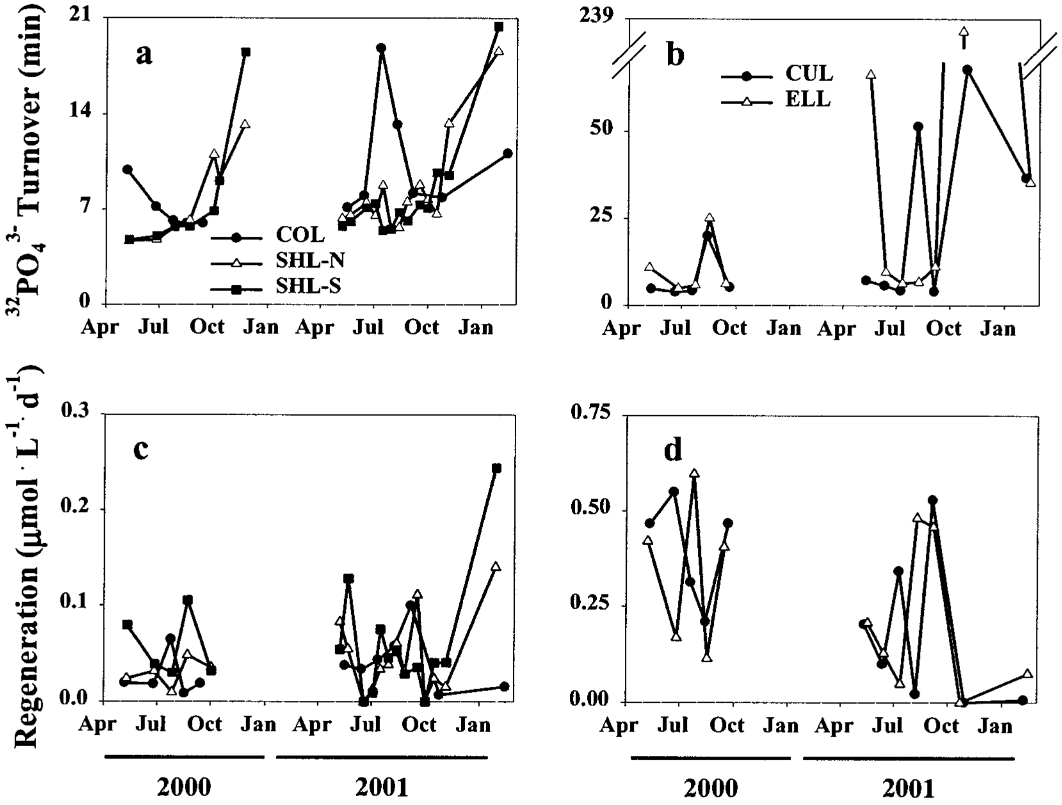

TP (µmol · L^{-1})
0.50
0.25
0.00
a
COL
SHL-N
SHL-S
3
2
1
0
b
CUL
ELL
TN (µmol · L^{-1})
20
10
0
c
60
30
0
d
Chl*a* (µg · L^{-1})
3
2
1
0
e
30
20
10
0
f
Apr Jul Oct Jan Apr Jul Oct Jan
2000
2001

Figure 3.2. Temporal trends of PO_4^{3-} turnover time (a - b), and planktonic regeneration rate (c – d) in the five study basins from May 2000 – February 2002. Data for the three oligotrophic sites (COL, SHL-S and SHL-N) are presented on the left side of the figure and the data for the meso-eutrophic sites are presented on the right side of the figure.



a
b
c
d
$^{32}PO_4^{3-}$ Turnover (min)
Regeneration (µmol · L^{-1} · d^{-1})
21
14
7
0
239
50
25
0
0.3
0.2
0.1
0.0
0.75
0.50
0.25
0.00
COL
SHL-N
SHL-S
CUL
ELL
Apr
Jul
Oct
Jan
Apr
Jul
Oct
Jan
2000
2001

Figure 3.3. (a) Mean summer aerial planktonic P regeneration rate plotted as a function of mean summer aerial epilimnetic P concentration for the five study basins in 2000 and 2001 (*n* = 10). (b) The mean summer percent of the epilimnetic TP pool recycled per day through planktonic regeneration plotted as a function of the mean summer aerial epilimnetic P concentration for the five study basins in 2000 and 2001 (*n* = 10).

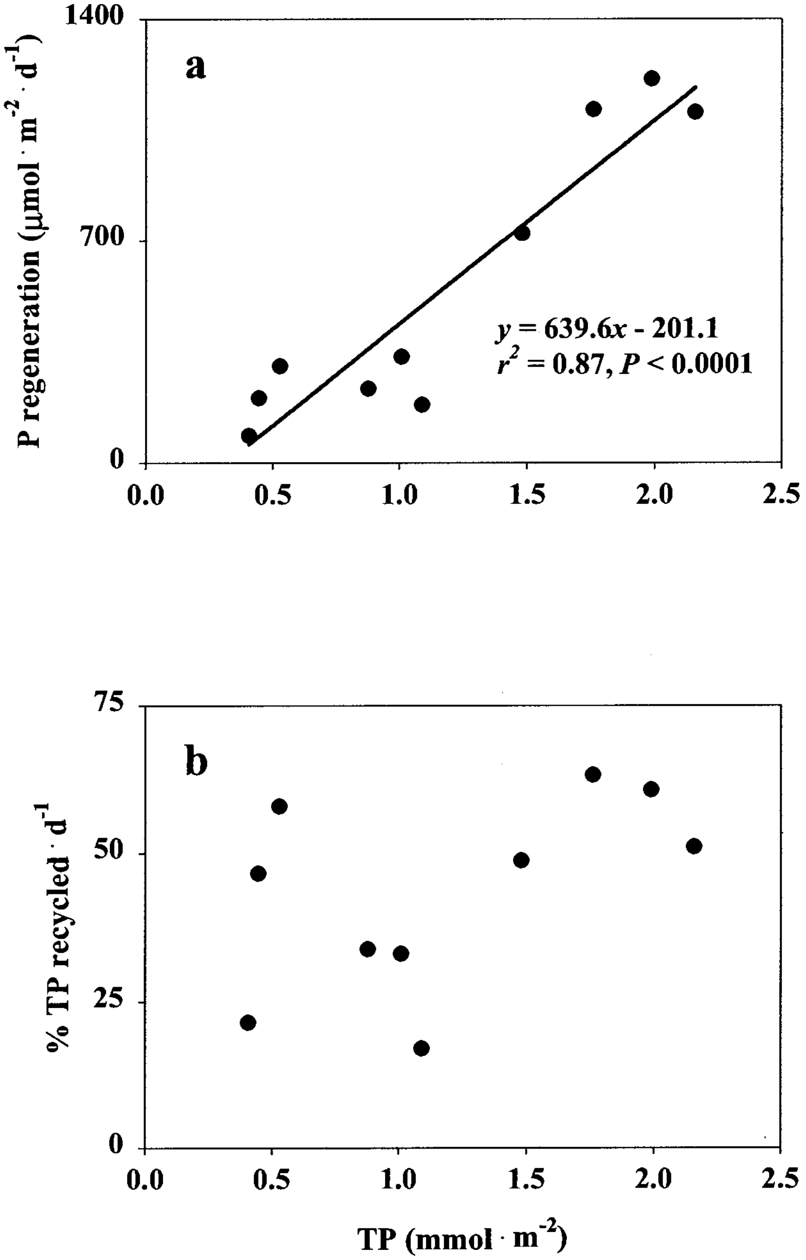

a
1400
700
0
0.0
0.5
1.0
1.5
2.0
2.5
P regeneration (μmol · m^{-2} · d^{-1})
$y = 639.6x - 201.1$
$r^2 = 0.87, P < 0.0001$
b
75
50
25
0
0.0
0.5
1.0
1.5
2.0
2.5
% TP recycled · d^{-1}
TP (mmol · m^{-2})

Figure 3.4. Temporal trends of zooplankton grazing rate (a - b) and the flux rate of PP<41 µm into zooplankton (c – d) in the five study basins from May 2000 – February 2002. Data for the three oligotrophic sites (COL, SHL-S and SHL-N) are presented on the left side of the figure and the data for the meso-eutrophic sites are presented on the right side of the figure.

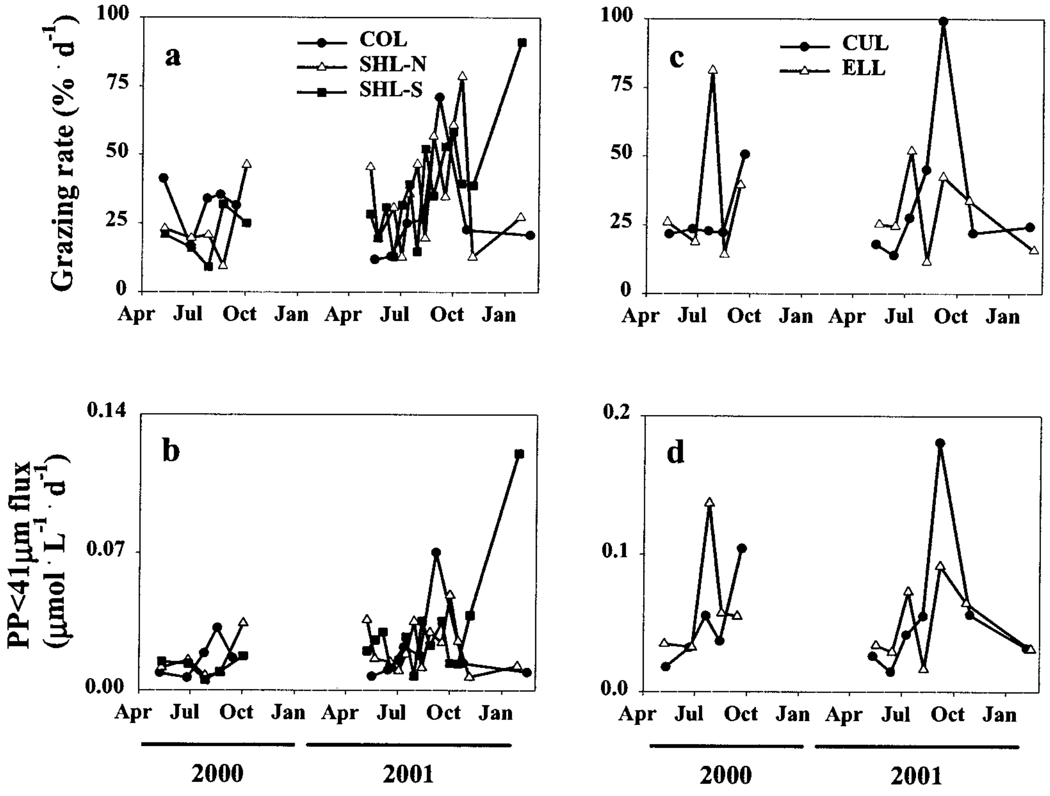

a
b
c
d
COL
SHL-N
SHL-S
CUL
ELL
Grazing rate (% · d^{-1})
PP<41μm flux (μmol · L^{-1} · d^{-1})
0
25
50
75
100
0.00
0.07
0.14
0.0
0.1
0.2
Apr Jul Oct Jan Apr Jul Oct Jan
2000
2001

Figure 3.5. (a) Mean summer aerial flux of PP <41 µm into zooplankton through grazing plotted as a function of mean summer aerial epilimnetic P concentration for the five study basins in 2000 and 2001 (*n* = 10). (b) The mean summer percent of the epilimnetic PP <41 µm pool ingested per day by zooplankton plotted as a function of the mean summer aerial epilimnetic P concentration for the five study basins in 2000 and 2001 (*n* = 10).

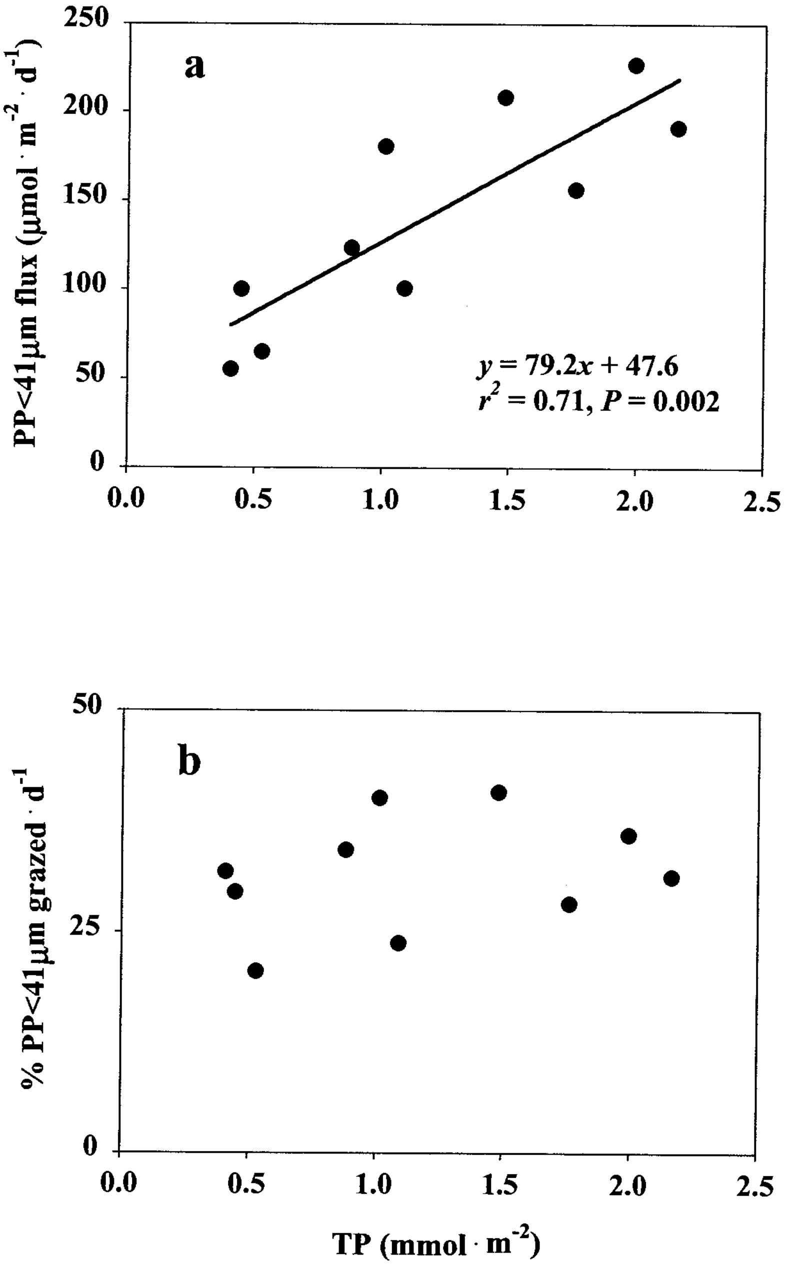

a
PP<41µm flux (µmol · m-2 · d-1)
250
200
150
100
50
0
0.0
0.5
1.0
1.5
2.0
2.5
y = 79.2x + 47.6
r2 = 0.71, P = 0.002
b
% PP<41µm grazed · d-1
50
25
0
0.0
0.5
1.0
1.5
2.0
2.5
TP (mmol · m-2)

Figure 3.6. Temporal trends of PP (>41 and <41 μm) sedimentation in the five study basins from May 2000 – February 2002. Data for the three oligotrophic sites (COL, SHL-S and SHL-N) are presented on the left side of the figure and the data for the meso-eutrophic sites are presented on the right side of the figure.

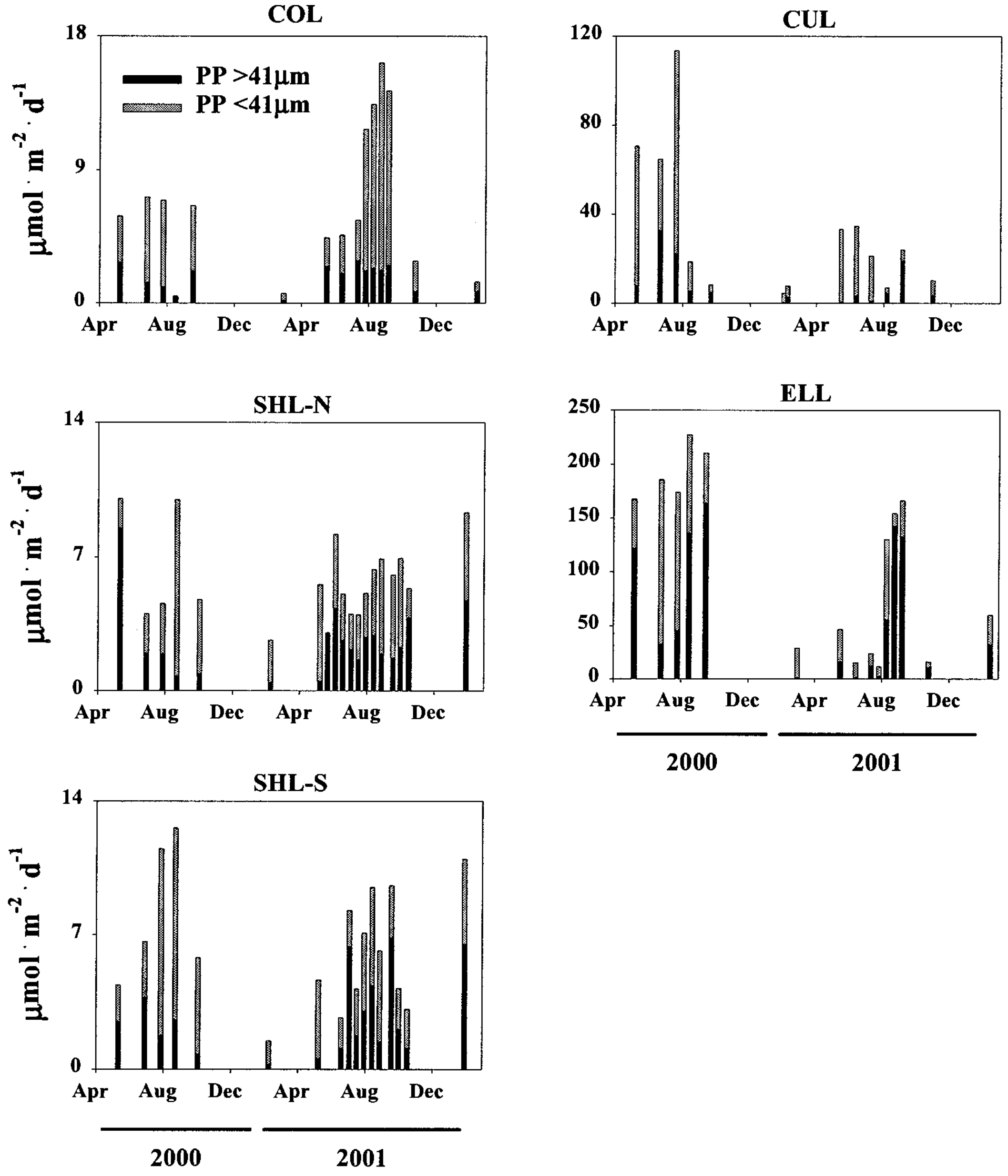

COL
CUL
SHL-N
ELL
SHL-S
PP >41µm
PP <41µm
µmol · m^{-2} · d^{-1}
18
9
0
120
80
40
0
14
7
0
250
200
150
100
50
0
14
7
0
Apr
Aug
Dec
Apr
Aug
Dec
2000
2001

Figure 3.7. (a) Mean summer aerial PP sedimentation flux of PP plotted as a function of mean summer aerial epilimnetic P concentration for the five study basins in 2000 and 2001 (*n* = 10). (b) The mean summer percent of the epilimnetic TP pool lost to sedimentation per day plotted as a function of the mean summer aerial epilimnetic P concentration for the five study basins in 2000 and 2001 (*n* = 10).

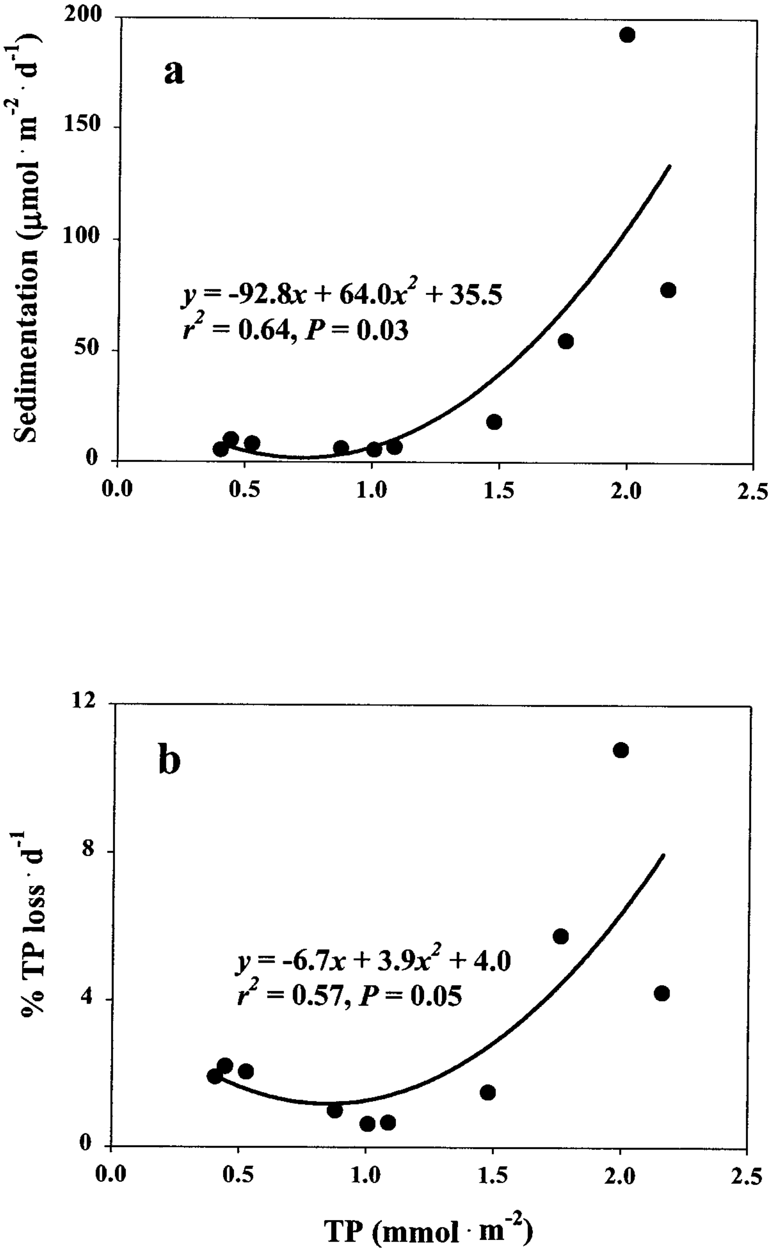

a
Sedimentation (μmol · m^{-2} · d^{-1})
200
150
100
50
0
0.0
0.5
1.0
1.5
2.0
2.5
$y = -92.8x + 64.0x^2 + 35.5$
$r^2 = 0.64, P = 0.03$
b
% TP loss · d^{-1}
12
8
4
0
0.0
0.5
1.0
1.5
2.0
2.5
$y = -6.7x + 3.9x^2 + 4.0$
$r^2 = 0.57, P = 0.05$
TP (mmol · m^{-2})

Figure 4.1. Bathymetric maps of Sooke Lake Reservoir and Shawnigan Lake, indicating their location in British Columbia and the north and south basin sampling sites in each water body.

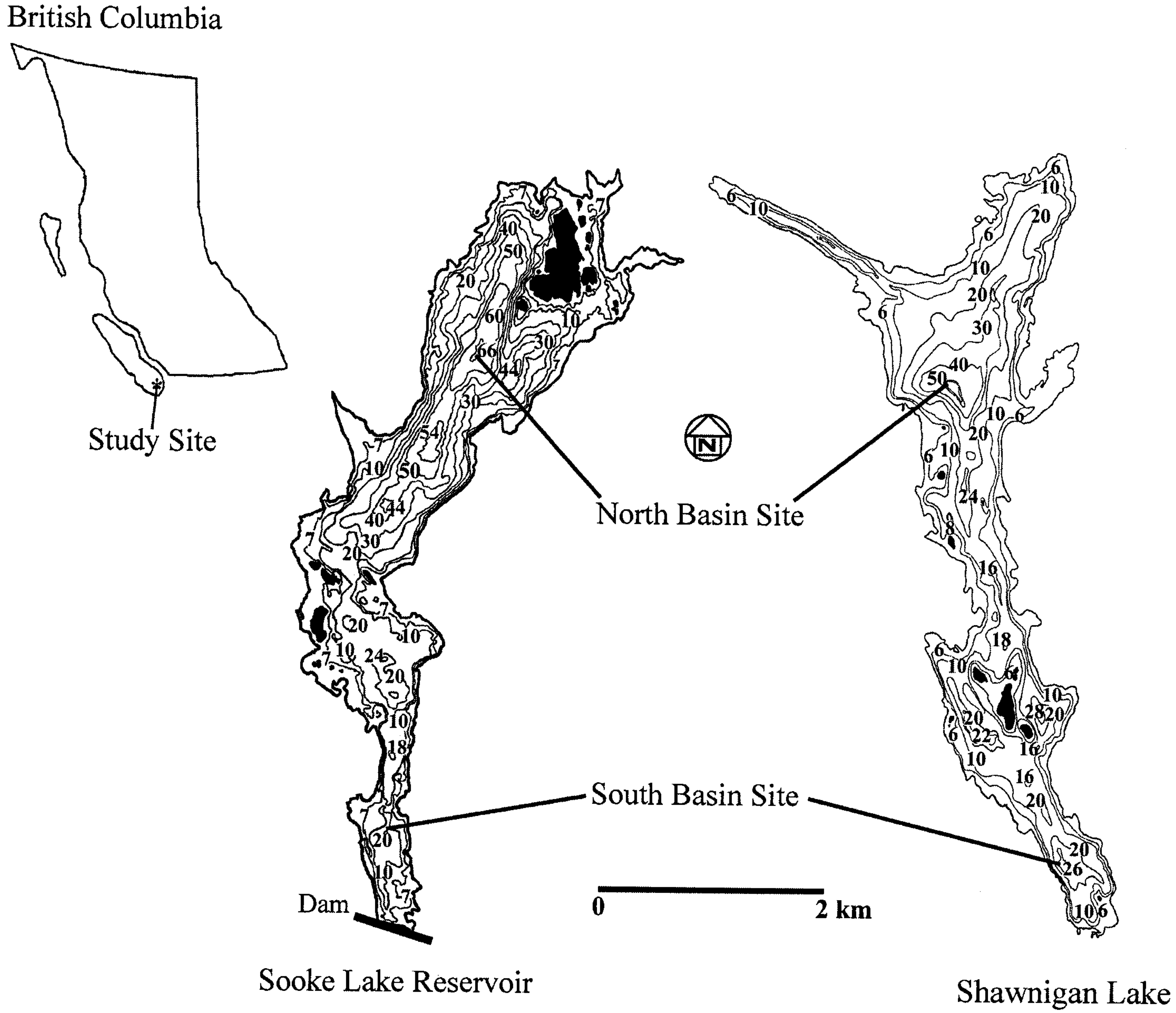

British Columbia
Study Site
North Basin Site
South Basin Site
N
0
2 km
Dam
Sooke Lake Reservoir
Shawnigan Lake

Figure 4.2. Water surface elevation (in meters above sea level – m.a.s.l.), total water body volumes, and north and south basin volumes of Sooke Lake Reservoir and Shawnigan Lake from December 1999 – March 2002.

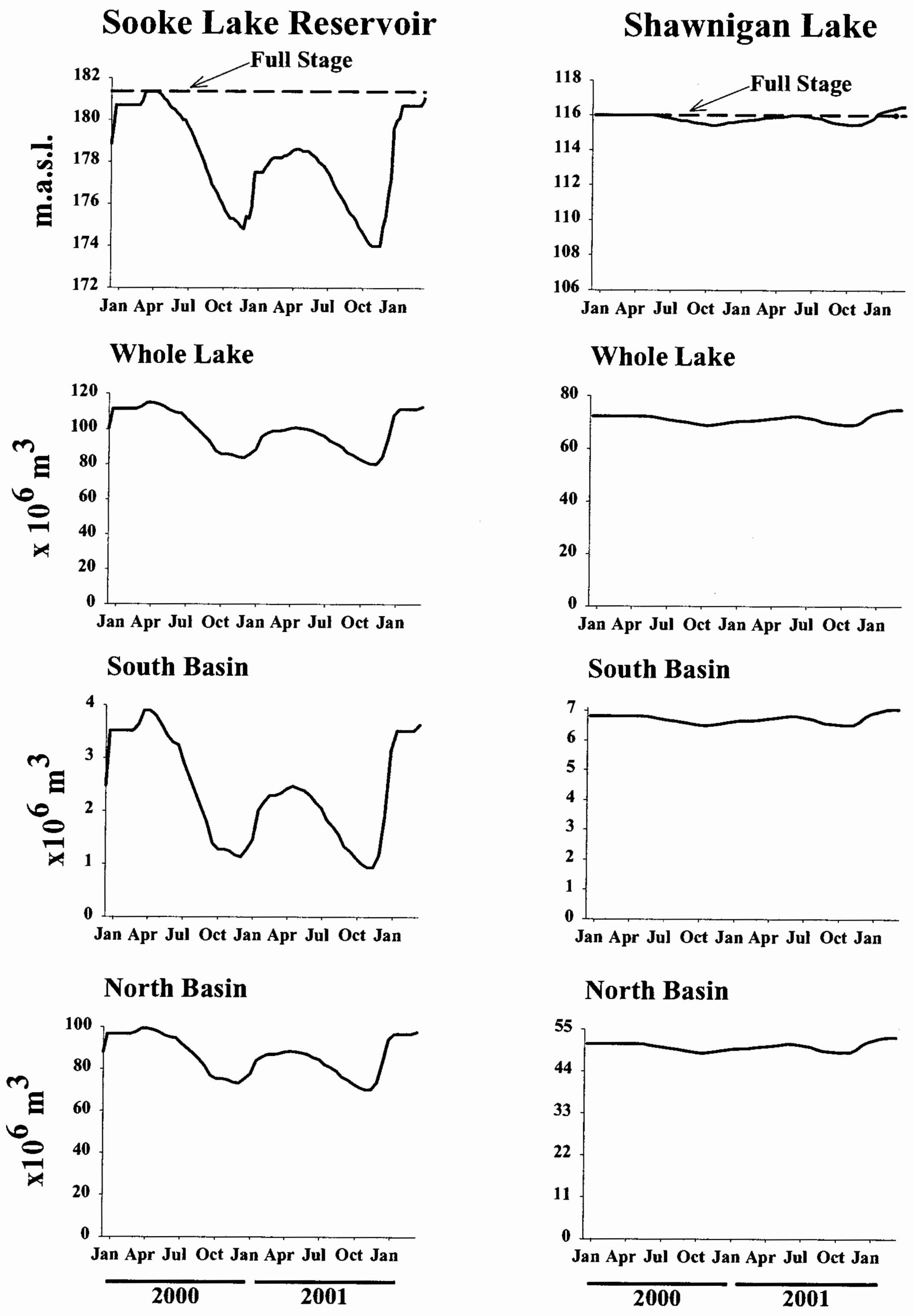

Sooke Lake Reservoir
Full Stage
m.a.s.l.
182
180
178
176
174
172
Jan Apr Jul Oct Jan Apr Jul Oct Jan
Whole Lake
x 10^6 m^3
120
100
80
60
40
20
0
Jan Apr Jul Oct Jan Apr Jul Oct Jan
South Basin
x10^6 m^3
4
3
2
1
0
Jan Apr Jul Oct Jan Apr Jul Oct Jan
North Basin
x10^6 m^3
100
80
60
40
20
0
Jan Apr Jul Oct Jan Apr Jul Oct Jan
2000
2001
Shawnigan Lake
Full Stage
118
116
114
112
110
108
106
Jan Apr Jul Oct Jan Apr Jul Oct Jan
Whole Lake
80
60
40
20
0
Jan Apr Jul Oct Jan Apr Jul Oct Jan
South Basin
7
6
5
4
3
2
1
0
Jan Apr Jul Oct Jan Apr Jul Oct Jan
North Basin
55
44
33
22
11
0
Jan Apr Jul Oct Jan Apr Jul Oct Jan
2000
2001

Figure 4.3. Precipitation (mm) data from the Sooke Lake Reservoir Dam meteorological station. (a) Total annual precipitation 1999 – 2001. Solid line is 104-year mean (1895 – 1999) and dashed lines are ± 1 standard deviation. (b) Monthly precipitation totals for 2000 and 2001. The solid line is the 104-year mean for each month and dashed lines are ± 1 standard deviation.

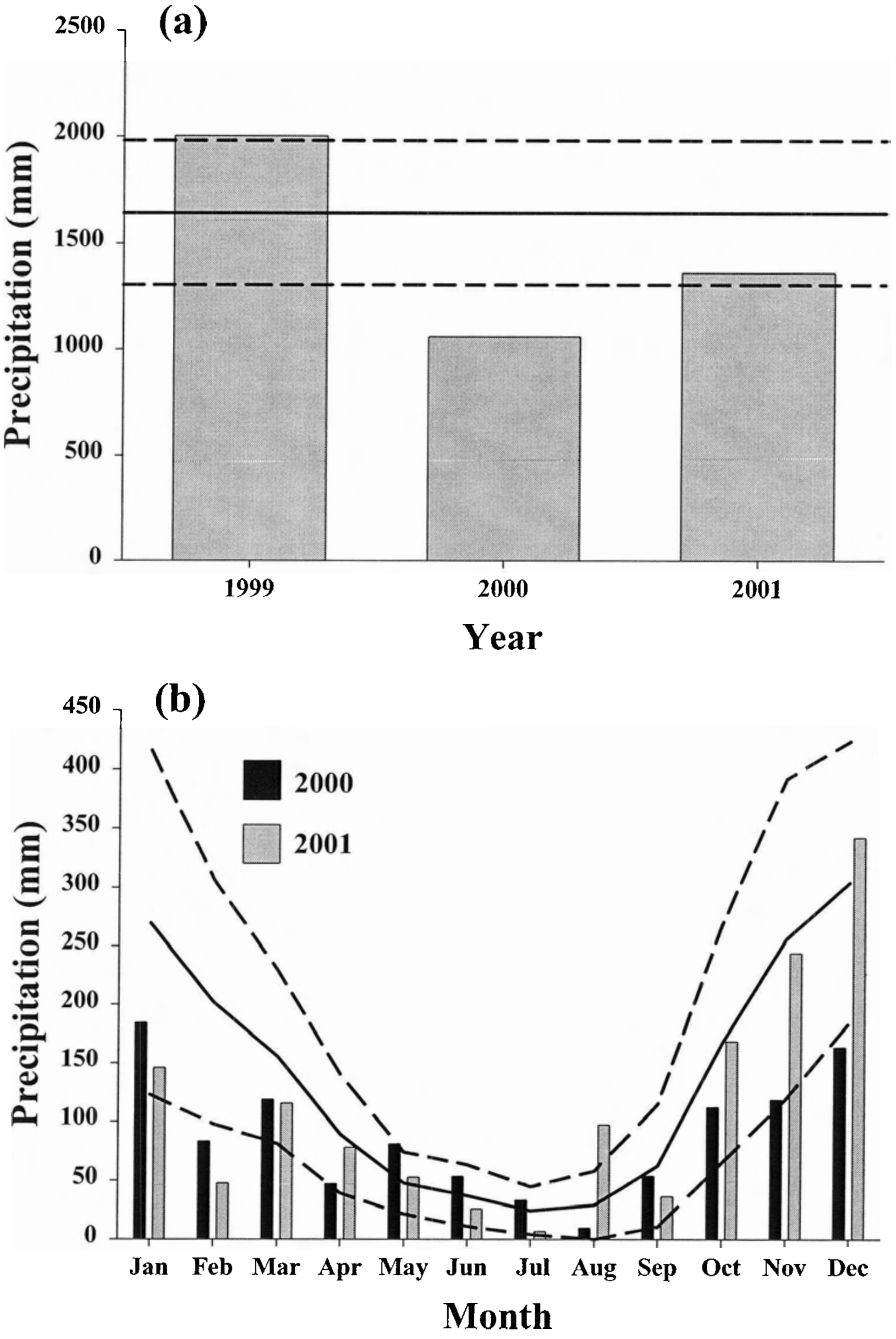

(a)
2500
2000
1500
1000
500
0
Precipitation (mm)
1999
2000
2001
Year
(b)
450
400
350
300
250
200
150
100
50
0
Precipitation (mm)
2000
2001
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

Figure 4.4. Monthly water flow rates (x10^6 m^3 day^{-1}) of Sooke Lake Reservoir and Shawnigan Lake from December 1999 – January 2002. Flow rates of stream inflow (Q_I), interbasin water transfer (Q_{IBT}), evaporation (Q_E), the drinking water outflow (Q_{DW}) and the Sooke Lake Reservoir dam outflow or the Shawnigan Lake outflow stream (both denoted Q_S) are presented for the whole water bodies and for the individual basins. Negative values are water losses and positive values are water inputs.

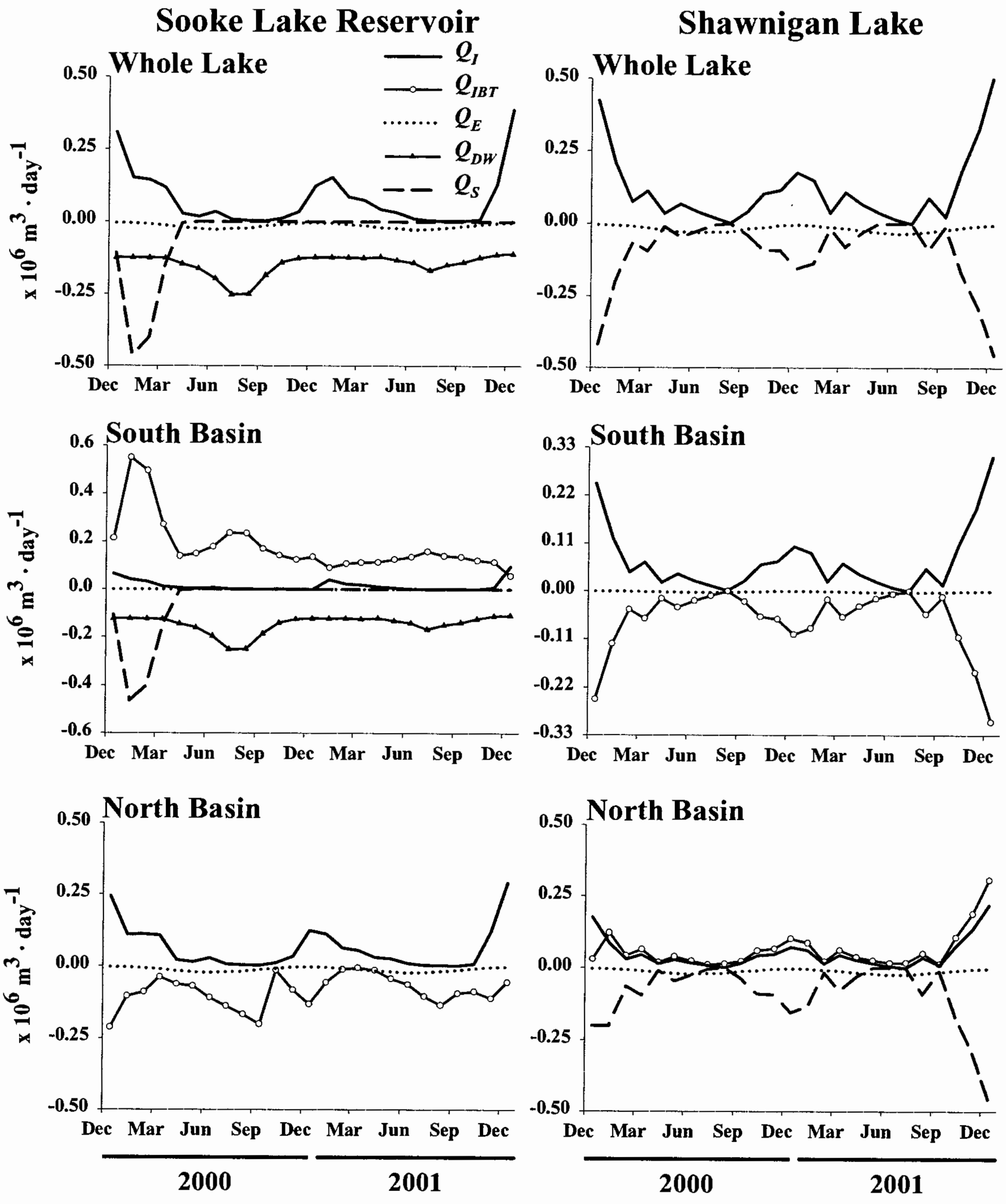

Sooke Lake Reservoir
Shawnigan Lake
Whole Lake
Q_I
Q_{IBT}
Q_E
Q_{DW}
Q_S
0.50
0.25
0.00
-0.25
-0.50
x 10^6 m^3 · day^{-1}
Dec Mar Jun Sep Dec Mar Jun Sep Dec
South Basin
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
0.33
0.22
0.11
0.00
-0.11
-0.22
-0.33
North Basin
2000
2001

Figure 4.5. Examples of monthly temperature profiles in 2000 (a – d) and 2001 (e – h) from Sooke south basin (a, e), Sooke north basin (b, f), Shawnigan south basin (c, g) and Shawnigan north basin (d, h). The lines at the top of the Sooke temperature represent basin water level. No lines are presented for Shawnigan because the water level only decreased ≤0.5 m in both years.

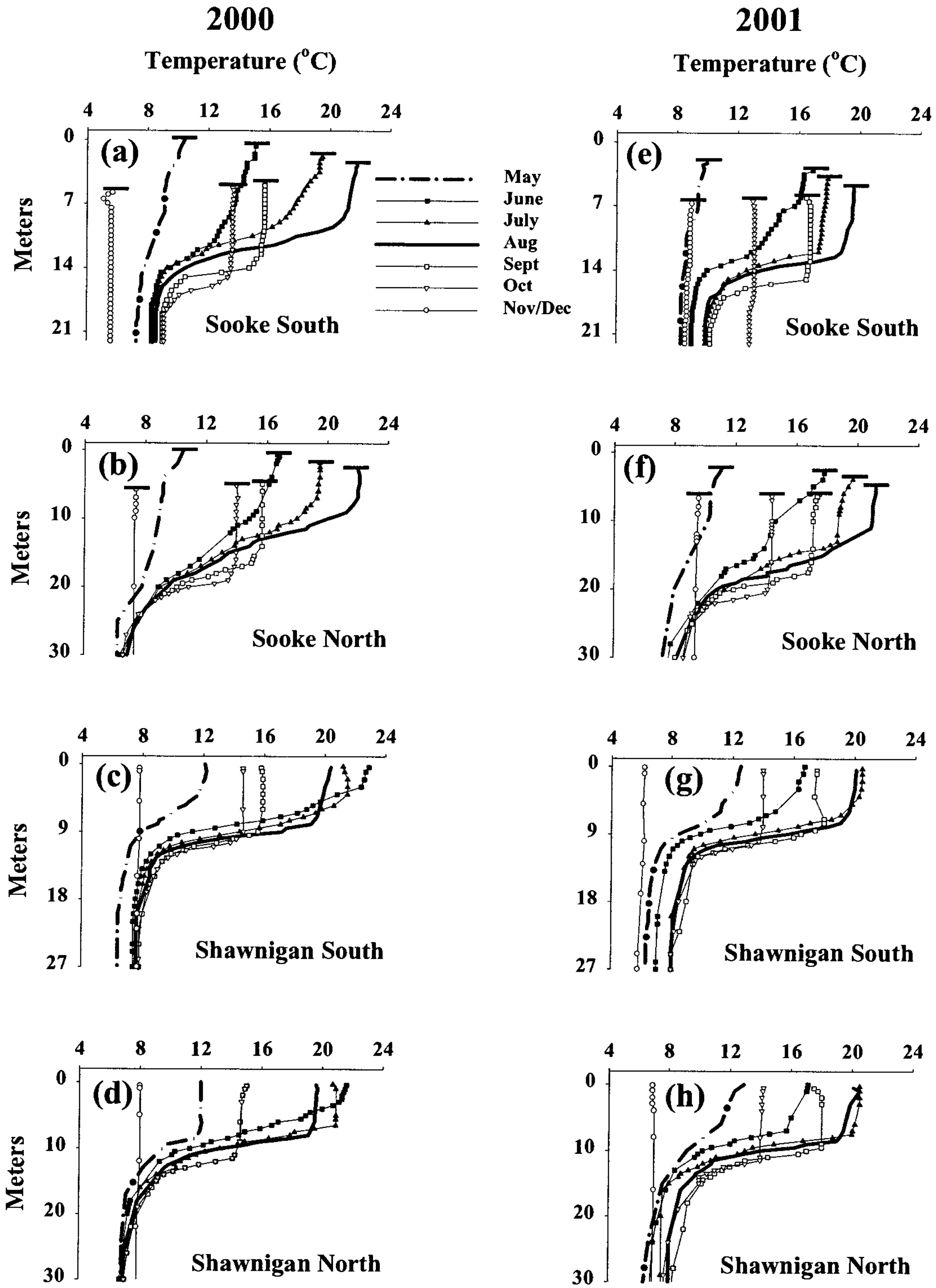

2000
Temperature (°C)
2001
Temperature (°C)
4 8 12 16 20 24
Meters
(a)
Sooke South
0 7 14 21
May
June
July
Aug
Sept
Oct
Nov/Dec
(e)
Sooke South
(b)
Sooke North
0 10 20 30
(f)
Sooke North
(c)
Shawnigan South
0 9 18 27
(g)
Shawnigan South
(d)
Shawnigan North
0 10 20 30
(h)
Shawnigan North

Figure 4.6. Longitudinal variation in water temperatures at specific depths (1, 5 and 10 m) within Sooke Lake Reservoir (a – c) and Shawnigan Lake (d – f) from April 2000 – Dec 2001.

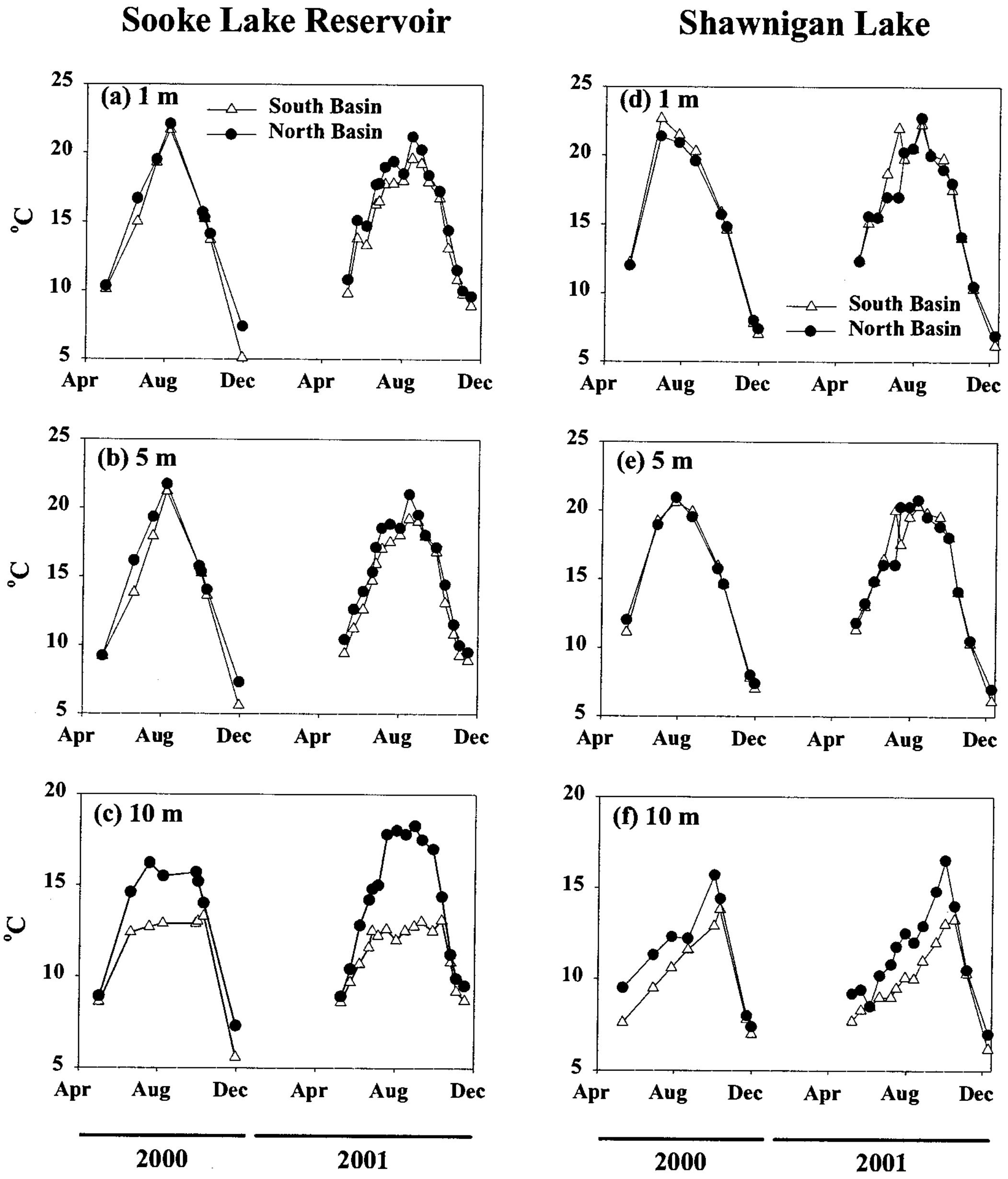

Sooke Lake Reservoir
Shawnigan Lake
(a) 1 m
(b) 5 m
(c) 10 m
(d) 1 m
(e) 5 m
(f) 10 m
South Basin
North Basin
°C
25
20
15
10
5
Apr
Aug
Dec
2000
2001

Figure 4.7. Schmidt stability indices (*S*) for the north and south basins of Sooke Lake Reservoir and Shawnigan Lake in 2000 and 2001. The dashed line is 2000 and the solid line is 2001.

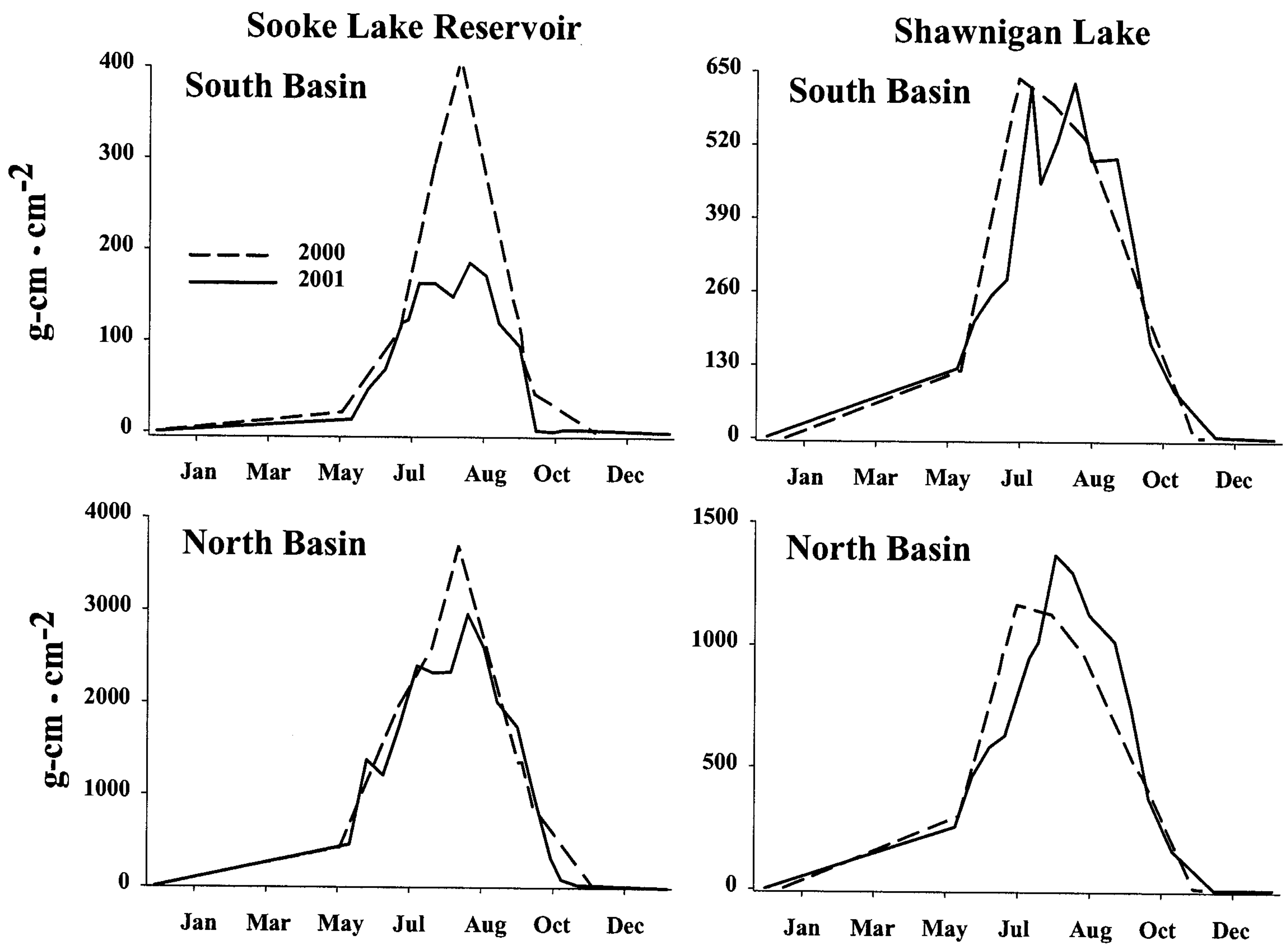

Sooke Lake Reservoir
Shawnigan Lake
South Basin
North Basin
g-cm • cm^{-2}
2000
2001
0
100
200
300
400
1000
2000
3000
4000
130
260
390
520
650
500
1500
Jan
Mar
May
Jul
Aug
Oct
Dec

Figure 4.8. Birgean summer heat budgets for the north and south basins of Sooke Lake Reservoir and Shawnigan Lake in 2000 and 2001. Heat content (megawatt m^{-2}) is plotted as a function of day of year (DOY). A 3rd or 4th order polynomial is fitted to the data and used to predict date of maximum heat content (H_M), the heat content of the basin on the date of maximum heat content (θ_{Hm}) and to calculate the Birgean summer heat budget (θ_S). Values for H_M, θ_{Hm} and θ_S (in megawatt m^{-2}) for each basin are given next to each line.

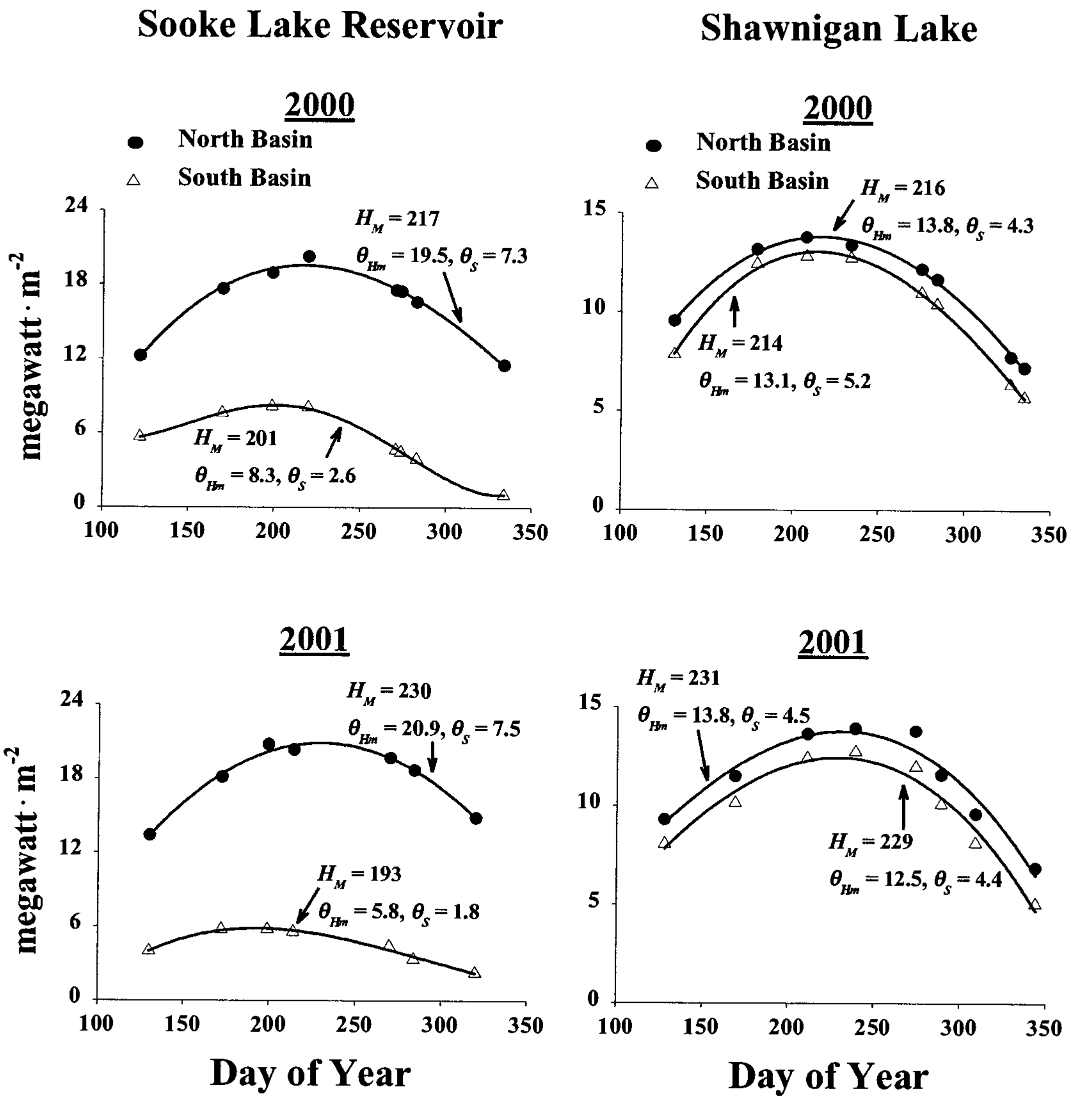

Sooke Lake Reservoir
Shawnigan Lake
2000
● North Basin
△ South Basin
H_M = 217
θ_{Hm} = 19.5, θ_S = 7.3
H_M = 201
θ_{Hm} = 8.3, θ_S = 2.6
2000
● North Basin
△ South Basin
H_M = 216
θ_{Hm} = 13.8, θ_S = 4.3
H_M = 214
θ_{Hm} = 13.1, θ_S = 5.2
2001
H_M = 230
θ_{Hm} = 20.9, θ_S = 7.5
H_M = 193
θ_{Hm} = 5.8, θ_S = 1.8
2001
H_M = 231
θ_{Hm} = 13.8, θ_S = 4.5
H_M = 229
θ_{Hm} = 12.5, θ_S = 4.4
megawatt · m^{-2}
0
6
12
18
24
0
5
10
15
100
150
200
250
300
350
Day of Year
Day of Year

Figure 4.9. Monthly heat fluxes (megawatt m^{-2} day^{-1}) into and out of Sooke Lake Reservoir and Shawnigan Lake from December 1999 – January 2002. Heat fluxes from the inflowing streams (Φ_I), the drinking water outflow (Φ_{DW}), the Sooke dam spill or the Shawnigan Lake outflow stream (both denoted Φ_S), evaporation (Φ_E), and the interbasin transfer of heat (Φ_{IBT}) are presented for the whole water body, the north and the south basin of both water bodies. Negative heat fluxes are heat losses from the system and heat influxes are positive values.

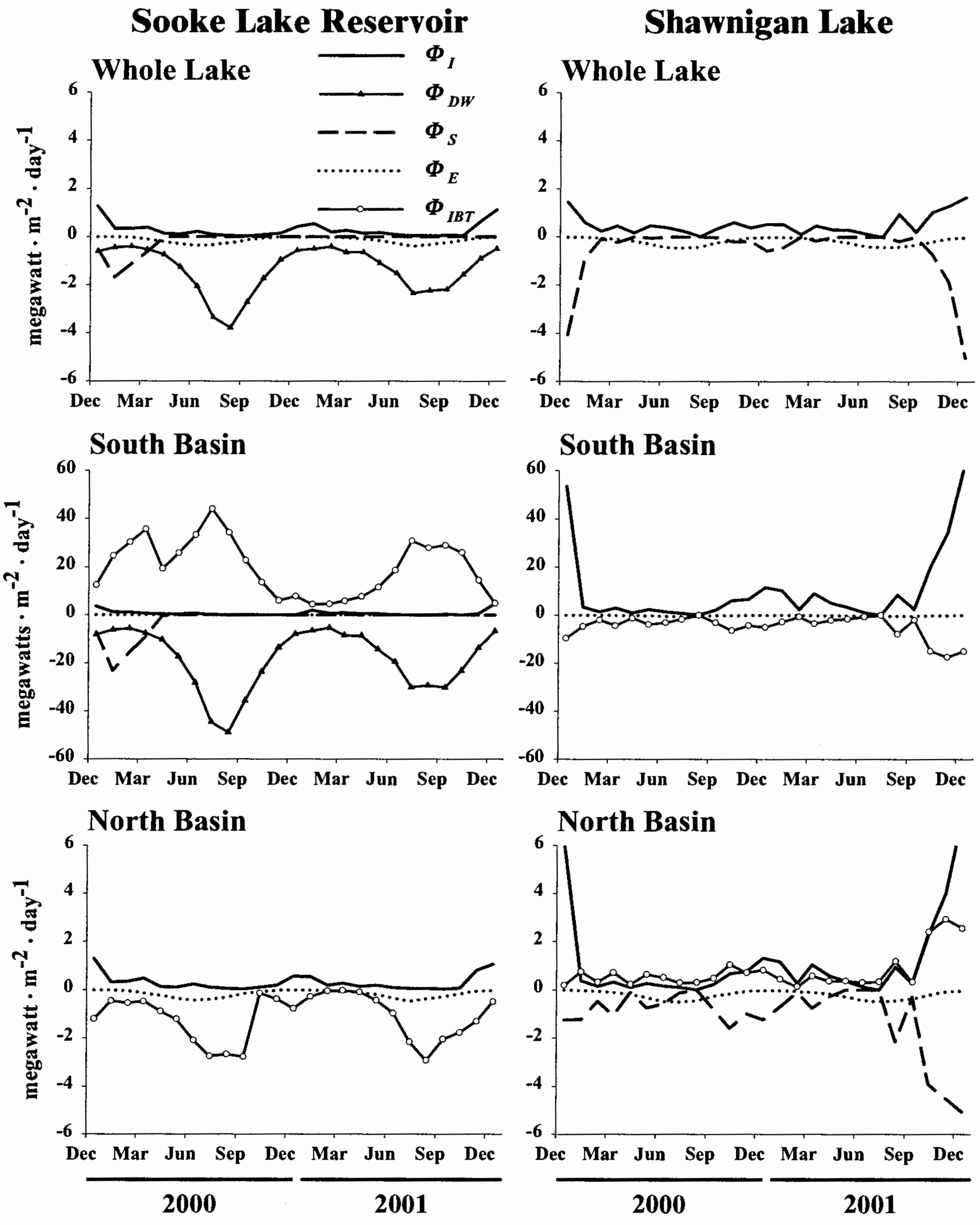

Sooke Lake Reservoir
Shawnigan Lake
Whole Lake
South Basin
North Basin
Φ I
Φ DW
Φ S
Φ E
Φ IBT
megawatt · m-2 · day-1
megawatts · m-2 · day-1
6
4
2
0
-2
-4
-6
60
40
20
0
-20
-40
-60
Dec
Mar
Jun
Sep
Dec
Mar
Jun
Sep
Dec
2000
2001

Figure 5.1. Bathymetric maps of Sooke Lake Reservoir and Shawnigan Lake, indicating their location in British Columbia and the north and south basin sampling sites in each water body.

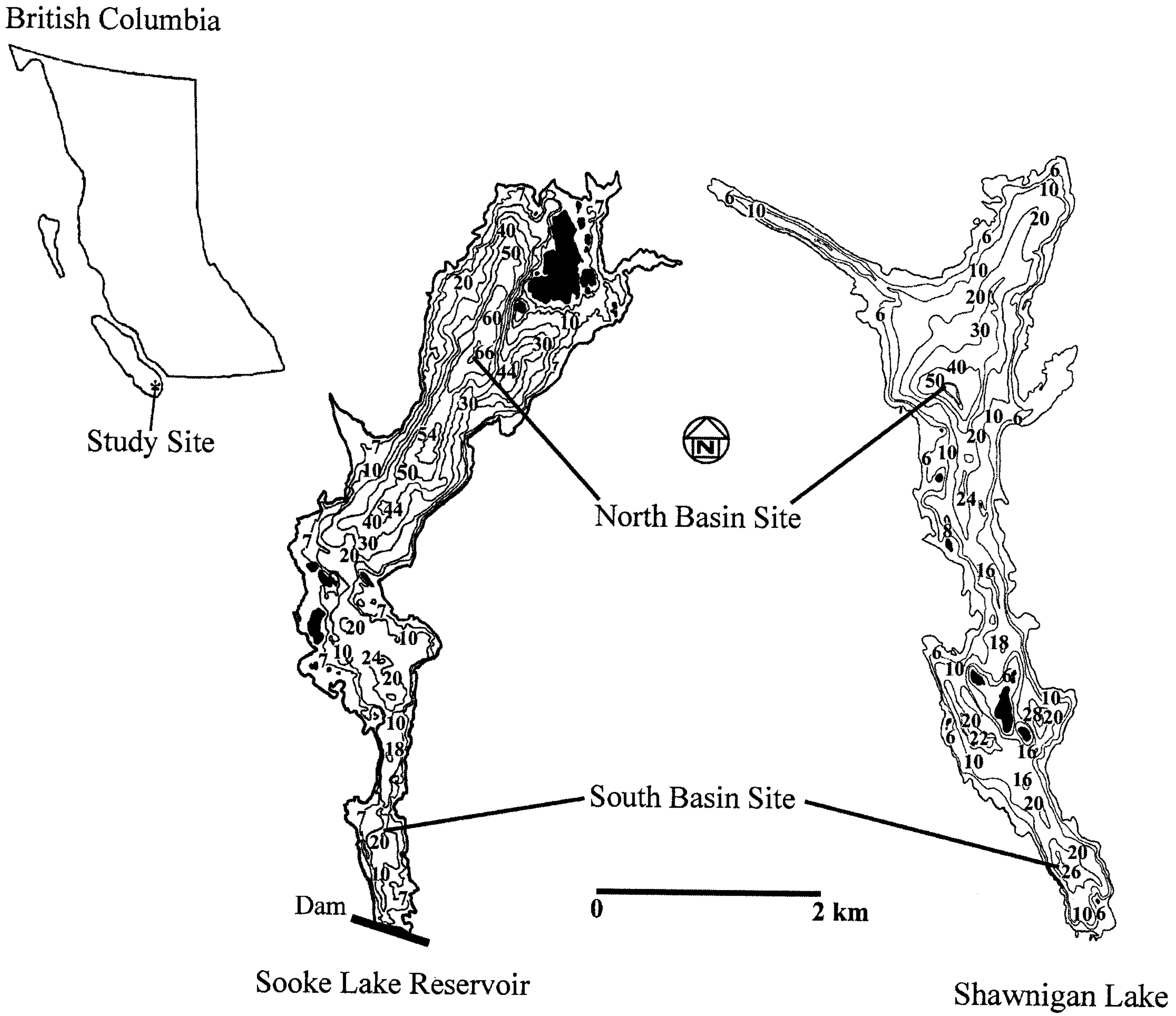

British Columbia
Study Site
North Basin Site
South Basin Site
Dam
0
2 km
Sooke Lake Reservoir
Shawnigan Lake
N

Figure 5.2. Basin volumes (x 10^6 m^3) of the north and south basins of Shawnigan Lake (a and b) and Sooke Lake Reservoir (c and d) from January 2000 – February 2002.

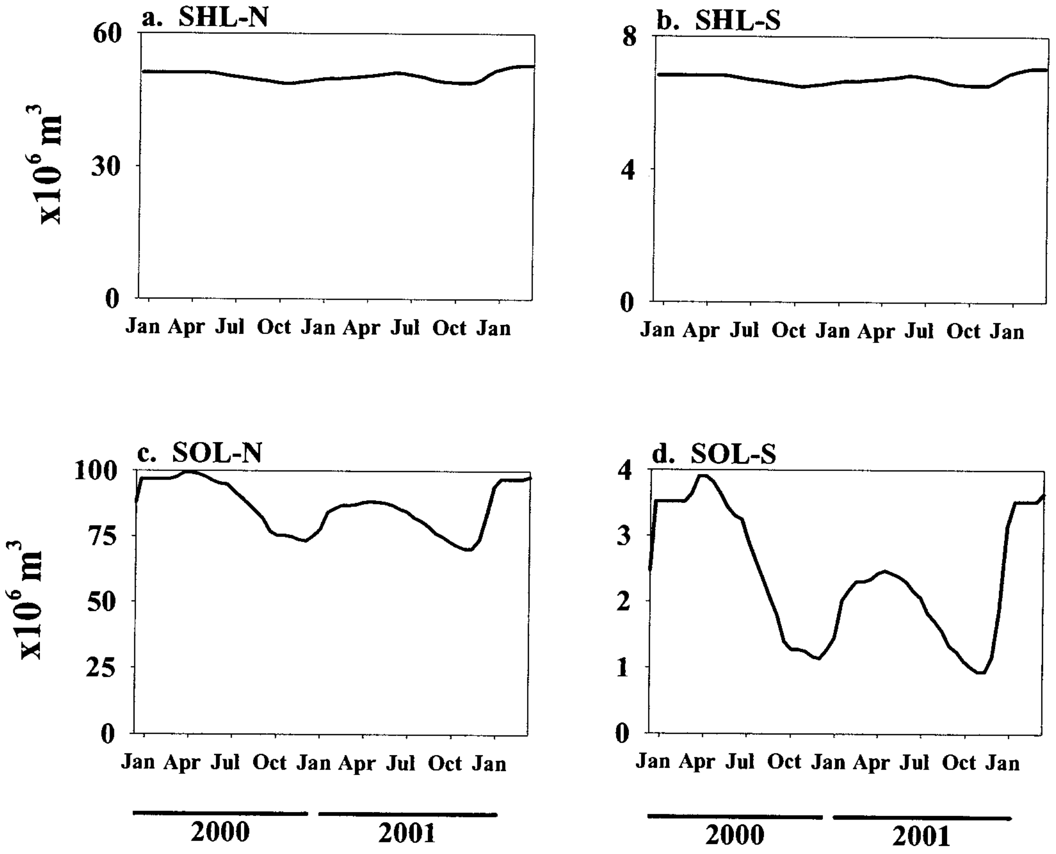

a. SHL-N
60
30
0
x10^6 m^3
Jan Apr Jul Oct Jan Apr Jul Oct Jan
b. SHL-S
8
4
0
Jan Apr Jul Oct Jan Apr Jul Oct Jan
c. SOL-N
100
75
50
25
0
x10^6 m^3
Jan Apr Jul Oct Jan Apr Jul Oct Jan
2000
2001
d. SOL-S
4
3
2
1
0
Jan Apr Jul Oct Jan Apr Jul Oct Jan
2000
2001

Figure 5.3. Percent hypolimnetic volume remaining on sequential sampling dates following the date of maximum epilimnetic temperature in the north and south basins of Shawnigan Lake (a and b) and Sooke Lake Reservoir (c and d) in 2000 and 2001.

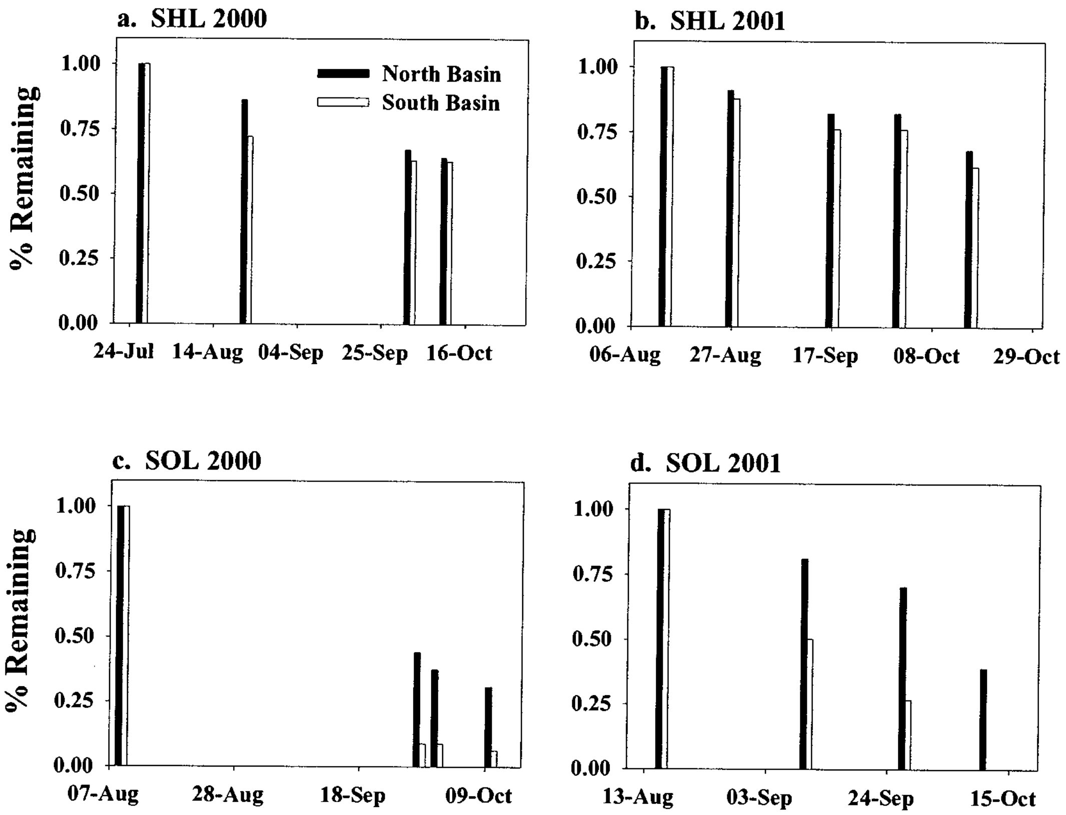

a. SHL 2000
b. SHL 2001
c. SOL 2000
d. SOL 2001
% Remaining
% Remaining
North Basin
South Basin
1.00
0.75
0.50
0.25
0.00
24-Jul
14-Aug
04-Sep
25-Sep
16-Oct
06-Aug
27-Aug
17-Sep
08-Oct
29-Oct
07-Aug
28-Aug
18-Sep
09-Oct
13-Aug
03-Sep
24-Sep
15-Oct

Figure 5.4. Seasonal changes in the residence time (in days) of the upper mixed layer of Shawnigan Lake (a and b) and Sooke Lake Reservoir (c and d) from May 2000 – February 2002. The time interval inside the vertical dashed lines indicated with a double-ended arrow represent the observed period of stratification in each summer.

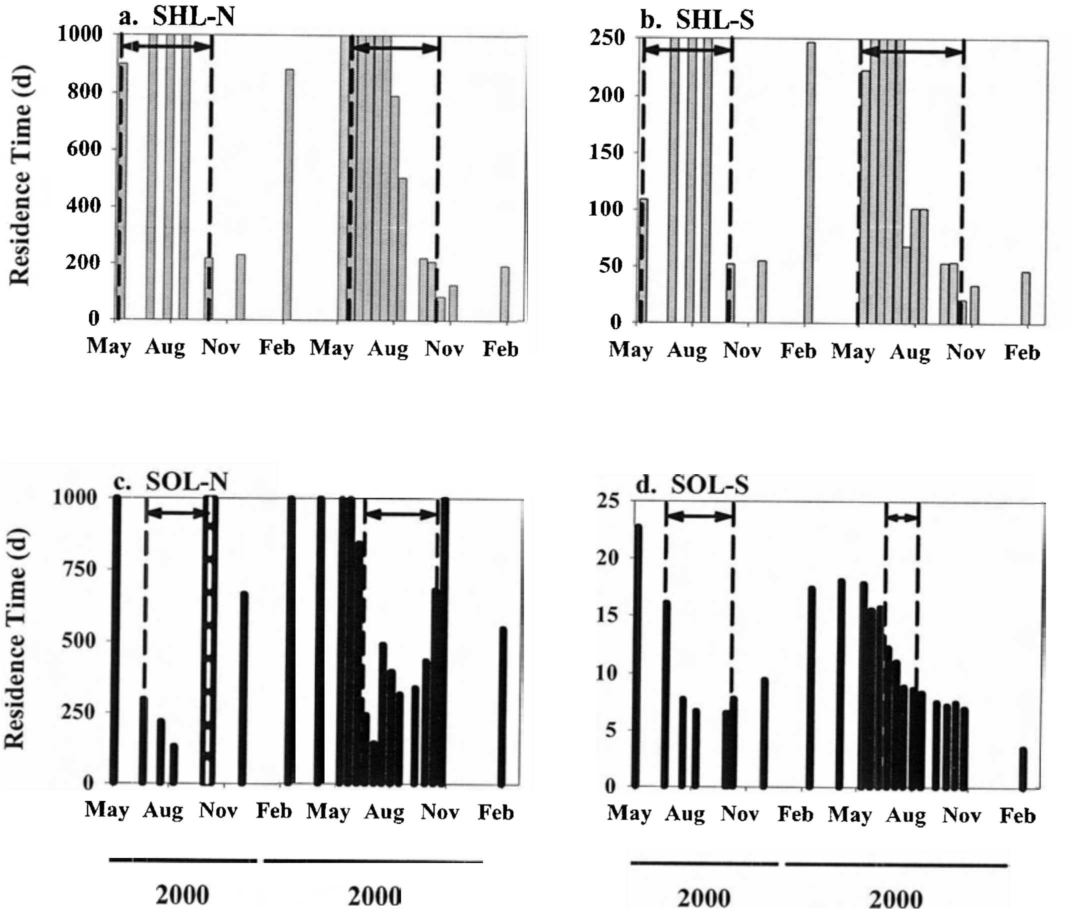

a. SHL-N
b. SHL-S
c. SOL-N
d. SOL-S
Residence Time (d)
Residence Time (d)
1000
800
600
400
200
0
250
200
150
100
50
0
1000
750
500
250
0
25
20
15
10
5
0
May
Aug
Nov
Feb
May
Aug
Nov
Feb
2000
2000
2000
2000

Figure 5.5. Epilimnetic and hypolimnetic TP concentrations of the north and south basins of Shawnigan Lake (a and b) and Sooke Lake Reservoir (c and d) from May 2000 – February 2002. Lines above temporal TP data on each graph represent the period of stratification and the number below lines is the duration (in days) of the summer stratification period in each summer.

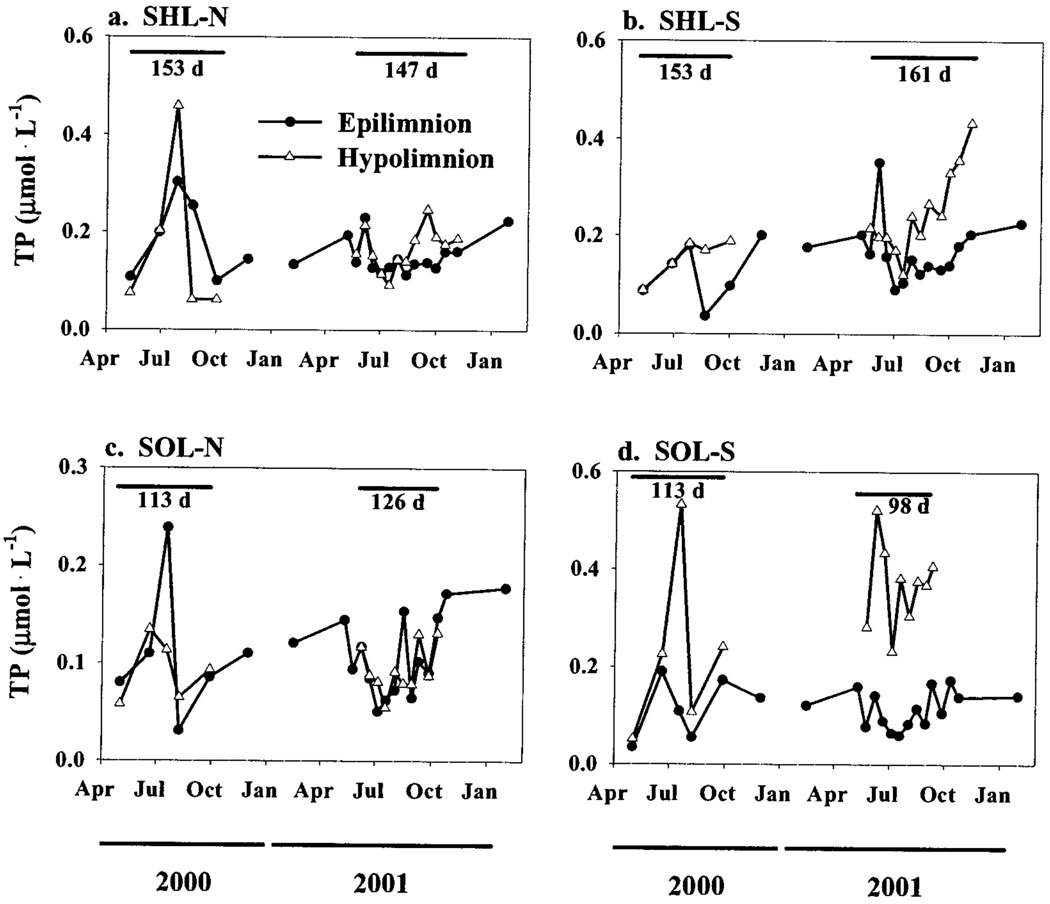

a. SHL-N
b. SHL-S
c. SOL-N
d. SOL-S
TP (µmol · L-1)
0.0
0.2
0.4
0.6
0.1
0.3
153 d
147 d
161 d
113 d
126 d
98 d
Epilimnion
Hypolimnion
Apr Jul Oct Jan Apr Jul Oct Jan
2000
2001

Figure 5.6. Epilimnetic TDP concentration during the stratification period of the north and south basins of Shawnigan Lake (a and b) and Sooke Lake Reservoir (c and d) from May 2000 – February 2002.

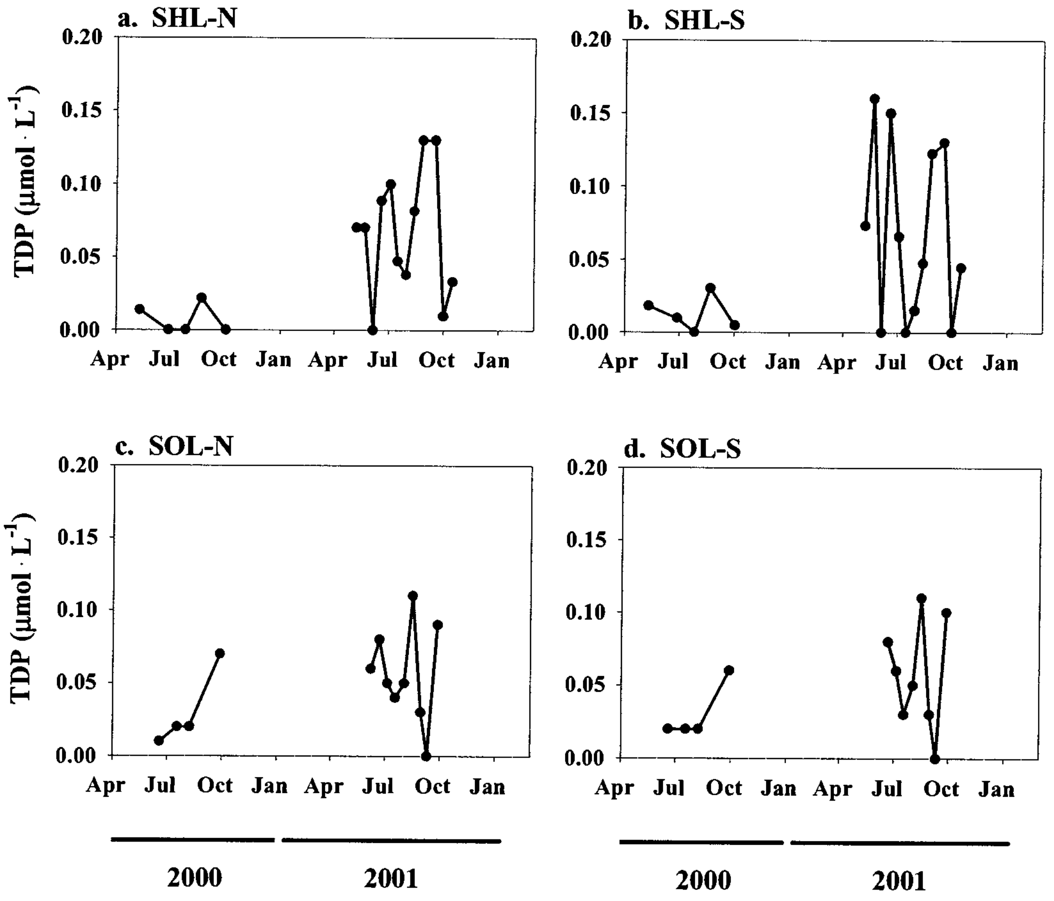

a. SHL-N
b. SHL-S
c. SOL-N
d. SOL-S
TDP (µmol · L^{-1})
0.20
0.15
0.10
0.05
0.00
Apr
Jul
Oct
Jan
2000
2001

Figure 5.7. Epilimnetic and hypolimnetic TN concentrations of the north and south basins of Shawnigan Lake (a and b) and Sooke Lake Reservoir (c and d) from May 2000 – February 2002. Lines above temporal TN data on each graph represent the period of stratification and the number below lines is the duration (in days) of the summer stratification period in each summer.

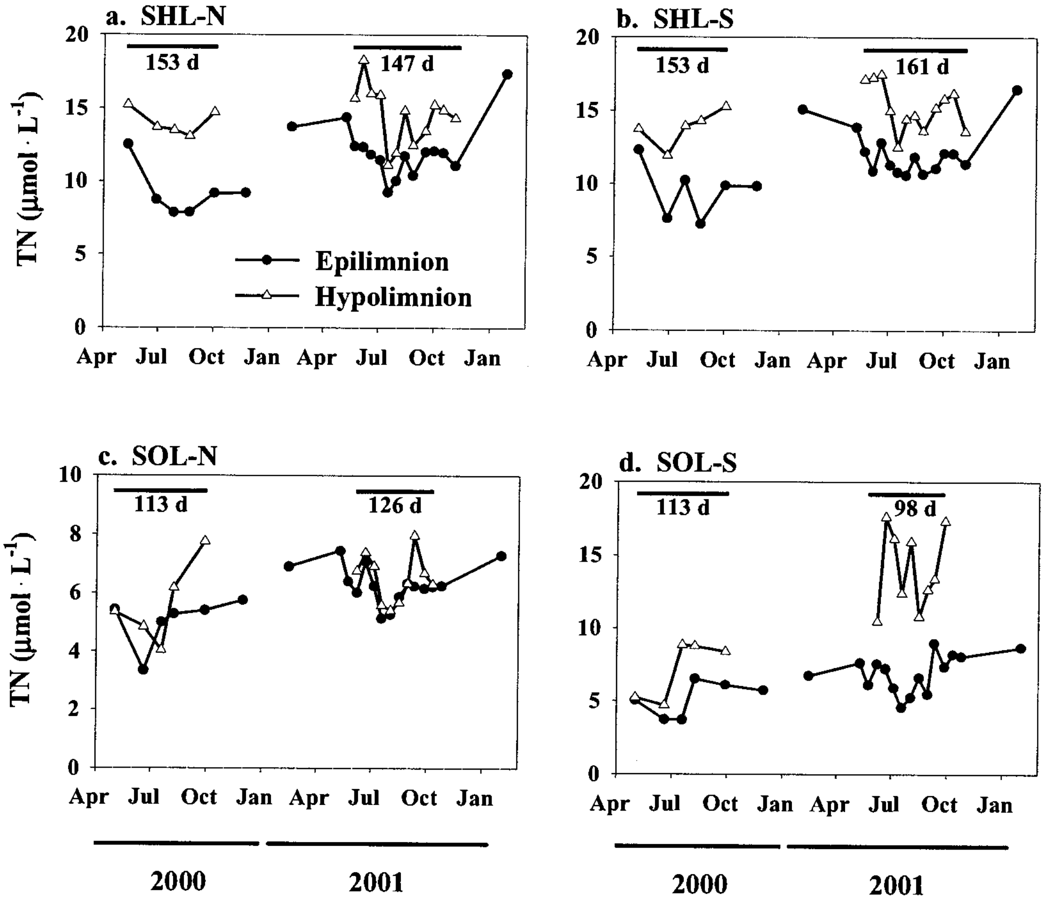

a. SHL-N
153 d
147 d
Epilimnion
Hypolimnion
b. SHL-S
153 d
161 d
c. SOL-N
113 d
126 d
d. SOL-S
113 d
98 d
TN (µmol · L^{-1})
20
15
10
5
0
10
8
6
4
2
0
Apr
Jul
Oct
Jan
Apr
Jul
Oct
Jan
2000
2001

Figure 5.8. Epilimnetic and metalimnetic Chl*a* concentrations of the north and south basins of Shawnigan Lake (a and b) and Sooke Lake Reservoir (c and d) from May 2000 – February 2002. Lines above temporal Chl*a* data on each graph represent the period of stratification and the number below lines is the duration (in days) of the summer stratification period in each summer.

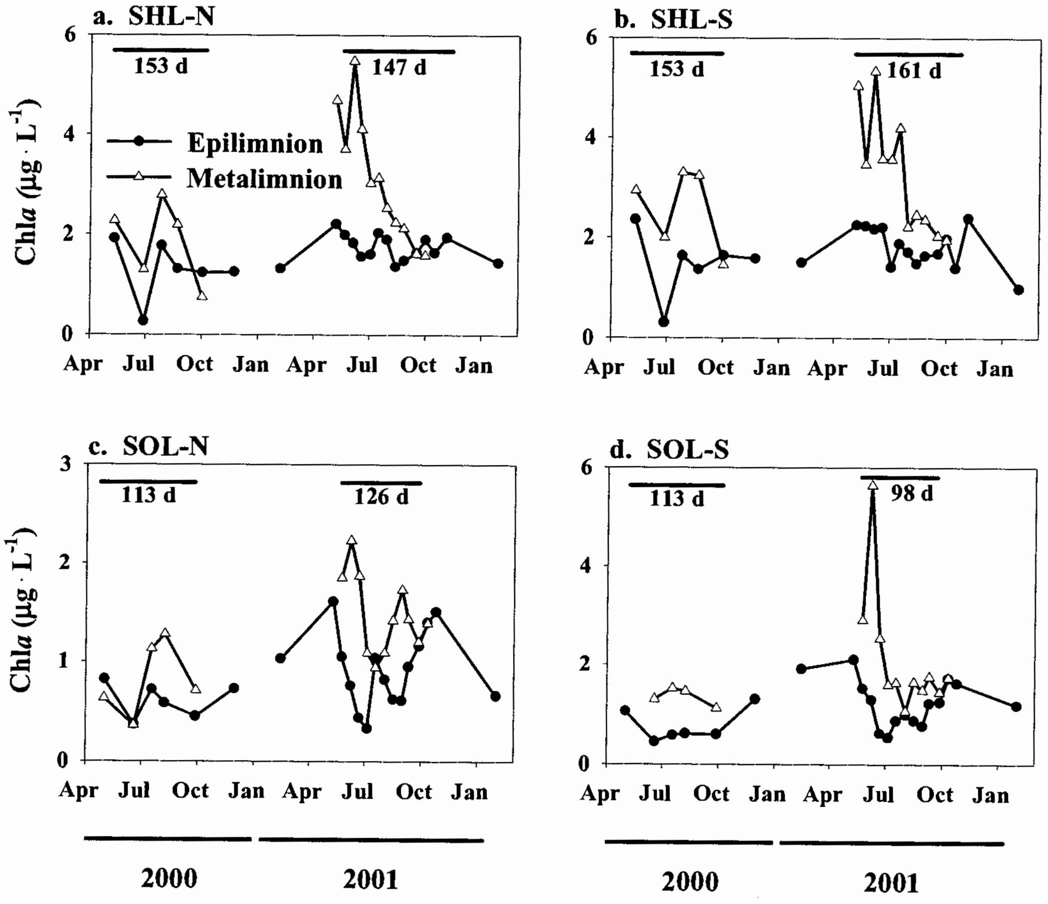

a. SHL-N
153 d
147 d
Epilimnion
Metalimnion
b. SHL-S
153 d
161 d
c. SOL-N
113 d
126 d
d. SOL-S
113 d
98 d
Chl*a* (μg · L^{-1})
0
2
4
6
0
1
2
3
Apr
Jul
Oct
Jan
Apr
Jul
Oct
Jan
2000
2001

Figure 5.9. Mean epilimnetic (a) TP, (b) TN and (c) Chl*a* during summer stratification of the north and south basins of Sooke Lake Reservoir from 2000 – 2003 plotted as a function of the minimum percent usable volume left in the reservoir from May-September of each year. Results of statistical analyses are presented in Table 5.4.

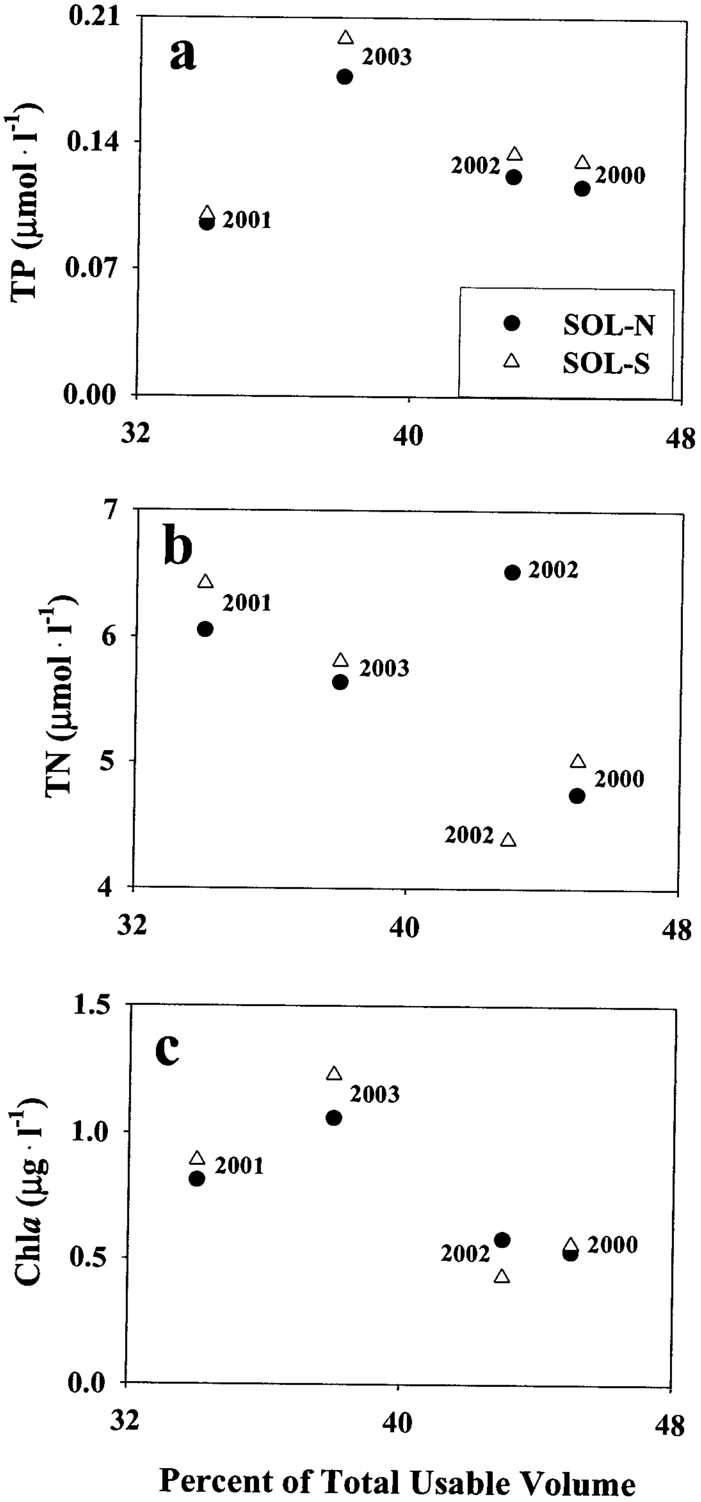

a
0.21
0.14
0.07
0.00
TP (µmol · l⁻¹)
2003
2002
2000
2001
● SOL-N
△ SOL-S
32
40
48
b
7
6
5
4
TN (µmol · l⁻¹)
2002
2001
2003
2000
2002
32
40
48
c
1.5
1.0
0.5
0.0
Chl*a* (µg · l⁻¹)
2003
2001
2002
2000
32
40
48
Percent of Total Usable Volume

Figure 5.10. Epilimnetic PO_4^{3-} turnover time (in minutes) of the north and south basins of Shawnigan Lake (a and b) and Sooke Lake Reservoir (c and d) from May 2000 – February 2002. Lines above temporal data on each graph represent the period of stratification and the number below lines is the duration (in days) of the summer stratification period in each summer.

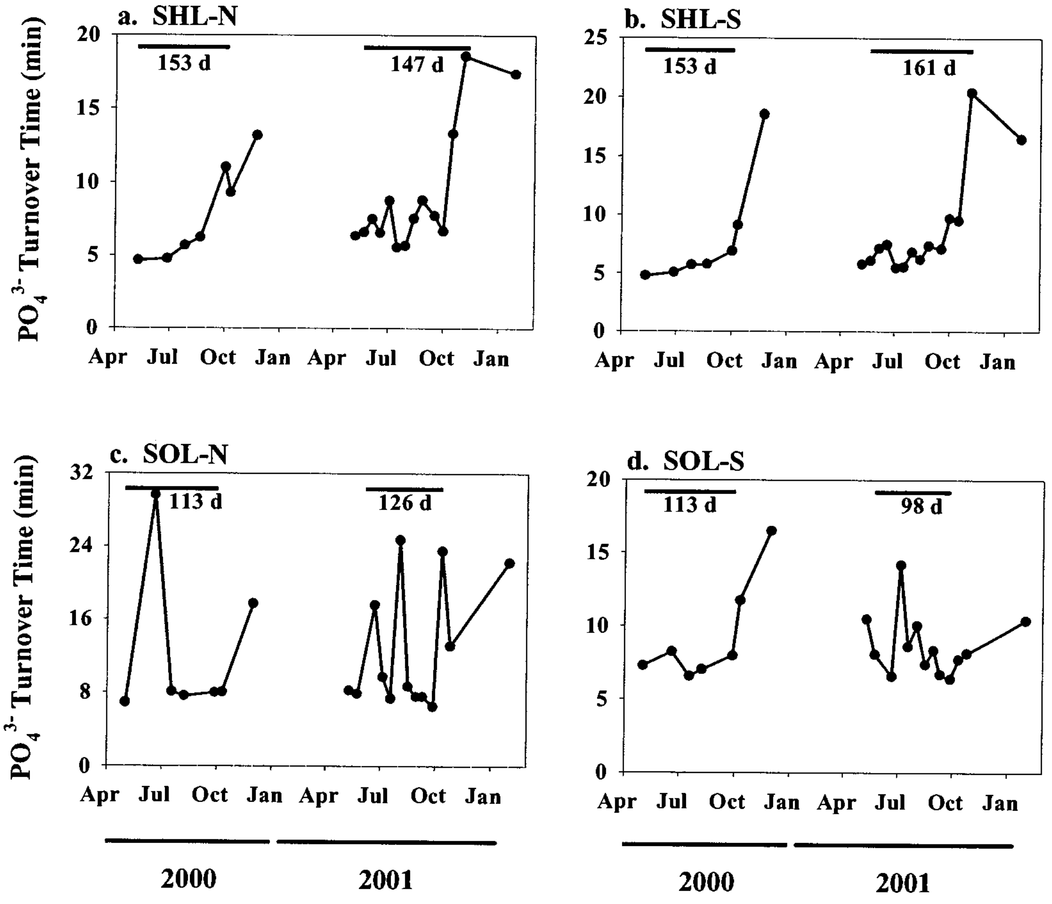
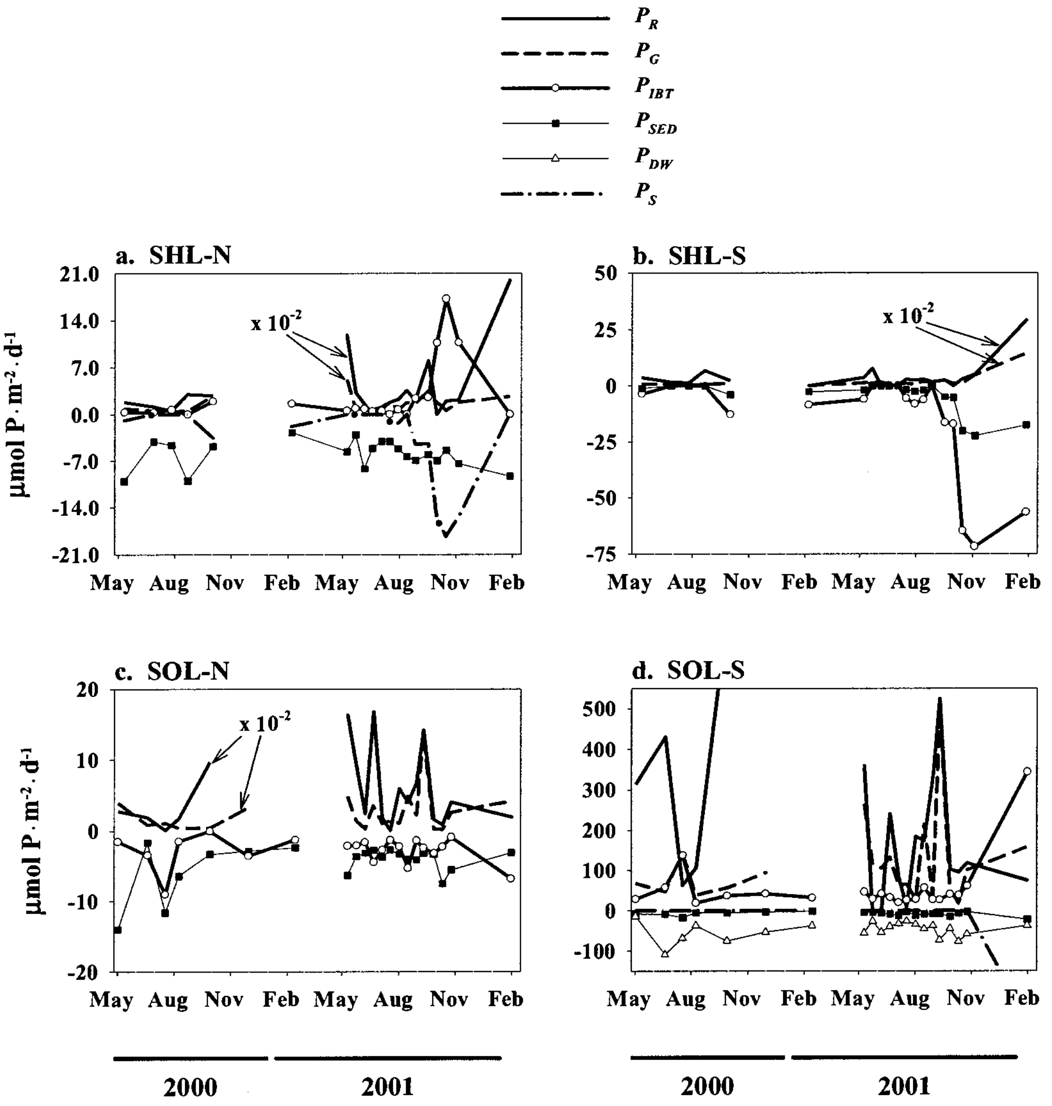

a. SHL-N
b. SHL-S
c. SOL-N
d. SOL-S
PO_4^{3-} Turnover Time (min)
153 d
147 d
153 d
161 d
113 d
126 d
113 d
98 d
0
5
10
15
20
25
8
16
24
32
Apr
Jul
Oct
Jan
2000
2001

Figure 5.11. Temporal P fluxes within (P_R, P_G), into (P_{IBT}), and out of (P_{SED}, P_{DW}, P_S) the north and south basins of Shawnigan Lake (a and b) and Sooke Lake Reservoir (c and d) from May 2000 – February 2002. Note that in Fig. 5.11a, b and c that *PR* and *PG* flux data are presented as x10^{-2} in order to accommodate the presentation of this data and the other fluxes on the same graph.


P_R
P_G
P_{IBT}
P_{SED}
P_{DW}
P_S
a. SHL-N
b. SHL-S
c. SOL-N
d. SOL-S
x 10^{-2}
µmol P · m^{-2} · d^{-1}
21.0
14.0
7.0
0.0
-7.0
-14.0
-21.0
50
25
0
-25
-50
-75
20
10
0
-10
-20
500
400
300
200
100
0
-100
May Aug Nov Feb May Aug Nov Feb
2000
2001