Scale of analysis and the influence of submerged macrophytes on lake processes

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Abstract

The goal of this thesis was to examine submerged macrophyte biomass, distribution, and ecosystem effects at scales large enough to incorporate the littoral zone into models of whole lake structure and function. Submerged macrophyte biomass and distribution was shown to be highly variable between growing seasons and primarily dependant upon air temperature and the timing of the onset of the growing season. Within a growing season, a mass balance study showed an undisturbed macrophyte bed to markedly lower phytoplankton biomass : total phosphorus ratios, although the net effect of the bed on the growing season phosphorus budget was minimal. The weedbed preferentially retained phytoplankton biomass while being a source of bacterial production to the open water. These findings were mirrored at the among lake scale, as planktonic respiration and bacterial production were higher in macrophyte dominated lakes than would be expected based on phytoplankton biomass alone. Further, phytoplankton biomass was lower than would be expected based on epilimnetic phosphorus levels, showing that the classical view of pelagic interactions that proposes phosphorus determines phytoplankton abundance, which in turn determines bacterial abundance through the production of organic carbon, becomes less relevant as macrophyte cover increases. Long term phosphorus accumulation in the littoral zone was shown to be linked to macrophyte biomass, and on average almost an order of magnitude higher than calculated from the growing season (June – October) phosphorus budget, suggesting that the bulk of phosphorus accumulation in weedbeds occurs outside of the growing season. Finally, sediment core data showed that while submerged weedbeds accumulate up to four times as much bulk sediment compared to the profundal zone, phosphorus accumulation in weedbeds is much less than observed in the profundal zone. These results strongly indicating that submerged macrophyte beds play a central role in trapping epilimnetic phosphorus and rapidly recycling it to lake biota.

Résumé

L'objectif de cette thèse était d'examiner la biomasse et la distribution des macrophytes immergés, ainsi que leurs effets sur l'écosystème, à des échelles spatiales suffisantes pour incorporer la zone littorale dans des modèles structuraux et fonctionels de lacs. La biomasse et la distribution des macrophytes variaient considérablement d'une année à l'autre, principalement en fonction de la température de l'air et du début de la saison de croissance. A une échelle locale, une étude de flux montre que, durant la saison de croissance, un large banc de macrophytes réduisait de façon importante le ratio biomasse de phytoplancton : phosphore total, alors que son effet sur le budget total en phosphore était minimal. Le banc conservait une grande partie de la biomasse phytoplanctonique entrant, et en favorisant la production bactérienne, libérer une biomasse de bactéries supérieure à sa sortie. Ces résultats se reflètent, lors de la comparaison de plusieurs lacs, par une respiration planctonique et une production bactérienne supérieures dans les lacs dominés par les macrophytes comparées aux valeurs de respiration et de production basées sur la biomasse phytoplanctonique seule. De plus, la biomasse phytoplanctonique était inférieure à la valeur attendue basée sur les concentrations de phosphore épilimnétique. Ceci montre que l'idée classique selon laquelle le niveau de phosphore détermine l'abondance de phytoplancton, qui à son tour détermine l'abondance de bactéries par la production de carbone organique, perd de sa signification lorsque le couvert macrophytique s'accroît. Sur le long terme, l'accumulation de phosphore dans la zone littorale était liée à la biomasse de macrophytes. Cette accumulation était en moyenne de près d'un ordre de grandeur supérieure à celle calculée à partir du budget du phosphore durant la saison de croissance (juin – octobre). Ce résultat laisse supposer que l'essentiel de l'accumulation du phosphore par les bancs de macrophytes se fait hors de la saison de croissance. Enfin, l'étude de carottes montre qu'en comparaison à la zone profonde, les bancs immergés accumulent près de quatre fois plus de sédiments mais beaucoup moins de phosphore. Ces résultats indiquent le rôle central des macrophytes immergés dans la capture du phosphore épilimnétique, et dans son recyclage rapide dans le biota du lac.

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Chapter 1

REMARKS ON STYLE AND AUTHORSHIP

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responsibilities of all authors of the co-authored papers. Under no circumstances can a co-author of such a thesis serve as an examiner for that thesis.

This thesis contains Four chapters, each of which has been prepared for publication in peer-reviewed scientific journals. The first chapter has been published in Aquatic Botany (Rooney and Kalff 2000, Aq. Bot. 68: 321-335), the second has been submitted to Ecosystems, the third to Hydrobiologia and the fourth to Limnology and Oceanography.

This thesis represents the results of my own independent research. All four chapters have been co-authored by my thesis supervisor, Jacob Kalff. Dr. Kalff contributed to the design, execution, analysis, and presentation of the results presented herein. Catherine Habel, while an undergraduate student, initiated the among weedbed portion of the research presented in Chapter 4 and is a co-author of the resulting paper.

CONTRIBUTIONS TO ORIGINAL KNOWLEDGE

Chapter 1 is the first study to document the influence of an earlier and warmer growing season on the biomass and distribution of submerged macrophytes in a series of north temperate lakes. Despite generally poorer underwater irradiance in the warmer 1998, I show that macrophytes colonized deeper and attained greater biomass in the lakes (g m^{-2}) compared to the cooler 1997. The significance of these results are three-fold. First, it documents the important, yet little recognized interannual variation in whole system macrophyte biomass. Second, earlier growing seasons, as predicted by climate change models, will result in greater biomass and distribution of submerged macrophyte communities, thereby modifying the structure and functioning of north temperate lakes. Third, the positive relationship between phytoplankton and whole system macrophyte biomass observed in Chapter 1 cautions that the negative relationship observed in highly eutrophic shallow systems does not appear applicable to deeper systems, such as those in the study area, characterized by lower macrophyte biomass to lake volume ratios

In Chapter 2, I use a mass balance approach to quantify the net influence of an undisturbed macrophyte bed on water column phosphorus, phytoplankton biomass (chlorophyll *a*) and bacterial production. Unlike the mesocosm studies that have dominated such macrophyte bed work, my approach allowed for the inputs of phosphorus, phytoplankton and bacterioplankton from outside of the weedbed as well as affording the opportunity to observe the system for four months, far longer than possible using a mesocosm approach. The results show that over the growing season, inputs and outputs of phosphorus are roughly in balance, indicating that weedbeds

receive a phosphorus subsidy outside of the growing season, likely during spring runoff. During the study, the weedbed had a consistent negative influence on phytoplankton biomass, while increasing bacterioplankton production, especially during a late summer export of phosphorus from the weedbed.

Chapter 3 is the first study to examine relationships among phosphorus, phytoplankton and bacterioplankton among lakes differing in macrophyte cover. The results show that the classical view of pelagic interactions, that proposes phosphorus determines phytoplankton abundance, which in turn determines bacterial abundance through the production of organic carbon, becomes less relevant as macrophyte cover increases.

Chapter 4 demonstrates that submerged macrophytes beds are net sinks for phosphorus, and that long term phosphorus accumulation rates are proportional to submerged macrophyte biomass. A comparison of profundal and weedbed accumulation rates revealed that weedbeds accumulated roughly twice as much bulk sediment per unit area as their profundal counterparts, but that phosphorus accumulation per unit bulk sediment was more than six times higher in profundal sediments compared to sediments in weedbeds. The findings yielded the first models predicting the extent of submerged macrophyte cover necessary to have a significant effect on whole lake sediment and phosphorus accumulation.

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I would first like to thank Jaap Kalff, my thesis supervisor, for giving me the opportunity to pursue my studies under his guidance. His encyclopedic knowledge of the literature is as impressive as his dedication to limnology. I have truly benefited from his broad view of the world.

I also thank Yves Prairie for serving as a member of my supervisory committee. Joe Rasmussen has helped me get through some muddy waters with his clarity of thought.

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My development as a scientist and as a person has benefited greatly from many 6th floor residents, past and present. Gilbert Cabana, Marc Trudel, Jessica Meeuwig, Adrian deBruyn, Graham Peers, Alice Parkes, Levi Cammack, Murray Humphries, Kevin McCann and Yvonne Vadeboncoeur have all either directly or indirectly helped me think or fight my way through the rough patches. Denis Réale was kind enough to translate my abstract.

Finally, I would like to dedicate this thesis to my family. They have been an incredible source of support and encouragement for the duration of this thesis. And, ofcourse, to the newest member of my family, Jacqueline, for your patience, your intellect, your sense of humour. You have contributed more than you know.

General Introduction

The success of limnology is due in no small part to the ease of sampling the small, abundant and homogeneously distributed organisms of the pelagic zone. Based largely on work done there, limnologists have made many fundamental contributions to population and community theory as well as to the understanding of energy and material flow in ecosystems (Kalff 2001). However, the pelagic focus has resulted in all too little attention to littoral zones and their role in lake dynamics. The limnological bias towards the pelagic zone was illustrated by Vadeboncoeur et al (2002) who, upon searching the BIOSIS literature database (1990-1999), reported that limnologists measured phytoplankton and bacterioplankton production about 10 times more often than periphyton and benthic bacterial production. However, littoral zones frequently contribute greater than 50% of whole lake primary production, especially in the shallow lakes that dominate the global landscape (Vadeboncoeur et al. 2002, Wetzel 1990). Moreover, submerged macrophyte beds influence numerous aspects of lake structure and function, from serving as habitat for littoral organisms to modifying nutrient and organic carbon cycling (See Jeppesen et al. 1998). Although limnologists have more recently acknowledged the intimate links between littoral and pelagic processes in lakes, the influence of submerged macrophytes on whole lake processes remains poorly understood.

One of the most important ways in which submerged macrophyte weedbeds influence lake structure and function is through modification of phosphorus (P) cycling (Barko and James 1998), as P is largely accepted as being the primary limiting nutrient in pristine north temperate zone freshwater ecosystems (Schindler 1977, Kalff 2001). Two primary goals of studying P dynamics in the littoral zone are the quantification of

weedbed influence on whole-lake P cycles and the linking of these effects to phytoplankton and bacterial dynamics in the water column. Despite much effort, the net effect of submerged weedbeds on P cycling and water column microbial metabolism remains unclear. In fact, there is not even consensus on whether submerged weedbeds are net sources or sinks of water column P (Granelli and Solander 1988, Barko and Smart 1998).

The influence of submerged macrophytes on phytoplankton is more apparent than on phosphorus. Mesocosm studies consistently report lowered phytoplankton biomass in the presence of submerged vegetation (Schriver et al 1995, Wigand et al. 2000). In Lake Veluwe, Netherlands, water clarity is greater within dense stands of *Chara* than in the turbid pelagic area (Van den Berg et al. 1998). The phenomenon of 'alternative stable states', in which a single lake switches between a clear water state with dense vegetation and a turbid water state dominated by phytoplankton, demonstrates the negative relationship between submerged macrophytes and phytoplankton among growing seasons (Jeppesen et al. 1990, van Donk et al. 1990, Scheffer et al. 1993). Finally, among lakes, water column transparency is greater than expected, based on water column phosphorus concentrations in lakes dominated by submerged macrophytes (Jeppesen et al. 1994, Faafeng and Mjelde 1998). The above studies amply demonstrate the negative effect of submerged macrophytes on phytoplankton biomass on a number of spatial and temporal scales.

Submerged macrophyte beds affect not only the phytoplankton, but also microbial metabolism in freshwater ecosystems. Until recently, it was assumed that bacterioplankton depend almost exclusively on phytoplankton derived dissolved organic

carbon for their metabolism (Cole 1988). That the ratio of phytoplankton production to planktonic respiration is below unity in oligotrophic lakes has, however, led researchers to implicate allochthonous sources of organic matter in bacterioplankton metabolism (e. g. delGiorgio and Peters 1993). In lakes dominated by submerged macrophytes, littoral sources of dissolved organic carbon (which are allochthonous to the epilimnion) have the potential to decouple phytoplankton-bacterioplankton relationships (Jeppesen et al. 1992, Pace 1993) because submerged macrophytes serve as an important source of DOC, increasing bacterioplankton metabolism (Hough and Wetzel 1975, Carpenter et al 1979, Wehr et al. 1999).

The classical view of pelagic interactions contends that phosphorus determines phytoplankton abundance, which in turn determines bacterial abundance (Currie 1990). Although submerged macrophytes influence each of these components in lakes, their net effect on whole lake scales is unclear. Based on previous research, submerged macrophytes negatively influence phytoplankton, provide organic substrate for bacterioplankton, and have the potential to alter phosphorus dynamics, although to what extent is poorly understood (Figure 1). While the majority of studies have examined these components individually, their tight interaction in the epilimnia of lakes makes their separation difficult.

The dearth of studies on the influence of submerged macrophyte beds on lake processes stems in part from the complexity of the littoral zone compared to the pelagic zone. Submerged macrophyte beds are internally heterogeneous and patchily distributed within lakes. Further, submerged macrophyte biomass and distribution varies throughout the course of a growing season as well as among growing seasons. Limnologists must

therefore be careful to design studies to address their questions at appropriate spatial and temporal scales. Unfortunately, the majority of the studies on the influence of macrophyte beds on lake processes have been carried out on small spatial scales (microcosm-mesocosms) over short time periods (minutes-weeks) (Figure 2). While such studies have provided useful insights into the processes and mechanisms of phosphorus cycling in weedbeds, they do not scale up well to ecosystem level of inquiry, and have resulted in considerable disagreement, such as whether submerged macrophyte beds are sinks or sources of phosphorus to the open water.

This thesis sets out to examine different aspects of a broad problem: submerged macrophyte biomass and distribution and their effect on whole lake phosphorus cycling and pelagic metabolism. Each chapter poses a question on spatial and temporal scales that are larger than the experimental manipulations that dominate the literature, and are of particular relevance to ecologists (Figure 2). In chapter 1, I quantify macrophyte biomass and distribution in 5 lakes in two climatically different growing seasons, providing evidence for major changes in lake structure and function on an interannual temporal scale. While it is well known that the lower limit of macrophyte distribution in lakes is generally determined by underwater irradiance within growing seasons (Spence 1982, Chambers and Kalff 1985), my results show that on larger temporal scale, air temperature and the timing of onset of the growing season are the primary determinant of macrophyte biomass and distribution among growing seasons.

The objective of chapter 2 was to quantify the net influence of a submerged macrophyte bed on water column phosphorus and microbial metabolism over the course of a growing season. A mass balance approach allowed for the monitoring of an

undisturbed weedbed over a 4-month growing season, far longer than possible using enclosures. The results from chapter 2 addressed two aspects of the influence of submerged macrophytes on lake processes, which are then examined at different scales in subsequent chapters (Figure 2). The first major finding was that the weedbed preferentially retained phytoplankton biomass while being a source of bacterial production to the open water, markedly lowering phytoplankton biomass : total phosphorus ratios in the process. The findings are subsequently compared to broader spatial scale observations in chapter 3 (Figure 2, see below). The second major finding of chapter 2 was that, although the weedbed was a net sink for phytoplankton biomass, it retained little of the inflowing phosphorus over the summer, with net phosphorus retention orders of magnitude lower than within weedbed phosphorus cycling rates reported in the literature. In chapter 4, I compare long term phosphorus accumulation rates to the phosphorus budget developed for the four month growing season in chapter 2 (Figure 2, see below).

Chapter 3 examines interactions among epilimnetic phosphorus, phytoplankton biomass and bacterioplankton metabolism in lakes varying in submerged macrophyte cover. On this large spatial scale, phytoplankton biomass was reduced in macrophyte dominated lakes, despite relatively high levels of soluble phosphorus, mirroring the results from chapter 2. Furthermore, planktonic respiration and bacterioplankton production were higher in macrophyte rich lakes than would be expected from phytoplankton biomass alone, pointing to a subsidization of bacterioplankton metabolism by macrophyte beds at the whole lake scale. The results show that the classical view of pelagic interactions that proposes phosphorus determines phytoplankton abundance,

which in turn determines bacterial abundance through the production of organic carbon, becomes less relevant as macrophyte cover increases.

Finally, in Chapter 4, I examine the influence of submerged macrophytes on long term (~ 115 yr) phosphorus and sediment accumulation rates. Whereas much of the debate surrounding the influence of submerged macrophytes on phosphorus cycling has resulted from short term studies, I chose to ask the question on a much longer temporal scale and compare the findings to a seasonal budget calculated in chapter 2 (Figure 2), showing that phosphorus and sediment accumulation in the littoral zone is proportional to macrophyte biomass.

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Figure 1. Schematic diagram illustrating the hypothesized influences of submerged macrophytes on phosphorus, phytoplankton, and bacterioplankton in lakes.

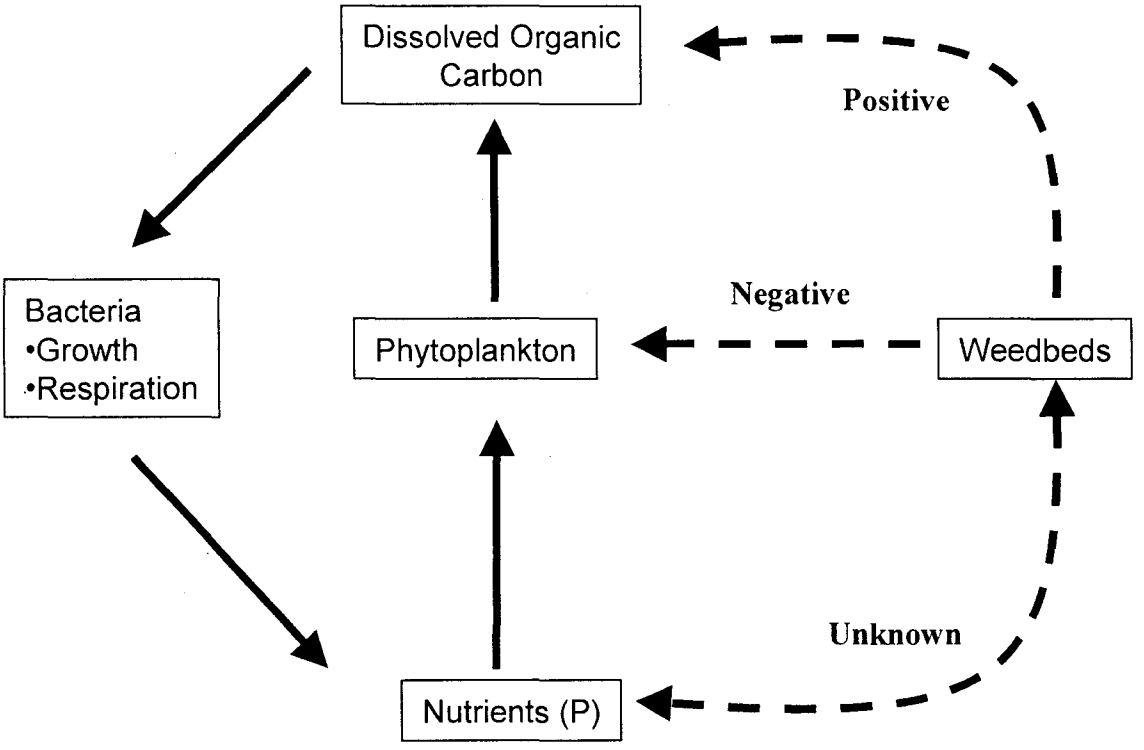
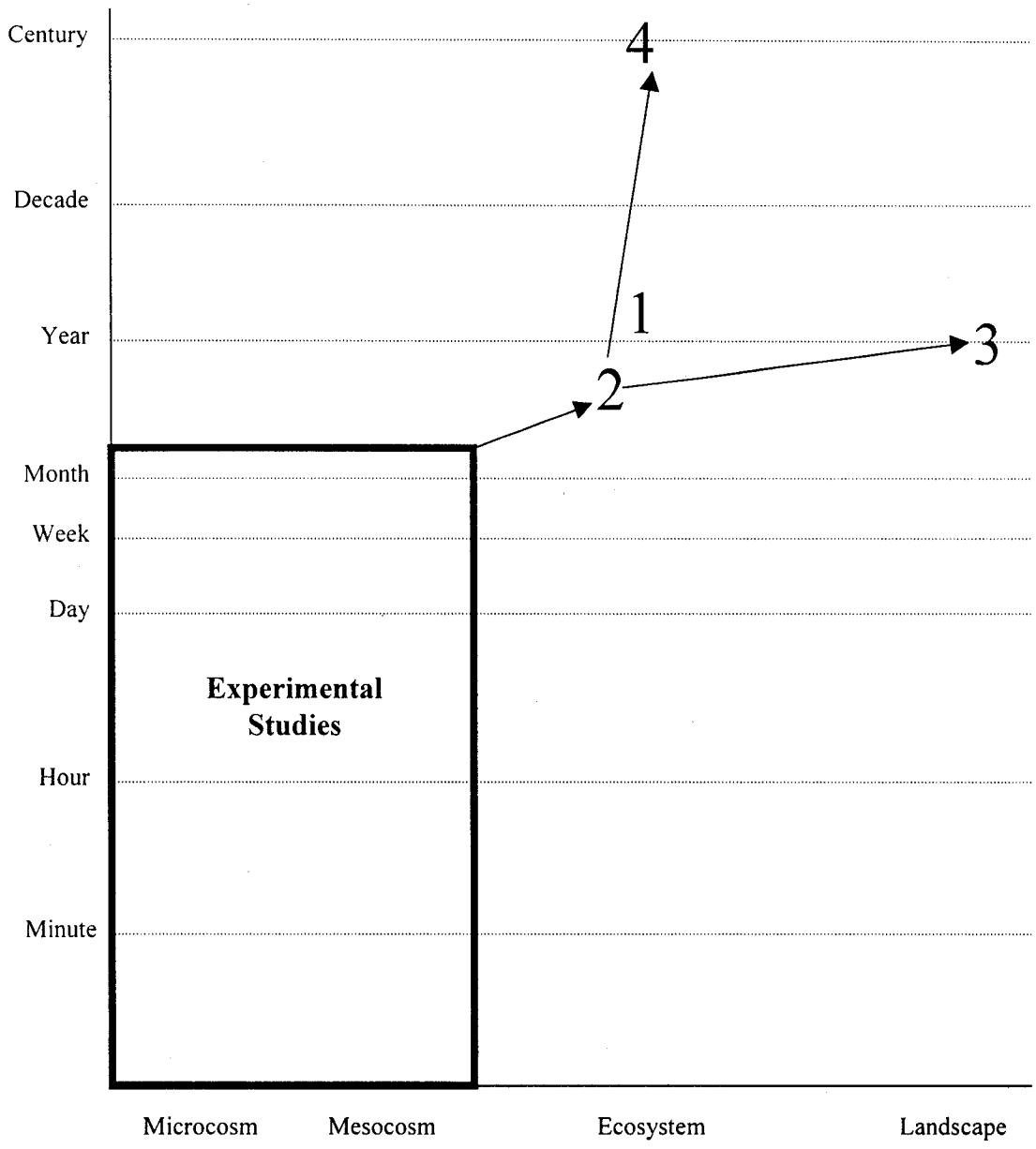

Dissolved Organic Carbon
Positive
Bacteria
•Growth
•Respiration
Negative
Phytoplankton
Weedbeds
Unknown
Nutrients (P)

Figure 1

Figure 2. Conceptual digram of the temporal and spatial scales addressed in this thesis.



Chapter 1- Interannual variation in whole lake biomass
Chapter 2- Mass balance of one weedbed over one growing season
Chapter 3- Among lake patterns in one growing season
Chapter 4- Long term (~115 yr) sediment and phosphorus accumulation

Figure 2

CHAPTER 1

Inter-annual variation in submerged macrophyte community biomass and distribution: the influence of temperature and lake morphometry.

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Abstract

We monitored the biomass and distribution of submerged macrophyte communities in five lakes in the Eastern Townships of Quebec, Canada, in two climatically different growing seasons. Early season warm temperatures allowed for much deeper macrophyte colonization (25-170%), an average of 300 g m^{-2} greater wet weight biomass (g m^{-2}) and a 45-1160% increase in whole lake biomass in warm 1998 compared to a cooler 1997. In contrast, the inter-year variation in underwater light climate had no effect on macrophyte colonization as water column turbidity was generally higher in the warmer year, although irradiance did affect the distribution and biomass within seasons. The positive relationship between phytoplankton and whole system macrophyte biomass observed in this study cautions that the negative relationship in highly eutrophic shallow systems does not appear applicable to deeper systems characterized by lower macrophyte biomass to lake volume ratios. Earlier growing seasons, as predicted by climate change models, would result in greater biomass and distribution of submerged macrophyte communities, thereby modifying the structure and functioning of north temperate lakes. The effect will be a function of lake morphometry and most pronounced in shallow systems.

Introduction

Submerged macrophyte communities influence many aspects of lake structure and function. Their physical structure determines fish, zooplankton, and benthos habitat in the littoral zones of lakes, influencing food web structure (Diehl and Kornijow 1998; Jeppesen et al. 1998; Beklioglu and Moss 1996; Cyr and Downing 1988). The plant beds serve as long term sinks for organic material (Benoy and Kalff 1999), and as short term sources of nutrients and metals to the water (Landers 1982; Jackson et al. 1994). At the whole lake scale, the pool of organic carbon represented by macrophyte communities tends to be large in shallow lakes (Wetzel and Hough 1973). Submerged plants therefore play an important role in carbon and nutrient flux within the predominantly shallow lakes that dominate the global landscape. Macrophytes also affect the use of lakes as recreational areas. Whereas swimmers might not appreciate macrophyte beds, most sport fishers look favourably upon extensive macrophyte beds. Ecological and lake management aspects of limnology are thus affected by changes in the distribution, specific biomass (weight per unit area) and the whole lake biomass of macrophytes.

Factors that influence the biomass and distribution of submerged macrophytes both among and within lakes have been well studied. Within lakes, the morphometric variables of sediment slope and community exposure are both negatively correlated to macrophyte biomass (Duarte and Kalff 1986). Among lakes, macrophyte biomass and distribution varies with lake morphometry (Duarte et al. 1986), latitude (Duarte and Kalff 1987), water transparency (Chambers and Kalff 1985; Dale 1986) and sediment characteristics (Barko et al. 1991;Barko et al. 1988; Anderson and Kalff 1988). The majority of studies on the distribution and biomass of macrophytes focus on factors that

vary in space within growing seasons. It is, however, unclear how such environmental factors influence macrophytes on longer temporal scales.

Many lines of evidence point to the influence that light levels have on macrophytes at many different scales. In his extensive review of macrophyte distribution within lakes, Spence (1982) reports an inverse relationship between the maximum depth of macrophyte colonization and the minimum vertical diffuse attenuation coefficient among systems. He concludes that the light regime is the principal determinant of macrophyte distribution within most lakes, while other factors (temperature, hydrostatic pressure, substrate conditions) have minor effects. In their comparative study, Chambers and Kalff (1985) produce strong empirical relationships between Secchi depth and maximum depth of colonization for angiosperms, bryophytes and charophytes. Additionally, experimental work demonstrates the limitation of submerged macrophyte growth at light levels comparable to those observed at the maximum depth of colonization in lacustrine and marine environments (Sand-Jensen and Madsen 1991; Markager and Sand-Jensen 1992). Longer term studies link eutrophication, and associated lower light levels, with decreases in macrophyte abundance (Rørslett et al. 1986, Blindow 1992).

Virtually no attention has been given to the impact of environmental factors, such as temperature, which operate on inter-annual time scales (Royle and King 1991). There is, however, a body of evidence which indicates that inter-annual fluctuations in temperature should have an effect on the distribution and biomass of macrophyte communities. Most physiological processes have temperature dependent steps, leaving rates subject to the influence of temperature. Laboratory manipulations show interactions

between light and temperature in determining shoot biomass, root biomass, and shoot density in macrophytes (Barko et al 1982). Other studies show submerged macrophytes to have a Q_{10} ranging from 2.3 to 3.5 (Madsen and Brix 1997). Further, plants acclimated to high temperatures have consistently higher photosynthetic capacities and light use efficiencies. The increased light use efficiency should allow plants growing in warmer water columns to grow deeper and cover larger lake bottom areas at a given irradiance. Unfortunately, a temperature effect is difficult to demonstrate in macrophyte beds where irradiance and temperature typically co-vary over the growing season, and where seasonal temperature changes tend to be moderate.

Studies on power plant cooling ponds and reservoirs allow a separation between the effects of temperature and irradiance on macrophyte communities. Grace and Tilly (1976) report a doubling of standing crop (mostly due to increased *Myriophyllum spicatum*) in the warm portions of a North Carolina cooling pond. In an Alberta, Canada lake, plant growth starts 2-3 months earlier in heated regions that receive cooling water from a coal fired electrical generating station (Haag and Gorham 1977). Other factors such as maximum biomass, time of flowering, and seed production are also affected by temperature in cooling ponds (Haag 1983).

A third line of evidence for the influence of temperature on macrophytes comes from an analysis of the macrophyte biomass and distribution among lakes in different geographical areas. Empirical and conceptual models developed by Duarte and Kalff (1987) show that temperature should influence the extent of macrophyte colonization. Changes in transparency in warmer low latitude lakes are predicted to result in greater changes in the extent of macrophyte colonization than similar light climate changes at

higher latitudes. The work, however, is not designed to allow a separation of temperature and light (day length) effects. Consequently, while there is physiological, small scale, and geographical evidence for the influence of temperature on macrophyte colonization within lakes, work at the whole lake scale has been lacking.

Although the influence of inter-annual changes in temperature on macrophytes has not been documented in lakes, a two year marine study shows that eelgrass communities exhibit higher biomass and production in a warm El Niño year, despite a decrease in nutrient availability (Nelson 1997). If temperature influences lacustrine macrophyte distribution above and beyond that produced by irradiance, the effect of such changes will be greatest in shallow lakes which constitute the majority of lakes worldwide. For a particular transparency, shallow lakes have a greater proportion of their sediment surface available for colonization than their deeper counterparts.

The importance of the effect of temperature on macrophyte community ecology is accentuated by a predicted increase in the temperature of the northern hemisphere resulting from an expected anthropogenically induced climate change. Predictive models are needed to address this issue. This paper has two different but linked objectives towards such models. The first is an analysis of the impact of temperature and light on the distribution and biomass of submerged macrophytes in five lakes during two quite different growing seasons. The second, and smaller objective, attempts to separate the influences of temperature and irradiance on macrophyte community distribution and biomass in the same and other north temperate lakes, using previously published data.

Methods

Field work was conducted on five lakes in the Eastern Townships region of southern Quebec, Canada (45°18' N, 72°15'W). The lakes were sampled in mid August of 1997 and 1998, the period of maximum submerged macrophyte biomass. Four macrophyte beds per lake were selected in 1997 so as to maximize the differences in the sediment slope and site exposure, the principal determinants of biomass (g m^{-2}) (Duarte and Kalff 1986). Pelagic zone thermal profiles were measured to determine the mixed layer depth. Six echosound transects were taken perpendicular to the shore to establish the maximum depth of macrophyte colonization (Z_c), which is easily distinguished from bare sediment on the printouts. Mean length of the weedbeds was calculated from the length of the echosounder printouts, the time of each transect, and the speed of the boat. At each site, two sets of triplicate quadrats (0.25 m^2) were taken, and all plants harvested by SCUBA divers at the depth of maximum submerged macrophyte biomass (MSMB).

Samples were taken to the laboratory and kept refrigerated until processed (within 2 days of collection). Roots were removed, the plants were washed free of detritus and/or loose epiphytes and then spun dry for at least 3 minutes in a salad spinner. Samples were weighed to the nearest 0.1g to yield the wet weight biomass.

The same four sites in each lake were re-visited in August 1998, and thermal profiles once again obtained in the open water. In addition to the 1997 protocol, echosound transects were obtained at an additional 6-8 sites per lake, again to establish Z_c and the length of weed beds.

The study lakes are all reasonably regular in shape, with no elongated bays or inlets, allowing for the percent lake area colonized to be determined as follows:

$$\%A = \frac{(r - Lw)^2}{r^2} \times 100$$

where %A is the percent of lake area colonized by submerged macrophytes, r is the mean lake radius, and L_w is the mean length of the weedbeds.

Based on the echosound tracings, we determined that the distribution of biomass on both sides of the depth of MSMB decreased linearly, with end points at the Z_c, and the shoreline. Mean transect wet weight biomass (g) was calculated and extrapolated to the area colonized per lake to provide an estimate of total lake macrophyte biomass. The relative impact of the submerged macrophytes on the open water was assessed by normalizing whole lake macrophyte biomass to the volume of the mixed layer. All macrophyte biomass in the lakes occurred above the thermocline.

We examined the inter-annual increase of within site biomass by regressing wet weight areal biomass at the depth of MSMB as measured in 1998 on measurements at the same sites in 1997. The slope of the regression was compared to the 1:1 line to determine if increases were related to site biomass ($g\ m^{-2}$). The intercept of the regression was the estimate of the average increase in macrophyte biomass ($g\ m^{-2}$) across all sites in all lakes.

Climatic data were obtained from the Global Surface Summary of Day site (NOAA 1999). Daily mean air temperatures at Mount Orford (45°18' N, 72°15'W, elevation 851m) were considered indicative of the mean air temperature of the lakes, which lie within 50 km of this site. Temperature was calculated as a three day running average and the cumulative degree days (the running sum of mean air temperatures from May 1st to August 31st). Hourly surface irradiance data (DOE 1999) from Lennoxville, Quebec (45°22' N, 71°52'W), located within 100km of the lakes, were considered to be

representative of lake surface irradiance. Irradiance data were summed for each day, and both cumulative and three day running average values calculated for May to September.

To estimate underwater light conditions, water clarity was estimated using open water chl *a* values. Water samples were taken between 4 and 6 times over the two growing seasons between early June and early September using an integrated tube incorporating the entire epilimnion. Samples were stored in opaque bottles, and brought to the laboratory within 4 hours of collection where they were filtered onto Whatman Type A/E glass fiber filters, the chlorophyll *a* extracted in 95% ethanol, and analyzed spectrophotometrically according to Bergman and Peters (1980).

The water light attenuation coefficients (K) were calculated using an empirical relationship derived from combined data sets (Rasmussen 1988, Duarte et al. 1987, Rooney, unpubl.) of Secchi depth (Z_{SD}) and chl *a* values for the 5 study lakes. Transparency was well correlated with chl a (r^2=0.92, n=24), allowing the estimation of underwater light attenuation coefficients. The equation describing the relationship between transparency (Z_{SD}), chl *a* and K is:

$$1/Z_{SD} = \frac{K_w}{\ln(I_o / I_z)} + \left[\frac{K_c}{\ln(I_o / I_z)}\right] \times Chla$$

Where Z_{SD} is Secchi depth, K_w is the partial attenuation coefficient for water, K_c is the partial attenuation coefficient for chlorophyll ($K = K_w + K_c$ x chl *a*), I_0 the surface irradiance, I_z the irradiance at Secchi depth, and the chl *a* concentration in mg m^{-3}. The light at Secchi depth was assumed to be 10% of surface irradiance (Megard et al. 1980). Light attenuation coefficients were interpolated between sampling dates. Daily irradiance totals were combined with estimated K values for each of the lakes to estimate the depth of the water column receiving 1 kJ m^{-2} of photosynthetically active radiation (PAR) over

the course of the summer. The light level of 1 kJ m^{-2} was chosen to standardize across all systems, and in all cases PAR was assumed to be 50% of total irradiance.

Within year relationships between depth of PAR penetration and both mean Z_c and areal wet weight at depth of MSMB were examined for 1997 and 1998. Values were log transformed in order to meet assumption of linearity before statistical tests (regression and ANCOVA). ANCOVA was used to test for an effect of year, underwater light conditions and an interaction between the two independent variables on macrophyte biomass and distribution.

Results

Table 1 outlines the morphometric features, average summer chlorophyll, total phosphorus values of the study lakes. Thermal stratification in both Roxton Pond and Lake Waterloo ended in early August in both study years.

The mean summer depth to which 1 kJ m^{-2} of photosynthetically active radiation (PAR) penetrated was correlated to the maximum depth of submerged macrophyte colonization (Z_c) (Figure 1a). The depth of PAR penetration was also correlated with the observed mean values for maximum submerged macrophyte biomass (MSMB) (Figure 1b). An ANCOVA revealed that both year and depth of PAR penetration displayed a significant effect on wet biomass at MSMB ($p < 0.05$), whereas there was only a year effect in predicting Z_c.

The maximum depth of macrophyte colonization (Z_c) was systematically deeper in 1998 than in 1997 (Figure 2a). The increase ranged from 0.5m to 2.5 m, with the smallest increase in humic Lake d'Argent (absorbance at 440nm in a 10cm cell = 0.135).

The increased depth of colonization (and resulting increased length of weedbeds) translated into a 20% to 170% gain in percent of lake area colonized (Figure 2c).

The average maximum submerged macrophyte biomass (MSMB, g m^{-2} wet weight) increased in all lakes, nearly tripling in Roxton Pond from 288 g m^{-2} to 824 g m^{-2} (Figure 2d). On a site-by-site basis, mean biomass in each of the 20 macrophyte communities either increased or remained the same in 1998 (Figure 3). The slope of the regression was not significantly different from the 1:1 line, but the intercept was significant ($p<0.01$), showing that the average quadrat biomass was approximately 300 g m^{-2} higher in 1998. The increase in whole lake biomass was a function of the lake area covered (Figure 2c) and the increase in biomass per unit area (g m^{-2}, Figure 2d). The whole lake biomass adjusted to the volume of the mixed layer showed the greatest increase in the shallower lakes (Figure 2e), increasing on average of 4 fold, with an over 12 fold increase in Roxton Pond.

The largest differences in inter-annual air temperature occurred early in the growing season. The daily air temperature was on average almost 6 °C higher in May 1998 than in 1997, but differed little more than 1 °C during the following three months (Figure 4a). In contrast, incoming irradiance was comparable in May of both years, but higher in June and July 1998, compared to 1997. Although May 1998 was warmer, the mean daily irradiance differed little between the two years (only 3% higher in May 1998) (Figure 4a). In fact, the cumulative light energy reaching the surface was higher in May 1997 than in 1998 (Figure 4b).

Even though the surface irradiance was higher in June 1998, three of the 5 lakes exhibited lower transparency resulting from elevated phytoplankton biomass (Figure 5). May transparency data are unfortunately not available.

Discussion

Light and temperature influenced the distribution and biomass of submerged macrophytes at different scales in our study. Within years, the maximum depth of macrophyte colonization (Z_c) and the maximum submerged macrophyte biomass (MSMB) were linked to the underwater irradiance (Figure 1). However, the early growing season temperature rather than the irradiance best explained differences in the biomass and distribution of the submerged plants between years. Yet other factors known to influence among lake macrophyte colonization patterns, such as littoral sediment slope (Duarte and Kalff 1986), water clarity (Chambers and Kalff 1985) and sediment conditions (Barko et al. 1982; Anderson and Kalff 1988) could not be responsible for the observed changes. Sediment slope and characteristics were constant, while underwater irradiance was similar or lower as a result of greater algal caused turbidity during the year of elevated macrophyte biomass. Rather, the month longer growing season in 1998 allowed for the average 4 fold increase in biomass accumulation and mean 74% increase in coverage.

Interestingly, the positive relationship between submerged macrophyte and phytoplankton biomass in our lakes contradicts the negative relationships observed in very shallow, highly eutrophic Dutch and Danish lakes (e.g. Jeppesen et al 1998, Scheffer et al. 1993). Mechanisms proposed to explain such negative relationships, such as zooplankton grazing, plant allelopathy, and increased phytoplankton sedimentation (see

Søndergaard and Moss 1998) are clearly not applicable as the relationship in our lakes was positive. The contrasting set of results points to a curvilinear relationship between phytoplankton and macrophyte production which is positive among somewhat deeper oligotrophic lakes characterized by high water volume to whole lake biomass ratio, and negative in shallow highly eutrophic systems associated with low transparency and water volume to macrophyte biomass ratio. Such a curvilinear relationship has been proposed within lakes over longer time scales (with respect to lake ontogeny), and along fertility gradients (as a result of eutrophication). In this study, the increased temperatures of 1998 coincided with increased mean summer total phosphorus concentrations (Table 1). Thus, our observations are consistent with the generalization that when nutrients become more available in relatively oligotrophic lakes, production of all primary producers tends to increase (Wetzel 1983, Hansson 1989).

Studies examining inter-annual variation in submerged macrophyte biomass and distribution are uncommon, and largely restricted to single systems subject to major changes resulting from well documented events. Royle and King (1991) document a greater than 300% increase in the colonized area of Lake Liddell, New South Wales between a drought and a non drought year, but note only minor changes in the following 5 years. The present study appears to be the first to document a systematic increase among lakes in macrophyte biomass and distribution between years.

While our sample size was too small to build quantitative models of light and temperature interactions, the data on macrophyte biomass and colonization points to such an interaction. Even though the lakes experienced a higher biomass and greater colonization in the warmer year, the response was not independent of the underwater

light climate. The smallest increases in the maximum depth of colonization (Z_c) were seen in humic lake d'Argent and in eutrophic (turbid) Lake Waterloo (Table 1). Conversely, the greatest increases were seen in Lake Brome and Roxton Pond, where light penetration was similar or increased between years.

The literature supports our findings of a light-temperature interaction. A re-analysis of data collected by Dale (1986) shows water column transparency (SD) to be the best among lake predictor of Z_c. Table 2 presents two models derived from data presented by Dale (1986). The first shows that SD explains 60% of the variation in maximum depth of macrophyte colonization among lakes. Even so, the second model which incorporates temperature (the depth of the 16°C isocline) increases the overall predictability of the model (SE_{est} 0.94), and the explained variation of Z_c to 74% (Table 2). This indicates that even within growing seasons, the thermal structure of lakes affects the distribution of submerged macrophytes. As thermal structure is linked to physical variables such as fetch (e.g. Hanna 1990, Shuter et al. 1983), it follows that the degree to which macrophyte communities can respond to temperature is a function of lake morphometry.

Our data and analysis based on regional observations provide insight into research on larger spatial scales. Duarte and Kalff (1987) demonstrated that angiosperms in lower latitude (warmer) lakes colonize deeper than those growing in lakes of similar transparency at higher latitudes. Our results corroborated their findings, showing that angiosperms colonized deeper during years characterized by an early warming of the water, independent of underwater irradiance. Duarte and Kalff (1987) postulate that the pattern with latitude could result from warmer water temperatures, greater incoming

irradiance, or a longer growing season. The higher May, 1998 air temperatures and the greater summer distribution of macrophytes in our lakes that year was analogous to a southward shift. But as the mean daily air temperatures in June, July and August, of the two years were virtually identical, it is clear that the greater biomass and distribution in 1998 results from a 4-6 week earlier onset of the growing season (personal observation of plant presence in lakes), and not to summer temperature or the irradiance differences during the remainder of the growing season (Figure 3a). Since the majority of the plants in these lakes reproduce asexually (rhizomes or fragments), an earlier start to the growing season allowed the plant communities more time to colonize deeper in the water column.

The 45% to 1160% between year increase in whole lake biomass with respect to the epilimnetic volume (Figure 1e) in 1998 would have a major effect on the quantities and concentrations of nutrients and organic carbon released into the epilimnion, especially during senescence. Submerged macrophyte communities release substantial quantities of metals (Jackson et al. 1994), as well as organic carbon (Godshalk and Wetzel 1978), and nutrients (Adams and Prentki, 1982; Landers 1982) that upon senescence influence the metabolism of the plankton (Rooney and Kalff in prep.). Furthermore, the area covered and plant biomass will affect the abundance and production of epiphytic algae (Catteneo and Kalff 1980), littoral zoobenthos (Rasmussen 1988) and zooplankton (Jeppesen et al. 1998).

While there has been considerable discussion regarding the expected effects of global climate change on lakes, the discussion to date appears to have been restricted to effects on the pelagic zone (See Schindler et al. 1990, Schindler 1997). But, the observation of an increase in biomass and production of subtidal eelgrass communities

(Nelson 1997), linked to warmer El niño years, is an indication of the influence of temperature on aquatic plant communities. This indicates that long term temperature increases will have a profound effect on the biomass and distribution of submerged macrophytes in inland waters. Shorter winters at high latitudes will allow for earlier, and therefore longer, growing seasons, thereby increasing both the depths of macrophyte colonization as well as the specific biomass of macrophytes within weedbeds. Shallow systems, with their associated shallow sloping littoral zones, would be among the most affected by higher temperatures and an associated longer growing season.

We demonstrated that the biomass and distribution of submerged macrophytes is greatly affected by inter-annual changes in temperature and length of growing season. In the study lakes, a mean increase in Z_c of over 1 m translated into a 20% to 170% increase in area colonized. In combination with an average 300 g m^{-2} increase in biomass, there was a 45% to 1160% increase in whole lake biomass, with the largest increases in the shallow lakes. The sensitivity of submerged macrophyte communities to higher temperatures and an earlier onset of the growing season indicates that the littoral plant communities, and the associated epiphyte, zooplankton, zoobenthic and fish communities, are particularly susceptible to long term climate changes. The relationship seen between littoral and pelagic biomass indicates that the two are positively coupled in our somewhat deeper and less productive lakes, and cautions that the mechanisms invoked to explain the observed negative relationships seen in shallow productive European systems are not universally applicable.

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Table 1. Morphometric characteristics, mean summer chlorophyll and total phosphorus values for 1997 and 1998 in the five study lakes located in the Eastern Townships, Quebec. Standard error values are given in parentheses.

Lake	Area (m^2)	Volume (m^3)	Maximum Depth (m)	Mean depth (m)	Mean Chl a ($\mu g\ l^{-1}$)		Mean total phosphorus ($\mu g\ l^{-1}$)	
					1997	1998	1997	1998
Brome	1.45×10^7	8.32×10^7	12.8	5.8	8.4 (2.4)	12.9 (1.6)	12.3 (2.5)	19.1 (0.9)
d'Argent	9.6×10^5	4.51×10^6	15.5	4.6	3.4 (0.2)	9.2 (5.4)	10.2 (2.1)	14.3 (5.7)
Magog	1.08×10^7	1.05×10^8	19.2	9.8	6.5 (0.9)	7.4 (0.8)	17.3 (3.4)	18.2 (2.3)
Roxton	1.79×10^6	5.6×10^6	5.5	3.2	19.8 (6.1)	15.7 (3.4)	18.6 (2.1)	20.2 (1.2)
Waterloo	1.5×10^6	4.35×10^6	4.9	2.9	25.5 (7.8)	65.4 (13.9)	26.5 (4.5)	44.7 (3.3)

Table 2. Regression models for predicting the maximum depth of macrophyte colonization (Z_c) using transparency (Z_{SD}) and the depth of the 16°C isocline ($Z_{16°C}$). Data is from Dale (1986). The number of sampling units for each regression is n, r^2 is the proportion of the sum of squares attributable to the regression, and SE_{est} is the standard error of the estimate for the regression.

Model	n	B_1 (Z_{SD})	B_2 ($Z_{16°C}$)	Intercept	r^2	SE_{est}
1	28	0.49*		1.46*	0.60	1.15
2	28	0.64*	0.37*	-0.15	0.74	0.94

* - $p<0.005$

Figure 1. The relationship between the log depth of 1 Kjoule m^{-2} PAR penetration and a) Maximum depth of macrophyte colonization (m); and b) Mean biomass at the depth of maximum submerged macrophyte biomass (g m^{-2}).

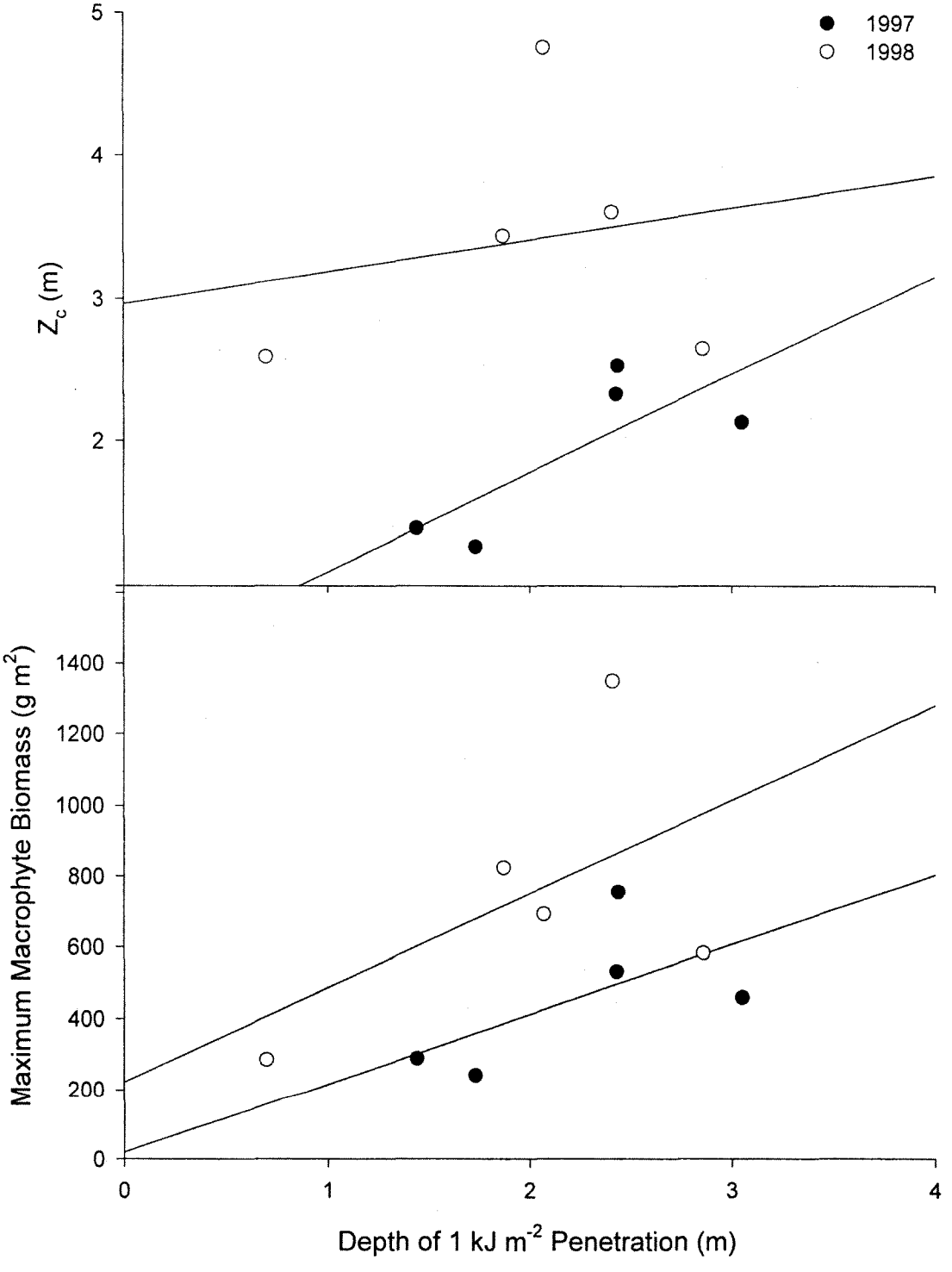
1997
1998
Z_c (m)
5
4
3
2
Maximum Macrophyte Biomass (g m^2)
1400
1200
1000
800
600
400
200
0
0
1
2
3
4
Depth of 1 kJ m^{-2} Penetration (m)

Figure 1

Figure 2. Distribution and biomass of submerged macrophytes in the five study lakes, for the years 1997 and 1998; a) Maximum depth of macrophyte colonization (Z_c); b) Percent of lake area colonized (%); c) Areal wet weight biomass (g m^{-2}); d) Wet weight macrophyte biomass relative to epilimnetic volume (B/V mg m^{-3}). Error bars indicate the standard error of the mean.

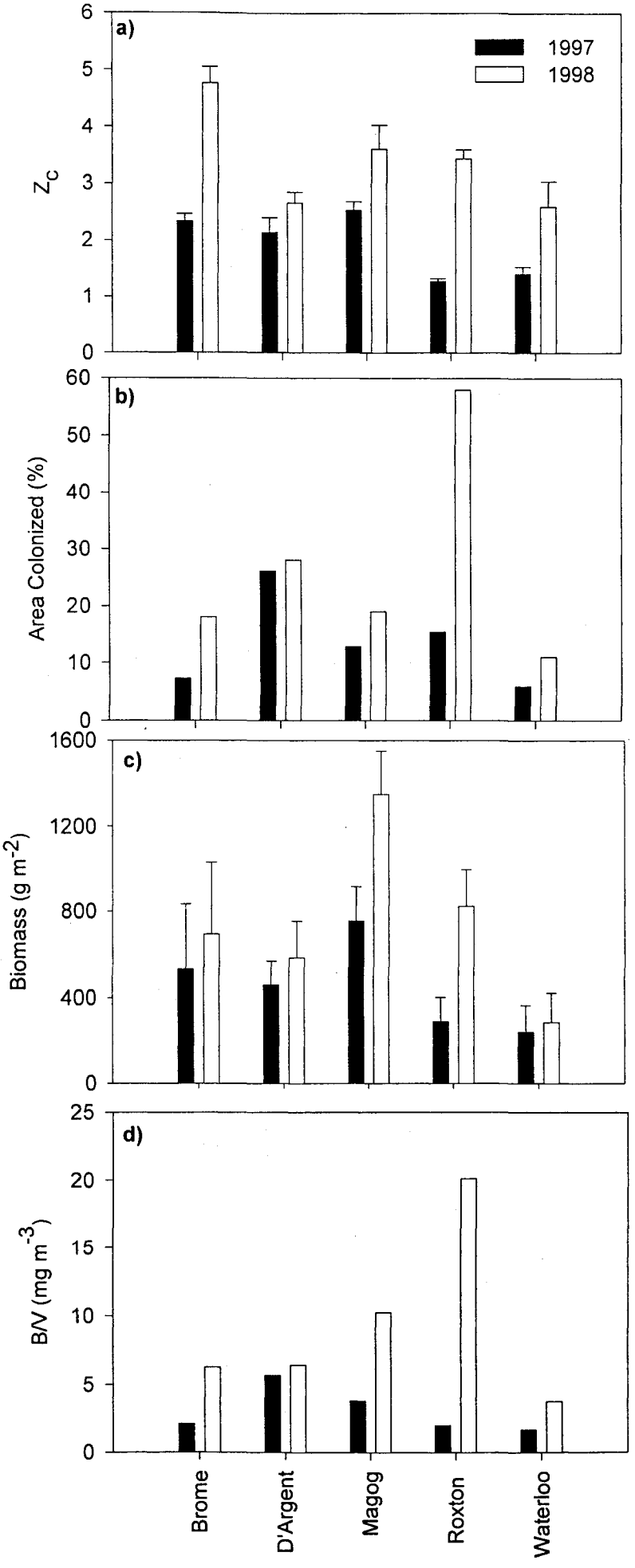
a)
1997
1998
Z_c
0
1
2
3
4
5
6
b)
Area Colonized (%)
0
10
20
30
40
50
60
c)
Biomass (g m^{-2})
0
400
800
1200
1600
d)
B/V (mg m^{-3})
0
5
10
15
20
25
Brome
D'Argent
Magog
Roxton
Waterloo

Figure 2

Figure 3. Mean site biomass (g m^{-2}) in 1998 versus 1997 in all twenty study sites. The 1:1 line represents no change in biomass from 1997 to 1998. The solid line is the linear regression, showing an average increase of 298 g m^{-2} per site ($r^2 = 0.62$).

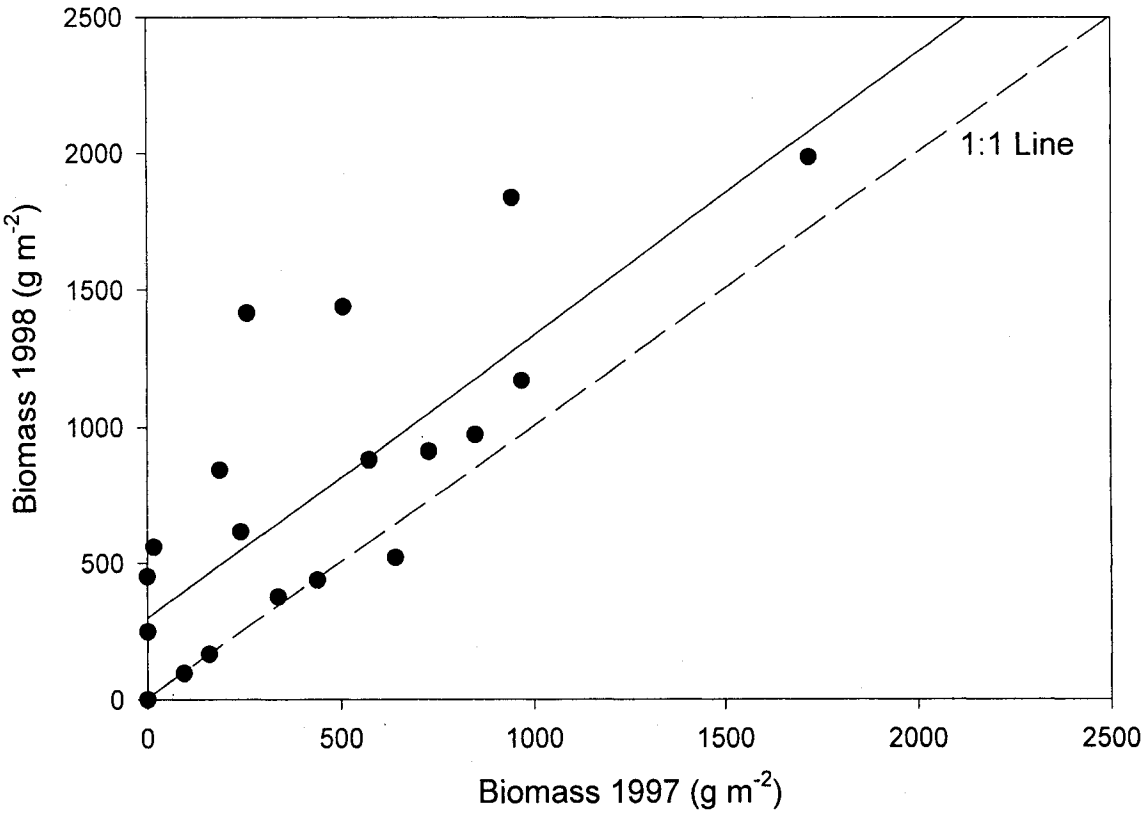
2500
2000
1500
1000
500
0
0
500
1000
1500
2000
2500
Biomass 1998 (g m-2)
Biomass 1997 (g m-2)
1:1 Line

Figure 3

Figure 4. **a)** Running 3 day mean air temperature (°C) and surface irradiance (PAR in MJ $m^{-2} hr^{-1}$) at Mt Orford (45° 18'N, 72° 15'W) and Lennoxville (45°22'N, 71° 52'W) respectively. Measurements presented are from May 1st to August 27th in 1997 (hatched line) and 1998 (solid line). **b)** Cumulative degree days and surface irradiance as in a). are from Mt. Orford (45°18' N, 72°15'W); (hatched line) and 1998 (solid line).

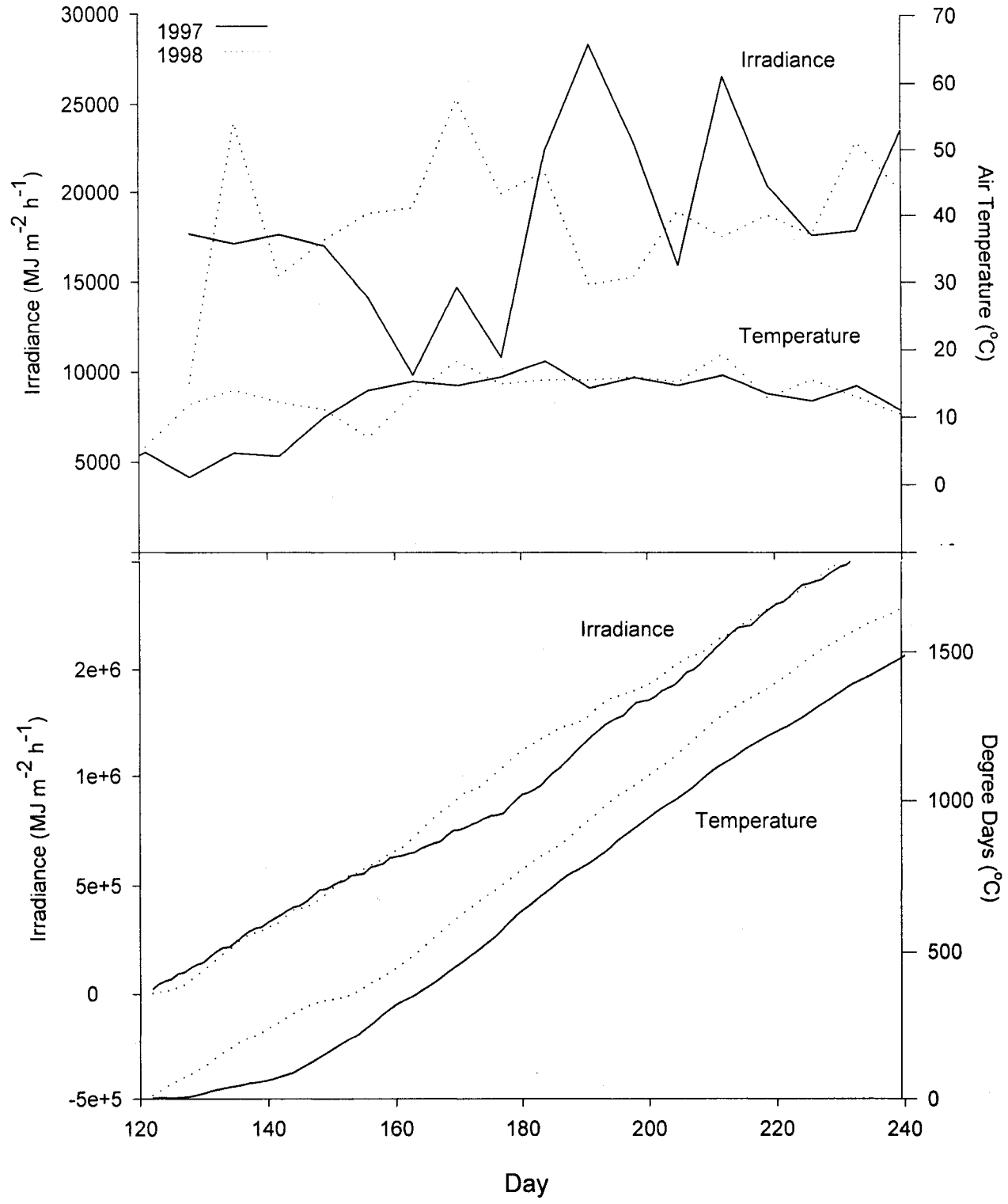
1997
1998
Irradiance
Temperature
Irradiance (MJ m-2 h-1)
Air Temperature (°C)
30000
25000
20000
15000
10000
5000
70
60
50
40
30
20
10
0
Irradiance
Temperature
Irradiance (MJ m-2 h-1)
Degree Days (°C)
2e+6
1e+6
5e+5
0
-5e+5
1500
1000
500
0
120
140
160
180
200
220
240
Day

Figure 4

Figure 5. Depth to which 1000 kJ m^{-2} (PAR) penetrated (m) in each of the five study lakes in 1997 (hatched line) and 1998 (solid line).

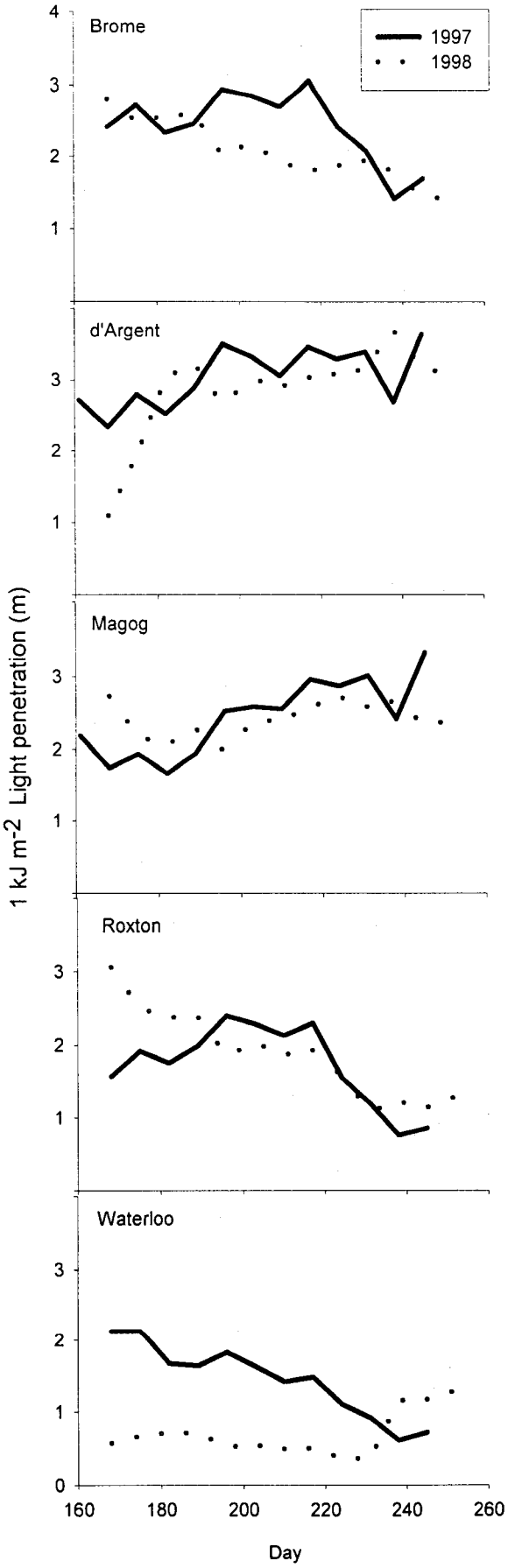
Brome
1997
1998
d'Argent
Magog
Roxton
Waterloo
1 kJ m-2 Light penetration (m)
Day
160
180
200
220
240
260
0
1
2
3
4

Figure 5

Connecting Statement

In the first chapter of this thesis, I analyzed the inter-annual variability in macrophyte biomass and distribution in 5 lakes, between two years. I show that in the warmer year (1998) macrophytes were more abundant, this despite lower mean underwater irradiance levels. These results show both that there is considerable interyear variation in whole lake macrophyte biomass and that the biomass and distribution of submerged macrophytes are susceptible to climate change, further emphasizing the need for ecosystem scale studies on their influence on lake structure and function. The following chapter documents the influence of a large submerged weedbed on water column phosphorus, phytoplankton biomass (chlorophyll *a*), and bacterioplankton production over a growing season using a mass balance approach. The results show that the presence of submerged macrophytes differentially modifies algae and bacteria in the water column, while modestly altering P dynamics over the summer.

CHAPTER 2

Submerged macrophyte bed effects on water column phosphorus, chl *a*, and bacterial production

Abstract

Submerged macrophytes are a major component of freshwater ecosystems, yet their net effect on water column phosphorus (P), algae, and bacterioplankton is not well understood. Here, we describe the results of a 4-month mass balance study that quantifies the net effect of a large (~5.5 ha) undisturbed macrophyte bed on these water column properties. The bed is located in a slow-flowing (0.05 - 0.1 cm sec^{-1}) channel between two lakes, allowing for the quantification of inputs and outputs. The P budget for the study period shows the macrophyte bed to be a small net sink for P (0.06 mg m^{-2} day^{-1}, range from -0.76 to +0.79 mg m^{-2} day^{-1}), demonstrating that loading and uptake processes in the weedbed roughly balance over the summer. Chlorophyll a was disproportionately retained relative to particulate organic carbon (POC), indicating the living component of the POC to be preferentially trapped. In contrast, bacterial production levels were consistently higher in water exiting the weedbed. Simulations based on the specific export of P and bacterial production measured in this study and submerged macrophyte cover in 5 nearby lakes varying in lake morphometry and epilimnetic conditions provide a first indication that the largest littoral zone contribution to the open water is the release of bacterial production rather than the pulse of P released following the late-summer onset of macrophyte senescence. The presence of submerged macrophytes therefore differentially modifies algae and bacteria in the water column, while modestly altering P dynamics over the summer.

Introduction

One of the most important ways in which submerged macrophyte beds influence lake structure and function is through modification of phosphorus (P) cycling (Barko and James 1998), with P being largely accepted as the primary limiting nutrient in pristine north temperate zone freshwater ecosystems (Schindler 1977, Kalff 2001). Two primary goals of studying littoral zone P dynamics are the quantification of the poorly understood influence of weedbeds on whole-lake P cycling and more specifically the linking of these effects on phytoplankton and bacterial dynamics of the water column. Despite considerable effort, the net effect of submerged macrophyte beds on P cycling and water column microbial metabolism remains unresolved.

There is no consensus on whether submerged weedbeds are net sources or sinks of water column P (Granéli and Solander 1988, Barko and James 1998). Submerged macrophyte beds include several types of primary producers (macrophytes, epiphytes, and benthic algae) that derive P from both the water column and sediments, as well as littoral zoobenthos and bacteria that modify P cycling in the littoral (Carpenter and Lodge 1986). The presence of submerged macrophytes further modifies the sediment-water interface, although their net effect on P flux is unclear (Stephen and others 1997). It is clear, however, that weedbed conditions that result in anoxia at the sediment surface result in enhanced P loading rates to the water column (James and others 1996). This comes about through increased sediment bacterial respiration rates resulting from high organic carbon loading in dense weedbeds. Further, factors influencing the net effect of weedbeds on P cycling are highly variable within growing seasons, and change with the

development and senescence of the plants. Weedbeds, therefore, act as both a sink and a source at different periods on a seasonal basis.

Early studies using ^{32}P as a tracer in whole lakes suggested that the littoral zone plays an important role in lake P cycling. Both Hutchinson and Bowen (1947) and Coffin and others (1949) reported ^{32}P in rooted aquatic plants after epilimnetic additions of $^{32}PO_4$. Rigler (1956) added ^{32}P to the epilimnion of macrophyte rich Lake Toussant (Ontario, Canada) and, after measuring loss of epilimnetic P to the hypolimnion, profundal sediments and outflow, inferred that 4% of epilimnetic P was lost to the littoral zone per day for a month after the addition. Despite this transfer, epilimnetic P concentrations did not change significantly, suggesting an exchange of P between the littoral and pelagic zones. Although these studies revealed a link between littoral and pelagic nutrient cycles, they were not designed to address the net effect of littoral communities on open water conditions, or how these effects change during the growing season.

Concerns about nutrient enrichment of lakes, and the finding that submerged macrophytes derive their P overwhelmingly from the rich sediment pool (e.g. Carignan and Kalff 1980) led to studies examining the potential of submerged macrophytes to act as a conduit for P from littoral sediment to the open water (internal loading). The majority of these studies measured rate processes at small spatial and temporal scales, and extrapolated findings to whole weedbed or lake scales. The studies generally concluded weedbeds to be net sources of P to the water column both during active growth (resulting from plant material turnover) and upon senescence of the plants (Prentki and others 1979, Carpenter 1980, Adams and Prentki 1982, Smith and Adams 1986). The

enduring importance of the studies is that they provide insight into the mechanisms of P cycling within the littoral. The predictions from these small scale studies of water column enrichment resulting from submerged macrophyte P release have not, however, been demonstrated in nature.

Mesocosm studies offer a spatial scale of analysis that is small enough to allow manipulation and large enough to contain most major elements of littoral zone. They have been used to compare water column properties of enclosures with and without macrophytes and with few exceptions (e.g. Landers 1982) have shown macrophyte enclosures to have lower abundances of both phytoplankton and bacterioplankton compared to denuded treatments (Schriver and others 1995, Søndergaard and others 1998, Wigand and others 2000). There are, however, not only advantages but also limitations to using the enclosure approach (See Schindler 1998). From a whole lake P cycling perspective, mesocosm work does not consider the import of P from the open water to submerged weedbeds, which occurs through sedimentation of particle associated P in the low energy environment and the uptake of soluble phosphorus (SP) by epiphytes. Moreover, enclosure experiments tend to be carried out over short time periods (days to weeks) so as to not allow conditions to diverge too greatly from natural conditions. Naturally, such experiments cannot reveal the impact of submerged macrophytes on a seasonal scale over which their influence on water column properties are expected to change. Lastly, the manipulations are sufficiently pronounced (e.g. they typically exclude top predators and reduce near shore turbulence) to make it uncertain whether conclusions drawn are valid for the weedbeds as a whole, let alone at larger temporal and spatial scales (Bloesch and others 1988, Schindler 1998).

Observational studies carried out over larger spatial and temporal scales typically report lower phytoplankton biomass in the presence versus the absence of submerged macrophytes. This has been observed over long temporal scales (within lakes among years), and at large spatial scales (among lakes)(Blindow and others 1993, Scheffer and Jeppesen 1998, Søndergaard and Moss 1998). Moreover, submerged macrophytes appear to modify the relationship between total phosphorus (TP) and chlorophyll *a* (chl *a*) in the pelagic zone. Faafeng and Mjelde (1998) note that in shallow, productive Norwegian lakes, chl *a* concentrations were lower in macrophyte-dominated lakes, given similar epilimnetic P concentrations. Similarly, Canfield and others (1984) reported the percentage of the water column infested with macrophytes (PVI) to be a significant negative predictor of epilimnetic chl *a* concentrations, once nutrient levels were accounted for. Although such modifications must influence the bacterioplankton in macrophyte-dominated lakes, large-scale observations of the links among P, phytoplankton, and bacterioplankton are lacking.

Linking nutrient, phytoplankton, and bacterioplankton dynamics in the pelagic zone has been a major goal of limnologists (e.g. del Giorgio and Peters 1994, del Giorgio and others 1999), but studies have largely ignored the influence of the littoral zone on these interactions. There is, however, evidence both from large scale observational work, and smaller scale manipulations that submerged weedbeds augment bacterioplankton production in the pelagic zone. Submerged macrophytes provide labile organic carbon to the open water, both during active growth and upon senescence (Hough and Wetzel 1975, Søndergaard 1981). Dried macrophyte tissue added to mesocosms results in elevated levels of both SP and bacterioplankton production in the water column (Wehr and others

1999). Production rates of bacterioplankton in excess of phytoplankton production have been cited as evidence for the dependence of bacterioplankton on weedbed production (Coveney and Wetzel 1992, Reitner and others 1999). The coincident stimulation of bacterial production and suppression of phytoplankton biomass associated with submerged macrophytes changes the dynamics of the microbial loop, and associated P cycling.

The present paper examines the effect of an undisturbed submerged macrophyte bed on water column P, chl *a* and bacterial growth over the summer using a mass balance approach. Located in a slow, unidirectional flowing body of water between two lakes, the large (~5.5 ha) study site allowed for the quantification at the whole weedbed and seasonal scale of inputs and outputs without modifying the natural environment. We believe that the findings at the scales selected will be useful in interpreting results based on small scale experimental work and on long term observations made at the whole lake scale.

Methods and Materials

Study Site

The site was a mixed species (Myriophyllum spicatum, Potamogeton robinsii, Elodea canadensis) submerged macrophyte bed receiving water from Fitch Lake and exporting water into the north end of Fitch Bay (45°05'N, 72°13'W) in Lake Memphremagog, Quebec, Canada (Figure 1). Fitch Lake is a meso-eutrophic lake with a maximum depth of 5m, a surface area of 1.86 km^2 and a 65 km^2 catchment area that includes an upstream lake (Lake Lovering). The bed, studied between June and October

of 1998, was 800m long, had an average of width 25m , a maximum depth of 2m and a mean depth of ~1m. A previous study used the same site for a mass balance of trace metals in submerged macrophyte beds (Jackson and others 1994).

Hydrological Balance of the study site

Water discharge was measured on each sampling date using a salt dilution technique in a centrally located 50 m stretch of the weedbed (Figure 1). A known amount of NaCl was injected at a point in the channel. Fifty metres downstream, the conductivity was measured every three minutes until the salt pulse passed, and the conductivity returned to pre-injection levels. A plot of salt concentration (relative to background) versus time was integrated, and the discharge calculated as the volume of solution injected divided by the time passage of the tracer pulse. Discharge was used to quantify the mass of materials and process rates entering and leaving the weedbed on each date.

The potential for inputs or dilution along the reach was minimal, as the direct drainage area of the channel was < 2% of the total drainage area of Fitch lake. The bordering land was 75% mixed deciduous and coniferous forest, with minimal cottage shoreline development. Conductivity measurements were taken on each sampling date at three depths, at nine stations along the reach (Figure 1). Conductivity of inflowing water from Fitch Lake (range 105-118 $\mu S\ cm^{-1}$) did not change spatially along the reach, providing further evidence for the absence of a significant lateral input of water and associated nutrients (Figure 2). At the outflow station, conductivity rose as the result of winds forcing water from downstream Lake Memphremagog (conductivity 138-150 μS

cm^{-1}) back into the sampling station (Figure 2). This necessitated a correction for dilution of the measurements made at the outflow site (see below). Mean dilution factors (the percent of water in an outflow sample that originated from downstream of the sampling site) averaged 24% in June, 15% in July, 25% in August, and 43% in September. The lone October sampling date experienced the highest dilution (54%). Water residence time of the bed showed a seasonal pattern, lowest in June, highest during July, and then decreasing again in August. Mean residence time was 13.5 days (range 10-18days). Calculated flow rates varied between 0.05 and 0.1 cm sec^{-1}, no higher than the 0.03 to 0.46 cm s^{-1} (mean 0.07 cm s^{-1}) reported in macrophyte communities elsewhere (Losee and Wetzel 1993). There was a weak, but positive relationship between the extent of Lake Memphremagog water dilution and residence time of the macrophyte bed (r^2 = 0.19, p=0.04).

On two sampling dates (June 21st and August 11th) conductivity and P concentrations were measured at the four sites downstream from the weedbed (Figure 1) to test the method used for correcting dilution factors. The relationship between conductivity and P concentration had r^2 values greater than 0.95 on both dates, showing conductivity to be suitable measure of mixing of downstream and macrophyte bed water.

Sampling

The reach was sampled 17 times between the 12th of June and the 12th of October 1998, averaging once every 8 days. The inflow site was in Fitch Lake, approximately 10 m upstream of the entrance to the macrophyte bed, while the outflow site was located 10

m downstream of the macrophyte bed, but still within the channel (Figure 1). Two 2 litre water samples were taken at a depth of 1m in acid washed opaque nalgene bottles at the two stations. Vertical conductivity measurements (every 0.5m) showed the in and out flowing water to be vertically homogeneous. Samples were taken to the laboratory and processed within 2 hours of collection.

Laboratory analysis

Glassware was acid washed overnight in15% HCl and rinsed three times with distilled water. For each of the variables triplicate samples were analyzed, unless otherwise indicated. Forty ml total phosphorus (TP) sub-samples were taken directly from containers. Water for soluble phosphorus (SP) analysis was filtered through pre-washed Gelman Type A/E filters (42.5mm diameter, mean 0.7 μm nominal pore size), and 40ml sub-samples taken. TP and SP were measured using the ascorbic acid method, following persulfate digestion (Griesbach and Peters 1991). Particulate phosphorus (PP) was obtained by difference.

Water for chl *a* analysis (200-400ml) was filtered onto Gelman Type A/E filters (42.5mm) and frozen. Chl *a* was extracted in 95% ethanol, and measured spectrophotometrically according to Bergmann and Peters (1980). Particulate organic carbon (POC) samples of 300 ml were filtered onto pre-combusted Gelman Type A/E filters (21mm), and dried at 85°C until a constant weight was achieved (approximately 48 hours). Filters were combusted at 425 °C for 4 hours to determine loss on ignition as an estimate of organic content.

A modification of the ^{3}H-Leu incorporation was used for the estimation of bacterial production (Smith and Azam 1992). Leucine incorporation was related to bacterial production as per Kirchman (1993);

$$\mathrm{Pr}oduction = Leu \times 131.2 \times (\%Leu)^{-1} \times (C/\mathrm{Pr}otein) \times ID \qquad (1)$$

where Leu is the rate of leucine incorporation (mol L^{-1} hr^{-1}), 131.2 is the formula weight of leucine, % Leu is the estimated fraction of leucine in protein (0.073), C/Protein is the estimated ratio of cellular carbon to protein (0.86), and ID is the estimated isotope dilution (2)(Smith and Azam 1992).

TP, SP, chl *a*, POC, and bacterial production were measured in Lake Memphremagog on three dates. As there were no significant differences found among the three dates, mean values were used in the calculations. Multiplying the difference between inflow and outflow (μg L^{-1}, or μg L^{-1} day^{-1}) by the discharge (L day^{-1}), correcting for dilution by Lake Memphremagog water yielded net export as follows:

Inflow: $$[X] \times Q \times 8.64 \times 10^{7} \qquad (2)$$

Outflow: $$\frac{[X] \times Q \times 8.64 \times 10^{7}}{[X_{Mem}] \times DF} \qquad (3)$$

where [X] is the volumetric value of the variable, Q is discharge (l sec^{-1}), 8.64 x 10^7 is a conversion constant, [x_{mem}] is the mean volumetric value of the variable in Lake Memphremagog (Table 1), and DF is the dilution factor calculated based on conductivities of Fitch Bay, Lake Memphremagog, and the outflow station. Paired inflow and outflow samples took into account the residence time of the macrophyte bed. Date versus value curves were integrated over the study period for each variable (TP, SP, chl *a*, POC, and bacterial production) at inflow and outflow stations. The difference between the integrated values was taken as the net effect of the weedbed on each variable over the study period.

Aboveground macrophyte biomass

In early August, six stations along the reach were sampled for the aboveground macrophyte biomass. Six randomly placed quadrats (0.25 m^2) were harvested by a SCUBA diver at each station. Plants were processed within 2 days. Roots were pinched off, and plants washed free of loose epiphytes, sediment and invertebrates. Plants were then spun in a lettuce spinner to remove excess water before being weighed to the nearest 0.1 g.

Statistical analysis

The means and standard deviations of inflow and outflow values were determined. Inflow and outflow chl *a* and TP were analyzed in two ways. First, chl *a* : TP ratios in the inflow and outflow were compared using paired-sample t-test. Second, we calculated the running correlation coefficients for inflow vs. outflow chl *a* : TP ratios

for 5-sample intervals over the course of the season, yielding 13 correlation coefficients. These were plotted against time, yielding a pattern of correspondence between inflow and outflow ratios.

Results

The mean aboveground wet weight macrophyte biomass was 700 g m^{-2} wet weight (SE = 180) in early August. Extrapolation yielded a biomass estimate of of 3.82 x 10^4 kg (wet weight) of macrophytes (SE = 5.99 x 10^2) in the reach. Submerged macrophytes in Lake Memphremagog have P contents between 0.22 and 0.50% (mean, 0.31%, measured between June and September) (Carignan and Kalff 1982). Consequently, the reach held between 12 and 27 kg P in aboveground tissue at the time of macrophyte sampling.

Mean water column attributes are given in Table 1. The water flowing into the reach is moderately P rich, and has chl *a* values characteristic of mesotrophic lakes. When concentrations were converted to net seasonal fluxes, the weedbed was a net sink for all materials (SP, PP, chl *a*, and POC) in the water column, although it retained the materials differentially. When expressed as percentage, the bed retained chl *a* > SP > POC > PP over the growing season (Table 2). Of the P retained, over 75% was SP. In contrast, bacterial production rates were higher in the exiting waters, with summed production rates more than double those entering (Table 2).

The weedbed modified the PP and SP levels differently. Most of the SP was retained in September, whereas PP was retained during July, followed by an export peak late August (Figure 3a). The net export of bacterial productivity occurred

overwhelmingly during August and roughly corresponded to the period of greatest PP export (Figure 3b).

Since the outflowing chl *a* concentrations varied little over time (mean=21.1, SD=4.8), the pattern of algal biomass (chl *a*) retention was driven by incoming concentrations, with the two well correlated over time ($r = 0.77$, $p < 0.001$). Algal biomass retention was highest in early and late summer, corresponding to the highest chl *a* concentrations of the inflowing water (Figure 3c). The pattern of POC export was similar to that of chl *a*, with most sampling dates showing the weedbed to be a sink for POC.

The yield of chl *a* per unit TP was significantly lower in outflowing than inflowing water (paired t-test $p < 0.01$). Variation within the study period followed a seasonal pattern (Figure 4a). The running correlations between inflow and outflow chl *a* : TP ratios were highly positive at the beginning and the end of the study period, indicating little effect of the macrophyte bed on the yield of chl *a* per unit phosphorus during the two periods. However, during the period of maximum macrophyte biomass there was a strong negative correlation between inflow and outflow ratios, with the inflow chl *a* : TP ratios increasing at a time when ratios in the outflowing water were declining (Figure 4b).

Discussion

The mass balance revealed the macrophyte bed to have a negative, but quite small effect on water column P (Table 2). The net TP summer retention (0.06 mg m^{-2} day^{-1}, range from -0.76 to +0.79 mg m^{-2} day^{-1}) was minor compared to estimates of P cycling in

such beds, indicating that processes of P loading and uptake are offsetting in macrophyte beds both within growing seasons and summed over the 4-month period (Table 3). These findings are in agreement with the only other similar nutrient mass balance study on a macrophyte bed conducted in an agricultural drainage ditch that found a negligible change in water column nutrient levels associated with the macrophyte presence (Hill 1986, Table 3). The small net retention by the two beds stands in contrast to orders of magnitude higher P cycling rates reported in the literature (Table 3).

Extrapolating from work on epiphyte production per unit macrophyte in Lake Memphremagog (Cattaneo and Kalff 1980), and assuming an epiphyte C:P molar ratio of 105:1, the epiphyte uptake rate of soluble phosphorus (SP) in the bed in midsummer (August 11th, 12 mg m^{-2} day^{-1}) is roughly 50 times greater than the amount entering the bed on that date. Similarly, the SP demand on the same date is high in comparison to the total calculated SP pool in the bed (19 mg m^{-2}), implying that about 63% of the SP was removed daily from the water, and that SP pool turnover time is on the order of 1.6 days. It is further evident from work on actively growing macrophytes in Lake Memphremagog (Carignan and Kalff 1982) that P release by is quite insufficient to supply the needed P to epiphytes (Table 3). An estimated macrophyte P release of only 0.37 mg m^{-2} day^{-1} (based on 700 g wet weight m^2) would provide roughly 3% of the daily epiphyte P demand, with the balance satisfied through rapid P recycling within the epiphytic biofilm (Riber and Wetzel 1987) and further supplemented by considerable P release from the sediments (Table 3).

Although the calculated P recycling rates within the bed were huge compared to the P input, the net weedbed P retention (input-output), which ultimately allows for the recycling, was but a small fraction of the annual P retention computed on the basis of long-term (~115 yr) sediment cores (Table 3). Annual P, sediment, and trace metal accumulation rates are a function of macrophyte biomass in Lake Memphremagog (Benoy and Kalff 1999, Rooney and others *in prep.*). Based on the average 700 g m^{-2} (above ground wet weight) of macrophyte biomass in the reach, we calculated an annual P accumulation rate between 88 and 179 mg P m^{-2} yr^{-1}, which when converted to mean daily retention is 4-8 times greater than measured by mass balance during the growing season (Table 3). The reasons and mechanisms responsible for the large discrepancy cannot be resolved here, but the data support the hypothesis that over-wintering plants serve as an effective trap outside the growing season not only for sediments, but also for P (Wetzel 1990, Wetzel and Søndergaard 1998). Further, the potential for P loading through particle deposition in weedbeds would be highest during spring runoff in the spring. Significant relationships exist between particulate phosphorus and discharge in headwater streams in Lake Memphremagog catchments (Prairie and Kalff 1988) and mean discharge values for the Clyde River (Newport, Vermont) flowing into Lake Memphremagog were, on average, four fold higher in April compared to the four months study period (USGS 1998).

In contrast to the small net retention of P during the summer, the biomass of algae (chl *a*) leaving the weedbed was much lower than entering over the summer period (Table 2). This pattern has been observed in other studies, and a number of plausible

explanations have been proposed (See Søndergaard and Moss 1998). Whatever the reason, the approximately two-fold greater retention of algal biomass compared to particulate organic carbon (POC, Table 2) composed of living and dead material indicates that the living component of the POC is much more effectively retained, probably through removal by zooplankton (Jeppesen and others 1998) and the abundant filter feeding unionid clams present in the weedbed (N. R. personal observation).

That phytoplankton-P relationships observed in pelagic zones become de-coupled in the littoral when currents move water and particles through large weedbeds is evident from a smaller retention of P (especially particulate phosphorus, PP) than algal particles, with the mean summer yield of chl *a* per unit P being 27% higher in inflowing than in outflowing water (paired t-test, $p=0.03$). Equivalent findings have been made in European lakes where those with extensive macrophyte beds have a lower phytoplankton biomass than predicted on the basis of water column TP (Blindow and others 1993, Scheffer and others 1993, Faafang and Mjelde 1998). Even so, the influence of the weedbed was not constant over the summer. Modification of chl *a* : TP ratios is greatest in mid-summer, the period corresponding to highest macrophyte biomass (Jackson and others. 1994), whereas ratios in inflowing and outflowing waters are similar in early and late summer (Figure 4).

The export of bacterial production was double that entering the macrophyte bed over the summer (Table 2). Although the bacterial abundance samples were unfortunately lost, the literature shows a coupling of bacterial production and biomass

(White and others 1991), making it clear that the macrophyte bed is a significant source of bacterial biomass and production to the open water, especially during late summer when macrophyte growth ends and the plants enter a period of high released of soluble material, including metals (Jackson and others 1994). The results provide support to literature findings of a greater bacterioplankton metabolism near or in the littoral zone than in the pelagic zone (Carpenter and others 1979, Murray and Hodson 1986, Güde 1990). Interestingly, the observed increases in bacterioplankton metabolism emanating from macrophyte beds in open systems are not seen in mesocosms when bacterial metabolism rates in macrophyte-colonized and bare-sediment mesocosms are compared (Tulonen and others 1996, Søndergaard and others 1998, Wigand and others 2000). Enclosure effects may be responsible for the discrepancies, quite possibly the outcome of a reduced turbulence and associated reduced release of macrophyte and sediment associated microbes. Further, the elimination of an external supply of nutrients, algal carbon, and bacteria could reduce levels of bacterioplankton, favouring surface associated microbes in the enclosures.

Even during the late summer period of greatest P export from the macrophyte bed (August 11th to August 29th) the net P export (Figure 3a) represented only 2-5% of the above-ground macrophyte P stock. If the present results reflect a greater generality, the largest littoral zone contribution to the open water during summer is the release of bacteria and bacterial production rather than the pulse of P released in late summer. By simulating the effect of P and bacterial production exported from the vegetated littoral zone during the peak exports for each (between August 11th and August 21st for P,

between August 29th and September 4th for bacterial production), we provide estimates of the late summer daily percent increase of both variables in the epilimnia of 5 nearby Township lakes (Table 4). These lakes represent a large range of morphometry, macrophyte colonization, and epilimnetic water properties. While projected daily subsidies of weedbed derived P to the epilimnetic pool never exceeded 1% per day, increases of up to 20% per day were projected for epilimnetic bacterial production in a clear-water, macrophyte dominated lake (Table 4).

The macrophyte bed served as a net trap for algal biomass but as a source of bacterial production to the open water during summer, while having a small influence on net P cycling. The overlapping peaks in late summer P export and bacterial production in the outflowing water point to an increase in the release rate of not only dissolved metals (Jackson and others 1994) but also of phosphorus, some of which is converted to bacterial protoplasm before being exported from the littoral zone. The hypothesis that macrophyte derived P stimulates bacterial production is supported by the literature. Small (< 1 mg l^{-1}) additions of macrophyte derived carbon to lake mesocosms results in significantly higher bacterioplankton growth rates and phosphorus levels when compared to controls and algal additions (Wehr and others 1999). It appears, therefore, that the presence of macrophyte beds change P dynamics such that energy flow is preferentially routed through the bacterioplankton.

In conclusion, the study shows that the incoming P trapped by the ~5.5 ha submerged macrophyte bed is almost balanced by export over the summer. Interestingly,

the phosphorus retained and accumulated in the macrophyte bed over the study period is only a small fraction of the annual P accumulation measured in Lake Memphremagog beds of similar biomass. The discrepancy is too large to be ascribed to experimental error and raises unanswered questions as to when and how the additional P measured in dated sediment cores is accumulated. Algal biomass (chl *a*) is much better retained in the bed during the growing season than POC, which includes presumably less-palatable (more recalcitrant) detritus component. Overlapping August peaks in PP export and bacterial production that occurred at the same time as a peak in the release of soluble trace metals measured in an earlier study (Jackson and others. 1994) suggests that the onset of macrophyte senescence is associated with leakage of soluble material from plants followed by enhanced bacterial production. This enhanced production appears to be of greater consequence to the open water than the aforementioned export of P from submerged macrophyte beds.

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Table 1. Mean inflow, outflow and Lake Memphremagog measurements (standard deviation in parentheses) over the course of the study period.

Variable	Mean In	Mean Out	Lake Memphremagog
Soluble Phosphorus ($\mu g\ l^{-1}$)	8.8 (4.1)	9.1 (3.4)	3.0 (0.1)
Particulate Phosphorus ($\mu g\ l^{-1}$)	15.8 (6.7)	16.8 (8.8)	10.0 (0.5)
Chlorophyll a ($\mu g\ l^{-1}$)	25.8 (10.9)	20.0 (9.9)	5.0 (0.3)
Particulate Organic Carbon ($mg\ l^{-1}$)	1.2 (0.3)	1.1 (0.4)	0.24 (0.02)
Bacterial production ($\mu g\ C\ l^{-1}\ day^{-1}$)	12 (18)	45 (68)	1.8 (0.1)

Table 2. Total seasonal import, export and retention from the Fitch Bay study reach determined by mass balance calculations.

Variable	Import	Export	Retention	Difference as % of Import
Soluble Phosphorus (g)	1692	1428	-265	-16
Particulate Phosphorus (g)	2659	2576	-83	-3
Chlorophyll *a* (g)	4663	2851	-1813	-39
Particulate Organic Carbon (kg)	221	187	-34	-15
Bacterial production (g C day^{-1})	3710	7670	3960	+107

Table 3. Summary of literature data on littoral P cycling and scale of study. Positive numbers indicate P loading to the water column, whereas negative numbers indicate removal of P from the water column. Biomass specific rates (*) are based on a mean weedbed biomass of 700 g m^{-2} (wet weight).

Process	Reference	Scale		Rate	
		Temporal	Spatial	mg P m^{-2} day^{-1}	
P release by actively growing macrophytes*	Carignan and Kalff 1982	12-30 hours	10 Plants in 1 weedbed	0.37	
P release from vegetated sediment	Andersen and Ring 1999	35-65 days	6 cores from 1 site in lake	Oxic	Anoxic
				1.3-2.5	7.2-9. 8
	James and others 1996	7-14 days	3 sites in lake	Oxic	Anoxic
				3.4-26.4	23.0
	Stephen and others 1997	16 hours	4 lakes, 6 cores per lake	~8 - 16	
Epiphyte uptake*	Cattaneo and Kalff 1980	5 months	10 sites in 1 lake	-12.5	
Sediment accumulation	Moeller and Wetzel 1988	~150	6 cores in 1 lake	-0.10	
	Rooney and others *in prep.*	~115 years	10 cores in 1 lake	-0.24 - -0.49	
	James and Barko 1997	18 years	55 cores in 1 reservoir	-21.9	
	Sand-Jensen 1998	3 months	6-18 beds in 4 streams	37.8 - 272.2	
Net Total Phosphorus Retention	Hill 1986	Growing season	1 Agricultural drainage ditch	< -0.001	
	Present Study	June-October	1 Weedbed	-0.059	

Table 4. Results of simulations estimating the contribution of macrophyte bed derived phosphorus and bacterial production to the epilimnia of 5 Eastern Township, Quebec, Lakes. Observed values of TP ($\mu g\ l^{-1}$) and bacterial production ($\mu g\ C\ l^{-1}\ day^{-1}$) are based on mean values for 5-7 samples taken in the summer of 1998. Macrophyte bed contributions were based on late summer exports of 0.59 mg P $m^{-2}\ day^{-1}$ and 0.45 mg C $m^{-2}\ day^{-2}$ for TP and bacterial production respectively determined in the Fitch Bay macrophyte bed, and extrapolated to the area colonized by submerged macrophytes in the other lakes.

				Observed Epilimnetic Values		Predicted Epilimnetic % increase day^{-1}	
Lake	Area (ha)	Percent Colonized	Epilimnetic Volume (m^3)	TP	Bacterial Production	TP	Bacterial Production
Waterloo	150	11	4.40×10^6	56	37.7	0.04	0.5
Brome	1417	18	8.16×10^7	21	12.0	0.09	1.2
Magog	927	19	5.79×10^7	19	6.6	0.10	2.1
d'Argent	108	28	3.79×10^6	16	9.6	0.30	3.8
Hertel	29	66	1.09×10^6	11	3.9	0.93	20.1

Figure 1. Map of the study site showing inflow sampling site in Fitch Lake and outflow sampling site flowing into Lake Memphremagog. Stations sampled for conductivity measurements used to characterize the hydrology of the site are shown with black circles. The outer edges of the macrophyte bed are denoted by a dashed line. The stretch of the site where discharge was measured is highlighted in the middle of the site.

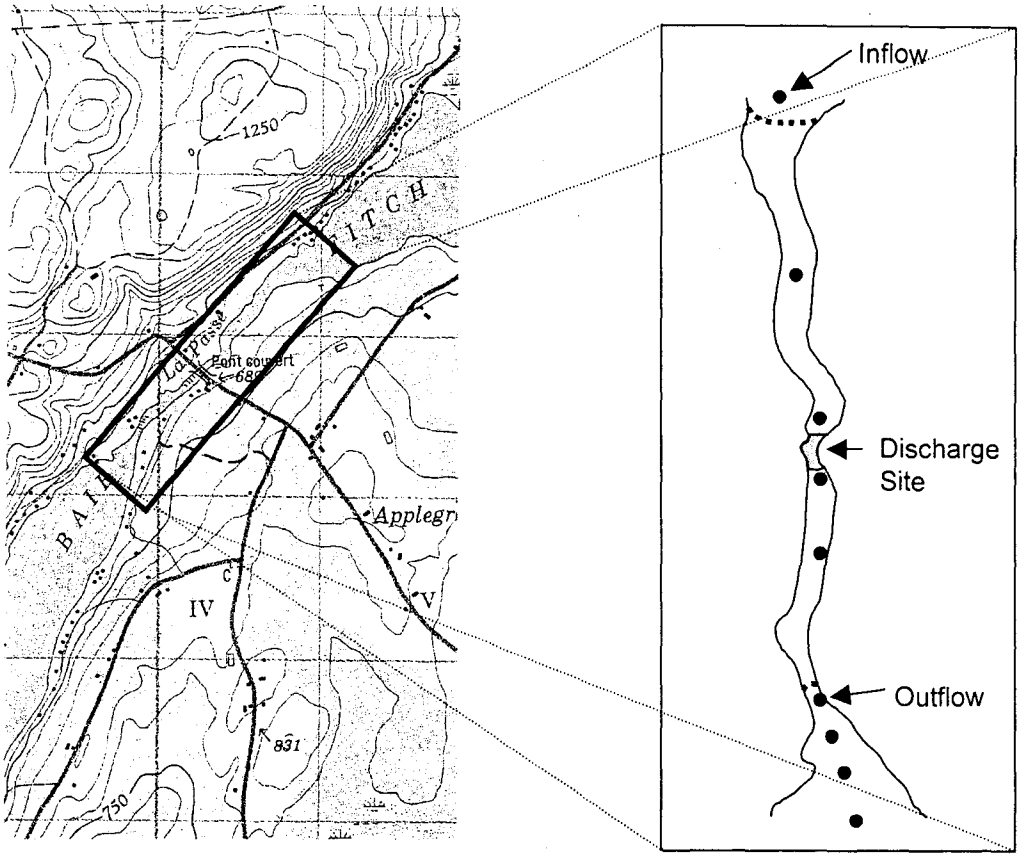
1250
ITCH
Applegr
IV
V
831
750
Inflow
Discharge
Site
Outflow

Figure 1

Figure 2. Mean (± 1 standard error) conductivity measurements at nine stations. Inflow and outflow stations are highlighted. The hatched bar shows the presence of submerged macrophytes.

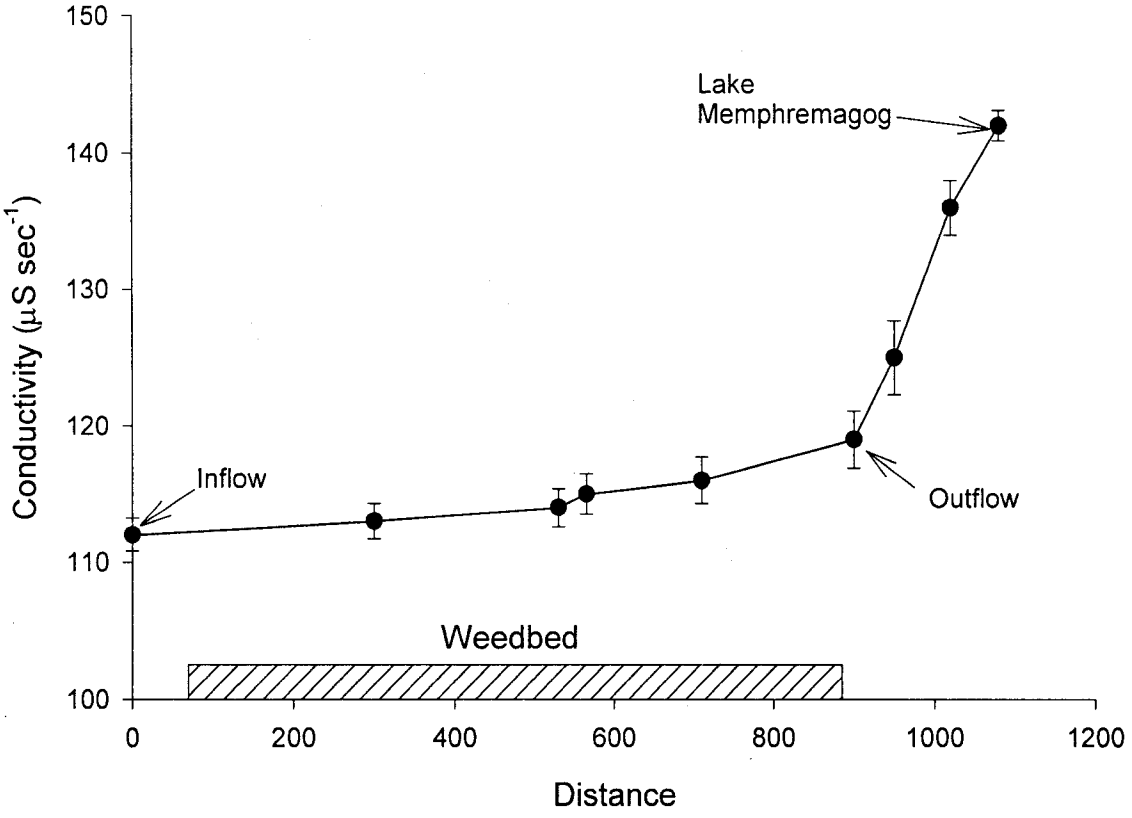
150
140
130
120
110
100
Conductivity (µS sec-1)
Lake
Memphremagog
Inflow
Outflow
Weedbed
0
200
400
600
800
1000
1200
Distance

Figure 2

Figure 3. Net export of a) phosphorus (SP and PP); b) bacterial production; c) chlorophyll *a* , and d) particulate organic carbon from June to October for Fitch Bay, Quebec as determined by mass balance.

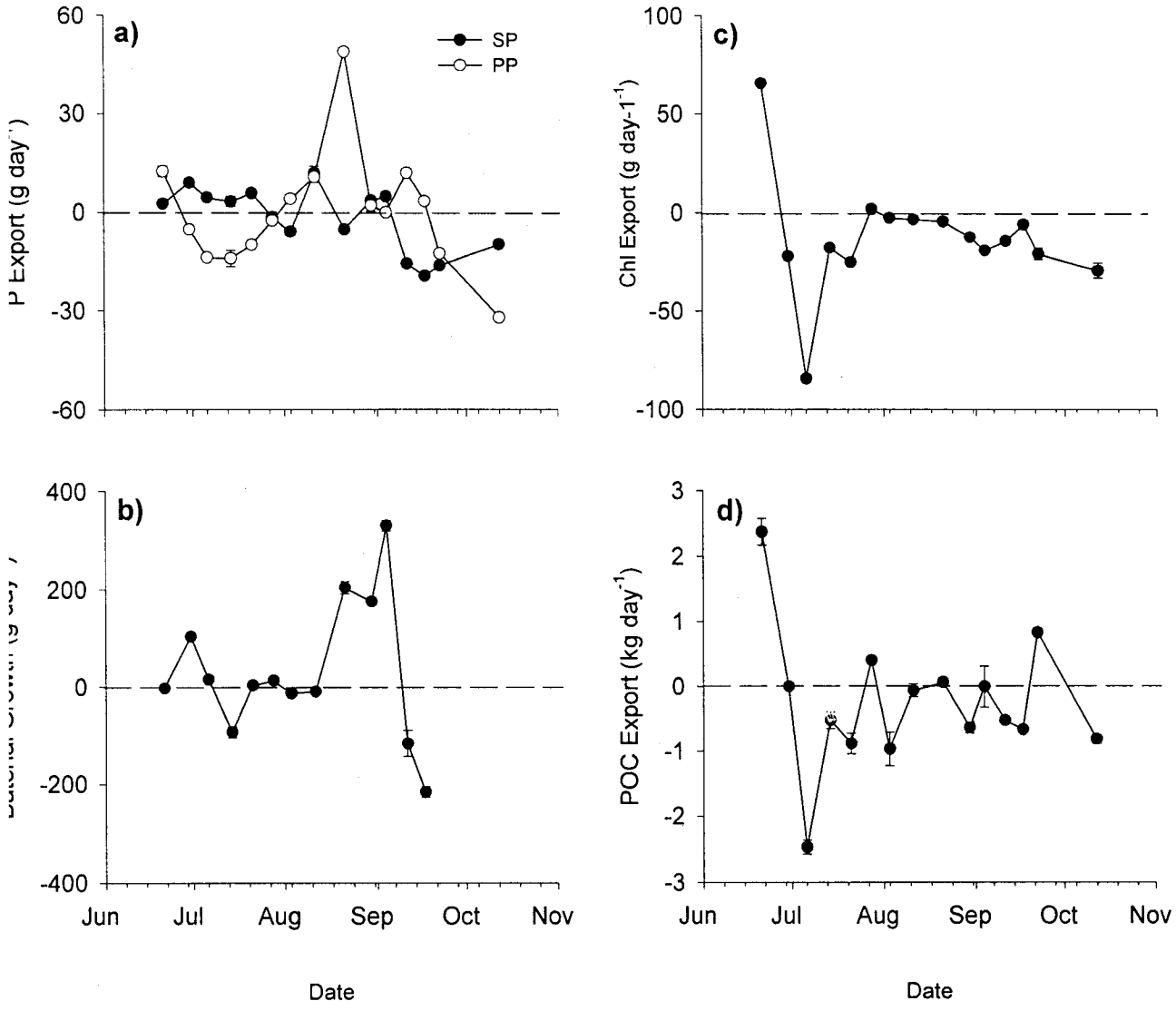
a)
SP
PP
60
30
0
-30
-60
c)
100
50
0
-50
-100
Chl Export (g day-1-1)
b)
400
200
0
-200
-400
d)
3
2
1
0
-1
-2
-3
POC Export (kg day-1)
Jun
Jul
Aug
Sep
Oct
Nov
Date
Date

Figure 3

Figure 4. a) Chlorophyll : TP ratios of samples taken at the inflow (black circles) and outflow (open circles) of the weedbed. b) Running 5-sample correlations coefficients (r) for inflow vs. outflow chl *a* : TP relationships (black circles) over the course of the study period.

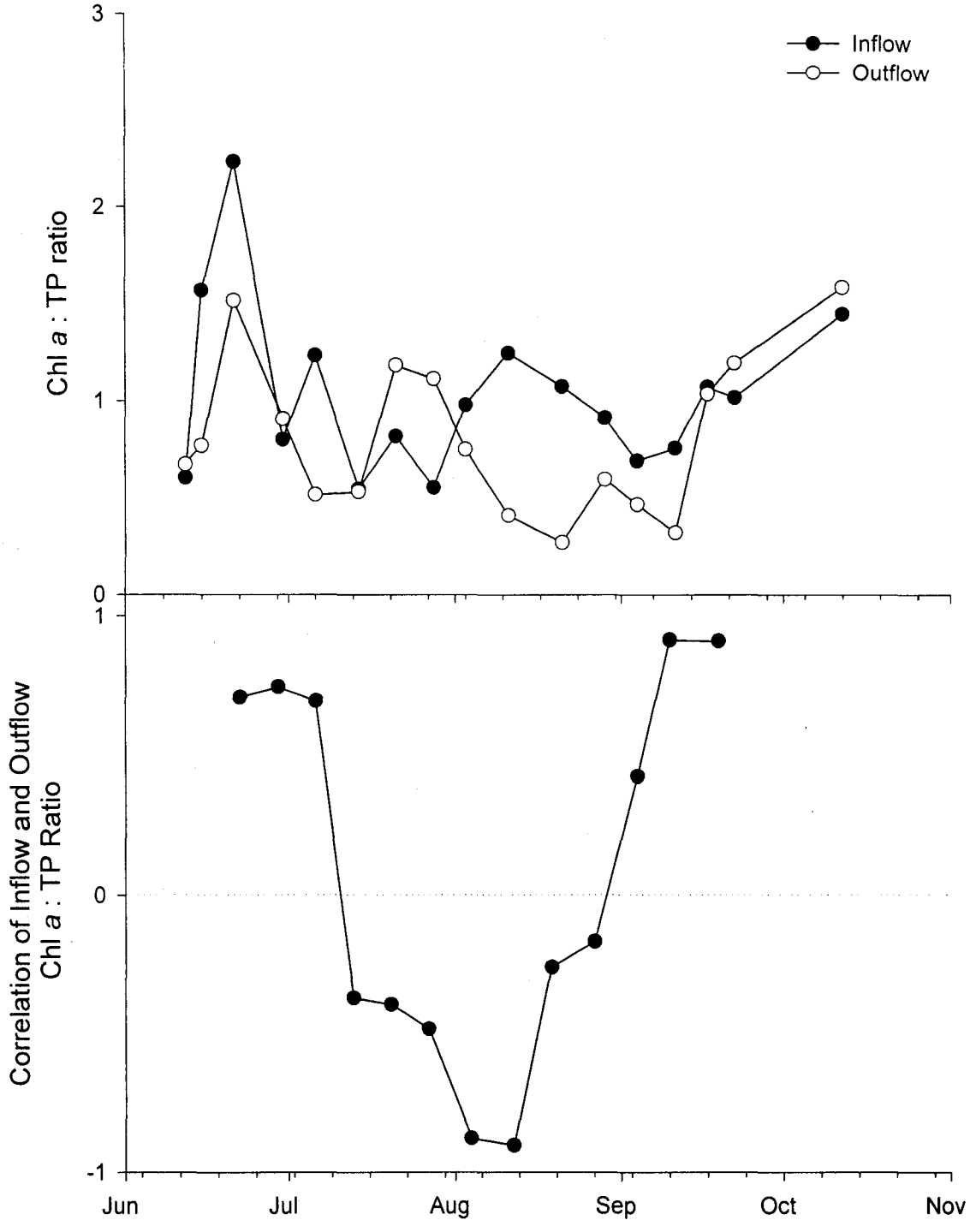
Inflow
Outflow
Chl a : TP ratio
3
2
1
0
Correlation of Inflow and Outflow
Chl a : TP Ratio
1
0
-1
Jun
Jul
Aug
Sep
Oct
Nov

Figure 4

Connecting Statement

In the preceding chapter, I quantified the influence of a large submerged macrophyte bed on water column phosphorus, phytoplankton biomass (chlorophyll *a*), and bacterioplankton production. Integrated over the summer, the weedbed had a net negative influence on phytoplankton biomass while increasing bacterioplankton production on the whole. The net growing season effect of the weedbed on phosphorus was modest, although a late summer peak in phosphorus export from the weedbed roughly corresponded to an increased export of bacterioplankton production from the system. Chapter 3 examines the relationships among epilimnetic phosphorus, phytoplankton biomass and bacterioplankton metabolism at a larger spatial scale (among lakes). Specifically, I test the hypotheses that phytoplankton biomass decreases with respect to epilimnetic phosphorus concentration and that plankton metabolism (respiration and bacterial production) increase with respect to phytoplankton biomass across a series of 9 lakes ranging from 0% to 66% of their sediment covered by submerged macrophytes.

CHAPTER 3

Interactions among epilimnetic phosphorus, phytoplankton biomass and bacterioplankton metabolism in lakes of varying submerged macrophyte cover

Abstract

The effect of submerged macrophytes on interactions among epilimnetic phosphorus, phytoplankton, and heterotrophic bacterioplankton has been acknowledged, but remains poorly understood. Here, we test the hypotheses that phytoplankton biomass decreases with respect to epilimnetic phosphorus concentration, and that planktonic respiration and bacterioplankton production increase with respect to phytoplankton biomass in nine lakes ranging from 0% to 66% of their sediment covered by submerged macrophytes. Increased macrophyte cover was associated with a lower fraction of particulate phosphorus in epilimnia, declining from over 80% of total phosphorus in a macrophyte free lake to less than 50% in a macrophyte dominated lake. Phytoplankton biomass (chlorophyll *a*) too was lower in macrophyte dominated lakes, despite relatively high levels of soluble phosphorus. Planktonic respiration and bacterioplankton production were higher in macrophyte rich lakes than would be expected from phytoplankton biomass alone, pointing to a subsidization of bacterioplankton metabolism by macrophyte beds at the whole lake scale. The results show that the classical view of pelagic interactions that proposes phosphorus determines phytoplankton abundance, which in turn determines bacterial abundance through the production of organic carbon, becomes less relevant as macrophyte cover increases.

Introduction

Phosphorus, phytoplankton and heterotrophic bacteria interact in the epilimnia of lakes to determine the flow of energy and the biogeochemical pathways at the base of pelagic food webs. Limnologists have traditionally studied these epilimnetic interactions with no reference to the presence of submerged macrophytes. There is, however, growing evidence that, at least in the shallow lakes that dominate the landscape worldwide, high levels of littoral production influences epilimnetic metabolism and phosphorus cycling.

Observations at a number of spatio-temporal scales have linked the presence of submerged macrophytes to lower levels of phytoplankton biomass. Mesocosm studies consistently report lowered phytoplankton biomass in the presence of submerged vegetation (Schriver et al., 1995; Wigand et al., 2000). In Lake Veluwemeer, Netherlands, water clarity is greater within dense stands of *Chara* than in the turbid pelagic area (Van den Berg et al., 1998). The phenomenon of alternative stable states, in which a single lake switches between a clear water state with dense vegetation and a turbid water state dominated by phytoplankton, shows the negative relationship between submerged macrophytes and phytoplankton among growing seasons (Jeppesen et al., 1990; van Donk et al., 1990; Scheffer et al., 1993). Finally, among lakes, water column transparency is greater than expected, based on water column phosphorus concentrations in lakes dominated by submerged macrophytes (Jeppesen et al., 1994; Faafeng & Mjelde, 1998). These studies demonstrate the negative effect of submerged macrophytes on phytoplankton biomass.

The net influence of submerged macrophytes on phosphorus dynamics is, however, less obvious than on phytoplankton biomass. While dense macrophyte beds can influence sediment redox conditions enough to increase sediment phosphorus release (James & Barko, 1991; James et al., 1996) the same plants also increase phosphorus accrual by dampening current and wave energies, increasing sedimentation and decreasing resuspension of particle associated phosphorus (Moeller & Wetzel, 1988; James & Barko, 1997; Rooney et al. *in prep.*). Comparative studies linking epilimnetic phosphorus concentrations and patterns of macrophyte colonization are unfortunately lacking, but it is evident that macrophytes thrive in lakes with low phytoplankton concentrations even at high phosphorus concentrations (Timms & Moss, 1984; Mjelde & Faffeng, 1997). Further, percent of lake volume infested with macrophytes (PVI) has been shown to explain residual variation in phosphorus – chlorophyll relationships in Florida lakes (Canfield et al., 1984). It appears therefore, that there is an interaction between phytoplankton and phosphorus that is dependent on macrophyte cover and that phosphorus cycling in shallow lakes may be better interpreted taking into account both macrophytes and phytoplankton.

Limnology has traditionally coupled bacterial and phytoplankton productivity in the epilimnia of lakes, the assumption being that bacterioplankton depend almost exclusively on phytoplankton derived organic carbon (DOC) for metabolism (Cole et al., 1988). That the ratio of phytoplankton production to planktonic respiration is below unity in oligotrophic lakes has, however, led researchers to implicate allochthonous sources of organic matter in bacterioplankton metabolism (delGiorgio & Peters, 1993). In lakes dominated by submerged macrophytes, littoral sources of dissolved organic

carbon (which are allochthonous to the epilimnion) have the potential to decouple phytoplankton-bacterioplankton relationships (Jeppesen et al., 1992; Pace, 1993) because submerged macrophytes serve as an important source of DOC, increasing bacterioplankton metabolism (Hough & Wetzel, 1975; Carpenter et al., 1979; Wehr et al., 1999). Submerged macrophytes, therefore, influence bacterioplankton metabolism directly through a supply of DOC to the epilimnion and indirectly by suppressing phytoplankton biomass. Even so, the combined impact of macrophyte beds on phytoplankton biomass and bacterioplankton metabolism has not been demonstrated at the whole lake scale.

Most studies mentioned above have drawn conclusions based on comparisons between macrophyte-free and macrophyte-dense areas, whether in enclosures or individual weedbeds. It has been unclear whether the patterns observed are detectable at the whole lake scale. Here, we report the results of a study that examines mean summer epilimnetic phytoplankton biomass (chl *a*), planktonic respiration, bacterioplankton production, and phosphorus concentrations in 9 lakes of lakes varying widely in submerged macrophyte cover. Specifically, we test the following hypotheses; 1) that phytoplankton biomass declines with respect to phosphorus concentration in macrophyte dominated lakes, and 2) that both epilimnetic respiration and bacterioplankton production increase with respect to phytoplankton biomass in macrophyte dominated lakes.

Methods and Materials

Field work was conducted in 9 lakes in the Eastern Townships region of southern Quebec, Canada (45°18'N, 72°15'W). Each lake was visited seven times between the

18th of June and 25th of September, 1998. Pelagic zone thermal profiles were measured to determine the mixed layer depth. Water samples were taken using an integrated tube incorporating the whole epilimnion. Acid washed opaque sampling containers were rinsed three times with sample water. Samples were stored in opaque bottles, and brought to the laboratory within 4 h of collection.

Laboratory analysis

Glassware was acid washed overnight in 15 % HCl and rinsed three times with distilled water. For each of the variables triplicate samples were analyzed, unless otherwise indicated. Forty ml total phosphorus (TP) sub-samples were taken directly from containers, and water for soluble phosphorus (SP) was filtered through pre-washed Gelman Type A/E filters (42.5mm diameter, mean 0.7 μm nominal pore size), and 40ml sub-samples taken. TP and SP were measured using the ascorbic acid method, following persulfate digestion (Griesbach & Peters, 1991). Particulate phosphorus (PP) was obtained as the difference between TP and SP.

Water for chl *a* analysis (200-400ml) was filtered onto Gelman Type A/E filters (42.5mm) and frozen. Chl *a* was extracted in 95% ethanol, and measured spectrophotometrically according to Bergmann and Peters (1980).

Planktonic respiration was measured as the decrease in oxygen concentration within the water samples per unit time. For each sample and date, six 60 ml bottles were filled, ensuring that the bottles were flushed at least three times each with sample water. Three were randomly chosen and measured immediately as initial oxygen controls and three were incubated at 18°C for 22-28 hours, and then assayed for oxygen concentration.

Dissolved oxygen concentrations were measured using a modification of the Winkler technique on a Metler Toledo DL-21 titrator.

A modification of the ^{3}H-Leu incorporation was used for the estimation of bacterial production (Smith & Azam, 1992). Six replicates and three blanks were used for estimates of bacterial production. Leucine incorporation was related to bacterial production as per Kirchman (1993);

$$\mathrm{Pr}oduction = Leu \times 131.2 \times (\%Leu)^{-1} \times (C/\mathrm{Pr}otein) \times ID \qquad (1)$$

where Leu is the rate of leucine incorporation (mol L^{-1} hr^{-1}), 131.2 is the formula weight of leucine, % Leu is the estimated fraction of leucine in protein (0.073), C/Protein is the estimated ratio of cellular carbon to protein (0.86), and ID is the estimated isotope dilution (2)(Smith & Azam, 1992).

Macrophyte colonization was quantified in mid August 1998. Ten to fourteen sites per lake were selected so as to maximize the differences in underwater sediment slope and site exposure, the principal determinants of submerged macrophyte biomass (Duarte & Kalff, 1986). At each site, six echosound transects were taken perpendicular to the shore to establish the maximum depth of macrophyte colonization (Z_c), which is easily distinguished from bare sediment on the echosounder printouts. Mean weedbed length was calculated from the length of the echosound printouts, transect time and boat speed (determined from a GPS unit).

Percent lake area colonized (% macrophyte cover) was calculated based on the length of the weedbeds, Z_c and bathymetric maps of each lake. Weedbed lengths were superimposed on bathymetric maps, and the area colonized was estimated by interpolating the extent of colonization among the beds along bathymetric contours.

Summer mean and standard error values were calculated for all epilimnetic variables. Relationships between macrophyte cover (%) and epilimnetic ratios were modeled using of linear regression analysis.

Results and Discussion

The lakes displayed a wide range of macrophyte cover and summer mean epilimnetic variables (Table 1). Correlation analysis including all sampling dates showed significant negative relationships between macrophyte cover (%) and epilimnetic variables (Table 2), with reduced phosphorus (both soluble and particulate), algal biomass, and planktonic respiration as macrophyte cover (%) increased. This finding is in agreement with the hypothesis that there is a switch from planktonic metabolism to dominance by littoral metabolism with increased macrophyte development (Wetzel & Søndergaard, 1998). However, the epilimnetic variables changed differentially with increased macrophyte cover, yielding further insight into the effect of submerged macrophyte beds on epilimnetic structure and function.

The present findings, although based on only nine lakes, point to a marked influence of submerged macrophytes on the biogeochemical phosphorus cycling among lakes. The percent particulate phosphorus systematically declines from > 80% in macrophyte free Lac Boivin to < 50% in macrophyte dominated Lac Hertel (Figure 1a). Mechanisms responsible for the observed decreases in water column turbidity (and presumably particulate phosphorus) in the presence of submerged macrophytes include increased zooplankton grazing (Jeppesen et al., 1998) and higher critical wind thresholds required to resuspend littoral zone sediments (Barko & James, 1998). Further, decreased

turbulence in weedbeds facilitates the sedimentation and retention of small particles that would otherwise be lost to the epilimnion (Petticrew & Kalff, 1992), and work on phosphorus accumulation in littoral sediments demonstrates that weedbeds are long term phosphorus traps (Rooney *et al.*, in prep.). Conversely, soluble phosphorus release from littoral sediments can result in the export of phosphorus to the open water (James & Barko, 1991). Although the present study does not permit the separation of mechanisms influencing particulate and soluble phosphorus dynamics, it is apparent that while epilimnetic soluble phosphorus levels decline with increasing macrophyte cover, the fraction of total epilimnetic phosphorus in soluble form increases.

Reported declines in phytoplankton biomass in the presence of submerged macrophytes (See Søndergaard & Moss, 1998) are supported here by a negative relationship between macrophyte cover and phytoplankton biomass (chl *a*) (Table 2). Further, the phytoplankton biomass to soluble phosphorus ratios are decline with increased macrophyte cover (Figure 1b), indicating that macrophyte beds mediate phosphorus-chlorophyll relationships in epilimnia. Similarly, at given phosphorus concentrations, the transparency of freshwater lakes is substantially higher in those dominated by macrophyte compared to lakes with low cover (Jeppesen et al., 1994; Faffeng & Mjelde, 1998). The uniform patterns observed are consistent with the hypothesis that in macrophyte dominated systems phytoplankton biomass is controlled by increased zooplankton grazing as opposed to phosphorus limitation (Jeppesen et al., 1998).

The present among lake results point to increased bacterioplankton subsidization with increased macrophyte cover. Algal biomass decreased more in macrophyte

dominated lakes than both planktonic respiration and bacterial production (Figure 1 c, d), pointing to a higher level of bacterioplankton metabolism in these systems than would be expected based on phytoplankton biomass alone. Clearly, not all of the increased bacterioplankton metabolism is attributable to the macrophytes, or the littoral zone in general because planktonic bacteria are nourished in part by organic matter from the catchment (see Kalff, 2001). Although the two sources cannot be distinguished here, our recent work (Rooney & Kalff, *in prep.)* notes submerged weedbeds as a source of pelagic zone bacterial production, with projected late summer increases in bacterioplankton production of 14% in lakes with 50% macrophyte cover. Although previous enclosure studies have shown bacterioplankton production in weeded enclosures to be high despite lower phytoplankton biomass (Søndergaard et al., 1998) this is the first study to note such a pattern among natural systems, providing evidence for a useful generality.

Epilimnetic levels of phosphorus, phytoplankton biomass, planktonic respiration and bacterioplankton production vary differentially among the nine lakes along a gradient of macrophyte cover. Present results show macrophyte cover (%) to explain about half of the observed variation in epilimnetic ratios among lakes varying widely in percent colonized, phosphorus concentration, phytoplankton biomass and planktonic metabolism. The results contradict the classical view of pelagic interactions in which phosphorus determines phytoplankton abundance, which in turn determines bacterial abundance through the production of organic carbon (Currie, 1990). While the generalizations are based on a yet modest number of lakes, the patterns are significant and provide quantitative evidence that the long held view that planktonic processes operate independently of the littoral zone is untenable.

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Table 1. Mean summer conditions of the 9 sampled lakes. Standard error values given in parentheses. SP = soluble phosphorus, PP = particulate phosphorus.

Lake	Macrophyte Cover (%)	SP ($\mu g\ l^{-1}$)	PP ($\mu g\ l^{-1}$)	Chl *a* ($\mu g\ l^{-1}$)	Respiration ($mg\ O_2\ l^{-1}\ day^{-1}$)	Bacterial Production ($\mu g\ C\ l^{-1}\ day^{-1}$)
Boivin	0	22 (2.3)	101 (8.2)	78 (9.7)	1.43 (0.27)	47 (14.6)
Bromont	4	8 (0.8)	18 (1.3)	16 (3.0)	0.62 (0.08)	12 (5.5)
Fitch	9	9 (1.6)	16 (2.5)	26 (4.1)	0.56 (0.16)	12 (6.8)
Waterloo	11	19 (2.2)	27 (12.0)	62 (15.7)	1.05 (0.15)	35 (19.7)
Brome	18	7 (1.0)	14 (2.0)	12 (2.5)	0.33 (0.08)	12 (5.4)
Magog	19	7 (0.9)	12 (2.5)	7 (0.8)	0.29 (0.06)	5 (1.2)
d'Argent	28	7 (1.6)	9 (4.1)	9 (5.3)	0.22 (0.06)	10 (4.8)
Roxton	58	8 (0.7)	14 (2.3)	15 (3.7)	0.47 (0.07)	15 (6.6)
Hertel	66	6 (0.6)	5 (0.7)	2 (0.3)	0.25 (0.06)	4 (1.0)

Table 2. Pearson correlation coefficients between measured variables among the nine lakes including all measurements throughout the study period. Asterisks: *-P<0.05; **-P<0.01; ***P<0.001. For abbreviations and units, see Table 1.

Variable	Macrophyte Cover	SP	PP	Chl *a*	Respiration	Bacterial Production
Macrophyte Cover	1					
SP	-0.40*	1				
PP	-0.52***	0.66***	1			
Chl *a*	-0.61***	0.70***	0.81***	1		
Respiration	-0.45**	0.68***	0.76***	0.75***	1	
Bacterial Production	ns	0.39*	0.49**	0.48**	0.46**	1

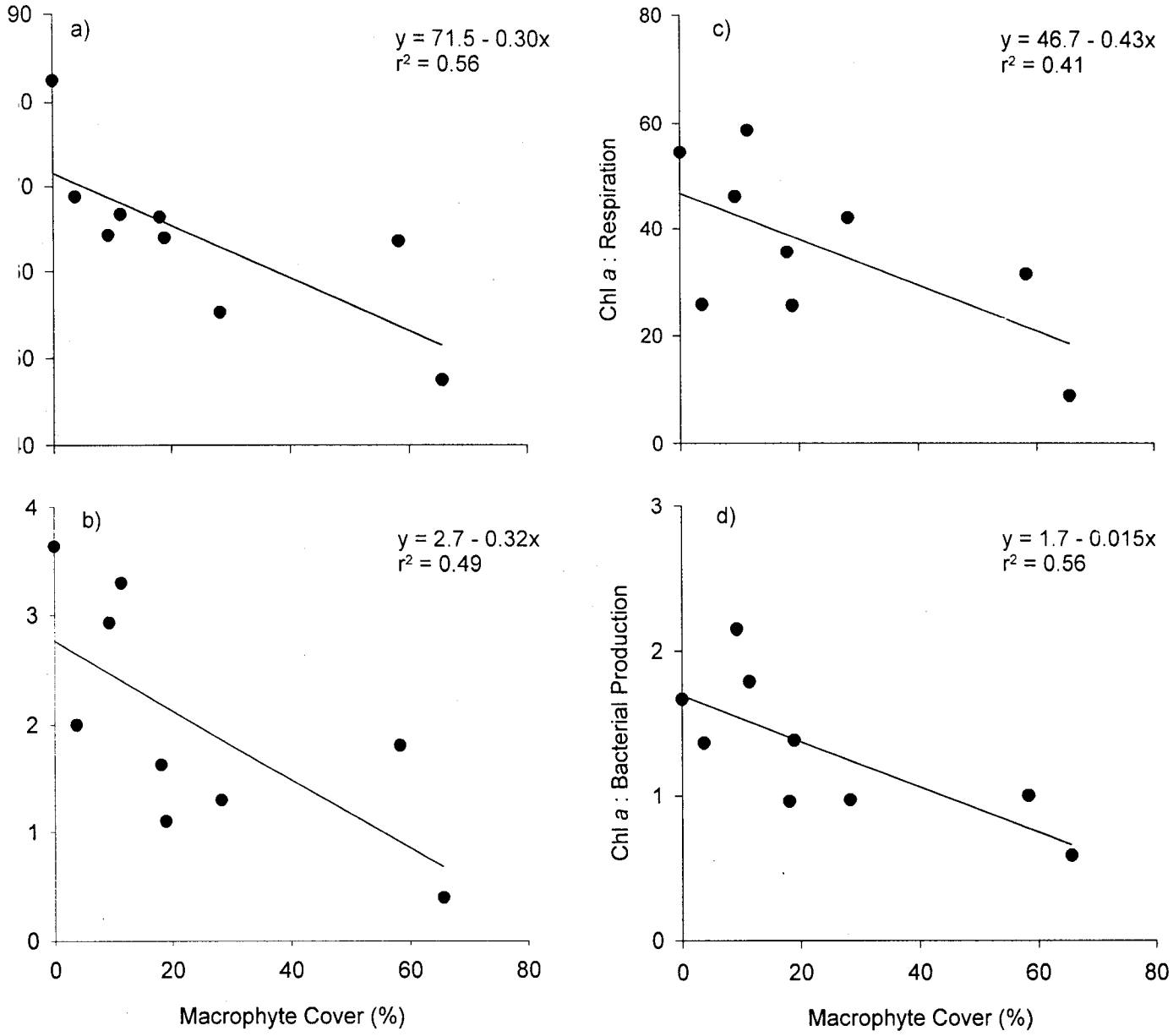
a)
y = 71.5 - 0.30x
r² = 0.56
c)
y = 46.7 - 0.43x
r² = 0.41
Chl a : Respiration
b)
y = 2.7 - 0.32x
r² = 0.49
d)
y = 1.7 - 0.015x
r² = 0.56
Chl a : Bacterial Production
Macrophyte Cover (%)
Macrophyte Cover (%)

Figure 1

Figure 1. Mean summer ratios of epilimnetic variables versus macrophyte cover (%) in 9 Quebec lakes. a) percent of epilimnetic total phosphorus in the particulate fraction; b) ratio of phytoplankton biomass (chl *a*) : soluble phosphorus; c) ratio of phytoplankton biomass (chl *a*) : planktonic respiration; d) ratio of phytoplankton biomass (chl *a*) : bacterial production.

Connecting Statement

Chapters 2 and 3 examine the influence of submerged weedbeds on phosphorus cycling and pelagic metabolism at large spatial scales, within growing seasons. The goal of Chapter 4 is to quantify the role of submerged macrophytes on phosphorus and sediment cycling over a much longer time scale (~115 yr). The advantage of using long term sediment core data is that it provides a time integrated expression that is not confounded by seasonal (Chapter 2) or interannual (Chapter 3) variation. Further, the results lend themselves to a comparison of littoral and profundal sediment and phosphorus dynamics, facilitating the integration of weedbeds into whole lake phosphorus cycling models.

CHAPTER 4

The role of submerged macrophyte beds in phosphorus and sediment accumulation

Abstract

We quantified the relationships between phosphorus and sediment accumulation and submerged macrophyte biomass both within a submerged macrophyte bed (MacPherson Bay), and among beds of varying biomass in Lake Memphremagog, Quebec, Canada. Stable Pb was used to date the sediments (~115 years) and generate five measurements of accumulation. We show macrophyte biomass to be the strongest predictor of littoral zone sediment and phosphorus accumulation rates both within and among weedbeds, yielding simple models for estimating long-term littoral zone sediment and phosphorus accumulation. Mean particle size at the depth of maximum submerged macrophyte biomass, as estimated from water content, was more similar to the mean particle size observed in profundal zones of lakes in the region than to bare littoral sediment, suggesting that weedbeds represent low energy littoral environments similar to profundal zones of sediment accumulation. Although weedbeds accumulated twice as much bulk sediment per unit area compared to their profundal counterparts, phosphorus accumulation per unit bulk sediment was more than six times higher in profundal sediments compared to sediments in weedbeds with a biomass of about 1000 g m^{-2} pointing to large post-depositional losses of sedimented phosphorus from macrophyte beds. Finally, extrapolation of the present results to 5 nearby lakes for which macrophyte biomass and distribution are known suggests, based on still limited data, that in lakes in which half of the sediment surface is colonized by submerged macrophytes, the littoral zone accounts for roughly one third of whole lake phosphorus and two thirds of whole lake bulk sediment accumulated annually.

Introduction

The distribution, transport, and ultimate fate of sediments have large effects on phosphorus (P) cycling in lakes (Canfield et al. 1982; Kalff 2001). With respect to the composition and long term accumulation of sediments, stratified lakes are generally divided into three zones. The zone of sediment accumulation (ZSA) located in deep sites of low underwater slope and energy is dominated by fine low density inorganic and organic particles (Håkanson and Jansson. 1983; Rowan et al. 1992), and is characterized by high rates of long term sediment accumulation. Located in just above the ZSA is the zone of discontinuous sediment accumulation (ZDA) where the accumulation of fine sediment particles is interrupted by periodic resuspension and transport during rare storm events. Finally, the zone of sediment erosion (ZSE) located in high energy shallow environments is characterized by coarse-grained dense inorganic sediments and low net sediment accretion rates. This pattern, however, does not hold where the littoral zone is colonized by submerged vegetation (James and Barko 1990; Benoy and Kalff 1999; Bindler et al. 2001).

Submerged macrophytes modify near-bed water flow and sediment composition, increasing the sedimentation rates of fine inorganic and organic particles, nitrogen, phosphorus and trace metals (Petticrew and Kalff 1992; Sand-Jensen 1998; Benoy & Kalff 1999). Long-term sediment accumulation rates measured over periods of decades to centuries are therefore high within the low turbulence vegetated littoral zone, decline to a minimum in the zone of highest turbulence beyond macrophyte beds, and rise to a second maximum in deeper profundal regions of lakes and reservoirs characterized by low turbulence (James and Barko 1990; Moeller and Wetzel 1988). The role of

macrophyte beds in the long-term accumulation and retention of sediments was dramatically demonstrated during the eutrophication of Lake Constance when an increase in algal turbidity lead to the disappearance of macrophyte beds, and the loss of the extensive sediment shelves deposited over centuries, as the result of increased nearshore turbulence (Schröder 1988). To our knowledge, only one study has examined relationships between macrophyte bed characteristics and long-term sediment accumulation. In Lake Memphremagog, Quebec total, bulk, organic, and anthropogenic lead accumulation rates at the depth of maximum submerged macrophyte biomass (MSMB) are linearly related to plant biomass (g m^{-2}) and biomass density (g m^{-3}) (Benoy and Kalff 1999). Increased long-term sediment accumulation in weedbeds results from the deposition and retention of water column and catchment derived particles, as well as the production and retention of organic matter produced within the littoral zone by macrophytes and epiphytes. Since these processes result in the import of external P to weedbeds, the extent to which macrophyte beds accumulate P should be a function of macrophyte bed attributes such as biomass and biomass density.

Both biomass and biomass density vary within macrophyte beds. Submerged macrophyte distribution is limited by turbulence near-shore (Chambers and Kalff 1987) and by light in deeper water (Chambers and Kalff 1985). Within beds, sediment characteristics and the light regime interact to determine plant biomass and its distribution (Anderson and Kalff 1988). With plant biomass attributes being the primary determinant of lead and sediment accrual among macrophyte beds determined at the depth of maximum submerged macrophyte biomass (Benoy and Kalff 1999), it seems plausible that there be an equivalent link between plant biomass and the sediment and P

accumulation rates not only at the depth of MSMB but also at different depths within macrophyte beds. As much of the P entering lakes is sorbed to particles (Prairie and Kalff 1988) or converted to particulate form by organisms, littoral zone sediment accumulation should be linked to P accumulation. Moreover, the extent to which macrophyte beds are a sink for P should be a function of bed characteristics such as biomass and biomass density.

It is clear that submerged macrophyte beds can act as a source or sink of P depending on the stage of plant development (Granéli and Solander 1988; Barko and James 1998). However, most studies that have quantified the influence of submerged weedbeds on P cycling have been carried out over short time periods (weeks-months) during the growing season only, ignoring nutrient cycling during the remainder of the year. Yet macrophyte stands are capable of acquiring and retaining nutrients even during periods of ice cover (Wetzel and Søndergaard 1998). One advantage of measuring long-term accumulation rates in weedbeds is, therefore, that accumulation outside of the growing season is taken into account.

A problem associated with measuring long-term sediment P accrual is its potential mobility in the sediment column (Carignan and Flett 1981) and the possibility of sediment P loss to the overlying water. Counteracting sediment processes do, however, result in sediment P immobilization in vegetated sediments. Precipitated calcite in hardwater lakes (Carignan 1985) and iron oxyhydroxide complexes that sorb soluble P in oxygenated surface sediments (see Kalff 2001) help prevent the diffusion of soluble P from the anoxic sediments below to the overlying water. Retention processes are further enhanced in macrophyte beds through a diffusion of dissolved oxygen from plant roots

into the surrounding sediments. Thus P, Fe, and Mn retention rates are 2-5 times higher in a *Littoella uniflora* bed than in nearby bare sediments (Christensen et al. 1997). Further, a high C:P ratio observed in littoral sediments (Moeller and Wetzel 1988) points to an incomplete microbial mineralization of the organic matter, shown directly by the presence of macrophyte fragments in weedbed sediments (LaZerte 1983).

Here, we use a sediment marker (stable lead) to determine long-term (~115 year) P accumulation within and among Lake Memphremagog weedbeds to estimate the importance of weedbeds as P traps and to use the relationships developed between plant biomass and the specific P and sediment accumulation (mg m^{-2} yr^{-1}) rates to provide a first estimate of the importance of macrophyte beds as sinks for P and sediments. Unfortunately, some of the P in the ~115 year profile may be derived from earlier deposited sediments which, following the deposition of additional sediment, created anoxic conditions that allowed a solublization and migration to within the 115 yr profile. If so, this would lead to an overestimation of P accumulation unless offset by an equivalent loss of P from the surface sediment to the overlying water as a result of periodic surface sediment anoxia (James et al 1996). While anoxia is unlikely at the macrophyte densities encountered (Table 1), it cannot be precluded. Not knowing the magnitude of the above processes, we calculate both P accumulation and what we call, for lack of a better term, a minimum P accumulation rate (see Methods and Materials). Measuring long-term accumulation rates has the advantage of giving a time-integrated expression not confounded by seasonal or inter-annual variation. The goal of the paper was to test two previously untested hypotheses. The first was to test the hypothesis that macrophyte biomass and biomass density are linked to long-term P accumulation within

and among submerged macrophyte beds. The second hypothesis is that relationships between macrophyte biomass characteristics and sediment and P accumulation rates at different depths within a single weedbed are not significantly different from those observed among beds at the depth of maximum submerged macrophyte biomass. If correct, this would greatly facilitate the modeling of sediment and P accumulation rates in the littoral zones of lakes.

Methods and Materials

Field work was conducted in oligo-mesotrophic Lake Memphremagog (Quebec, Canada – Vermont, USA), which provides a wide variety of littoral environments for comparative work (e.g. Duarte and Kalff 1986; Rasmussen 1988; Benoy and Kalff 1999). Lake Memphremagog is a long (45 km), narrow (1-4 km), and deep (Z_{mean} = 20 m, Z_{max} = 107 m) dimictic lake (Figure 1).

Among weedbeds

Sampling for the among weedbed portion of the study took place in October 1998. Ten sites were selected to examine among weedbed variation in sediment and P accumulation patterns (Figure 1), with the sites a subset of those examined by Benoy and Kalff (1999). At each site, sediment cores (tube inner diameter, 5.7 cm) were collected by SCUBA diver from the depth of maximum submerged macrophyte biomass (MSMB), determined to be 2.7 ± 0.5 m using empirical relationships derived by Chambers and Kalff (1985). Cores were immediately returned to the laboratory, and extruded using a vertical extrusion system at one of three section intervals (1, 1.5, or 2 cm) to obtain at least 10 sections per core where possible. Sediments were transferred to clean, pre-

weighed 25 ml polyethylene scintillation vials and weighed to the nearest 0.1 g to obtain sediment wet weight. Sediments were dried at 85 °C until constant weight (~48 hours) to determine water content (%) and bulk sediment weight. Sub samples (~1 g) were burned for 2 hours at 550 °C to determine loss on ignition (LOI) as an estimate of organic content (Dean 1974).

Phosphorus (P) analysis was carried out following a modification of the ignition method (Anderson 1976). Between 3 and 10 mg of burnt sediment was boiled in 10 ml of 1N HCl for 15 minutes. Each sample was then diluted to 40 ml with double distilled deionized water and assayed for P using the ascorbic acid method following persulfate digestion (Griesbach and Peters 1991).

Macrophyte biomass (g m^{-2}), biomass density (g m^{-3}), and the depth of the lead horizon at each of the sites were taken from Benoy and Kalff (1999).

Within Weedbed

Sampling for the within-bed portion of the study was done in August 1999. Three transects were sampled in a weedbed located in MacPherson Bay, a large (~1km^2) embayment on the eastern shore of Lake Memphremagog (Figure 1 inset). Macrophyte composition was heterogeneous, with macrophytes nearest the shore being dominated by isoetids and sequentially moving away from shore, *Myriophyllum spicatum*, *Potamogeton spp.* and *Elodea canadensis*. Sampling for accumulation rates (ARs) and aboveground macrophyte biomass was done at 7 sites along each of three transects, for a total of 21 sites.

Triplicate quadrats (0.25 m^2) were placed at each site, and plant height was measured *in situ*, providing estimates of weedbed canopy height to be used to calculate macrophyte biomass density (g m^{-3}, Benoy and Kalff 1999). All plants within quadrats were harvested, taken back to the laboratory and processed within 24 hours of collection. Macrophytes were washed free of epiphytes, detritus and invertebrates, roots were pinched off, and plants were then spun in a lettuce spinner to remove excess water. Plant biomass was weighed to the nearest 0.1 g to obtain fresh weight.

Sediment cores (inner diameter 5.7 cm) were taken from a fourth quadrat at each site. Cores were returned immediately to the laboratory, and processed as in the among weedbed portion of the study.

Sediment Analysis

Stable Pb was selected as the most suitable marker for dating sediment cores, as it has been shown to be a replicable and reliable marker in for both profundal and littoral sediments in lakes in this region (Blais and Kalff 1995, Benoy and Kalff 1999). The subsurface enrichment of stable Pb is the result of coal burning, and mining and smelting activities in southern Quebec and adjacent regions starting in the mid 1880s. Consequently, all ARs are based on a ~115 year interval (Blais et al. 1995, Benoy and Kalff 1999). There is a high degree of agreement between accumulation rates determined using stable lead and other markers (^{210}Pb, *Ambrosia* pollen, ^{137}Cs) in Ontario and Quebec lakes (Blais and Kalff 1995).

All laboratory glassware used for Pb analysis was acid washed in 15 % HCl and twice rinsed in double-distilled deionized water. All reagents were AnalaR-grade acids

from BDH. Dried sediment samples (~1 g) were crushed by mortar and pestle, and digested in a dilute aqua regia ($3HCl:3H_2O:HNO_3$) at 85°C for 1 h. After digestion, samples were cooled, and brought to a final volume of 25 ml in polyethylene volumetric flasks using double-distilled deionized water. Samples were centrifuged at 3000 rpm for 10 minutes to remove suspended solids. Concentrations of Pb were measured using a flame atomic absorption spectrometer (Perkin Elmer 3100). Pb extraction efficiencies were assessed using standard reference material (Buffalo River sediment, No. 2704, U.S. National Bureau of Standards). The extraction efficiency of the medium for Pb was 100 %, and the extraction reproducibility was 10 %, both of which are within limits set by the U.S. National Bureau of Standards.

Accumulation Rate determination

The depth used to calculate accumulation rates (ARs), as in Blais et al. (1995) and Benoy and Kalff (1999), was the point in the sediment profile where anthropogenic Pb burden was greater than background burden by a factor of two (Figure 2a). When two or more points of inflection were encountered in the sediment column, shallower rather than deeper points were considered to avoid artificially inflating of the depth of the sediment marker.

Five measures of accumulation were used. Total sediment accumulation rate (TSAR, mm yr^{-1}) refers to the depth of material that has accumulated with respect to the lead horizon. TSAR was corrected for compaction by using elastic bands placed at the sediment-water interface at the time of core collection to indicate the difference between the sediment depth in the core tube and the surrounding sediment:

$$Total\ SAR = \frac{[(\sum s_i \times si_a \times (td - md)]}{115\ yr} \quad (1)$$

where s_i = *i*th section, si_a = section interval, td = total depth (mm), and md = mud depth. Bulk (BSAR) and organic (OSAR) accumulation rates were calculated using the dry weight and ashed weight of the sediment sections, respectively. Both ARs are expressed in g m^{-2} yr^{-1}:

$$Bulk\ and\ Organic\ SAR = \frac{(\sum m_i) \times si_b \times 392}{115\ yr} \quad (2)$$

Where m_i = mass at the *i*th section, either dry weight or organic content (g), and si_b = corrected section interval (si_a x td/md). The value of 392 converts the areal measurement of accumulation from that of a core tube area (25.5 cm^2) to square meters.

Two measurements of P accumulation were developed (PSAR and MinPSAR). PSAR was calculated using bulk dry weight and sediment P concentrations (μg g^{-1} dry weight). PSAR is expressed in mg m^{-2} yr^{-1}:

$$PSAR = \frac{\sum[(P_i \times W_D) \times si_b] \times 392}{115\ yr} \quad (3)$$

where P_i = P concentration at the *i*th horizontal section (μg g^{-1} dry weight), W_D = dry weight of the *i*th section, si_b = corrected section interval (si_a x td/md) and the value of 392

converts the areal measurement of accumulation from that of the core tube. MinPSAR was calculated using the background concentrations of P (μg g^{-1} dry weight) as determined in the deep portions (> 115 yrs) of the cores (Figure 2b). This provides a minimum estimate of P accumulation:

$$Min\ PSAR = \frac{\sum[(P_B \times W_D) \times si_b] \times 392}{115\ yr} \qquad (4)$$

where P_B = background P concentration (lowest μg g^{-1} dry weight in sediment core), W_D = dry weight of the *i*th section, si_b = corrected section interval (si_a x td/md) and the value of 392 converts the areal measurement of accumulation from that of the core tube.

Statistical analyses were performed using SYSTAT software (1998). Correlation and regression analysis were used to develop predictive models for the measured accumulation rates.

Results

The large ranges of underwater slope, biomass, and sediment water content show that a wide variety of littoral environments were considered in the study (Table 1). Nineteen cores were examined for the within weedbed portion of the study. Two (Transect 2, cores 1 and 2, nearest the shore) were eliminated because they lacked identifiable lead horizons. Figure 3 shows profiles of Pb, organic content, and P in sediment cores taken at different sites within the weedbed. Including all stations, peak Pb concentrations (mean = 20.4 μg g^{-1} , SE = 9.2, n = 19) were significantly higher than

background levels (mean = 8.8 $\mu g\ g^{-1}$, SE = 5.9, n = 19) according to a paired t-test ($P < 0.0001$).

Patterns of within weedbed sediment accumulation were comparable among the three transects measured. In general, macrophyte biomass increased from the near-shore sites to a peak in the center (and densest portion) of the weedbed, and then declined as measurements moved toward the open water (Figure 4 a, b, c). Sediment ARs followed a similar pattern, with most rates attaining their highest values in the middle of the weedbed (Figure 4).

Of the three predictor variables (biomass, biomass density, and underwater slope), only biomass was coupled to within weedbed sediment accumulation (Table 2). Sediment water content (%) was correlated with biomass and accumulation rates (Table 2). Organic sediment accumulation (OSAR) showed the highest correlation with biomass, whereas MinPSAR was least correlated, although the correlation coefficient was significant at the $P = 0.05$ level (Table 2). Whereas neither underwater slope nor biomass density were linked to any of the ARs, all accumulation rates were correlated with each other (Table 2).

Among weedbeds, biomass was again the overall best predictor of ARs, being significantly related to TSAR, OSAR, PSAR, and MinPSAR (Table 3). Water content was not significantly correlated with biomass or any ARs among sites. Biomass density ($g\ m^{-3}$) was correlated only with TSAR (Table 3). As in Table 2, variation in underwater slope was too small to allow it to be a significant predictor of any ARs.

ANCOVA of the within and among portions of the study showed no significant differences between grand means and slopes of the relationships between biomass and

sediment ARs for TSAR, BSAR, and PSAR (Figure 5 a, b, d,), allowing the data from both portions of the study to be pooled for regression analysis.

Linear regression analysis was used to construct models predicting sediment accumulation within weedbeds, among weedbeds, and for pooled data where ANCOVA allowed. Biomass was a significant predictor of all ARs within the weedbed, accounting for the largest variation in OSAR, followed by BSAR, PSAR, TSAR, and finally MinPSAR (Table 4). Prediction of ARs among weedbeds was generally better than those within weedbed, with the exception of BSAR (Table 4). Pooling data from the two portions of the study decreased the SE_{est} and increased significance of the regression models for TSAR and PSAR, although it did not increase the R^2 of the relationships (Table 4).

Discussion

The results show macrophyte biomass to be a good predictor of long-term sediment and P accumulation in the littoral zone. It is particularly noteworthy that models predicting among site total (TSAR), bulk (BSAR), and P (PSAR) measured at the depth of maximum submerged macrophyte biomass (MSMB) do not differ significantly from the within weedbed ARs measured over a similar range of biomass (Figure 5), showing the accumulation rates (ARs) to be a function of local biomass rather than where along transects within a weedbed, or where in the lake, measurements were made.

The minimum estimate of P accumulation (MinPSAR) places a lower limit on the amount of P accumulated during the past 115 years because with a known mobility of P in sediment cores (Carignan and Flett 1981), there is a possibility that some of the total P accumulated (PSAR) is the result of a migration from below the lead horizon. However,

any resulting overestimate appears to be small. If P mobility was responsible for the observed biomass - PSAR relationships, one would expect macrophyte biomass and background P concentration (> 115 years, Figure 2) to be correlated, which they were not ($r = -0.2$, $p = 0.43$). Further, PSAR was better correlated with other measures of sediment accumulation than was MinPSAR (Table 3), indicating that the total P accumulated during the 115 yr period was associated with sedimenting particles. Even though MinPSAR sets a lower limit, estimates were on the same magnitude as those of PSAR (Table 1), and both show the weedbeds to be long term sinks for phosphorus.

The high correlation between P accumulation rates and the other measures of sediment accumulation (TSAR, BSAR, OSAR) over the 115-year period (Table 2, Table 3) shows P accumulation to be closely linked to other long-term rates of sedimentation in the littoral zone. However, within individual cores, the amount of P ($g\ m^{-2}$) per stratum was not correlated with bulk sediment ($g\ m^{-2}$) for pooled strata ($r = 0.01$, $p = 0.93$), indicating that bulk sediment and P become decoupled once incorporated into the sediments. This decoupling reflects an increase in bulk weight per stratum in deeper sections as a result of compaction, and a decrease in [P] ($\mu g\ g^{-1}$) with increasing sediment depth, presumably the result of an upward diffusion of soluble P under anoxic conditions in deeper sediment (Carignan and Flett 1981) and high rates of P recycling at the sediment water interface. With the largest pool of P in the upper sediment horizons (Figure 2), it is susceptible to loss to the overlying water, resulting from surface sediment anoxia (James et al. 1996) or biological activity in the weedbeds (see below). Nonetheless, the results indicate that, over long time periods, increased sedimentation of

particles and associated P is proportional to macrophyte biomass and outweighs any P losses that may occur.

Submerged macrophytes not only influence rates of sedimentation (Benoy and Kalff 1999) but also surficial sediment particle size distribution, with plant surface area a significant predictor of surface sediment clay content (Petticrew and Kalff 1992). This is particularly important here, as small particles disproportionately sorb phosphorus (Clay and Wilhm 1979). Here, an analysis of surface sediment (0-5 cm) water content allows for the comparison of weedbed sediments to profundal and bare littoral sediments, as it is as an excellent predictor of mean sediment particle size (Phi = -0.93 + 0.09 x water content, $r^2 = 0.93$, Rowan et al. 1992). Estimated sediment particle diameter at higher biomass sites (> 1 kg m^{-2}) was 12 μm (range 7 - 41 μm, n=14) and much closer to reported profundal values averaging 7 μm for glacial lakes in this region (Rowan and Kalff 1991) than to bare littoral sediments in Lake Memphremagog (~300 μm, Benoy 1997). Even at lower biomass sites (<1 kg m^{-2}), mean sediment particle size, although much more variable, was much smaller (mean = 52 μm, range 4 - 323 μm, n=15) than in bare littoral sediment. Therefore, even a modest plant density reduces turbulence sufficiently to allow for the permanent sedimentation of relatively fine particles.

While mean sediment particle size in dense weedbeds is similar to that of profundal sediment, there are notable differences between ARs in the profundal zone of Lake Memphremagog (Flett and Marshall 1983) and those measured in weedbeds. The mean bulk sediment accumulation rate among sites was more than double that of mean profundal BSARs measured in two basins of Lake Memphremagog, with the densest weedbeds having BSARs almost 4 fold higher than mean profundal rates (Figure 6a). In

contrast, PSARs in the weedbeds were on average less than half that of profundal rates of P accumulation (Figure 6b), with only the densest weedbeds exhibiting PSARs similar to profundal rates. Therefore, weedbeds accumulate far less P per unit bulk sediment than their profundal counterparts. In fact, phosphorus accumulation per unit bulk sediment accumulation was more than six times higher in profundal sediments compared to sediments in weedbeds with a biomass of 1000 g m^{-2}.

The fine particles sedimenting in the both weedbeds and the profundal zone are, based on the loss on ignition of surface sediments, largely inorganic (weedbed mean 88% inorganic, profundal mean 87% inorganic). Assuming the origin of these inorganic particles to be the same (the catchment), and an almost total P retention by the aerobic profundal sediment surface, the much lower PSAR : BSAR ratio measured in the weedbed cores compared to the profundal cores implies a large loss of P following sedimentation in the weedbeds. Based on bulk sediment accumulation, weeded littoral regions with macrophyte biomass of 1000 g m^{-2} receive roughly 1600 mg P m^{-2} yr^{-1}, but must lose over 1300 mg m^{-2} yr^{-1} of this phosphorus to balance the long-term P accumulation rates. Export of this P from weedbeds as a result of sediment anoxia (James et al. 1996) is unlikely at the relatively modest macrophyte biomass encountered here (Table 1). However, with macroinvertebrate biomass about four fold greater in Lake Memphremagog weedbeds than in the nearby littoral zone of sediment erosion, (Rasmussen and Rowan 1997) it is likely that shallow water fish obtain much of their nutrition from within weedbeds, exporting a significant fraction of the P recycled from the sediment-water interface to the open water. In fact, there is rapidly growing evidence for the importance of a littoral zone energy subsidy to the pelagic zone. Of 15 species of

fish examined by Vadeboncoeur et al. (2002), the average species obtained 65% of its diet either directly or indirectly from zoobenthos, not including littoral zooplankton. Assuming that zoobenthic and littoral zooplankton production is fueled by primary production within the littoral zone, fish feeding would provide a plausible mechanism for some or all of the export of phosphorus from weedbeds, thereby providing an important littoral - pelagic link in lakes.

While the above discussion addressed the specific areal rates (mg m^{-2} yr^{-1}) of long-term sediment accumulation, the importance of the littoral and profundal zones as sites of P accumulation is a function of lake morphometry and the relative size of the littoral and profundal zones. In large and deep Lake Memphremagog, characterized by steep underwater slopes, the vegetated littoral zone covers <2% of the surface area, making the littoral zone an insignificant sink for P in absolute terms. The importance of weedbeds as sinks for P and sediment can be expected to be much greater in shallow lakes with a much larger fraction of the bottom covered by macrophytes.

Whole lake accumulation rates: an exploration

We extrapolated the per unit area estimates of littoral and profundal bulk and P accumulation rates as a function of macrophytes biomass to five nearby lakes for which we collected macrophyte biomass and distribution data (Table 5). The lakes share a similar climate, geology and land use, but differ appreciably in morphometry and littoral characteristics, thereby providing an indication of the range of influence of the littoral zone on whole lake sediment accumulation among lakes. The extrapolation, based on a small data set, suggests that macrophyte beds account for more than half of the annual

bulk sedimentation in lakes where greater than one third of the sediment surface is colonized by submerged macrophytes. The same analysis suggests that macrophytes must cover a much larger fraction (about two-thirds) of the sediment surface for the littoral zone to retain half of the P accumulated in sediments (Table 5). The primary value of the simple models lies not in the relevance of the estimated impacts to lakes everywhere, but rather to serve as an indication of the magnitude of macrophyte cover required to have a major impact on sediment and P distribution in lakes. In the same vein, the estimated impacts serve as a reminder of the importance of vegetated littoral zones as traps of sediments, nutrients, and contaminants, something generally overlooked as the result of the emphasis in limnology on the pelagic zone and profundal sediments.

In summary, although macrophyte beds can act alternatively as sources and sinks of water column P over short time scales (Granéli and Solander 1988, Barko and James 1998), the present results demonstrate that weedbeds are major sediment and P sinks, with rates of total, bulk, organic matter and P accumulation linked to macrophyte biomass. Although both submerged weedbeds and the profundal zone of sediment accumulation accumulate fine particles, weedbeds accumulate far more (bulk) sediment per unit area than their profundal counterparts, while retaining about six times less P per unit bulk sediment (Figure 6). These results point to a considerable loss of P from recently sedimented particles to the open water. Extrapolations of the specific accumulation rates to five nearby lakes for which macrophyte cover is known points to a major role of submerged weedbeds in the trapping and cycling of P in lakes.

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Table 1. Summary statistics for within and among portions of the study, including mean, minimum, maximum, and standard deviation of all variables measured in Lake Memphremagog, Quebec.

Variable	Mean		Minimum		Maximum		Standard Deviation	
	Among	Within	Among	Within	Among	Within	Among	Within
Mean Biomass, g m^{-2}	845	987	78	0	1767	2603	567	597
Mean Biomass Density (g m^{-3})	530	280	39	0	876	759	268	213
Slope (%)	7.9	4.1	2.1	2.7	28.4	7.5	7.4	1.7
Water Content (%)	75.5	68.2	62.0	23.9	87.8	84.3	7.3	17.8
TSAR, mm yr^{-1}	1.15	1.14	0.08	0	1.83	2.02	0.66	0.54
BSAR g m^{-2} yr^{-1}	588	507	88	0	1130	1167	371	248
OSAR g m^{-2} yr^{-1}	57	51	2	0	139	123	47	33
PSAR, mg m^{-2} yr^{-1}	193	246	14	0	498	616	154	149
Min PSAR mg m^{-2} yr^{-1}	114	120	14	0	276	287	100	79

Table 2. Correlation matrix of all measured variables from the within weedbed portion of the study. Significance levels are given below the table.

	Biomass	Biomass Density	Slope	Water Content	TSAR	BSAR	OSAR	PSAR	Min PSAR
Biomass	1.00								
Biomass Density	-	1.00							
Slope	-	-	1.00						
Water Content	0.52*			1.00					
TSAR	0.73***	-	-	0.77***	1.00				
BSAR	0.79***	-	-	0.48*	0.78***	1.00			
OSAR	0.82***	-	-	0.70**	0.88***	0.86***	1.00		
PSAR	0.74***	-	-	0.61**	0.72**	0.86***	0.81***	1.00	
MinPSAR	0.54*	-	-	0.52*	0.52*	0.64**	0.60**	0.85***	1.00

- Not significant
* P<0.05
** P<0.01
*** P<0.001

Table 3. Correlation matrix of all measured variables from the among weedbed portion of the study. Significance levels are given below the table.

	Biomass	Biomass Density	Slope	Water Content	TSAR	BSAR	OSAR	PSAR	Min PSAR
Biomass	1.00								
Biomass		1.00							
Density	-								
Slope	-	-	1.00						
Water Content	-	-	-	1.00					
TSAR	0.81*	0.72*	-	-	1.00				
BSAR	-	-	-	-	0.81*	1.00			
OSAR	0.87**	-	-	-	0.89**	-	1.00		
PSAR	0.79*	-	-	-	0.90**	0.76*	0.92**	1.00	
MinPSAR	0.92**	-	-	-	0.83*	-	0.94***	0.93**	1.00

- Not significant
* P<0.05
** P<0.01
*** P<0.001

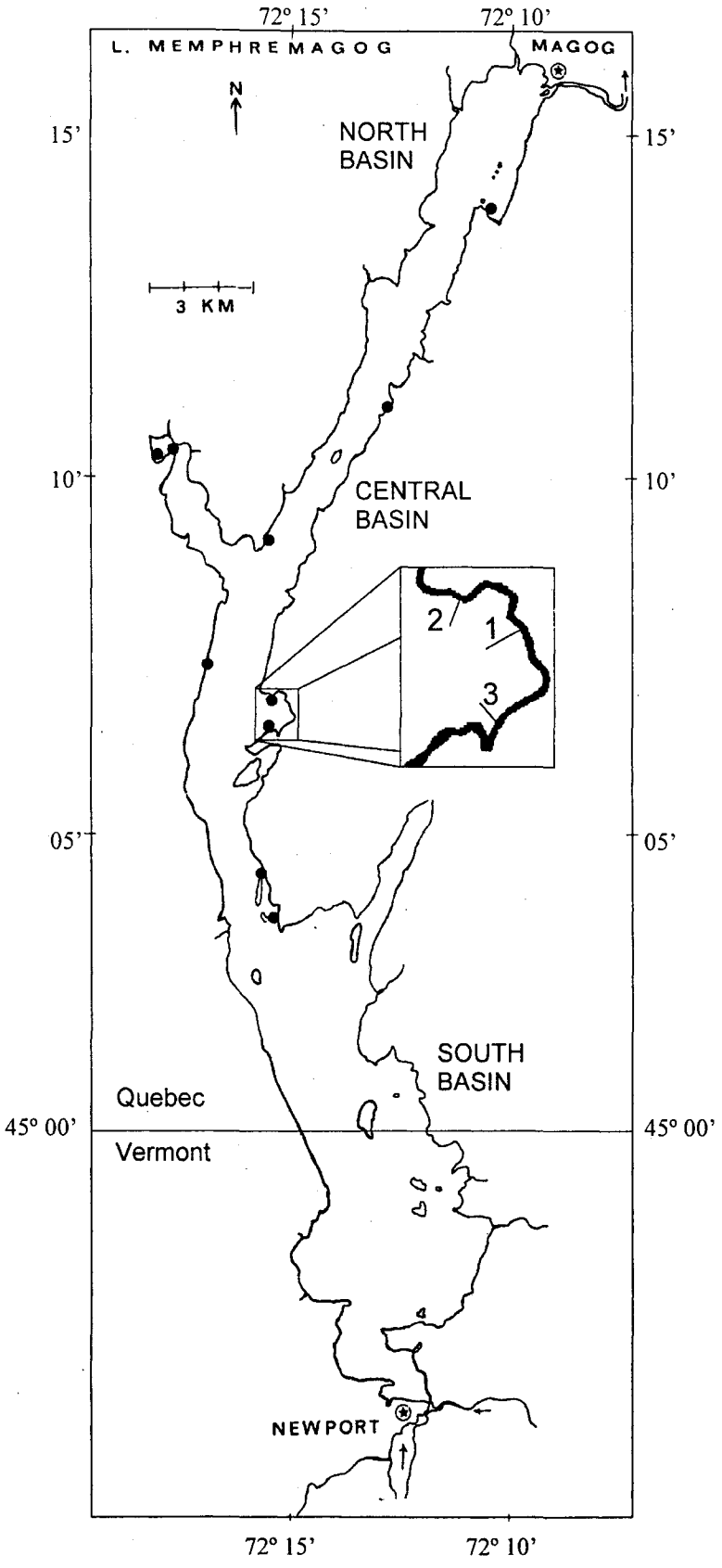
Table 4. Regression models of SARs with the independent variable being macrophyte biomass. Models are given for within weedbed, among weedbeds, and where allowed by ANCOVA pooled for both portions of the study. SE_{est} is the standard error of the estimate for each model. Significant intercepts for the models are denoted with an asterisk. Units are biomass (kg m^{-2}), TSAR (mm yr^{-1}), BSAR (g m^{-2} yr^{-1}), OSAR (g m^{-2} yr^{-1}), PSAR (mg m^{-2} yr^{-1}), and MinPSAR (mg m^{-2} yr^{-1}).

Dependent Variable	n	Coefficient (Biomass)	SE_{est}	Intercept	R^2	Regression P value
TSAR						
Within	19	0.67	0.15	0.49*	0.50	<0.001
Among	10	1.05	0.21	0.24	0.73	<0.001
Pooled	29	0.77	0.13	0.42	0.57	<0.001
BSAR						
Within	19	330	63	181*	0.59	<0.001
Among	ns	ns	ns	ns	ns	ns
Pooled	29	330	75	225	0.39	<0.001
OSAR						
Within	19	44	7.4	8.1	0.65	<0.001
Among	10	76	12.5	-4.0	0.80	<0.001
Pooled	nd	nd	nd	nd	nd	nd
PSAR						
Within	19	184	40	65.3	0.53	<0.001
Among	10	225	53	2.6	0.65	0.003
Pooled	29	198	31	42.1	0.58	<0.001
MinPSAR						
Within	19	70	26	51.4	0.25	0.016
Among	10	164	23	-24.4	0.84	<0.001
Pooled	nd	nd	nd	nd	nd	nd

Table 5. Morphometric and macrophyte characteristics of the 5 lakes in the Eastern Townships, Quebec, used in the whole-lake sediment accumulation simulation. Estimates of the proportion of bulk (BSAR) and phosphorus (PSAR) are given, using estimates of accumulation in vegetated and bare sediments of the lake.

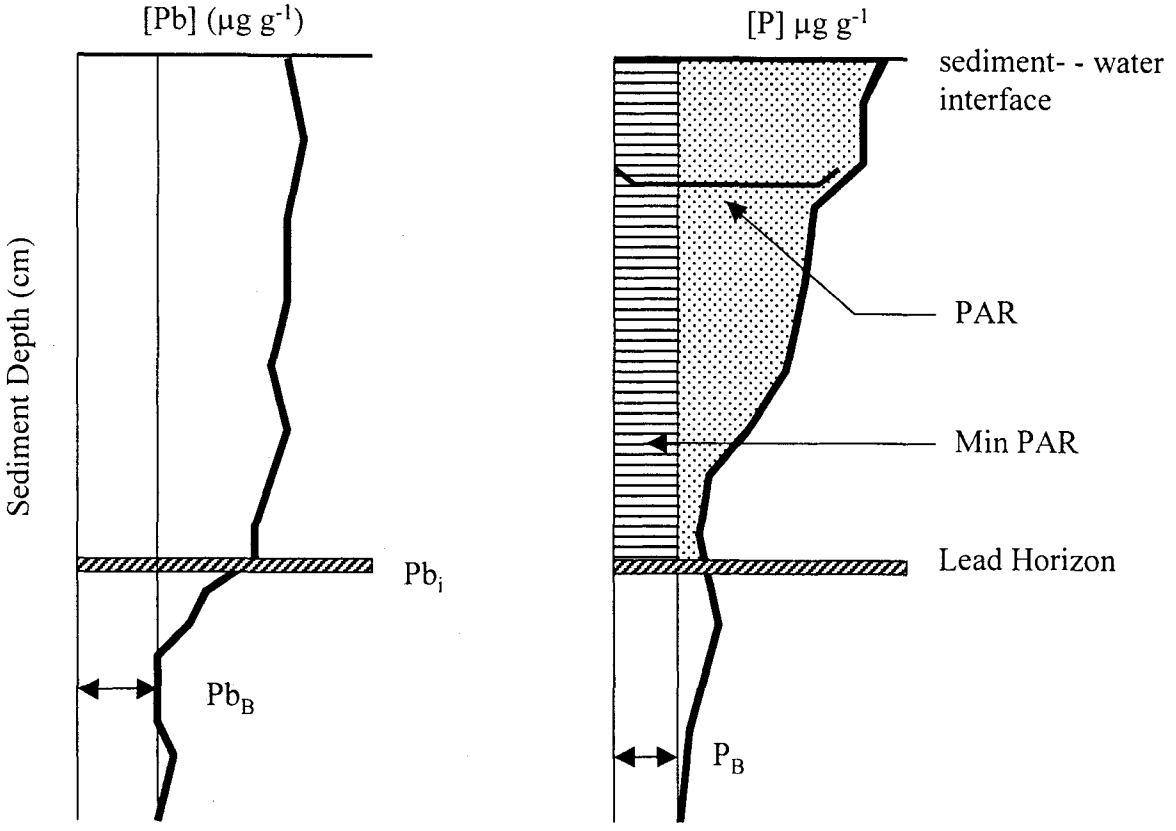
	Measured Variables					Predicted	
Lake	Area (ha)	Z_{max} (m)	Z_{mean} (m)	% of Lake Colonized	Mean Biomass (g m^{-2})	% BSAR in macrophyte beds	% PSAR in macrophyte beds
Waterloo	150	6	2.9	11	143	26	7
Brome	1417	12	5.8	18	195	33	10
Magog	927	18	7.7	19	675	35	10
D'Argent	108	16	5.4	28	212	58	23
Hertel	29	9	4.7	66	890	80	47

Figure 1. Map of Lake Memphremagog (Quebec-Vermont), showing study sites. Sites for the among weedbed portion of the study are shown with black circles, and the site for the within weedbed portion of the study is shown in the inset.



Neil Rooney, Jacob Kalff and Catherine Habel
Figure 1

Figure 2. Idealized profiles showing a) Parameters used to establish the depth where anthropogenically derived stable lead is initiated (early 1880s). Pb_i denotes the Pb concentration at a specific sediment depth (ith section) and Pb_B refers to the natural background level; b) Parameters used to establish rates of phosphorus accumulation. P_B refers to the background phosphorus concentration in the core.



Neil Rooney, Jacob Kalff and Catherine Habel
Figure 2

Figure 3. Three exemplary profiles take from the within weedbed portion of the study: a) Transect 1, quadrat 5; b) Transect 2, quadrat 6; c) Transect 3 quadrat 2. Figures for each site include organic content (%), Pb concentrations ($\mu g\ g^{-1}$), and TP concentration ($\mu g\ g^{-1}$ dry weight).

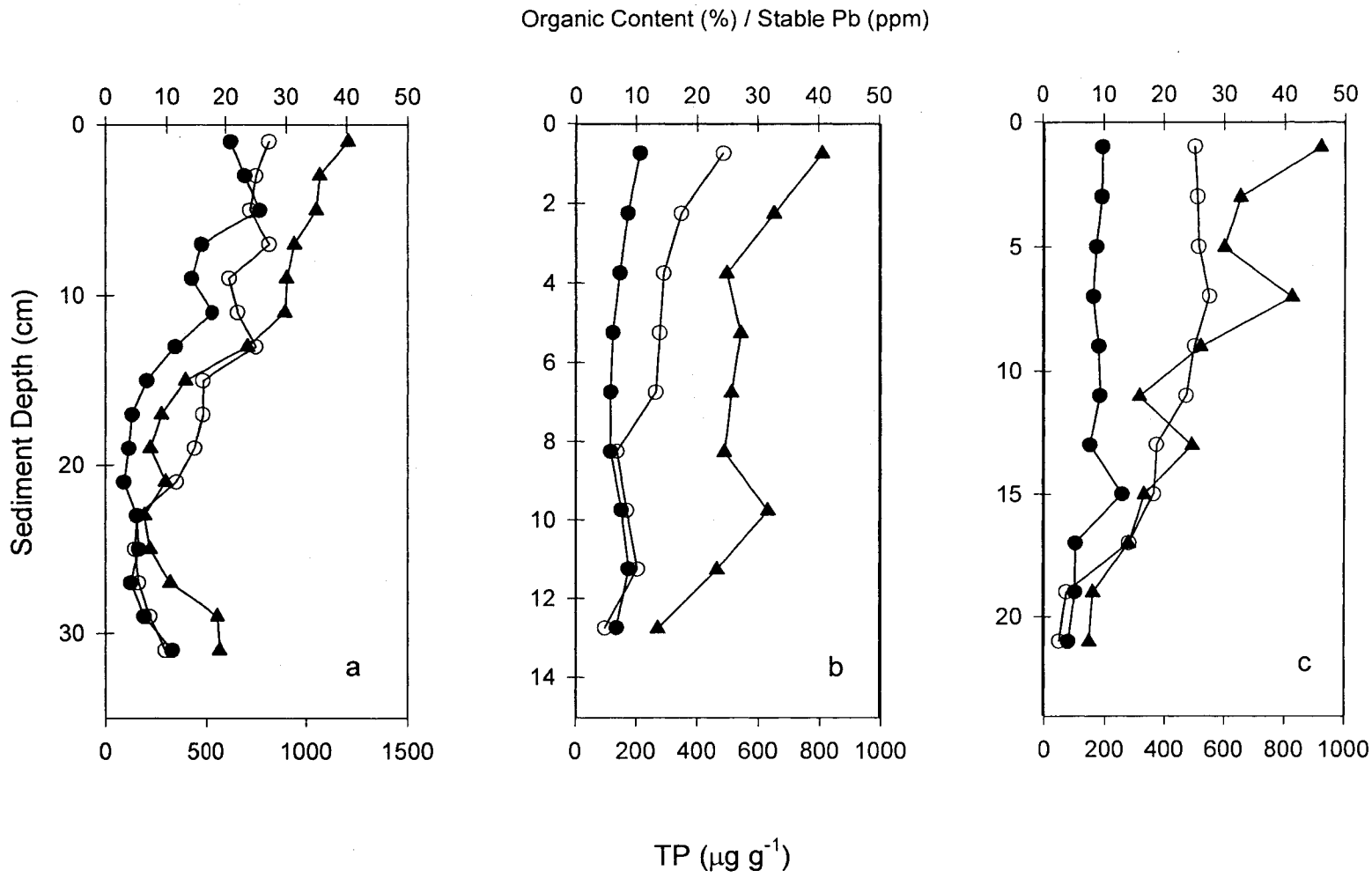

Organic Content (%) / Stable Pb (ppm)
Sediment Depth (cm)
TP (μg g-1)
a
b
c
Organic Content (%)
Stable Pb (ppm)
TP (μg g-1)

Figure 3

Figure 4. Relation of macrophyte bed characteristics to distance from shore for each of the three transects. The top panel (a, b, c) shows macrophyte biomass and TSAR. The second panel (d, e, f) shows BSAR and OSAR. The third panel (g, h, i) shows PSAR and MinPSAR a. See text for explanation of abbreviations.

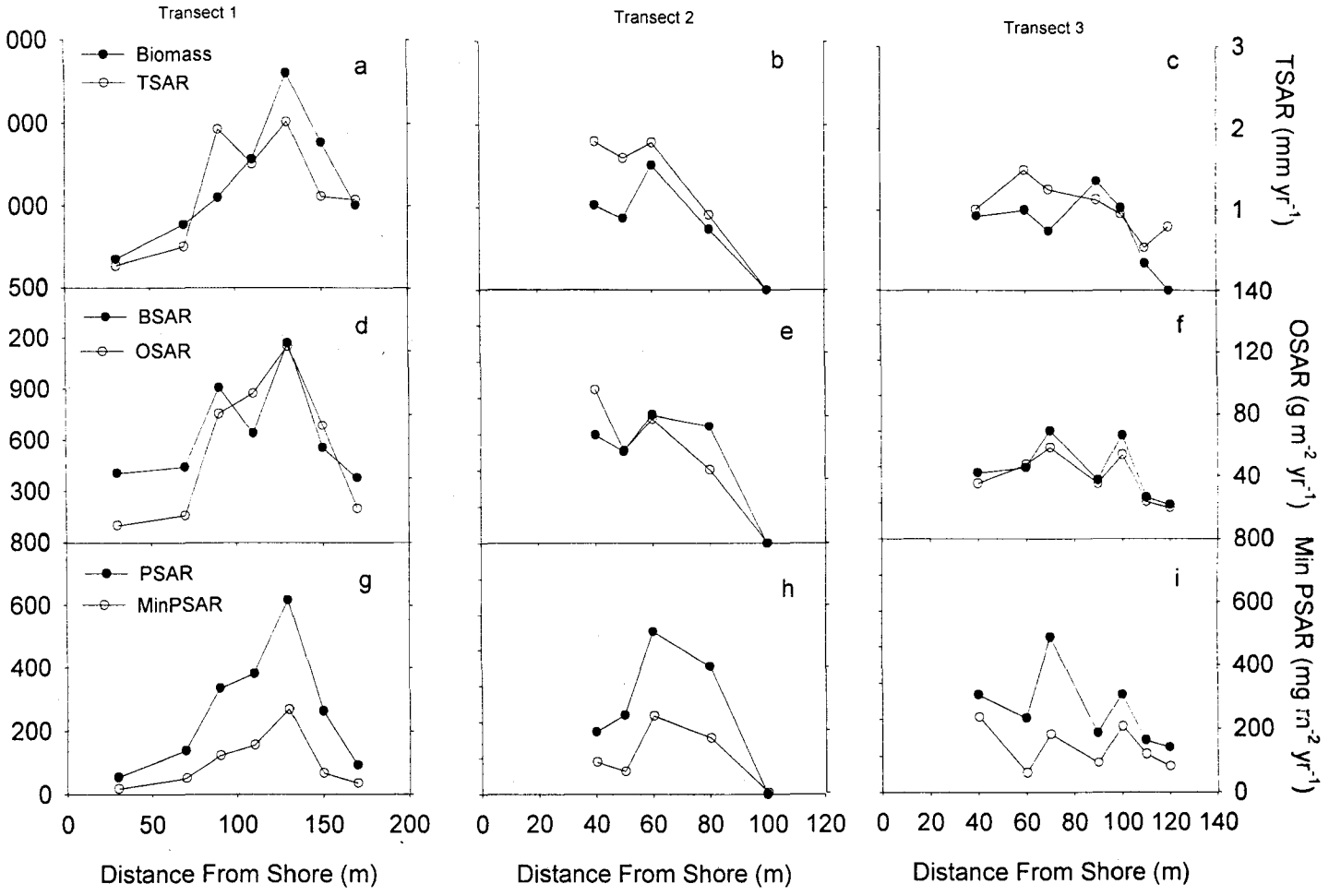

Transect 1
Transect 2
Transect 3
Biomass
TSAR
BSAR
OSAR
PSAR
MinPSAR
a
b
c
d
e
f
g
h
i
TSAR (mm yr-1)
OSAR (g m-2 yr-1)
Min PSAR (mg m-2 yr-1)
Distance From Shore (m)
Distance From Shore (m)
Distance From Shore (m)

Figure 4

Figure 5. Bivariate plots of the relationship between five SARs and macrophyte biomass. Black circles represent measurements for the within weedbed portion of the study and open circles represent measurements taken among weedbeds at the depth of MSMB. a) TSAR; b) BSAR; c) OSAR; d) PSAR; and e) MinPSAR. Linear regressions are plotted for pooled data when allowed for by ANCOVA, and separately for each portion of the study when slopes are significantly different. Regression equations are given in Table 4.

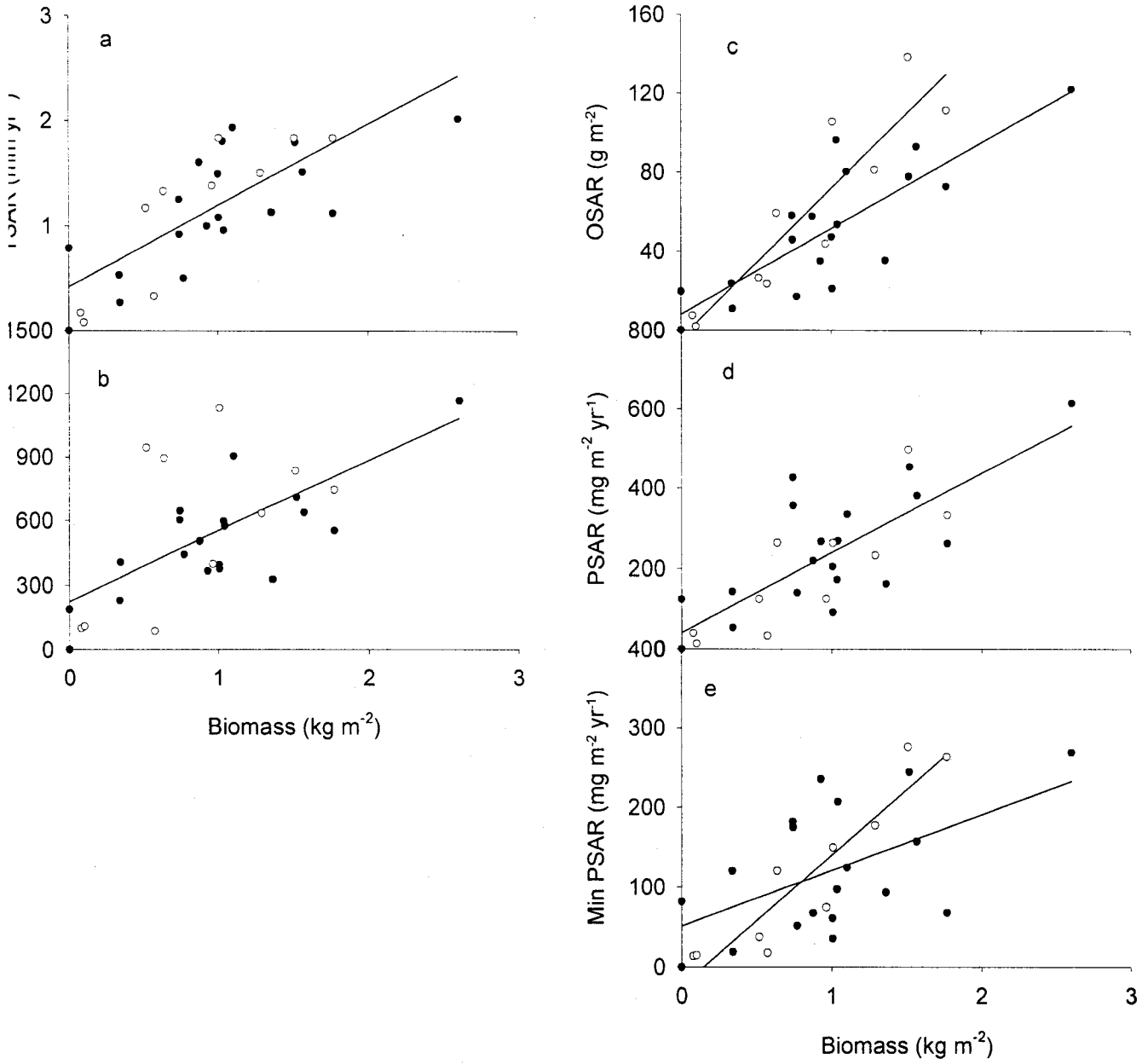

a
b
c
d
e
Biomass (kg m-2)
Biomass (kg m-2)
OSAR (g m-2)
PSAR (mg m-2 yr-1)
Min PSAR (mg m-2 yr-1)

Figure 5

Figure 6. Box plots of sediment accumulation rates in the littoral and profundal zones of Lake Memphremagog. The horizontal bars indicate the median, 25^{th}, and 75^{th} percentiles and the error bars represent the 10^{th} and 90^{th} percentiles for a) Bulk sediment accumulation rate; and b) phosphorus sediment accumulation rate. Profundal data from Flett and Marshall 1983.

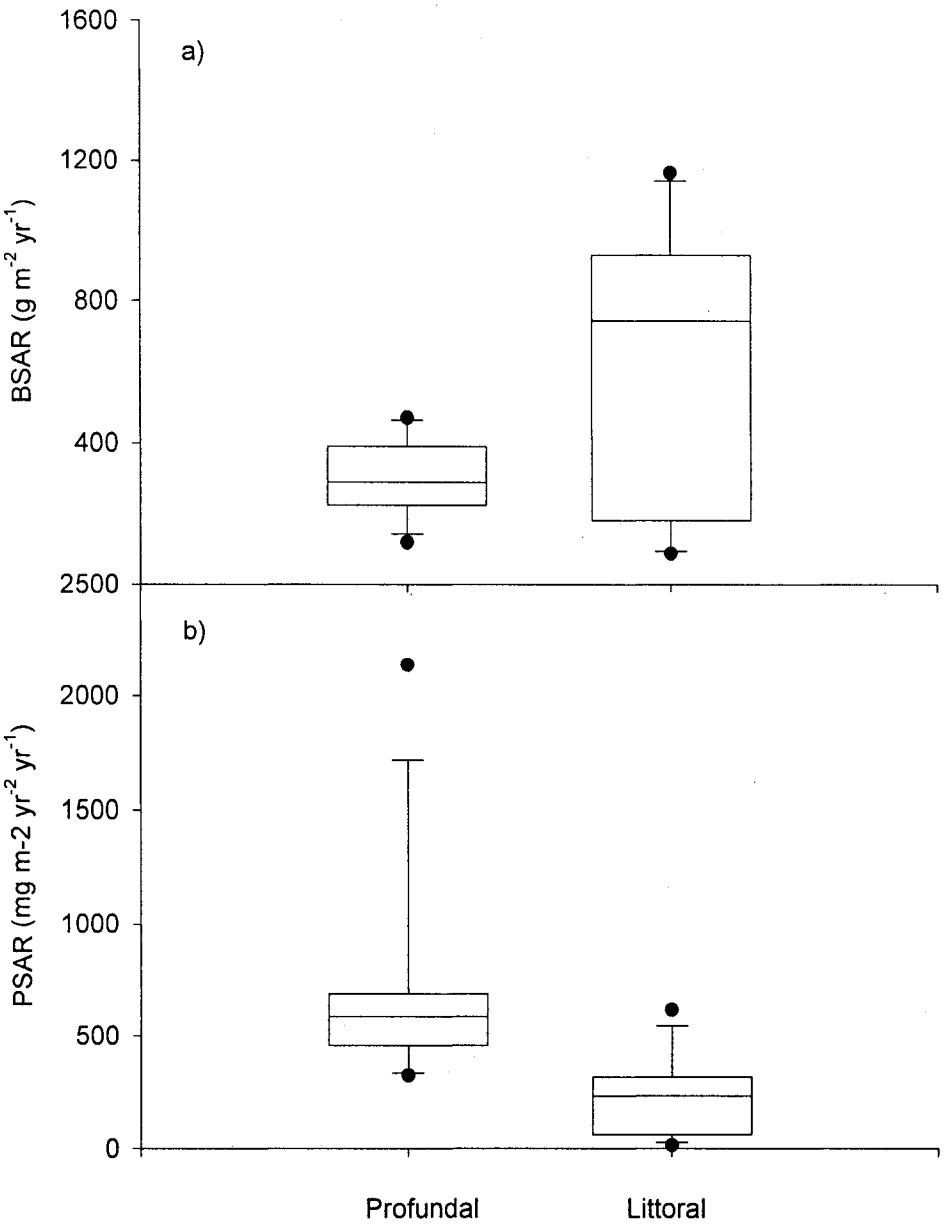

a)
b)
BSAR (g m-2 yr-1)
PSAR (mg m-2 yr-2 yr-1)
1600
1200
800
400
2500
2000
1500
1000
500
0
Profundal
Littoral

Figure 6

General Conclusion

In an article entitled *Effects of submersed macrophytes on ecosystem processes*, Carpenter and Lodge (1986) pointed out that limnologists had focused almost exclusively on environmental factors that determine the biomass and distribution of submerged macrophytes in lakes, largely ignoring the influence of these plants on ecosystem processes. Since then, limnologists have examined the influence of submerged macrophytes on water column nutrients and biota at small scales, but have been slow to incorporate the littoral zone into models of whole lake structure and function. The concept of 'alternative equilibrium' in shallow productive lakes (Scheffer et al 1993) illustrated the general negative relationship between phytoplankton and submerged macrophytes at whole lake scales, and spawned a considerable amount of work that explored the mechanisms responsible for this general relationship (See Jeppesen et al. 1998). Basic relationships between submerged macrophyte distribution and lake phosphorus cycling and bacterioplankton metabolism, however, have remained less clear. It was with this in mind that I embarked on this thesis.

A central theme of this thesis is that macrophyte effects on ecosystem processes are scale dependent, and Chapter 1 provides an introduction to the concept. In contrast to the generally observed negative relationship between phytoplankton and macrophytes observed at other scales (Blindlow and others 1993, Scheffer and Jeppesen 1998, Søndergaard and Moss 1998), between two growing seasons macrophyte distribution, phytoplankton biomass and epilimnetic phosphorus concentrations increased in lakes as a result of an earlier and warmer growing season. On an inter-annual temporal scale, therefore, macrophyte and phytoplankton production can be positively correlated. Within

the 1998 growing season, however, submerged macrophytes are indeed associated with lower phytoplankton biomass both within (Chapter 2) and among (Chapter 3) systems.

Concern about nutrient enrichment of lakes, and the finding that submerged macrophytes derive their P almost exclusively from the rich sediment pool (e.g. Carignan and Kalff 1980) led to studies examining the potential for submerged macrophytes to act as a conduit for P from the littoral sediment to the open water (internal loading). While many studies cited submerged weedbeds as net sources of phosphorus to the open water (Prentki and others 1979, Carpenter 1980, Adams and Prentki 1982, Smith and Adams 1986), predictions of water column enrichment resulting from submerged macrophyte P release were not, however, demonstrated in nature. In Chapter 2, I show that although a large, undisturbed weedbed was a source of phosphorus to the open water in the late summer, this was roughly balanced over the summer by the weedbed being a net sink for phosphorus at other points in the growing season. In contrast to the moderate influence of the weedbed on whole lake phosphorus dynamics, late summer onset of senescence was linked to a marked increase in bacterioplankton production which, when extrapolated to five nearby lakes, predicted marked increases in bacterioplankton production in macrophyte dominated lakes.

The difficulty in scaling up from observations made at smaller scales to whole lake scales has recently become a topic of discussion in limnology (Harris 1994, Kalff 2001). In Chapter 3, I test hypotheses that are generated based on the results of the mass balance study of Chapter 2. This chapter demonstrates that epilimnetic levels of phosphorus, phytoplankton biomass, planktonic respiration and bacterioplankton production vary differentially among lakes along a gradient of macrophyte cover. Phytoplankton biomass

(chlorophyll *a*) was lower in macrophyte dominated lakes, despite relatively high levels of soluble phosphorus. Further, planktonic respiration and bacterioplankton production were higher in macrophyte rich lakes than would be expected from phytoplankton biomass alone, pointing to a subsidization of bacterioplankton metabolism by macrophyte beds at the whole lake scale. These results are consistent with those found in Chapter 2, and show that the classical view of pelagic interactions that proposes phosphorus determines phytoplankton abundance, which in turn determines bacterial abundance through the production of organic carbon, becomes rapidly less relevant as macrophyte cover increases.

An examination of phosphorus and sediment accumulation in weedbeds (Chapter 4) provided the thesis with the most significant insight into the role of submerged macrophyte beds on phosphorus cycling. The results clearly show macrophyte beds to be a phosphorus sink over long (~115 yr) time periods and that the degree to which weedbeds are both phosphorus and sediment sinks is a function of macrophyte biomass. The sediment core approach was initially chosen, as it has the advantage of giving a time integrated expression not confounded by seasonal or interannual variation, which can be significant (Chapters 1 and 2). Two more important aspects of weedbed effects on phosphorus cycling emerged from the analysis. First, when compared to the results of the mass balance study (Chapter 2), the results indicate that the majority of phosphorus accumulation by weedbeds does not occur during the summer, when plants are most metabolically active. Instead, high spring runoff events, generally associated with increases in total suspended solids, appear to provide a source of largely inorganic particulate bound phosphorus to weedbeds. Second, that weedbeds accumulate far less

phosphorus per unit bulk sediment compared to the profundal zone (while accumulating the same fine particles) indicates that the majority of particle associated phosphorus that is deposited in weedbeds is recycled back into the pelagic zone. The results from the mass balance (Chapter 2) show that this export does not occur in the water or the plankton during the summer, whereas there is support in the literature for an export of phosphorus from weedbeds through fish feeding on littoral benthos (Vadeboncoeur et al. 2002).

In conclusion, the broad goal of this thesis was to examine submerged macrophyte biomass, distribution, and ecosystem effects at scales large enough to incorporate the littoral zone into whole lake models. Field based observations of unperturbed weedbeds provided insights that would be invisible during small-scale experimental manipulations. Combined, the results demonstrate the importance of submerged macrophyte beds in modifying pelagic metabolism and phosphorus cycling at the whole lake scale, and represent an important first step in incorporating weedbeds into whole lake structure and function.

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Appendix A

Appendix A consists of the mean macrophyte bed characteristics for lakes analyzed in Chapters 1 and 3.

Lake	Mean weedbed Length (m)	Plant Depth (m)	Mean Biomass MSMB (gm-2)	Area (m2)	Area Colonized	Percent Colonized
1997						
Brome	99	2.33	531	14169698	1021635	7.21
D'Argent	79	2.13	458	1083495	283230	26.14
Magog	123	2.53	755	9265515	1186939	12.81
Roxton	60	1.27	288	1790000	275425	15.39
Waterloo	21	1.40	241	1500000	87987	5.87
1998						
Biovin	0	0.00	0	130000	0	0.00
Bromont	23	1.48	752	4807692	175930	3.66
Fitch	42	2.18	700	2430000	226545	9.32
Waterloo	43	1.28	285	1500000	171287	11.42
Brome	133	3.39	691	14169698	2565378	18.10
Magog	180	3.62	1350	9265515	1750972	18.90
D'Argent	91	2.36	582	1083495	306626	28.30
Roxton	204	3.64	824	1790000	1042903	58.26
Hertel	93	5.59	1781	290000	190116	65.56

Appendix B

Appendix B Consists of variables and measurements used in the mass balance study (Chapter 2)

SP = Soluble phosphorus

TP = Total phosphorus

PP = Particulate phosphorus

Chla = Chlorophyll *a*

Respiration = Total plankton oxygen consumption

Bacterial production = Bacterioplankton production estimated using ^{3}H – leucine incorporation

Date	Discharge (l sec-1)	Percent Fitch	In SP (mg/m3)	Out SP (mg/m3)	In TP (mg/m3)	Out TP (mg/m3)	In PP (mg/m3)	Out PP (mg/m3)	In Chla (mg/m3)	Out Chla (mg/m3)
6/12	15.80	0.56	7.78	8.66	33.32	28.55	25.54	19.90	20.11	17.85
6/15	15.80	0.56	4.71	4.96	28.91	28.35	24.21	23.38	45.32	19.92
6/21	22.60	0.83	4.81	6.14	23.73	27.94	18.92	21.79	53.02	40.10
6/30	18.50	0.90	9.41	8.96	28.50	25.62	19.09	16.66	22.83	22.62
7/6	17.92	0.92	6.33	8.50	23.45	23.05	17.12	14.55	28.91	11.77
7/14	17.26	0.94	10.47	11.78	23.05	22.70	12.58	10.91	12.55	11.95
7/21	16.68	0.75	7.49	8.87	18.51	20.00	11.03	11.13	15.13	21.38
7/28	16.10	0.86	7.90	9.18	20.10	20.67	12.21	11.49	11.10	21.87
8/3	15.60	0.85	8.24	3.56	15.95	17.68	7.71	14.13	15.62	12.66
8/11	19.21	0.87	6.53	12.41	17.96	26.48	11.44	14.08	22.39	10.80
8/21	22.10	0.65	5.26	2.97	20.04	29.56	14.78	26.59	21.55	9.00
8/29	19.85	0.63	21.30	6.30	22.31	19.48	1.01	13.18	20.37	10.81
9/4	18.17	0.61	13.88	6.96	28.42	21.86	14.55	14.90	19.64	9.94
9/11	16.20	0.58	11.95	9.94	36.26	19.84	24.31	9.90	27.43	6.80
9/17	14.52	0.56	9.45	5.68	29.35	17.10	19.90	11.42	31.52	14.44
9/22	13.12	0.54	4.84	4.03	27.87	13.58	23.03	9.55	28.40	11.91
10/12	7.50	0.46	9.74	6.61	20.34	13.53	10.61	6.92	29.52	13.83

Date	In Respiration (mg O2 l-1 day-1)	Out Respiration (mg O2 l-1 day-1)	Mean In POC (mg l-1)	Mean Out POC (mg l-1)	In Bacterial Production (gC l-1 day-1)	Out Bacterial Production (gC l-1 day-1)
6/12			1.05	0.84	1.77E-06	5.50E-07
6/15	0.07	0.41			6.09E-07	7.74E-07
6/21	1.73	0.22	2.06	1.66	2.16E-07	3.95E-07
6/30	0.19	0.45	1.32	1.30	3.51E-06	6.62E-06
7/6	0.67	0.40	1.60	0.65	5.68E-07	1.42E-06
7/14	1.03	1.55	1.23	1.01	4.50E-07	8.29E-07
7/21			1.30	0.89	2.95E-07	1.34E-06
7/28	0.39	0.70	1.14	1.32	5.70E-07	1.64E-06
8/3	0.57	0.35	1.30	0.61	1.06E-08	4.74E-07
8/11	0.57	0.50	1.16	0.88	2.22E-07	3.05E-07
8/21	0.23	0.24	0.89	0.76	7.87E-07	7.10E-06
8/29	0.43	0.51	0.86	0.53	1.52E-08	7.67E-06
9/4	0.36	0.31	0.89	1.05	6.71E-06	1.51E-05
9/11	0.68	0.44	1.05	0.50	2.12E-06	6.60E-07
9/17	0.07	0.13	1.15	0.43	7.31E-07	9.29E-07
9/22	1.90	0.45	0.67	1.17		
10/12	0.71	0.54	0.95	0.68		

Appendix C

Appendix C consists of epilimnetic measurements made in the summer of 1998. Data was used in analysis in Chapter 3.

Lake	Date	SP	Standard Deviation	TP	Standard Deviation	Chl a	Standard Deviation	Respiration	BP
Boivin	06/18/98	23.0	0.73	91.5	2.07	79.8	9.35	1.6	14.3
Boivin	07/07/98	66.5		72.5	2.15	53.4	3.88	0.5	25.3
Boivin	07/30/98	24.2	0.44	133.4	2.39	69.1	2.25	1.6	53.0
Boivin	08/13/98	29.6	1.28	129.9	2.21	93.4	3.96	2.5	84.2
Boivin	08/20/98	21.9	1.54	151.5	5.29	110.0	2.41	1.9	57.0
Boivin	09/08/98	18.5	1.28	131.1	3.87	100.6	7.83	0.6	
Boivin	09/22/98	11.8	0.96	96.3	1.70	39.5	3.18	1.3	
Brome	06/15/98	3.4	1.08	15.9	0.76	6.9	1.09	0.2	14.5
Brome	07/03/98	9.2	1.55	19.3	0.83	6.7	1.12	0.1	23.6
Brome	07/29/98	5.5	2.39	13.4	0.09	9.3	0.69	0.2	5.0
Brome	08/12/98	6.0	0.68	19.1	2.67	11.0	1.08	0.3	7.5
Brome	08/20/98	6.1	0.71	18.8	0.96	6.2	0.37	0.2	8.5
Brome	09/03/98	10.4	0.63	32.8	10.07	18.6	1.49	0.5	28.0
Brome	09/17/98	9.5	0.52	29.4	0.78	22.8	5.92	0.7	
Bromont	06/27/98	9.2	1.41	25.0	1.61	19.2	0.04	0.4	5.1
Bromont	07/04/98	6.3	0.95	19.2	2.82	12.7	0.17	0.5	0.2
Bromont	07/31/98	7.2	0.95	28.8	1.13	32.2	0.43	0.4	1.0
Bromont	08/14/98	10.8	1.26	28.0	4.53	17.0	0.73	0.9	14.7
Bromont	08/23/98	6.5	1.29	23.4	1.85	9.9	5.87	0.9	39.2
Bromont	08/28/98	10.3	0.40	26.6	1.45	11.8	1.77	0.6	9.6
Bromont	09/23/98	5.7	0.53	28.3	3.24	9.2	4.11	0.6	
d'Argent	06/18/98	14.5	0.45	47.1	1.20	40.8	0.94	0.0	7.1
d'Argent	06/29/98	5.7	0.17	9.7	0.43	4.4	1.39	0.2	34.7
d'Argent	07/30/98	1.2	0.39	6.1	1.15	5.5	1.08	0.1	8.4
d'Argent	08/13/98	5.8	0.45	10.1	1.89	3.5	0.26	0.5	5.8
d'Argent	08/19/98	6.0	1.23	7.9	1.05	3.7	1.00	0.2	1.7
d'Argent	08/27/98	7.8	1.37	12.5	1.49	2.1	0.07	0.2	0.6
d'Argent	09/21/98	9.5	0.89	19.7	2.88	5.9	0.25	0.4	
Hertel	06/22/98	6.7	1.20	12.2	1.39	2.1	0.11	0.3	6.9
Hertel	07/06/98	5.0	0.70	9.3	1.81	2.6	0.41	0.3	3.2
Hertel	07/31/98	3.8	0.41	7.3	0.36	3.5	0.43	0.0	4.8
Hertel	08/14/98	6.4	0.63	14.0	3.67	1.5	0.40	0.3	6.1
Hertel	08/23/98	8.9	4.19	11.4	2.41	2.4	0.24	0.1	4.4
Hertel	08/26/98	5.0	0.26	12.1	1.69	2.4	0.15	0.4	1.3
Hertel	09/23/98	4.9	1.04	11.4	0.34	1.3	0.20	0.4	
Magog	06/17/98	8.7	2.76	18.5	3.36	6.4	0.14	0.2	5.4
Magog	07/03/98	9.0	2.38	26.1	1.37	11.2	1.56	0.1	1.9
Magog	07/30/98	3.9	0.39	11.7	1.48	6.3	3.81	0.3	11.1
Magog	08/12/98	6.4	0.62	7.7	0.27	5.6	0.32	0.2	5.5
Magog	08/19/98	3.8	0.30	18.7	1.67	5.1	0.81	0.3	5.1
Magog	09/02/98	9.5	0.32	30.4	5.48	8.1	0.66	0.4	2.7
Magog	09/17/98	5.7	1.06	17.1	2.62	8.7	0.74	0.5	
Roxton	06/17/98	8.8	0.35	18.8	2.65	4.9	0.12	0.7	6.0
Roxton	07/06/98	9.3	0.49	16.9	1.97	8.7	0.43	0.5	4.8
Roxton	07/31/98	7.3	0.49	16.5	0.46	4.5	1.63	0.2	10.6
Roxton	08/13/98	9.6	0.18	25.1	3.54	11.3	2.09	0.4	4.3
Roxton	08/20/98	4.7	0.60	18.5	4.75	26.9	4.88	0.3	13.1
Roxton	09/04/98	8.5	0.57	29.1	2.52	27.1	0.37	0.5	49.8
Roxton	09/23/98	9.1	1.84	32.4	5.31	19.9	3.21	0.7	
Waterloo	06/17/98	14.0	0.22	59.8	1.52	79.9	3.33	1.9	1.9

Lake	Date	SP	Standard Deviation	TP	Standard Deviation	Chl a	Standard Deviation	Respiration	BP	
Waterloo	06/29/98	20.0	1.03	46.8	4.44	45.3	2.99	1.2		139.2
Waterloo	07/29/98	8.3		35.0	1.19	43.0	0.68	0.7		27.7
Waterloo	08/12/98	19.3	3.55	38.2	1.52	72.3	3.85	0.9		5.6
Waterloo	08/19/98	26.8	2.76	42.1	0.33	142.6	11.24	0.9		15.9
Waterloo	08/27/98	25.0	1.67	53.9	3.50	27.5	1.54	0.9		16.9
Waterloo	09/21/98	18.2	6.10	43.5	0.38	22.1	13.11	0.9		

Appendix D

Appendix D consists of site characteristics and sediment accumulation rates used in chapter 4.

TSAR = Total sediment accumulation

BSAR = Bulk sediment accumulation

OSAR = Organic sediment accumulation

PSAR = Phosphorus sediment accumulation

MinPSAR = Minimum estimate of phosphorus sediment accumulation

Study	Site	Biomass (g m-2)	TSAR (mm yr-1)	BSAR (g m-2 yr-1)	OSAR (g m-2 yr-1)	PSAR (mg m-2 yr-1)	MinPSAR (mg m-2 yr-1)
Within	T1Q1	344	0.27	406.18	10.92	54.64	18.43
Within	T1Q2	771	0.5	442.26	17.1	140.39	51.45
Within	T1Q3	1103	1.93	903.89	80.56	334.3	124.51
Within	T1Q4	1566	1.51	639.06	93.15	380.91	157.03
Within	T1Q5	2603	2.02	1166.96	122.82	615.59	268.96
Within	T1Q6	1767	1.12	554.08	73.23	262.74	67.61
Within	T1Q7	1007	1.08	376.22	21.15	92.8	35.19
Within	T2Q3	1036	1.8	596.77	96.38	173.44	97.2
Within	T2Q4	877	1.6	504.54	57.9	219.94	67.42
Within	T2Q5	1517	1.79	708.96	78.08	453.34	244.42
Within	T2Q6	744	0.92	645.5	46	355.8	174.8
Within	T2Q7	0	0	0	0	0	0
Within	T3Q1	929	1	366.24	35.09	267.25	235.47
Within	T3Q2	1005	1.49	394.71	47.4	204.8	60.89
Within	T3Q3	742	1.25	601.56	58.3	426.98	181.65
Within	T3Q4	1360	1.13	328.14	35.5	162.93	93.23
Within	T3Q5	1042	0.96	574.87	53.84	268.23	206.7
Within	T3Q6	339	0.53	228.83	23.73	143.89	120.17
Within	T3Q7	0	0.79	189.06	19.66	124.38	81.45
Among	1	78	0.17	101.3	7.44	40.08	13.55
Among	2	100	0.08	109.83	1.91	14.28	14.28
Among	3	519	1.17	941.91	26.54	125.29	37.22
Among	4	574	0.33	88	23.57	34.47	17.45
Among	5	638	1.33	893.86	59.55	264.21	120.47
Among	6	964	1.38	398.83	44.05	126.34	74.44
Among	7	1009	1.83	1129.71	105.72	263.23	149.53
Among	8	1289	1.5	634.58	81.58	232.78	177.36
Among	9	1510	1.83	833.86	139.07	497.55	276.02
Among	10	1767	1.83	744.83	111.78	332.23	263.28

Appendix E

Appendix E consists of raw sediment core data used to calculate sediment accumulation rates in Chapter 4

Transect	Core	Depth (cm)	Dry Weight (g)	Water Content (%)	%organic	Organic Matter (g)	Mean P (micro g g-1)	[Pb] ppm
1	1	1	56.1	32.4	4.4	2.4	179.3	10.2
1	1	3	68.4	20.7	1.3	0.9	97.8	9.3
1	1	5	73.4	20.2	1.5	1.1	122.1	4.3
1	1	7	72.7	16.4	1.0	0.7	180.7	4.7
1	1	9	77.5	21.1	1.0	0.8	151.7	6.0
1	1	11	79.0	21.1	0.5	0.4	74.9	8.3
1	1	13	80.0	19.9	0.6	0.5	138.8	4.5
1	1	15	78.7	19.1	0.9	0.7	54.2	5.3
1	1	17	77.6	19.2	1.2	1.0	36.5	6.9
1	1	19	74.8	22.9	1.8	1.4	110.4	7.1
1	1	21	76.5	19.0	1.4	1.1	159.7	6.3
1	2	0.5	16.8	48.3	4.4	0.7	314.2	9.2
1	2	1.5	19.5	38.9	3.5	0.7	343.8	8.9
1	2	2.5	18.5	36.7	3.2	0.6	317.2	9.3
1	2	3.5	26.8	30.7	3.6	1.0	414.2	10.1
1	2	4.5	27.0	26.2	3.4	0.9	229.6	8.3
1	2	5.5	26.9	31.5	5.0	1.4	292.0	11.1
1	2	6.5	28.0	26.0	2.9	0.8	175.5	4.9
1	2	7.5	33.2	22.1	4.2	1.4	158.2	5.1
1	2	8.5	37.1	15.7	1.2	0.4	248.2	5.8
1	2	9.5	36.3	16.8	0.7	0.3	158.0	5.2
1	2	10.5	36.7	19.3	0.7	0.3	233.4	4.3
1	2	11.5	39.0	22.3	0.5	0.2	118.0	5.5
1	2	12.5	43.8	20.0	0.4	0.2	101.8	2.4
1	2	13.5	40.6	17.7	0.7	0.3	136.0	2.7
1	2	14.5	37.7	26.1	0.6	0.2	109.2	4.0
1	2	15.5	45.6	15.9	0.5	0.2	182.9	4.4
1	2	16.5	32.6	24.0	3.2	1.0	178.9	4.1
1	2	17.5	25.1	24.4	2.6	0.7	203.9	5.8
1	3	1	12.0	74.0	13.7	1.6	415.9	18.6
1	3	3	15.7	71.4	12.8	2.0	404.8	19.7
1	3	5	17.8	67.7	13.5	2.4	437.9	25.6
1	3	7	20.7	64.0	12.6	2.6	430.3	23.4
1	3	9	20.3	64.6	12.6	2.6	534.5	23.4
1	3	11	22.0	63.6	10.2	2.2	394.4	28.3
1	3	13	27.8	55.9	8.7	2.4	469.4	26.1
1	3	15	32.2	51.5	7.3	2.3	409.4	23.4
1	3	17	32.4	53.1	8.0	2.6	416.7	25.3
1	3	19	34.2	42.9	5.2	1.8	283.4	23.6
1	3	21	41.8	39.4	5.0	2.1	129.0	14.4
1	3	21	38.3	50.1	7.0	2.7	146.3	7.6
1	4	1	6.4	84.3	19.6	1.3	1179.2	27.2
1	4	3	12.6	76.1	25.9	3.3	1016.6	25.8
1	4	5	11.9	77.2	17.2	2.0	979.1	27.2
1	4	7	14.8	73.1	16.1	2.4	916.6	30.4
1	4	9	19.3	65.8	22.4	4.3	740.9	28.6

Transect	Core	Depth (cm)	Dry Weight (g)	Water Content (%)	%organic	Organic Matter (g)	Mean P (micro g g-1)	[Pb] ppm
1	4	11	22.3	61.1	15.0	3.3	652.0	22.4
1	4	13	29.3	55.0	8.2	2.4	537.0	27.8
1	4	15	38.3	45.0	14.0	5.4	309.7	20.6
1	4	17	40.9	43.7	10.2	4.2	358.7	19.4
1	4	19	51.8	35.7	3.3	1.7	211.2	10.4
1	4	21	59.2	30.9	2.5	1.5	140.9	6.4
1	4	23	53.8	35.5	4.1	2.2	306.3	5.2
1	4	25	18.1	70.6	26.0	4.7	324.4	5.8
1	4	27	39.3	46.5	7.9	3.1	236.7	4.8
1	4	29	60.9	31.3	2.4	1.5	253.9	6.0
1	5	1	7.1	81.3	20.8	1.5	999.2	27.2
1	5	3	15.6	68.3	23.1	3.6	866.3	25.0
1	5	5	14.2	69.3	25.6	3.6	835.8	24.0
1	5	7	22.0	57.6	15.7	3.5	814.1	27.2
1	5	9	34.5	24.8	14.1	4.8	792.6	20.6
1	5	11	49.3	29.1	17.6	8.7	761.1	22.0
1	5	13	40.1	35.0	11.4	4.6	635.9	25.0
1	5	15	31.3	50.9	6.7	2.1	369.0	16.0
1	5	17	43.6	38.6	4.3	1.9	264.1	16.0
1	5	19	52.0	33.7	3.8	2.0	212.9	14.6
1	5	21	47.8	35.4	3.0	1.4	286.1	11.6
1	5	23	50.2	40.6	5.1	2.5	181.9	5.2
1	5	25	45.7	39.4	5.4	2.5	206.6	4.8
1	5	27	43.4	39.8	4.1	1.8	305.5	5.4
1	5	29	38.8	45.6	6.3	2.4	526.4	7.2
1	5	31	36.5	48.9	10.9	4.0	515.5	9.8
1	6	1	6.4	81.5	22.8	1.5	767.4	24.8
1	6	3	14.7	73.5	27.6	4.1	645.2	24.0
1	6	5	17.1	69.2	17.0	2.9	707.2	24.2
1	6	7	21.7	61.1	11.3	2.4	586.3	22.6
1	6	9	31.3	49.1	15.9	5.0	436.3	18.8
1	6	11	39.6	42.2	11.0	4.3	479.3	13.8
1	6	13	38.9	43.7	5.7	2.2	221.2	12.2
1	6	15	44.0	37.3	19.3	8.5	154.0	6.2
1	6	17	42.2	41.8	28.5	12.0	93.3	5.2
1	6	19	38.2	46.2	6.2	2.4	195.7	4.6
1	6	21	51.2	35.0	9.7	5.0	103.0	3.6
1	6	23	47.1	38.5	8.9	4.2	127.1	3.4
1	6	25	49.4	38.1	7.0	3.4	135.1	3.6
1	6	27	55.5	33.8	9.4	5.2	122.6	4.6
1	7	1	27.1	50.1	5.8	1.6	267.3	13.0
1	7	3	41.4	40.3	5.2	2.1	325.6	12.0
1	7	5	46.8	36.3	5.9	2.8	164.8	12.2
1	7	7	45.7	35.9	4.0	1.8	93.5	6.6
2	3	1	6.6	83.3	25.9	1.7	412.0	27.6

Transect	Core	Depth (cm)	Dry Weight (g)	Water Content (%)	%organic	Organic Matter (g)	Mean P (micro g g-1)	[Pb] ppm
2	3	3	8.7	81.1	19.1	1.7	548.0	27.5
2	3	5	12.5	77.1	23.5	2.9	387.1	31.3
2	3	7	13.3	74.7	18.0	2.4	390.4	32.1
2	3	9	17.2	68.7	12.4	2.1	322.3	43.0
2	3	11	19.9	76.3	13.6	2.7	293.1	39.5
2	3	13	24.0	61.9	17.7	4.2	314.6	35.8
2	3	15	19.8	64.4	11.2	2.2	260.2	39.0
2	3	17	21.6	63.8	10.6	2.3	187.4	29.0
2	3	19	22.5	60.0	20.9	4.7	186.0	24.5
2	3	21	16.9	65.4	15.1	2.5	198.9	20.1
2	3	23	18.5	66.7	11.1	2.1	161.4	14.1
2	3	25	26.4	56.9	10.4	2.8	160.9	8.5
2	3	27	25.1	59.2	11.2	2.8	166.0	10.9
2	4	1	8.7	82.0	16.6	1.4	512.5	27.4
2	4	3	14.8	72.0	16.2	2.4	592.7	30.1
2	4	5	14.9	73.1	13.9	2.1	510.9	34.3
2	4	7	17.2	68.6	12.5	2.2	463.1	36.5
2	4	9	23.3	62.1	10.6	2.5	305.6	37.9
2	4	11	25.2	60.2	9.5	2.4	453.5	36.0
2	4	13	25.0	60.8	9.2	2.3	408.0	27.0
2	4	15	25.6	59.4	9.8	2.5	386.3	13.0
2	4	17	23.4	63.1	10.4	2.4	278.4	9.8
2	4	19	23.2	61.6	10.8	2.5	133.5	11.6
2	5	1	11.0	78.7	13.6	1.5	951.9	33.0
2	5	3	16.8	70.6	14.7	2.5	906.8	33.6
2	5	5	22.6	63.7	13.2	3.0	738.0	36.2
2	5	7	25.8	59.4	9.3	2.4	689.9	35.4
2	5	9	29.0	52.9	8.8	2.5	565.4	29.2
2	5	11	27.0	55.0	9.9	2.7	594.5	11.2
2	5	13	23.0	61.6	13.1	3.0	576.4	20.0
2	5	15	27.9	54.8	10.8	3.0	543.1	14.4
2	5	17	34.1	47.3	9.8	3.3	522.4	11.4
2	5	19	36.0	49.0	7.1	2.6	344.5	5.4
2	6	0.75	10.9	72.3	10.6	1.2	808.0	24.4
2	6	2.25	17.3	62.4	8.6	1.5	651.3	17.4
2	6	3.75	22.1	73.7	7.3	1.6	498.3	14.5
2	6	5.25	27.8	46.1	6.1	1.7	543.0	13.9
2	6	6.75	31.0	42.4	5.7	1.8	513.1	13.2
2	6	8.25	32.2	38.4	5.7	1.8	489.6	6.8
2	6	9.75	29.5	44.5	7.5	2.2	631.3	8.4
2	6	11.25	27.0	48.2	8.7	2.4	465.1	10.2
2	6	12.75	32.8	41.9	6.7	2.2	270.6	4.8
2	7	0.5	34.8	23.9	1.8	0.6	320.1	6.2
2	7	1.5	35.5	16.5	1.5	0.5	333.8	8.2
2	7	2.5	35.2	18.3	1.5	0.5	373.2	7.7

Transect	Core	Depth (cm)	Dry Weight (g)	Water Content (%)	%organic	Organic Matter (g)	Mean P (micro g g-1)	[Pb] ppm
2	7	3.5	36.9	18.0	0.9	0.3	297.9	7.2
2	7	4.5	40.5	17.6	0.8	0.3	330.2	9.2
2	7	5.5	37.4	20.9	2.1	0.8	201.5	7.6
2	7	6.5	30.8	25.3	7.8	2.4	453.9	6.6
2	7	7.5	22.9	36.5	12.8	2.9	681.9	7.8
2	7	8.5	25.8	27.3	3.0	0.8	423.6	10.4
2	7	9.5	36.6	22.0	0.9	0.3	251.1	8.4
2	7	10.5	38.7	19.8	0.5	0.2	267.4	11.0
2	7	11.5	38.1	18.9	2.8	1.1	237.4	7.6
3	1	0.5	7.2	78.3	8.8	0.6	930.7	26.2
3	1	1.5	6.9	75.3	9.6	0.7	985.6	27.6
3	1	2.5	6.5	76.9	9.5	0.6	827.1	27.4
3	1	3.5	8.6	71.7	9.4	0.8	779.0	29.8
3	1	4.5	8.4	69.9	9.3	0.8	726.7	30.8
3	1	5.5	9.4	68.3	9.0	0.8	734.2	29.8
3	1	6.5	10.1	66.2	9.2	0.9	782.6	30.4
3	1	7.5	10.8	67.0	9.6	1.0	647.3	26.5
3	1	8.5	10.9	63.7	9.9	1.1	647.5	28.9
3	1	9.5	11.0	63.5	9.2	1.0	692.2	25.8
3	1	10.5	12.1	63.4	9.9	1.2	550.8	21.4
3	1	11.5	10.3	65.4	11.2	1.1	686.5	23.2
3	1	12.5	4.1	65.4	15.9	0.6	630.8	7.7
3	2	1	6.9	79.3	9.8	0.7	922.0	25.0
3	2	3	9.6	78.3	9.7	0.9	653.2	25.4
3	2	5	14.0	70.4	8.8	1.2	599.1	25.6
3	2	7	14.0	66.7	8.3	1.2	825.8	27.4
3	2	9	16.0	64.4	9.2	1.5	520.4	24.9
3	2	11	16.3	63.6	9.4	1.5	316.3	23.6
3	2	13	16.5	63.3	7.8	1.3	492.0	18.6
3	2	15	15.4	62.3	13.1	2.0	332.8	18.2
3	2	17	12.2	70.2	34.5	4.2	279.3	14.0
3	2	19	23.0	51.4	5.3	1.2	160.1	3.6
3	2	21	23.1	48.6	4.2	1.0	148.2	2.4
3	3	1	15.5	72.1	10.1	1.6	949.0	24.0
3	3	3	22.8	61.5	9.7	2.2	897.2	24.1
3	3	5	21.5	65.1	9.1	1.9	786.6	27.4
3	3	7	25.2	59.2	9.5	2.4	720.7	21.5
3	3	9	25.2	59.3	10.6	2.7	569.4	23.9
3	3	11	21.8	64.7	10.2	2.2	699.3	45.1
3	3	13	22.5	63.9	10.3	2.3	756.2	46.4
3	3	15	29.8	53.9	8.6	2.5	468.0	22.1
3	3	17	46.6	42.2	5.0	2.3	386.3	4.7
3	3	19	35.3	52.0	6.8	2.4	223.0	4.1
3	3	21	4.0	60.0	10.8	0.4	380.5	4.9
3	4	1	17.9	71.1	10.9	2.0	650.9	24.5

Transect	Core	Depth (cm)	Dry Weight (g)	Water Content (%)	%organic	Organic Matter (g)	Mean P (micro g g-1)	[Pb] ppm
3	4	3	20.0	66.7	11.1	2.2	456.9	25.8
3	4	5	19.6	66.1	10.4	2.0	515.6	27.5
3	4	7	20.9	64.7	10.6	2.2	451.8	25.0
3	4	9	22.2	64.9	11.1	2.5	433.2	22.7
3	4	11	25.1	58.4	8.1	2.0	322.2	8.4
3	4	13	34.7	49.3	7.0	2.4	252.5	3.8
3	4	15	31.9	51.3	6.4	2.0	239.9	3.3
3	5	1	20.0	55.0	10.5	2.1	629.6	13.6
3	5	3	23.5	59.2	10.0	2.4	619.5	17.8
3	5	5	38.2	43.0	8.5	3.3	562.0	16.0
3	5	7	31.3	50.4	7.9	2.5	426.3	19.0
3	5	9	31.6	48.0	7.9	2.5	343.9	18.4
3	5	11	31.6	47.3	12.1	3.8	297.3	9.4
3	5	13	30.7	49.5	14.2	4.3	303.6	6.4
3	5	15	30.4	46.7	13.9	4.2	417.7	4.0
3	5	17	31.9	50.3	14.5	4.6	371.3	4.4
3	5	19	30.9	49.9	15.1	4.7	338.1	3.2
3	5	21	27.5	52.1	15.3	4.2	328.4	4.2
3	5	23	29.1	51.2	13.4	3.9	361.8	4.0
3	6	1	14.2	70.0	11.6	1.7	786.7	25.2
3	6	3	30.0	51.6	10.7	3.2	603.9	19.4
3	6	5	25.9	54.6	9.3	2.4	570.8	28.4
3	6	7	21.2	60.5	10.3	2.2	441.5	17.2
3	6	9	22.2	61.2	11.5	2.6	556.3	14.2
3	6	11	24.8	55.8	14.2	3.5	507.3	15.8
3	6	13	24.3	54.0	14.3	3.5	539.6	11.6
3	6	15	13.8	73.7	15.8	2.2	568.3	13.9
3	6	17	19.3	65.8	16.1	3.1	511.2	
3	6	19	19.5	64.8	15.3	3.0	549.4	11.3
3	6	21	17.0	70.6	13.8	2.4	486.4	13.9
3	6	23	15.9	70.9	13.7	2.2	613.2	14.1
3	6	25	17.4	70.6	13.7	2.4	491.2	12.7
3	6	27	17.6	69.1	13.1	2.3	635.7	13.3
3	7	0.75	7.8	77.9	11.9	0.9	642.5	27.7
3	7	2.25	5.6	77.4	10.9	0.6	850.3	28.5
3	7	3.75	8.5	72.8	10.3	0.9	677.4	35.0
3	7	5.25	11.1	67.9	9.1	1.0	725.6	31.8
3	7	6.75	13.1	65.5	9.7	1.3	685.0	31.0
3	7	8.25	11.9	63.1	11.3	1.3	471.8	31.2
3	7	9.75	14.5	58.4	9.3	1.3	432.1	16.2
3	7	11.25	17.2	55.2	8.4	1.4	663.7	13.2
3	7	12.75	20.6	50.8	6.2	1.3	399.9	11.2
3	7	14.25	15.2	56.5	8.1	1.2	534.6	11.4
3	7	15.75	16.6	58.5	7.8	1.3	510.6	9.1
3	7	17.25	9.7	69.7	26.4	2.6	418.2	7.9