Factors influencing the abundance of sediment-associated algae in two isolated ponds and a turbid channel of Delta Marsh, Manitoba.

By

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A Thesis Submitted to the Faculty of Graduate Studies in Partial Fulfillment of the Requirements for the Degree of Master of Science

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Factors Influencing the Abundance of Sediment-Associated Algae in Two Isolated Ponds and a Turbid Channel of Delta Marsh, Manitoba

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A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of Manitoba in partial fulfillment of the requirements of the degree of Master of Science

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at the other end of the phone. I love you! And of course, I would like to thank Grant for putting up with me for the last 2 years!

ABSTRACT

Three sampling methods were used to determine the biomass (chlorophyll *a* content and algal biovolume) of sediment-associated algae (SAA = epipelon + plocon) at three sites in Delta Marsh, Canada during a two-year period. I hypothesized that the importance of SAA in wetlands has been substantially under-estimated due to sampling bias of the standard lens-paper trapping method towards only motile constituents of the assemblage. In addition to the lens paper method, SAA biomass was measured in intact surface sediment cores and in wet slurries aspirated under vacuum from the sediment surface. Sediment slurries yielded the highest Chl *a* values (15-280 mg/m^2) followed by sediment cores (5-25 mg/m^2) whereas estimates using the lens tissue method were consistently <5 mg/m^2. Algal biovolumes followed similar trends.

Other determinants of underwater irradiance (macrophyte cover, nutrient concentration, water depth and turbidity) also correlated with SAA chlorophyll. The measured environmental variables could explain 47% of the variation in SAA chlorophyll in 1998 and 54% in 1999. Contrary to my hypotheses, water depth did not affect SAA chlorophyll. Also, SAA chlorophyll did not decrease with increasing macrophyte abundance. I suspect that the species of macrophyte (shape and form) affected the presence of SAA chlorophyll. Furthermore, high sediment and sediment pore-water nutrient concentration did not determine the magnitude of SAA abundance. SAA chlorophyll was negatively related to phytoplankton biomass at the sites. Results of this study have clear implications for food web structure in turbid lacustrine wetlands, where phytoplankton and SAA represent the only food resources for benthic and planktonic herbivores.

1. INTRODUCTION

The role of algae in wetlands is largely unknown (Klarer & Millie 1992). Recent studies indicate that macrophytes are not the predominant food resource, as had been concluded previously (Murkin 1989), and that algae have a larger role in the wetland food web than previously thought (R. McDougal, pers. comm.). Wetlands are known to provide habitat for waterfowl, migratory birds and small mammals as well as spawning grounds for fish, reptiles and invertebrates (Mitsch & Gosselink 1993). They are also sites of high primary productivity and a sink for nutrients (Reeder 1994). Most prairie wetlands are surrounded by agricultural land or urban areas and are, therefore, increasingly subject to allogenic phosphorus and nitrogen inputs. These nutrient additions are known to increase planktonic algal biomass and the primary production of prairie wetlands (Murkin *et al.* 1994, Goldsborough & Robinson 1997, McDougal 1997). However, there are other algal assemblages to be considered when looking at total primary production in wetlands.

There are five assemblages of algae present in prairie wetlands: phytoplankton, metaphyton, epiphyton, epipelon and plocon (Goldsborough & Robinson 1996). Phytoplankton, algae entrained in the water column, is thought to contribute most significantly to the primary production of wetlands (Lowe 1996). Metaphyton consists of floating mats of filamentous green algae. Epiphyton refers to algae growing on submersed and emergent macrophytes. Sediment-associated algae, also known as epipelon, include the algae growing on the sediment surfaces and consist of motile diatoms and unicellular flagellates. Another sediment-associated algal assemblage, plocon, forms a non-migratory crust on the sediment surface. It is often seen when it detaches from the sediment and rises to the water surface. This is thought to occur due to either increased photosynthesis that causes air bubbles to accumulate and dislodge this algal crust. The assemblage that I

have chosen to name sediment-associated algae (SAA) encompasses both epipelon and plocon.

Few studies have been done on the proportionate contributions of all algal assemblages to state whether SAA play a significant role in wetland primary production (Goldsborough & Robinson 1996). Indeed, there are minimal data on the role and biomass of benthic algae in wetlands (Crumpton 1989). This is surprising considering a unique feature of wetlands is that they provide abundant colonizable substrata. In addition, benthic algae, more specifically SAA, have been documented through the literature as playing a role in nutrient cycling (Jansson 1980, Hansson 1989, Wetzel 1993), providing habitat for other organisms, and helping stabilize the sediment substratum (Holland *et al.* 1974, Grant *et al.* 1986).

SAA have rarely been studied in freshwater wetlands and thus little is known about their abundance and role in primary production. Therefore, it has been assumed that the contribution of these assemblages to the total primary production of wetlands is insignificant. I suspect that this assumption may be incorrect because it is based on data collected in a way that may underestimate total biomass. Therefore, the purposes of the research described in this thesis were two-fold.

1.1 Objectives

The first objective was to determine a method that accurately measures the biomass (Chl *a*) and biovolume of SAA in wetlands. Three comparative techniques were used that consisted of 1) collecting an intact sediment core and removing the uppermost 3 mm (2) aspirating under vacuum sediment surfaces into a wet slurry and (3) trapping motile algae from the sediment slurries in tissue paper. Sediment samples were taken from the slurries before and after tissue trapping for Chl *a* analysis and biovolume measurements. The second objective was to characterize the abiotic environment (water depth, light extinction, turbidity, sediment pore-water

chemistry, sediment phosphorus and nitrogen) at the sediment-water interface at three sites in a prairie wetland using these sampling methods and to assess correlations with SAA Chl *a*. This study was conducted within Delta Marsh MB, Canada at three sites (Blind Channel, Crescent Pond, Saline Pond) that differed in their water depth, sediment composition and macrophyte cover. Samples were collected biweekly during the ice-free seasons of 1998 and 1999.

1.2 Hypotheses

I suspected that the widely used lens tissue trapping technique (Eaton & Moss 1966), would underestimate the biomass (Chl *a*) of SAA because this technique accounts for only motile epipelic algae whereas wetland sediment may contain both motile and non-motile components. I assumed that SAA Chl *a* in the intact sediment core would yield the highest measurements because it takes into account both the motile and the non-motile algae. If the lens paper was trapping the motile algae then the sum of the Chl *a* content of the slurry after tissue trapping and lens tissue should equal that of the slurry before tissue trapping. The slurry before tissue trapping and the intact sediment core should give comparable Chl *a* measurements because they are both sampling surface sediments that include both motile and non-motile algae.

Water depth, solar irradiance, macrophyte cover and nutrient concentration are the environmental variables known to affect SAA Chl *a* (Lassen *et al.* 1992, Murkin *et al.* 1994, Blumenschine *et al.* 1997, Garrigue 1998). Most of these abiotic and biotic factors are co-dependent. The effect of the combination of all measured environmental factors on SAA Chl *a* was determined by multiple regression analysis. This thesis, therefore, examines several predictions based on hypotheses:

1) Saline Pond should have the highest SAA chlorophyll because it is the shallowest site. As water depth increases, less light will reach the sediment-water interface.

The scattering and absorption of light by macrophytes, phytoplankton and suspended particulates will reduce the incident light reaching the SAA, thereby limiting algal growth.

2) SAA chlorophyll will be lower in vegetated sites compared to unvegetated sites because as macrophyte abundance increases less light will reach the sediment surface and algal growth will be limited. If macrophyte abundance is the controlling factor then Crescent Pond will have a clear water column but should still have the lowest SAA chlorophyll and Blind Channel will be the most turbid but have the highest.
3) The higher the nutrient concentration in the sediment and the interstitial pore-water the higher the SAA chlorophyll because nutrient concentration and algal abundance are positively correlated. Algal growth at the sediment-water interface has been documented to regulate the efflux of phosphorus, limiting availability for phytoplankton. In turn, this should lead to a lower abundance of phytoplankton because the increased SAA on the sediment surface should reduce the amount of nutrients released to the overlying water column.
4) SAA abundance will peak in spring and autumn. I suspect this is because phytoplankton and macrophyte abundance are low during these seasons and irradiance reaching the sediment water interface will be at a maximum. In spring, the absence of macrophytes, and in autumn the senesce of macrophytes, would allow maximum light to reach the sediment surface to stimulate SAA growth. Less SAA would be present in the summer due to lower light at the sediment caused by overlying phytoplankton blooms.
5) The occurrence of plocon is dependent on high solar irradiance and minimal wind velocity because plocon was only observed by late afternoon on calm sunny days.

Although there are problems associated with using Chl *a* as a surrogate for algal biomass, it was the most efficient method under the circumstances of this study. Measurements were coupled with biovolume measurements to account for any discrepencies. The constraints of using Chl *a* as an indicator of algal biomass are discussed in this thesis.

1.3 Organization of the thesis.

This thesis consists of six sections following this one. The next section is a review of the literature on the methods for sampling SAA and a review of the biotic and abiotic factors that affect its growth. The third section describes the sampling methods that took place during the 1998 and 1999 field seasons as well as laboratory and statistical analyses. The fourth and fifth sections, Results and Discussion, are separated into two parts based on the objectives: 1) methodological implications and 2) ecological implications. The last two sections are a summary of the major findings of this thesis and a list of the literature cited.

2. LITERATURE REVIEW

2.1 Wetlands

Wetlands are among the most productive and biogeochemically diverse ecosystems on earth (Stanley & Ward 1997). They are difficult to define because of their hydrology, size, location and human influence (Mitsch & Gosselink 1993). In fact, there are many definitions for a wetland. It is generally defined as a shallow-water or littoral-dominated system (generally <2m in depth), with standing water, continuously waterlogged soil and vegetation tolerant of saturated soil (Goldsborough & Robinson 1996). Wetlands are ecotones situated between terrestrial and aquatic environments and are influenced by both systems. Most prairie wetlands are surrounded by either agricultural land or urban areas and are therefore increasingly subject to allogenic inputs of phosphorus and nitrogen, as well as fertilizers and pesticides. They are often referred to as buffer zones because of their ability to act as sources, sinks or transformers of nutrients. This has lead to the widespread use of natural and constructed wetlands for cleaning polluted water (Brix 1997). Wetlands serve many other functions that include preventing flooding, providing habitat for waterfowl, migratory birds and small mammals, as well as a spawning ground for fish, reptiles and invertebrates (Mitsch & Gosselink 1993).

Wetlands comprise 6% of the land surface area of the world (Mitsch & Gosselink 1993). They are found on every continent except Antarctica. In Canada, 14% of our land area, 127 million hectares, is considered wetland and 40% of those wetlands are found in Manitoba (Zoltai 1988). Wetlands cover 43% of Manitoba's terrestrial landscape (Halsey *et al.* 1997) althouth mostly in the form of treed bog and fen. Prairie wetlands make up a small proprotion of Manitoba wetlands most of which have been drained over the past century for agricultural use or expanding urban development. Wetlands were always considered to be "sinister or

forebidding" and to have little economic value. Prior to 1970, wetlands were hastily drained but now that their value is known, laws have been implemented, especially in the USA, for their protection (Mitsch & Gosselink 1993).

2.2 Algae in wetlands

Algae are a major component of wetlands. Their role is biological, chemical and physical. Because of their small size, high availability and rich nutritive value, they provide an important food source for both invertebrate and vertebrate consumers (Campeau *et al.* 1994). They are referred to either as planktonic, suspended in the water column, or benthic, living on or in association with a substratum. An individual alga may be benthic or planktonic at one time or another, but many species are characteristically found in just one state. Some major taxonomic groups that can be characterized as benthic algae include species from the Divisions Chlorophyta (green algae) and Bacilliarophyta (diatoms). A unique feature of wetlands is that they provide abundant colonizable substrata for benthic algae because of their shallow waters and profuse submersed and emergent vegetation.

There are five assemblages of algae present in prairie wetlands, one that is planktonic and four that are benthic. Phytoplankton, algae entrained in the water column, is thought to be the dominant primary producer of lentic ecosystems (Lowe 1996). Benthic forms includes metaphyton which consists of floating mats of filamentous green algae that was originally attached to macrophytes, epiphytic algae growing on submersed and emergent macrophytes and sediment-associated algae (SAA), which includes epipelon and plocon. Epipelon includes the algae growing on the sediment surfaces and consists of motile diatoms and unicellular flagellates such as *Euglena*. The other SAA assemblage, plocon, consists of algae that have detached from the sediment surface due to the accumulation of gas (oxygen, methane or hydrogen sulphide) and dislodge the algal mat from the sediment surface.

According to the four quasi-stable states of a freshwater wetland predicted in a model by Goldsborough & Robinson (1996), one of the above algal assemblages is dominant depending on the stage of the wetland development. The "lake marsh state" is dominated by phytoplankton, the "sheltered marsh state" by metaphyton, the "open marsh state" by epiphyton and the "dry marsh state" by epipelon (Figure 1). These four states are affected by water level, turbidity, nutrient concentration, macrophyte abundance, and grazing pressure.

2.3 Sediment-associated algae (SAA)

Throughout the literature, algae inhabitating the sediment have been referred to by several different names. Epipelon is probably the most common term used although it is not inclusive of all the algae living in the sediment as it only refers to motile algae. Some SAA are motile, moving up and down vertically, due to light, salinity, oxygen (Moss 1977) and others do not. Therefore, more appropriate terms used to refer to algae inhabiting the sediments include: sediment-associated algae (Sullivan & Moncreiff 1988), sediment-attached algae, sediment-associated periphyton (Hansson 1988, 1990, 1992, Davis & Steinman 1998), sediment-attached periphyton (Hansson 1988, 1990), sediment-dwelling algae (Hansson 1992, Vinebrooke & Leavitt 1999), microphytobenthos (Delgado 1989, deJonge & Colijn 1994, Kuhl *et al.* 1994, Garrigue 1998), microbenthos (Diaz *et al.* 1997), benthic microalgae (Pinckney & Zingmark 1991,1993, Cahoon & Cooke 1992, Kendrick *et al.* 1996), edaphic algae (Gallagher & Daiber 1974, Sullivan & Moncreiff 1988) and epibenthic algae (Hall & Fisher 1985). Periphytic algae is a ubiquitous term referring to algal growth upon a substratum (Wetzel 1983), therefore terms such as sediment-associated periphytic algae and sediment-attached periphytic algae are more descriptive. The term edaphic algae is used to refer to algae growing in terrestrial soil and is commonly used when referring to SAA in salt marshes. I have chosen to

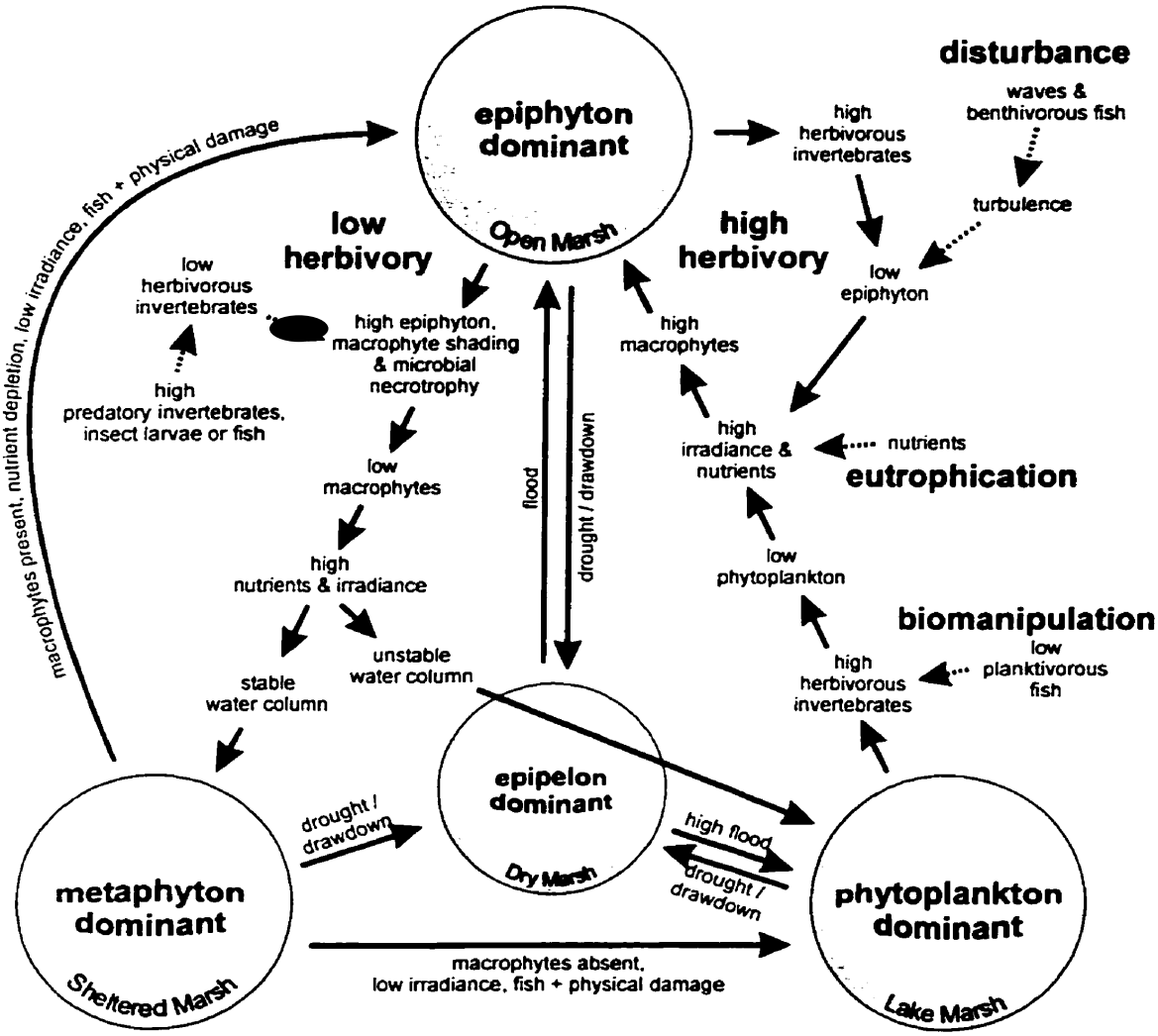

Figure 1: Conceptual diagram of the relative importance of four algal assemblages at various stages of wetland development (Goldsborough & Robinson 1996).

use the term sediment-associated algae (SAA= epipelon + plocon) as it encompasses all algae found in association with the sediment whether motile or not. It also includes plocon, algae that was formerly part of the sediment and have been dislodged.

Benthic algae are important primary producers in streams, lakes and wetlands. They are the dominant primary producers in streams where they serve as the main source of energy for higher trophic levels (Stevenson 1996). Most research in lakes has been done on planktonic algae because of the general perception that they are the major primary producers in these ecosystems (Lowe 1996), however, benthic algae still make a significant contribution to the total algal productivity especially in shallow littoral-dominated lakes (Lowe 1996). Evidence from invertebrate grazing studies indicate that benthic algae, in wetlands, contributes significantly to nutrient storage and food chain support (Hann 1991, Campeau *et al.* 1994). In wetlands, too few studies have been done on the proportionate contributions of all algal assemblages to be able to state whether benthic algae also play a significant role in wetland primary production (Goldsborough & Robinson 1996). In addition, benthic algae, more specifically SAA have been documented through the literature as playing a role in nutrient cycling (Jansson 1980, Hansson 1989, Wetzel 1993). SAA mediate nutrient efflux rate from the sediment to the water column (Jansson 1980, Hansson 1989). This can be explained in two ways: 1) the algae assimilate the nutrients and/or 2) the aerobic microzone created by algal photosynthesis prevents the efflux of reduced nutrient species (Carlton & Wetzel 1988, Hansson 1989). SAA also play an important role in creating habitats for invertebrates and stabilizing the sediment interface (Holland *et al.* 1974, Grant *et al.* 1986). SAA can cover the sediment floor of the marsh like a carpet keeping soil particles from being disturbed and in the meantime invertebrates burrow into it.

One the most abundant insects, chironimids, develop as larvae in the sediment and disrupt the epipelic community through bioturbation.

I will discuss research to date about different methods used to sample SAA, as well as the abiotic and biotic factors that regulate the biomass and productivity of SAA in lakes, streams and wetlands. The effect of abiotic factors such as light, temperature, oxygen concentration, water depth, nutrient availability, sediment composition, and salinity will be evaluated. The biotic factors to be addressed include the presence of phytoplankton, macrophytes, fish, and invertebrates. The effect of these factors can not be looked at individually as many factors are inter-dependent.

2.4 Sampling methods for sediment chlorophyll

SAA are not as commonly studied as phytoplankton because this assemblage is more difficult to sample and analyse and was originally thought not to be as important to ecosystem function. There are methodological problems associated with sampling SAA. SAA chlorophyll may be estimated from artificial substrata, such as tiles, clay pots or acrylic rods or directly from the sediment. Artificial subtrata give an erroneous picture of algal chlorophyll whereas chlorophyll extracted directly from the sediment is more accurate although this analysis includes detrital pigments (Hansson 1988). No artificial substrata can simulate natural sediment. Blumenschine *et al.* (1997) found a strong potential for nutrients to accumulate in algae growing on hard surfaces. In mesocosms in Long Lake MI, they observed a higher biomass of Chl *a* on plastic strips than in the epipelon and phytoplankton indicating that these strips do not represent either assemblage. In fact, algae that would have been originally part of either the epipelon or phytoplankton preferred to grow on the plastic strips.

The lens tissue trapping method of Eaton & Moss (1966) is the accepted method for collecting epipelic algae. Sediment slurries are aspirated from the

sediment surface, brought back to the lab and allowed to settle in darkened containers. Any excess water is removed and lens paper is placed directly on the sediment. The sample is then placed in direct sunlight. The principle behind this method is that the algae migrate up by positive phototaxis into the lens paper. Hickman (1969) found that the amount of chlorophyll extracted from the lens tissue depended on the number of times the bottle that contained the lens tissue was shaken. A drawback to this method is that it only takes into account the motile algae and not all the algae potentially in the sediment.

Numerous researchers have used sediment cores of various diameters to retrieve an undisturbed column of sediment and the overlying water with little disturbance of the sediment-water interface (Hansson 1988, deJonge & Colijn 1994, Blumenschine *et al.* 1997, Lassen *et al.* 1997, McCormick *et al.* 1998). Carlton & Wetzel (1985) devised a box corer sampling method that was deployed by SCUBA, and collected a total sample volume (sediment and water) of approximately 30 litres. The advantage of this large diameter core was that there is less edge effect. This means that as the core enters the sediment it disturbs a smaller percentage of the algal crust on the core surface than would a smaller core. A lightweight inexpensive core sampler for use in shallow water, was designed by Davis and Steinman (1998). This hand held gravity corer consisted of PVC pipe of variable length and was designed with a detachable end, so that the sediment core can be removed intact for experiments involving metabolism and nutrient uptake. The appropriate corer to use depends upon the objective of your study, your economical and physical resources and the aquatic system in which you work.

Determination of chlorophyll *a* (Chl *a*) is one of the most common methods used for estimation of algal biomass (Hansson 1988). However, there are some methodological problems, not necessarily exclusive to sediment chlorophyll but intensified in the sediment. The first problem is the increase of Chl *a* content in

algal cells in a low light environment. This can be resolved by coupling Chl *a* measurements with productivity and biovolume measurements. The second problem is the different extraction efficiency of different solvents. The most widely used solvents for extracting photosynthetic pigments are acetone, ethanol and methanol. Hansson (1988) found that acetone extracted more chlorophyll than methanol from sediment samples. He also showed that the water content of the sediment sample and freeze-drying prior to extraction affected the ability of a solvent to extract chlorophyll. The third problem concerns the estimation of degradation products of chlorophyll. In sediment samples, degraded chlorophyll, known as phaeopigments, are more prominent than in other algal assemblages. The most common method for their analysis is the addition of acid. Acid degrades the chlorophyll molecule by cleaving the Mg^{+} ion and the phytol hydrocarbon chain to form chlorophyll derivatives. The concentration of detrital pigments in sediment samples can be higher than in phytoplankton so samples can be partitioned with hexane to eliminate interference of degraded pigments (Cahoon *et al.* 1993). The hexane hyperphase retains carotenes, Chl *a*, Chl *b*, and pheophytin since these compounds retain the non-polar chain. The hexane hypophase contains Chl *c*, some carotenoids and chlorophyll degradation products that lack the phytol chain. Therefore partitioning with hexane eliminates two classes of degradation products from the active chlorophyll (Whitney & Darley 1979). The fourth problem is the possible inclusion of non-algal chlorophyll such as from detritus as well as metabolically inactive algal chlorophyll in dead or senescent cells. Again these Chl *a* measurements can be justified by being coupled with algal species identification and enumeration.

2.5 Abiotic factors influencing sediment-associated algal biomass

2.5.1 Light

Light is a key limiting factor for SAA photosynthesis but several processes are responsible for absorbing light in shallow waters (Kjeldson *et al.* 1996, Lassen *et al.* 1997, Garrigue 1998). Light attenuates exponentially as it penetrates the water column before it reaches the algae at the sediment surface. Light attenuation occurs because water, dissolved organic matter, suspended inorganic particles, phytoplankton, and macrophytes scatter and absorb light, limiting the number of photons that actually reach the algae on the sediment for photosynthesis (Lassen 1997). Not all wavelengths of light are equally extinguished through the water column. The percentage absorption is very high in the infrared region of the spectrum, decreases in the lower wavelengths to a minimum absorption in the blue, and then increases again in the violet and ultraviolet wavelength (Wetzel 1983). Once light reaches the sediment it is further attenuated by a vertical matrix of algal cells that comprise the sediment-associated assemblage (Hill 1993). Stanley (1976) observed in several Alaskan tundra ponds, that rapid light extinction limited photosynthesis to a thin zone (2 cm) near the sediment surface where live cells were being continuously mixed to deeper sediments (5 cm). This mixing occurred due to wind, feeding benthic invertebrates, burrowing chironomid larvae and methane and carbon dioxide bubbles produced from subsurface decomposition.

Recent studies have shown that ozone layer depletion is responsible for increases in global warming and ultraviolet radiation (Tominaga 1992). UV-B (280 - 320 nm) and UV-A (320 - 400 nm) are becoming more of a concern for aquatic ecosystems (Vinebrooke & Leavitt 1999). UV radiation might have a more pronounced impact in shallow water where a higher proportion of biota are exposed to high UV irradiance. In an alpine Alberta lake, UV radiation was found to have no

adverse affect on motile epipelon because these algae are capable of active avoidance via vertical migration through the sediment. They have the capacity to regulate their exposure to UV by adjusting their position in the sediment to avoid high irradiance yet they can exploit periods of photolytically enhanced resource availability. The stimulation of epipelon by UV-A radiation may involve phosphorus release following UV induced photolysis of organic iron-phosphorus complexes. On the other hand, UV radiation did suppress attached epilithic algae as they lack any means of protection (Vinebrooke & Leavitt 1999).

In a three year study of benthic algae in a Danish stream, Kjeldson *et al.* (1996) found that epipelon development was affected by light availability while epilithon composition and peak biomass was affected by invertebrate grazing. Sabbe (1993) found epipelon to be affected by an increase in total sky irradiance on the days prior to sampling. This indicates that epipelic production was related to light availability and that a certain amount of time (at least 2 days in this case) was needed between a period of high irradiance and an algal population increase.

One of the most notable characteristics of epipelic algae is its tolerance of darkness for many days (Moss 1977). However, epipelic algae do not survive under anaerobiosis for long and must rely on rapid movement to regain the sediment surface. It is believed that this algal assemblage may have a circadian rhythm of movement in which they are at the sediment surface when light is available and retreat to the sediment in the dark. This vertical migration has been shown to be diurnal (Brown *et al.* 1972). This rhythm may also reduce the risk of dislodgement of the cells by invertebrates or tides and currents (Moss 1977).

Irradiance reaches its maximum in the upper 0-0.5mm of a coastal sandy sediment (Lassen *et al.* 1992, Kühl *et al.* 1994). Therefore only Chl *a* contained in the top sediment layers is photosynthetically active and thus responsible for primary production. Interestingly, a higher Chl *a* content was found in the second centimetre

than in the first for a few cores. This may reflect the effect of bioturbation by burrowing invertebrates (Garrigue 1998). Kühl *et al.* (1994) found that light attenuation coefficients in the sediment decreased with increasing particle size and infrared light penetrated deeper than visible light in coastal sediments.

The productivity of epipelic algae in an estuary also exhibited regular periodicity that was a function of both light and tidal cycles (Pinckney & Zingmark 1991). This periodicity in epipelic algal production (range 28-460 µmol O_2/mg Chl *a*/hr) could be explained by the vertical rhythmic migrations of motile diatoms that are also influenced by tidal and light cycles.

The epipelic algal productivity in Hastings Lake, Alberta was found to be closely correlated with both light levels and biomass, measured as Chl *a* (Jenkerson & Hickman 1983). Kairesalo (1977) found that solar radiation was more important than water temperature in determining the epipelic production in a deep oligotrophic Finnish lake. However, it is difficult to look at individual effects of light and temperature on any algal community as these two parameters are usually positively correlated (Wetzel 1983). Both light penetration and water temperature were found to be the most important environmental factors affecting epipelic algae in a subarctic lake in northern Sweden. The algae compensated for low light by increasing chlorophyll concentration but the production remained the same (Björk-Ramberg 1983).

2.5.2 Temperature

Both water and sediment temperatures are important factors regulating SAA growth. The main source of heat is solar radiation, hence the coupling of light and temperature effects (Wetzel 1983). In temperate lakes of moderate depth, thermal stratification occurs whereas in streams and wetlands the water column is typically isothermal except possibly in a heavily vegetated water column during long quiescent periods. In shallow waters, sediments can absorb significant quantities of solar

radiation due to their dark colour and this heat may be transferred to the water (Wetzel 1983).

Different species of algae have different temperature optima for growth (DeNicola 1996). In the Severn estuary, England, Underwood (1994) found a significant correlation between surface sediment temperature and relative abundance for eight of twelve dominant diatom species. However, temperature alone could not explain the apparent seasonal progression up and down the estuary. Jenkerson & Hickman (1983) found that the cyanophycean algae in Hastings Lake, AB, including *Lyngbya lagerheimii, Merismopedia glauca, M. tenuissima,* and *Microcystis aeruginosa,* were associated with higher temperatures whereas *Coelosphaerium naegelianum* developed best at low temperatures.

The biomass of epipelic algae in two Alberta lakes was found to have a negative correlation with temperature (Hickman 1978). Again, there is a lot of controversy among scientists over whether it is light or temperature that regulates epipelic biomass. Solar radiation was found to have more of an effect on determining productivity than water temperature in a southern Finnish lake (Kairesalo 1977). In Marion Lake, BC the water temperature accounted for over 70% of the variation in epipelic algal community production (Hargrave 1969). Comparing the productivity of epipelic algae in tundra ponds and a lake in Alaska, Stanley (1976) found that the epipelic production was higher in the ponds because of lower light intensities, lower water temperature and a shorter ice free period in the lake.

The differences in temperature with water depth are minor in wetlands, given their generally shallow depth and the high amount of wind mixing that occurs particularly in prairie wetlands (Goldsborough & Robinson 1996).

2.5.3 Water depth

The depth of the water column is one factor that influences the percent of surface irradiance that reaches the sediment and thereby, influences the abundance and productivity of SAA. Therefore the importance of the benthic community as primary producers plays a more significant role in streams and wetlands than in lakes.

The benthic community is an important primary producer particularly in shallow lakes, but become less important in deep lakes as they are often light-limited (Hickman 1978). Stanley (1976) found that, benthic algal production was insignificant in deep Alaskan lakes, equal to planktonic production in medium depth lakes and more productive in shallow lakes. In these nutrient poor lakes and ponds, depth determined the relative proportion of production by planktonic and benthic algae but not the total production. Garrigue (1998) speculated that the decrease in Chl *a* with increasing water depth in a lagoon in New Caledonia, likely reflected the reduced light availability in deeper areas. Jenkerson & Hickman (1983) found no consistent pattern in epipelon biomass with respect to depth in Hastings Lake, Alberta. However, they observed that the primary productivity or epipelic algae was consistently greater at 0.25 m and then decreased rapidly with increasing depth. They also found that species composition was distinct at different depths. *Navicula crytocephala*, *N. gracilis, N. hungarica v. capitata, Achnanthes* sp. and *Anabaena flos aquae* were prevalent in shallow water, whereas *Nitzschia gracilis, N. palea*, *Oscillatoria subbrevis* and *Trachelomonas granulosa* dominated in deeper water. Stevenson *et al.* (1985) studied 20 poorly buffered lakes in New Hampshire and found that the total biovolume of benthic algae decreased with water depth, indicating that some benthic algae species had adapted to low light and were perhaps facultative heterotrophs. Contrary results were found in Marion Lake, BC, where

Hargrave (1969) found that the photosynthetic efficiency of epibenthic algae ranged from 0.4 to 3.1% and increased with depth of water over the sediment.

Water depth is one of the most important variables that defines a wetland and therefore its algae (Goldsborough & Robinson 1996). It affects directly and indirectly the nutrients, light, temperature, and macrophyte abundance in the wetland. The shallowness of wetlands can result in extensive resuspension of the sediments by wind. This leads to a thoroughly mixed turbid water column. The role of water depth is further complicated since most wetlands experience regular fluctuations in water level by cycles of flooding and drought (Goldsborough & Robinson 1996).

Robinson *et al.* (1997a) looked at the responses of both planktonic and benthic algae to fluctuations in water level in a series of cells constructed within a prairie wetland. Epipelic algae was found to be of greatest abundance (mean 4.2-4.9 mg Chl *a*/m^2) in the intermediate depth cells (65-75 cm) and shallow cells (35-55 cm) and lowest (mean 3.2 mg Chl *a*/m^2) in the deep cells (95-115 cm). The mean epipelon biomass in all cells, at all sampling times, ranged from < 0.1 to 17.5 mg Chla/m^2 (mean 4.0 mg Chl *a*/m^2). This represented 1% of the total of all algal biomass. As the water deepened, epipelon biomass decreased and phytoplankton increased. This transition to the "lake marsh" state in which phytoplankton dominates was consistent with a conceptual model of wetland algae (Goldsborough & Robinson 1996). In this four state model it is the "dry marsh" state, with low water depth and abundant vegetation where epipelon is dominant.

The proportionate contributions of the four assemblages to total algal production were compared by Robinson *et al.* (1997b) at different water levels. The photosynthetic efficiency (amount of carbon fixed per unit of chlorophyll per unit of light) was higher for epiphyton than epipelon. The mean epipelon productivity was 31 mg C/ m^2/d over the five-year study but varied from <1 to 157 mg C/m^2/d with no inter-annual trend. The highest epipelon productivity of epipelon was found in the

intermediate water level cells (47 mg C/m^2/d), followed by the low and high cells, (32 mg C/m^2/d and 15 mg C/m^2/d, respectively). Therefore, the epipelon contributed to <1 to 3 % of total algal productivity. The turnover rate (lifecycle), of epipelon was found to be highest in the intermediate cells and ranged between 9 to 91 days.

2.5.4 Oxygen

Aside from water itself, oxygen is the most fundamental component of aquatic ecosystems (Wetzel 1983). Dissolved oxygen is essential to the metabolism of all aerobic organisms. The oxygen distribution in the water column and sediment is due to the balance between inputs from the atmosphere and photosynthesis, and outputs due to microbial oxidations (Wetzel 1983). Mortimer (1941) was the first to demonstrate that the presence of an oxidized microzone at the sediment surface inhibited phosphorus release. Epipelic algae were found to form and break down this oxidized microzone daily mediating the release of phosphorus from the sediment to the overlying water (Carlton & Wetzel 1988). During daylight, photosynthetically active epipelic algae oxidize the sediments and Fe (III) hydroxides can bind phosphate as a precursor to the formation of hydroxyapatite. At night, the microzone becomes anoxic Fe (III) is reduced and phosphorus is released (Carlton & Wetzel 1988).

Microelectrodes are often used to measure the rate of photosynthesis of epipelic algae in intact sediments. Carlton and Wetzel (1988) observed, that epipelic algal photosynthesis within the photic zone of lakes undergoes diel fluctuations in the extent of the oxygen penetration into the sediment. They used radiolabelled phosphate to examine the effects of sediment oxygen dynamics on the release of phosphorus from the sediment, and observed that the microzone around the epipelic algae became oxygenated when the sediment was illuminated and ^{32}P release from the deeper sediment was inhibited. However, during darkness, the microzone became anoxic and phosphorus was released to the overlying water faster.

In a shallow eutrophic Danish lake, Lassen (1997) observed pronounced diurnal fluctuations in the oxygen concentration in the uppermost 3 mm of the sediment and in the approximately 3 mm thick flocculent microalgal layer covering the sediment. At dawn, the oxygen penetrated less than 1 mm into the sediment but oxygen penetrated down 5 mm by noon and reached a maximum of more than 450% of atmospheric saturation. The oxygen level in the entire water column reached 150% saturation at the same time.

The benthic algal production of Marion Lake, BC was measured by following the changes in dissolved oxygen weekly in undisturbed sediment cores throughout an entire year. Hargrave (1969) found that the epipelic production was directly related to temperature, light, and respiration, and inversely related to day length. The sedimentary chlorophyll was found to be stratified vertically with the highest concentration occurring in the upper few centimetres of sediment that corresponded to the depth of oxygen penetration.

Oxygen microelectrodes have been used to analyze the distribution of the diffusive boundary layer at the sediment-water interface in relation to surface topography and flow velocity (Jorgensen-Marais 1990). The diffusive boundary layer is the thin layer of water adjacent to the sediment surface through which molecular diffusion is the dominant transport mechanism for dissolved material. It plays an important role in the exchange of nutrients and gases across the sediment-water interface. The surface roughness is also important for both the thickness and topography of the diffusive boundary layer. Jorgensen-Marais (1990) found that diffusion through the diffusive boundary layer constituted an important rate limitation to the oxygen uptake of the sediment and that the mean effective thickness of the diffusive boundary layer decreased as the velocity of the overlying water increased.

2.5.5 Nutrients

Algae, both planktonic and benthic, require micro- and macronutrients to grow and reproduce. Phosphorus and nitrogen are the most commonly investigated macronutrients because they are most likely to limit algal growth (Borchardt 1996). Phytoplankton receives nutrients from the water column whereas SAA can obtain nutrients from the sediment or the overlying water (Borchardt 1996). This dual nutrient source is probably a competitive advantage for SAA, particularly in shallow lakes and wetlands (Hansson 1990).

Nutrient addition to aquatic systems is an increasing problem as lakes, streams and wetlands are being encroached by urban development and the use of fertilizers in agricultural fields is increasing. The effect of nutrient addition on phytoplankton has been studied (Campeau 1990, Gabor *et al.* 1994, Murkin *et al.* 1994, Blumenshine *et al.* 1997, Goldsborough & Robinson 1997, McDougal 1997). Only a few studies have been concerned with nutrient effects on benthic algae in wetlands. Algae often require more nutrients when light and temperature conditions are less than optimal for growth (Borchardt 1996).

In wetlands and shallow lakes, no experimental study measuring epipelon biomass has detected any change due to nutrient addition (Campeau 1990, Gabor *et al.* 1994, Murkin *et al.* 1994, Blumenshine *et al.* 1997, McDougal 1997). This lack of response by epipelon would suggest that the nutrients added became unavailable or were made unsuitable for uptake before reaching the sediment. On the other hand epipelon was so nutrient efficient that further addition simply made no difference. Murkin *et al.* (1994) did not provide an explanation for how or why nutrient addition did not increase epipelon biomass. Campeau (1990) added even higher levels of nutrients to Narcisse wetland, MB and still did not increase epipelic algal production. It was concluded, by Campeau (1990) that there must have been rapid uptake and/or transformation of nutrients within the water column. The lack of

response by epipelon observed in the Narcisse wetland and in other marsh enrichment studies may reflect the epipelic algae's ability to use the enriched nutrient pool in marsh sediments. The sediment and the biota are the two major nutrient pools in a wetland but, in the case of McDougal (1997), biological consumption of the press and pulse additions of inorganic nutrients (nitrogen and phosphorus) was low compared to losses to the sediment.

Numerous studies have examined the effects of nutrients on phytoplankton biomass, productivity and taxonomic composition in lakes. Very little research has been done on benthic algae, particularly epipelon due to the logistic difficulty and expense in working on lake bottoms. Carlton and Wetzel (1988) found that epipelic algae growing upon organic lake sediments developed into dense (mean 30.2 ± 8.3 mg/m^2 Chl *a* content) but thin communities (<1 mm thick) that were loosely attached mat-like aggregations and that mediated phosphorus fluxes from the sediment to the overlying water. Hansson (1990) thought, from his research in Swedish lakes, that this algal assemblage might reduce phosphorus availability in the overlying water by up to 44%. This could potentially affect nutrient availability for phytoplankton (Carlton & Wetzel 1988, Hansson 1990, Van Luijn 1995, Blumenschine *et al.* 1997, Lassen 1997). In a study by Van Luijn (1995) benthic diatoms reduced the nutrient release from the sediment and may actually have accelerated the process of recovery from eutrophication. This can be explained by the fact that there was less nutrient available for phytoplankton growth so light extinction remained low which profited benthic diatoms growth. In turn, this increased oxic layer gives a longer diffusion path for nitrate-N (Van Luijn 1995). Axler and Reuter (1996) proposed that epipelic algae is are potentially important sink for nitrate added to the epilimnion of a Californian lake. They observed that 56% of the nitrate that disappeared from the water column was incorporated into the epipelic

algae and sediment. Unfortunately, they did not determine what percentage of the nitrate was incorporated only into the epipelic algae.

In five prairie parkland lakes in Alberta, Hickman (1978) found that few nutrients gave a highly significant correlation with epipelon biomass. The exceptions were nitrate-N and dissolved silica which were correlated positively with biomass. In four other Alberta lakes, Hickman (1978) found that there was no correlation between epipelon biomass and the nutrient status of the water. This indicates that the sediment was probably providing most of the nutrients for the epipelic algae.

Algal nutrient uptake can be described by the Michealis-Menten model of enzyme kinetics. This model, however, does not apply to phosphorus as algae are luxury consumers of phosphorus. Therefore, Droop (1968), proposed that algal growth was best described as a function of the intracellular concentration of the limiting nutrient. Portielje and Lijklema (1994) found that the maximum storage capacity of phosphorus per unit of algal dry weight was positively correlated to the level of external nutrient loading whereas the phosphorus uptake rate was negatively correlated. This was observed in three test ditches, in the Pleistocene part of the Netherlands, receiving different levels of external phosphorus and nitrogen. In addition, the efficiency with which a species is capable of phosphorus uptake and storage, during periods of enhanced availability, determines its competitive ability.

Little is known about competitive abilities and optimum ratios of nutrients of benthic algae (Borchardt 1996). Ecological theory predicts that competition for limiting resources is important in structuring natural communities. For example, Fong *et al.* (1993) found that resource competition occurred between benthic and planktonic primary producers in microcosms, adjacent to the Tijuana estuary just north of the US Mexico border. The strength of the interaction depended on the supply rate of the resource. Algae, with a low K_s (substrate concentration that yields half the maximum rate) are better competitors when the nutrient supply is low while algae

with a high maximum uptake rate have the advantage when the nutrient supply is high. Fong *et al* (1993) hypothesized that the strength of the resource competition among different algal groups was also dependent on the amount competition between phytoplankon and a combination of floating and attached green macroalgae and attached cyanobacterial mats. The resource competition between benthic and planktonic primary producers is probably not as important in deeper systems where the competition for nutrients is not as extensive or in sites with high water column turbidity where the SAA are more likely to be light limited.

An increase in sediment Chl *a* concentration after fertilization (addition of 0.5 g/m^2/yr phosphorus and 5 g/m^2/yr nitrogen) of a subarctic lake was observed (Björk-Ramberg 1983). This was not caused by a change in biomass of epipelic algae but by an increase in the chlorophyll concentration. This was most likely due to the decreased sunlight due to the increase in phytoplankton biomass (from 2.3 to 39 g C/m^2) as a result of fertilization. Therefore, the algae on the sediment compensated for low light by increasing they chlorophyll concentration and the algal productivity remained constant throughout the three years of the experiment. Consequently, the concentration of nutrients in the water and sediment had no observed effect on the variation in the epipelic production indicating that the nutrients did not limit production (Björk-Ramberg 1983).

2.5.6 Sediment composition

The sediment of aquatic ecosystems is composed of organic matter in various stages of decomposition, particulate mineral matter, and inorganic matter of biogenic origin such as diatom frustules and calcium carbonate particles (Wetzel 1983). It is the site of major biological activity that includes microbial degradation of organic matter and recycling of nutrients. The sediment has been found to be an important source and sink of nutrients in aquatic ecosystems. McDougal *et al.* (1997) found

that the sediment could account for most, if not all of the phosphorus removal from a pulse treatment that was added to enclosures in Delta Marsh, MB. The phosphorus content of macrophytes and algae was small so biological consumption was low compared to losses to sediments. Conversely, Vaithiyanathan and Richardson (1997) found that luxury uptake of phosphorus by algae and macrophytes, and their subsequent deposition of detrital tissue, resulted in high levels of phosphorus in the sediment. As stated before, the benthic microalgae may regulate the flux of phosphorus between the sediment and the water column and thereby, limit phytoplankton growth (Carlton & Wetzel 1988, Hansson 1990, Van Luijn 1995, Blumenschine *et al.* 1997, Lassen 1997). After fertilizing a subarctic lake in Sweden, Björk-Ramberg (1983) found that the concentration of total nitrogen and total phosphorus in the sediment explained 4% of the variation in the epipelic algal production while the concentration of molybdate reactive phosphorus and inorganic nitrogen in the water column was uncorrelated with epipelic production.

Sediments are sinks for organic matter, the breakdown of which can result in exchanges of nutrients with the water column. During summer months, sediments represent important sources of phosphate and ammonium to the water column (Rizzo 1990). Through denitrification, sediments can be sinks for nitrate. This is an important pathway for removal of excess anthropogenic nitrogen inputs (Rizzo 1990).

Sediment particle size and texture may potentially affect the biomass and species composition of the epipelic community. Algal biomass may vary between site with different sediment composition because light penetration through different soil types varies (Kühl 1994). Also the water and organic matter content of a sediment sample affects the ability of various solvents to extract chlorophyll (Hansson 1988). However, Underwood (1994) found no significant relationship between the abundance of any epipelic taxon and sediment particle size, in the Severn estuary, England. He did observe a relationship between certain species and sediment water

content with *Navicula phyllepta* favouring drier firmer sediments and *Coscinodiscus* sp. 1 being more abundant on wetter less firm sediments. Jenkerson and Hickman (1983) observed that the texture of the sediment influenced algal species composition in that *Navicula hungaria v. capitata* and *Achnanthes* sp. increased as the proportion of sand in the sediment increased. At sites where the sediment was more organic, *Oscillatoria subbicuis, Trachelomonas granulosa, Nitzschia gracilis* and *N. palea* were dominant.

Sediment disturbances by wind, bioturbation by burrowing invertebrates and gas bubbles produced from subsurface decomposition could affect the productivity of SAA negatively. Wind creates water currents that can resuspend surface sediments, larvae of chironomids lead to deeper mixing and gas bubbles dislodge the epipelic algae (Stanley 1976). Therefore, the sediment stability more likely affects Chl *a* concentration where waves resuspend the upper centimetres of sediment (Kendrick *et al.* 1996).

2.5.7 Salinity

Salinity describes the summed ionic composition of water. The proportion of anions and cations in the water and sediment may influence the metabolism and distribution of many organisms especially algae and macrophytes because of the reduced solubility of oxygen as salt concentration increases (Wetzel 1983).

Claps (1996) found that the number of epipelic algal species increased, along the salinity gradient, from the headwater to the mouth of the Samborombon River in Argentina, a tributary to the Rio de la Plata estuary. This higher species diversity resulted from the presence of freshwater, brackish and marine species. The epipelic density decreased from the headwater to the mouth because cyanophytes disappeared. This may be explained by the hydrological variability caused by the tide that impeded their settlement. Conversely, Underwood (1994)

found no difference in the diversity of the epipelic algal community at three sites, in the Severn Estuary along a salinity gradient. In addition, he also found greater seasonal variation in species composition on the upper fresher mudflats of the estuary because of the longer period of tidal exposure that resulted in greater variability in temperature and salinity.

2.5.8 Wind

Wind-induced waves can have a significant effect on water movement and sediment resuspension in shallow lakes and wetlands (Wetzel 1983). Resuspension of sediment may have important biological consequences for macrophytes and SAA. It increases water column turbidity so less light reaches the sediment-water interface. However, wind also disturbs the sediment and may release phosphorus for phytoplankton (Ogilvie & Mitchell 1998). The most frequent effect of resuspension is an increase in chlorophyll concentration in the sediment (Hamilton & Mitchell 1996, 1997). It may be higher than the baseline concentration, reflecting cumulative effects of earlier resuspension events. Therefore, the effects of resuspension on Chl *a* concentration may have been underestimated in previous studies. Resuspension in shallow eutrophic lakes often decrease the TN:TP ratio in the water so they approach those of the sediment which leads to nitrogen relief of algae (Ogilvie & Mitchell 1998).

Sabbe (1993) has studied the relationship between wind speed and epipelic cell abundance in the sediment. He found that the small but significant contribution of wind speed to a multiple regression equation used to predict cell abundance, in a Dutch estuary, points to a negative effect of wind speed on the epipelic cell abundance in the sediment.

2.6 Biotic factors influencing sediment-associated algal biomass

There has not been as much research on the biotic factors that affect SAA biomass and productivity as has been done on the abiotic factors. Most measurements of biotic factors and SAA were taken simultaneously but not intentionally to draw any causal relationship.

2.6.1 Phytoplankton

SAA can obtain high biomass (Moss 1968, Hansson 1988a) and may contribute up to 80% of the primary production in subarctic Swedish lakes. Little research has been done on the direct effect of phytoplankton on SAA. However, numerous studies have included simultaneous measurements of both the phytoplankton and SAA. SAA and phytoplankton coexist but their biomass differs spatially and temporally. Both assemblages require light and nutrients for growth. SAA can limit nutrient availability for phytoplankton by reducing the efflux of nitrogen and phosphorus from the sediment (Carlton & Wetzel 1988, Hansson 1990, Van Luijn 1995, Blumenschine *et al.* 1997, Lassen 1997). On the other hand, if nutrients are not limiting for phytoplankton they may proliferate and reduce light availability for SAA. This shift from nutrient limitation to light limitation in epipelon caused by phytoplankton was observed in temperate and subarctic lakes (Hansson 1992).

In wetlands, phytoplankton is the dominant algal assemblage when water and nutrient levels are high and few macrophytes are present (Goldsborough & Robinson 1996). SAA is dominant when the water level is low, water transparency is high and few macrophytes are present (Goldsborough & Robinson 1996). In Delta Marsh, epipelon and phytoplankton contributed 1% of total algal biomass but phytoplankton biomass increased as water depth increased, which is consistent with the early stages in a transition to a "lake wetland" in which phytoplankton dominate (Robinson *et al.* 1997).

In the following studies, the direct relationship between phytoplankton and epipelon production has been documented. In the bays of the Ebro Delta in northeast Spain, the chlorophyll *a* content in the top 3 mm of the sediment was similar to that in the phytoplankton in the water column but its production was only one quarter (Delgado 1989). The biomass of the benthic microalgae (mean 36.4 mg Chl *a*/m^2) always exceeded the phytoplankton biomass (mean 8.2 mg Chl *a*/m^2) in Onslow Bay, North Carolina. However, the average benthic microalgal productivity (24.9 mg C/m^2/hr) was lower than the integrated water column productivity (27.4 mg C/ m^2/hr) (Cahoon & Cooke 1992). These findings can be explained by the increase in Chl *a* content in the SAA to adapt to the low light environment.

In tundra ponds of Alaska, Stanley (1976) found that epipelic production (4-10 g C/m^2/yr) was greater than phytoplankton productivity (1 g C/m^2/yr). Several studies that have dealt with coastal intertidal areas such as the Georgia salt marshes, the Danish Waddin Sea, the BC sandflat and the New England Estuary found that epipelic productivity ranged from 100-200 g C/m^2/yr and in every study was greater then planktonic productivity.

2.6.2 Vegetation

Aquatic vascular plants are defining features of a wetland. They can be either emergent or submergent. The role of macrophytes in wetlands include stabilizing the soil surface, reducing the current velocities of the water, shading algae below, and providing surface area for epiphytic algal growth (Brix 1998). Most studies on primary production in wetlands have been based solely on measurements of macrophytes biomass and production and they have, therefore, underestimated total primary production by ignoring significant contributions from algal photosynthesis (Brinson *et al.* 1981). A recent study comparing primary production of macrophytes and algae found that algal biomass equaled or exceeded

macrophyte biomass when all algal assemblages were included in the measurement (R. McDougal, pers. comm.).

Scheffer *et al.* (1993) proposed a model comprising two alternative stable states; a clear water state dominated by macrophytes and a turbid state, without macrophytes, dominated by phytoplankton. Submersed macrophytes enhance water quality while high turbidity prevents their growth due to light limitation. According to Scheffer *et al.* (1993) these two alternative stable states are possible in shallow lakes over a range of intermediate nutrient concentrations. Vegetation can stabilize a clear water state in shallow lakes up to a relatively high nutrient concentration but once the system has switched to a turbid state it takes a strong nutrient reduction to enable recolonization of macrophytes. Reducing the nutrient concentration rarely leads to change to the clear water state. But, reducing the fish stock can switch a turbid state to a clear state. The reduction of planktivorous fish allows zooplankton to peak and graze down phytoplankton and there would be less sediment resuspension.

Lougheed *et al.* (1998) found that the loss of submergent macrophytes in Cootes Paradise, a coastal wetland of Lake Ontario, could be explained by the decrease in water clarity. This was caused by increased carp (*Cyrinus carpio*) disturbance during spawning and feeding. They also observed a more diverse macrophyte community (>7 species) in clear water sites. Macrophytes help to stabilize the sediment and are also important sources and sinks of nutrients to the sediment (Brix 1997). In the absence of both emergent and submergent macrophytes in the spring, light penetration through the water column is high and the exposed sediments can be colonized by SAA. Once macrophytes develop in the summer, the sediment surface is shaded (Kjeldson *et al.* 1996). In the fall, the macrophytes start to senesce and light reaching the sediment surface increases.

A significant effect of vegetation on epipelon production was observed by Murkin *et al.* (1994) in enclosures, in a prairie wetland in the Interlake region of Manitoba. Unvegetated enclosures had higher levels of epipelon production than nearby vegetated sites, particularly early in the growing season. This can be explained by the increased amount of light available at the substrata in enclosures without macrophytes. Wrubleski (1991) showed experimentally that epipelon biomass in Delta Marsh, MB, increased when he removed a dense *Potomageton pectinatus* overstory. In addition, macrophytes may out compete epipelon for sedimentary nutrients or release allelo-chemicals that selectively inhibit growth of epipelic algae (Stephen *et al.* 1997). Macrophytes, that do not root into sediments, such as *Ceratophyllum demersum,* require nutrient uptake from the water and may compete successfully with phytoplankton, leaving sediment nutrients available for SAA. Macrophytes have a competitive advantage over phytoplankton due to their ability to accumulate nitrogen early in the season, compete for light and allelopathy (Mjelde & Faafeng 1997).

A decrease in epipelic algal production has been shown to coincide with macrophyte spring growth in streams (Lassen 1997). A canopy of submerged macrophytes had a significant impact on light transmission to the sediment surface. In enclosures with 100% macrophyte cover only 8% of incident light reached the sediment surface compared to 37% that reached the sediment in enclosures without macrophytes. The presence of vegetation also had a significant effect on epipelic algal productivity. From May to July the productivity in enclosures with macrophytes decreased to less than 20% of the productivity in May when macrophytes were absent whereas productivity in the enclosures without macrophytes remained constant throughout the growing season.

2.6.3 Herbivory

SAA provide a concentrated source of energy for grazing animals. The grazing electivity of the grazer determines if an algal species will be grazed. Grazer selectivity is based on the morphological and/or nutritional differences between the algal taxa. Most species of SAA are adnate and therefore have a negative electivity and are not easily grazed (L.G. Goldsborough, pers. comm.). This leads to different patterns of grazing pressure on the phytoplankton and SAA. Phytoplankton biomass is strongly dependent on grazing. In contrast, benthic grazing organisms consume less than 15% of the epipelic production (Campeau *et al.* 1994). Unfortunately, there has been limited research done on the effect of grazers on the epipelic algal community.

In lakes, grazers are the main biotic disturbance to benthic algae. They impact the epipelic community either by direct consumption or by dislodging the cells from the substratum. Grazers range from protozoa to bottom feeding fish (Lowe 1996). Grazing by invertebrates and to a lesser extent fish is a secondary source of biomass loss for epipelic algae.

Wetlands are spawning and feeding ground for fish, waterfowl, muskrats and beavers (Mitsch & Goselink 1993). These animals disrupt the sediment, destroy emergent and submerged macrophytes and in the process disrupt the benthic algal community. The common carp (*Cyrinus carpio*) graze uprooting vegetation while searching for food and resuspend the sediment (Lougheed *et al.* 1998). Carp activity, especially during spawning, disturb the sediment for epipelic growth and also increase the turbidity of the water column limiting light reaching the epipelon. Lougheed *et al.* (1998) found that wetlands without carp tended to have clearer water and a diverse (>7 species) and a dense community of macrophytes (>20 plants/m^2).

Wetland algae and algal detritus have a high nutritive value compared to vascular plant litter (Campeau *et al.* 1994). Algae is also an important source to herbivores because of its availability during the ice-free period compared to macrophytes and insects. Epipelon is especially important due to its availability throughout the growing season unlike higher plants that senesce in the fall and do not emerge until the following summer. However, there is no direct evidence that grazing disturbance does effect the epipelic algal abundance. Campeau *et al.* (1994) found no increase in epipelon biomass, in enclosures deployed in a nutrient-poor marsh of the Interlake region of Manitoba, after additions of nitrogen and phosphorus. According to Blumenschine *et al.* (1997), who excluded invertebrates from their mesocosms in Long Lake, MI, increased grazing did not explain the lack of response of epipelon to nutrient addition. Benthic consumers may benefit from an increase in phytoplankton biomass by filter-feeding or collecting newly sedimented phytoplankton.

2.6.4 Seasonal variation

No single factor can account for seasonal fluctuations in SAA chlorophyll. A combination of % surface irradiance, nutrient concentration, temperature, and physical disturbances at the sediment, the presence of phytoplankton and zooplankton grazing contribute to these fluctuations. Robinson *et al.* (1997 a & b) found there was no seasonal variation in SAA biomass in enclosures in Delta Marsh, MB when water levels were fluctuated. However, differences in algal biomass, production and species composition between years were observed.

Epipelic cell numbers, in the Garmat Ali river of Iraq, showed two peaks. The largest peak occurred in autumn while the other was earlier in the summer (Al-Saadi *et al.* 1996). Kassim & Al-Saadi (1994) also found peaks in the epipelic

community (87.3%) in August and April that were dominated by diatoms in the marsh areas of southern Iraq.

Seasonal fluctuations in the epipelon biomass of five prairie parkland lakes in central Alberta were observed by Hickman (1978). He found that peaks in epipelic biomass occurred in late spring and autumn. Midsummer peaks did occur at shallow littoral stations but they were dominated by *Chlorococcocales* sp. This genus is not associated with the sediment and therefore, could not be part of the epipelic algal assemblage. Winter peaks were also dominated by algae of planktonic origin. Hickman (1978) found the autumn maxima biomass to be greater than the spring due to the extremely short growing period between ice break up and summer. Water temperature, light intensity and photoperiod also increased rapidly toward the summer values so that spring conditions were present for a short time. Algal production, in a salt marsh in Delaware, was greatest at low tide in winter and highest at high tide in summer but total daily production was not significantly different at different seasons (Gallagher & Daiber 1974). The annual productivity of the epibenthic algal community of a brackish marsh, in Delaware, was 10% of the estimated net aerial productivity of the terrestrial grass canopy in this area. In this case, productivity increased in the summer due to increased temperature.

2.7 Summary of the literature

There has been a modest amount of research on SAA in lakes, streams and wetlands. Still, the majority of studies in algal ecology are devoted to phytoplankton research. The main reason for this is the lack of knowledge of the importance of this assemblage, as well as the logistic difficulty and expense in collecting these samples.

Several factors seem to be of minor importance in determining SAA biomass including temperature, substratum characteristics and herbivory but a great deal of

variation can be explained by light and nutrient availability (Hansson 1992). Although carp bioturbation of sediments is one of the major factors in wetland degradation, all abiotic and biotic factors may contribute to the increase in water turbidity and nutrient concentration including wind suspension, benthic herbivores, algal concentration, nutrient loading and substatum type (Lougheed *et al.* 1998).

Not only do abiotic and biotic factors influence SAA biomass, but this algal assemblage affects them. The presence of this SAA biofilm, affects nutrient fluxes at the sediment-water interface and limits phosphorus efflux to phytoplankton in the water column. The presence of algae on the sediment also alters the dissolved oxygen and carbon dioxide concentrations in the sediment pore-water, thereby altering the pH and redox conditions in the sediment and the overlying water (Woodruff *et al.* 1999).

There is a definite need for more research on SAA and the biotic factors that affect its growth. A standard method for sampling this assemblage should also be established. This community warrants further research as it may be a significant contributor to the total algal production in wetlands.

3. METHODS

3.1 Study site

This study was conducted in Delta Marsh, a 22,000 hectare prairie wetland on the south shore of Lake Manitoba, Canada. The focus of this study was on three sites within the west unit of Delta Marsh adjacent to the Portage Diversion - Blind Channel, Crescent Pond, Saline Pond (Figure 2 & 3, Table 1).

The Blind Channel is a flat-bottomed, 45 m wide Assiniboine River paleochannel (Rannie *et al.* 1989) and is vegetated by submersed macrophytes (*Potamogeton zosteriformis, P. pectinatus, Myriophyllum sibiricum, Ceratophyllum demersum* and *Chara* sp.) in the open water and emergents (*Typha x glauca* and *Phragmites australis*) along the channel edges.

Crescent Pond is an enclosed pond surrounded by an extensive zone of emergent vegetation in depths up to 40-60 cm (Hooper & Robinson 1976). Formerly a part of the Assiniboine paleochannel, this pond has been encroached by cattails and its size has decreased by 34% over the past 50 years (Goldsborough 1987). *Typha x glauca*. is the most dominant emergent macrophyte. According to Hooper & Robinson (1976) *Potamogeton pectinatus* L. was the dominant submerged macrophyte although I observed the dominant macrophyte, based on visual estimates of pond surface cover, to be *Lemna trisulca*, followed by *Ceratophyllum demersum*. *Potamogeton petinatus* L. was rare during this study.

Saline Pond is a borrow pit by the west dike of the Portage Diversion, that was excavated during the construction of the diversion channel in 1968. The emergent vegetation consists of *Typha x glauca* and the pond is surrounded by patches of *Salicornia rubra*. The submersed vegetation was dominated by *Potamogeton pectinatus* L. The sites also differed with respect to their water chemistry and sediment composition (see Results).

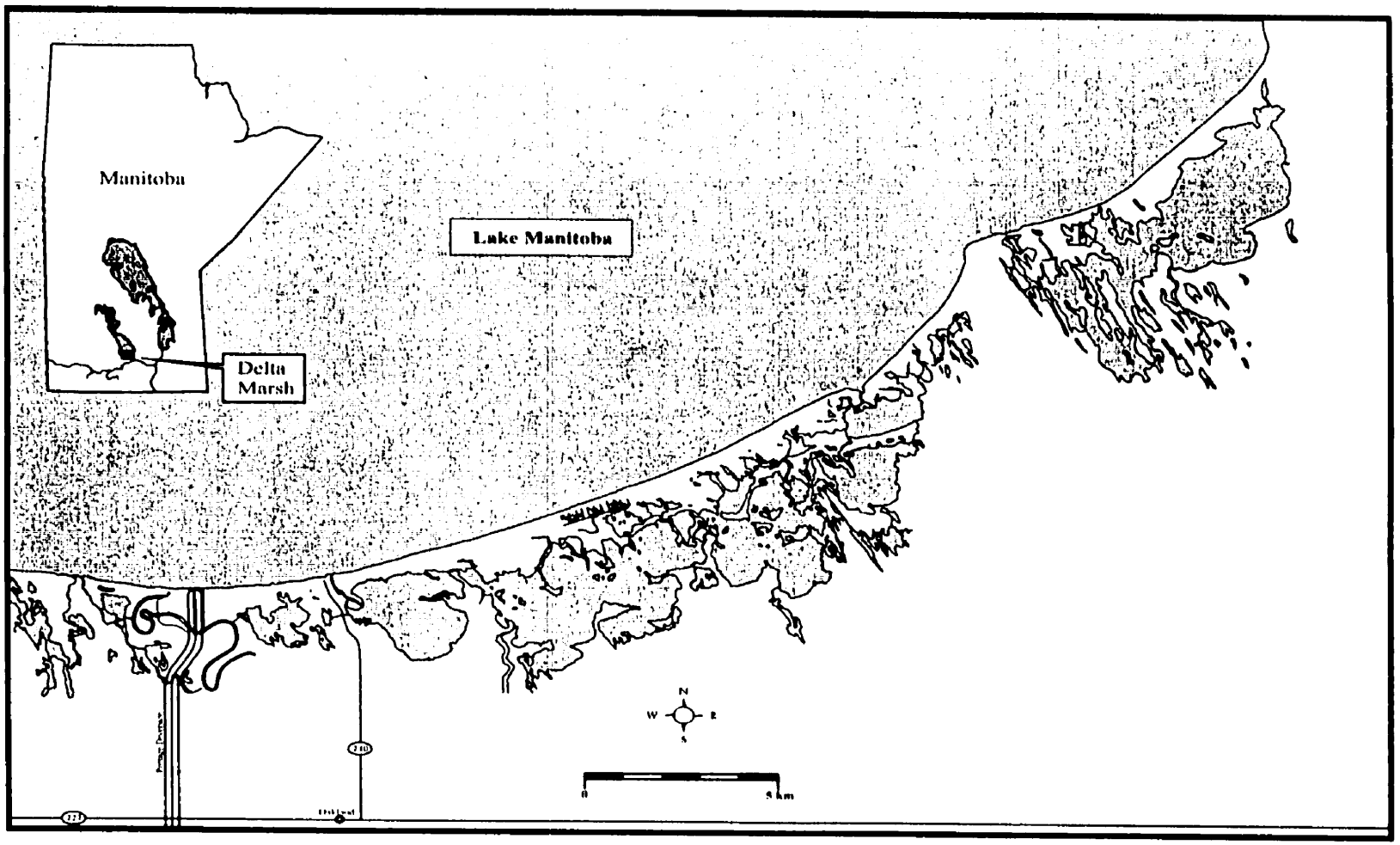

Figure 2: Delta Marsh, MB Canada; a 22000 hectare wetland on the south shore of Lake Manitoba

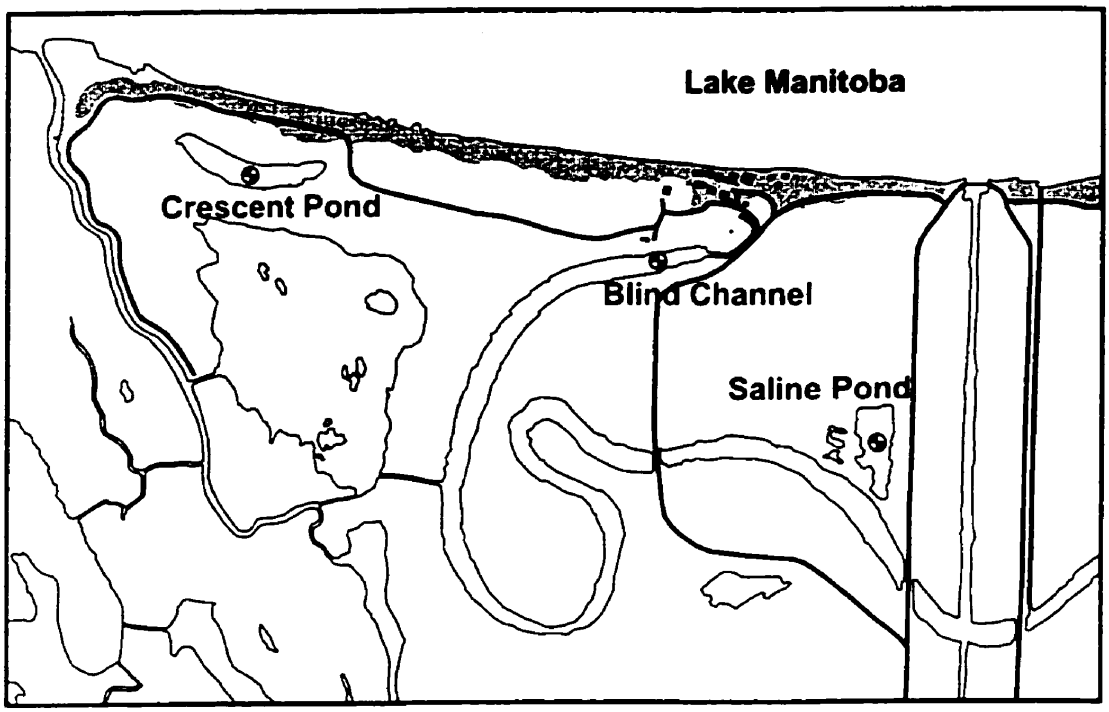

Figure 3: Schematic diagram of the three sampling sites within Delta Marsh, MB.

Table 1: Surface area and depth (at sediment sample collection sites) in Blind Channel, Crescent Pond and Saline Pond (seasonal means ± SE, n = 40). Superscript letters represent significant Scheffé *post hoc* comparisons between sites, with a critical p value = 0.05.

	Blind Channel	Crescent Pond	Saline Pond	*p value*
Area (ha)	na	3.4	2.3	
Mean depth (cm)				
1998	97^{A} (± 4)	94^{A} (± 2)	65^{B} (± 3)	*0.001*
1999	91^{A} (± 4)	93^{A} (± 4)	65^{B} (± 4)	*0.001*

3.2 Field season 1998

Six surficial sediment and integrated water samples were collected biweekly from June until October at each of the three sites. Samples alternated monthly between being collected along transects and at one point to obtain a degree of spatial heterogeneity. A random spot in the pond was selected and the canoe was rotated around to get six samples in close proximity without disturbing the sediment surface. All samples were collected from an anchored canoe to minimize sediment disturbance during sampling. At each sample location within each site the water depth was recorded, a sediment slurry, a sediment core and a water sample were collected for analysis of water chemistry and phytoplankton biomass.

3.2.1 Sampling methods and analyses

Water column samples were collected at each site by dipping a 1 L polypropylene bottle. Water samples were analyzed for pH, alkalinity (acid titration; APHA 1992), total reactive phosphorus (acid molybdate method; Stainton *et al.* 1977), ammonium-N (hypochlorite method; Stainton *et al.* 1977), nitrate+nitrite-N (UV spectrophotometric method; APHA 1992), and soluble reactive silica (acid molybdate method; Stainton *et al.* 1977). Conductivity was measured at each site using a YSI Model 30 conductivity meter.

In situ sediment slurries were collected at six randomly selected locations in each of the three sites (Blind Channel, Crescent Pond, Saline Pond) at biweekly intervals. A plastic tube (diameter = 0.45 cm), attached to a side-arm flask and a hand-operated vacuum pump, was used to aspirate the surface sediments enclosed within a 10 cm diameter PVC tube that was embedded in the surface sediments. When 500 mL was collected, its contents were transferred into a 1 L sample bottle by rinsing with distilled deionized water (DDW). A volume of 500 mL was chosen as it corresponds to a depth of 6.4 cm.

At the lab, the contents of the plastic sample bottles were emptied into separate blackened 2 L plastic containers and left undisturbed in the dark for approximately 24 hours. After the sediment had settled the overlying water was removed by suction using the side arm flask and hand-operated vacuum pump, so as not to disturb the settled sediment. Samples (2 cm^3) were taken from the slurry using an open-ended 5 mL syringe for analysis of chlorophyll *a*, sediment dry weight and algal species identification and enumeration.

Once the sun had set, the blackened beakers containing the sediment were transported to the field station's weather station. There, any remaining free-standing water was siphoned off and the sediment was covered with lens paper filters, pre-cut to the same diameter as the darkened plastic containers (8.8 cm). The lens paper served to trap the motile sediment-associated algae that migrated towards sunlight. Each darkened plastic bottle was covered with a clear plastic bag and left undisturbed on the weather station platform overnight. To account for the temporal variability in the upward motility of algal taxa, the lens tissue papers were placed on each sample, first from sun up to 10 am, second from 10 am to 2 pm and third from 2 pm to 7 pm. Again, any excess water that accumulated throughout the day was removed at these times with a Pasteur pipette. When the lens papers were removed, they were cut in half. One half was placed in a plastic centrifuge tube for chlorophyll *a* analysis while the other half was placed in a 20 mL scintillation vial to be preserved in Lugol's solution for algal identification. After the last tissue trap was removed, 2 cm^3 samples were taken from the bulk sediment slurries for analysis of chlorophyll *a*, sediment dry weight and algal species identification using the same procedure as before tissue trapping. This was done to determine whether there were any remaining sediment-associated algae that did not migrate into the lens paper. The dry weight of the remaining sediment slurry was weighed and compared to the

amount of sample collected in the open-ended syringe to determine what percentage of the slurry was sampled.

After the sediment slurry was collected the PVC tube used for slurry collection was left in the sediment so as not to disturb the sediment-water interface. Then, a clear plastic tube (6.3 cm diameter) was lowered vertically into the sediment to collect an intact core. A rubber stopper was placed in the top of the tube. The tube was gently lifted, to create suction, and before it broke the water surface, a plastic disk was placed on the bottom of the tube. A core extruder pole was placed under this disk and the stopper was removed. Then, the core barrel was gently lowered down the extruder causing the gradual extrusion of the sediment core at the barrel top. Approximately 3 mm of the uppermost intact sediment layer were scraped off and collected for analysis of chlorophyll *a*, sediment dry weight, sediment phosphorus and algal identification. Only samples with obviously intact surfaces were used; otherwise, the core was discarded and a new sample was collected.

Total chlorophyll *a* (chlorophyll and pheophytin; µg/L) was used as an indicator of sediment-associated algal biomass. Lens tissue papers and 2 cm^3 samples of the sediment slurries and sediment cores collected in an open-ended syringe were frozen for at least 24 hours prior to analysis to disrupt algal membranes. Samples were then placed in 5mL of 90% methanol in the dark overnight. All samples were centrifuged for 10 minutes before being analysed spectrophotometrically at 665nm and 750nm (Marker *et al.* 1980).

Chlorophyll values in Chl *a* per cm^2 or g were converted to mg/m^2 of marsh bottom. For sediment slurries and cores, this calculation was done by determining the percentage of the entire slurry or core and that was sampled in the 2 cm^3 syringe. This percentage was used to determine the area of the 2 cm^3 syringe from the known area of the slurry or core.

Water, organic matter and carbonate mineral content of the sediment slurry was analysed before and after tissue trapping and the sediment core. Following the method of Dean (1974) clay crucibles were dried overnight at 105°C and immediately weighed. Moist sediment was collected using an open-ended syringe 2 cm^3 and transferred to the crucible. These samples were dried overnight and reweighed to determine the water content of the sediment (% of wet weight). The dry sample was then incinerated in a muffle furnace at 550°C for 1 hour, which caused all organic material in the sample to be combusted and given off as inorganic CO_2. The difference in the weight of the sample before and after incineration reflected the organic matter content of the sample (% of dry weight). This sample was then incinerated at 950°C, which caused the carbonate minerals to be converted to CO_2 and thus the difference in the weight before and after incineration reflected the carbonate content (% of dry weight).

To prepare samples for algal identification, lens papers were vigorously shaken in 10 mL of DDW to dislodge the algae trapped in the lens filter fibres. The lens paper was then removed and 2 mL Lugol's iodine solution was added. Sediment core and slurry samples (2 cm^3) were diluted in 10 mL of DDW before the addition of 2 mL Lugol's solution. Samples were kept in the dark until identification and enumeration. This preservation technique was good for several months provided the sample does not become bleached by the sun.

A Palmer counting cell containing 100 µL was used with light microscopy. Lens tissue samples were diluted 1:1 with DDW and sediment samples were diluted 1:4. Slides were first examined at the lowest magnification (100x) to focus on the plane containing algal cells, then adjusted to 400x. Algal cells were counted in 20 field of views along a linear transect in the middle of the Palmer cell. Since the volume of the sample, the area of the counting chamber and the diameter of the field of view are known, the number of cells of each species per unit sample volume

was calculated. However, biomass reported in the form of cell counts is essentially useless since there is considerable size range amongst algal species. Dimensions of the cells were measured, using similar geometric forms for each taxon encountered, to permit the calculation of cell volumes. This was done for each significant species and sufficient measurements were made to provide an acceptable standard error. One genus, *Navicula*, was divided into two categories, based on size. Algal species identification and enumeration was done for three replicates of each sampling method for one sampling date in August. This date was used because the sampling techniques had been practiced and the SAA community had been established. However, this community does not represent the two field seasons.

For phytoplankton a 1 L water sample was collected, 500 mL of which was used for phytoplankton total chlorophyll analysis (µg/L). Water samples were filtered through glass microfibre filters (Whatman GF/C), neutralized with $MgCO_3$ and frozen for subsequent chlorophyll analysis. The samples were then placed in 5ml of 90% methanol for 24 hours in the dark and analysed as described above.

From the sediment cores, 2 cm^3 of sediment was collected using an open-ended syringe and placed in pre-weighed 20 mL scintillation vials for sediment phosphorus analysis. The samples were dried overnight at 105°C and then reweighed. The samples were ignited at 550°C for 1 hour. Sediment was then transferred into 125 mL Erlenmeyer flasks with 25 mL 1N HCl and boiled for 8 minutes. After cooling, samples were diluted to 100 mL in a volumetric flask with distilled water and decanted into glass centrifuge tubes. To clear the sample, they were centrifuged at 3000 rpms for 5 minutes. The clear supernatant (10 mL) was placed in 20 mL scintillation vials and 2 mL of mixed molybdate reagent was added. After colour development had occurred (approximately 30 minutes) absorbance was measured spectrophotometrically at 885 nm (Stainton *et al.* 1977).

Pore water samples were collected by inserting a "peeper" (Hesslein 1976) to the desired depth in the sediment. The peeper was made of acrylic and consisted of 38 milled grooves every 1.5 cm centimetres. The grooves were filled with DDW and covered with polyester membrane filter paper (pore size of 2 microns, Osmonics Inc.). The peeper was attached to a 2" x 2" wooden stake that was used to position the peeper at the required sediment depth. The depth from the water surface to the sediment and the depth from the water surface to the top of the peeper were recorded. Peepers were placed in Blind Channel, Crescent Pond or Saline Pond every three weeks. A week later the depths were remeasured, the peeper was removed and transported back to the laboratory. Pore water samples (3.5 mL) were withdrawn from each groove by puncturing the membrane with a 5 mL syringe and placed in a 5 mL volumetric flask. DDW was added to make the volume up to 5 mL. Alternate grooves were analysed for total reactive phosphorus (acid molybdate method; Stainton *et al.* 1977) while remaining grooves were analysed for ammonium-N (hypochlorite method; Stainton *et al.* 1977). In late summer a test was conducted in which a peeper filled with DDW was immersed in a water basin and parged with nitrogen gas prior to placement in the marsh sediments. The peeper water was then anaerobic and not introducing any oxygen into the anaerobic sediments. This was done to determine whether adding aerobic water (peeper not parged in nitrogen gas) lowered the ammonia concentrations found in the sediment pore water.

3.3 Field season 1999

3.3.1 Study site

The second field season was also conducted at the same three sites. Five samples at each of these three sites were collected biweekly between May and September 1999. Samples were collected at the centre of the ponds and samples were taken at the same approximate location. In Blind Channel samples were

collected from the west of the enclosures to the mouth of the canoe ditch. Crescent Pond samples were collected from the west to the east end of the pond and Saline Pond's from the south and continued to the north end. At each sample location within each site the water depth and light profiles were recorded. Two sediment slurries, a sediment core and a macrophyte sample were also collected. A 1L polyethylene bottle was filled with a water sample for analysis of phytoplankton chlorophyll and turbidity.

3.3.2 Sampling methods and analyses

Light readings were taken above and below water surface and at 10 cm intervals through the water column until the sediment surface was reached. The percent of surface water irradiance reaching the sediment surface was calculated using a regression.

Surface water samples were analysed for Turbidity (NTU) using a Hach 2100 A turbidimeter.

In situ sediment slurries were collected and processed as they were in 1998 except for one alteration. Instead of removing and replacing lens tissue papers at 10 am, 2 pm and 7 pm, only one lens paper, per darkened plastic bottle, covered the sediment and was removed at 7pm. This was done since there was found to be no temporal variability in Chl *a* biomass between the three tissue traps collected in 1998.

This year (1999) an additional slurry was collected. This core slurry was collected using the same clear plastic tube (6.3 cm diameter) used for the sediment core collection. The plastic tube was lowered into the sediment, a rubber stopper was placed in the top end to create suction and the tube was gently lifted. A plastic disk was placed on the bottom of the tube before the tube was lifted out of the water. The plastic tube was then placed on top of the extruder pole, the rubber

stopper was removed and the core was gently lowered down the extruder. The core was lowered until there was approximately 10 cm of water remaining above the sediment-water interface. At this point a plastic tube (4.5 mm diameter) attached to a side-arm flask and a hand-operated vacuum pump, was used to aspirate the surface sediments within the clear plastic tube. This collection was more controlled then the previous slurry collection since you could see the sediment-water interface. When 200 mL was collected, its contents were transferred to a 500 mL sample bottle by rinsing with distilled deionized water and transported to the laboratory. A volume of 200 mL was collected because it corresponds to a vertical depth of 6.4 cm. This is the same vertical depth as the larger less controlled 500 mL *in situ* slurry collected from a PVC pipe.

The 200 mL slurry samples were emptied into blackened yogurt containers and left undisturbed in the dark for approximately 24 hours. These samples were then processed using the same method as the 500 mL *in situ* slurries. Again, only one tissue trap was placed over the sediment and was removed at 7pm.

Sediment cores were collected and processed using the same methods as in 1998. However, in 1999 special care was taken to collect only 6.5 mL of sediment that corresponds to a vertical depth of 2.2 mm. Additional sediment cores were collected at the three sites in order to determine the vertical profiles of Chl *a* concentration in the sediments. On 7 June 1999 three cores were collected at each of the three sites. For each core, sediment samples were collected at a depth of 3 mm, 6 mm and 9 mm and analysed for Chl *a*.

Chlorophyll *a* was used as a surrogate for biomass pigment production. Chlorophyll analysis was processed by the same method as in 1998.

A 1 L water sample was collected of which 200mL were filtered through glass microfibre filters (Whatman GF/C), neutralized with $MgCO_3$ and frozen for chlorophyll analysis.

Macrophytes were collected by placing an open ended barrel (54 cm diameter) in the marsh and clipping all macrophytes present in that area using garden shears. The clipped plant material was retrieved using a kitchen strainer. Macrophyte abundance was estimated by drying the plant material at 100°C in a drying oven. Dry weights were converted to g/m^2 of marsh bottom. Prior to drying, macrophytes were identified to species.

Sediment phosphorus content was analysed biweekly for the three sites using the same method as in 1998. Sediment nitrogen and carbon were analysed at the Freshwater Institute (Department of Fisheries and Oceans) using the methods of Stainton *et al.* (1977). C:N, C:P and N:P molar ratios were calculated.

Pore water samples were collected by inserting a "peeper" to the desired depth in the marsh sediment. The peeper was made of acrylic and consisted of twelve milled grooves (Figure 4). These peepers were smaller in length (25 cm) then those used in 1998 (66.5 cm) because I was only interested in a few centimetres above and below the sediment-water interface.

Three peepers were placed simultaneously in each of the three sites, Blind Channel, Saline Pond and Crescent Pond on 30 July, 13 August, and 25 August. In the Blind Channel, two peepers were placed west of the enclosures and one at the mouth of the canoe ditch. Peepers were placed at the south, middle and north end of Saline Pond and the west, middle and east end of Crescent Pond. All peepers were placed in the centre of either the channel or the pond.

The grooves of each peeper were filled with DDW and covered with polyester membrane paper (pore size 2 microns, Osmonics Inc.). Each groove contained 10 mL of DDW. The peepers were then parged in nitrogen gas for 24 hours, attached to a 2" x 2" wooden stake and placed in the marsh sediments. The depth from the water surface to the peeper, and from the water surface to the sediment were measured to ensure that two thirds of the peeper was below the sediment-water

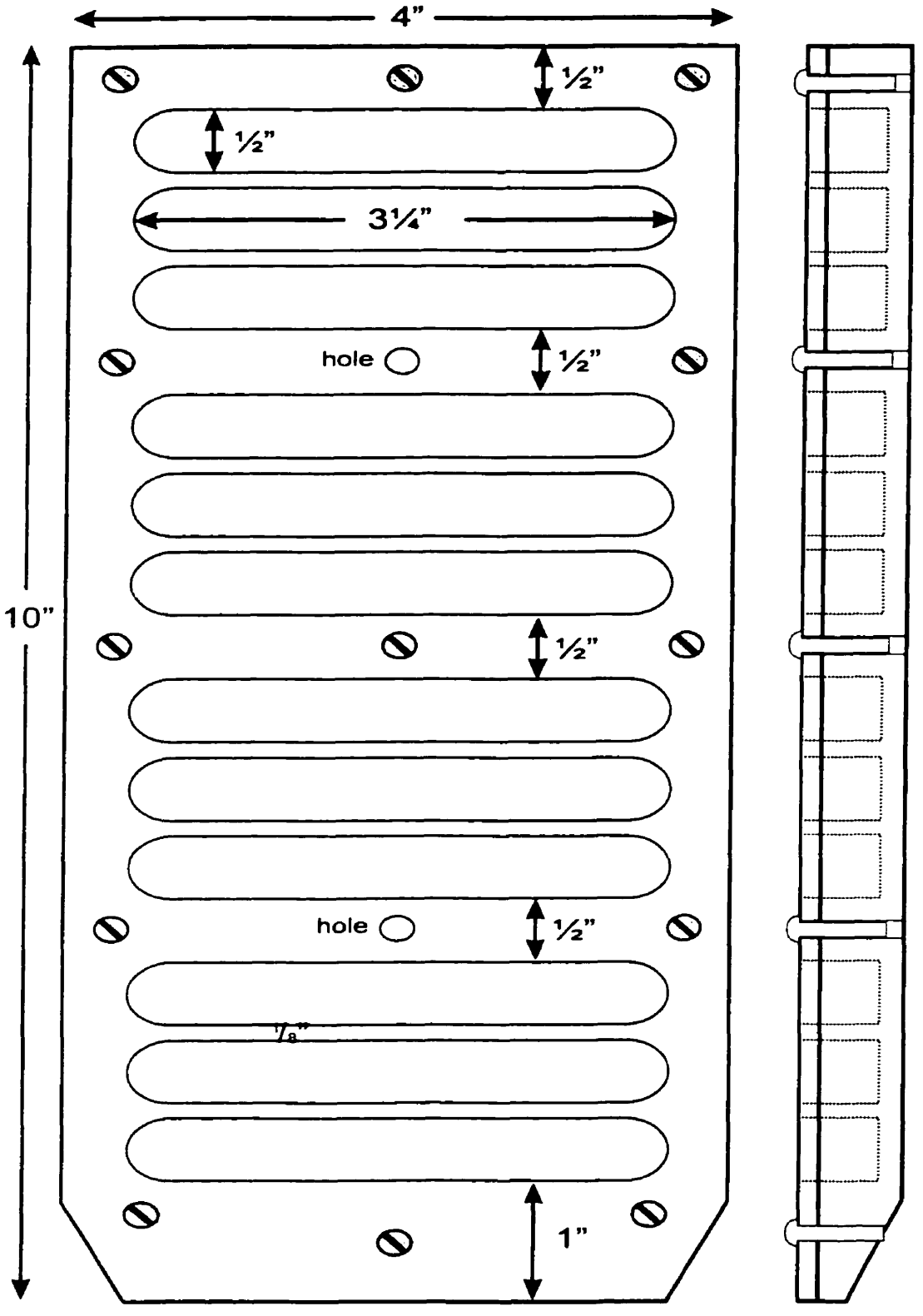

Figure 4: A schematic diagram of a "peeper" used to analyze sediment pore-water in 1999.

interface. A week later the depths were remeasured, the peeper was removed and transported back to the laboratory. Pore water samples (5 mL) were withdrawn twice from every groove, with a 5 mL syringe and placed in a 5mL volumetric flask for the 30 July and 13 August samples. Every groove was analysed for soluble reactive phosphorus (acid molybdate method; Stainton *et al.* 1977) and ammonium-N (hypochlorite; Stainton *et al.* 1977). However these samples could not be adequately diluted afterwards to get an accurate reading in the spectrophotometer. Therefore, the peepers that were placed in the marsh on 25 August were diluted by half (2.5 mL were withdrawn from the groove and made up to 5 mL with DDW) before the reagents were added for both NH_3-N and TRP analysis.

An attempt was made to quantify the frequency and abundance of plocon within a 1 m^2 area. A 1 m^2 enclosure was placed in the canoe ditch and in the Blind Channel. The enclosures consisted of 4 wooden 2" x 2" stakes attached to a 40 cm wide curtain. The curtain was placed around the stakes so it extended 20 cm above and below the air-water interface. This would prevent wave action from blowing the plocon away from the sediment from which it rose, but it would still enable water movement throughout the water column. Everyday, in late afternoon, both the canoe ditch and the Blind Channel were observed for the presence of plocon.

3.4 Statistical analysis

One-factor analyses of variance (ANOVA) were used to determine the effect of sampling method and site on Chl *a* content of SAA and the effect of sampling method and site on algal biovolume. A one-factor ANOVA compared differences between or among sample means, testing a null hypothesis that the groups represented random samples from populations with the same means (Harris 1995). The null hypothesis was rejected when $p < 0.05$ and the conclusion was drawn that the means of the sampling sites or sampling method differed significantly.

Scheffé multiple comparisons were performed following a significant analysis of variance. The Scheffé procedure was chosen because it is a *post hoc* test for an hypothesis about differences in means after an analysis of variance has led to the conclusion that the means are unlikely to represent random samples from the same population. This approach is conservative and less powerful than the Tukey HSD (Honestly Significant Difference) test but it does enable comparisons involving more than two means (Harris 1995).

Two-factor repeated measures ANOVAs were also performed to look at the effect of the interaction of site and sampling method on SAA Chl *a*. A repeated measures ANOVA was possible because all samples were collected biweekly over a 15 week period.

A forward stepwise multiple regression was used to predict the abundance of SAA chlorophyll from the measured biological, physical and chemical parameters. The analysis is a search method that computes a sequence of regression equations by successively adding variables that increase the correlation coefficient until you have arrived at a "best" set of independent variables and added variables do not improve the predictive power significantly (Neter & Wasserman 1974). However, it should be noted that the variables selected are not necessarily the ones that control the system directly. The three sites were first analysed separately to look at habitat heterogeneity within the site. Then the data were compiled to form one regression model per sampling year to determine the underlying ecological factors that affect SAA chlorophyll. Regression analysis was used because I wanted to investigate a number of independent variables simultaneously and determine which variables best explained the variation in SAA chlorophyll. SAA chlorophyll collected from the sediment core was used because it was found to be the best method for sampling SAA.

A discriminant analysis was used to look at the effect of daily PAR and wind speed on the occurrence of plocon at the water surface. This analysis was used to test the difference between alternative binary states (presence and absence of plocon) and to explore which variable was most useful for discriminating the state predominating on a given sample day. Data were log-transformed prior to analyses to reduce the variance. All statistical analyses were performed using Microsoft Excel 97 and SPSS Systat 8.0 software. A summary of the statistical analysis is provided in an Appendix.

4. RESULTS

4.1. Methodological implications

In 1998, sampling method had a significant effect on SAA chlorophyll content ($p = 0.001$). The lens tissue papers removed from the slurries at 10 am, 2 pm and 7 pm did not collect significantly different SAA chlorophyll from each other (Figure 5). According to *post hoc* comparisons, the sum of the lens tissue yielded significantly lower SAA chlorophyll (1.4 ± 0.1 mg/m^2) than the other sampling methods (44.7 ± 4.2 mg/m^2, 59.8 ± 7.5 mg/m^2 and 15.4 ± 1.2 mg/m^2, Table 2).

In situ sediment slurries before and after tissue trapping had the highest chlorophyll throughout the sampling period (Figure 6). Mean seasonal chlorophyll content of the sediment slurry after tissue trapping was higher (59.8 ± 7.5 mg/m^2) than the sediment slurry before tissue trapping (44.7 ± 4.2 mg/m^2) but *post hoc* comparisons revealed they were not significantly different (Table 2). The chlorophyll content of both slurries was significantly higher than that of the sediment core (15.4 ± 1.2 mg/m^2). Sediment cores contained approximately ten times more chlorophyll *a* content than the lens tissues (Table 2). A thick algal crust layer was often observed through the core barrel (Figure 7).

Algal biovolume in sample was calculated for one sampling cycle on 6, 7 & 10 August (Table 3). There was a significant effect of sampling method on algal biovolume ($p = 0.001$). Algal biovolumes were higher in the lens tissue trap placed on the sediment slurries between 10 am – 2 pm than the other two tissue papers placed on the slurries between dawn and 10 am or 2 pm – 7 pm. However, according to *post hoc* comparisons none of these differences were significant. All lens tissue papers had significantly lower mean biovolumes (4.1 ± 0.9 mL/m^2, 6.5 ± 1.1 mL/m^2, 3.7 ± 0.6 mL/m^2) than *in situ* sediment slurries (584.4 ± 119.3 mL/m^2 and 718.8 ± 140.7 mL/m^2, before and after tissue trapping respectively) and sediment cores

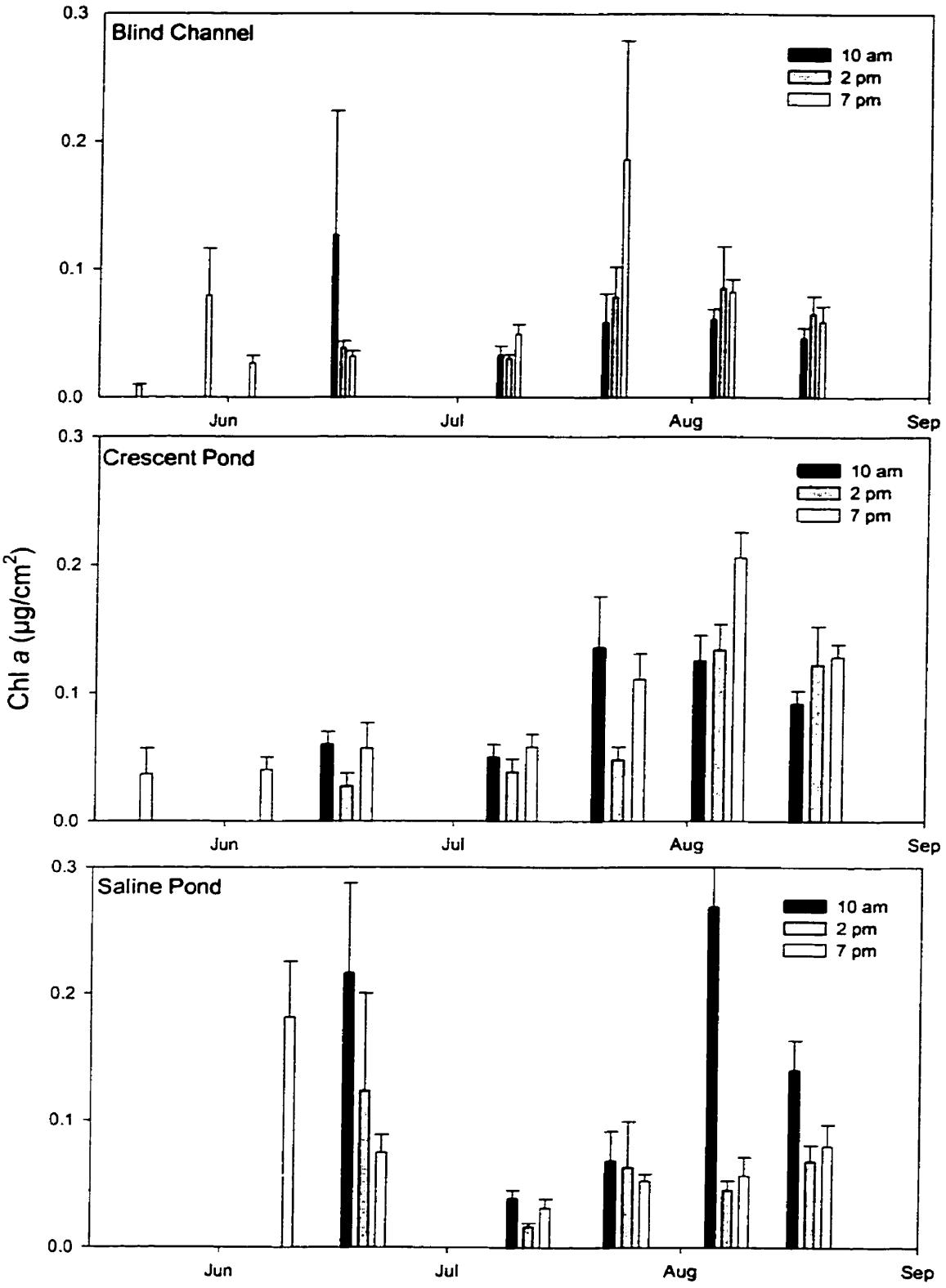

Figure 5: SAA Chl *a* (µg/cm² ± SE, n = 6, 1998) from the lens tissue trapping technique at three sites: i) Blind Channel ii) Crescent Pond iii) Saline Pond.

Table 2: Mean seasonal (1998) total chlorophyll *a* (mg/m^2 ± SE, n = 48) of SAA in Blind Channel, Crescent Pond, and Saline Pond, depending on the sample method used. Plocon and phytoplankton (mg/m^2 ± SE, n = 6 and 48, respectively) are reported here for comparison. Superscript uppercase letters represent significant Scheffé *post hoc* comparisons between sites, and superscript lowercase letter represent significant comparisons between methods, all with a critical p value = 0.05.

Sampling method	Overall Mean	Blind Channel	Crescent Pond	Saline Pond	p value
Lens tissue trapping	1.4^{a} (0.1)	0.8^{A} (0.1)	1.4^{B} (0.2)	2.1^{B} (0.2)	0.001
Sediment slurry before tissue trapping	44.7^{b} (4.2)	14.6^{A} (2.6)	28.9^{B} (3.0)	84.4^{C} (8.5)	0.001
Sediment slurry after tissue trapping	59.8^{b} (7.5)	22.3^{A} (4.4)	34.0^{B} (5.5)	122.1^{C} (17.5)	0.001
Sediment core	15.4^{c} (1.2)	8.3^{A} (1.4)	15.6^{B} (2.0)	21.3^{C} (2.2)	0.001
Plocon	na	151.7 (14.3)	127.6 (20.4)	na	na
Phytoplankton	15.8 (1.0)	25.1^{A} (1.7)	11.5^{B} (1.2)	10.9^{B} (1.2)	0.001

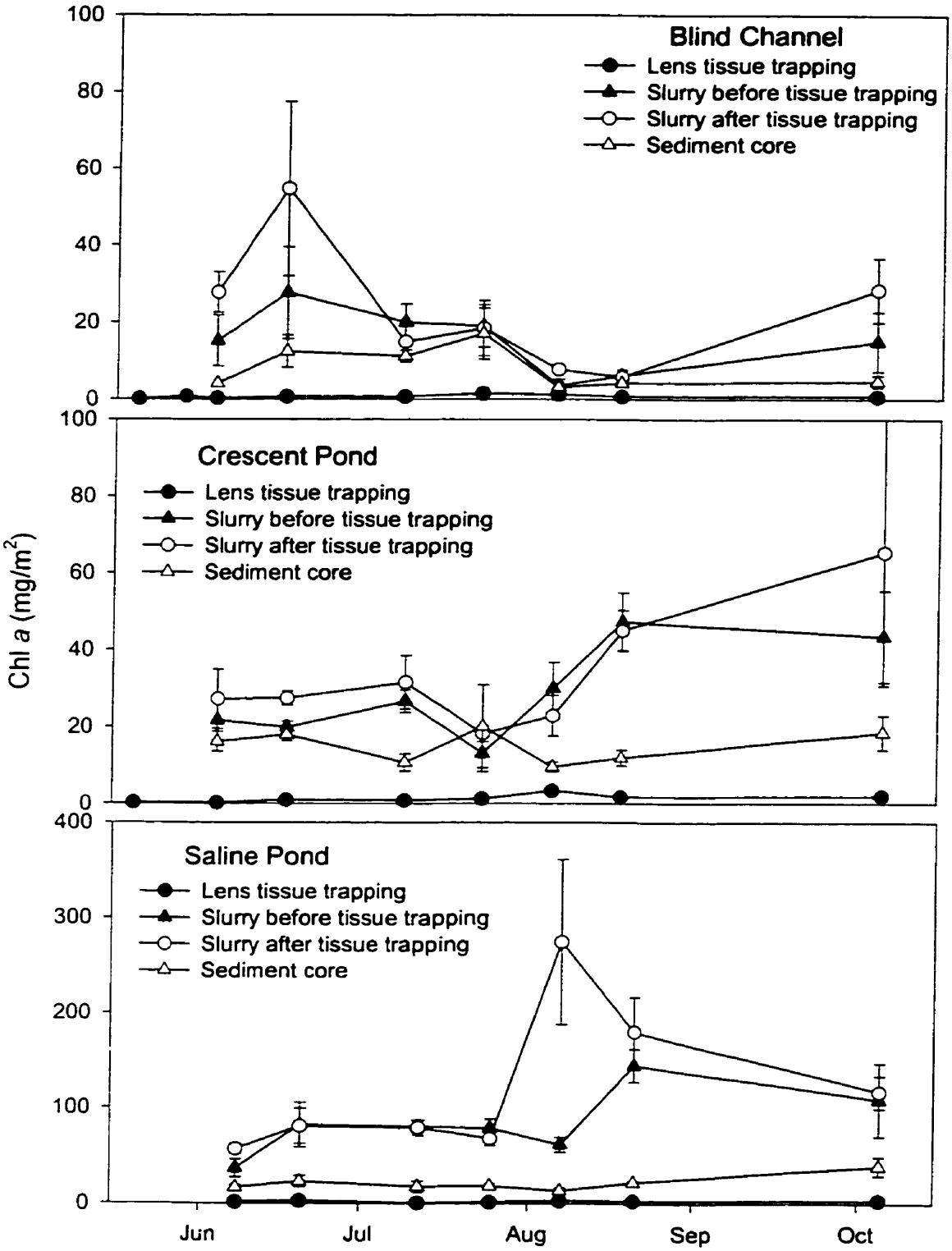

Figure 6: Mean total Chl *a* (mg/m^2 ± SE, n = 6, 1998) of SAA for lens tissue paper, sediment slurry before and after tissue trapping and an intact sediment core. Note the change in scale for the Saline Pond graph.

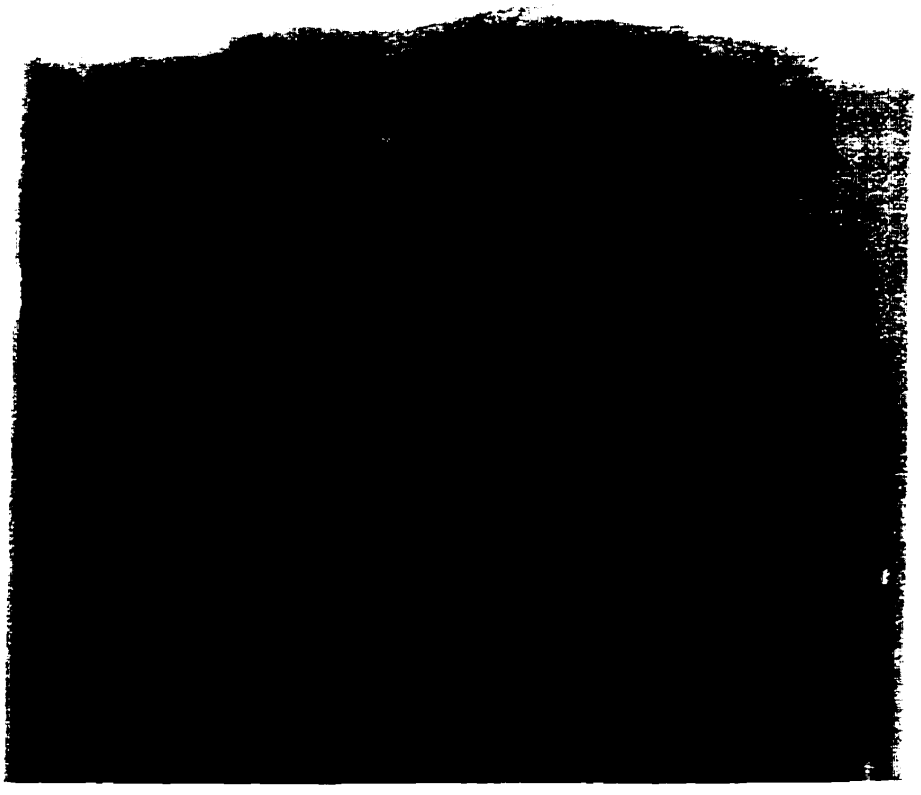

Figure 7: An intact sediment core collected from the canoe channel into Blind Channel, 1998, showing a visible algal crust layer.

Table 3: Mean biovolume ($mL/m^2 \pm SE$) of SAA depending upon sampling method used (n= 3). Samples were collected on 6,7 & 10 August 1998. Superscript uppercase letters represent significant Scheffé *post hoc* comparisons between sites, and superscript lowercase lettters represent significant comparisons between methods, all with a critical p value = 0.05.

Sampling method	Overall Mean	Blind Channel	Crescent Pond	Saline Pond	*p value*
Lens tissue 10am	4.1^{a} (0.9)	5.9 (2.4)	3.5 (0.8)	2.8 (0.6)	*0.373*
Lens tissue 2pm	6.5^{a} (1.1)	8.3 (1.8)	4.2 (1.6)	7.2 (2.0)	*0.321*
Lens tissue 7pm	3.7^{a} (0.6)	5.4^{A} (0.9)	1.8^{B} (0.7)	4.0^{A} (0.5)	*0.035*
SUM of lens tissue	14.4^{a} (1.4)	19.6 (2.4)	9.5 (2.2)	14.1 (3.5)	*0.053*
Slurry before tissue trapping	584.4^{b} (119.3)	439.9^{A} (45.6)	333.5^{A} (59.5)	979.8^{B} (212.0)	*0.026*
Slurry after tissue trapping	718.8^{b} (165.5)	682.0 (100.1)	286.2 (68.2)	1188.1 (330.8)	*0.054*
Sediment core	140.7^{c} (31.6)	171.4 (91.8)	79.3 (16.6)	171.4 (21.0)	*0.446*

(140.7 ± 31.6 mL/m^2). Slurries before and after tissue trapping did not have significantly different algal biovolumes. The biovolume calculated from the sediment core was significantly different than the slurry before and after tissue trapping (Table 3).

The algal biovolume collected from the sum of the lens tissue papers was highest in Blind Channel (19.6 ± 2.4 mL/m^2) which contradicts findings for Chl *a* content. However, there was no difference between sites ($p = 0.053$). Algal biovolumes from either sediment slurries or cores followed the same trends as Chl *a* with highest values found in Saline Pond. Surprisingly, Crescent Pond had a lower algal biovolume but a higher Chl *a* content than Blind Channel but the difference was not significant (Table 3).

The percentage of total cell biovolume was calculated for seven benthic algal indicator genera present in these samples. The percentage of genera present was different for each sampling method. A single method did not sample one genus more prominently except the lens tissue trapping technique. *Euglena* sp. represented the highest % in lens tissue paper at all three sites (Table 4). Genera present for each sampling method and in each site are reported in a table in the Appendix.

In 1999, a one factor ANOVA revealed that sampling method had a significant effect on SAA chlorophyll content ($p = 0.001$). Lens tissue papers were collected at 7 pm from two kinds of slurries: the *in situ* slurries and the core slurries. *Post hoc* pairwise comparisons of the lens paper collected from the *in situ* sediment slurries and the controlled core slurries yielded significantly lower SAA chlorophyll than sediment slurries and cores (Table 5). Both lens tissue trapping techniques yielded SAA chlorophyll that was always less than 5 mg/m^2 and no seasonal trend was observed throughout the sampling period (Figure 8). There was no significant difference between mean seasonal chlorophyll in the tissue traps collected from *in situ* (1.2 ± 0.1 mg/m^2) and core slurries (0.9 ± 0.1 mg/m^2). Contrary to the 1998 field

Table 4: The percentage of total cell biovolume for seven benthic algal genera of SAA depending upon sampling method used (n = 3): i) lens tissue paper collected at 10am, 2pm and 7pm, ii) sediment slurries before (A) and after (B) tissue trapping iii) sediment core. Samples were collected from Blind Channel, Crescent Pond and Saline Pond on 6, 7, 10 Aug 1998.

Blind Channel	Lens tissue			Slurry	Slurry	
	10am	2pm	7pm	A	B	Core
% *Caloneis*	5.9	2.3	4.3	4.5	3.7	4.7
% *Cymatopleura*	3.1	0.0	0.0	5.3	4.8	0.0
% *Epithemia*	22.6	18.7	34.9	12.9	16.7	8.0
% *Euglena*	2.4	0.8	1.3	0.0	0.6	1.4
% *Navicula* (sm)	7.0	3.7	5.1	5.5	5.5	2.1
% *Navicula* (la)	0.7	0.3	0.5	1.0	0.4	0.7
% *Oscillatoria*	0.8	0.0	0.0	0.0	0.0	0.0
% *Surirella*	0.0	0.0	2.5	2.0	2.4	2.8

Crescent Pond	Lens tissue			Slurry	Slurry	
	10am	2pm	7pm	A	B	Core
% *Caloneis*	2.2	3.7	4.3	1.9	0.6	0.0
% *Cymatopleura*	0.0	4.3	0.0	2.9	0.0	0.0
% *Epithemia*	15.8	21.1	12.4	9.0	8.7	10.0
% *Euglena*	4.0	6.6	3.9	2.3	2.2	18.8
% *Navicula* (la)	14.7	3.3	9.6	5.6	1.6	6.2
% *Navicula* (sm)	5.8	2.6	8.1	2.4	2.8	6.9
% *Oscillatoria*	0.0	0.4	0.0	0.0	0.0	4.2
% *Surirella*	0.0	0.0	0.0	2.2	0.0	0.0

Saline Pond	Lens tissue			Slurry	Slurry	
	10am	2pm	7pm	A	B	Core
% *Caloneis*	10.9	0.0	0.0	1.3	1.2	0.5
% *Cymatopleura*	0.0	0.0	0.0	4.1	1.8	2.5
% *Epithemia*	15.8	12.3	8.3	8.6	8.4	1.9
% *Euglena*	14.8	5.8	6.9	0.0	0.0	0.0
% *Navicula* (la)	4.9	3.8	6.8	5.4	2.8	4.2
% *Navicula* (sm)	9.1	1.5	1.9	1.4	1.7	4.6
% *Oscillatoria*	3.3	3.3	0.0	0.0	0.0	0.0
% *Surirella*	0.0	3.7	23.4	3.0	5.4	0.0

Table 5: Mean seasonal (1999) total chlorophyll *a* ($mg/m^2 \pm SE$, n = 48) of SAA in Blind Channel, Crescent Pond and Saline Pond depending upon sampling method used. Phytoplankton chlorophyll *a* ($mg/m^2 \pm SE$, n = 48) is reported here for comparison. Plocon was not sampled in 1999. Superscript uppercase letters represent significant Scheffé *post hoc* comparisons between sites, and superscript lower case letters represent significant comparisons between methods, all with a critical p value = 0.05.

Sampling method	Overall Mean	Blind Channel	Crescent Pond	Saline Pond	*p value*
In situ slurry					
Lens tissue trapping	1.2^{a} (0.1)	0.8^{A} (0.2)	1.1^{A} (0.3)	1.7^{B} (0.4)	*0.004*
Sediment slurry before tissue trapping	43.4^{b} (3.3)	20.0^{A} (2.1)	44.6^{B} (4.6)	66.6^{C} (6.7)	*0.001*
Sediment slurry after tissue trapping	47.1^{b} (4.6)	17.8^{A} (1.6)	43.0^{B} (4.4)	84.1^{C} (11.1)	*0.001*
Core slurry					
Lens tissue trapping	0.9^{a} (0.1)	0.8 (0.2)	0.8 (0.1)	1.2 (0.3)	*0.137*
Sediment slurry before tissue trapping	29.5^{b} (3.1)	15.6^{A} (2.4)	20.6^{A} (2.5)	54.6^{B} (8.1)	*0.001*
Sediment slurry after tissue trapping	25.9^{b} (3.1)	9.1^{A} (1.3)	17.1^{A} (2.4)	52.6^{B} (7.8)	*0.001*
Sediment core	9.6^{c} (0.8)	3.6^{A} (0.6)	10.0^{B} (1.1)	15.1^{B} (1.9)	*0.001*
Phytoplankton	24.6 (2.0)	42.1^{A} (3.8)	19.9^{B} (2.5)	11.8^{B} (1.7)	*0.001*

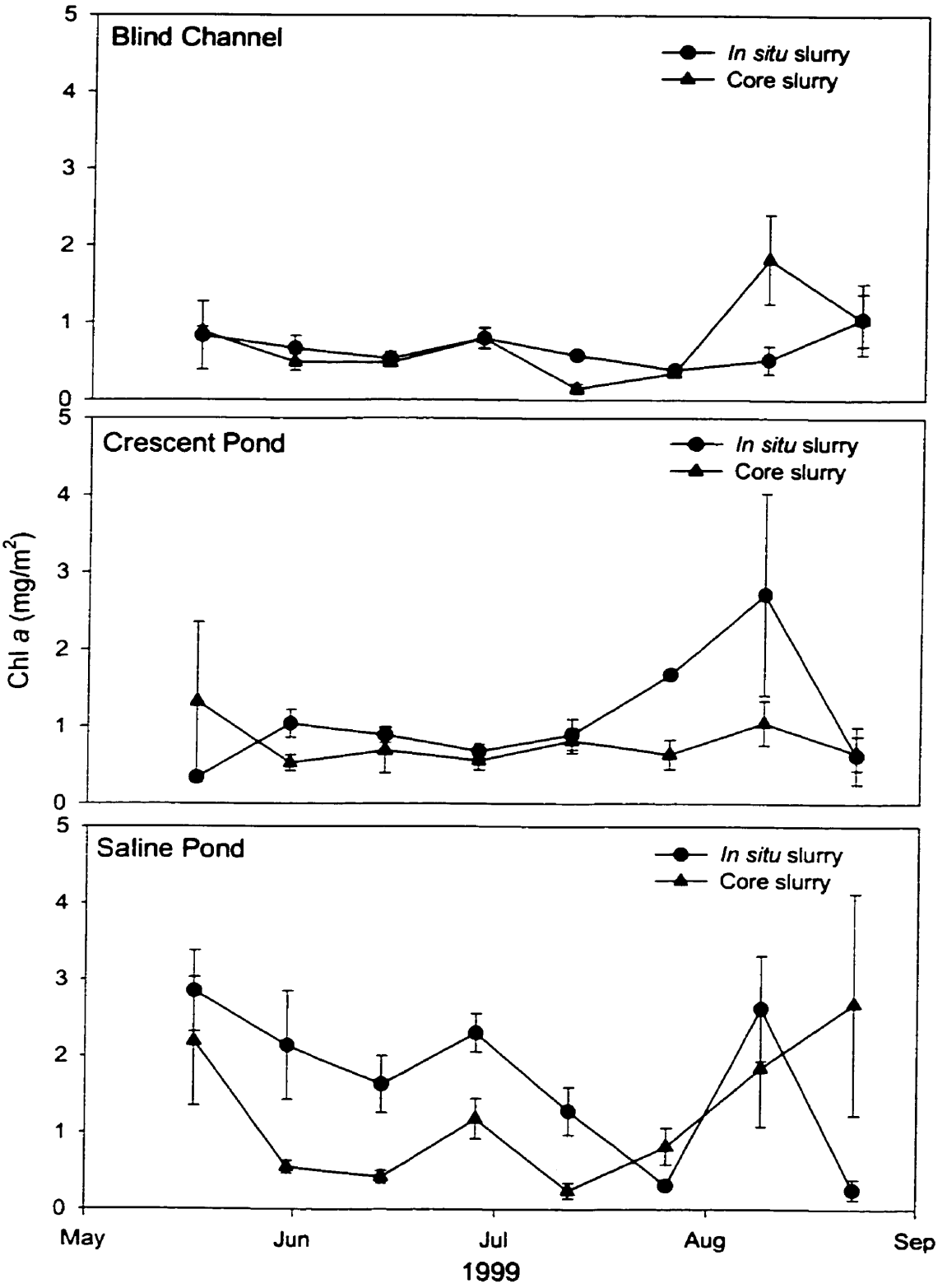

Figure 8: Mean total Chl *a* ($mg/m^2 \pm$ SE, n = 5, 1999) of SAA trapped on lens tissue papers placed on *in situ* and core sediment slurries.

season, the mean seasonal chlorophyll content of the *in situ* slurries after tissue trapping (47.1 ± 4.6 mg/m^2) was lower, but not significantly ($p = 0.001$) than those before tissue trapping (43.4 ± 3.3 mg/m^2, Table 5). As in 1998, sediment cores had approximately ten times the chlorophyll *a* content of the lens tissues.

The mean seasonal SAA chlorophyll of the *in situ* slurries before and after tissue trapping were higher (43.4 ± 3.3 mg/m^2, and 47.1 ± 4.6 mg/m^2) than that of the controlled core slurries (29.5 ± 3.1 mg/m^2, and 25.9 ± 3.1 mg/m^2) but were not significantly different (Table 5). The mean of the chlorophyll content before and after tissue trapping for both the *in situ* slurry and the core slurry showed no seasonal trends (Figure 9). Averaging the before and after chlorophyll content was possible due to the insignificance of a student t-test. Again, the *in situ* slurry had a greater chlorophyll content (43.4 ± 3.3 mg/m^2 and 47.1 ± 4.6 mg/m^2) than the core (9.6 ± 0.8 mg/m^2), and core slurries (29.5 ± 3.1 mg/m^2 and 25.9 ± 3.1 mg/m^2, Figure 10) even though the *in situ* slurry and the core slurry were sampled to the same vertical depth (6.4 cm) into the sediment. Of the four types of slurries none had significantly different SAA chlorophyll. The mean seasonal sediment core chlorophyll (9.6 ± 0.8 mg/m^2) was significantly less than all slurries. As in the 1998 field season, there was no seasonal variation in any of the sampling methods throughout the sampling period (Figure 10).

4.2 Ecological implications

4.2.1 Sediment-associated algae

In 1998, sampling site had a significant effect on SAA chlorophyll content regardless of sampling method (all $p = 0.001$). The chlorophyll content of SAA varied between three sites in Delta Marsh: Blind Channel, Crescent Pond and Saline Pond (Table 2). Using the lens tissue technique, Saline Pond (2.1 ± 0.2 mg/m^2) and Crescent Pond (1.4 ± 0.2 mg/m^2) had significantly higher mean seasonal SAA

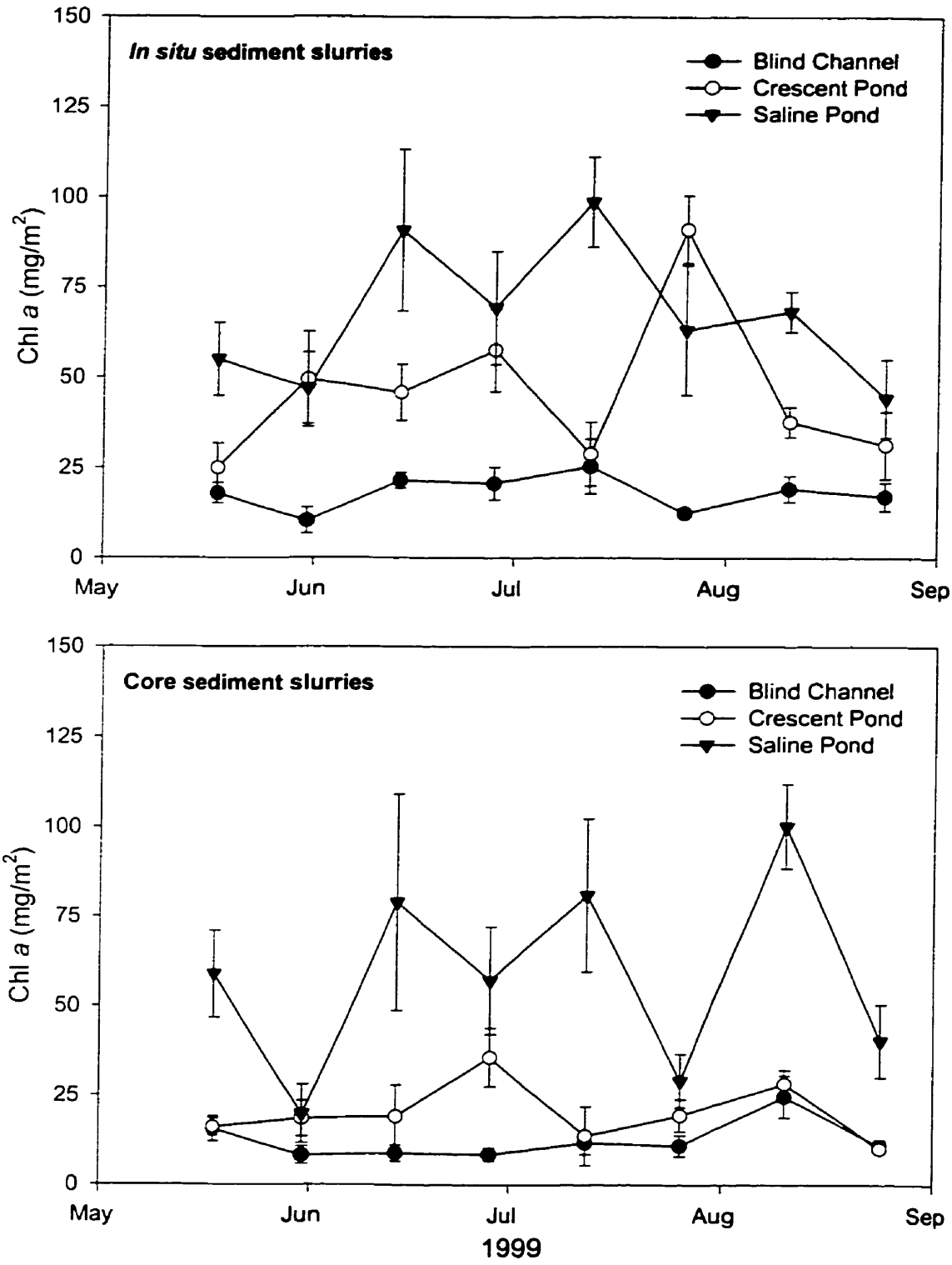

Figure 9: Mean total Chl *a* (mg/m^2 ± SE, n = 5) of *in situ* sediment slurries and core sediment slurries before and after tissue trapping during the 1999 sampling period.

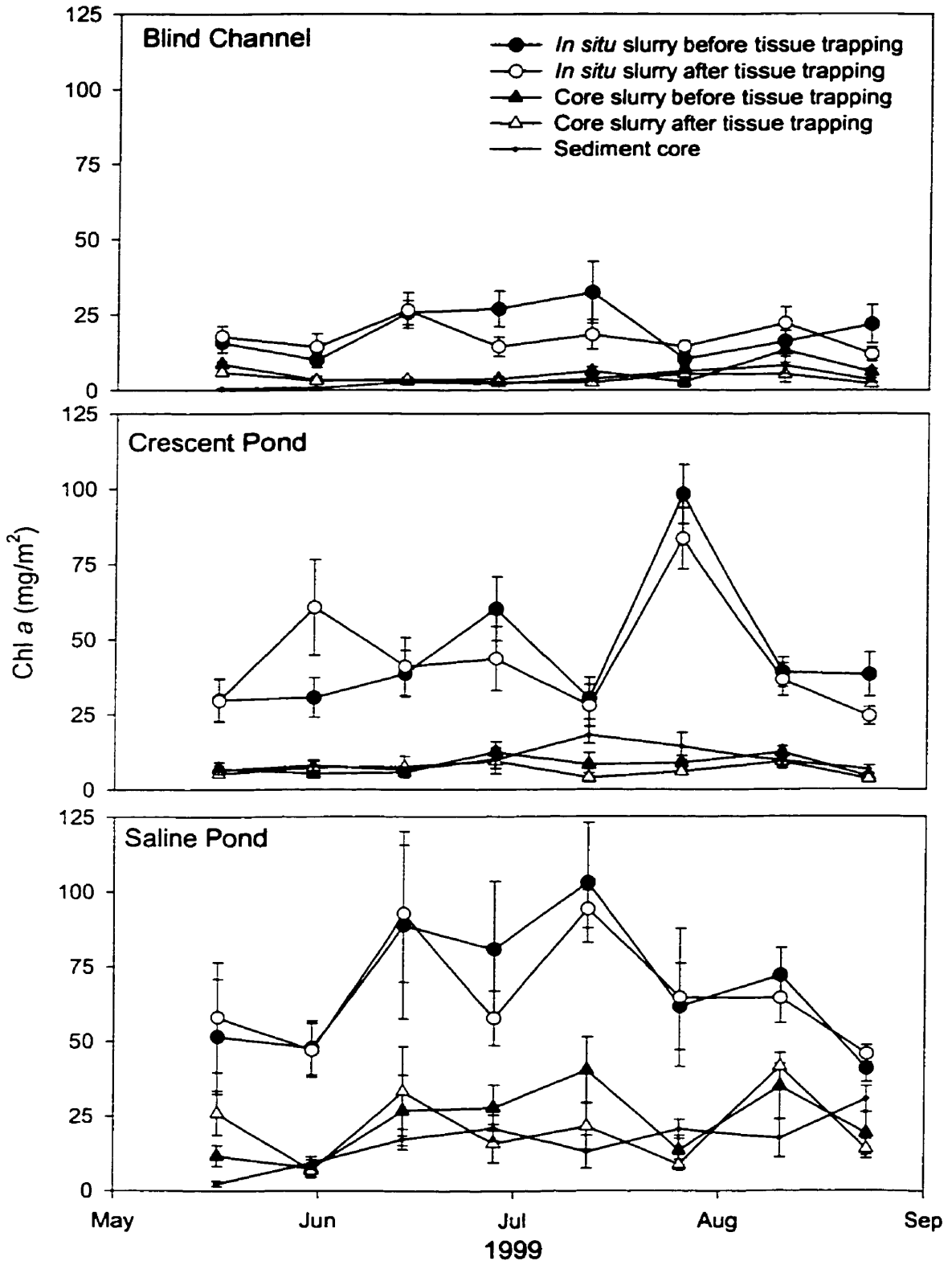

Figure 10: Mean total Chl *a* (mg/m^2 ± SE, n = 5) of SAA in Blind Channel, Crescent Pond and Saline Pond for the 1999 sampling period.

chlorophyll than Blind Channel (0.8 ± 0.1 mg/m^2, p = 0.001). The *in situ* sediment slurries and the sediment cores at the three sites all had significantly different mean seasonal SAA chlorophyll (p = 0.001, Table 2). Saline Pond always had the highest SAA chlorophyll content and Blind Channel the lowest regardless of sampling method used (Table 2). There was no consistent seasonal trend in SAA chlorophyll at the three sites.

A two-factor repeated measures ANOVA revealed a significant effect of site (p = 0.001) and sampling method (p = 0.001) on SAA chlorophyll. However, the interaction of site and method had only a marginally significant effect on SAA chlorophyll (p = 0.050).

Sampling site had a significant effect on SAA biovolume. Algal biovolume measurements in August 1998 followed a slightly different trend than chlorophyll *a*. Saline Pond had the highest biovolume in sediment slurries and cores but the lowest biovolume was observed in Crescent Pond (Table 3). However the sum of the lens tissue was highest in Blind Channel (19.6 mL/m^2). Both the 10 am and 2 pm lens tissues showed no difference in algal biovolume between the three sites (p = 0.373 and p = 0.321 respectively). The lens tissue collected at 7 pm had significantly higher algal biovolume in Blind Channel (5.4 ± 0.9 mL/m^2) and Saline Pond (4.0 ± 0.5 mL/m^2) than Crescent Pond (1.8 ± 0.7 mL/m^2, p = 0.035). The algal biovolume in the slurry before tissue trapping was not significantly different between Blind Channel (439.9 ± 45.6 mL/m^2) and Crescent Pond (333.5 ± 59.5 mL/m^2) but both had a significantly smaller biovolume than Saline Pond (979.8 ± 212.0 mL/m^2, p = 0.026). The algal biovolume of the slurry after tissue trapping and the sediment core were not significantly different between the three sites (p = 0.054 and p = 0.446, Table 3).

In the Blind Channel, *Epithemia* sp. was the most prominent genus regardless of sampling method (Table 4). *Epithemia* sp. was also the most prominent in the

lens tissue and the slurries collected from Crescent Pond, but *Navicula* sp. (large class) was the greatest percentage in the core. In Saline Pond, *Epithemia* sp. was again the most highly represented genus in the lens tissues collected at 10 am and 2 pm and the sediment slurries. *Surirella* sp. was the most abundant in lens tissues collected at 7 pm and *Navicula* sp. (small class) in the core. It was surprising that *Oscillatoria* sp. and *Lyngbya* sp. were comparatively rare considering that plocon samples were mostly cyanobacterial trichomes (visual observations, Figure 11).

In 1999, the chlorophyll *a* content of the *in situ* slurry lens tissues was not significantly different between Blind Channel (0.8 ± 0.2 mg/m^2) and Crescent Pond (1.1 ± 0.3 mg/m^2) but both were significantly less than Saline Pond (1.7 ± 0.4 mg/m^2, $p = 0.004$, Table 5). The chlorophyll *a* content of the sediment, whether in the form of a slurry or an intact core was always highest in Saline Pond, followed by Crescent Pond and Blind Channel. The SAA chlorophyll in the *in situ* slurry before and after tissue trapping was significantly different at all sites ($p = 0.001$, Table 5).

There was no significant difference between the three sites in the chlorophyll content of the lens tissues collected from the core slurry ($p = 0.137$, Table 5). There was no significant difference between mean seasonal SAA chlorophyll in the core slurry before tissue trapping in Blind Channel (15.6 ± 2.4 mg/m^2) and Crescent Pond (20.6 ± 2.5 mg/m^2) but both were significantly less than that in Saline Pond (54.6 ± 8.1 mg/m^2, $p= 0.001$). The same trend was observed for SAA chlorophyll in the core slurry after tissue trapping (Table 5).

The sediment core yielded significantly higher SAA chlorophyll values in Saline Pond (15.1 ± 1.9 mg/m^2) and Crescent Pond (10.0 ± 1.1 mg/m^2) than Blind Channel (3.6 ± 0.6 mg/m^2, $p = 0.001$).

A two-factor repeated measures ANOVA revealed a significant effect of site ($p = 0.001$) and sampling method ($p = 0.001$) on SAA chlorophyll. The interaction of site and sampling method was also significant ($p = 0.013$).

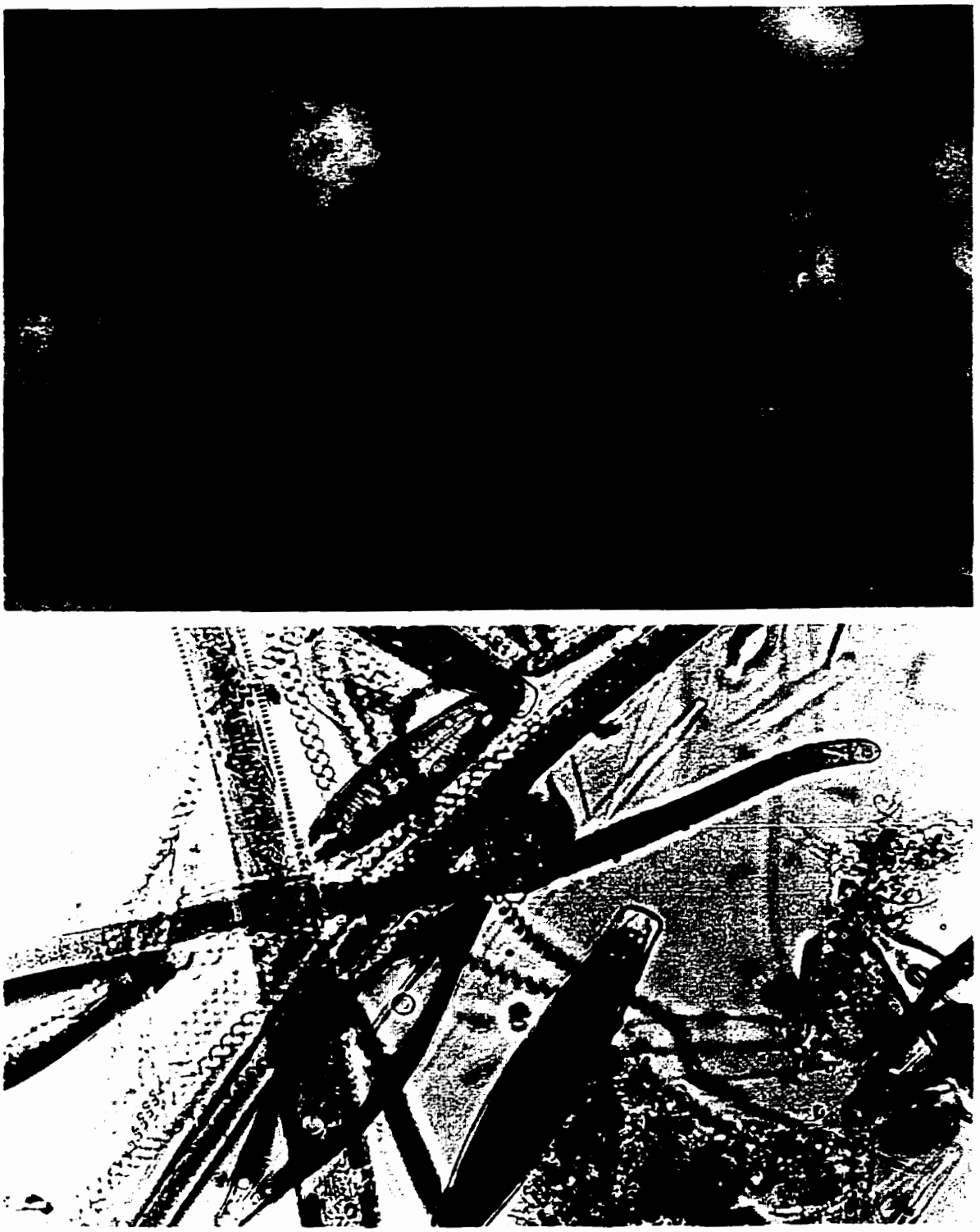

Figure 11: Photomicrographs of plocon from Blind Channel, 1998. Whole samples were placed between a glass slide and coverslip, wetted and squashed with gentle force. Diatoms and cyanobacteria were the prominant algal taxa.

Nine cores were collected on the 7 June 1999 to assess the vertical distribution of chlorophyll in the sediments of Blind Channel, Crescent Pond and Saline Pond (Figure 12). The first 3 mm had the highest chlorophyll content (overall mean = 3.2 ± 0.5 mg/m^2) which decreased for each subsequent 3 mm interval. This was consistent for all three sites and Saline Pond consistently had the highest SAA chlorophyll at 3 mm, 6 mm and 9 mm; however, none were significantly different ($p = 0.158$, $p = 0.108$, $p = 0.474$) for the three sites, respectively.

4.2.2 Other biological parameters

Phytoplankton chlorophyll *a* (mg/m^2) followed the reverse trend of SAA chlorophyll in 1998. Differences between sites were significant ($p = 0.001$). Blind Channel had the highest mean seasonal phytoplankton chlorophyll (25.1 ± 1.7 mg/m^2) followed by Crescent Pond (11.5 ± 1.2 mg/m^2) and Saline Pond (10.9 ± 1.2 mg/m^2, Table 2). There was no seasonal trend throughout the sampling period but by October there was clear separation with Blind Channel having the highest phytoplankton chlorophyll (29.4 ± 3.6 mg/m^2) followed by Crescent Pond (20.2 ± 3.8 mg/m^2) and Saline Pond (4.8 ± 1.3 mg/m^2, Figure 13).

Phytoplankton chlorophyll at the three sites in 1999 followed the same trend as in 1998 with Blind Channel having the highest mean seasonal chlorophyll (42.1 ± 3.8 mg/m^2) and Saline Pond the lowest (11.8 ± 1.7 mg/m^2). There was no difference between means for Crescent Pond and Saline Pond. Again this was the opposite trend than what was observed in the chlorophyll content of SAA (Table 5). Phytoplankton chlorophyll was higher throughout the sampling period in Blind Channel except for one sampling date at the end of May (Figure 14).

Submersed macrophytes were first observed on 14 and 15 June but not collected until 28 and 29 June. Macrophytes were only present at one site in Blind Channel compared to all five sites in the two ponds. *Potamogeton pectinatus* was

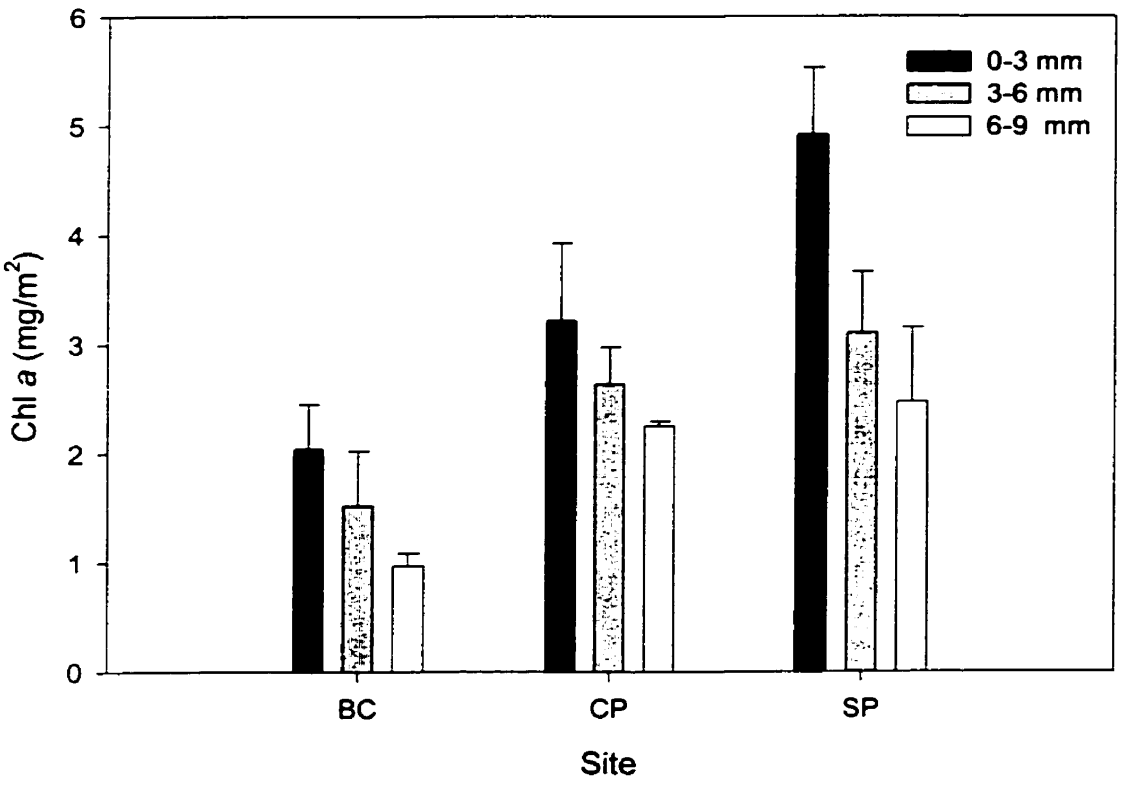

Figure 12: Mean total Chl *a* (mg/m^2 ± SE, n = 3) of SAA of three sediment cores taken in the Blind Channel, Crescent Pond and Saline Pond on 7 June 1999. Samples were taken at three depth intervals (0-3mm, 3-6mm, 6-9mm). There were no significant differences between sites or between depths within a site.

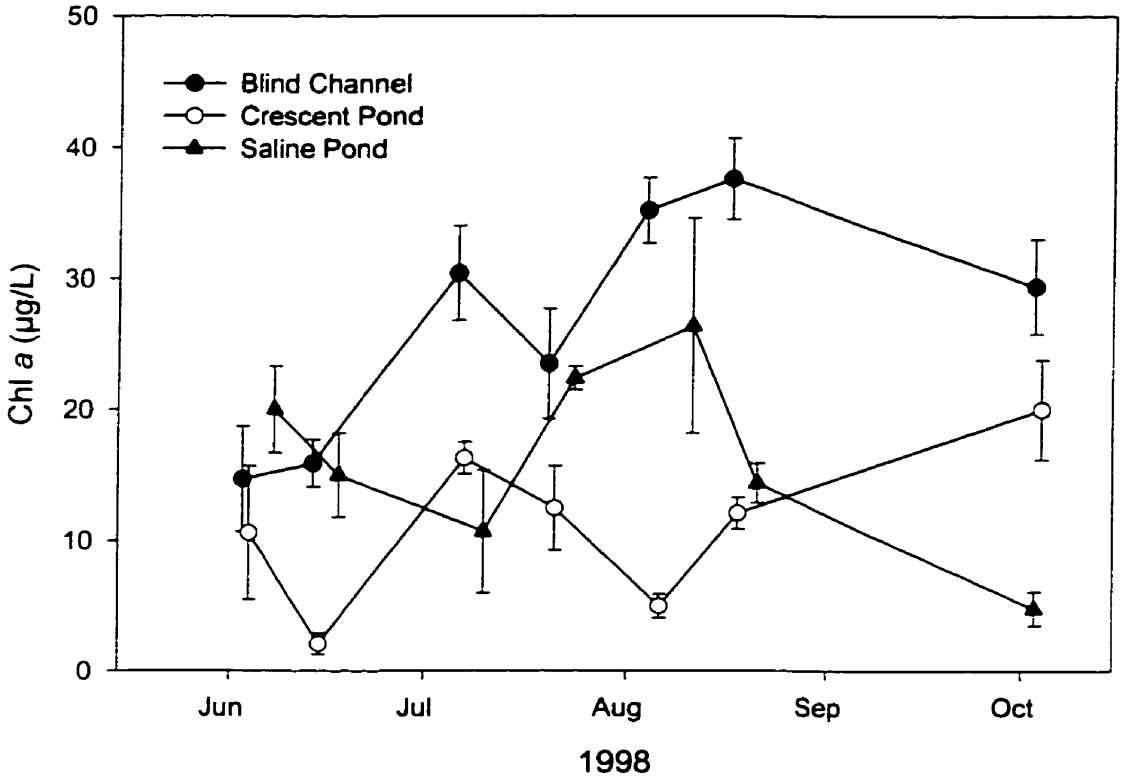

Figure 13: Mean total Chl *a* ($mg/m^2 \pm SE$, n = 6) of phytoplankton in Blind Channel, Crescent Pond and Saline Pond during the 1998 sampling period.

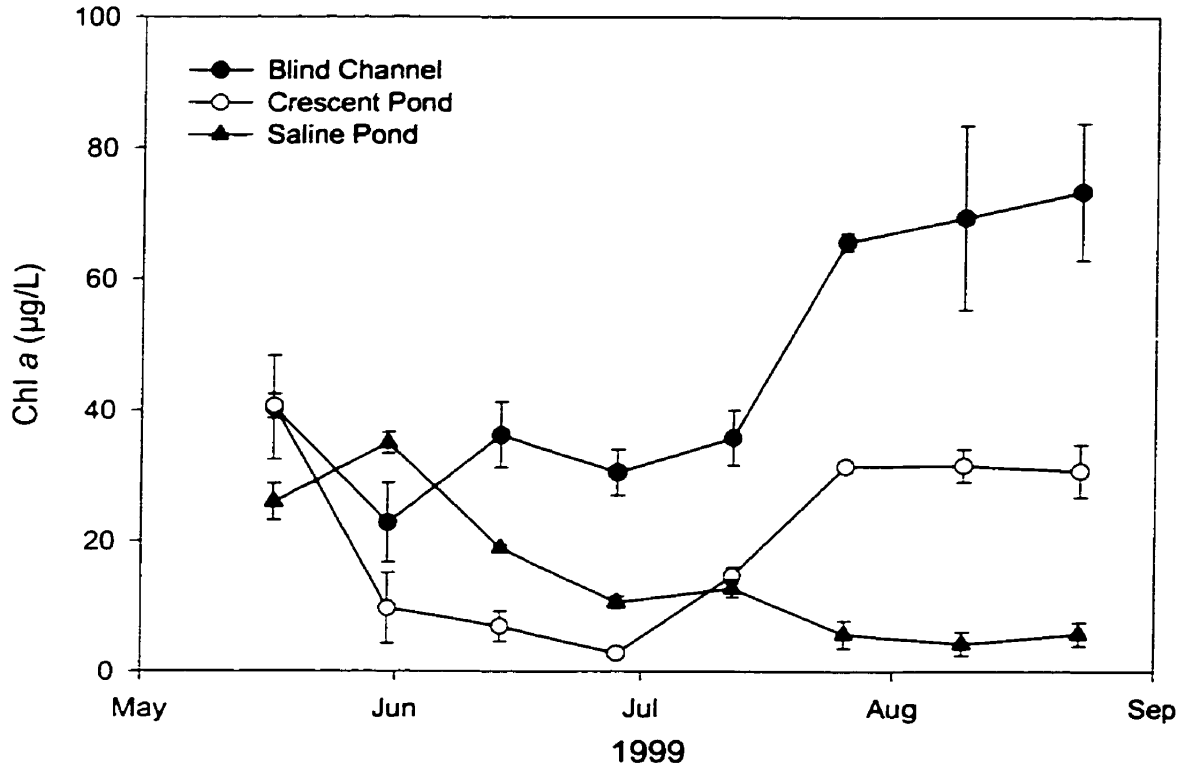

Figure 14: Mean total Chl *a* (mg/m^2 ± SE, n = 5) of phytoplankton for Blind Channel, Crescent Pond and Saline Pond for the 1999 sampling period.

present in both Blind Channel and Saline Pond. The dominant submersed macrophyte in Crescent Pond was *Lemna trisulca* followed by *Ceratophyllum demersum*. *Ceratophyllum* was also present in Blind Channel. Crescent Pond had the highest biomass of macrophytes throughout the growing season until 28 August when the macrophytes started to senesce. Macrophyte abundance increased steadily in Saline Pond throughout the summer to a maximum dry weight of 162 ± 65 g/m^2 (Figure 15). Mean seasonal dry weight of macrophytes in Blind Channel (34.8 ± 16.6 g/m^2), Crescent Pond (81.4 ± 12.6 g/m^2) and Saline Pond (79.3 ± 17.9 g/m^2) were not significantly different from each other ($p = 0.367$).

An increase in phytoplankton chlorophyll, in Blind Channel, in mid-July was followed by a sharp increase in macrophyte abundance by late July. Both macrophyte and phytoplankton abundance reached a plateau by mid August (Figure 14 & 15). Crescent Pond had a period of low phytoplankton chlorophyll in June when macrophytes were starting to develop. Phytoplankton abundance increased in July along with macrophytes and they both leveled off in August (Figure 14 & 15). Saline Pond had its highest phytoplankton chlorophyll at the beginning of June then it decreased to a low point in mid July that coincided with an increase in macrophyte abundance. Macrophyte abundance in Saline Pond then continued to increase throughout the sampling period (Figure 15). By late August the same separation as in 1998 was observed with Blind Channel having the highest phytoplankton chlorophyll (73.3 ± 10.5 mg/m^2) followed by Crescent Pond (30.7 ± 4.0 mg/m^2) and then Saline Pond (5.7 ± 1.8 mg/m^2, Figure 14).

4.2.3 Physical parameters

In 1998, adult carp (*Cyrinus carpio)* were present in Blind Channel but not in Crescent Pond or Saline Pond. This, along with wind induced wave action, increased the turbidity of the water column (visual observation) reducing the incident light

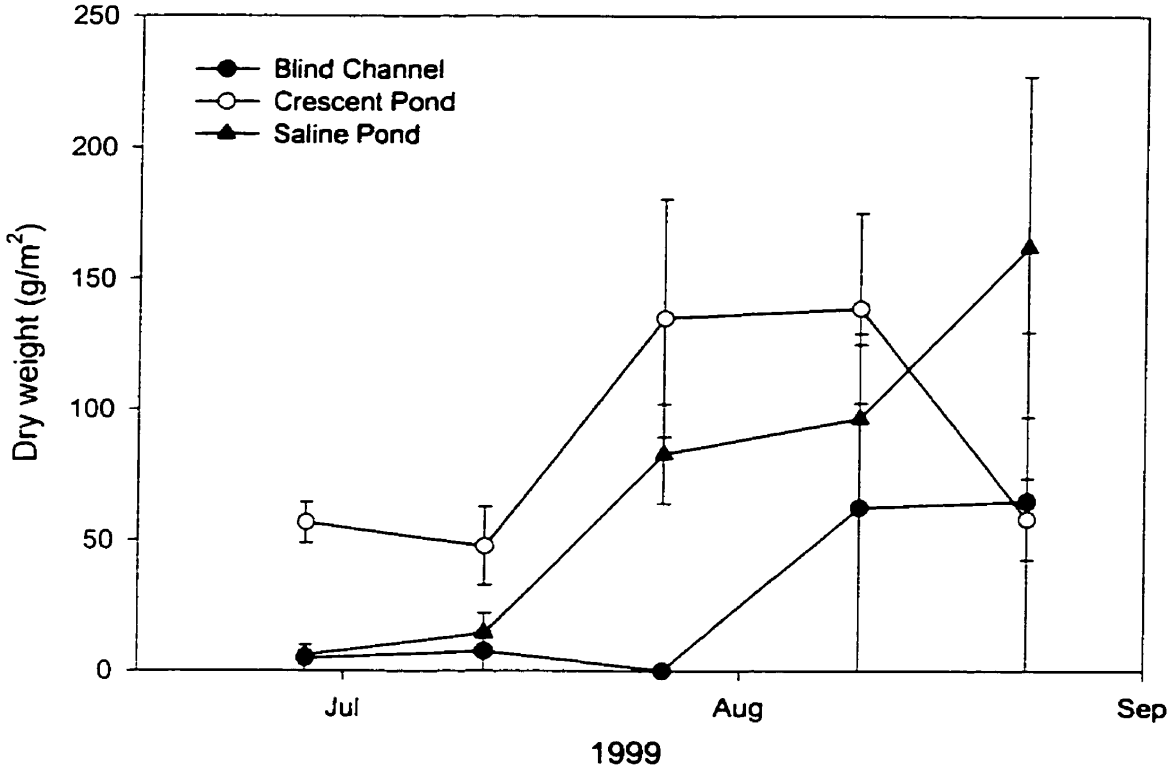

Figure 15: Macrophyte dry weight (mg/m^2 ± SE, n = 5) present in Blind Channel, Crescent Pond and Saline Pond during the 1999 sampling period.

available for phytoplankton and SAA growth but also disturbed the substrata for SAA colonization. Unfortunately, water column turbidity and light profiles were not measured.

Water depth at sampling sites was significantly lower at Saline Pond (65 ± 3 cm) than Blind Channel and Crescent Pond ($p = 0.001$) The mean depth of Blind Channel (97 ± 4 cm) and Crescent Pond (94 ± 2 cm) at the sampling sites were not significantly different from each other (Table 1).

Mean seasonal water depth in 1999 was also not significantly different between Blind Channel (91 ± 4 cm) and Crescent Pond (93 ± 4 cm) but these two sites were significantly deeper than Saline Pond (65 ± 4 cm) ($p = 0.001$, Table 1). The turbidity of Saline Pond was high (40 NTU) in May relative to the other summer months. This was attributed to the presence of spawning carp in the spring which were not present in the 1998 field season. Blind Channel and Crescent Pond followed the same trend with a decrease in turbidity in late June (Figure 16) coinciding with the establishment of submersed macrophyte beds. Blind Channel had the highest mean seasonal turbidity (11.9 ± 3.7 NTU) followed by Saline Pond (9.7 ± 3.5 NTU) and Crescent Pond (3.4 ± 0.6 NTU), although there was no significant difference between Blind Channel and Saline Pond ($p = 0.001$). By the end of the summer, the turbidity of Saline Pond (4.8 ± 0.2 NTU) was as low as that of Crescent Pond (5.0 ± 0.0 NTU).

The percentage of surface irradiance that reached the sediment-water interface varied between 1-35% at the three sites (Table 6). The light profiles at the three sites fluctuated because of partly cloudy days and the presence of submersed macrophytes. More than half the sites sampled received >15% incident irradiance at the sediment surface. Only on 12 July was Blind Channel significantly different than the other two sites ($p = 0.012$). The light extinction coefficient was highest in Saline Pond throughout the sampling period (Figure 17).

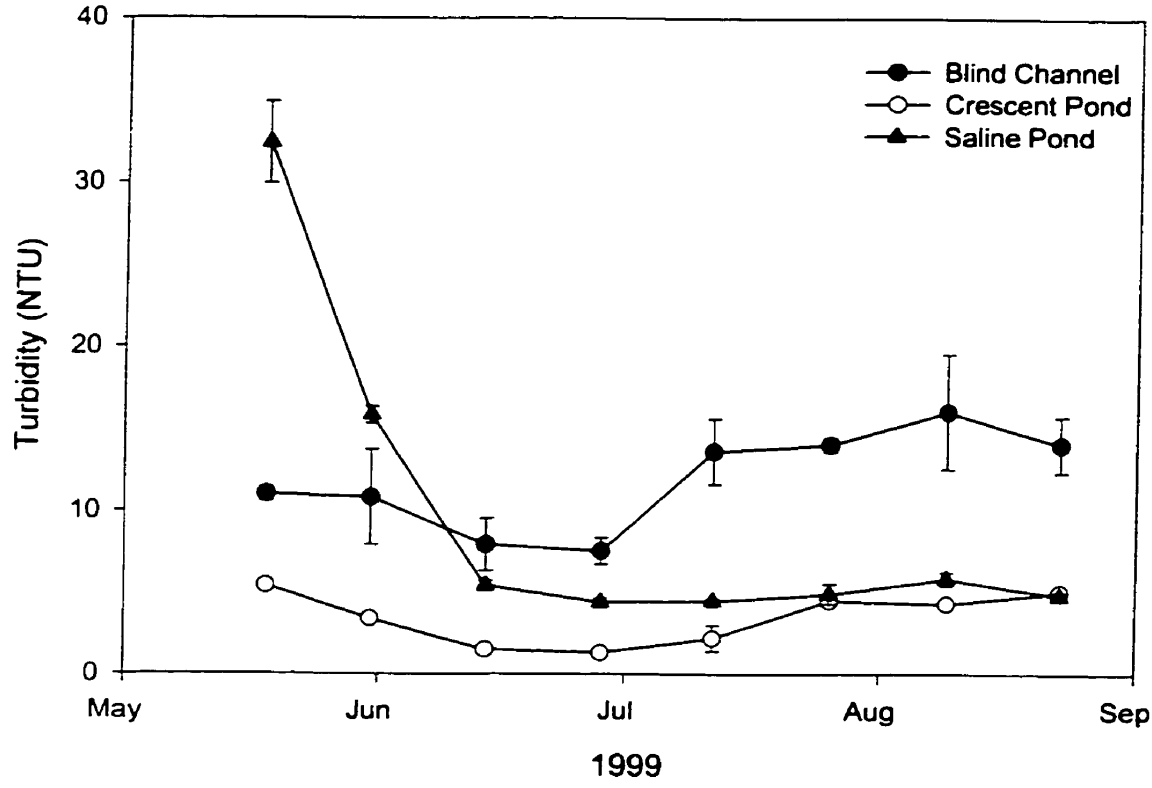

Figure 16: Mean water column turbidity (NTU ± SE, n = 5) for Blind Channel, Crescent Pond and Saline Pond for the 1999 sampling period.

Table 6: Mean percent incident irradiance (± SE, n = 5) reaching the sediment-water interface in Blind Channel, Crescent Pond and Saline Pond during the 1999 sampling period. Superscript letters represent significant Scheffé *post hoc* comparisons between sites with a critical p value = 0.05.

Date	Blind Channel	Crescent Pond	Saline Pond	*p value*
31-May	4.7 (3.3)	8.5 (0.4)	5.0 (2.8)	*0.510*
14-Jun	3.5 (1.2)	6.6 (0.7)	6.4 (1.5)	*0.158*
28-Jun	5.6 (0.7)	20.8 (8.3)	15.2 (1.6)	*0.212*
12-Jul	1.0^{A} (0.3)	30.3^{B} (6.4)	30.9^{B} (7.7)	*0.012*
10-Aug	32.8 (9.1)	10.1 (5.7)	20.6 (7.1)	*0.124*
24-Aug	24.8 (15.0)	16.6 (4.3)	33.8 (4.0)	*0.287*

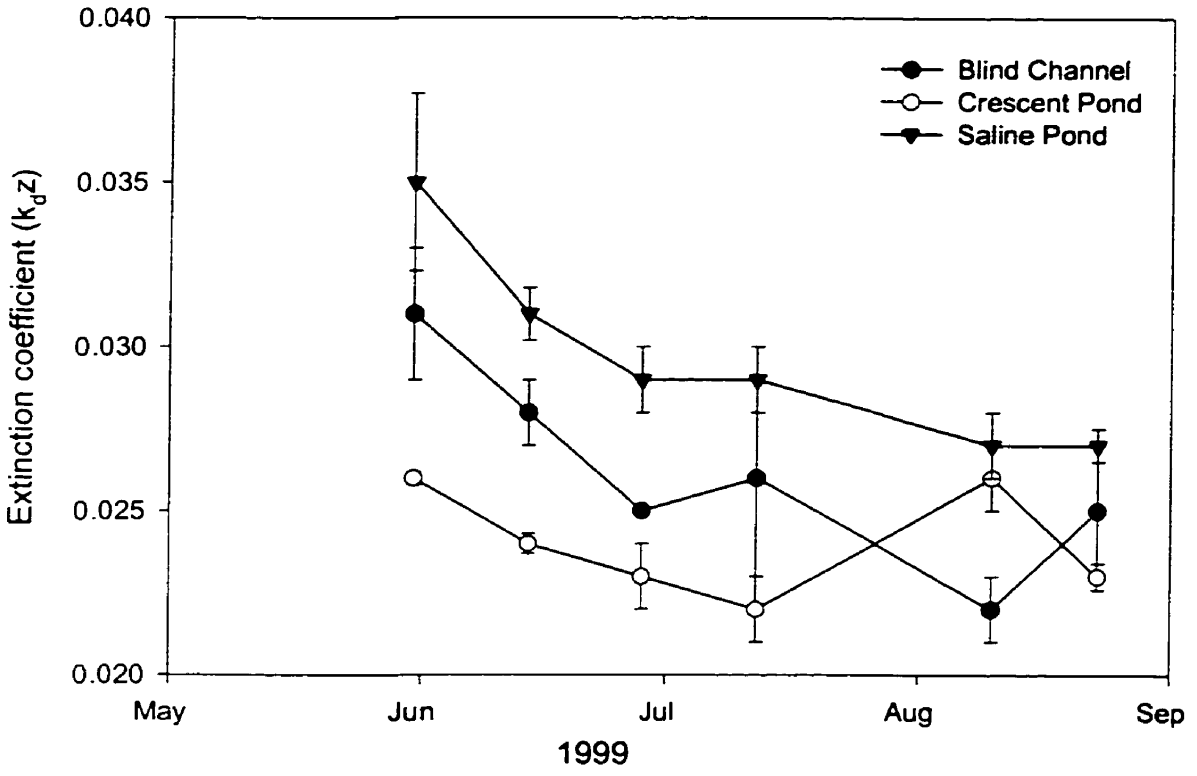

Figure 17: Light extinction coefficients ($k_dz \pm SE$) between 0-50 cm for Blind Channel, Crescent Pond and Saline Pond (n = 5, 1999).

4.2.4 Chemical parameters

In 1998, levels of NH_3-N in the water column were consistently below detection (< 50µg/L) at the three sites. Mean levels of NO_3-N were highest in Saline Pond (43 ± 10 µg/L), because of a peak in mid August and in October (Figure 18), but not significantly different from the other two sites (p = 0.082). The highest levels of mean total reactive phosphorus (TRP; 90 ± 20 µg/L) were found in Blind Channel. This was significantly (p = 0.001) higher than Crescent Pond (29 ± 3 µg/L) and Saline Pond (24 ± 8 µg/L). TRP concentration in Blind Channel increased continually until the end of July and then gradually decreased (Figure 19). Crescent Pond had the highest levels of silica (2160 ± 100 µg/L, Table 7) although not significantly different (p = 0.593) than Blind Channel (1675 ± 88 µg/L) and Crescent Pond (1974 ± 57 µg/L). There were no seasonal trends in silica. Water conductivity and alkalinity were significantly higher in Saline Pond, than Blind Channel which, in turn, was significantly higher than Crescent Pond (p = 0.001, Table 7).

Surficial marsh sediments in Blind Channel and Crescent Pond were similar with respect to water, organic matter and carbonate content (Table 8). On the other hand, Saline Pond had a significantly lower water (57.8 ± 1.1 % dry weight) and organic matter content (7.6 ± 0.4 % dry weight) and higher carbonate content (8.4 ± 0.2 % dry weight) (p = 0.001). Mean sediment conductivity in Saline Pond was significantly higher than Crescent Pond and Blind Channel (p = 0.001, Table 8).

Sediment interstitial pore-water contained NH_3-N as high as 3 mg/L and TRP as high as 2 mg/L (Figure 20). These may be underestimates because the peepers used in collecting samples were not parged with N_2 prior to being placed in the marsh. This meant that highly oxygenated water was introduced into the anoxic sediment environment, possibly converting NH_3-N to NO_3-N. Nevertheless, NH_3-N and TRP were 30x and 20x more abundant, respectively, in the sediment interstitial water than in the water column.

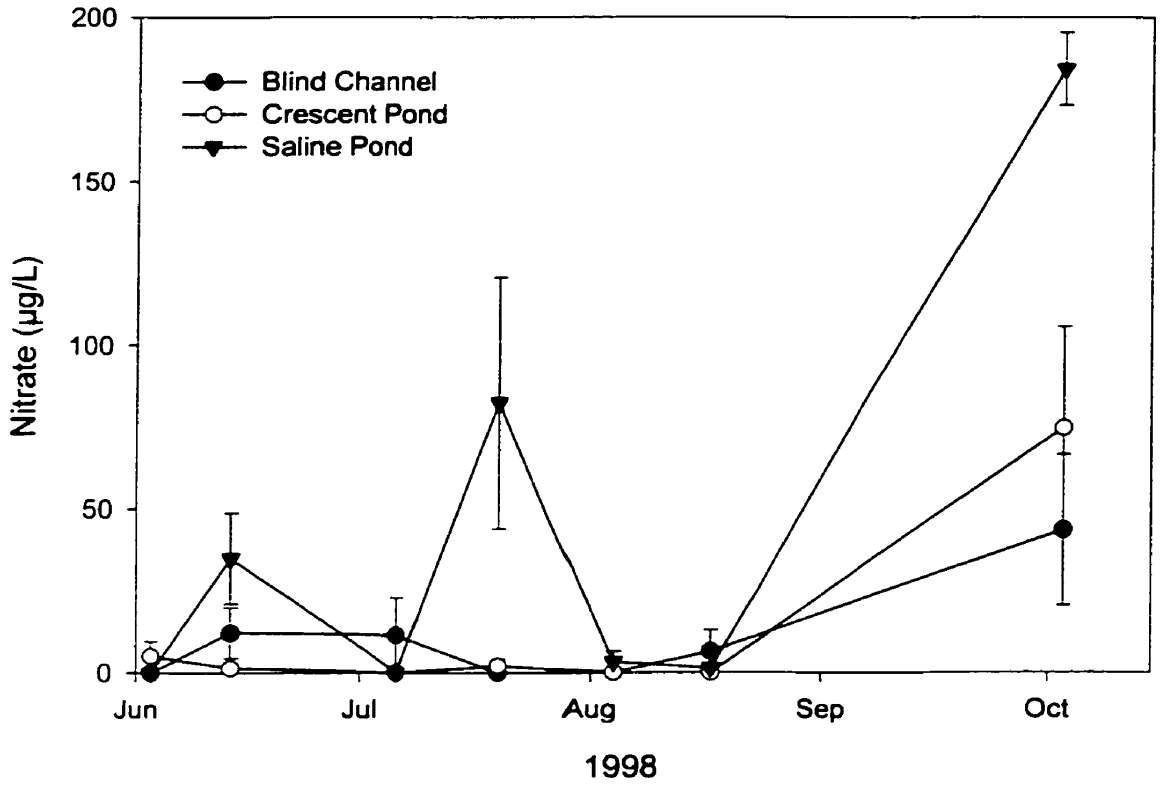

Figure 18: Nitrate concentrations (µg/L ± SE, n = 6) in Blind Channel, Crescent Pond and Saline Pond throughout the 1998 sampling period.

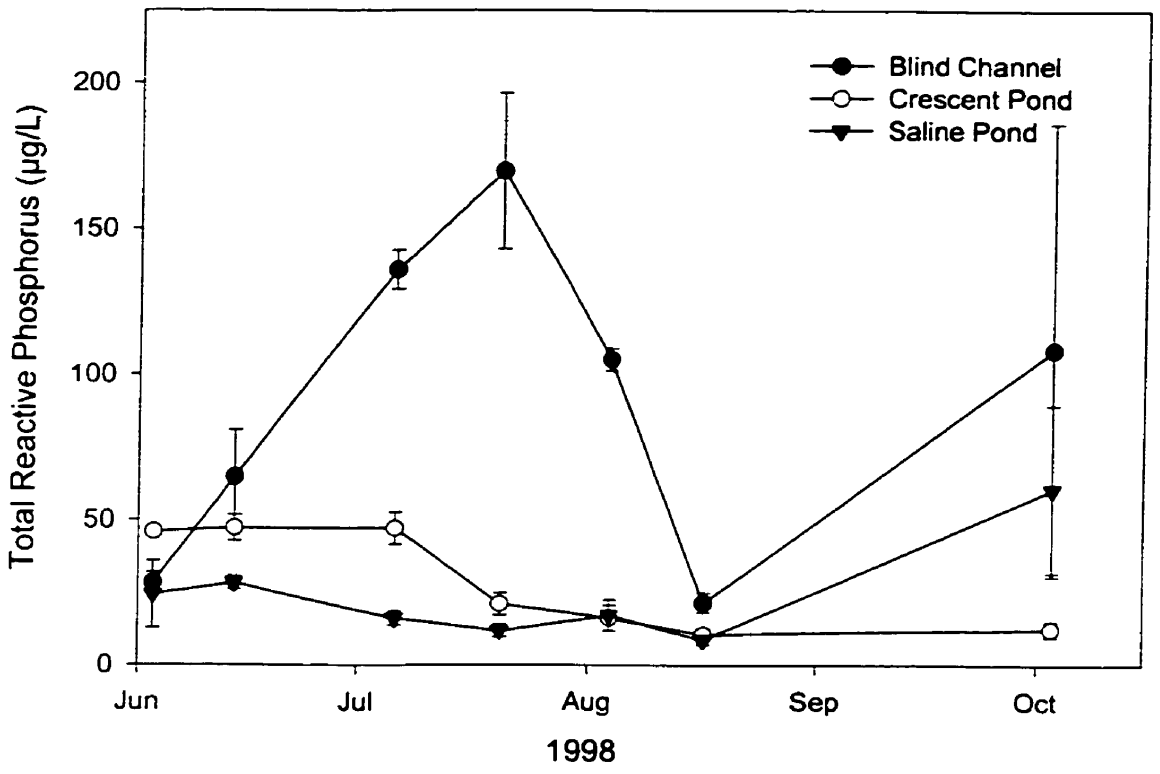

Figure 19: Total reactive phosphorus (µg/L ± SE, n = 6) in Blind Channel, Crescent Pond and Saline Pond throughout the 1998 sampling period.

Table 7: Chemistry of integrated water column samples taken from Blind Channel, Crescent Pond and Saline Pond in 1998 (seasonal means ± SE, n= 35). Superscript letters represent significant Scheffé *post hoc* comparisons between sites, with a critical p value = 0.05.

	Blind Channel	Crescent Pond	Saline Pond	*p value*
Ammonia-N (µg/L)	< 50	< 50	< 50	*na*
Nitrate-N (µg/L)	10 (7)	11 (5)	44 (10)	*0.082*
Total reactive phosphorus (µg/L)	90^{A} (20)	29^{B} (3)	24^{B} (8)	*0.001*
Silica (µg/L)	1675 (88)	2160 (100)	1974 (57)	*0.593*
Alkalinity $CaCO_3$(mg/L)	306^{A} (8)	285^{B} (4)	433^{C} (7)	*0.001*
Conductivity (µS/cm)	1409^{A} (15)	1196^{B} (12)	1906^{C} (14)	*0.001*

Table 8: The composition and chemistry of surficial marsh sediments in Blind Channel, Crescent Pond and Saline Pond (seasonal means ± SE, n= 40). Superscript letters represent significant Scheffé *post hoc* comparisons between sites, with a critical p value = 0.05.

	Blind Channel	Crescent Pond	Saline Pond	*p value*
Composition 1998				
Water content (% wet wt)	76.7^{A} (10.3)	80.7^{A} (1.1)	57.8^{B} (1.1)	*0.001*
Organic matter (% dry wt)	18.7^{A} (0.5)	21.1^{A} (0.9)	7.6^{B} (0.4)	*0.001*
Carbonates (% dry wt)	4.8^{A} (0.3)	5.0^{A} (0.3)	8.4^{B} (0.2)	*0.001*
Chemistry 1999				
Conductivity (µS/cm)	1024^{A} (4)	1173^{A} (65)	1757^{B} (126)	*0.001*
Total phosphorus (mg/gdw)	0.3^{A} (0.02)	0.5^{B} (0.06)	0.2^{C} (0.02)	*0.001*
Total nitrogen (mg/gdw; n=18)	8.3^{A} (0.3)	9.0^{A} (0.2)	1.3^{B} (0.3)	*0.001*
Total carbon (mg/gdw; n=18)	96.3^{A} (2.3)	108.3^{B} (1.5)	36.0^{C} (4.2)	*0.001*

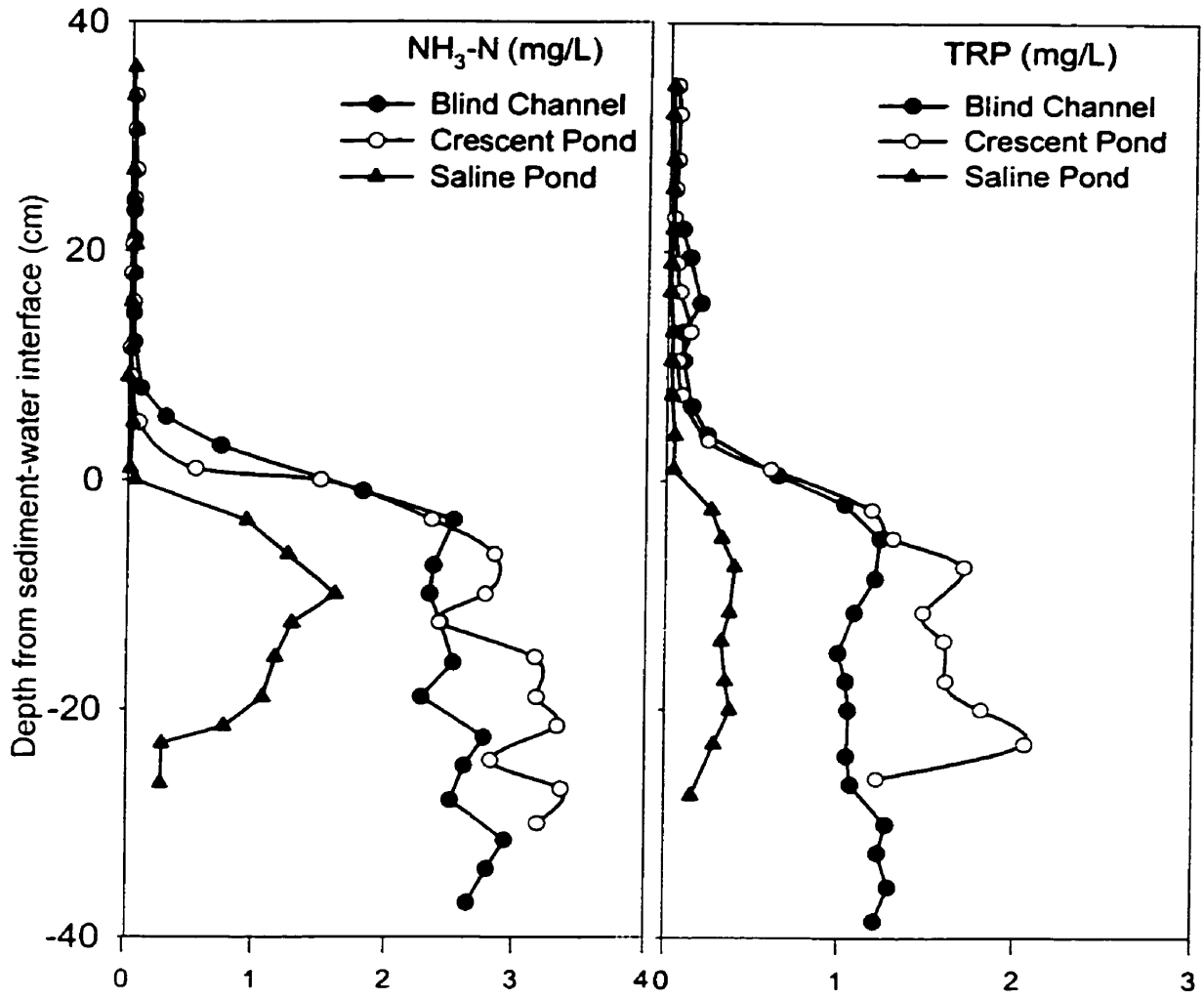

Figure 20: Ammonium-N and total reactive phosphorus concentrations above and below the sediment-water interface (n = 4, 1998) in Blind Channel, Crescent Pond and Saline Pond.

Sediment chemistry analysis in 1999 revealed that sediments in Crescent Pond contained more total reactive phosphorus (491 ± 59 µg/g dw) than those from Blind Channel (291 ± 17 µg/g dw) which, in turn, was higher than Saline Pond (150 ± 17 µg/g dw, $p = 0.001$, Table 8). Sediment phosphorus concentrations in all three sites were relatively constant over time (Figure 21). Levels of total nitrogen were the same in Crescent Pond (9.0 ± 0.2 mg/g dw) and Blind Channel (mean 8.3 ± 0.3 mg/g dw, $p = 0.001$) but lower in Saline Pond (1.3 ± 0.3 mg/g dw). Total carbon values followed the same trend as nitrogen and phosphorus with the highest values in Crescent Pond (108.3 ±1.5 mg/g dw) followed by Blind Channel and Saline Pond (Table 8). There was a significant difference between the sites ($p = 0.001$).

Sediment C:N molar ratios were highest in Saline Pond (27.0 ± 1.8 mol/mol and 45.4 ± 8.1 mol/mol) for July and August respectively (Table 9) There was a significant difference between sites in both July and August ($p = 0.001$ and $p = 0.005$, respectively). The increase in August for Saline Pond can be explained by a decrease in nitrogen from July (1.9 mg/g dw) to August (0.8 mg/g dw).

C:P molar ratios were higher in Blind Channel than the other two sites for July and August but not significantly ($p = 0.157$ and $p = 0.158$, respectively). The increase in C:P ratio in August in Blind Channel was the result of a decrease in total phosphorus (from 265 µg/g dw to 228 µg/g dw).

N:P molar ratios were significantly higher in Blind Channel than the other two sites for both July ($p = 0.003$) and August ($p = 0.001$) samples. The N:P ratios increased from July to August in Blind Channel and Crescent Pond but decreased in Saline Pond. Saline Pond shifted to a nitrogen-limited environment (N:P < 15) in August while the other two remained phosphorus limited (N:P > 15). The C:N:P ratios of Blind Channel (959:71:1), Crescent Pond (672:48:1), and Saline Pond (696:22:1) are in between those found in the experimental lake area (ELA) boreal forest soil (1730:35:1) and ELA streams (280:22:1) (Hecky *et al.* 1993)

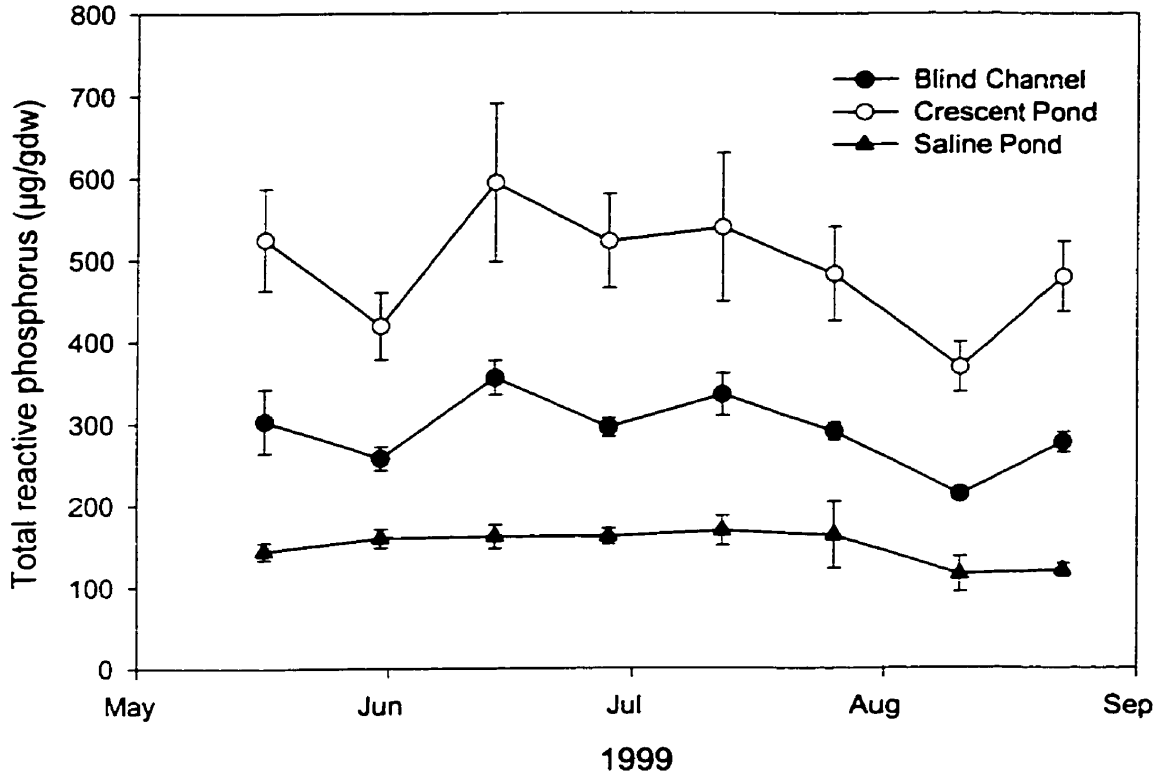

Figure 21: Total reactive phosphorus (µg/gdw ± SE, n = 5, 1999) present in marsh sediments of Blind Channel, Crescent Pond and Saline Pond.

Table 9: Mean sediment C:N, C:P, N:P (mol/mol) and C:Chl *a* (mol/mg) ratios (± SE) for Blind Channel, Crescent Pond and Saline Pond (July & August 1999, n = 3). Superscript letters represent significant Scheffé *post hoc* comparisons between sites, with a critical p value = 0.05.

		Blind Channel	Crescent Pond	Saline Pond	*p value*
C: N					
	July	13.6^{A}	14.1^{A}	27.0^{B}	*0.001*
		(0.1)	(0.2)	(1.8)	
	Aug	13.6^{A}	14.0^{A}	45.4^{B}	*0.005*
		(0.4)	(0.1)	(8.1)	
C:P					
	July	898.0	645.7	794.3	*0.157*
		(46.3)	(71.0)	(108.2)	
	Aug	1045.6	723.5	664.3	*0.158*
		(57.2)	(42.8)	(210.6)	
N:P					
	July	66.1^{A}	45.5^{B}	29.7^{B}	*0.003*
		(3.8)	(4.5)	(4.2)	
	Aug	76.7^{A}	51.7^{B}	15.4^{C}	*0.001*
		(2.7)	(3.5)	(6.0)	
C:Chl *a*					
	July	1.1^{A}	0.4^{B}	0.3^{B}	*0.022*
		(0.2)	(0.1)	(0.0)	
	Aug	1.0^{A}	0.3^{B}	0.2^{B}	*0.043*
		(0.3)	(0.1)	(0.1)	

All C:Chl *a* ratios were less than 4.2 mol/mg and remained constant indicating that there is no degree of nutrient deficiency for the SAA (Hecky *et al.* 1993).

The concentration of the NH_3-N and TRP in the interstitial pore-water reached levels as high as 5 mg/L (Figure 22). Crescent Pond again had the highest concentration of nutrients in the sediment pore-water. The dramatic increase in NH_3-N and TRP occurred approximately 5 cm above the sediment-water interface indicating that there was a nutrient-rich microzone immediately above the sediment surface.

4.3 Plocon

The total chlorophyll *a* content of plocon was measured for six samples collected from Blind Channel (151.7 ± 14.3 mg/m^2) and Crescent Pond (127.6 ± 20.4 mg/m^2) in 1998. Samples were collected randomly when plocon occurred (Figure 23) and when time allowed. The magnitude of these SAA chlorophyll values were approximately 10x that of sediment cores and 100x that of lens tissues (Table 2).

Plocon occurred after numerous days of consistently high photosynthetic active radiation (PAR > 500 mol/m^2/hr, Figure 24) in 1999. A discriminant analysis revealed that daily PAR had no effect on determining presence or absence of plocon (Wilks' λ = 0.991 p = 0.437). However, daily PAR two and three days prior had a significant effect on plocon occurrence (Table 10). PAR on one and four days prior had no effect on plocon occurrence. The effect of cumulative daily PAR between 1 June and 1 September did have a significant effect on plocon occurrence regardless of the length of the lag period (Table 10).

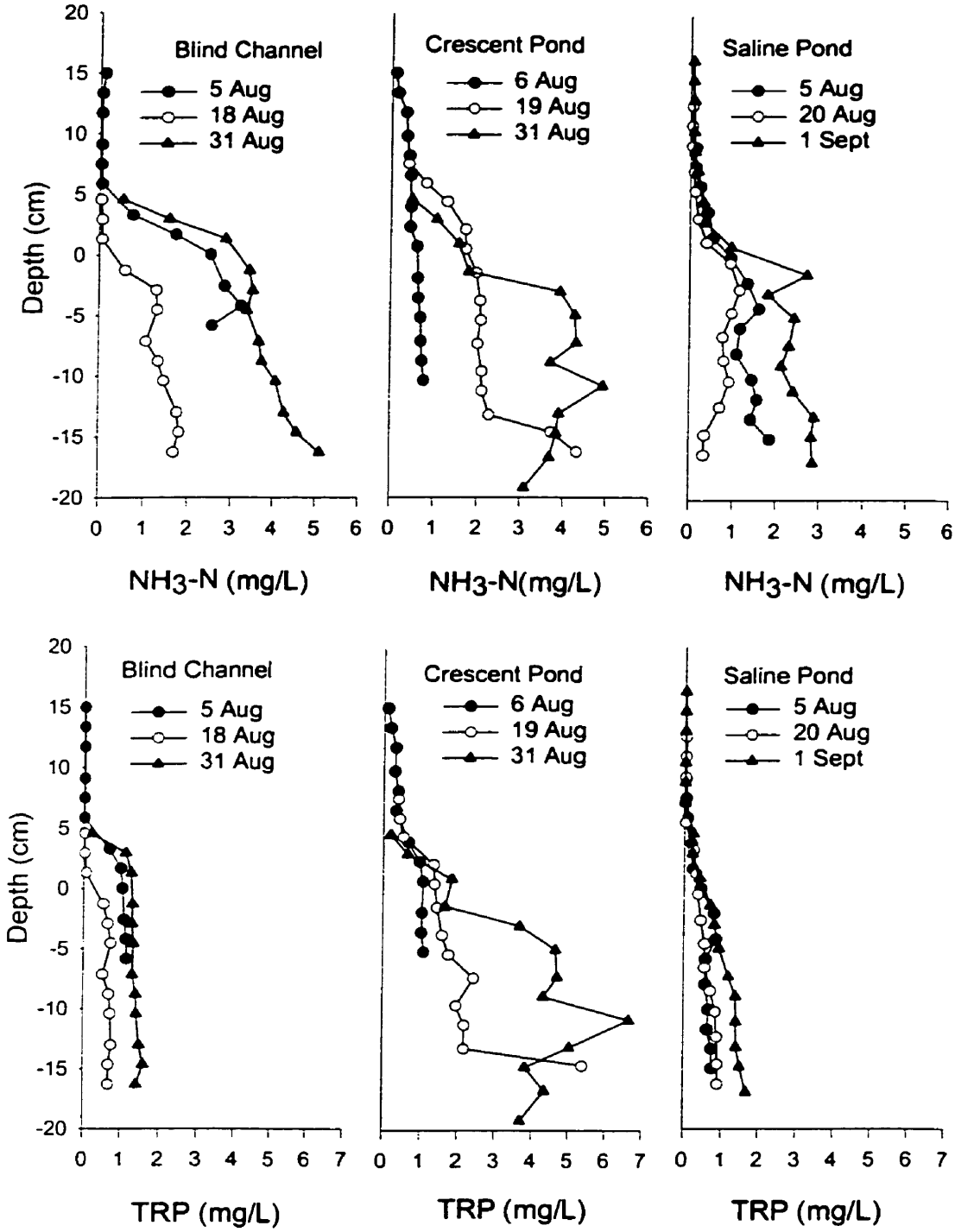

Figure 22: Ammonium-N and total reactive phosphorus concentrations (n = 3, 1999) above and below the sediment-water interface in Blind Channel, Crescent Pond and Saline Pond.

Figure 23: Plocon floating in the canoe channel leading to Blind Channel, 1999.

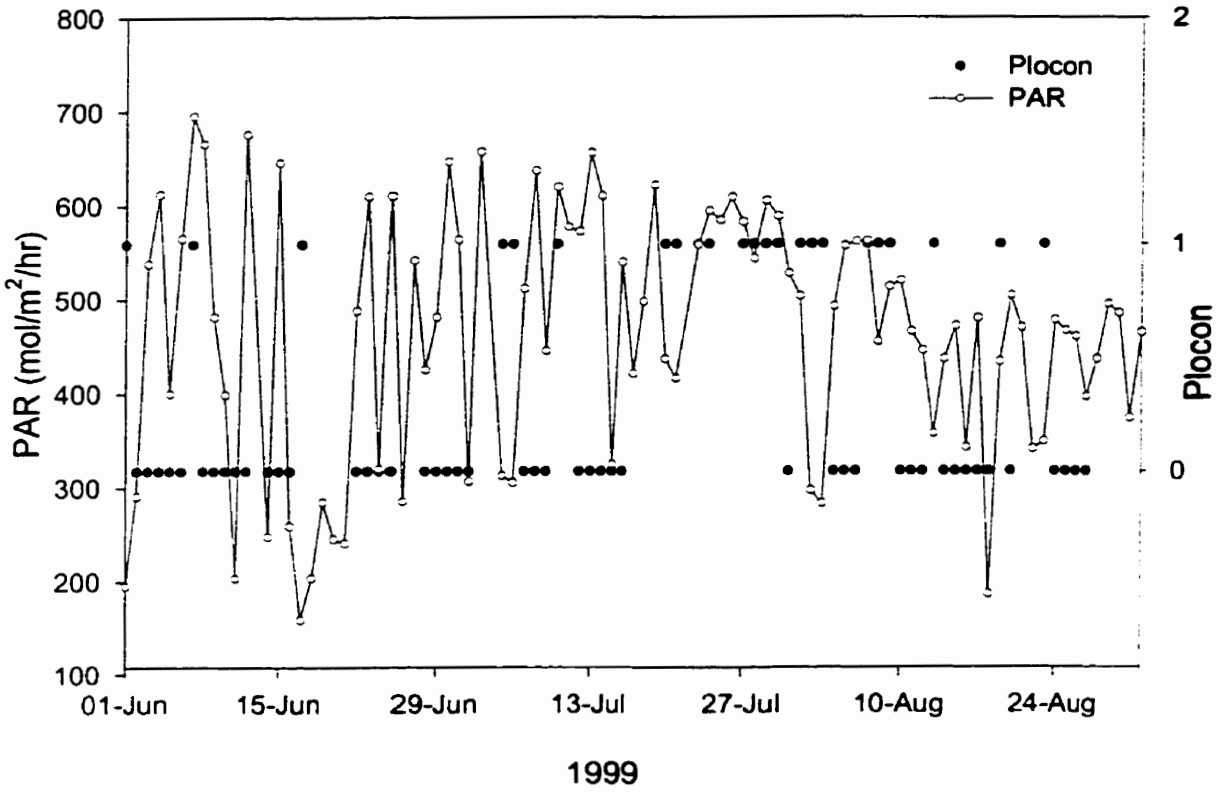

Figure 24: Daily mean photosynthetic active radiation (PAR) observed at the Environment Canada weather station at Delta Marsh, MB and the occurrence of plocon (presence (1) and absence (0)) observed in the canoe ditch of the Blind Channel (1999).

Table 10: The effect of PAR on the day of plocon occurrence and the effect of cumulative PAR one to four days prior to plocon occurrence. These results are based on a discriminant analysis (Wilks' λ).

	PAR *p value*	Cumulative PAR *p value*
No lag	*0.437 ns*	*0.033*
1 day lag	*0.780 ns*	*0.022*
2 day lag	*0.015*	*0.016*
3 day lag	*0.043*	*0.024*
4 day lag	*0.161 ns*	*0.033*

4.4 Multiple regression analysis

The independent variables included in the development of a forward stepwise multiple regression model for 1998 included sediment water content, organic matter and carbonate content, water depth, phytoplankton abundance, turbidity, water column total reactive phosphorus concentration, water column silica concentration, water column conductivity and alkalinity, and time of sample collection.

Sediment water content explained 31% of the variability in SAA chlorophyll in Blind Channel ($p = 0.016$, Table 11). When time of sample collection and water depth were added to the regression model the predictive power increased to 73.5%. Sediment water content, time of sample collection, and water depth all contributed significantly to the model ($p = 0.001$, $p = 0.034$ and $p = 0.004$, respectively). According to a forward stepwise regression all variables were poorly correlated ($r^2 = 0.000$) with SAA in Crescent Pond, and there was not a "best" set of independent variables to determine SAA chlorophyll. Phytoplankton chlorophyll explained 12.6% of the variability in SAA chlorophyll in Saline Pond but was not significant ($p = 0.148$). When water column conductivity was added to the regression model the predictive power increased to 25.3% (Table 11). This model was still poor because there was still a lot of unaccounted variability.

When the three sites were considered together, sediment carbonate content had a significant positive effect on SAA chlorophyll at the three sites ($p = 0.001$) and could explain 26.9% of the variability in SAA chlorophyll. As the cumulative regression model became more complex, the sediment water content ($p = 0.111$), water column alkalinity ($p = 0.002$) and time of sample collection ($p = 0.001$) explained 43.6% of the variability in SAA chlorophyll.

The independent variables included in the forward stepwise multiple regression model for 1999 included phytoplankton and macrophyte abundance, water depth,

Table 11: The major environmental variables that affect SAA chlorophyll at three sites in Delta Marsh (1998), as identified by forward stepwise multiple regression.

Site	Step	Variable	r^2	*p value*
Blind Channel	1	Sediment water content	0.310	*0.016*
	2	Sediment water content +	0.631	*0.001*
		Time		*0.003*
	3	Sediment water content +	0.735	*0.001*
		Time +		*0.034*
		Water depth		*0.004*
Crescent Pond		None		
Saline Pond	1	Phytoplankton chlorophyll	0.126	*0.148*
	2	Phytoplankton chlorophyll +	0.253	*0.060*
		Water column conductivity		*0.131*
All sites	1	Sediment carbonate content	0.269	*0.001*
	2	Sediment carbonate content +	0.347	*0.010*
		Time		*0.020*
	3	Sediment carbonate content +	0.409	*0.522*
		Time +		*0.004*
		Water column alkalinity		*0.032*
	4	Water column alkalinity +	0.404	*0.001*
		Time		*0.001*
	5	Water column alkalinity +	0.436	*0.111*
		Time +		*0.002*
		Sediment water content		*0.001*

Table 12 : The major environmental variables that affect SAA chlorophyll at three sites in Delta Marsh (1999), as identified by forward stepwise multiple regression.

Site	Step	Variable	r^2	*p value*
Blind Channel	1	Sediment conductivity	0.335	*0.007*
	2	Sediment conductivity +	0.439	*0.048*
		Water depth		*0.094*
	3	Sediment conductivity +	0.528	*0.015*
		Water depth +		*0.028*
		Macrophyte abundance		*0.100*
Crescent Pond		Light	0.226	*0.019*
Saline Pond	1	Turbidity	0.325	*0.014*
All sites	1	Sediment conductivity	0.249	*0.001*
	2	Sediment conductivity +	0.423	*0.001*
		Turbidity		*0.001*
	3	Sediment conductivity +	0.499	*0.001*
		Turbidity +		*0.001*
		Sediment phosphorus		*0.004*
	4	Sediment conductivity +	0.523	*0.001*
		Turbidity +		*0.001*
		Sediment phosphorus +		*0.012*
		Light		*0.095*
	5	Sediment conductivity +	0.542	*0.001*
		Turbidity +		*0.001*
		Sediment phosphorus +		*0.004*
		Light +		*0.076*
		Phytoplankton chlorophyll		*0.141*

water column turbidity, % surface light at the sediment-water interface, sediment conductivity, sediment total reactive phosphorus, and time of sample collection.

Sediment conductivity, water depth and macrophyte abundance explained 53% of the variation in SAA chlorophyll in Blind Channel (Table 12). Light explained 22.6% of the variability in SAA chlorophyll in Crescent Pond and had a positive significant effect ($p = 0.019$). No other variables met the criteria for inclusion in the regression model. In Saline Pond, 32.5% of SAA chlorophyll could be explained by water column turbidity ($p = 0.014$). Turbidity was found to be negatively correlated ($r = -0.673$) to SAA chlorophyll. Again, no other variable could improve the regression model.

When the three sites were considered together, sediment conductivity explained the most variation in SAA chlorophyll (24.9 %, $p = 0.001$). The predictive power of the forward stepwise regression model was improved to 54.2 % by adding water column turbidity, sediment phosphorus, light and phytoplankton chlorophyll. Of these five variables, sediment conductivity, water column turbidity and sediment phosphorus all contributed significantly to the multiple regression ($p= 0.001$, 0.001 and 0.004, respectively; Table 12).

5. DISCUSSION

5.1 Methodological implications

5.1.1 Evaluation of sampling methods

The lens tissue trapping technique of Eaton and Moss (1966) is a standard method for collecting epipelic algae and there is a considerable amount of data published in the literature that were collected in this manner. Because it relies on the phototactic response to sample illumination, this technique samples only the motile algae in the sediment. On the positive side, it samples only viable cells thereby reducing the amount of detrital and degraded pigments interfering with estimates of algal chlorophyll. This procedure also enables the observation of temporal differences in algal migration. Lens tissue papers can be placed and removed from sediment slurries at different times of the day and for varying durations.

The lens tissue trapping technique is an adequate method for sampling epipelic algae but not SAA for the following reasons. First, not all SAA are motile and therefore using this technique does not account for all the algae potentially present in the sediment, some of which are non-motile. I found that some of the motile algae in the sediment migrated to the surface of the sediment, as indicated by Chl *a* measurements after tissue trapping, but did not get trapped in the fibres of the lens tissue. Second, allowing the algae to migrate from deeper sediments meant that sampling was occurring vertically deeper into the sediment. Third, Hickman (1969) found that the amount of Chl *a* extracted from the lens paper depended upon the number of times the lens paper was shaken to dislodge the algae from the paper. I avoided this problem by extracting the Chl *a* directly from the lens tissue with methanol. Another deterrent to using this method is that it is laborious and time consuming, requiring about twelve hours to fully process one sample.

The *in situ* slurry method is a relatively easy and inexpensive way to collect SAA. This method collects both the motile and non-motile fractions of the sediment flora. However, it has numerous disadvantages, starting with the collection of the slurry in the field. Because this sample is collected *in situ,* the sediment surface cannot be seen in a turbid water column which means that the evenness with which the area delineated by the PVC pipe is sampled is unknown. The aspiration technique involved in collecting a sediment slurry disturbs the sediment and increases the chance that phytoplankton or detrital material is included in the sample. A further problem arises during chlorophyll analysis due to the long time period that occurs between sample collection and analysis. The *in situ* slurry needs to settle before the tissue trapping experiment begins. Therefore, the Chl *a* sample from the sediment slurry "before tissue trapping" has been sitting in the dark for 24 hours. By the time the sediment slurry has been sampled for Chl *a* for the "after tissue trapping" sample, the samples have been removed from the marsh for 48 hours (36 hours in the dark and 12 hours outdoors in the sun). During this time, algal chlorophyll may change due to growth. The Chl *a* content was found to be higher in the sediment slurry "after tissue trapping" because the algae migrated by phototaxis to the sediment surface and did not get trapped in the fibres of the lens tissue paper. The algae are in direct sunlight all day and are reproducing in the time frame between being collected from the marsh and Chl *a* analysis.

The core slurry method is a more controlled way to obtain a sediment slurry. The sediment-water interface in a clear coring tube can be seen readily so the whole area can be aspirated equally. However, there are two disadvantages to this method. First, the sediment is disturbed slightly during collection because of the edge effect in a small diameter corer and the mixing of sediment and water that inevitably occurs while aspirating the sediment. As for the *in situ* slurry, the long lag time between sample collection in the marsh and Chl *a* extraction can be problematic.

The coring method collects an intact sediment sample with little disturbance and Chl *a* extraction occurs immediately. This method also allows for finer resolution in sampling depth. Using the sediment core technique, samples can be collected at millimetre depth increments whereas slurries only permit sampling depths in centimetres. According to Cyr (1998), only the surface few millimetres of sediment should be collected in order to isolate actively photosynthesizing algae. However, the core can include detrital phytoplankton and macrophyte chlorophyll. Other problems associated with this technique include disturbance created by the edge effect of the core and disturbance caused by degassing from the sediment. I found that both these effects are generally minimal but they can disrupt the sediment surface.

5.1.2 Evaluation of hypotheses based on sampling methods

I hypothesized that the lens tissue trapping technique would underestimate SAA Chl *a* because it only samples motile algae. I also expected that, if the lens paper was trapping the motile algae efficiently, the sum of the Chl *a* of the slurry after tissue trapping and the lens tissue should equal that of the slurry before tissue trapping. This was not the case, indicating that the lens tissue was not even trapping all the motile algae. I hypothesized that the more controlled core slurry method would account for the deviation in Chl *a* between the *in situ* and the core, and it would yield Chl *a* measurements closer to that of the intact sediment core. However, Chl *a* values in the core slurry were again higher than those of the intact sediment core. I hypothesized that the sediment core would give the highest Chl *a* content and would be comparable to that of the slurries because they are both sampling surface sediments that include motile and non-motile algae. However, the overall mean seasonal Chl *a* values of the *in situ* and core slurries (43.4 and 25.9 mg/m^2, respectively) were significantly higher than the sediment core (9.6 mg/m^2).

Based on the foregoing, I conclude that the best method for sampling SAA is collecting an intact sediment core because it samples all the algae in association with the sediment. There is relatively little disturbance to the sediment and the sediment-water interface can be viewed while the sample is collected. Samples should be collected between 3-9mm in depth in this system. There is also minimal time delay between sample collection and Chl *a* analysis. One disadvantage to this method is the edge effect because of the small core diameter. The edge of the sediment core is disturbed due to the force exerted when a corer is pushed into and pulled out of the marsh bottom. The ratio of the proportion of the disturbed edge to the intact sediment surface is larger than if a corer of greater diameter is used. Core diameters ranging from 1 - 7 cm have been used to retrieve a column of sediment (Carlton & Wetzel 1985, Hansson 1988, deJonge & Colijn 1994, Blumenschine *et al.* 1997, Lassen 1997, McCormick *et al.* 1998). The appropriate core size depends upon the objective of the study, the economic and physical resources available, and the aquatic system of interest. A hand held gravity corer consisting of variable length plastic pipe is inexpensive and easy to use in shallow water. This device can be made with material readily available at hardware stores. This corer can be modified to accommodate a detachable end, allowing the sediment core to be removed intact inside a plastic cylinder for chamber studies involving metabolism or nutrient uptake. A box corer, sampling sediment and water, can also be used for studying metabolism of microorganisms in sediment under *in situ* conditions and are used in deeper water. They are usually deployed with SCUBA and allow sampling at a larger scale. Besides edge effects, another disadvantage to coring is the sediment disturbance occurring when methane pockets in cores of highly organic sediments are dislodged. Cores should be collected quickly before the gas bubbles rise to the sediment surface.

The standard lens tissue trapping method is a good method to account for temporal migration in the motile constituents of SAA. However, this method could be improved by collecting intact sediment cores and placing lens paper directly on the undisturbed column of sediment.

5.1.3 Evaluation of algal biomass analyses

I used chlorophyll *a* as a surrogate for algal biomass in this study. It was chosen because numerous samples were processed weekly, and it is a simple and inexpensive procedure. It is also a widely adopted standard so there is abundant published data available for comparisons. Chlorophyll *a* is one of the most common estimators of algal biomass (Hansson 1988). However, there are some methodological problems, not necessarily exclusive to sediment chlorophyll, which have been discussed in the Literature Review section of this thesis.

It is plausible that the Chl *a* content measured in my SAA samples could be a function of increased Chl *a* per algal cell as an adaptation to their low light environment. However, when samples from a single date were analyzed for both chlorophyll and biovolume, both metrics followed similar trends. According to Hansson (1988) acetone extracts more chlorophyll than methanol from sediment samples. If this is the case then the measurements of SAA Chl *a* in this thesis are under-estimations because all chlorophyll analyses were done with methanol. Hansson (1988) also showed that the amount of chlorophyll extracted with methanol and acetone increased with decreasing water content. Freeze-drying prior to chlorophyll extraction increased the extraction efficiency because the reduced water content improved the exposure of the sample to the solvent. Saline Pond had significantly lower water content, lower organic matter content, and higher carbonate content than Blind Channel and Crescent Pond (all $p = 0.001$) but a higher SAA Chl *a* content (regardless of sampling method). This high Chl *a* measurement in Saline

Pond could be explained by the higher extraction efficiency for sediment with these characteristics. The limited capability of estimating degradation products and the possible inclusion of non-algal chlorophyll was problematic.

Algal biovolumes were calculated for 54 samples collected in a single sampling interval, to determine if the different methods were preferentially sampling certain genera. A single method did not sample one genus more prominently except the lens tissue trapping technique. This method collected the highest percentage of *Euglena* sp. Algal biovolumes were compared to chlorophyll measurements to determine if Chl *a* measurements are representative of algae present in the sediment. Algal biovolume measurements did provide more detailed information about the SAA assemblage than Chl *a* analysis. Measurements of algal biovolume were highest in lens paper placed on the sediment slurry between 10 am and 2 pm indicating that there was possibly temporal migration in the motile component of SAA.

There is undoubtedly some interference from degraded pigments in SAA Chl *a* samples. It would have been instructive to analyze sediment samples by HPLC (high performance liquid chromatography) to distinguish the degradation products of Chl *a* that were present and also to quantify other pigments and their degradation products that were present in the samples. Unfortunately, the high cost of this method put it beyond the resources of this study.

5.1.4 Recommendations

In this thesis, it would have been instructive to collect a core slice to a depth of 6.4 cm, the same depth as that collected for the sediment slurries, in order to make a more direct comparison between the two sampling techniques for SAA. Based on a sediment core collected from Blind Channel in March 1999, a core slice to a depth of 6.4 cm corresponds to approximately 19 mg/m^2 (Goldsborough unpublished). This is approximately 5x more than my sediment core measurements

and not significantly different from *in situ* slurry measurements.

For future research on SAA in wetlands, I recommend the following:

1. Intact sediment cores should be collected with a large enough diameter to reduce the disturbance caused by the edge effect. The proportion of the disturbed edge to the intact sediment surface increases as the diameter of the core decreases. I observed that a core diameter of approximately 6 cm was adequate to obtain an intact sediment surface with minimal disturbance.
2. Core slices should be collected at millimeter increments to avoid missing small-scale vertical profiles within a core where the depth of photosynthesizing algae varies depending on soil type and environmental conditions. This would be useful for comparisons to other studies in which cores are collected to varying depths and it would also enable better understanding of the food resource available to benthic invertebrates.
3. SAA abundance should be analyzed by HPLC because it provides information on all pigments as well as their degradation products. However, given that it is expensive and not readily available to many researchers, spectrophotometric chlorophyll *a* analysis as well as identification and enumeration is the best compromise for measuring algal abundance. This will ensure that Chl *a* measurements are from viable algal cells and not detritus or macrophytes. Samples should be freeze dried and extracted with acetone.

5.2 Ecological implications

5.2.1 Site Description

Blind Channel had the highest abundance of phytoplankton chlorophyll but lowest abundance of macrophytes and SAA compared to the other two sites. Carp were present in the channel in both years and the water column was extremely turbid. Blind Channel had the lowest concentration of NO_3-N and silica but the

highest concentration of TRP in the water column compared to the other sites. Like Crescent Pond, the sediment composition was high in water and organic matter but low in carbonates relative to Saline Pond. The sediments of the channel had the lowest conductivity of the three sites. The phosphorus and carbon concentrations in the sediments were low relative to Crescent Pond but higher than Saline Pond. The pore-water TRP and NH_3-N concentrations were slightly less than Crescent Pond.

Crescent Pond was covered extensively by a thick mat of duckweed. This pond had the highest abundance of macrophytes relative to the other sites. The abundance of phytoplankton and SAA chlorophyll were both in between the values for Blind Channel and Crescent Pond. Crescent Pond had a mean water depth approximately equal to that of Blind Channel (93 cm). However by comparison, its water column was very clear and no fish were present. This site had the lowest water column TRP but highest sediment phosphorus, nitrogen and carbon concentrations. It also had the highest concentration of sediment pore-water nitrogen and phosphorus.

Saline Pond had the highest SAA chlorophyll and lowest phytoplankton chlorophyll of the three sites. Submersed macrophytes were present and increased in abundance throughout the growing season. Both the sediment and water column had the lowest concentration of phosphorus compared to Blind Channel and Crescent Pond. The sediment also had low water and organic matter content but high carbonate content relative to the other two sites. Saline Pond is a recent pond that was dug out in 1968 whereas Crescent Pond and Blind Channel are part of post glacial Assiniboine River and are approximately 2000 to 2500 years old (Teller & Last 1981). They have been around for a long period of time allowing organic matter to accumulate. This site also had the highest sediment and water column conductivity. Carp were not present in the pond in 1998 but were present in the

spring of 1999. The water column was therefore turbid in the spring due to spawning carp and became clearer throughout the growing season because of the establishment of macrophytes.

5.2.2 Sediment-associated algae

The chlorophyll *a* measurements from the lens tissue papers and sediment cores in Delta Marsh were comparable to other wetland studies (Table 13). However, most studies where sediment cores have been collected were in salt-water marshes. These marshes have a high abundance of SAA probably because of exposed tidal mudflats that increase the irradiance for the algae. Another problem with comparing core Chl *a* measurements between studies is that core slices are collected from varying depths (2 mm to 10 cm). Nevertheless, there is a clear trend of sediment core Chl *a* being roughly ten-fold higher than lens tissue Chl *a*. No one has looked at the Chl *a* content in the sediment slurry prior to and after tissue trapping before so no comparisons can be made to other freshwater marshes.

5.2.3 SAA, phytoplankton and macrophytes

SAA and phytoplankton coexist but their biomass differs spatially and temporally. Both assemblages require light and nutrients for growth. A shift from nutrient limitation to light limitation in SAA caused by phytoplankton has been observed in temperate and subarctic lakes (Hansson 1992).

SAA chlorophyll was always highest in Saline Pond followed by Crescent Pond and Blind Channel regardless of sampling technique used. Phytoplankton chlorophyll had the reverse trend with Blind Channel having the highest chlorophyll followed by Crescent Pond and Saline Pond (Tables 2 & 5). There are two possible explanations. First, the high abundance of SAA regulated the flux of nutrients from the sediment to the water column limiting the nutrient availability to phytoplankton. Second, the high abundance of phytoplankton reduced the incident irradiance that

Table 13: A comparison of lens tissue and sediment core SAA chlorophyll collected from Delta Marsh, MB and other wetlands, estuaries and shallow lakes (* denotes from salt-water marshes).

Sampling method	Wetland	Chlorophyll *a* (mg/m^2)	Reference
Lens tissue	Delta Marsh, MB	0.2 - 4.5	Present study
	Blind Channel, MB	2.0 - 3.0	McDougal *et al.* (1997)
	MERP cells, MB	0.1 - 17.5	Robinson *et al.* (1997)
	Garmat ali River, Iraq	2.0 - 35.0	Al-Saadi et al. (1996)
	Narcisse, MB	1.0 - 2.0	Campeau *et al.* (1994)
	Narcisse, MB	7.5 - 12.0	Gabor *et al.* (1994)
	Narcisse, MB	0.4 - 4.8	Murkin *et al.* (1994)
	Narcisse, MB	0.4 - 4.2	Murkin *et al.* (1991)
	Lake Wabamun, AB	1 - 14	Hickman (1974)
Sediment Core	Delta Marsh, MB	0.5 - 35	Present study
	Blind Channel, MB	6.5 - 29	Goldsborough (unpublished)
	Killarney Lake, MB	21 - 433	Richmond (1997)
	Ems Estuary, Netherlands*	29 - 247	DeJonge & Colijn (1994)
	Stellwagen Bank Bay, MA, USA*	10 - 109	Cahoon *et al.* (1993)
	North Inlet Estuary, SC, USA*	20 - 25	Pinckney & Zingmark (1993)
	North Inlet Estuary, SC, USA*	19 - 25	Steward *et al.* (1992)
	Graveline Bay Marsh, MI, USA*	57 - 160	Sullivan & Moncreiff (1988)
	East Galveston Bay, TX, USA*	231	Hall & Fisher (1985)
	Erickson potholes, MB	13 - 435	Shamess (1980)

could reach the sediment-water interface for the SAA (Carlton & Wetzel 1988, Hansson 1990, Van Luijn 1995, Blumenschine *et al.* 1997, Lassen 1997). Whether SAA are nutrient or light limited varies between sites and depends upon the nutrient concentration in the sediments and the water column and the light environment.

There is evidence of both possibilities (SAA regulating nutrient flux, and phytoplankton reducing light penetration) at the three sites. In Blind Channel, the increase in phytoplankton abundance reduced light reaching the sediment-water interface because macrophyte abundance was low. The high abundance of phytoplankton in Blind Channel could be explained by high water column nutrients from the sediments, and from senescing macrophytes or the possible inclusion of resuspended SAA Chl *a* in phytoplankton measurements. Also, carp disturbed the sediment releasing nutrients and increasing the water column turbidity. This reduced the incident light that could reach the sediment-water interface. I suspect that in Crescent Pond the SAA are regulating the flux of nutrients from the sediment because of the nutrient-rich sediment and clear nutrient-poor water column. Phytoplankton abundance was not high enough in Crescent Pond to reduce light penetration but the mat of macrophytes was sufficiently dense to do so. Saline Pond had the highest concentration of SAA but lowest concentration of nitrogen and phosphorus in the sediments. SAA could be luxuriously consuming nutrients in the sediment, and limiting the amount that gets into the water column available for phytoplankton. This, in turn, resulted in a low phytoplankton abundance that allowed more incident light to reach the sediment-water interface.

Another explanation could be that phytoplankton was favoured in sites where there was adequate wind fetch, wherein water circulation by wind activity helped to keep phytoplankton cells entrained. Settling occurred at sites where wind-induced mixing was low so there was a higher abundance of SAA. The most exposed site,

Blind Channel, had the highest phytoplankton abundance whereas Saline Pond, the least exposed site, has lowest abundance.

The general trend observed at all three sites was high macrophyte abundance when phytoplankton abundance was low and vice versa. The site with the highest phytoplankton, Blind Channel, had the fewest macrophytes (34.8 g/m^2 dry wt). Crescent Pond had the highest abundance of macrophytes of the three sites (81.4 g/m^2 dry wt) and low phytoplankton abundance (19.9 mg Chla/m^2). As macrophyte abundance increased, turbidity decreased and SAA abundance increased. Blind Channel had only one sampling location with macrophytes and the lowest amount of SAA Chl *a*. Saline Pond and Crescent Pond had a higher macrophyte abundance and a higher SAA Chl *a* than Blind Channel.

Water column turbidity also affected light attenuation. The light extinction coefficients at the three sites varied with the combined effects of cloud cover, and the absorption and scattering of light by macrophytes, phytoplankton and suspended particulates. Sampling where macrophytes were not present would have been subjective and not indicative of the light environment for SAA.

SAA Chl *a* was smaller in 1999 than 1998 at all three sites regardless of sampling method. This could be due to inter-annual environmental variability or more accurate sampling during the second field season. The decrease in SAA chlorophyll content in Saline Pond was suspected to be due to the presence of carp in 1999. Carp disturbed the sediment making the water column visibly turbid, thereby lowering the amount of light that could reach the sediment surface. Carp also disturbed the sediment surface for SAA colonization. Lougheed *et al.* (1998) found that increased carp disturbance during spawning and feeding led to the loss of submergent macrophytes and a decrease in water clarity in Cootes Paradise, a coastal wetland of Lake Ontario. In Blind Channel, macrophyte abundance has decreased over the past 10 years (L.G. Goldsborough, pers. comm.). However,

there are no data to assess whether the number of carp have increased over this same period. Lougheed *et al.* (1998) also observed a more diverse (>7 species) and dense community of macrophytes (>20 plants/m^2) in clear water sites. Crescent Pond, the clearest site of three studied here, had the highest number of macrophyte species and no carp.

5.2.4 Conceptual models

Blind Channel and Crescent Pond are examples of the two alternative stable states in the shallow lake model of Scheffer *et al.* (1993). Blind Channel was very turbid and had no macrophytes whereas Crescent Pond was extremely clear and had lots of macrophytes. However, water clarity and macrophytes are not the only parameters that differed between the sites. The turbid site, Blind Channel, was dominated by phytoplankton and the clear water site, Crescent Pond, was dominated by SAA and epiphyton (Table 14). The biomass of primary producers was > 2x higher in the clear state (126 g/m^2) than the turbid state (55 g/m^2).

Saline Pond had carp in the spring of 1999 but not at all in 1998. The pond was clear in 1998 and turbid in 1999 (5-35 NTU). Macrophytes were still present in Saline Pond possibly because this pond was in the process of switching from a clear water state to a turbid state but also because of its shallow water depth. This shallowness would enable more incident light to reach the sediment-water interface and would also force carp to retreat into the Blind Channel later in the summer, as water levels fell.

Phytoplankton is the dominant algal assemblage in the "Lake State" in a wetland four stable state model of Goldsborough & Robinson (1996) when water and nutrient levels are high, few macrophytes and fish are present and the water column transparency is low. Blind Channel would be considered to be in this state (Table 14). In the "Dry State" SAA is dominant, the water level is low, water

Table 14: Mean algal and macrophyte biomass (g/m^2) and their percentage of total biomass in three sites in Delta Marsh during the 1999 sampling period. Biomass was converted from chlorophyll to dry weight using a factor of 0.25% (Goldsborough unpublished).

	Blind Channel	%	Crescent Pond	%	Saline Pond	%
Phytoplankton	17	30	8	6	5	5
Epipelon	0	1	0	0	1	1
SAA *(Sediment core)*	2	3	4	3	6	6
Epiphyton	9	16	27	21	22	21
Macrophytes	28	50	87	69	72	68
Total	**55**		**126**		**106**	

transparency is high and few macrophytes are present. I believe that Saline Pond is switching to this state from the "Open State" dominated by epiphyton. If the water level decreases and/or the abundance of macrophytes decrease SAA will become the dominant algal assemblage in this pond. A decrease in macrophyte abundance is likely because of increased turbidity and direct macrophyte damage caused by carp. Crescent Pond is also considered to be in the "Open State" dominated by epiphytic algae (Table 14).

My results were consistent with those of Robinson *et al.* (1997a) who found that SAA biomass in isolated cells of Delta Marsh decreased and phytoplankton increased as the water column. Their SAA measurements were made using the lens tissue technique and can therefore be assumed to be under-estimates.

5.2.5 Nutrients

Many freshwater lakes are phosphorus limited but there are too few data to assess whether this generalization applies to freshwater wetlands (Goldsborough & Robinson 1996). Phosphorus occurs in wetlands as orthophosphate or organically bound phosphates. Orthophosphate is the only form of soluble inorganic phosphorus useable by algae and macrophytes (Wetzel 1983). Phosphate is extremely reactive and interacts with many cations (Fe and Ca) to form insoluble compounds. The availability of phosphate is also reduced by the adsorption to particulate compounds (clays, hydroxides and carbonates). The sediment conductivity was significantly higher in Saline Pond than the other two sites which is indicative of high ion concentration. There are no data on sediment ion concentrations for this site but there are data for water column calcium (55 mg/L), magnesium (275 mg/L), potassium (24 mg/L), and iron (< 0.01 mg/L) (Goldsborough 1994). The low phosphorus concentration in the sediment of Saline Pond could be explained by phosphorus complexes with these ions (Wetzel 1983) that renders phosphorus

unavailable for algal consumption. The ability of sediments to retain phosphorus beneath an oxidized microzone at the sediment water interface is related to several factors. Mortimer (1941) found that the presence of an oxidized microzone at the sediment surface inhibited phosphorus release. A decrease in the redox potential of the microzone following the onset of anoxic conditions reduced Fe(III) releasing phosphorus. Carlton and Wetzel (1988) found that the release of phosphorus was inhibited during daylight because of photosynthesizing epipelic algae oxygenating the sediment.

Phytoplankton receives nutrients from the water column whereas SAA can obtain nutrients from the sediment and the overlying water (Borchardt 1996). This dual nutrient source is probably a competitive advantage for SAA, particularly in shallow lakes and wetlands (Hansson 1990). There could be a trade off between nutrient and light acquisition with phytoplankton receiving more light and less nutrients whereas SAA has more nutrients available and less light. Although, sediment and sediment pore-water nutrient concentration may be more indicative of the environment that SAA inhabit than water column nutrient concentration. Sediment pore-water TRP ranged from 1 to 7 mg/L and NH_3 ranged from 1 to 5 mg/L. This is comparable to wetlands in Point Pelee National Park, Ontario (TRP approximately 4 mg/L, NH_3 from 20 to 25 mg/L, Mayer *et al.* 1999). There was a sharp increase in phosphorus and nitrogen concentration at, or slightly above, the sediment-water interface in my nutrient profiles (Figures 20 & 22). There may be a nutrient-rich microzone 5 cm above the sediment, possibly caused by nutrients diffusing from the sediment into the overlying water column. Beside the possibility of *in situ* cross-contamination between chambers in the peeper, a third possibility is that the peeper moved vertically while in the sediments.

In this study, nutrient levels measured in pore-water using peepers were probably lower than actual concentrations existing in sediment interstices for three

reasons. First, the reagents used in TRP and NH_3 analyses could not be digested at such high concentrations in the allocated 24 hours and needed to be left longer. Second, peepers were parged with nitrogen gas prior to being placed in the marsh, but I could not ascertain whether all oxygen in the peeper was removed by this treatment. The peepers also became slightly oxygenated during transit to the marsh sites and again during retrieval and return to the lab. The results of these factors would be lower NH_3 measurements due to NH_3 oxidation to NO_3.

Chemical analyses of sediments from the three sample sites indicate severe deficiency of some nutrients. C:P molar ratios from Delta Marsh sediments ranged from 645 to1045 mol/mol. These ratios are higher than those reported for a wetland at Point Pelee National Park (475-600 mol/mol; Mayer *et al.* 1999). Hecky *et al.* (1993) reported that a C:P molar ratio > 258 indicates severe phosphorus deficiency. When the C:N molar ratio > 14.6 there is severe nitrogen deficiency and when the N:P molar ratio is greater than 22 the system is considered phosphorus deficient. C:N, C:P and N:P molar ratios showed that there was nitrogen and phosphorus limitation occurring at the three sites while the C:Chl *a* ratio indicated that there was no degree of deficiency (all ratios < 4.2). Organic matter could be skewing the C:N and C:P molar ratios because sediment total reactive phophorus and total nitrogen ranged from 0.1-0.5 mg/gdw and 1-10 mg/gdw respectively. These values are considered adequate to support algal growth (Healy & Hendzel 1979). The low C:Chl *a* ratios could possibly be explained by a lot of detrital Chl *a* or non-algal Chl *a* that might be skewing the ratio.

5.2.6 Evaluation of hypotheses

The effect of the combination of all measured environmental factors on SAA chlorophyll was evaluated by multiple regression. The amount of variation in SAA chlorophyll that could be predicted by these variables ranged from 0 to 73.5%. In

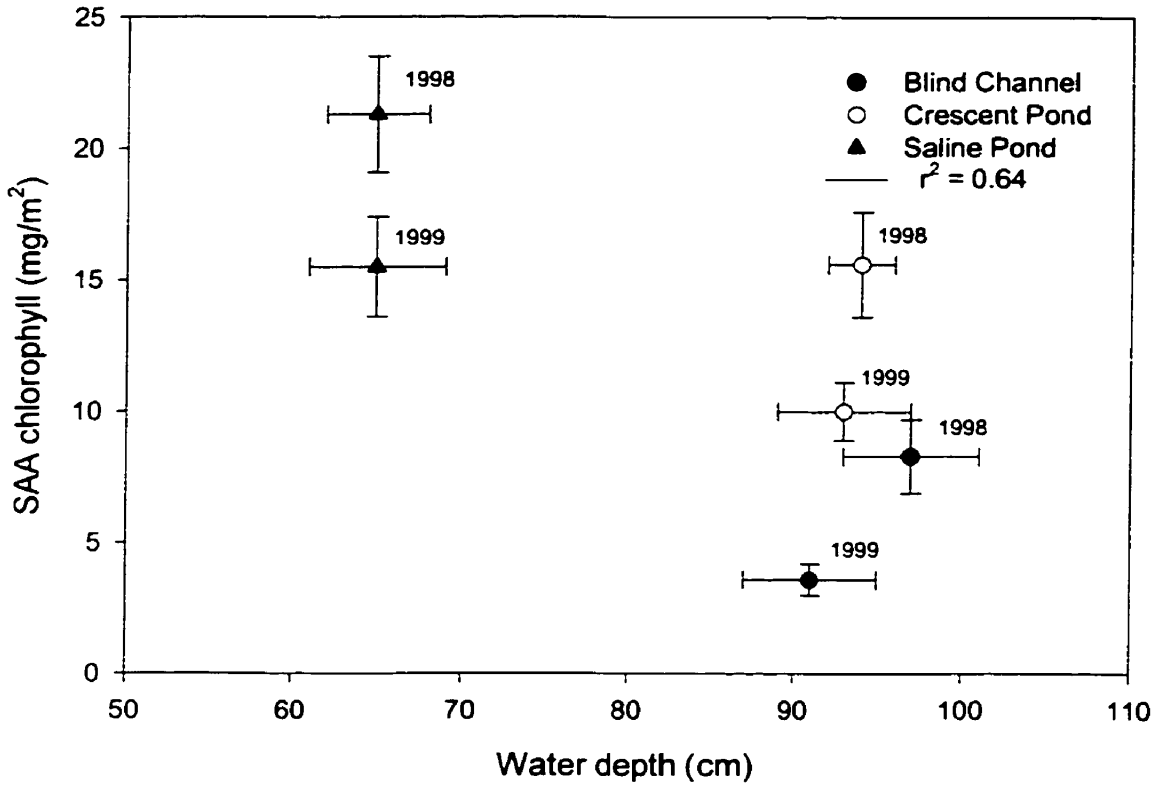

Figure 25: The relationship between mean seasonal SAA chlorophyll (mg/m^2 ± SE) based on sediment cores and water depth (cm ± SE) for Blind Channel, Crescent Pond and Saline Pond (1998 and 1999).

other words, there was considerable unaccounted variation in SAA production. There were five hypotheses posed at the beginning of this study based on an examination of literature dealing with SAS and its ecology. This thesis, therefore, examined predictions arising from these hypotheses:

Hypothesis #1: Saline Pond should have the highest SAA chlorophyll of the three sites because it is the shallowest.

Saline Pond had the highest SAA chlorophyll in both years relative to Blind Channel and Crescent Pond and it was the shallowest site (Figure 25, $r^2 = 0.64$). According to a forward stepwise regression, water depth did contribute to Blind Channel SAA chlorophyll, but not to Saline Pond or the cumulative models for all three sites. Phytoplankton chlorophyll and water column conductivity in Saline Pond explained 25.3% of the variation in SAA chlorophyll. However, turbidity measurements done in 1999 were correlated significantly with SAA Chl *a* ($p = 0.014$), explaining 32.5% of the variation in SAA Chl *a* at this site. No other single variable could improve the predictive power of this model. Water depth was correlated with time; that is, depth decreased over the season.

Hypothesis #2: SAA chlorophyll will be lower in vegetated sites compared to unvegetated sites because, as macrophyte cover increases, less light will reach the sediment surface and algal growth will be limited.

SAA chlorophyll at the three sites did not correlate inversely with macrophyte biomass. Instead, contrary to my hypothesis, macrophyte abundance increased as SAA chlorophyll increased (Figure 26). The difference in macrophyte abundance in Saline Pond and Crescent Pond was insignificant; however, Saline Pond did have significantly higher SAA chlorophyll than Crescent Pond ($p = 0.001$). The effect of macrophyte abundance on SAA chlorophyll depended upon the shape and structure

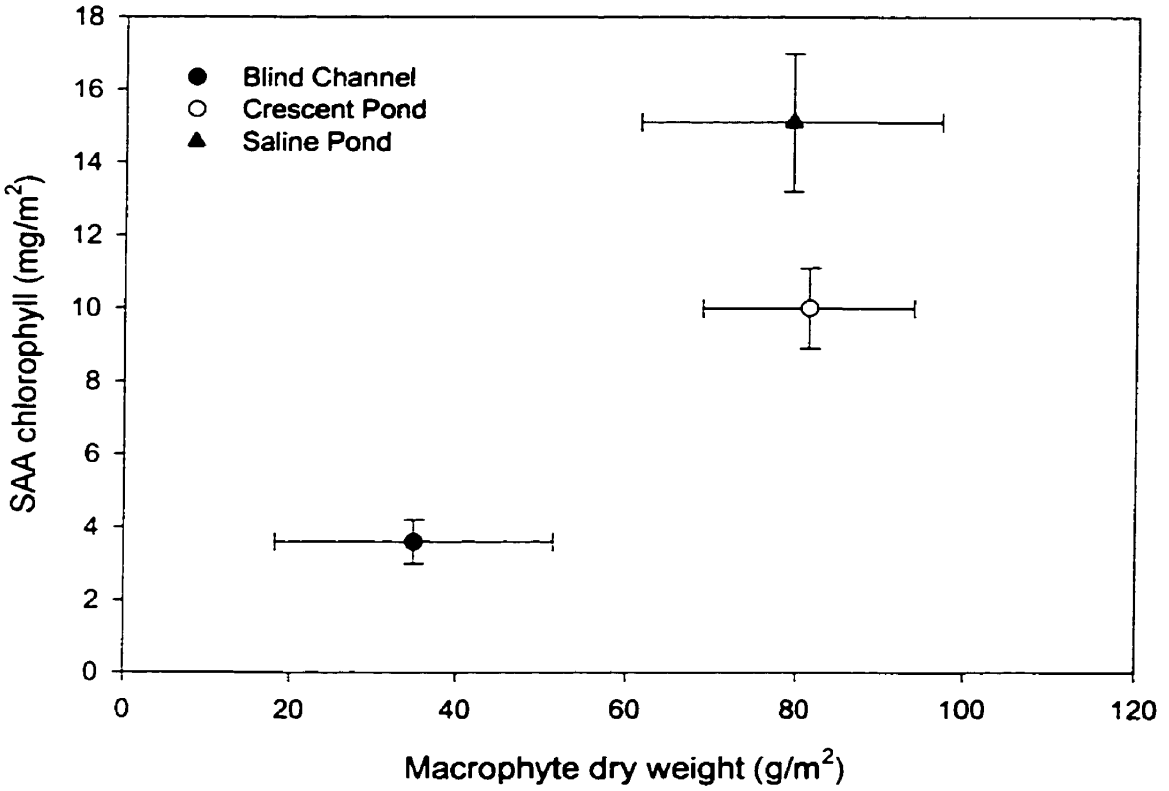

Figure 26: The relationship between mean seasonal SAA chlorophyll (mg/m^2 ± SE) based on sediment cores amd macrophyte dry weight (g/m^2 ± SE) for Blind Channel, Crescent Pond and Saline Pond (1999).

of the predominant macrophyte species at each site. In Crescent Pond, *Lemna trisulca,* a floating, ivy-leaved macrophyte that covered the water surface, was predominant. *Potamogeton pectinatus,* a rooted macrophyte with needle-like leaves was predominant in Saline Pond. More light was able to penetrate to the sediment surface in Saline Pond than in Crescent Pond because of difference in the structure of these macrophytes. Also, I suspect that *Lemna trisulca* has more surface area per gram of dry weight for epiphytic algal colonization. Macrophytes that do not root into sediments, such as *Lemna trisulca,* require nutrient uptake from the water and may compete successfully with phytoplankton, leaving sediment nutrients available for SAA. This could explain the high sediment phosphorus (491 ± 60 µg/gdw) in Crescent Pond and the high SAA Chl *a* and low phytoplankton abundance. Macrophytes also help to stabilize the sediment reducing water columnn turbidity and are also important sources and sinks of nutrients to the sediment (Brix 1997). It seems to be the structure of the leaves rather than if the macrophyte is rooted or not that affects the presence of SAA chlorophyll.

It is possible that the inability to distinguish between algal and macrophyte Chl *a* might have enhanced Chl *a* measurements, although algal biovolume measurements were also highest at the vegetated sites. It is also possible that the increasingly vegetated sites may have increased SAA abundance because of detached and sedimented epiphytic algae that may be taxonomically indistinguishable from SAA taxa.

Hypothesis #3: The higher the nutrient concentration in the sediment and the interstitial pore-water the higher the SAA chlorophyll because nutrient concentration and algal abundance are positively correlated.

This hypothesis was not supported by these data. The highest SAA chlorophyll was found in Saline Pond, the site with the lowest nutrient concentration in its

sediment and interstitial pore-water. In a forward stepwise multiple regression for the three sites, sediment phosphorus was negatively correlated to SAA chlorophyll ($r = -0.665$). There are two possible explanations for the low phosphorus concentration in Saline Pond sediments. First, the phosphorus measurements could be underestimates because if the sediment is prone to form calcium complexes with phosphorus that are not detected by the phosphorus analysis method used here. Second, the macrophytes in Saline Pond were rooted in the bottom, and took up sediment phosphorus. Also, rooted macrophytes increase the sediment release rate of phosphorus during the growing season (Stephen *et al.* 1997). The high Chl *a* measurements could be a function of increased chlorophyll extraction efficiency in sediment with low water content such as occurred at this site.

Hypothesis #4: The biomass of SAA will peak in spring and autumn because phytoplankton and macrophyte abundance are low at that time of year and irradiance reaching the sediment-water interface will be at a maximum.

There was no seasonal trend in SAA chlorophyll at any of the three sites. High water column turbidity in the spring and macrophyte abundance in the autumn could be keeping SAA chlorophyll from reaching peaks at these times. However, in the forward stepwise regression model for 1998, time of sample collection did explain 44% of the variation in SAA along with water column alkalinity and sediment water content.

Hypothesis #5: The occurrence of plocon is dependent on high solar irradiance and minimal wind velocity because plocon is only observed by late afternoon on calm sunny days.

This study successfully showed that plocon occurrence could be explained by high solar irradiance but not wind velocity. Plocon occurred after at least two

days of consistently high photosynthetic active radiation. A discriminant analysis revealed that daily PAR had no effect on determining presence or absence of plocon. However, plocon occurred after two or three days of high PAR (>500 mol/m^2/hr). The effect of cumulative daily PAR did have a significant effect on plocon occurrence. The magnitude of plocon chlorophyll values were approximately 10x that of sediment cores and 100x that of lens tissues. Plocon may not only have a higher biomass than SAA but may also have a higher rate of primary productivity. This assemblage could be actively photosynthesizing at such a high rate and producing gas bubbles that it dislodged itself from the sediment and rose to the water surface. Wind speed did not affect the presence of plocon in this study. However, I studied a quiet, calm site sheltered from wind because plocon rarely occurs in open areas of the marsh where wind is higher.

5.2.7 Ecosystem support

Organic carbon in aquatic systems comes from two sources: 1) allochthonous carbon which is contributed externally by the surrounding terrestrial system and 2) autochthonous carbon, synthesized internally by autotrophic organisms such as algae and macrophytes. Stable isotope analyses have shown that herbivore "signatures" often match those of wetland algae more closely than macrophytes (Sullivan & Moncreiff 1990, Keough *et al.* 1996, Neill & Cornwell 1997). Algae and algal detritus have a high nutritive value and are readily available to herbivores. In contrast, plant litter is a low quality food (high C:N ratio) and may require microbial degradation before being used by invertebrates (Campeau *et al.* 1994). However, carbon budgets do not directly reflect food quality or utilization by consumers. Some carbon is rapidly assimilated (labile) whereas other carbon forms are slowly assimilated (refractory) (Lamberti 1996).

Macrophytes have been thought to be the predominant food resource for secondary producers in wetlands (Murkin 1989), but recent studies indicate that algae play a larger role in wetland primary production (Robinson *et al.* 1997a). Most studies on algal production look at phytoplankton because it is easy to collect and is thought to contribute the most to primary production (Lowe 1996). The role of benthic algae in aquatic food webs has received relatively little attention when compared to studies on phytoplankton in pelagic food webs. From the methodological component of this thesis, it would appear that production of SAA in wetlands has been under estimated by the standard lens tissue method. Because phytoplankton was considered the most abundant assemblage, it was also considered to be the main food source for benthic and planktonic herbivores. Results of this study have clear implications for the wetland food web, especially when macrophytes are absent and phytoplankton and SAA represent the only food source. There are several open water bodies in the 22,000 hectares of Delta Marsh, such as Cadham Bay, Clandeboye Bay and Simpson Bay, where submersed macrophytes have been in decline since at least the 1970s (Wrubleski & Anderson 1999). Instead, phytoplankton and SAA is conspicuous at these sites; for example, SAA can be seen covering the sediment during periods of low water level (Figure 27). Therefore, it is probable that these assemblages are the major contributors to primary production and, as such, are a more important food source for benthic and planktonic herbivores. Future research needs to be devoted to algal-herbivore interactions in wetlands, especially those in which submersed macrophytes are absent.

Estimates of biomass of the major algal assemblages and macrophytes and their percentage of total biomass differ between Blind Channel, Crescent Pond and Saline Pond (Table 14). Epiphytic algae was estimated as a percentage of macrophyte biomass, based on other studies from Delta Marsh (McDougal *et al.* 1997, McDougal *et al.* in press). Chlorophyll measurements (mg/m^2) were converted

Figure 27: Green patches of SAA on an exposed mudflat at low water level in Canvasback Bay, Delta Marsh, 1999. Photo taken by Dale Wrubleski (Ducks Unlimited Canada).

to dry weight (g/m^2) by multiplying by a factor of 0.4 (Goldsborough, unpublished data). SAA contributed approximately 3% of the biomass in both Blind Channel and Crescent Pond and 6% in Saline Pond. Phytoplankton biomass contributed approximately 30% in Blind Channel but only 6% in Crescent Pond. The percentage of phytoplankton biomass in Saline Pond (5%) was less than that of SAA, indicating that in this site SAA could be of greater or equal importance to phytoplankton in the food web. Measurements of productivity are needed to determine whether phytoplankton is being turned over at a faster rate than SAA. Robinson *et al.* (1997b) found that the contribution by algae to total primary productivity was greater than 70% in Delta Marsh MERP cells and stated that this was an underestimate of their significance to the wetland food web because the turnover time for algal biomass is typically measured in days (Robinson *et al.* 1997b) as compared to months or years for macrophytes.

Phytoplankton biomass is strongly controlled at the time of invertebrate grazing. In contrast, in a wetland in the Interlake region of Manitoba, benthic grazing organisms consumed less than 15% of the epipelic production (Campeau *et al.* 1994). Chl *a* measurements from the top 0.5 cm of sediment are often used to calculate SAA biomass but this may lead to underestimates of the biomass available to grazers. In this case, only 35 to 60 % of the total biomass is taken into account (de Jonge & Colijn 1994). Grazers such as *Arenicola marina* and *Mya arenaria* are able to exploit the top 10 to 20 cm of the sediment (de Jonge & Colijn 1994). In this thesis, sediment cores were only sampled to a depth of 2.1 mm and sediment slurries were collected to a depth of 6.4 cm. Therefore, my SAA biomass measures may still be under estimates of what is available to benthic invertebrates.

5.3 Recommmendations

If I were to undertake a third sampling season or advise another researcher on a similar project I would suggest collecting all environmental variables measured in 1998 and 1999. This would increase the predictive power of regression models and reduce the unexplained variation. The frequency of sample collection may have to be decreased (monthly) to enable all environmental variables to be collected. Only sediment cores would be collected because they were found to be the best method for collecting SAA. Algal biovolume measurements would be calculated for each sediment core collected because it assures that chlorophyll measurements are in fact from algal species and would provide more detailed information. Chl *a* measurements would still be taken to compare to other freshwater wetlands.

More studies on SAA would be beneficial for future research on wetland production. Since a site difference was observed, the nature of food web support could be different in different parts of the marsh. Therefore, increasing the number of sample sites within the Delta Marsh by extending sampling east of the Portage Diversion would be valuable. The number of sample sites within a pond could be reduced because no variability was observed within the ponds. Also, there are other variables that I would recommend measuring which include sand, silt, clay and cation concentrations (Ca and Fe) in the sediment. The proportion of silt or clay may be higher in Saline Pond which may influence which if any algal taxa migrate to the sediment surface. Sediment cation concentrations in Saline Pond could be useful to explain the low phosphorus concentration. It would be instructive to measure epiphytic algae so that all algal assemblages were measured and the relative percentages of algal assemblages under different environmental variables throughout the marsh could be determined. Productivity measurements of SAA should also be measured to see how the rate of turnover differs from that of phytoplankton to assess their relative importance in the wetland food web. In terms

of wetland management, a long term study needs to be done on the effect of carp and reduced macrophyte abundance in Delta Marsh, in particular their effect on SAA abundance.

6. CONCLUSIONS

SAA (epipelon + plocon) is more abundant in freshwater wetlands than previously thought. The sampling method used to quantify its abundance had a significant effect on the results. The lens tissue trapping technique (Eaton & Moss 1966) was appropriate for sampling the motile component of sediment algae (epipelon) but it grossly underestimated the non-motile algae inhabiting the marsh sediments (SAA). A standard method for collecting SAA is needed so comparisons can be made between freshwater wetlands, lakes and estuaries. I believe that collection of an intact sediment core for SAA measurements is the best method to date and it should become the standard for future studies.

A combination of biological, physical and chemical factors affected SAA chlorophyll. In 1998, the major environmental variables that explained 47% of the variation in SAA chlorophyll were water column alkalinity, time of sample collection, and sediment water content. In 1999, sediment conductivity, turbidity, sediment phosphorus, light and phytoplankton chlorophyll collectively explained 54% of the variation in SAA chlorophyll. Much variation remained unexplained but if all variables in 1998 or 1999 datasets were measured simultaneously the amount of variation could be reduced. Contrary to my hypotheses, water depth did not affect SAA abundance. SAA chlorophyll did not decrease with increasing macrophyte abundance although I suspect that the species of macrophyte (shape and form) did affect the quantity of SAA chlorophyll. High sediment and sediment pore-water nutrient concentration did not determine the magnitude of SAA abundance.

The percentage of SAA biomass of total algal and macrophytes biomass differed spatially within the marsh. In Saline Pond, SAA made up a slightly larger percentage of algal biomass than phytoplankton indicating that SAA could be of greater or equal importance in the wetland food web. As macrophyte abundance decreases in Delta Marsh, phytoplankton and SAA could become more important food sources for benthic and planktonic herbivores.

7. LITERATURE CITED

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Appendix

ANOVA Tables 1998

Dependent variable on " Site"	n	df	F ratio	P value
Lens tissue	117	2	15.71	0.001
Sediment core	107	2	25.63	0.001
Slurry before	118	2	62.54	0.001
Slurry after	122	2	66.06	0.001
% WAT	66	2	130.83	0.001
% OM	66	2	268.14	0.001
% CARB	66	2	43.91	0.001
Water depth	123	2	40.27	0.001
Phytoplankton	117	2	27.05	0.001
Alkalinity	125	2	388.24	0.001
Nitrate	33	2	2.718	0.082
SRP	125	2	21.66	0.001
Silica	112	2	0.525	0.593
Conductivity	85	2	729.76	0.001

Biovolume by different methods on "Site"	n	df	F ratio	P value
Lens 10 am	9	2	1.169	0.373
Lens 2 pm	9	2	1.382	0.321
Lens 7 pm	9	2	6.167	0.035
Slurry before	9	2	7.124	0.026
Slurry after	9	2	4.940	0.054
Sediment core	9	2	0.928	0.446
Lens total	9	2	4.963	0.053

	n	df	F ratio	P value
"Method" on Chl a	764	6	139.42	0.001
"Method" on Biovolume	54	5	14.75	0.001
"Site" on Chl a	764	2	23.75	0.001
"Site" on Biovolume	54	2	11.29	0.001

Repeated measures	n	df	F ratio	P value
"Site"	9	2	24.165	0.001
"Method"	9	3	156.68	0.001
Interaction "Site" x " Method"	9	6	2.364	0.050

ANOVA Tables 1999

Dependent variable on " Site"	n	df	F ratio	P value
Insitu slurry before	103	2	29.69	0.001
Insitu slurry after	102	2	42.12	0.001
Lens paper (*Insitu*)	98	2	8.58	0.004
Core slurry before	89	2	13.86	0.001
Core slurry after	88	2	22.14	0.001
Lens paper (core)	86	2	2.029	0.138
Core	93	2	22.38	0.001
Phytoplantkon	100	2	25.32	0.001
Macrophytes	43	2	1.028	0.367
Water depth	105	2	37.27	0.001
Light	77	2	6.148	0.003
Turbidity	102	2	42.21	0.001
Conductivity	95	2	38.47	0.001
Sediment phosphorus	95	2	202.09	0.001

	n	df	F ratio	P value
"Method" on Chl a	608	6	284.49	0.001
"Site" on Chl a	608	2	113.37	0.001

Repeated measures	n	df	F ratio	P value
"Site"	8	2	65.25	0.000
"Method"	8	6	127.45	0.000
Interaction "Site" x " Method"	8	12	2.391	0.031

Vertical profiles	n	df	F ratio	P value
Blind Channel	9	2	2.034	0.212
Crescent Pond	9	2	1.116	0.387
Saline Pond	9	2	4.314	0.069

Sediment chemistry	n	df	F ratio	P value
C:P (July)	9	2	2.56	0.157
N:P (July)	9	2	18.74	0.003
C:N (July)	9	2	47.88	0.001
C:Chla (July)	9	2	7.78	0.022
C:P (August)	9	2	2.55	0.158
N:P (August)	9	2	49.94	0.001
C:N (August)	9	2	14.95	0.005
C:Chla (August)	9	2	5.55	0.043

Plocon (n=89)	λ	df	F ratio	P value
PAR	0.9905	1	0.658	0.437
1 day lag	0.999	1	0.078	0.781
2 day lag	0.916	1	6.717	0.015
3 day lag	0.939	1	4.279	0.043
4 day lag	0.970	1	1.99	0.163
Cumulative PAR	0.934	1	4.70	0.034
Cumulative 1 day lag	0.924	1	5.479	0.022
Cumulative 2 day lag	0.917	1	6.075	0.016
Cumulative 3 day lag	0.925	1	5.368	0.024
Cumulative 4 day lag	0.932	1	4.727	0.033

Appendix: Genera present by site and by method of sample collection (A=before and B=after tissue trapping, C= Core).

	Blind Channel						Crescent Pond						Saline Pond					
	10am	2pm	7pm	A	B	C	10am	2pm	7pm	A	B	C	10am	2pm	7pm	A	B	C
Achnanthes		x		x	x			x						x	x	x	x	x
Amphora				x	x	x	x	x	x	x	x	x		x	x	x	x	x
Anabaena				x			x	x		x			x	x				
Caloneis	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x
Chroococus							x											
Cocconeis	x	x	x	x	x	x		x		x	x	x		x		x	x	x
Cymatopleura				x	x			x		x						x	x	x
Cymbella	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x
Desmidium																		x
Diatoma	x		x															
Epithemia	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Euglena	x	x				x	x	x		x	x	x	x	x	x	x		
Eunotia										x	x							
Fragelaria		x	x	x	x	x	x			x	x					x	x	x
Gomphonema	x			x	x	x	x	x		x	x	x	x	x			x	x
Gyrosigma	x	x	x	x	x	x	x	x		x			x	x	x	x	x	x
Lyngbya	x	x			x		x	x	x	x	x		x				x	x
Merismopedia										x	x	x						
Mougeotia	x		x	x	x			x	x	x	x	x	x	x		x	x	
Navicula (la)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Navicula (sm)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Nitzschia	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Oscillatoria								x				x	x					
Pediastrum		x		x	x	x	x	x		x	x	x						

	Blind Channel						Crescent Pond						Saline Pond					
	10am	2pm	7pm	A	B	C	10am	2pm	7pm	A	B	C	10am	2pm	7pm	A	B	C
Pinnularia		x	x	x	x	x		x		x	x			x		x	x	x
Rhopolodia	x	x		x	x	x	x	x			x		x	x	x	x	x	x
Scenedesmus				x	x	x	x		x	x	x	x	x	x	x	x	x	x
Spirulina				x	x	x	x	x	x	x		x	x			x		x
Staurastrum		x	x	x	x		x			x								
Stephanodiscus		x		x	x						x					x	x	x
Surirella				x	x	x				x				x	x	x	x	
Synedra				x	x	x										x	x	

Multiple Regression
Blind Channel 1998

SYSTAT Rectangular file C:\Bourne\Statistics\1998\BC MR 98.syd,

CORE	WAT	OM	CARB	DEPTH	PHYTO
ALK	SRP	SILICA	COND	WEEK	

24 case(s) deleted due to missing data.
Step # 0 R = 0.000 R-Square = 0.000

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In							
1 Constant							
Out	Part. Corr.						
2 WAT	0.557	.	.	1.00000	1	7.186	0.016
3 OM	0.368	.	.	1.00000	1	2.501	0.133
4 CARB	0.372	.	.	1.00000	1	2.567	0.129
5 DEPTH	0.404	.	.	1.00000	1	3.113	0.097
6 PHYTO	-0.154	.	.	1.00000	1	0.389	0.541
7 ALK	0.175	.	.	1.00000	1	0.507	0.487
8 SRP	0.381	.	.	1.00000	1	2.718	0.119
9 SILICA	-0.180	.	.	1.00000	1	0.534	0.476
10 COND	-0.250	.	.	1.00000	1	1.070	0.316
11 WEEK	-0.482	.	.	1.00000	1	4.833	0.043

Dependent Variable CORE
Minimum tolerance for entry into model = 0.001000
Forward stepwise with Alpha-to-Enter=0.150 and Alpha-to-Remove=0.150

Step # 1 R = 0.557 R-Square = 0.310
Term entered: WAT

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In							
1 Constant							
2 WAT	6.678	2.491	0.557	1.00000	1	7.186	0.016
Out	Part. Corr.						
3 OM	0.053	.	.	0.64319	1	0.042	0.841
4 CARB	0.498	.	.	0.99461	1	4.950	0.042
5 DEPTH	0.539	.	.	0.99411	1	6.138	0.026
6 PHYTO	-0.411	.	.	0.90565	1	3.054	0.101
7 ALK	0.135	.	.	0.98673	1	0.277	0.606
8 SRP	0.409	.	.	0.99429	1	3.018	0.103
9 SILICA	-0.150	.	.	0.99002	1	0.346	0.565
10 COND	-0.432	.	.	0.96609	1	3.444	0.083
11 WEEK	-0.682	.	.	0.97971	1	13.059	0.003

Step # 2 R = 0.794 R-Square = 0.631
Term entered: WEEK

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In							

1	Constant							
2	WAT	7.656	1.901	0.638	0.97971	1	16.228	0.001
11	WEEK	-0.063	0.017	-0.573	0.97971	1	13.059	0.003
Out		Part. Corr.						
3	OM	0.345	.	.	0.59368	1	1.886	0.191
4	CARB	0.063	.	.	0.53341	1	0.055	0.818
5	DEPTH	0.531	.	.	0.93824	1	5.496	0.034
6	PHYTO	-0.207	.	.	0.76081	1	0.624	0.443
7	ALK	0.246	.	.	0.98253	1	0.899	0.359
8	SRP	0.339	.	.	0.93321	1	1.818	0.199
9	SILICA	-0.140	.	.	0.98517	1	0.281	0.604
10	COND	0.228	.	.	0.37136	1	0.764	0.397

Step # 3 R = 0.857 R-Square = 0.735
Term entered: DEPTH

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In							
1 Constant							
2 WAT	7.827	1.669	0.652	0.97784	1	22.002	0.000
5 DEPTH	0.005	0.002	0.333	0.93824	1	5.496	0.034
11 WEEK	-0.054	0.016	-0.493	0.92465	1	11.879	0.004
Out	Part. Corr.						
3 OM	0.248	.	.	0.55133	1	0.854	0.372
4 CARB	0.074	.	.	0.53341	1	0.072	0.792
6 PHYTO	-0.265	.	.	0.75998	1	0.979	0.341
7 ALK	-0.055	.	.	0.69976	1	0.039	0.846
8 SRP	0.236	.	.	0.86182	1	0.767	0.397
9 SILICA	-0.185	.	.	0.98422	1	0.461	0.509
10 COND	0.139	.	.	0.35464	1	0.255	0.622

Multiple Regression
Crescent Pond 1998

SYSTAT Rectangular file C:\Bourne\Statistics\1998\CP MR 98.syd,

CORE	WAT	OM	CARB	DEPTH	PHYTO
ALK	SRP	SILICA	COND	WEEK	

26 case(s) deleted due to missing data.
Step # 0 R = 0.000 R-Square = 0.000

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In							
1 Constant							
Out	Part. Corr.						
2 WAT	-0.093	.	.	1.00000	1	0.114	0.741
3 OM	-0.195	.	.	1.00000	1	0.513	0.486
4 CARB	0.160	.	.	1.00000	1	0.340	0.570
5 DEPTH	-0.108	.	.	1.00000	1	0.155	0.701
6 PHYTO	0.052	.	.	1.00000	1	0.035	0.855
7 ALK	0.091	.	.	1.00000	1	0.110	0.746
8 SRP	0.135	.	.	1.00000	1	0.241	0.632
9 SILICA	0.218	.	.	1.00000	1	0.649	0.435
10 COND	-0.190	.	.	1.00000	1	0.490	0.496
11 WEEK	-0.075	.	.	1.00000	1	0.074	0.790

Dependent Variable CORE
Minimum tolerance for entry into model = 0.001000
Forward stepwise with Alpha-to-Enter=0.150 and Alpha-to-Remove=0.150

Nothing to do!

Multiple Regression
Saline Pond 1998

SYSTAT Rectangular file C:\Bourne\Statistics\1998\SP MR 98.syd,

CORE	WAT	OM	CARB	DEPTH	PHYTO
ALK	SRP	SILICA	COND	WEEK	

15 case(s) deleted due to missing data.
Step # 0 R = 0.000 R-Square = 0.000

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In							
1 Constant							
Out	Part. Corr.						
2 WAT	0.082	.	.	1.00000	1	0.107	0.748
3 OM	0.126	.	.	1.00000	1	0.260	0.617
4 CARB	0.163	.	.	1.00000	1	0.438	0.517
5 DEPTH	-0.084	.	.	1.00000	1	0.113	0.741
6 PHYTO	-0.355	.	.	1.00000	1	2.309	0.148
7 ALK	-0.317	.	.	1.00000	1	1.783	0.200
8 SRP	-0.130	.	.	1.00000	1	0.275	0.607
9 SILICA	0.120	.	.	1.00000	1	0.235	0.634
10 COND	-0.217	.	.	1.00000	1	0.789	0.388
11 WEEK	-0.148	.	.	1.00000	1	0.356	0.559

Dependent Variable CORE
Minimum tolerance for entry into model = 0.001000
Forward stepwise with Alpha-to-Enter=0.150 and Alpha-to-Remove=0.150

Step # 1 R = 0.355 R-Square = 0.126
Term entered: PHYTO

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In							
1 Constant							
6 PHYTO	-0.218	0.144	-0.355	1.00000	1	2.309	0.148
Out	Part. Corr.						
2 WAT	0.018	.	.	0.96649	1	0.005	0.945
3 OM	0.288	.	.	0.87470	1	1.360	0.262
4 CARB	0.018	.	.	0.82563	1	0.005	0.946
5 DEPTH	-0.086	.	.	0.99993	1	0.113	0.742
7 ALK	-0.217	.	.	0.87161	1	0.741	0.403
8 SRP	-0.180	.	.	0.98871	1	0.504	0.488
9 SILICA	0.183	.	.	0.98102	1	0.519	0.482
10 COND	-0.381	.	.	0.88746	1	2.553	0.131
11 WEEK	-0.163	.	.	0.99985	1	0.407	0.533

Step # 2 R = 0.503 R-Square = 0.253
Term entered: COND

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In							

1	Constant							
6	PHYTO	-0.296	0.145	-0.482	0.88746	1	4.143	0.060
10	COND	-4.356	2.726	-0.378	0.88746	1	2.553	0.131

Out		Part. Corr.						
2	WAT	0.069	.	.	0.95298	1	0.067	0.800
3	OM	0.264	.	.	0.86221	1	1.053	0.322
4	CARB	-0.036	.	.	0.81110	1	0.018	0.895
5	DEPTH	-0.279	.	.	0.84424	1	1.181	0.296
7	ALK	-0.092	.	.	0.75854	1	0.120	0.734
8	SRP	-0.342	.	.	0.89120	1	1.854	0.195
9	SILICA	0.134	.	.	0.95598	1	0.255	0.622
11	WEEK	0.118	.	.	0.58397	1	0.198	0.663

Multiple Regression
All sites 1998

SYSTAT Rectangular file C:\Bourne\Statistics\1998\All MR 98.SYD,

CORE	WAT	OM	CARB	DEPTH	PHYTO
ALK	SRP	SILICA	COND	WEEK	

42 case(s) deleted due to missing data.
Step # 0 R = 0.000 R-Square = 0.000

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'p'
In							
1 Constant							
Out	Part. Corr.						
2 WAT	-0.359	.	.	1.00000	1	7.240	0.010
3 OM	-0.444	.	.	1.00000	1	12.060	0.001
4 CARB	0.519	.	.	1.00000	1	18.047	0.000
5 DEPTH	-0.261	.	.	1.00000	1	3.580	0.064
6 PHYTO	-0.408	.	.	1.00000	1	9.808	0.003
7 ALK	0.456	.	.	1.00000	1	12.867	0.001
8 SRP	-0.216	.	.	1.00000	1	2.404	0.127
9 SILICA	0.182	.	.	1.00000	1	1.685	0.200
10 COND	0.337	.	.	1.00000	1	6.294	0.015
11 WEEK	-0.499	.	.	1.00000	1	16.223	0.000

Dependent Variable CORE
Minimum tolerance for entry into model = 0.001000
Forward stepwise with Alpha-to-Enter=0.150 and Alpha-to-Remove=0.150

Step # 1 R = 0.519 R-Square = 0.269
Term entered: CARB

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'p'
In							
1 Constant							
4 CARB	1.064	0.250	0.519	1.00000	1	18.047	0.000
Out	Part. Corr.						
2 WAT	0.033	.	.	0.46932	1	0.051	0.822
3 OM	-0.034	.	.	0.31915	1	0.055	0.816
5 DEPTH	-0.034	.	.	0.79508	1	0.056	0.814
6 PHYTO	-0.312	.	.	0.91233	1	5.177	0.027
7 ALK	0.192	.	.	0.59810	1	1.843	0.181
8 SRP	-0.097	.	.	0.93092	1	0.455	0.503
9 SILICA	0.128	.	.	0.97979	1	0.803	0.375
10 COND	0.029	.	.	0.62519	1	0.041	0.840
11 WEEK	-0.327	.	.	0.75834	1	5.760	0.020

Step # 2 R = 0.589 R-Square = 0.347
Term entered: WEEK

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'p'
In							

1	Constant							
4	CARB	0.740	0.275	0.361	0.75834	1	7.263	0.010
11	WEEK	-0.043	0.018	-0.321	0.75834	1	5.760	0.020

Out		Part. Corr.						
2	WAT	-0.025	.	.	0.45566	1	0.029	0.865
3	OM	-0.117	.	.	0.30300	1	0.649	0.425
5	DEPTH	-0.199	.	.	0.65643	1	1.939	0.170
6	PHYTO	-0.212	.	.	0.77433	1	2.216	0.143
7	ALK	0.307	.	.	0.55527	1	4.906	0.032
8	SRP	-0.103	.	.	0.93092	1	0.500	0.483
9	SILICA	0.150	.	.	0.97825	1	1.076	0.305
10	COND	0.216	.	.	0.49105	1	2.300	0.136

Step # 3 R = 0.640 R-Square = 0.409
Term entered: ALK

Effect		Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In								
1	Constant							
4	CARB	0.227	0.351	0.111	0.42849	1	0.417	0.522
7	ALK	1.192	0.538	0.333	0.55527	1	4.906	0.032
11	WEEK	-0.053	0.018	-0.401	0.70404	1	8.985	0.004

Out		Part. Corr.						
2	WAT	0.292	.	.	0.22345	1	4.288	0.044
3	OM	0.179	.	.	0.13368	1	1.522	0.224
5	DEPTH	0.007	.	.	0.36736	1	0.002	0.962
6	PHYTO	-0.166	.	.	0.74769	1	1.302	0.260
8	SRP	-0.015	.	.	0.85314	1	0.010	0.919
9	SILICA	0.124	.	.	0.96732	1	0.716	0.402
10	COND	-0.096	.	.	0.13109	1	0.429	0.516

Step # 4 R = 0.636 R-Square = 0.404
Term removed: CARB

Effect		Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In								
1	Constant							
7	ALK	1.422	0.402	0.397	0.98273	1	12.495	0.001
11	WEEK	-0.059	0.015	-0.447	0.98273	1	15.776	0.000

Out		Part. Corr.						
2	WAT	0.230	.	.	0.26435	1	2.635	0.111
3	OM	0.074	.	.	0.23335	1	0.256	0.615
4	CARB	0.094	.	.	0.42849	1	0.417	0.522
5	DEPTH	-0.005	.	.	0.37365	1	0.001	0.971
6	PHYTO	-0.159	.	.	0.75030	1	1.225	0.274
8	SRP	-0.014	.	.	0.85328	1	0.009	0.925
9	SILICA	0.127	.	.	0.96881	1	0.768	0.385
10	COND	-0.055	.	.	0.15080	1	0.144	0.706

Step # 5 R = 0.660 R-Square = 0.436
Term entered: WAT

Effect		Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In								
1	Constant							

2	WAT	1.669	1.028	0.346	0.26435	1	2.635	0.111
7	ALK	2.444	0.744	0.683	0.27805	1	10.802	0.002
11	WEEK	-0.066	0.015	-0.498	0.90890	1	18.743	0.000

Out		Part. Corr.						
3	OM	-0.102	.	.	0.13574	1	0.481	0.492
4	CARB	0.206	.	.	0.36219	1	2.041	0.160
5	DEPTH	0.023	.	.	0.36821	1	0.025	0.875
6	PHYTO	-0.145	.	.	0.74535	1	0.988	0.325
8	SRP	0.007	.	.	0.84634	1	0.002	0.961
9	SILICA	0.180	.	.	0.93177	1	1.542	0.221
10	COND	0.041	.	.	0.12680	1	0.078	0.782

Multiple Regression
Blind Channel 1999

SYSTAT Rectangular file C:\Bourne\Statistics\1999\BC MR 99.syd,
created Mon Mar 06, 2000 at 16:22:56, contains variables:

CORE PHYTO MACRO DEPTH LIGHT TURB
COND SEDP WEEK

8 case(s) deleted due to missing data.
Step # 0 R = 0.000 R-Square = 0.000

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In							
1 Constant							
Out	Part. Corr.						
2 PHYTO	-0.011	.	.	1.00000	1	0.002	0.963
3 MACRO	0.152	.	.	1.00000	1	0.427	0.521
4 DEPTH	-0.537	.	.	1.00000	1	7.290	0.015
5 LIGHT	0.282	.	.	1.00000	1	1.555	0.228
6 TURB	-0.011	.	.	1.00000	1	0.002	0.962
7 COND	0.579	.	.	1.00000	1	9.074	0.007
8 SEDP	-0.501	.	.	1.00000	1	6.034	0.024
9 WEEK	0.525	.	.	1.00000	1	6.860	0.017

Dependent Variable CORE
Minimum tolerance for entry into model = 0.001000
Forward stepwise with Alpha-to-Enter=0.150 and Alpha-to-Remove=0.150

Step # 1 R = 0.579 R-Square = 0.335
Term entered: COND

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In							
1 Constant							
7 COND	1.459	0.484	0.579	1.00000	1	9.074	0.007
Out	Part. Corr.						
2 PHYTO	-0.061	.	.	0.99551	1	0.064	0.803
3 MACRO	-0.176	.	.	0.76883	1	0.545	0.470
4 DEPTH	-0.395	.	.	0.82053	1	3.140	0.094
5 LIGHT	0.234	.	.	0.97354	1	0.980	0.336
6 TURB	-0.144	.	.	0.96792	1	0.358	0.558
8 SEDP	-0.314	.	.	0.77295	1	1.862	0.190
9 WEEK	0.167	.	.	0.43400	1	0.488	0.494

Step # 2 R = 0.662 R-Square = 0.439
Term entered: DEPTH

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In							
1 Constant							
4 DEPTH	-0.008	0.005	-0.355	0.82053	1	3.140	0.094
7 COND	1.080	0.506	0.428	0.82053	1	4.561	0.048

Out		Part. Corr.						
2	PHYTO	0.082	.	.	0.88387	1	0.108	0.747
3	MACRO	-0.400	.	.	0.64327	1	3.041	0.100
5	LIGHT	0.207	.	.	0.96105	1	0.715	0.410
6	TURB	0.054	.	.	0.74947	1	0.048	0.830
8	SEDP	-0.218	.	.	0.69670	1	0.798	0.385
9	WEEK	0.158	.	.	0.43265	1	0.411	0.531

Step # 3 R = 0.727 R-Square = 0.528
Term entered: MACRO

Effect		Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In								
1	Constant							
3	MACRO	-0.120	0.069	-0.373	0.64327	1	3.041	0.100
4	DEPTH	-0.012	0.005	-0.501	0.68653	1	5.858	0.028
7	COND	1.376	0.507	0.546	0.72831	1	7.366	0.015

Out		Part. Corr.						
2	PHYTO	-0.150	.	.	0.66132	1	0.344	0.566
5	LIGHT	0.240	.	.	0.96007	1	0.914	0.354
6	TURB	-0.138	.	.	0.61566	1	0.290	0.598
8	SEDP	-0.280	.	.	0.69057	1	1.275	0.277
9	WEEK	0.138	.	.	0.42981	1	0.290	0.598

Multiple Regression
Crescent Pond 1999

SYSTAT Rectangular file C:\Bourne\Statistics\1999\CP MR 99.syd,
created Mon Mar 06, 2000 at 17:17:58, contains variables:

CORE PHYTO MACRO DEPTH LIGHT TURB
COND SEDP WEEK

12 case(s) deleted due to missing data.
Step # 0 R = 0.000 R-Square = 0.000

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In							
1 Constant							
Out	Part. Corr.						
2 PHYTO	0.031	.	.	1.00000	1	0.022	0.885
3 MACRO	0.293	.	.	1.00000	1	2.073	0.164
4 DEPTH	0.149	.	.	1.00000	1	0.498	0.488
5 LIGHT	0.476	.	.	1.00000	1	6.438	0.019
6 TURB	-0.216	.	.	1.00000	1	1.075	0.311
7 COND	0.121	.	.	1.00000	1	0.328	0.573
8 SEDP	0.027	.	.	1.00000	1	0.016	0.900
9 WEEK	0.118	.	.	1.00000	1	0.311	0.583

Dependent Variable CORE
Minimum tolerance for entry into model = 0.001000
Forward stepwise with Alpha-to-Enter=0.150 and Alpha-to-Remove=0.150

Step # 1 R = 0.476 R-Square = 0.226
Term entered: LIGHT

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In							
1 Constant							
5 LIGHT	0.350	0.138	0.476	1.00000	1	6.438	0.019
Out	Part. Corr.						
2 PHYTO	0.141	.	.	0.96365	1	0.428	0.520
3 MACRO	0.170	.	.	0.89868	1	0.627	0.437
4 DEPTH	0.185	.	.	0.99915	1	0.744	0.398
6 TURB	-0.110	.	.	0.93348	1	0.255	0.619
7 COND	0.112	.	.	0.99769	1	0.266	0.611
8 SEDP	0.002	.	.	0.99722	1	0.000	0.991
9 WEEK	0.084	.	.	0.99137	1	0.151	0.702

Multiple Regression
Saline Pond 1999

SYSTAT Rectangular file C:\Bourne\Statistics\1999\SP MR 99.syd,
created Tue Mar 07, 2000 at 16:41:16, contains variables:

CORE PHYTO MACRO DEPTH LIGHT TURB
COND SEDP WEEK

11 case(s) deleted due to missing data.
Step # 0 R = 0.000 R-Square = 0.000

Effect		Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In								
1	Constant							
Out		Part. Corr.						
2	PHYTO	-0.176	.	.	1.00000	1	0.514	0.484
3	MACRO	0.288	.	.	1.00000	1	1.450	0.246
4	DEPTH	-0.155	.	.	1.00000	1	0.395	0.538
5	LIGHT	0.480	.	.	1.00000	1	4.782	0.044
6	TURB	-0.570	.	.	1.00000	1	7.695	0.014
7	COND	-0.115	.	.	1.00000	1	0.215	0.649
8	SEDP	0.182	.	.	1.00000	1	0.545	0.471
9	WEEK	0.363	.	.	1.00000	1	2.431	0.139

Dependent Variable CORE
Minimum tolerance for entry into model = 0.001000
Forward stepwise with Alpha-to-Enter=0.150 and Alpha-to-Remove=0.150

Step # 1 R = 0.570 R-Square = 0.325
Term entered: TURB

Effect		Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In								
1	Constant							
6	TURB	-0.673	0.243	-0.570	1.00000	1	7.695	0.014
Out		Part. Corr.						
2	PHYTO	0.225	.	.	0.66921	1	0.801	0.385
3	MACRO	-0.054	.	.	0.67514	1	0.044	0.837
4	DEPTH	0.324	.	.	0.59795	1	1.763	0.204
5	LIGHT	0.195	.	.	0.61346	1	0.592	0.454
7	COND	-0.043	.	.	0.98037	1	0.028	0.869
8	SEDP	0.194	.	.	0.99849	1	0.588	0.455
9	WEEK	-0.004	.	.	0.58778	1	0.000	0.987

Multiple Regression
All sites 1999

SYSTAT Rectangular file C:\Bourne\Statistics\1999\All MR 99.SYD,
created Sun Mar 12, 2000 at 16:34:34, contains variables:

CORE PHYTO MACRO DEPTH LIGHT TURB
COND SEDP WEEK

31 case(s) deleted due to missing data.
Step # 0 R = 0.000 R-Square = 0.000

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In							
1 Constant							
Out	Part. Corr.						
2 PHYTO	-0.417	.	.	1.00000	1	12.596	0.001
3 MACRO	0.322	.	.	1.00000	1	6.949	0.011
4 DEPTH	-0.384	.	.	1.00000	1	10.349	0.002
5 LIGHT	0.398	.	.	1.00000	1	11.314	0.001
6 TURB	-0.392	.	.	1.00000	1	10.868	0.002
7 COND	0.499	.	.	1.00000	1	19.914	0.000
8 SEDP	-0.234	.	.	1.00000	1	3.477	0.067
9 WEEK	0.119	.	.	1.00000	1	0.857	0.358

Dependent Variable CORE
Minimum tolerance for entry into model = 0.001000
Forward stepwise with Alpha-to-Enter=0.150 and Alpha-to-Remove=0.150

Step # 1 R = 0.499 R-Square = 0.249
Term entered: COND

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In							
1 Constant							
7 COND	1.371	0.307	0.499	1.00000	1	19.914	0.000
Out	Part. Corr.						
2 PHYTO	-0.346	.	.	0.93604	1	8.038	0.006
3 MACRO	0.198	.	.	0.89766	1	2.405	0.126
4 DEPTH	-0.139	.	.	0.67543	1	1.166	0.285
5 LIGHT	0.390	.	.	0.98403	1	10.584	0.002
6 TURB	-0.481	.	.	0.99751	1	17.785	0.000
8 SEDP	-0.011	.	.	0.79651	1	0.008	0.930
9 WEEK	-0.035	.	.	0.91234	1	0.073	0.788

Step # 2 R = 0.650 R-Square = 0.423
Term entered: TURB

Effect	Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In							
1 Constant							
6 TURB	-0.409	0.097	-0.418	0.99751	1	17.785	0.000
7 COND	1.428	0.272	0.520	0.99751	1	27.586	0.000

Out		Part. Corr.						
2	PHYTO	-0.037	.	.	0.51735	1	0.081	0.776
3	MACRO	-0.006	.	.	0.73826	1	0.002	0.963
4	DEPTH	-0.204	.	.	0.67105	1	2.511	0.118
5	LIGHT	0.275	.	.	0.87134	1	4.759	0.033
8	SEDP	-0.364	.	.	0.56801	1	8.840	0.004
9	WEEK	0.018	.	.	0.90199	1	0.020	0.888

Step # 3 R = 0.707 R-Square = 0.499
Term entered: SEDP

Effect		Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In								
1	Constant							
6	TURB	-0.580	0.108	-0.593	0.71135	1	28.977	0.000
7	COND	0.998	0.293	0.363	0.75538	1	11.559	0.001
8	SEDP	-0.576	0.194	-0.367	0.56801	1	8.840	0.004

Out		Part. Corr.						
2	PHYTO	0.177	.	.	0.39015	1	1.835	0.181
3	MACRO	0.007	.	.	0.73732	1	0.003	0.956
4	DEPTH	0.022	.	.	0.42490	1	0.028	0.867
5	LIGHT	0.219	.	.	0.83383	1	2.882	0.095
9	WEEK	0.099	.	.	0.86668	1	0.565	0.455

Step # 4 R = 0.724 R-Square = 0.523
Term entered: LIGHT

Effect		Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In								
1	Constant							
5	LIGHT	0.123	0.072	0.170	0.83383	1	2.882	0.095
6	TURB	-0.504	0.115	-0.515	0.60293	1	19.122	0.000
7	COND	0.982	0.289	0.358	0.75462	1	11.554	0.001
8	SEDP	-0.508	0.195	-0.323	0.54356	1	6.776	0.012

Out		Part. Corr.						
2	PHYTO	0.196	.	.	0.38861	1	2.227	0.141
3	MACRO	-0.063	.	.	0.67104	1	0.222	0.639
4	DEPTH	0.037	.	.	0.42321	1	0.077	0.782
9	WEEK	-0.014	.	.	0.64516	1	0.011	0.916

Step # 5 R = 0.736 R-Square = 0.542
Term entered: PHYTO

Effect		Coefficient	Std Error	Std Coef	Tol.	df	F	'P'
In								
1	Constant							
2	PHYTO	0.163	0.109	0.217	0.38861	1	2.227	0.141
5	LIGHT	0.129	0.072	0.179	0.83053	1	3.263	0.076
6	TURB	-0.685	0.166	-0.700	0.28265	1	16.923	0.000
7	COND	1.031	0.288	0.375	0.74499	1	12.831	0.001
8	SEDP	-0.665	0.220	-0.423	0.41852	1	9.147	0.004

Out		Part. Corr.						
3	MACRO	-0.053	.	.	0.66902	1	0.156	0.694

4 DEPTH	-0.009	.	.	0.40007	1	0.004	0.947
9 WEEK	-0.020	.	.	0.64464	1	0.022	0.882