The significance of waterfowl feces as a source of nutrients to algae in a prairie wetland

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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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ABSTRACT

In situ enclosures in Delta Marsh, Canada were used to determine the responses of planktonic and benthic algae, and submersed macrophytes, to repeated additions of waterfowl feces from mallard ducks (*Anas platyrhynchos*) and Canada geese (*Branta canadensis*). Two types of feces loading were examined. In 1995, two feces pulses were added to duplicate enclosures, four weeks apart. The treatments were: 1) a high feces load (containing 2.421 g/ m^2N and 0.806 g/m^2P), 2) a low feces load (0.242 g/m^2N and 0.0806 g/m^2P), and 3) untreated controls. In 1996, eight weekly additions of waterfowl feces were added to triplicate enclosures, representing the same cumulative load as added to each high feces load enclosure in 1995. The treatments were: 1) high feces load (0.722 g/m^2 N and 0.240 g/m^2 P) and 2) untreated controls.

In the high feces load enclosures in both 1995 and 1996, total P, soluble reactive P and ammonia-N in the water column increased significantly after feces application. However, biomass, productivity and particulate P of algae (phytoplankton, epiphyton, metaphyton, and epipelon) did not respond significantly to nutrients released from the waterfowl feces, even when loading exceeded estimated natural values (488.9 g/m^2 versus 1.28 g/m^2 wet weight, respectively). These results contradict previous studies which showed that waterfowl do make substantial contributions to the nutrient requirements of wetland algae and macrophytes. I propose that at least three hypotheses may explain the mitigated response to waterfowl feces additions, as follows: 1) feces were deplete in N, relative to P, as compared to the ambient N:P ratio in Delta Marsh, suggesting that feces provided insufficient quantities of the growth-limiting resource; 2) fecal nutrients were not available for algal uptake because they were rapidly adsorbed in the sediments; 3) feces additions did stimulate algal production but the increase was immediately and entirely transferred to consumers so an increase in invertebrates with treatment concealed the algal response.

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1. INTRODUCTION

Wetlands comprise about 14% of Canadian land area. They are predominantly littoral-dominated ecosystems with more or less permanently waterlogged sediments (Goldsborough and Robinson 1996). Wetlands are viewed as nutrient sinks, where they reduce pollution by trapping P and other chemicals in their sediment (Kusler *et al.* 1994). The combination of wetland plants and microbes found in the wetland ecosystem is highly efficient at transforming nutrients, metals and other compounds (Richardson and Marshall 1986). Therefore, wetlands are often seen as buffer zones between aquatic and terrestrial systems, tools to be used to enhance water quality (Kadlec and Bevis 1990). Wetlands also provide habitat and food for large populations of breeding waterfowl (Murkin and Kadlec 1986; Leschisin *et al.* 1992). However, much of the land area once covered by wetlands has been drained for agriculture (Mitsch and Gosselink 1993) and it is no longer available for use by waterfowl. Therefore, those wetlands that do remain support large waterfowl populations and, as a result, they should theoretically serve as major sinks for nutrients associated with waterfowl (Parmenter and Lamarra 1991).

Waterfowl may influence the eutrophication of lakes either positively or negatively (Gere and Andrikovics 1992). If they feed in the water and excrete on land the eutrophication process is delayed. However, if they feed on land and excrete in the water, this increase in nutrient loading has the potential to quicken eutrophication. Therefore, the role waterfowl play in regulating plant communities is two-fold: they are viewed as consumers, removing macrophytes and invertebrates (Bazely and Jefferies 1989; Hanson and Butler 1990, 1994; Gere and Andrikovics 1992; Hargeby *et al.* 1994), and they are viewed as contributors, adding nutrients from their feces and decaying carcasses (Parmenter and Lamarra 1991; Gere and Andrikovics 1992; Manny *et al.* 1994).

To date, research has focused primarily on the effect that waterfowl have on lakes (Manny *et al.* 1994; Staicer *et al.* 1994) but their role in regulating plant communities in wetlands remains unresolved. Research previously conducted concerning waterfowl and wetlands

has concentrated on habitat selection and food habits of waterfowl (Murkin and Kadlec 1986; Leschisin *et al.* 1992); however, the impact of waterfowl on the trophic status of a wetland has yet to be resolved.

The primary producers of wetlands are stimulated by additions of inorganic nutrients (Campeau *et. al* 1994; Gabor *et. al.* 1994; Murkin *et. al.* 1994; McDougal *et al.* 1997). Wetlands are important habitats for waterfowl as they provide food, breeding and nesting sites (Murkin and Kadlec 1986; Batt *et. al.* 1989; Swanson and Duebbert 1989; Leschisin *et. al.* 1992; Merendino *et. al.* 1995). Inorganic N and P are released from waterfowl feces (Bazely and Jefferies 1985; Gere and Andrikovics 1992; Manny *et. al.* 1994; Marion *et. al.* 1994) but effects of these nutrients on the primary producers have not been examined in a wetland.

In this thesis, the response of algae and macrophytes to repeated waterfowl feces additions was determined using *in situ* littoral enclosures in Delta Marsh. I hypothesized, based on results of past nutrient enrichment experiments at this site, that additions of feces from mallard ducks (*Anas platyrhynchos*) and Canada geese (*Branta canadensis*), both of which are common visitors to prairie marshes, would result in a significant change in the quantity and productivity of the macrophyte and algal communities. I hypothesized that nutrients released by the decomposing feces would be assimilated by the plants, leading to increased primary productivity and biomass. I also hypothesized that the addition of feces would alter the composition of the algal assemblage, shifting the system from an epiphyte-dominated system to a phytoplankton-dominated one. I evaluated these hypotheses by monitoring vertical light extinction, water chemistry, algal photosynthesis (inorganic C assimilation rate), algal biomass (total chlorophyll), and macrophyte abundance. In order to assess whether the algal and macrophyte components benefited from nutrients liberated by the feces, I measured their P content following feces additions. I hypothesized that proportionate P content of algae should increase in enclosures receiving feces loading.

I tested two types of feces loading. In 1995 (year 1), two large pulses of waterfowl feces were added four weeks apart to simulate the nutrient input from a large, transient waterfowl flock. In 1996 (year 2), many smaller additions (press) of waterfowl feces were added at weekly intervals, representing the same cumulative load as in 1995 with the press intended to simulate the inputs from a resident flock. Despite these different input regimes, I did not attempt to approximate natural levels of loading; rather, additions were selected to represent approximately the same total P input to experimental enclosures as was added in prior experiments in Delta Marsh (McDougal *et al.* 1997).

2. LITERATURE REVIEW

2.1 Wetlands

Wetlands are dynamic parts of our landscape, each different from the next, each found in diverse physical regions, yet all with one characteristic in common: their fluctuating water levels (Kusler *et al.* 1994). Wetlands are unique ecosystems that adapt and thrive after "disastrous events" such as floods, hurricanes, fires and droughts (Moss 1988; Kusler *et al.* 1994). During a flood, a wetland acts as a temporary reservoir, minimizing the flood's damage by "spreading out the water" and, therefore, increasing the time it would take the flood to reach its maximum height (Moss 1988). On the other hand, a drought exposes the wetland bottom wherein a diverse seed bank exists allowing annuals and emergent species to flourish (van der Valk and Davis 1978; Poiani and Johnson 1989, 1993).

Wetlands provide a great variety of habitat and subsequently encourage large and diverse populations of birds, mammals, fish, reptiles and invertebrates to inhabit them (Moss 1988; Mitsch and Gosselink 1986; Murkin and Kadlec 1986; Leschisin *et al.* 1992; Kusler *et al.* 1994). The flora and fauna of wetlands are interdependent; therefore, any alteration of the habitat can have a ripple effect throughout the ecosystem. Timms and Moss (1984) observed that the loss of submerged plants in the Broadlands of Norfolk, U.K. lead to devastating reductions of organisms down the food chain. There was a reduction of habitat for invertebrates and the number of herbivorous birds that once populated the wetland decreased. As well, the density and diversity of fish declined because the absence of aquatic plants no longer provided them with a habitat suitable for spawning and a refuge from prey. Another example where variations in wetland habitat influenced the populations that live there was observed by Murkin and Kadlec (1986) in Delta Marsh, Manitoba. They determined that the presence of breeding waterfowl in the spring was positively correlated with macroinvertebrate densities. This suggests that invertebrate distribution and abundance are an important factor in habitat selection by waterfowl.

Wetlands are sometimes viewed as buffer zones, tools to enhance water quality. When a

wetland is encroached by agriculturally active land it is subject to excess nutrient loading from animal waste, fertilizers and pesticides applied to food and forage crops (Neely and Baker 1989). Therefore, their capacity to act as "large sponges" (Moss 1988), able to absorb nutrients and sediments, is one of great value. The combination of plants and microbes found in wetlands allows a high efficiency for modifying nutrients, metals and other compounds. For example, nitrogen, when in the form of nitrate (NO_3-N) can be removed from the water through denitrification by aerobic and anaerobic bacteria (Moss 1988; Kusler *et al.* 1994).

The total primary production of vascular plants in littoral-dominated systems, such as wetlands, is high (Brisson *et al.* 1981); however, one cannot discount the significant proportion that algae contribute (Hooper and Robinson 1976; Cattaneo and Kalff 1980; Robarts *et al.* 1995). Algae are a major component in wetlands providing a fundamental food source to higher trophic levels because of their size, availability, and nutritive value (Robarts *et al.* 1995; Goldsborough and Robinson 1996) while Campeau *et al.* (1994) suggests that vascular plant litter is a lower quality food source for invertebrates, serving primarily as a habitat and substratum for algal growth.

Crumpton (1989) noted that research on the role algae have in wetlands is limited. Research to this point has primarily concentrated on the role algae have in lakes, therefore a comparison between wetlands and shallow water lakes (lakes that are less than 2 m) should be made. Both aquatic systems share the same phenomenon of two stable states (Scheffer *et al.* 1993): a clear water state where aquatic vegetation (macrophytes) is dominant, and a turbid state where phytoplankton is dominant (Hosper and Jagtman 1990). Assuming there is a critical point between the two states and the mechanism that triggers one state over the other can be determined, the system can effectively be manipulated to the desired state. However, in order to manipulate the system, the mechanism which regulates one states over the other must be understood.

Hargeby *et al.* (1994) observed that a shift from a turbid water state to a clear water state

in a shallow eutrophic lake, Lake Krankesjon, Sweden resulted in the reappearance of breeding and migrating waterfowl. During the mid 1970s there was a decrease in waterfowl which coincided with the disappearance of submerged macrophytes; however, there were no limnological studies to explain this decline in vegetation. By the early 1980s the water became turbid and rich in phytoplankton, while submerged macrophytes and waterfowl remained scarce. In the mid 1980s vegetation expanded spatially, coinciding with an increase in waterfowl usage.

Vegetation enhances the clarity of the water, where the roots stabilize the substrata, reducing resuspension of the sediments (Dieter 1990). Macrophytes provide refuge to benthic macroinvertebrates such as snails and isopods from planktivores and they also tend to out compete phytoplankton for nutrients (Keough 1994). This decrease in phytoplankton results in a subsequent decrease in zooplankton, primarily Cladocera (Campeau *et al.* 1994). The changes that occurred in Lake Krankesjon were such that the populations of waterfowl were able to reestablish themselves.

2.2 Algae of wetlands

Based on the model of prairie marsh vegetation dynamics proposed by van der Valk and Davis (1978), Goldsborough and Robinson (1996) proposed a model for wetland development which predicts the relative abundance of four algal communities. These communities are (1) phytoplankton, algae entrained in the water column; (2) epiphyton, algae that is attached and growing on submersed vascular and non-vascular plants; (3) metaphyton, algae that originates as attached algae, but detaches to form floating and subsurface mats; and (4) epipelon, algae that inhabits soft sediments. Their model suggests that nutrient loading ("bottom-up control"), grazing pressure ("top-down control"), and water level fluctuations can effect the development of a wetland such that it will shift towards one out of four stable states where one of the four algal assemblages listed above will dominate (Fig. 1).

The lake marsh state is characterized by high water levels where emergent vegetation can not establish, a turbid water column and high nutrient levels which allow for phytoplankton

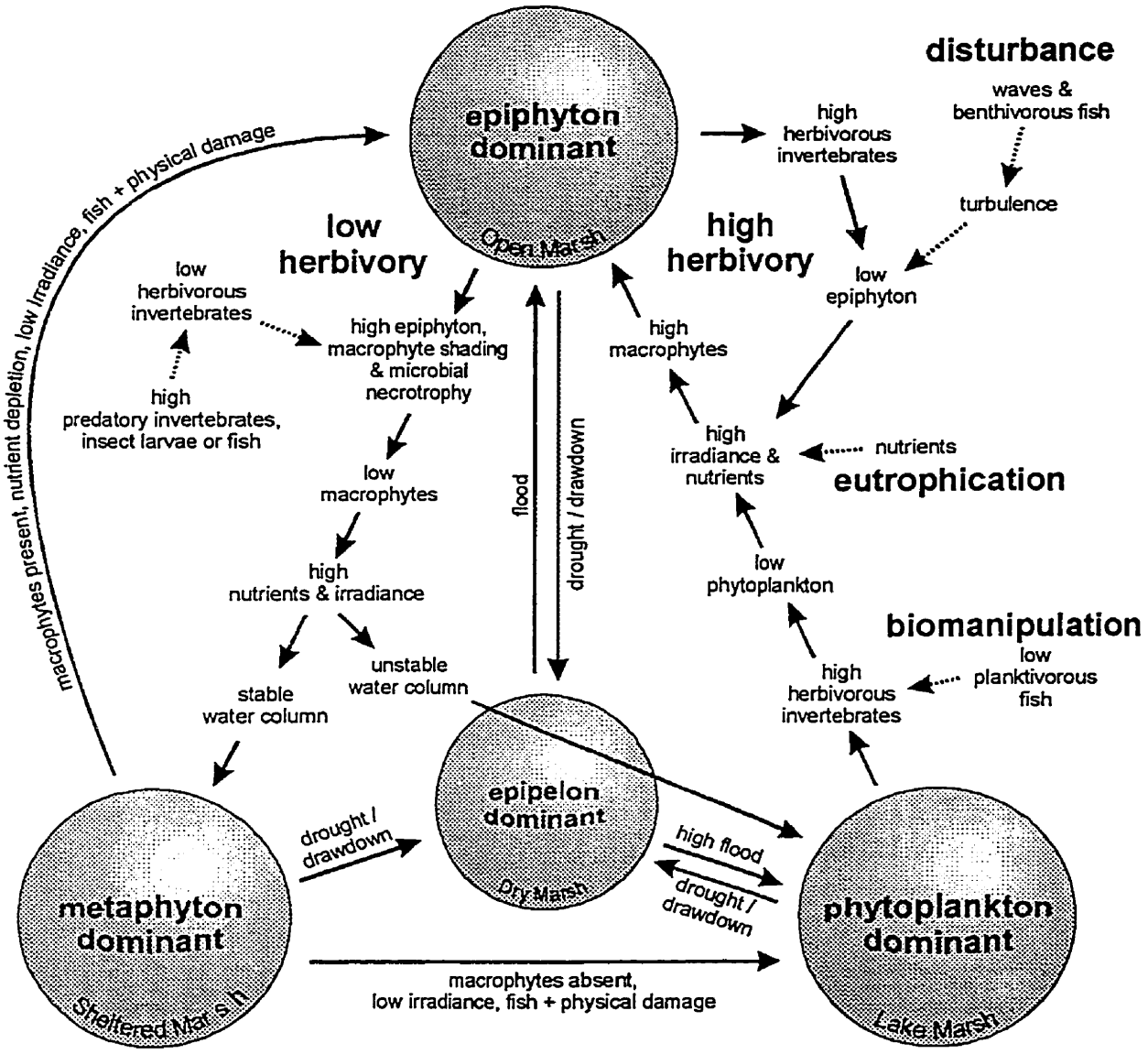

Figure 1. Conceptual diagram of the relative importance of four algal assemblages at various stages of wetland development (Goldsborough and Robinson 1996).

to dominate. Due to the turbidity of the lake marsh state, subsurface irradiance is low and insufficient to support the development of the other three algal communities. In the absence of macrophytes, whose roots normally stabilize the bottom, sediment resuspension occurs and substratum availability for epiphyton is minimal.

In periods that follow a drought where water levels remain at very low levels a dry marsh state is reached. In this state, the loss of aquatic plants and the subsequent increase in irradiance of the sediment surface stimulates production by epipelic algae. The open marsh state is reached when the water level of the dry marsh increases and aquatic macrophytes develop or when top-down pressures exerted by herbivorous invertebrates on the phytoplankton-dominated lake marsh state become too great. In the open marsh state epiphyton dominates due to the presence of macrophytes which provide colonizable surfaces for them. However, this combined presence of macrophytes and epiphytes shades the sediments thereby reducing the abundance of epipelon. Phytoplankton is out-competed for nutrients by the abundance of other primary producers. Disturbances such as wind and benthivorous fish (carp) and high herbivory maintain epiphyton biomass at levels which do not hinder macrophyte growth, for without these natural disturbances epiphyton would shade the macrophytes leading to their decline (Goldsborough and Robinson 1996). Without the presence of macrophytes the system would shift back to the lake marsh state and phytoplankton would dominate.

In the absence of wind action, epiphyton grows profusely such that it detaches from the surface of macrophytes and forms large metaphyton mats, shifting the wetland into the sheltered marsh state. These metaphyton mats that develop shade the macrophytes and epiphyton thereby altering the dominant algal community.

2.3 Effects of nutrient enrichment on primary production

The life forms in an aquatic ecosystem are linked together through predator-prey relationships in a food chain. Food chains follow the same general pattern where nutrients supply phytoplankton which in turn are ingested by zooplankton which are consumed by planktivores and or larger invertebrates which are then eaten by piscivores (Reynolds 1994).

Within one ecosystem there may be over a hundred food chains integrated into a complex pattern called a food web. To examine the "big picture" one must consider the combined effects of both cascading trophic interactions (top-down) and nutrient loading (bottom-up) for the management of water quality. It is the nutrient availability found at each trophic level that predetermines the potential productivity of an ecosystem but, as well, it is the top-down forces that, in the end, regulate the actual productivity of that system (Gutierrez *et al.* 1994; Reynolds 1994; McQueen *et al.* 1986; Carpenter *et al.* 1985).

Many researchers suggest that aquatic productivity and the onset of eutrophication are determined by abiotic factors alone, primarily nutrient inputs (bottom-up) (Dillon and Rigler 1974; Schindler 1978). If the algal crop size is determined by nutrient supply it stands to reason that control of water quality can be maintained by manipulating the nutrient content of an aquatic system and thereby directly influencing the algal communities.

An experiment that examined the response of periphyton (attached algae), to nutrient enrichment (bottom-up manipulation) was conducted by Jacoby *et al.* (1991) in Lake Chelan, Washington. Lake Chelan is divided into two distinct regions where one is the recipient of inflow from nutrient-rich tributaries. They found those areas nearest the nutrient-rich tributaries had a 10 to 100-fold increase in periphyton biomass (50-150 mg chl *a*/m^2) compared to those areas distant from the nutrient-rich tributaries (<1-20 mg chl *a*/m^2). Periphyton also increased with nutrient enrichment in Walker Branch, Tennessee, a relatively shallow, low-nutrient stream (<1m) underlain with gravel and organic sediments. Rosemond *et al.* (1993) showed that with the addition of both N and P to the stream increased periphyton biomass and primary productivity by over 100% from the controls.

Limnocorrals in Toolik Lake, Alaska were used by O'Brien *et al.* (1992) to study the effects of inorganic nitrogen and phosphorus additions. The additions dramatically increased phytoplankton biomass from < 5 µg/L to 80 µg/L. They also observed an increase in zooplankton densities, primarily daphnids, in the limnocorrals that received the highest nutrient concentration suggesting that the zooplankton responded positively to high

phytoplankton densities. Therefore, manipulation of the ecosystem via a bottom-up reaction did occur in this experiment.

Murkin *et al.* (1994) determined that algae in an oligotrophic wetland in the Interlake region of Manitoba responded positively to nutrient enrichment using *in situ* enclosures. The enclosures received bi-weekly nutrient additions of 0 and 0, 800 and 30, and 1600 and 60 µg/L inorganic nitrogen (NH_4NO_3) and phosphorus (H_3PO_4), respectively. Biomass of phytoplankton, epiphytes and metaphyton all increased throughout enrichment period; however, there was no effect on epipelon.

In another series of enclosure experiments at the same site, Gabor *et al.* (1994) examined the response of algae to two treatments of dissolved inorganic N and P (6200 µg/L N, 420 µg/L P and 3100 µg/L N, 210 µg/L P) and, one treatment of organic N and P (ground alfalfa 6200 µg/L N, 420 µg/L P) as compared to untreated control enclosures. Phytoplankton biomass increased in all fertilization treatments with a corresponding increase in zooplankton densities, primarily cladocerans and copepods. These positive relationships between nutrients and algal abundance indicate the productivity of an aquatic system can be controlled from bottom-up forces (resource limitation).

2.4 Role of animals in nutrient cycling of aquatic systems

Until recently, research has suggested that it is solely a manipulation of top-down forces such as increased piscivores, decreased planktivores and increased zooplankton grazing which influence plant and algal biomass in an aquatic system (Spencer and King 1984; Faafeng and Brabrand 1990; Carvalho 1994). However, some researchers challenge this conclusion, suggesting that there are other factors involved in the top-down forces affecting algal biomass, separate to zooplankton grazing. These include indirect addition of nutrients liberated from sediments by burrowing insects and benthivorous fish, and direct addition of nutrients into the water column via excrement and decaying carcasses.

Phillips *et al.* (1994) reviewed the effect of fish removal on sediment efflux of phosphorus in a series of shallow lakes, the Norfolk Broads in England. For one lake, Hoveton Great

Broad, they found that large populations of benthic chironomid larvae developed following fish removal, coinciding with an increase in total phosphorus released from the sediments (from 0.03 mg/L to 0.1 mg/L). When the chironomid larvae decreased the following month, phosphorus released from the sediments decreased. They suggested that it was the action of the burrowing chironomids which lowered the redox potential thereby decreasing the sediment binding capacity for phosphorus.

Cline *et al.* (1994) showed that benthivorous fish (*Cyprinus carpio* and *Ictalurus punctatus*) have an indirect impact on turbidity of the water column by stimulating algal production due to nutrient release from the bottom. They found that enclosures which contained sediment and abundant benthivorous fish had increased levels of NO_3+NO_2-N as compared to sediment-free enclosures. They also found that those enclosures with sediment had an increased level of oxygen production (primary production) and no effect on the abundance of the zooplankton community. All of these results imply that increased productivity was probably due to the sediment efflux of nitrogen, caused by the bioturbation of the benthivorous fish and not by decreased grazing pressure.

Tatrai *et al.* (1990) also studied the effect benthivorous bream (*Abramis brama*) have on nutrient cycling in a large eutrophic shallow lake, Lake Balaton, Hungary. They showed that there was an increase in both phytoplankton biomass and productivity in experimental enclosures that contained high fish biomass that could not be attributed to zooplankton predation because, in the presence of high fish biomass, the number of copepods and cladocerans increased. They also found an increase in ^{3}H-thymidine consumption by bacteria indicating a growing organic substrate in these enclosures probably due to bioturbation by benthivorous fish, releasing nutrients from the sediment.

Vanni and Findlay (1990) and Vanni and Layne (1997) have suggested another mechanism by which fish may indirectly recycle nutrients in which they alter the composition of grazers and hence change the rates at which zooplankton (grazers) recycle nutrients. Zooplankton grazing rates increase with body size, so when large-bodied zooplankton are removed by

fish, the proportion of small-bodied zooplankton increases. Small-sized zooplankton not only have decreased grazing rates as compared to large-sized zooplankton and they also have a higher "mass specific excretion rate" (Bartell 1981). Therefore, communities made up of small zooplankton species will recycle nutrients to phytoplankton faster than large-species zooplankton. This increase in nutrient cycling, coupled with a decrease in grazing rates, will allow for enhanced phytoplankton biomass.

Fish have a direct effect on nutrient enrichment through the excretion of wastes as demonstrated in an experiment conducted simultaneously as the one above by Cline *et al.* (1994). They found that enclosures which contained no sediment and omnivorous fish (*Dorosoma cepedianum*) had increased levels of NO_3+NO_2-N in the water column, but these nutrient levels did not increase when added to enclosures with sediment. These results suggest that omnivores play a role in nutrient cycling via physiological processes such as excretion.

Matveev *et al.* (1995) observed that the addition of planktivorous mosquitofish (*Gambusia holbrooki*) to mesocosms did not suppress zooplankton populations but, in fact, increased phytoplankton production. They suggested that fish stimulated algal growth by enriching the water column with excreted nutrients. Schindler (1992) suggested that the sockeye salmon (*Oncorhynchus nerka*) which invade Little Lagoon from Chilko Lake, British Columbia early each June increase internal nutrient loading to phytoplankton with fish excreta and feces as well as those nutrients released from decaying fish carcasses. Schindler divided his enclosures into two equal volume compartments using a 116-μm-mesh screen thereby isolating the planktivorous fish from the zooplankton and phytoplankton communities, so that he could observe the direct effects of nutrient recycling and not predation on the plankton communities. Total plankton biomass increased in the fish-less compartments of his enclosures, confirming that direct nutrient addition by fish was important in algal production because 95% of the variation in phytoplankton biomass could be predicted solely by P excretion rates.

Fish also affect nutrient addition through mortality and subsequent decomposition of

carcasses. Parmenter and Lamarra (1991) observed that carrion decomposition from rainbow trout (*Oncorhynchus mykiss*) carcasses in Kemmerer Marsh, Wyoming, contributed substantial amounts of nutrients during a ten-month period. They noted that fish carrion lost 95% of its total N and 60% of its total P. Threlkeld (1988) found that outdoor tanks with dead fish (*Menidia beryllina*) had increased algal chlorophyll fluorescence, decreased water transparency and increased large herbivorous zooplankton, while those tanks with live fish displayed the opposite results. Threlkeld suggested it was the nutrients released from decaying fish tissue that caused an increase in phytoplankton production because there was an increase in large grazing zooplankton.

2.5 Role of waterfowl in wetlands

The role that waterfowl play in wetlands remains unresolved. To date, research has concentrated on habitat selection and food habits of waterfowl (Murkin and Kadlec 1986; Leschisin *et al.* 1992; Blankespoor *et al.* 1994; Hoyer and Canfield 1994; Staicer *et al.* 1994; Tamisier and Boudouresque 1994). Limited research has focused on the role of waterfowl in lakes and those few studies that have occurred in wetlands (Murkin and Kadlec 1986; Leschisin *et al.* 1992; Merendino *et al.* 1995) have yet to shed light onto the role that waterfowl play in influencing the primary productivity of freshwater wetlands.

Waterfowl have the ability to influence the eutrophication of lakes either positively or negatively (Gere and Andrikovics 1992). If they feed in the water and excrete on land the eutrophication process is delayed. However, if they feed on land and excrete in the water, this increase in nutrient loading has the potential to quicken eutrophication. Therefore, the role waterfowl play in regulating plant communities is two-fold: they are viewed as consumers, removing macrophytes and invertebrates (Bazely and Jefferies 1989; Gere and Andrikovics 1992; Hanson and Butler 1990, 1994; Hargeby *et al.* 1994), and they are viewed as contributors, adding nutrients from their feces and decaying carcasses (Gere and Andrikovics 1992; Manny *et al.* 1994; Parmenter and Lamarra 1991).

The importance of waterfowl as consumers has been shown clearly in lakes where increases

in plant biomass have followed increases in the populations of herbivorous waterfowl. For example, Hanson and Butler (1990, 1994) noted that the density of waterfowl on Lake Christina, a shallow prairie lake in Minnesota, increased when the lake shifted from a high turbidity, phytoplankton-dominated system to a clear, submersed macrophyte- and periphyton-dominated system in response to fish removal. The changes in the lake corresponded with an increase in the number of diving ducks using the lake during fall migration.

Similar observations were made by Hargeby *et al.* (1994) during their study in Lake Krankesjon, a shallow eutrophic lake in Sweden. Here they observed that a shift from phytoplankton to submerged macrophytes caused structural changes to higher trophic levels and altered the trophic food web. With the shift towards increased submersed plants, the number of resting and breeding waterfowl increased, the density of planktonic Cladocera decreased, and the benthic macroinvertebrate assemblage became more diverse and became dominated by plant-associated forms like snails.

Lauridsen *et al.* (1993) observed that waterfowl grazing influenced macrophyte development in a shallow lake, Lake Vaeng, Denmark. The object of their study was to determine if the delay in the colonization of submerged macrophytes was the result of sediment composition or grazing pressure exerted by waterfowl. They transplanted pondweed (*Potamogeton crispus*) to pots with two kinds of sediment found in Lake Vaeng (organic-rich mud and sand) and placed them in fenced and unfenced areas. Lauridsen *et al.* found that macrophytes grew on both kinds of substrata but, grew 6.5 times more in a station from which grazing waterfowl, primarily coots (*Fluca atra*), were excluded as compared to unfenced macrophytes.

Waterfowl may provide nutrients to wetlands in the form of excretion products and carrion. Manny *et al.* (1994) examined the impact of Canada geese (*Branta canadensis*) and mallard ducks (*Anas platyrhynchos*) on Wintergreen Lake, Michigan. They investigated annual P loads from external sources, such as waterfowl and devised a nutrient load response model enabling them to determine whether waterfowl degrade water quality. They calculated that

27% of all N and 70% of all P entering Wintergreen Lake was contributed by Canada geese and mallards. A large population of birds breed and roost in Lake Grand-Lieu, France where Marion *et al.* (1994) calculated they contributed 5800 kg N and 2000 kg P in one year and 7640 kg N and 2530 kg P the following year. However, these inputs represented only < 1% of total N and 2% of total P and < 1% of total N and 7% of total P, making their role of nutrient contributors small as compared to inputs from human sewage. However, they calculated the birds would have contributed 36% of the annual N and 95% of the annual P prior to initiation of sewage inputs.

Wetlands provide habitat and food for large populations of breeding waterfowl (Leschisin *et al.* 1992; Murkin and Kadlec 1986). For example, the northern prairie pothole region produces 50 to 80% of North America's waterfowl population (Batt *et al.* 1989). However, much of the land area once covered by wetlands has been drained for use in agriculture (Mitsch and Gosselink 1993) and is no longer available for waterfowl use. Those wetlands that do remain support large waterfowl populations and should theoretically serve as major nutrient pools (Parmenter and Lamarra 1991).

Colonial nesting birds add nutrients from their feces and decaying carcasses, thereby countering the "negative" effects waterfowl have on reducing plant biomass. Baxter and Fairweather (1994) compared the nutrient levels of the water column and surface sediments in wetlands in New South Wales that had egret (*Egretta* sp.) colonies and areas in the same region with similar physical characteristics that had no colonies. As compared to areas where egrets were absent, wetlands with the egret colonies had a greater concentration of N and P in the water column (16.2 mg/L and 18.7 mg/L, respectively) and surface sediments (2.9 mg/L and 1.4 mg/L, respectively). This suggests colonial nesting birds add nutrients to their surroundings either from their feces, dropped or regurgitated food, or from dead birds.

Parmenter and Lamarra (1991) observed that carrion decomposition from waterfowl carcasses in Kemmerer Marsh, Wyoming, contributed substantial amounts of nutrients. They noted that waterfowl carrion lost 65% of their total N and 30% of their total P over a period

of 10 months suggesting that waterfowl contributions should be taken into account when determining nutrient budgets of a wetland. Gere and Andrikovics (1992) observed that not only do waterfowl remove significant amounts of N and P (1,500 breeding pairs of cormorants removed 12.5 tonnes/year N and 3.1 tonnes/year P) but, through their excretions of feces, they re-supplied nutrients back into the Kis-Balaton, Hungary, possibly influencing lake eutrophication. Feces from lesser snow geese (*Anser caerulescens caerulescens*) made significant N contributions to macrophytes in a salt marsh, La Pérouse Bay, Manitoba (Bazely and Jefferies 1985). In plots that received snow goose feces, the mean standing crop increased from 22 g/m^2 to 195-204 g/m^2 over a 72-day period whereas plots that did not receive any nutrient addition only increased to 122 g/m2. As well, the N content of *Puccinellia phryganodes* shoots receiving feces increased from 1.43 to 2.63% dry weight. Both observations indicate that addition of snow goose feces increased the standing crop of macrophytes due to an increase in nutrients received by the plants.

2.6 Enclosure and whole lake experiments

Enclosures or limnocorrals provide a method to conduct *in situ* experiments. Enclosures are contained compartments that are assumed to have the same environmental conditions and communities as the natural aquatic system that the researcher wants to examine. Therefore, they provide the researcher with an opportunity to monitor conditions of an aquatic system when they are unable to manipulate that system in its entirety (Cruikshank *et al.* 1983; Bloesch *et al.* 1988).

Bloesch *et al.* (1988) points out that enclosure experiments avoid the limitations of small scale laboratory experiments which often have different environmental conditions (light and nutrients) and community structure (only a few of the species) from what occurs naturally. On the other hand, laboratory experiments allow the control of environmental conditions so that an understanding of the physiological processes affecting community structure can be gained. DeNoyelles *et al.* (1980) used lab and *in situ* continuous culture chambers to compare the phytoplankton of lakes at the Experimental Lakes Area of NW Ontario (L239, L226,

L223) to alterations in light, nutrient (P) and cadmium concentration. They found that there was no difference in phytoplankton species distribution between control cultures in the laboratory and *in situ* as compared to the lake community.

Enclosure studies are not without their faults. These include issues related to their size and replicability (Bloesch *et al.* 1988; Carpenter and Kitchell 1992; O'Brien *et al.* 1992). For example, horizontal advection is reduced due to the presence of enclosure walls. Bloesch *et al.* (1988) believe that without this continuous lateral mixing of waters between the enclosure and the surrounding aquatic system, difference in the physical and chemical properties will arise, subsequently affecting the constituent biological communities. They attribute this and the lack of vertical mixing to the size of the enclosures and recommended response they observed would be the same as that observed in a whole lake study because the controlling mechanisms would still be the same, yet the degree of the response may not fluctuate within the same range.

O'Brien *et al.* (1992) suggested that shading and temporal factors contributed by reduced turbulence in the Bloesch *et al.* (1988) experiment. In their three year study using limnocorrals to determine the effect of nutrient and fish additions on phytoplankton and zooplankton populations, O'Brien *et al.* (1992) found that response from the control enclosures and the surrounding lake were similar. They found that there was little difference between the water quality parameters (oxygen concentration, pH ammonia, SRP) of the control enclosures and the lake itself.

In their comment concerning the legitimacy of biomanipulation experiments, DeMelo *et al.* (1992) proposed that size of the enclosure is not a factor which should limit the validity of the results. They offer the suggestion that because "whole lake" studies encompass the entire physical and biological components that make up the system it is (1) difficult to find a similar system to use as a reference (control) point and (2) difficult to control independent variables. Both factors lead to results that are unlikely to be reproduced and unlikely to pinpoint the exact components which control the system.

No matter the debate, the majority of researchers agree that enclosures are valuable tools in determining how physical and biological parameters affect each other and how each are influenced by allochthonous factors. Difficulty in replicability occurs when researchers attempt to manipulate whole systems as they manipulated enclosures, expecting to obtain similar results. Enclosures should be used cautiously as guidelines, understanding that they have their limitations (as stated above) as well as their merits.

3. MATERIALS AND METHODS

3.1 Aquarium Experiments

Aquarium experiments were conducted during 1995 to find if waterfowl feces liberate inorganic nutrients following application to water under conditions similar to those occurring in *in situ* enclosures and, if so, to measure the duration of the release.

3.1.1 Experiment #1

This experiment was performed in a laboratory at the University Field Station (Delta Marsh) that received no direct natural light. Four glass aquaria (0.49 m long x 0.27 m deep x 0.27 m high) were filled with 36 L of carbon-filtered well water. Two hundred milliliters of water was removed from each aquarium immediately and analyzed for soluble reactive P (SRP), ammonia-N (NH_3-N) and nitrate-N (NO_3-N) using methods described by Stainton *et al.* (1977). One liter of water was removed from two aquaria, and each sample was mixed with 40.05 g of fresh waterfowl feces, collected from Mallard ducks (*Anas platyrhynchos*) and Canadian Geese (*Branta canadensis*), until a uniform slurry was obtained. The feces slurries were added to the same aquaria from which the water had been removed. The remaining two aquaria, where nothing was removed or added, served as controls. The four aquaria were covered with plastic wrap (Saran Wrap) and the time was recorded (0 hours). Every 12 hours for 96 hours, 200 mL of water from each aquarium was removed and analyzed as above. At the end of the 96-hour period, nutrient analyses continued at daily intervals for one week (12 - 19 June). The plastic wrap was replaced over the aquaria following removal of water samples to reduce evaporative losses.

3.1.2 Experiment #2

For a second set of experiments at the University Field Station (Delta Marsh), the same four aquaria each received 4 L fresh sediment, collected next to the canoe ditch wharf at the station. Thirty-four liters of unfiltered marsh water taken near the sediment collection site was poured into each aquarium. Suspended sediment was allowed to settle for 48 hours before feces were added. Following the settling period, 200 mL of water was removed from

each aquarium and analyzed for SRP, NH_3-N, and NO_3-N as before. One liter of water was removed from two aquaria and mixed with 12.228 g of fresh waterfowl feces, collected from Mallard ducks (*Anas platyrhynchos*) and Canadian Geese (*Branta canadensis*), until a uniform slurry was obtained. The quantity of feces was chosen to approximate the same proportional load as applied to high feces loading enclosures in 1995 (see below). The feces slurries were then added back to the aquaria. The aquaria were not covered by plastic wrap during this experiment. The two remaining aquaria, where nothing was removed or added, served as controls. Every six hours for 24 hours following the feces additions, 200 mL of water was removed from each aquarium and analyzed as above. After the 24 hours, nutrient analysis was performed every 12 hours for a 72 hour period then every 24 hours for another 72 hour period, for a total duration of one week (21 - 28 August).

3.1.3 Experiment #3

Five glass aquaria were placed under direct, natural light in the south greenhouse on the roof of the Buller Building at the University of Manitoba. Each aquarium was filled with 4 L of fresh sediment, collected near the canoe ditch wharf at the University Field Station (Delta Marsh) and 34 L of dechlorinated City of Winnipeg tap water, poured directly on top of the sediment and left undisturbed for 48 hours to allow the sediment to resettle. Then, 200 mL of water was removed from each aquarium and analyzed for SRP, NH_3-N and NO_3-N as before. One liter of water was removed from two aquaria and mixed with same quantity of waterfowl feces as used in experiment #2, to simulate high feces loading. The feces had been frozen and were thawed a day before the experiment began. One liter of water was removed from two other aquaria and mixed as before with 1.223 g of thawed waterfowl feces. This quantity of feces was intended to simulate the same proportion load as applied to low feces loading enclosures (see below). The remaining aquarium, where nothing was removed or added served, as a control. Following feces addition, 200 mL of water was removed from each aquarium and analyzed for SRP, NH_3-N and NO_3-N every 4 hours over a 24 hour period. After the 24 hour period, nutrient analysis was performed at regular intervals for one week (28 October - 4 November).

3.1.4 Experiment #4

The final aquarium experiment was conducted under direct, natural light in the greenhouse on the roof of the Buller Building. The five aquaria were set-up and water was sampled and processed for SRP, NH_3-N and NO_3-N following the same procedure as used in experiment #3 with one exception. The sediment was removed from the canoe ditch wharf at the University Field Station (Delta Marsh) three weeks prior to the experiment and frozen until it was required. The experiment was performed over a one-week period (18 - 25 November). As in experiment #3, there were three treatments (high feces load, low feces load, control).

3.2 Field Experiment Year 1 (1995)

3.2.1 Study Site and Enclosure Set-up

Delta Marsh is a 21,870 hectare prairie wetland in south-central Manitoba (Fig. 2) which supports a wide and unique diversity of habitats and biota. The marsh has dense beds of submersed aquatic plants (*Potamogeton zosteriformis* (Fern.), *P. pectinatus* (L)., *Myriophyllum sibiricum* (Fern.), *Ceratophyllum demersum* (L)., and *Chara* sp.), and emergent reed beds (*Typha* X *glauca* (Godron)., *Phragmites australis* (Cav.) bordered by willows (*Salix* spp.). Delta Marsh is separated from the south shore of Lake Manitoba by a sand ridge and bordered by agricultural land at its southern edge.

A series of floating, littoral enclosures, 5 m x 5 m in size, were constructed to examine the algal and plant community responses to waterfowl feces additions (Fig. 3). The enclosures were supported by high density foam blocks fastened under 40 cm wide wooden walkways which allowed the enclosure edges to float just above the water surface. A translucent plastic curtain (6-mil) was suspended from each frame. A metal rod at the base of each curtain was embedded into the sediments (~30 cm) to anchor the curtains and prevent lateral water flow between the enclosures and the surrounding marsh. Each enclosure contained approximately 20,000 L of water. The enclosures were anchored on 23 May in the center of Blind Channel where the water depth was about 1 m. Gee-type minnow traps were placed in each enclosure after curtain deployment and these remained throughout the experiment. Fathead minnows

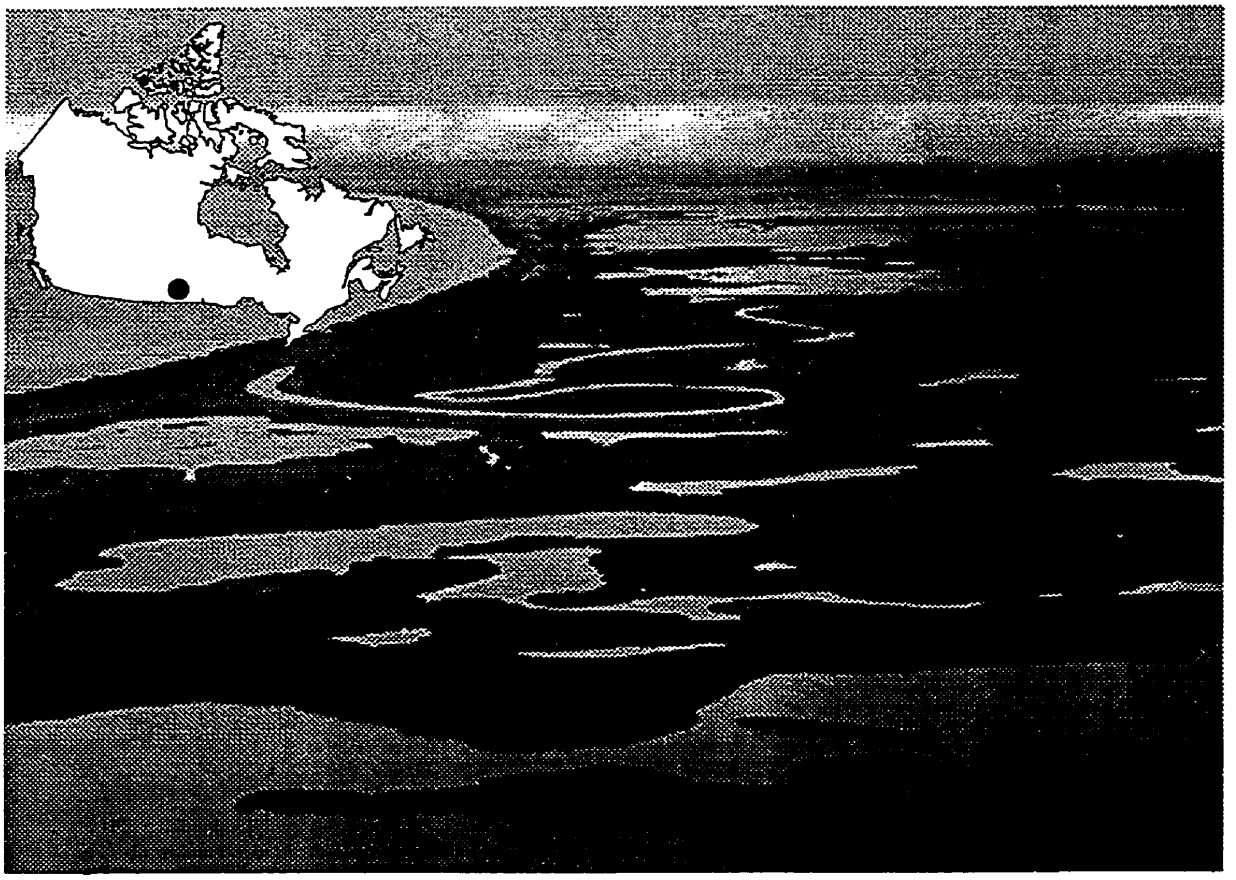

Figure 2. Aerial view of Delta Marsh in south-central Manitoba (location at dot in inset map). This study was conducted near the northern end of the meandering Blind Channel, near Lake Manitoba in the background left.

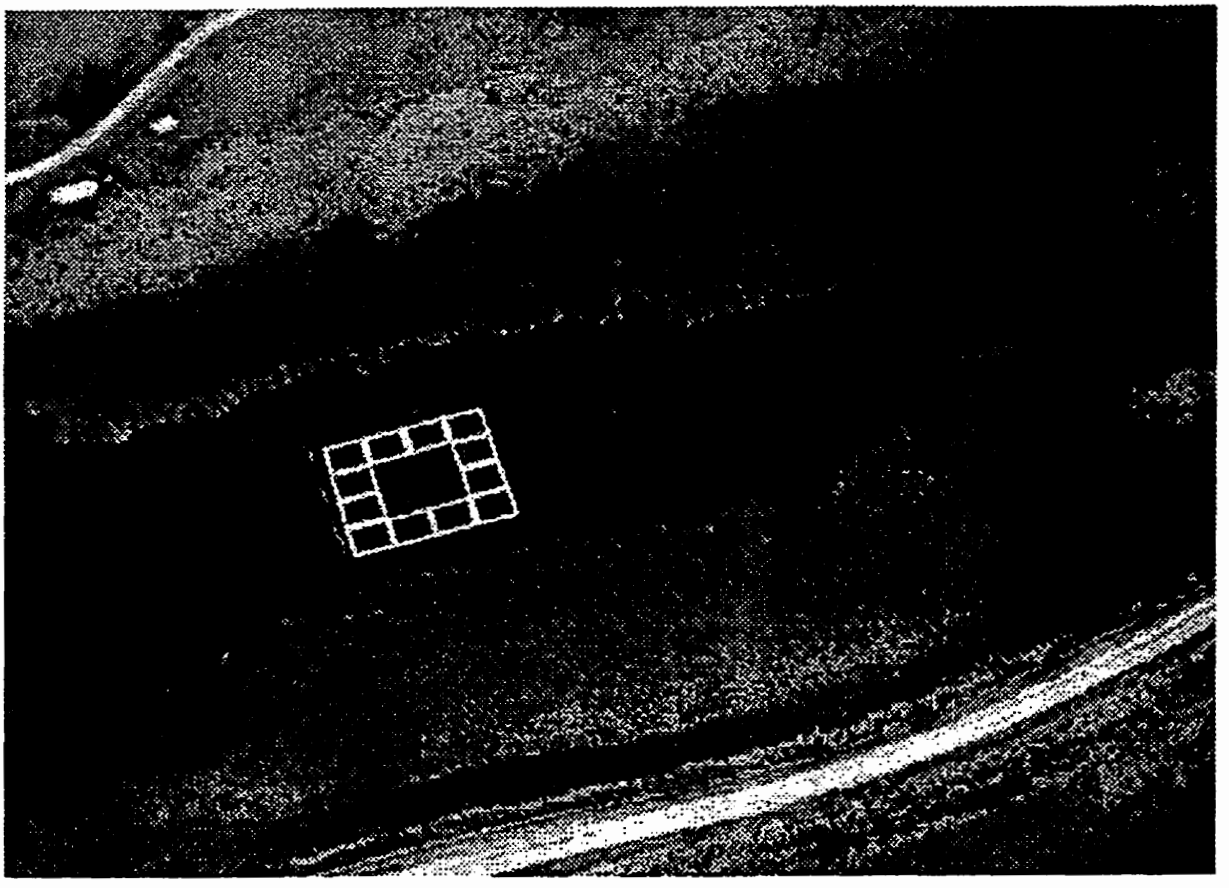

Figure 3. Aerial view of twelve experimental enclosures deployed in the center of the open water area of Blind Channel, of which six randomly selected enclosures were used in these experiments in 1995 and 1996. Each square enclosure measured 5 m on a side.

(*Pimephales promelas*) and sticklebacks (*Gasterosteidae*) were the primary fish removed from the traps. The first enclosure sampling began on 6 June and the last sampling occurred on 30 August.

3.2.2 Collection, mixing, and addition of feces

Experimental additions of the waterfowl feces were intended to approximate the total inorganic P load (20.14 mg/enclosure P) added during inorganic nutrient enrichment experiments conducted at the same site in 1994 (McDougal *et al.* 1997). Fresh, intact feces from Canada geese (*Branta canadensis*) and/or mallard ducks (*Anas platyrhynchos*) were collected from captive and wild flocks at the Delta Waterfowl and Wetlands Research Station between May and July, and stored at -30°C until required for experimental additions. The feces were thawed and mixed to make a consistent moist slurry which was poured uniformly over the surface of the target enclosure. The slurry initially remained at the water surface, but it was mixed into the water column by gentle agitation using a wooden paddle. Four of the six experimental enclosures were pulsed (spiked) with the feces slurry on 28 June and 21 July.

The first addition consisted primarily of Canada goose feces that contained 14.0 mg P/g dry weight, 5.72 mg N/g dry weight and a moisture content of 80.9% (Table 1). Two different loads of N and P were added to the enclosures such that the experimental treatments were as follows: 1) a high feces addition to two randomly selected enclosures, each of which received 287.6 g wet weight/m^2 feces representing 0.769 g/m^2 P and 0.314 g/m^2 N, 2) a low feces addition to two randomly selected enclosures, representing 0.0769 g/m^2 P and 0.0314 g/m^2 N, and 3) two untreated controls that received no feces additions.

The second experimental addition was comprised entirely of Mallard duckling feces that contained 17.4 mg P/g dry weight, 52.3 mg N/g dry weight and a moisture content of 77% (Table 2). The enclosures assigned to the high feces treatment each received 201.30 g wet weight/m^2 feces representing 0.806 g/m^2 P and 2.421 g/m^2 N. The low feces enclosures received 0.0806 g/m^2 P and 0.242 g/m^2 N. As before, the controls received no feces additions.

Table 1. Chemical composition of Canada Goose feces added to experimental treatment enclosures in Year 1 on 28 June 1995. The units represent the quantities per gram of dry weight. The quantity labeled "Nitrogen" is total N (the sum of inorganic and inorganic N forms). Similarly, the quantity labeled "Phosphorus" is the sum of both inorganic and organic P forms.

Component	**Concentration**
Nitrate (mg/g)	< 0.05
Ammonium (mg/g)	2.58
Total organic N (mg/g)	3.14
Nitrogen (mg/g)	5.72
Phosphorus (mg/g)	14.0
Potassium (mg/g)	12.5
Sodium (mg/g)	2.84
Calcium (mg/g)	21.4
Magnesium (mg/g)	6.38
Sulphur (mg/g)	3.07
pH	6.9
Conductivity (mS/cm)	7.99
Moisture (%)	80.9

Table 2. Chemical composition of Mallard duckling feces added to experimental treatment enclosures in Year 1 on 21 July 1995 and weekly in Year 2 starting on 5 July 1996. The units represent the quantities per gram of dry weight. The quantity labeled "Nitrogen" is total N (the sum of inorganic and inorganic N forms). Similarly, the quantity labeled "Phosphorus" is the sum of both inorganic and organic P forms.

Component	Concentration
Nitrogen (mg/g)	52.3
Phosphorus (mg/g)	17.4
Potassium (mg/g)	17.5
Sodium (mg/g)	3.47
Moisture (%)	77.0

3.2.3 Sampling and Analysis

Photosynthetically active radiation (PAR) at 10 cm depth intervals was measured biweekly, on sunny, cloud-free days, using a Li-Cor LI-185 meter and a LI-192SA submersible quantum sensor. Turbidity was measured weekly using a Hach Model 2100B turbidimeter. Dissolved oxygen was measured weekly, in the evening, at 10 and 50 cm depths using a YSI Model 51B meter. Surface water samples (~ 15 cm) were collected weekly and analyzed for SRP, NH_3-N, soluble reactive silicon (Stainton *et al.* 1977), and NO_3-N (APHA 1992). Alkalinity and pH were measured concurrently with measurements of algal C assimilation (see below). Additional surface water samples from each enclosure were delivered to Norwest Labs (Winnipeg) for analysis of total P (TP), nitrate+nitrite-N (NO_x-N) and total Kjeldahl N (TKN) using standard methods (APHA 1992).

At weekly intervals through the experiment, I measured the biomass and photosynthesis of the four algal assemblages known to occur in Delta Marsh. These were **phytoplankton**, algae entrained in the water column; **periphyton**, attached algae growing on submersed surfaces; **epipelon**, algae inhabiting soft sediments; and **metaphyton**, algae that originates as attached algae, but detaches to form floating and subsurface mats.

Phytoplankton

Phytoplankton was sampled at three randomly selected positions in each enclosure at weekly intervals. Depth-integrated samples were collected with a 5.5 cm diameter Plexiglas plastic tube. Four liters of the collected sample was filtered through a 52 μm plankton net to remove zooplankton. One liter of the filtrate was retained for analysis and the remaining 3 L were returned to the enclosure.

Phytoplankton productivity (μgC/L/h) was determined by measuring the rate of inorganic ^{14}C assimilation (Robinson *et al.* 1997b). Fifty milliliters were taken from the original 1 L water sample and dispensed in two equal portions into screw-cap tubes, one of which was blackened with elastic tape. Each of the sub-samples was inoculated with a $NaH^{14}CO_3$ solution (0.5 μCi/mL, 37 kBq/mL) and placed in a 25°C water bath under saturating irradiance (500

μmoles/m²/s) for four hours. The samples were then removed from the bath and collected onto 2.4 cm glass microfiber filters (Whatman GF/C) under gentle vacuum. The filters were placed over concentrated HCl for at least 1 minute, which volatilized remaining inorganic ^{14}C, and placed into vials containing 5 mL of Beckman ReadySafe™ liquid scintillation cocktail. The radioactivity of each vial was determined using a Beckman LS 3801 scintillation counter. Sample radioactivity (dpm) was corrected for color quenching using the H-number method.

Phytoplankton productivity was determined according to the formula:

$$\mu gC/L/h = \frac{dpm_S \times DIC \times 1.06}{dpm_T \times V \times T}$$

where dpm_S is the radioactivity of each sample corrected for dark uptake; DIC of marsh water (μgC/L) as determined from alkalinity, pH and temperature (APHA 1992); 1.06 is an isotope discrimination factor (Strickland and Parsons 1972); dpm_T is the radioactivity of added ^{14}C; V is the sample volume (25 mL); and T is the incubation time (hours).

Phytoplankton biomass was determined by measuring its total chlorophyll content (Robinson *et al.* 1997a). Sub-samples (400 mL) were taken from each of the original 1 L water samples and collected onto 4.7 cm glass microfiber filters (Whatman GF/C) under vacuum. The filters were neutralized with a saturated $MgCO_3$ solution and stored at -30°C for later analysis. Each filter was immersed in 5 mL of 90% methanol for 24 hours in the dark at room temperature. A portion of the sample was transferred into a cuvette and its absorbance was read at two wavelengths, 665 nm and 750 nm, against a blank of 90% methanol using a Milton-Roy Spectronic 601 spectrophotometer. Each sample was then injected with 50 μL of 10^{-3} N HCl, allowed to stand in the dark for one hour, then its absorbance was re-read at the same settings as before. The two sets of readings were used to calculate the total chlorophyll content (native chlorophyll plus degradation products) (μg/L) of each sample using the equation of Marker *et al.* (1980).

Phytoplankton chlorophyll values (μg/L) were multiplied by estimates of enclosure volume

(based on daily depth measurements) at the time of sampling and divided by enclosure surface area (25 m^2) to extrapolate to units of wetland area (mg/m^2). As well, phytoplankton photosynthesis values (µg C/L/h) were divided by phytoplankton chlorophyll values (µg/L) to determine the rate of C assimilated per unit chlorophyll (µg C/chl-a/h) or biomass-normalized photosynthesis (Robinson *et al.* 1997b).

Additional phytoplankton sub-samples (200 mL) were taken from each of the original 1 L samples, collected onto 4.7 cm glass microfiber filters (Whatman GF/C), and stored at 4°C for later analysis of total particulate P (µg/L) (Andersen 1976). The samples were combusted at 550°C in a muffle furnace and boiled in 25 mL 1 N HCl for 10 minutes thereby converting polyphosphates to orthophosphate. The P concentration was quantified spectrophotometrically using the acid molybdate method (Stainton *et al.* 1977). A standard curve for P was developed by analyzing samples of known P concentration using the same method. Data were extrapolated to units of wetland area (mg/m^2 P) using the same method as for chlorophyll data.

Periphyton

Periphyton were sampled weekly using 90 cm long, 0.65 cm diameter acrylic rods that served as artificial substrata for attached algae (Goldsborough *et al.* 1986). These rods were pre-notched at specific lengths, with each segment used for measurements of algal productivity, biomass, particulate P, or identification (Fig. 4). Sixty-four rods were positioned on 24 May (13 days before the experiment started) so an 8 x 8 grid was fashioned in each enclosure. The rods were not sampled for three weeks allowing time for algal colonization of the rods. Three rods were sampled randomly from each enclosure each week, starting on 8 June, using a 7.0 cm diameter plastic tube that fastened around therod while simultaneously taking a water column sample that surrounded the rod. The water was carefully removed from the tube so as not to disturb the periphyton on the rod. This water was filtered through a 100 µm plankton net for zooplankton analysis (Pettigrew *et al.* 1998). The rods were snapped at the notched points with needle-nose pliers and the segments for total chlorophyll

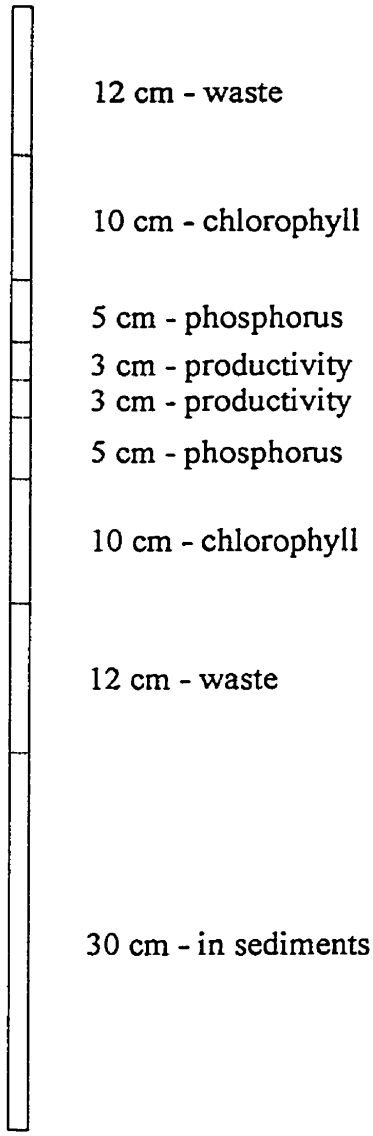

Figure 4. Schematic showing the segmentation of acrylic rods (0.64 cm diameter, 90 cm long) used as artificial substrata for periphytic algae in experimental enclosures.

analysis (2 x 10 cm segments/rod), particulate P analysis (2 x 5 cm segments/rod), and algal identification (5 cm segment/rod) were placed in separate empty tubes, while the segments for productivity analysis (2 x 3 cm segments/rod) were placed in tubes with 25 mL of pre-filtered (Whatman GF/C) marsh water previously taken from the enclosures.

Periphyton productivity ($\mu g/cm^2/h$), chlorophyll ($\mu g/cm^2$), and total P ($\mu g/cm^2$) were determined using the same basic procedures as performed for phytoplankton samples. For productivity and chlorophyll measurements, intact rod segments were retained during analysis. Periphyton chlorophyll data ($\mu g/cm^2$) were multiplied by estimates of submersed macrophyte surface area (m^2/m^2) at the time of sampling to extrapolate to units of wetland area ($\mu g/m^2$). Biomass-normalized photosynthesis for periphyton was determined using the same calculation as used for photoplankton. For P analysis, periphytic algae were scraped from their substratum using a soft bristled paint brush into a petri dish containing a minimal amount of water. The contents of the dish were collected onto 2.4 cm glass microfiber filters (Whatman GF/C) for analysis. Data were extrapolated to units of wetland area (mg/m^2 P) using the same method as for epiphyton chlorophyll data.

Epipelon

Epipelon was sampled at three randomly selected sites in each enclosure at bi-weekly intervals. A small plastic tube, attached to a side-arm flask and a hand-operated vacuum pump, was used to suction up the surface sediments (~ 2 mm deep) enclosed within a 10 cm diameter PVC tube that was embedded in the surface sediments in the enclosure. When the flask was filled, its contents were transferred into a 1 L sample bottle for transport to the laboratory.

The contents of the plastic sample bottles were emptied into blackened 2 L plastic bottles and left undisturbed in the dark for approximately 24 hours. Then, 400 mL of the overlying water of each sample were filtered through 4.7 cm glass microfiber filters (Whatman GF/C), from which 40 mL were taken for measurements of alkalinity and pH. Three flasks, each containing 100 mL of the filtered water, were refrigerated at 4°C overnight. The

blackened beakers containing the sediment were transported to the field station's weather station. There, any overlying water was siphoned off and the sediment was covered with lens paper tissues (Whatman #1), pre-cut to the same diameter as the beaker (9.02 cm). The lens paper served to trap the upwardly migrating epipelic algae. Each beaker was covered with a clear plastic bag, held in place by an elastic band, and left undisturbed on the weather station platform overnight. The following morning (07:00), any excess water that had collected underneath the lens paper was carefully siphoned off with a glass pipette attached to the hand-operated vacuum pump. At 10:00, the lens papers were removed and placed into the corresponding 100 mL of filtered water. The flasks containing the lens paper were shaken vigorously for 15 minutes to dislodge the epipelon trapped in the lens filter fibers. Epipelon C assimilation rate ($\mu g/cm^2/h$) was measured using 50 mL of the water containing the suspended algal cells while the remaining 50 mL was filtered for total chlorophyll (mg/m^2 of wetland area) determination using the same procedures as for phytoplankton samples. Epipelon biomass-normalized photosynthesis was calculated using the same formula as for photoplankton.

Sediment

To measure total sediment P content, two milliliters of fresh sediment were removed from each of the blackened beakers using a syringe. The sediment samples were put into pre-weighed vials, dried at 100°C for 24 hours, and re-weighed. The samples were then processed using the same procedure as for phytoplankton samples.

Feces

Samples of the feces slurry were taken and analyzed for P content both times the feces additions were made to the enclosures. The feces samples were put into pre-weighed vials, dried at 100°C for 24 hours and re-weighed. The samples were then processed using the same procedure as for phytoplankton samples.

Macrophytes

Submersed macrophytes were sampled bi-weekly at three randomly selected positions in each enclosure, starting on 12 June. The sampler was modified from Pip and Stewart (1976) and enclosed all macrophytes in 0.09 m^2 of the enclosure bottom. Following collection, macrophytes were rinsedfree of phytophilous invertebrates using water from the enclosure, placed into a glass jar and shaken vigorously to dislodge epiphytes. The cleaned macrophyte samples were brought back to the lab where a sub-sample was taken to measure its surface area (length and diameter of stems and leaves). Small sub-samples, sorted by plant species, were placed in pre-weighed aluminum dishes, dried at 100°C for 24 hours, and weighed. This allowed me to establish empirical relationships between the surface area (cm^2) and weight (g) of macrophyte species in the enclosures. Plant tissue not used in surface area measurements was placed in pre-weighed aluminum plates and dried at 100°C for 24 hours, re-weighed, and used to calculate macrophyte biomass in the enclosure (g/m^2). A sub-sample of the dry macrophyte tissue was placed in pre-weighed glass vials for total P analysis (µg/g) using the same method as for algal samples. The total volume of water used to clean the macrophytes, containing dislodged epiphyton, was recorded, but only 1 L was used for analysis of epiphyton biomass. Known volumes (200 - 400 mL) of the sample were filtered 4.7 cm (Whatman GF/C) for analysis of epiphyton chlorophyll and total P (µg/gdw). Epiphyton chlorophyll and total P (µg/gdw) were multiplied by macrophyte biomass (gdw/m^2) at the time of sampling to extrapolate to units of wetland area (µg/m2).

Invertebrates

Invertebrates were sampled bi-weekly for particulate P using funnel traps. Funnel traps consist of a Plexiglas plate with three holes through which three funnels, each 10 cm in diameter, were attached. The stems of the funnels extended into 125 mL sample bottles where invertebrates were trapped. This method collects those invertebrates that undergo nightly vertical migration (Whiteside and Williams 1975). The traps were submerged so that the funnels and sample bottles filled with enclosure water and then they were inverted

and gently lowered into the enclosures until they rested on the bottom. Two traps per enclosure were positioned randomly in the evening at ~ 19:00 and collected in the morning approximately 12 hours later. Collection involved slowly lifting the traps to just below the water surface where they were inverted and brought above the surface so the water collected in the funnel could be poured off. The contents of the 125 mL sample bottles were then filtered through a 52 μm plankton net into pre-weighed glass vials. The samples were brought back to the lab where they were dried at 100°C for 24 hours and re-weighed and processed for particulate P using the same procedure as for phytoplankton samples.

3.3 Field Experiment Year 2 (1996)

3.3.1 Study Site and Enclosure Set-up

The enclosure experiment conducted in 1996 occurred at approximantely the same site as the experiment in 1995. The enclosures were anchored on 11 June in the center of Blind Channel at a water depth of about 1 m. Once the curtains were anchored into the sediment each enclosure was seined to remove adult fish. The fish caught in each enclosure, primarily Fathead Minnows (*Pimephales promelas*) and Sticklebacks (*Gasterosteidae*), were counted and removed. Gee-type minnow traps were then placed in each enclosure for the duration of the experiment and any fish caught were removed from the enclosures.

3.3.2 Collection, mixing, and addition of feces

Experimental additions of waterfowl feces approximated the total load added to one of the high load enclosures (12.2 kg/enclosure wet weight) in 1995. I eliminated the low loading treatment used in Year 1. This enabled me to increase treatment replication from two to three, thereby increasing the statistical power of the experiment and my ability to detect significant responses to feces additions. Fresh, intact feces from Canada geese (*Branta canadensis*) and mallard ducks (*Anas platyrhynchos*) were collected from wild flocks at the Delta Waterfowl and Wetlands Research Station on 4 July, and stored at -30 °C until required for experimental additions. Unused feces collected in 1995, which had been stored in sealed plastic bags at -30 °C, were also used in the 1996 experiment. Three randomly selected

enclosures received an aqueous slurry of waterfowl feces once a week beginning on 5 July with the final application on 23 August.

The experiment additions consisted primarily of mallard duckling feces containing 17.4 mg P/g dry weight, 52.3 mg N/g dry weight and a moisture content of 77% (Table 2). In 1995, the two high feces enclosures each received a total load of 12.2 kg wet weight of feces. The same total load per enclosure as in 1995 was divided into weekly press additions so that each week, for 8 weeks, 1.5 kg wet weight of feces was applied to each enclosure. Three randomly selected enclosures were pressed weekly with 1.5 kg wet weight feces containing 0.240 g/m^2 P and 0.722 g/m^2 N. The three remaining control enclosures received no feces additions throughout the experiment.

3.3.3 Sampling and Analysis

Measurements of vertical light extinction, turbidity, dissolved oxygen, temperature, concentrations of NH_3-N, NO_3-N, NO_x-N, TKN, SRP, and TP, algal photosynthesis (C assimilation rate), algal biomass (total chlorophyll), and macrophyte abundance were monitored in the six enclosures between June and August at the same frequency and with the same methods as in 1995. Deviations are described below.

Forty-two acrylic rods were positioned in a 7 x 6 grid in each enclosure on 13 June as substrata for periphyton. The rods were not sampled for two weeks allowing time for algal colonization of the uppermost 60 cm of each rod. Three rods were randomly sampled from each enclosure each week, starting on 27 June.

Submersed macrophytes were sampled weekly at two randomly selected positions in each enclosure, starting on 26 June, using a Downing Box sampler (Downing 1984). The procedure for sampling macrophytes was changed in 1996 because there was concern that the sampler modified from Pip and Stewart (1976) was compressing the macrophytes as it passed down through the water column, so they were not sampled and total plant biomass (per m^2 of bottom) was underestimated. The Downing Box was less prone to such problems, but it does not sample a quantitative area, so independent estimates of aerial abundance

were used with the PVC cylinder. The sampler consisted of a hinged Plexiglas box (30.5 cm x 11 cm x 19 cm) that could be opened to enclose macrophytes near the surface of the water column. Following collection, macrophytes were rinsed of phytophilous invertebrates using a known volume of C-filtered water (500 mL or 250 mL, depending on the macrophyte biomass collected), placed into a glass jar and shaken vigorously to dislodge epiphytes. The contents of the jar were then poured through a steel sieve (53 μm) with a basin underneath to collect water containing the epiphytes. A measured amount of C-filtered water (500 mL or 250 mL) was used to rinse the macrophytes, the jar and the basin. The total volume of water used to clean the macrophytes (1 L or 500 mL) was recorded and transferred into a plastic sample bottle. These samples were brought back to the lab for analysis of epiphyton biomass (chlorophyll content). The macrophyte samples were processed as before.

Macrophyte biomass was measured four times during the experiment (17 June, 15 July, 12 August, and 27 August) using a 77 cm diameter PVC cylinder. The sampler enclosed all macrophytes contained in 0.45 m^2 of the enclosure bottom. Collected macrophytes were brought back to the lab where a sub-sample was taken to measure its surface area (length and diameter of stems and leaves). The remaining sample was sorted by species and placed in pre-weighed aluminum plates, dried at 100°C for 24 hours, re-weighed, and used to calculate macrophyte biomass in the enclosure (g/m^2).

3.4 Statistical Analysis

The statistical analysis for all parameters in both years was performed using one-factor analysis of variance (ANOVA) to detect significant differences between treatments. One-factor ANOVA compares differences between or among sample means, where it imposes no restriction on the number of means (Howell 1992). The null hypothesis was rejected when $p = 0.05$ and the treatments were said to be significantly different. A repeated-measures ANOVA was not used because the treatment concentration was not constant over time. Therefore, each sampling date was analyzed separately. The analysis was performed using Microsoft Excel Version 5.0a for Power Macintosh™. Reported values are all given as mean ± SE.

4. RESULTS

4.1 Aquarium Experiments

4.1.1 Experiment #1 (Fig. 5)

NO_3-N was present in the control aquaria at time 0 hours at 0.06 mg/L and increased to 0.2 mg/L for 46 hours. NO_3-N levels then decreased to 0.17 mg/L and remained at this concentration for the duration of the experiment. In the aquaria that received the waterfowl feces there was no NO_3-N present for 46 hours. At 60 hours, however NO_3-N was detected at 0.09 mg/L where it increased significantly ($p=0.042$) 34 hours later to reach a maximum concentration of 0.26 mg/L. Following this peak, concentrations remained constant at 0.14 mg/L for the duration of the experiment.

NH_3-N increased with time in the feces load treatment and was significantly different ($p<0.05$) from the control treatment that had no detectable amounts of NH_3-N present.

SRP concentrations in the feces load treatment were significantly higher ($p<0.05$) than the control treatment throughout the experiment which had no detectable amounts of SRP present. The highest SRP concentration occurred 12 hours after the feces slurry was added (1.76 mg/L), following after which concentrations decreased with time.

4.1.2 Experiment #2 (Fig. 6)

There was no NO_3-N detected in either treatment for the duration of Experiment 2. NH_3-N concentrations in the feces aquaria varied with time, but there was an overall increase while the control treatment remained relatively constant. SRP concentrations in the feces treatment increased with time and were significantly higher ($p<0.05$) than the control treatment which remained constant and low (<0.2 mg/L)

4.1.3 Experiment #3 (Fig. 7)

Changes in NO_3-N concentrations between the three treatments did not occur until 82 hours, after which, the high and low feces load levels increased from 0 mg/L to 0.15 mg/L and 0.02 mg/L, respectively. NO_3-N levels continued to increase with time in both the high and low feces load treatments for the duration of the experiment where concentrations were

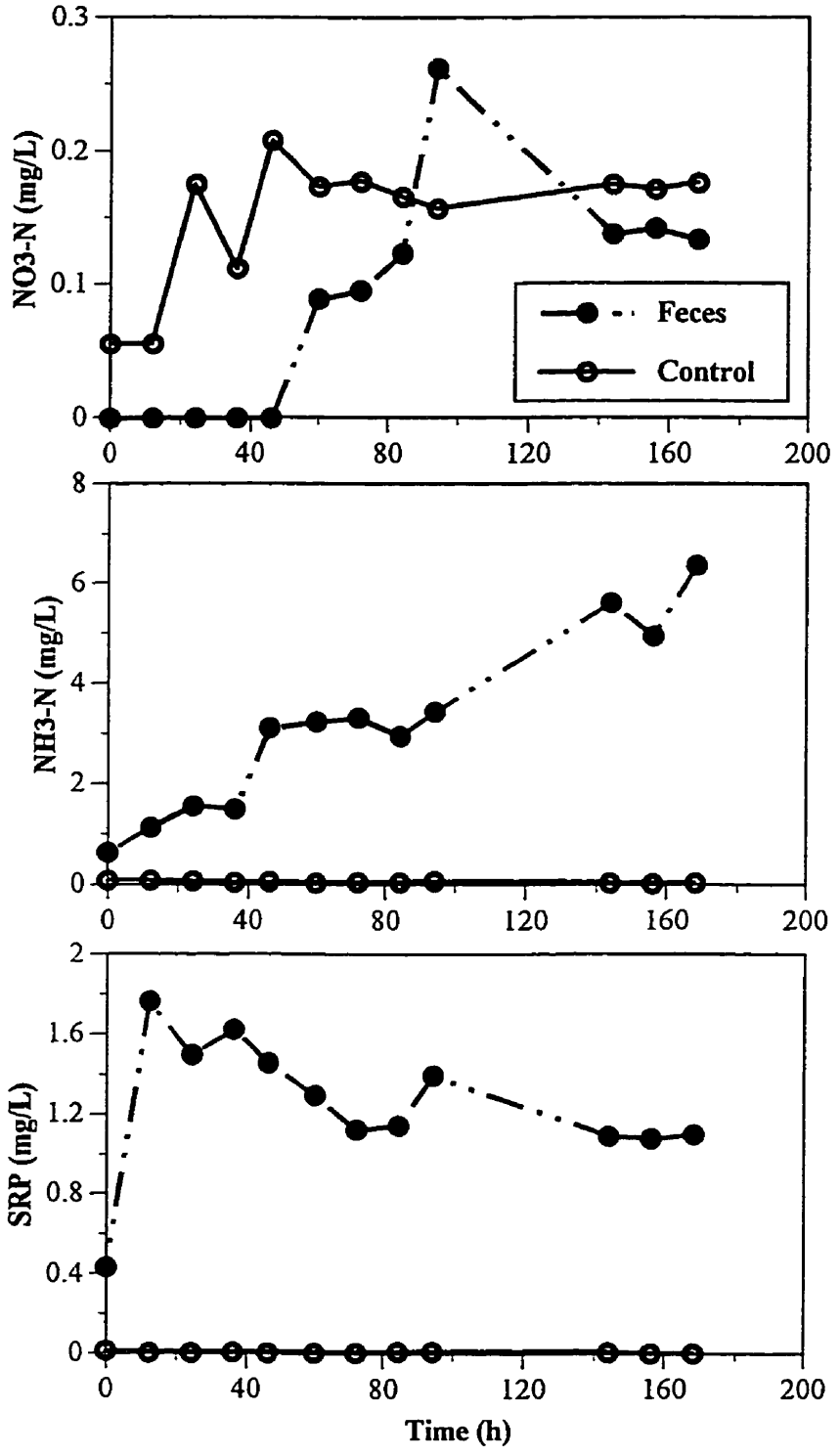

Figure 5. NO_3-N, NH_3-N and SRP concentrations (mg/L) liberated from waterfowl feces in the water column of two treatment aquaria during a 180-h period. Two aquaria received randoms amounts of the waterfowl feces slurry (closed circles) while two aquaria served as untreated controls (open circles).

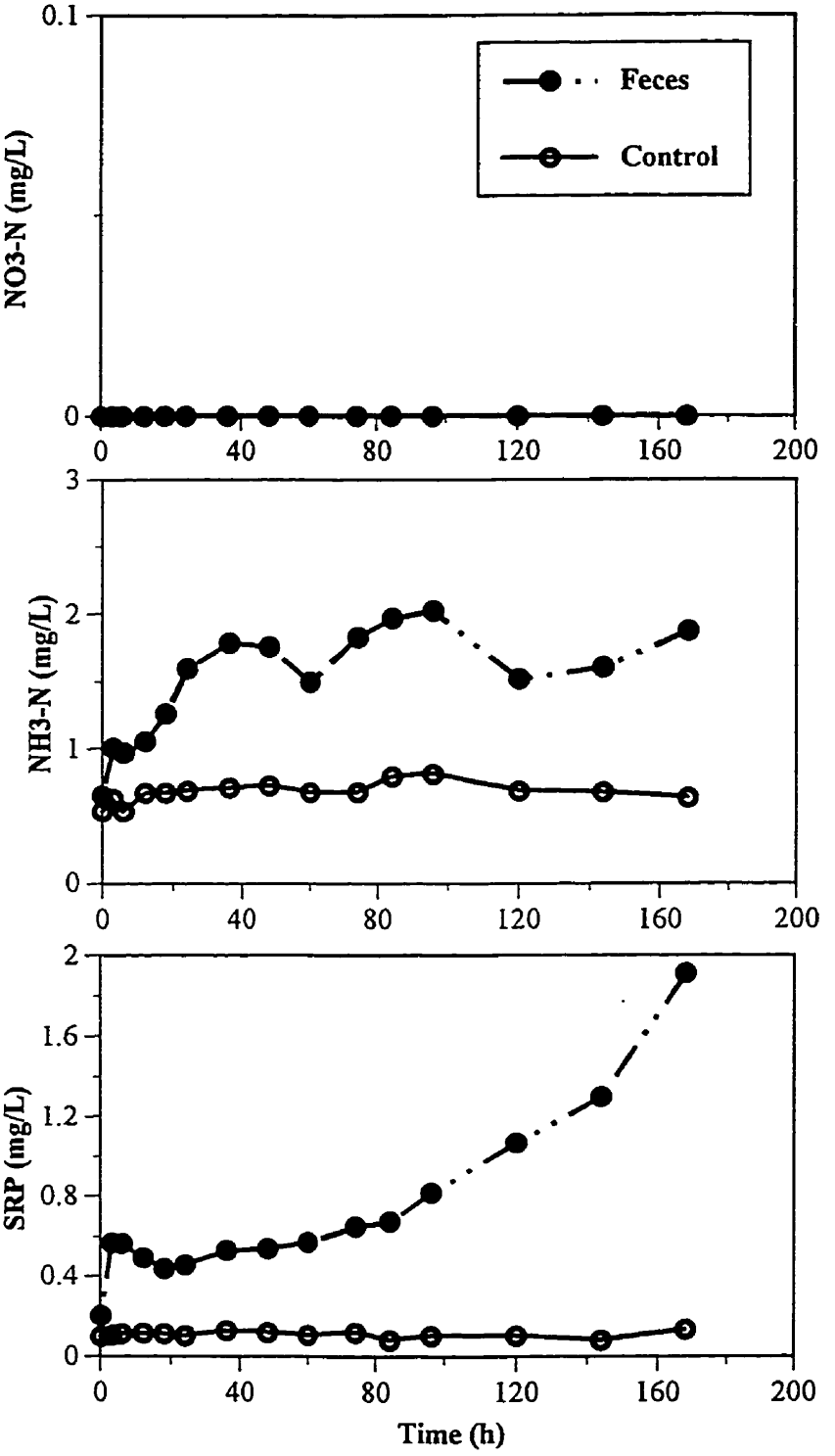

Figure 6. NO_3-N, NH_3-N and SRP concentrations (mg/L) liberated from waterfowl feces in the water column of two treatment aquaria during a 180-h period. Two aquaria received the same proportional load as applied to high feces loading enclosures in 1995 (closed circles) while two aquaria served as untreated controls (open circles). All aquaria contained 4L of fresh marsh sediment.

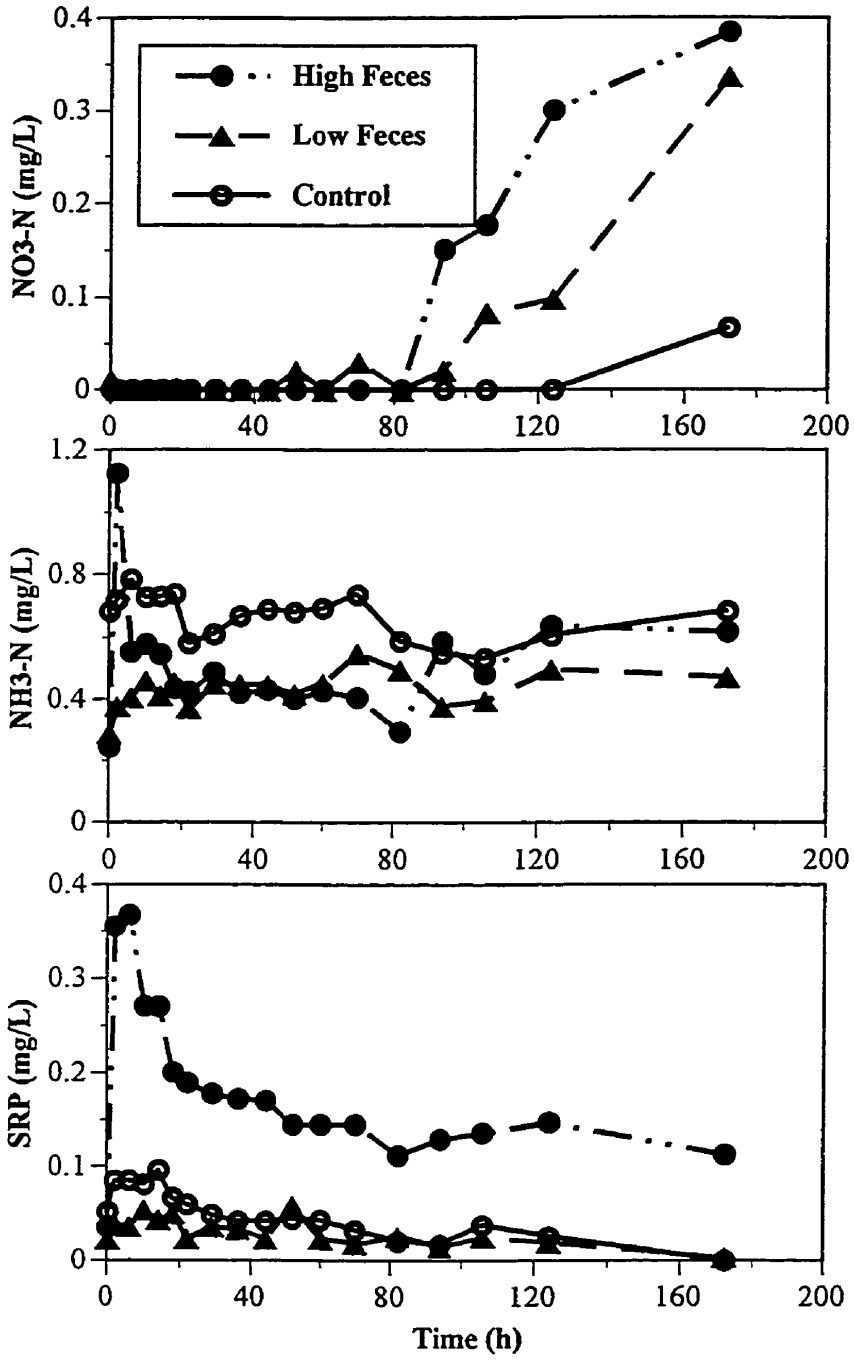

Figure 7. NO_3-N, NH_3-N and SRP concentrations (mg/L) liberated from waterfowl feces in the water column of three treatment aquaria during a 180-h period. Two aquaria received the same proportional load as applied to high feces loading enclosures in 1995 (closed circles), two aquaria received the same proportional load as applied to low feces loading enclosures in 1995 (closed triangles) while one aquarium served as an untreated control (open circles). All aquaria contained 4L of fresh marsh sediment.

always highest in the high feces load treatment. There were no significant differences between treatments on any of the sampling times ($p>0.05$).

The concentration of NH_3-N varied with time in all treatments. There was a significant difference between treatments at times 0, 2 and 4 hours ($p=0.018$, 0.009, and 0.03, respectively) while during the other sampling times, there was no significant difference between treatments ($p>0.05$). The greatest fluctuation in concentrations occurred in the high feces load treatment two hours after the feces slurry was added NH_3-N levels went from 0.24 mg/L to 1.13 mg/L. NH_3-N concentrations then decreased to approximately 0.5 mg/L where they remained around this level for the duration of the experiment.

SRP increased for the first six hours of the experiment in the high feces load treatment after which, SRP levels gradually decreased with time. Concentrations increased from 0.035 mg/L time 0 hour to 0.36 mg/L at time 2 hour to 0.37 mg/L at time 6 hour and then began to decrease at 10 hours to 0.27 mg/L. The low feces load and control treatments remained relatively constant and low with concentrations not exceeding 0.1 mg/L. There was no significant difference ($p>0.05$) between treatments at any of the sampling times.

4.1.4 Experiment #4 (Fig. 8)

Significant differences ($p<0.05$) occurred between treatments for only the first ten sampling times with respect to changes in NO_3-N concentrations after which, there was no significant difference ($p>0.05$) between treatments. Following feces additions to the high and low load treatments, NO_3-N concentrations were highest in the low feces load treatment than the high feces load treatment, where values remained constant at approximately 0.25 mg/L for the duration of the experiment. The NO_3-N levels in the high feces load treatment were less than 0.15 mg/L for the first 40 hours of the experiment, where they increased to levels reaching those of the low feces load treatment. There was no NO_3-N detected in the control treatment.

NH_3-N concentrations in all treatments varied with time, but they were significantly higher in the high feces load treatment than the other two treatments for the first 60 hours of the experiment. However, after 80 hours the NH_3-N concentrations in the three treatments were relatively similar and there was no significant difference between them.

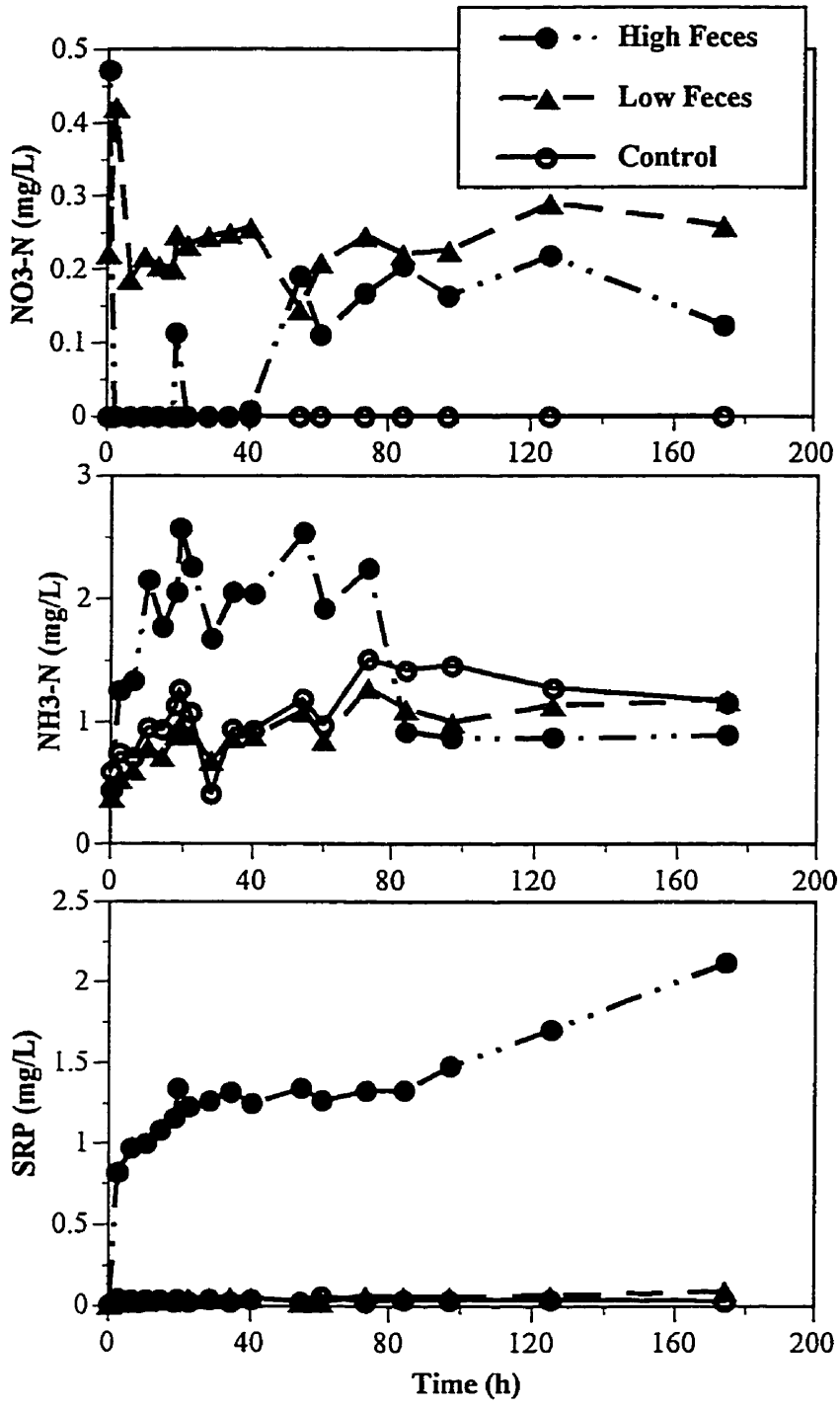

Figure 8. NO_3-N, NH_3-N and SRP concentrations (mg/L) liberated from waterfowl feces in the water column of three treatment aquaria during a 180-h period. Two aquaria received the same proportional load as applied to high feces loading enclosures in 1995 (closed circles), two aquaria received the same proportional load as applied to low feces loading enclosures in 1995 (closed triangles) while one aquarium served as an untreated control (open circles). All aquaria contained 4L of thawed marsh sediment.

SRP concentrations in the low feces load and control treatments were constant and neither exceeded 0.06 mg/L. SRP levels increased with time in the high feces load treatment upon receiving the feces addition, yet there was no significant difference ($p>0.05$) between treatments.

4.2 Year 1 (1995)

4.2.1 Physical Data

Vertical attenuation coefficient (k_d) and macrophyte biomass varied during the experiment, but did not differ significantly ($p > 0.05$) between treatments (Appendix A).

Water was turbid (> 2 NTU) in all the enclosures at the beginning of the experiment (Fig. 9), but declined with time due to the protection against the effects of wind and fish on the resuspension of bottom sediments provided by the enclosure curtains. As well, as the experiment progressed, so did the growth of macrophytes, reducing resuspension of sediments where their roots stabilize the substrata. Following the first and second feces additions, turbidity between the treatments varied significantly (p = 0.009 and 0.02, respectively). However, by the next sampling date there was no difference between treatment probably due to the settling of the feces addition.

4.2.2 Chemical Data

Dissolved oxygen at 10 cm, alkalinity and pH varied during the experiment, but did not differ significantly ($p > 0.05$) between treatments (Appendix A).

Dissolved oxygen levels in the evening, 50 cm from the water surface (Fig. 10) showed a negative trend with time from the mean initial readings on the 13 June in the high, low and control enclosures (14.8 ± 0.2, 15.0 ± 0 and 15.0 ● 0 mg/L, respectively) to the mean final readings on the 28 August (5.65 ± 2.4, 2.40 ± 1.7, and 2.00 ± 0.9 mg/L, respectively). Significant variation (p = 0.008) between the treatments and the controls occurred once on 23 July with mean dissolved oxygen readings in the high feces load enclosures of 4.0 mg/L ± 0.4, in the low feces load enclosures of 7.6 ± 0.2 mg/L and in the control enclosures of 7.6 ± 0.4 mg/L.

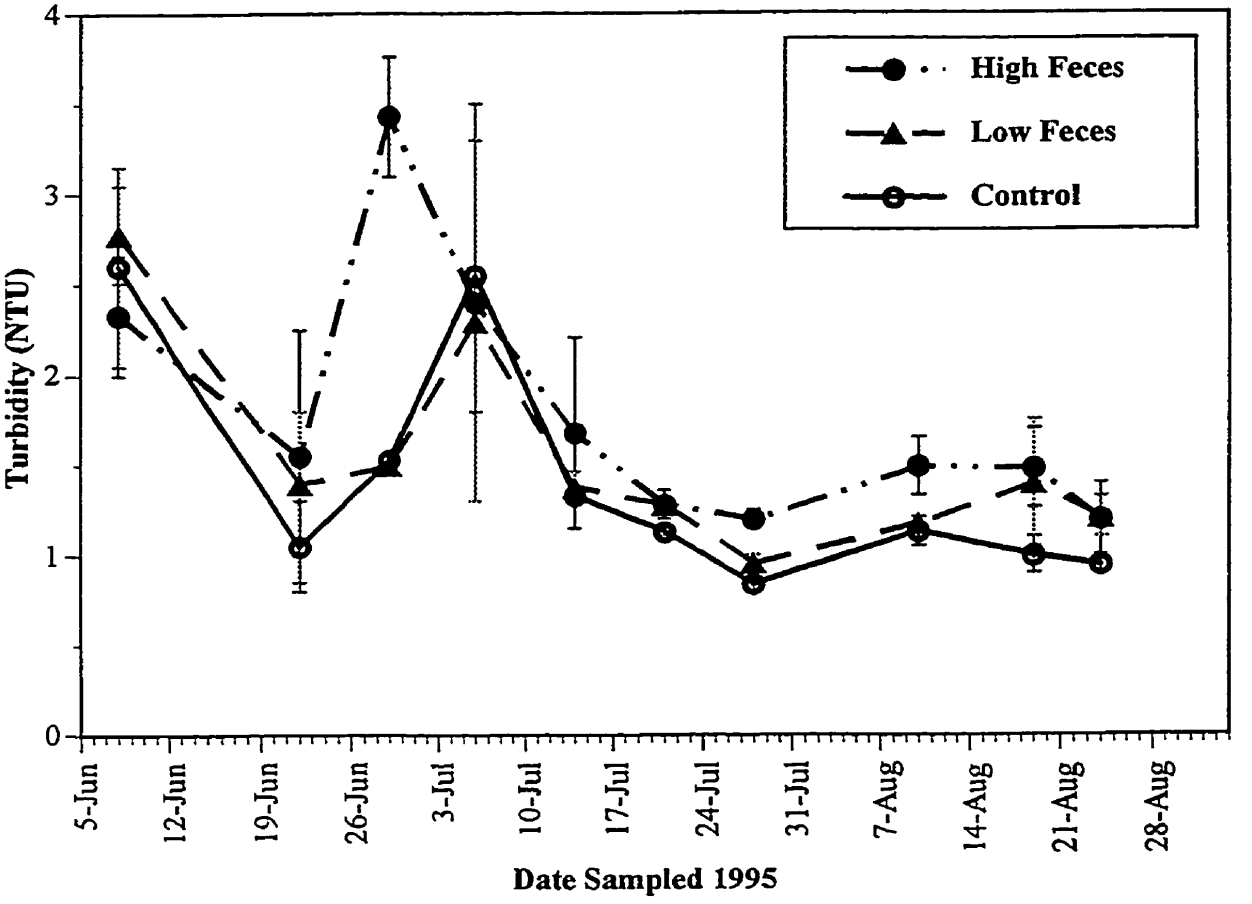

Figure 9. Water column turbidity (NTU ± SE, n = 2) during a 12-week sampling period in control (open circles), low feces load (closed triangles) and high feces load (closed circles) enclosures, 1995. Feces additions were made on 28 June and 21 July.

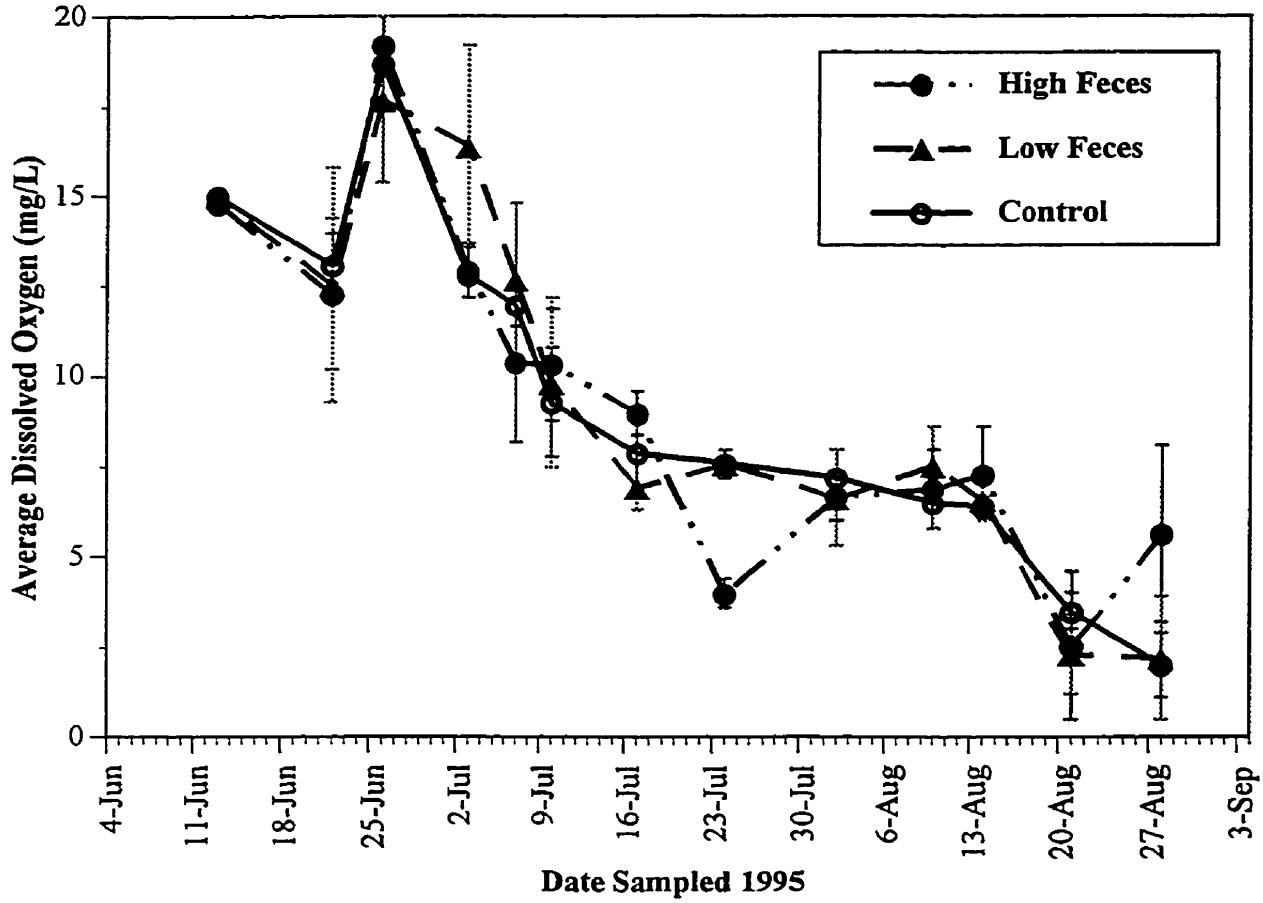

Figure 10. Dissolved oxygen concentration in the evening, 50 cm from water surface (mg/L ● SE, n = 2), during a 12-week sampling period in control (open circles), low feces load (closed triangles), and high feces load (closed circles) enclosures, 1995. Feces additions were made on 28 June and 21 July.

The concentration of nitrate-nitrite, as analyzed by Norwest Labs, varied with time in all treatments, yet remained low (< 0.05 mg/L) during the 13-week experimental period (Fig. 11). Two sampling dates expressed significant difference between treatments where p = 0.005 on 16 June and p = 0.03 on 25 August. The enclosures were not manipulated until the fifth week of the experimental period, suggesting that on 16 June (week 3) the higher value observed in the low treatment enclosures was not a treatment effect, but instead a settling effect where the enclosures had yet to reach constancy. The nitrate-nitrite concentration did increase in the high feces load treatment after the first feces addition on 28 June from 0.006 mg/L ± 0.001 to 0.020 mg/L ± 0.006, but did not increase after the second feces addition on 21 July. Therefore, I suggest it was not a treatment effect on 25 August (week 13) which caused a significant p-value, but rather a seasonal effect of macrophyte senescence, which in turn released P, causing N-limitation in the high feces load treatment.

TKN increased with time in the high feces load treatment, yet remained relatively constant in both the low feces load and control treatments (Fig. 12). After the first feces addition, the TKN value increased from 1.28 mg/L ± 0.11 to 3.00 mg/L ± 0.56, while after the second addition the TKN value increased from 1.81 mg/L ± 0.09 to 2.26 mg/L ± 0.44. The larger difference between TKN concentrations after the first addition than after the second addition was probably due to the time lag between additions and sampling dates. TKN was determined one day after the first feces addition, but seven days after the second feces addition. There were significant differences between treatments on 4 August (p = 0.05) and 18 August (p = 0.05).

Total P concentration followed a similar trend as TKN where there was a gradual increase with time in the high feces load treatments while the low feces load and control treatments remained relatively constant and low (Fig. 13). A significant difference between the treatments and the controls occurred once on 29 June, one day following the first feces addition (p = 0.05). The high feces treatment increased TP from 0.15 mg/L ± 0.03 to 0.27 mg/L ± 0.07, while both the low feces treatment and controls showed a decrease in TP concentration.

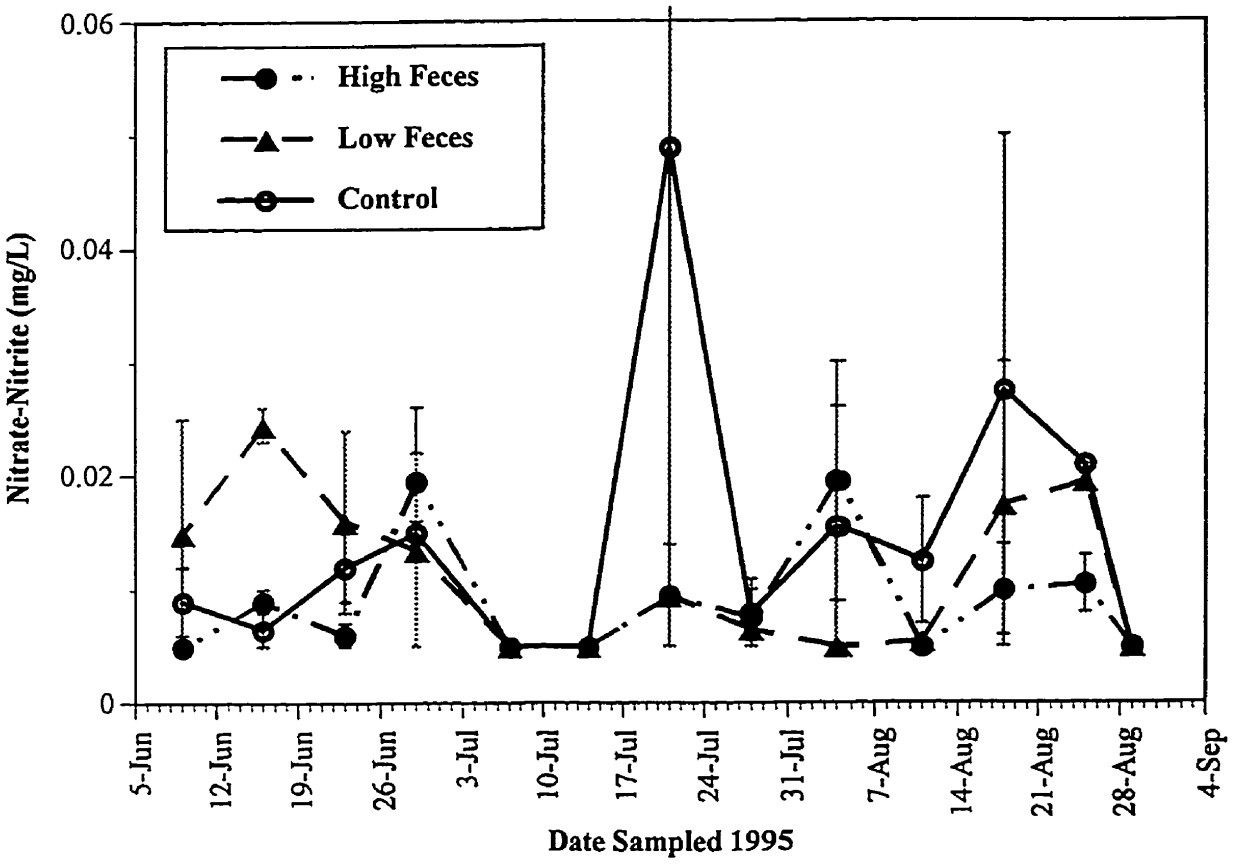

Figure 11. Nitrate-nitrite-N concentration (mg/L ± SE, n = 2), as analyzed by Norwest Labs, in the water column during a 13-week sampling period in control (open circles), low feces load (closed triangles) and high feces load (closed circles) enclosures, 1995. Feces additions were made on 28 June and 21 July.

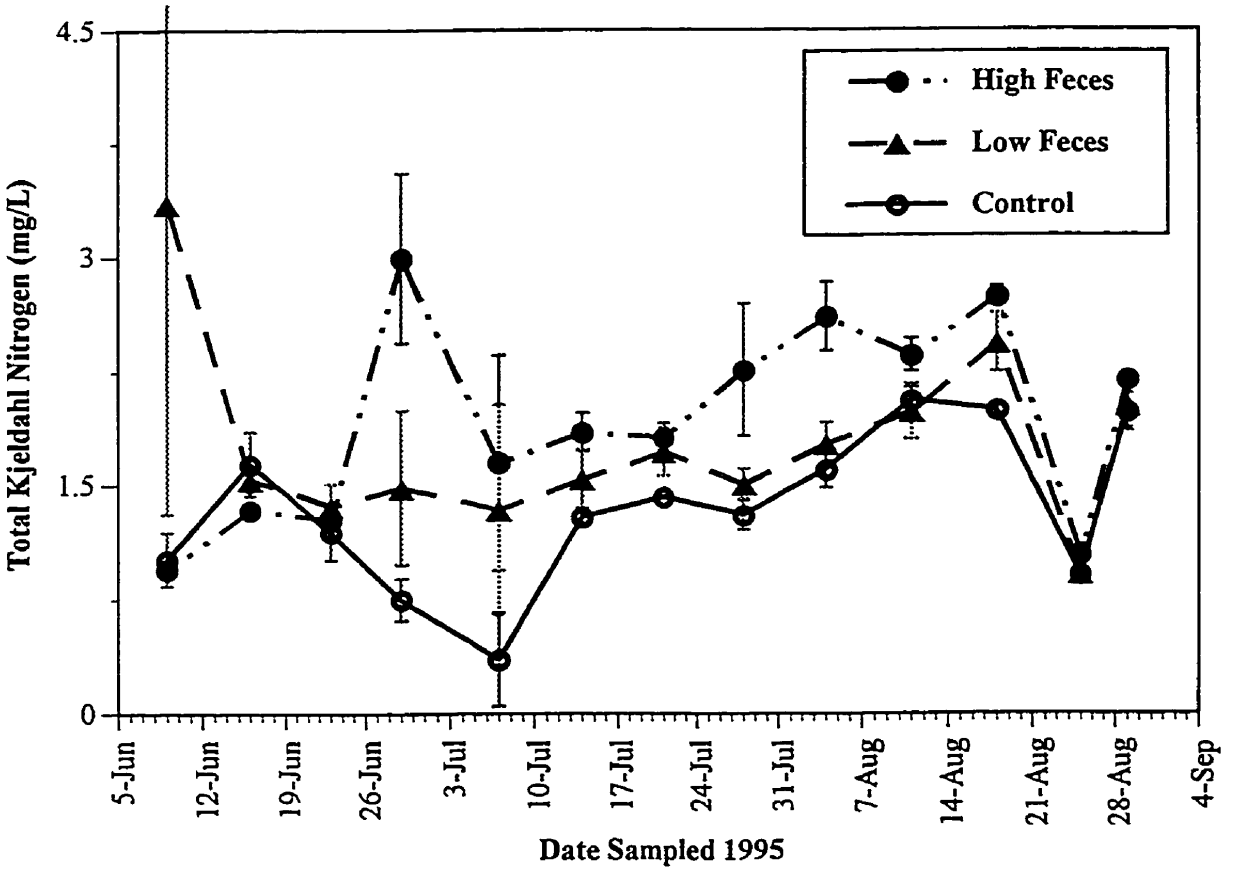

Figure 12. TKN concentration (mg/L ± SE, n = 2) in the water column during a 13-week sampling period in control (open circles), low feces load (closed triangles) and high feces load (closed circles) enclosures, 1995. Feces additions were made on 28 June and 21 July.

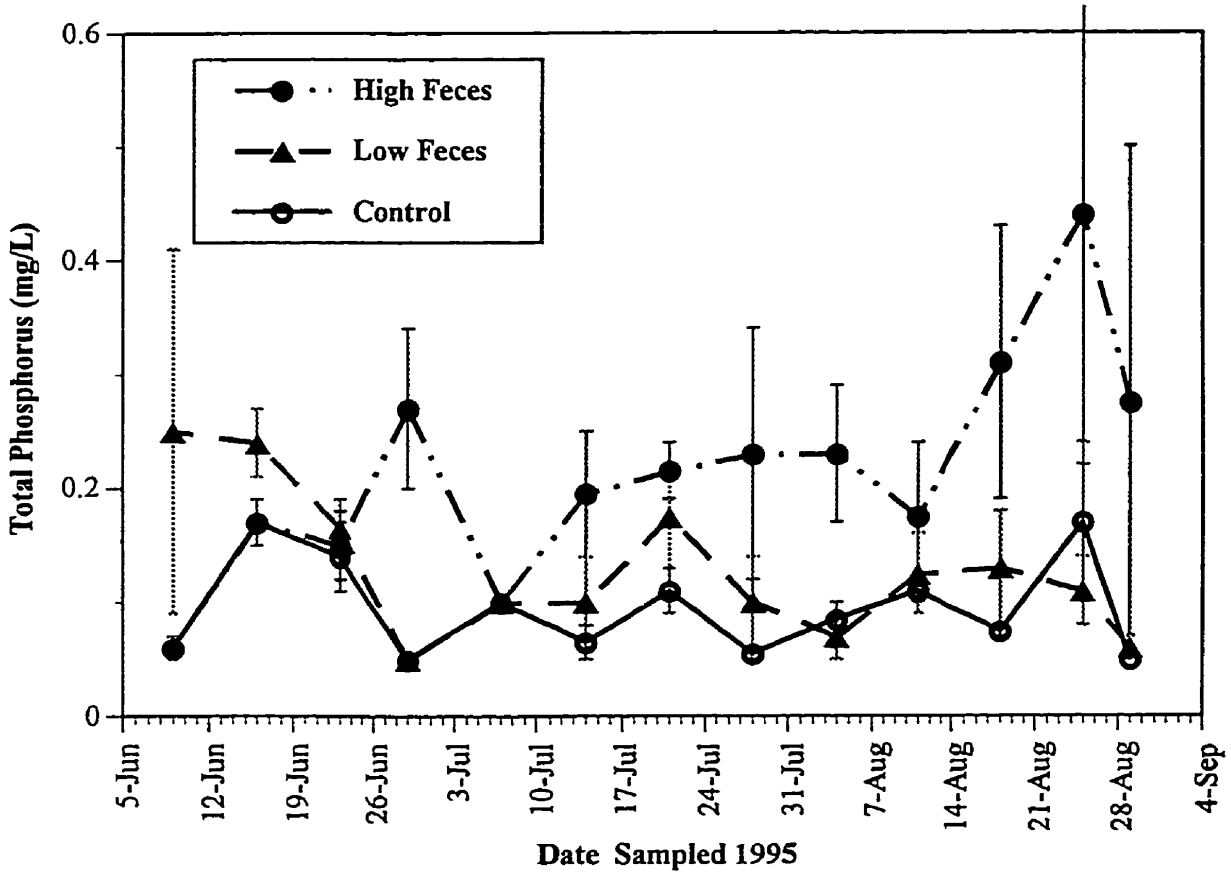

Figure 13. Total phosphorus concentration (mg/L ± SE, n = 2) in the water column during a 13-week sampling period in control (open circles), low feces load (closed triangles) and high feces load (closed circles) enclosures, 1995. Feces additions were made on 28 June and 21 July.

Within one week of the first addition there was a decrease in the TP concentration in the high feces treatment which was not observed after the second addition. Following the second addition, there was an increase in TP in the high feces concentration from 0.22 mg/L ± 0.025 to 0.23 mg/L ± 0.11, however there was no significant difference between treatments. Again, the low feces load treatment and the controls did not increase TP after the second addition. TP peaked on 25 August in the high feces load treatment (0.44 mg/L ± 0.22), yet there was no significant difference between treatments.

NH_3-N differed significantly between treatments after each feces addition where p = 0.00034 on 28 June and $p = 0.0053$ on 21 July (Fig. 14). The maximum NH_3-N concentration was observed in the high feces treatment enclosures after the first and second additions (1.035 mg/L ± 0.033 and 0.671 mg/L ± 0.004, respectively). The low feces treatment also increased after the feces additions where maximum concentrations reached 0.094 mg/L ± 0.046 and 0.093 mg/L ± 0.091 respectively. Following the feces additions the NH_3-N concentrations in the high and low feces load treatments decreased within 24 hours, yet remained significantly different ($p < 0.05$) from each other after the addition on 28 June. However, 24 hr. following the second feces addition on 21 July, NH_3-N concentrations levels remained low during the remainder of the experiment with no significant difference between treatments.

SRP levels increased with time in both the high and low feces load treatments upon receiving the feces additions while the control was no greater than 0.054 mg/L ± 0.007 (Fig. 15). SRP concentrations peaked significantly after each feces addition ($p = 0.0016$ and 0.0022, respectively) in the treatment enclosures. Following the first feces addition SRP in the high feces load treatment was 0.695 mg/L ± 0.058, while in the low feces load treatment SRP concentration was 0.108 mg/L ± 0.021. Levels were highest after the second feces addition in both high and low feces treatments (1.399 mg/L ± 0.081 and 0.218 mg/L ± 0.114, respectively). Values in both treatments decreased within 24 hours of the feces additions, yet a significant difference ($p > 0.05$) between treatments continued 4 days following both additions.

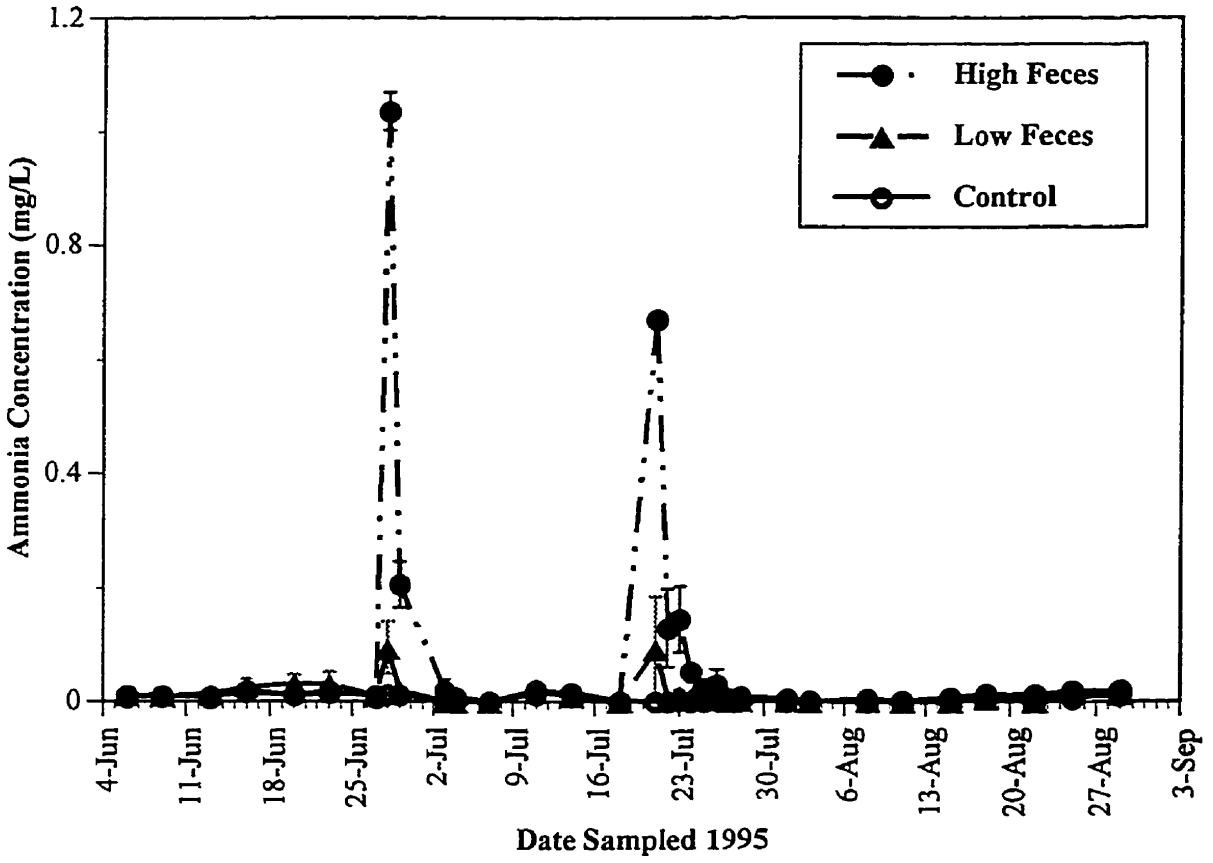

Figure 14. NH_3-N concentration (mg/L ± SE, n = 2) in the water column during a 13-week sampling period in control (open circles), low feces load (closed triangles), and high feces load (closed circles) enclosures, 1995. Feces additions were made on 28 June and 21 July.

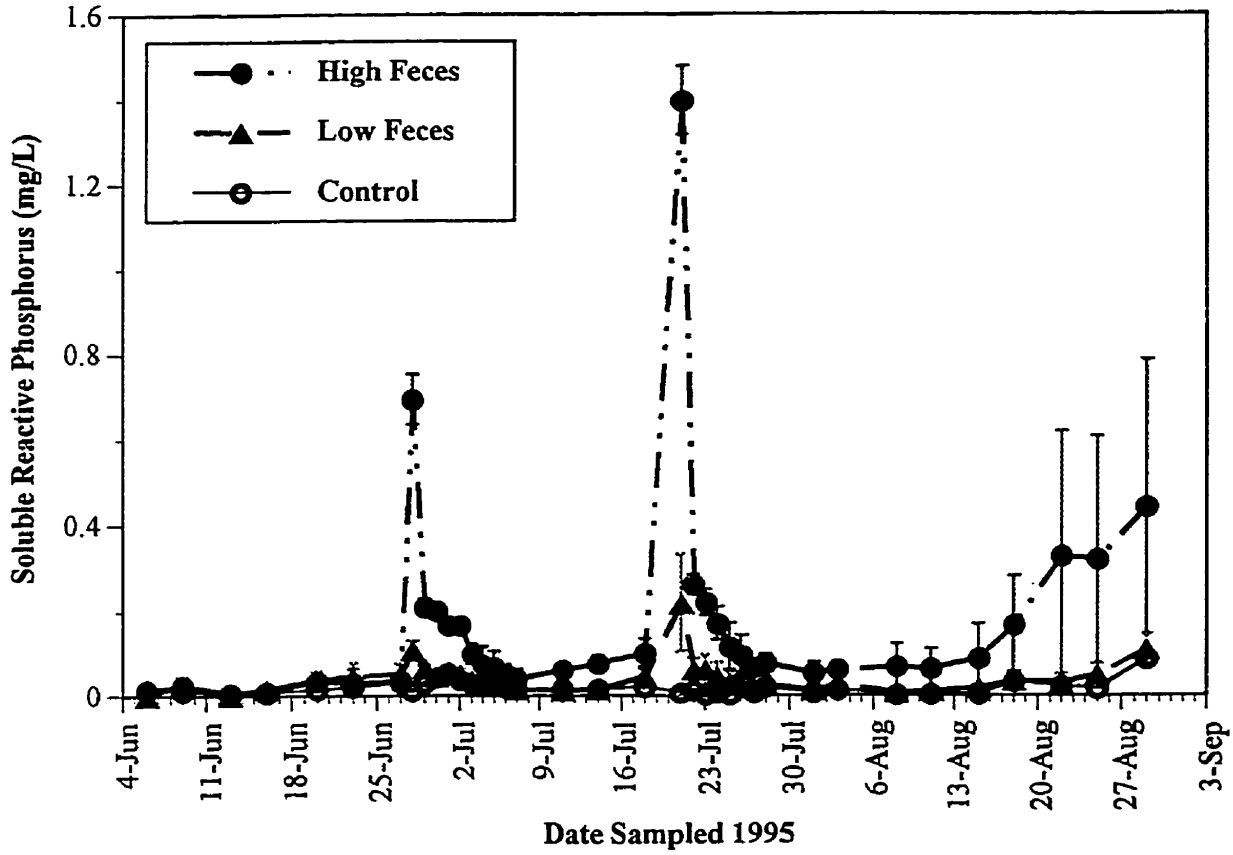

Figure 15. SRP concentration (mg/L ± SE, n = 2) in the water column during a 13-week sampling period in control (open circles), low feces load (closed triangles), and high feces load (closed circles) enclosures, 1995. Feces additions were made on 28 June and 21 July.

Soluble reactive silicon concentrations varied throughout the duration of the 13-week experiment (Fig. 16) and differed significantly on three separate sampling dates. On 13 June $p = 0.02$, however this was prior to feces addition and therefore not relevant to the purpose of this study. Trends between the three treatments were similar for the month of June and the first two weeks of July but there was a deviation between the treatments after week 6. The high feces load treatment continued to decrease, reaching the lowest level on 25 July (0.134 mg/L ± .017), while the low feces load and control treatments remained constant (1.487 mg/L ± 0.777 and 1.737 ± 0.757 mg/L, respectively), displaying little variation between them. There was no significant difference between treatments until week 12, where the trends observed following week 6 were reversed. On 22 and 25 August ($p = 0.013$ and $p = 0.021$, respectively), the high feces load enclosures had higher levels of soluble reactive silicon than the other two treatments.

4.2.3 Biological Data

Phytoplankton

Changes in phytoplankton chlorophyll, photosynthesis and particulate P concentrations varied over time in all treatments with no significant effect ($p > 0.05$) of feces additions (Figs. 17, 18 and 19). Levels peaked in the high feces load treatment (30.04 µg/L ± 27.21, 309.32 µg C/L/h ± 285.82 and 7.91 µg/L ± 4.48, respectively) following the feces addition on 28 June, yet declined within one week. Chlorophyll concentrations remained low (< 5 µg/L) in both the low feces load and control treatments following the first feces addition, but increased after the second feces addition on 21 July. Productivity remained low throughout the remainder of the experiment in all three treatments. By mid-July particulate P concentrations were low in the three treatments, with little variation in trends between them. Particulate P concentrations increased in the three treatments mid-August and peaked on 29 August where the highest concentration in the low feces load treatment (14.93 µg/L ± 3.26). Also during the month of August, phytoplankton chlorophyll increased in the three treatments where again, the highest values reached were in the low feces treatment (56.82 µg/L ± 11.38).

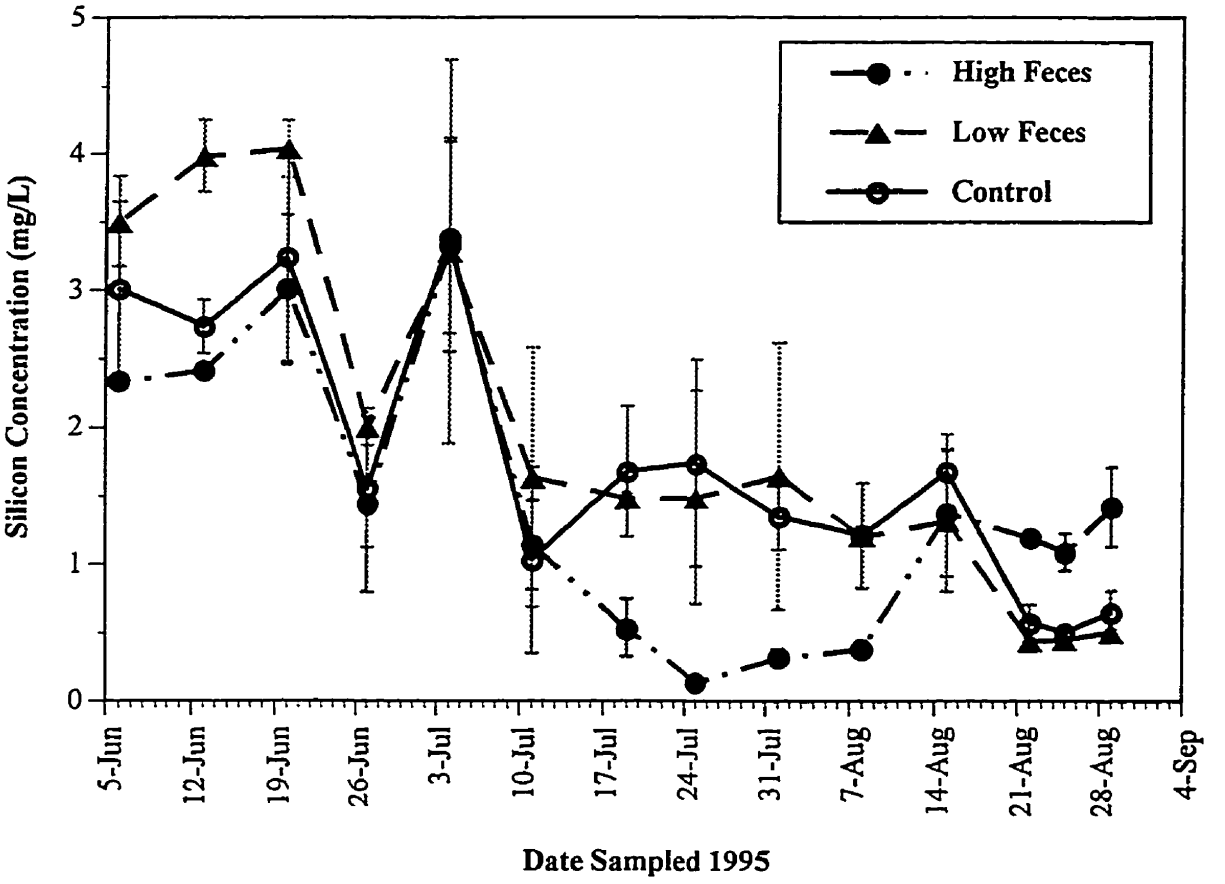

Figure 16. Soluble reactive silicon concentration (mg/L ± SE, n = 2) in the water column during a 13-week sampling period in control (open cirlces), low feces load (closed triangles), and high feces load (closed circles) enclosures, 1995. Feces additions were made on 28 June and 21 July.

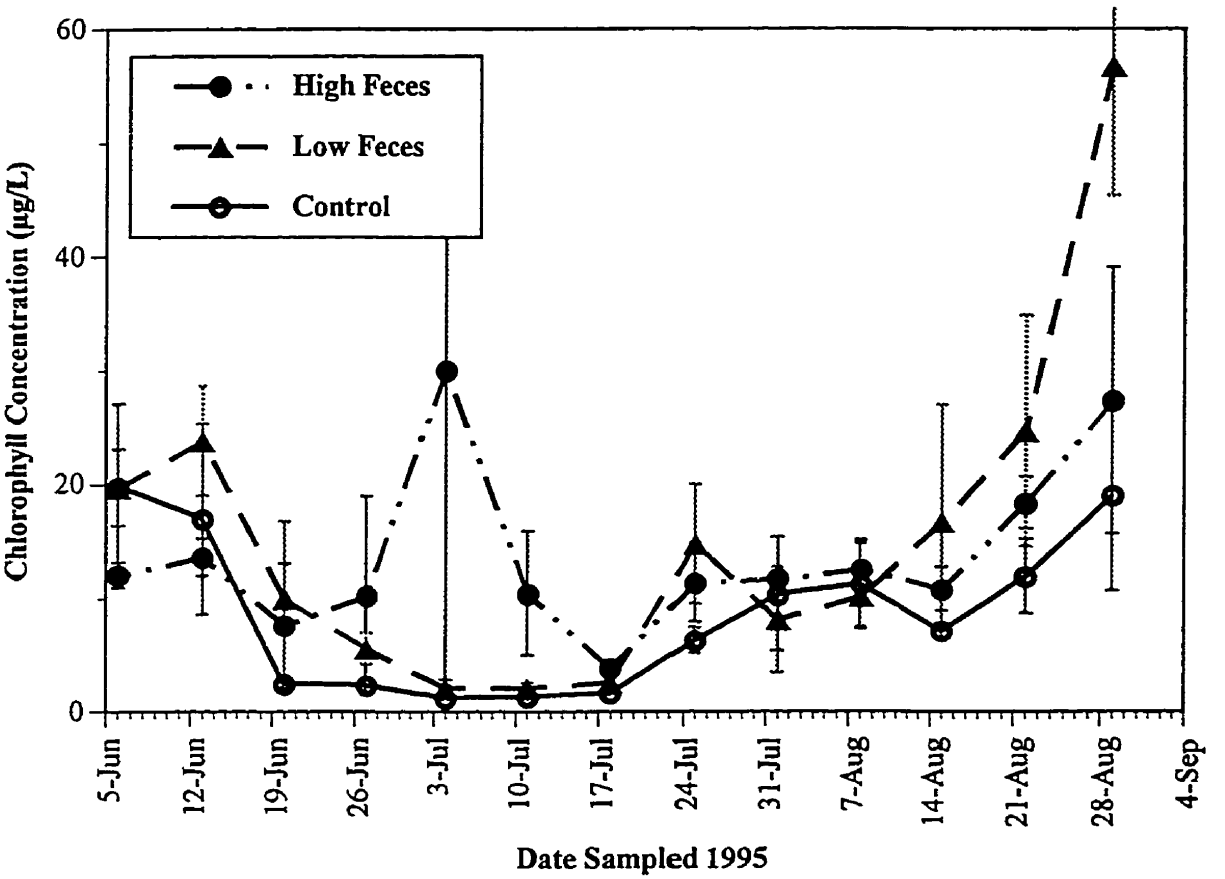

Figure 17. Phytoplankton chlorophyll concentration (µg/L ± SE, n = 2) during a 13-week sampling period in control (open circles), low feces load (closed triangles), and high feces load (closed circles) enclosures, 1995. Feces additions were made on 28 June and 21 July.

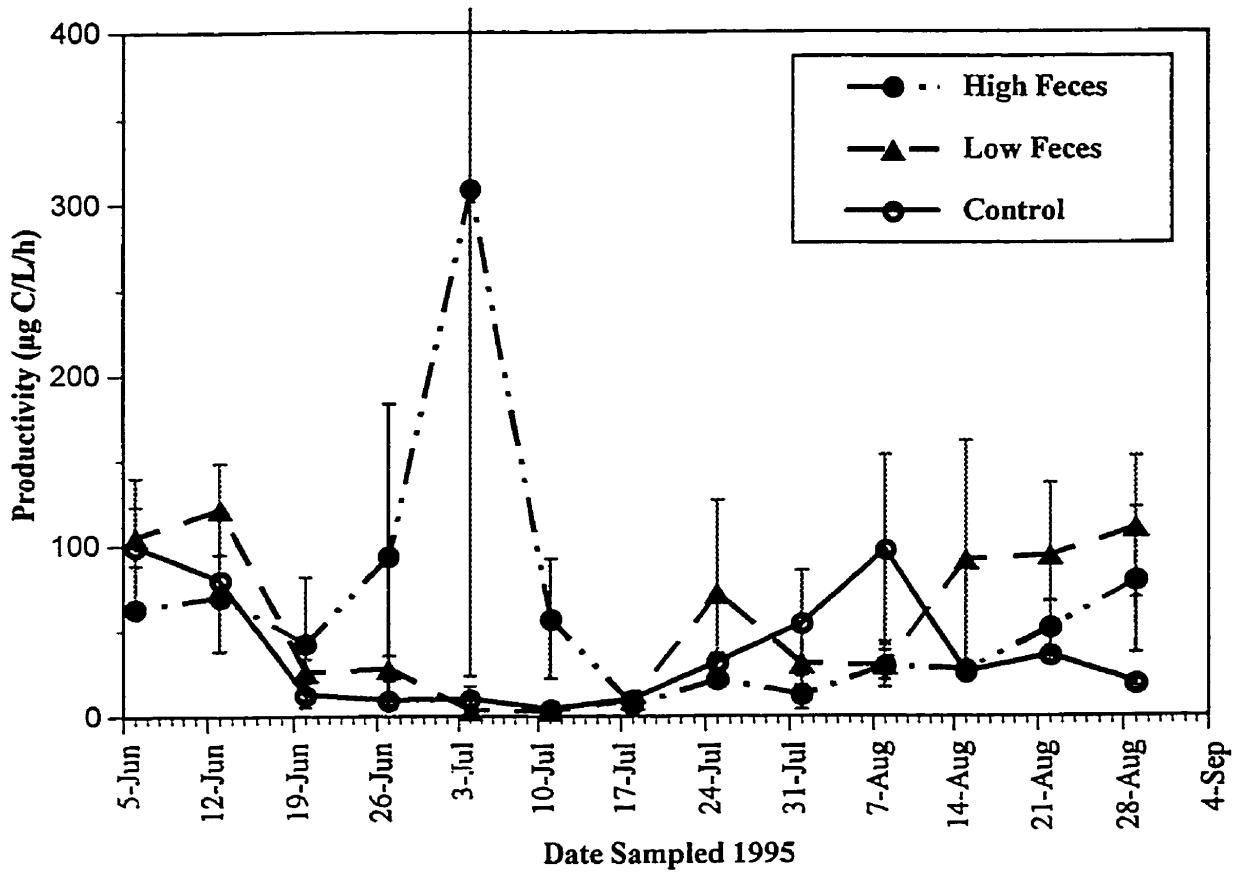

Figure 18. Phytoplankton photosynthetic rate (µgC/L/h ± SE, n = 2) during a 13-week sampling period in control (open circles), low feces load (closed triangles), and high feces load (closed circles) enclosures, 1995. Feces additions were made on 28 June and 21 July.

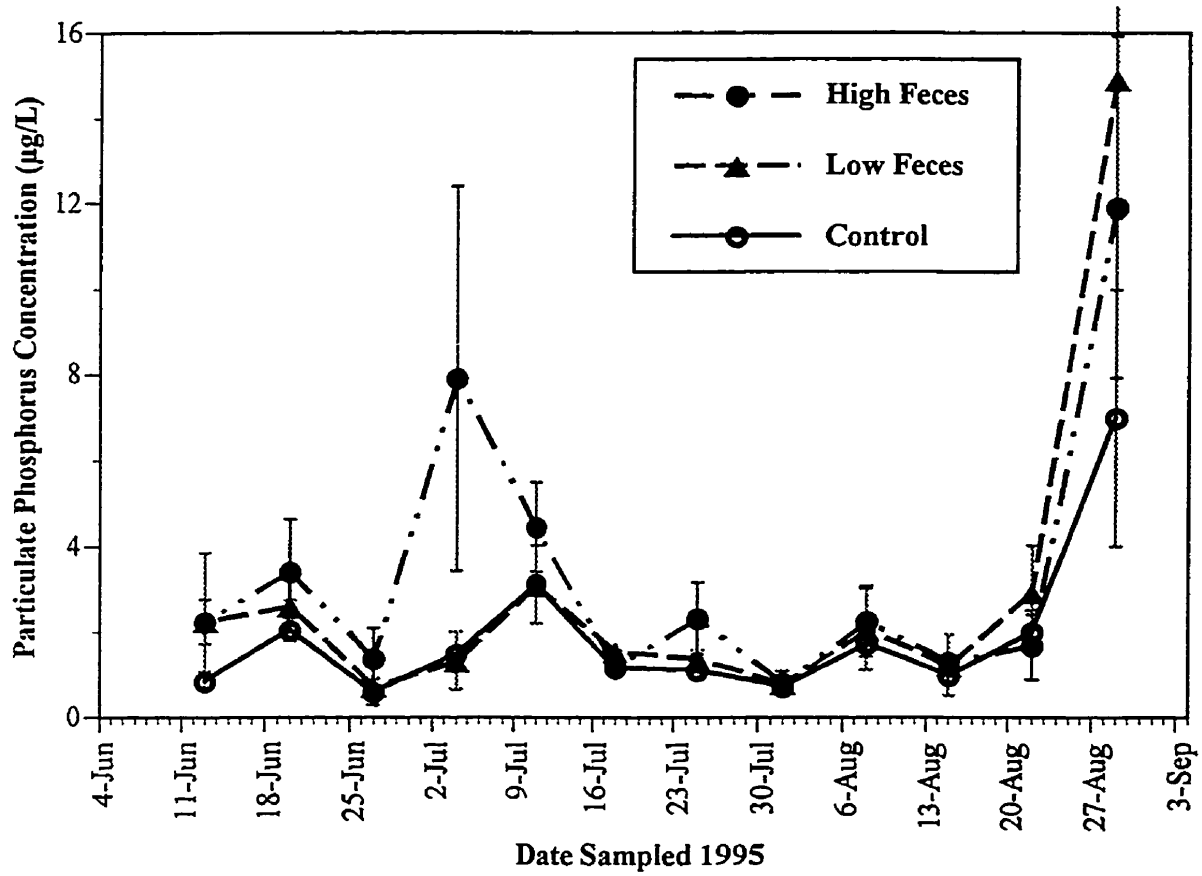

Figure 19. Phytoplankton particulate P concentration (µg/L ± SE, n = 2) during a 13-week sampling period in control (open circles), low feces load (closed triangles) and high feces load (closed circles) enclosures, 1995. Feces additions were made on 28 June and 21 July.

The biological data to follow, like the parameters measured for phytoplankton, varied during the experiment, but did not differ significantly ($p>0.05$) between treatments. Data are summarized in Table 3.

Periphyton

Three different pattern of trends were observed in periphyton chlorophyll, photosynthesis and particulate P concentrations. Periphyton chlorophyll concentrations in the control enclosures were consistently low (~ 0.6 $\mu g/cm^2$) throughout the duration of the experiment. Following each feces addition there was an increase in chlorophyll concentrations in the high and low feces load treatments. The low feces load treatment peaked after the first feces addition (1.41 $\mu g/cm^2 \pm 0.86$), while the high feces load treatment increased yet remained around control levels (0.64 $\mu g/cm^2 \pm 0.20$). One week after the addition, the low feces treatment remained at the same concentration (1.41 $\mu g/cm^2 \pm 1.07$) and the high feces load treatment increased (1.30 $\mu g/cm^2 \pm 0.41$). However, two weeks after the first feces addition, chlorophyll levels in both the high and low feces load treatments decreased, reaching similar levels (0.51 $\mu g/cm^2 \pm 0.23$ and 0.53 $\mu g/cm^2 \pm 0.06$, respectively) until the second addition. Then periphyton chlorophyll increased in the high and low feces load treatments (2.04 $\mu g/cm^2 \pm 0.44$ and 0.90 $\mu g/cm^2 \pm 0.51$, respectively), and decreased the following week. Throughout August chlorophyll levels in the low feces load treatment remained similar to levels in the control treatment while levels in the high feces load treatment increased. There were no significant difference between treatments on any of the dates analyzed for chlorophyll.

Prior to the end of July there was no significant difference between periphyton productivity in the three treatments. There was however, a significant increase ($p = 0.036$) in productivity after the second feces addition on 27 July, but values decreased the following week and during the month of August the trends between the three treatments were the same and remained low.

There was no significant difference between periphyton particulate P in the three treatments until mid-August. Throughout the experiment, particulate P concentrations in the control

Table 3. Mean (range in parentheses) of biological data measured for periphyton, epipelon, sediment, macrophyte, epiphyton and invertebrates for experimental enclosures (1995). None of the treatments varied significantly ($p>0.05$).

Parameter	High Feces	Low Feces	Control
Periphyton			
Chlorophyll ($\mu g/cm^2$)	0.84 (0.09 - 2.04)	0.62 (0.20 - 1.40)	0.38 (0.07 - 0.60)
Photosynthesis ($\mu gC/cm^2/h$)	2.60 (0.29 - 15.64)	2.37 (0.42 - 11.82)	1.41 (0.25 - 6.19)
Particulate P ($\mu g/cm^2$)	0.04 (0.006 - 0.11)	0.07 (0.006 - 0.28)	0.02 (0.005 - 0.06)
Epipelon			
Chlorophyll ($\mu g/cm^2$)	0.08 (0.05 - 0.13)	0.08 (0.04 - 0.11)	0.10 (0.04 - 0.20)
Photosynthesis ($\mu gC/cm^2/h$)	0.05 (0.02 - 0.08)	0.06 (0.03 - 0.11)	0.11 (0.02 - 0.36
Sediment			
Particulate P ($\mu g/gdw$)	167.42 (142.00 - 187.56)	157.76 (139.87 - 180.81)	149.12 (128.00 - 165.42)
Macrophyte			
Particulate P ($\mu g/gdw$)	469.22 (351.71 - 661.22)	605.14 (396.21 - 846.81)	537.69 (361.66 - 698.52)
Epiphyton			
Chlorophyll ($\mu g/gdw$)	85.84 (20.86 - 204.64)	95.64 (23.09 - 232.38)	47.18 (13.40 - 113.84)
Particulate P ($\mu g/gdw$)	5.93 (0.69 - 8.26)	9.51 (1.50 - 30.36)	4.64 (0.22 - 12.73)
Invertebrates			
Particulate P ($\mu g/gdw$)	935.94 (585.30 - 1880.65)	693.78 (371.72 - 1034.20)	929.06 (417.77 - 1305.93)

were steady (≤ 0.06 $\mu g/cm^2$) and did not vary with time. Concentrations peaked in the low feces load treatment (0.28 ± 0.25 $\mu g/cm^2$) on 29 June, but decreased steadily until eventually particulate P levels fell to those of the control. Particulate P levels fluctuated in the high feces load treatment, but gradually increased with time, reaching a maximum after the second feces addition (0.11 ± 0.025 $\mu g/cm^2$). However, two weeks following the feces addition, the concentration in the high feces load treatment decreased and remained similar to the other two treatments until the conclusion of the experiment.

Epipelon

Epipelon chlorophyll concentrations and photosynthesis showed no treatment effects. No significant difference ($p > 0.05$) due to feces additions was detected in the two parameters among the three treatments throughout the sampling period.

Sediment

Feces additions had no significant effect ($p > 0.05$) on sediment particulate P where the concentrations in all treatments increased with time. During the first week of August, the last time sediment particulate P was sampled, the control treatment concentration decreased from the previous sampling date, below both feces treatments.

Macrophyte

Macrophyte particulate P concentrations varied over time, but did not differ significantly among treatments ($p > 0.05$).

Epiphyton

Throughout the 7-week sampling period in which epiphyton chlorophyll and particulate P were measured, no significant differences among treatments were found in either parameter.

Invertebrates

Invertebrate particulate P concentrations varied over time, with no significant differences among treatments.

4.3 Year 2 (1996)

4.3.1 Physical Data

Turbidity, vertical attenuation coefficient (k_d) and macrophyte biomass varied during the experiment, but did not differ significantly ($p > 0.05$) between treatments (Appendix A).

4.3.2 Chemical Data

Dissolved oxygen at 10 and 50 cm, nitrate-nitrite, soluble reactive silicon and alkalinity varied during the experiment, but did not differ significantly ($p > 0.05$) between treatments (Appendix A).

TKN varied with time in the two treatments (Fig. 20), but an overall increase was observed in both feces load (from 1.52 mg/L ± 0.11 to 2.32 mg/L ± 0.09) and control (from 1.53 mg/L ± 0.11 to 1.88 mg/L ● 0.04) enclosures. Throughout the experiment, the TKN concentrations in the feces load enclosures were equal to or greater than the concentrations in the controls and on two sampling dates in late August significant difference between treatments were noted ($p = 0.009$ on 23 August and $p = 0.010$ on 28 August).

The total P concentration increased throughout the experiment in both treatments (Fig. 21). The feces load increased from 0.14 mg/L ± 0 to 0.41 mg/L ± 0.05 while the control increased from 0.17 mg/L ± 0.04 to 0.29 mg/L ± 0.01. TP concentrations were higher in the feces load enclosures than in the controls two weeks following the first feces addition, and remained higher than the control values to the end of the experiment. A significant difference ($p = 0.009$) between the treatments occurred once on 23 August.

After the first feces application, ammonia (NH_3-N) levels increased, but returned to control levels the following week (Fig. 22). The concentrations between the treatments began to diverge by late July. On 26 July and 9 August there were significant differences between treatments ($p = 0.025$ and $p = 0.049$, respectively). The feces load treatment continued to have higher NH_3-N concentrations than the controls to the end of the experiment. There was a gradual increase in NH_3-N levels in the feces load enclosures where the maximum concentration was reached on 23 August (0.100 mg/L ± 0.039), following which the

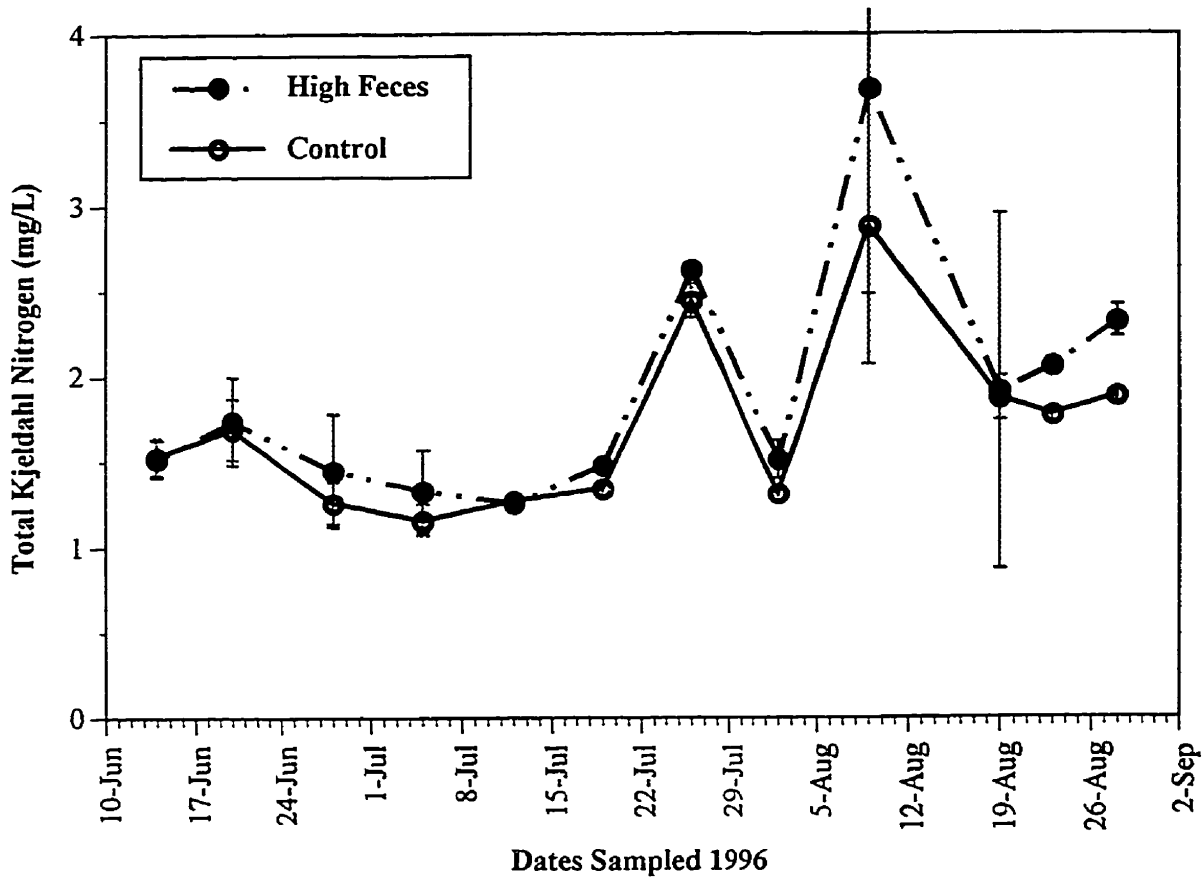

Figure 20. TKN concentration (mg/L ± SE, n = 3) in the water column during a 12-week sampling period in control (open circles) and high feces load (closed circles) enclosures, 1996. Feces additions began on 5 July and continued once every week following the initial application. The final addition was made on 23 August.

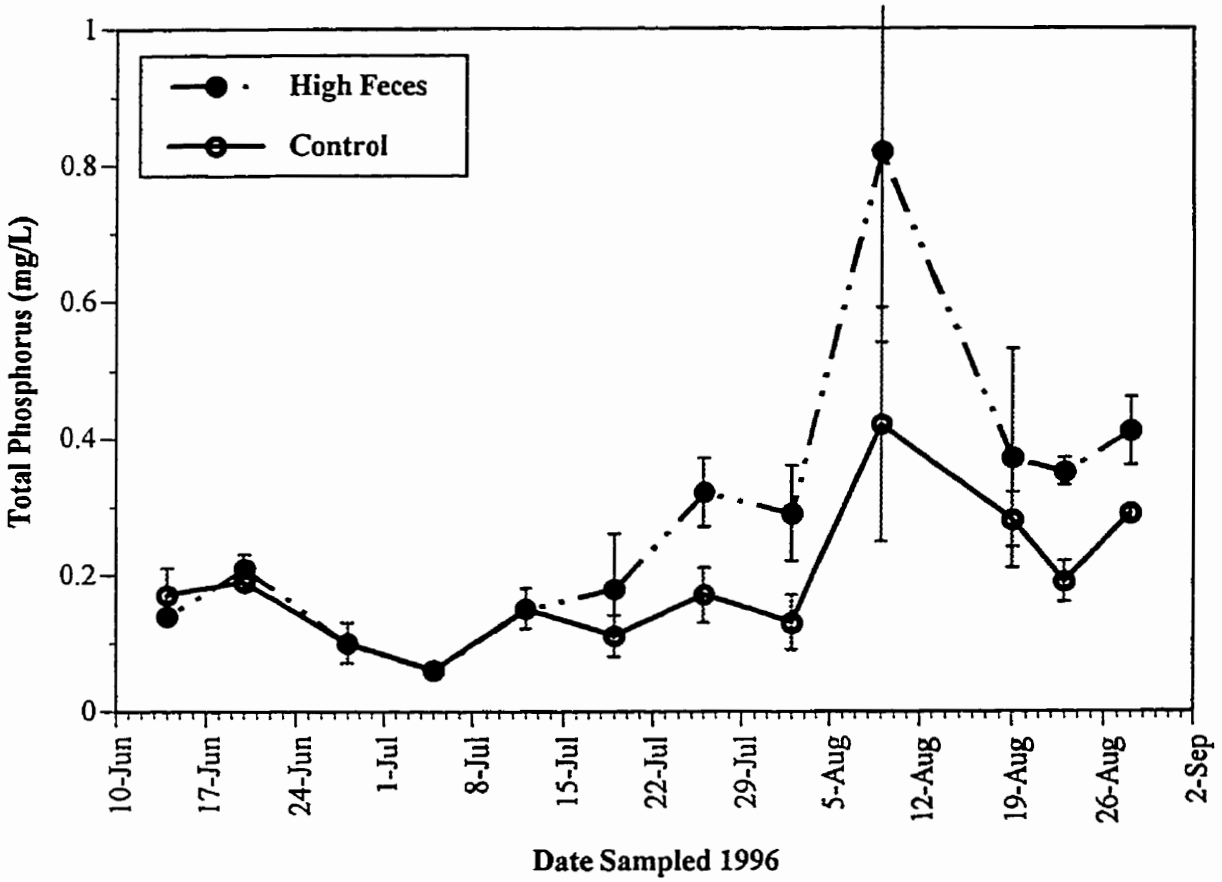

Figure 21. Total phosphorus concentration (mg/L ± SE, n = 3) in the water column during a 12-week sampling period in control (open circles) and high feces load (closed circles) enclosures, 1996. Feces additions began on 5 July and continued once every week following the initial application. The final addition was made on 23 August.

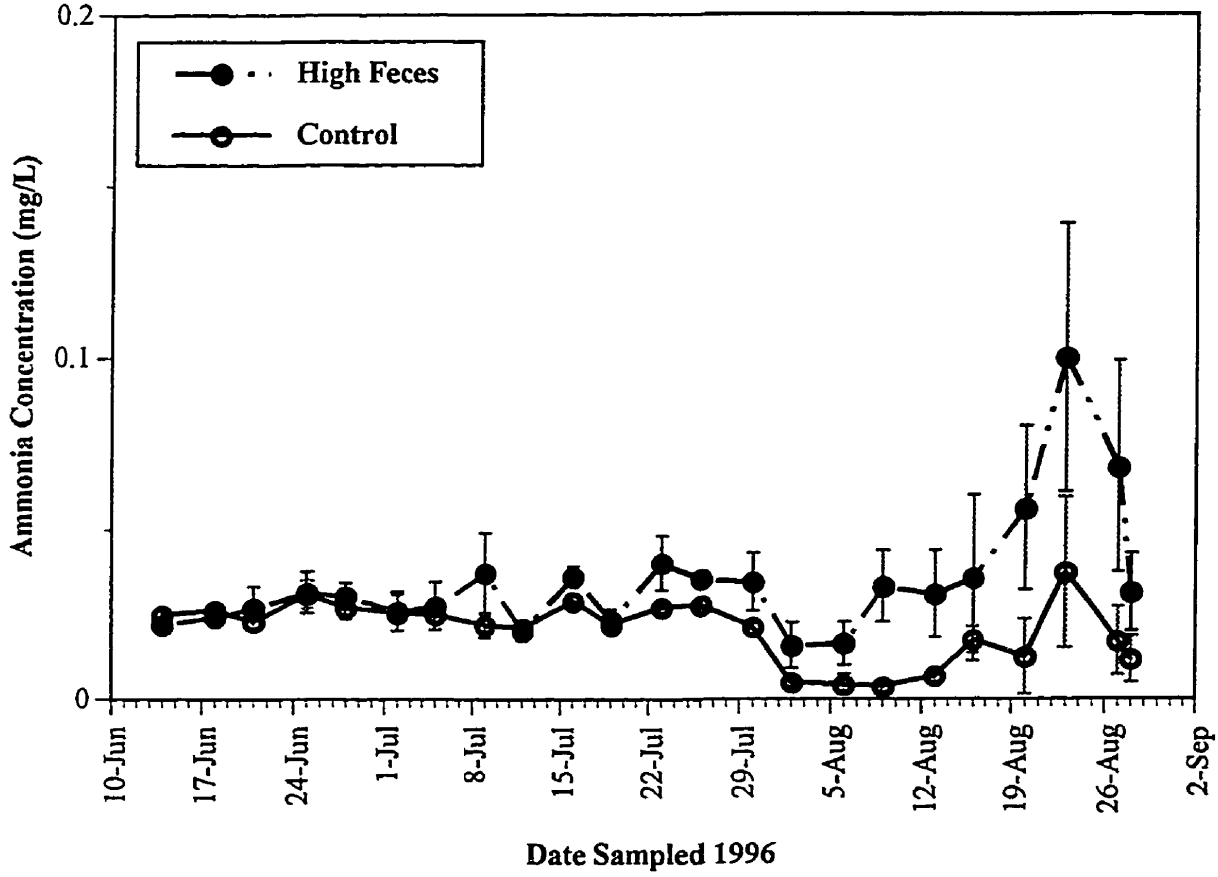

Figure 22. NH_3-N concentration (mg/L ± SE, n = 3) in the water column during a 12-week sampling period in control (open circles) and high feces load (closed circles) enclosures, 1996. Feces additions began on 5 July and continued once every week following the initial application. The final addition was made on 23 August.

concentrations decreased to levels observed at the beginning of the experimental period.

Prior to the feces additions, there was a decrease in the SRP concentrations (Fig. 23) and the levels of the control were higher than those of the enclosures designated for feces addition. From mid-July SRP concentrations in the feces load treatment were two times higher than those in the controls (< 0.1 mg/L) and remained so throughout the experiment. On 6 August, there was a significant difference ($p = 0.040$) between the feces load treatment (0.28 mg/L ● 0.061) and the control (0.078 mg/L ± 0.031). Significant differences between treatments were also calculated on each of the last four sampling dates 20, 23, 27 and 28 August (p = 0.017, 0.0051, 0.014, and 0.0036, respectively).

pH increased with time in both treatments and values were always higher in the control treatment (Fig. 24). There were a significant differences in pH between treatments on the 2, 13 and 14 of August ($p = 0.021$, 0.013 and 0.048, respectively).

4.3.3 Biological Data

Phytoplankton

Changes in phytoplankton chlorophyll (Fig. 25) and productivity (Fig. 26) concentrations over time increased after the feces additions began, however the level of concentrations were highest in the controls. There was no significant effect ($p > 0.05$) of feces addition in either parameter. Phytoplankton particulate P decreased prior to feces additions in both treatments and remained at a constant level in the control treatment during the remainder of the experiment (Fig. 27). The particulate P concentrations continued to decrease after the feces additions were applied, yet no significant difference between treatments was detected.

The biological data to follow, like the parameters measured for phytoplankton, varied during the experiment, but did not differ significantly ($p>0.05$) between treatments. Data are summarized in Table 4.

Periphyton

Feces additions increased periphyton chlorophyll and photosynthesis concentrations within a week of the first addition, however concentrations then decreased during the following

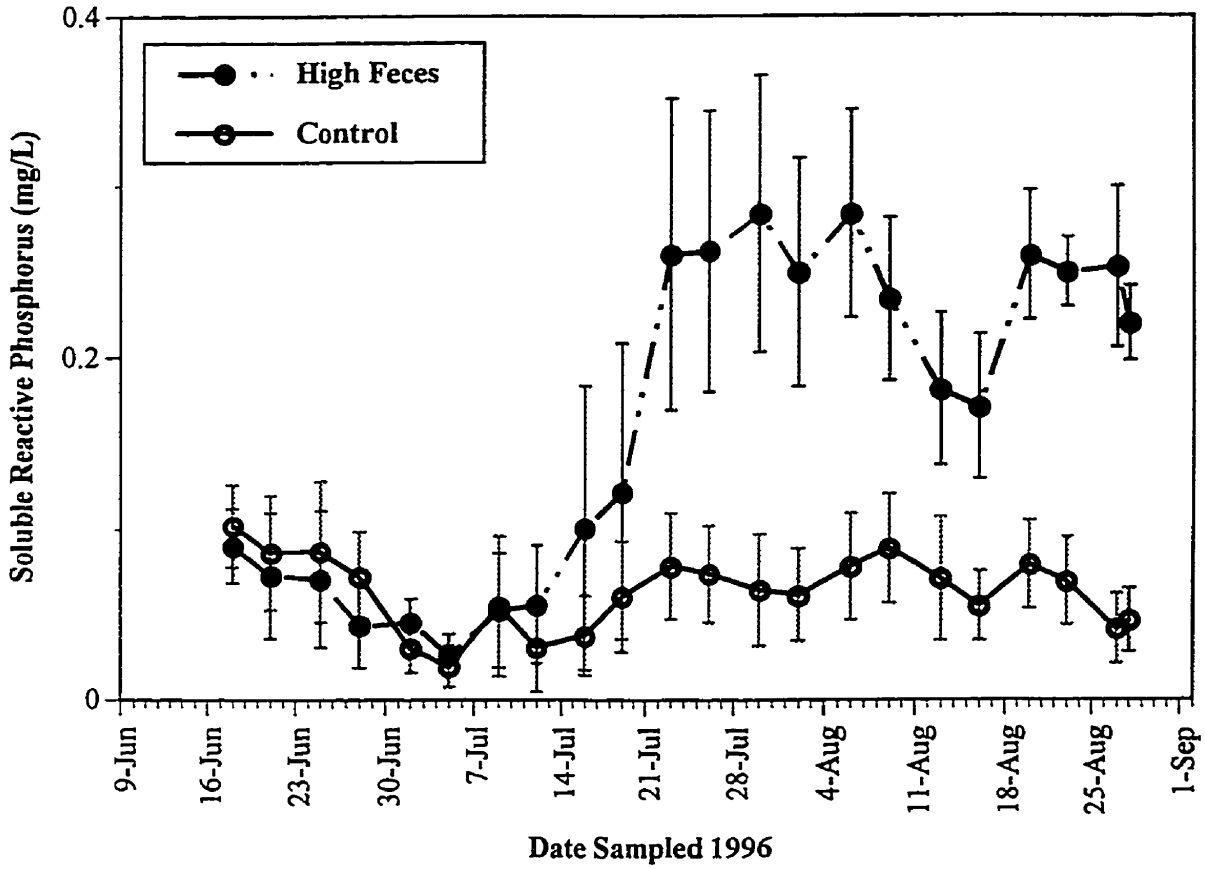

Figure 23. SRP concentration (mg/L ± SE, n = 3) during an 11-week sampling period in control (open circles) and high feces load (closed circles) enclosures, 1996. Feces additions began on 5 July and continued once every week following the initial application. The final addition was made on 23 August.

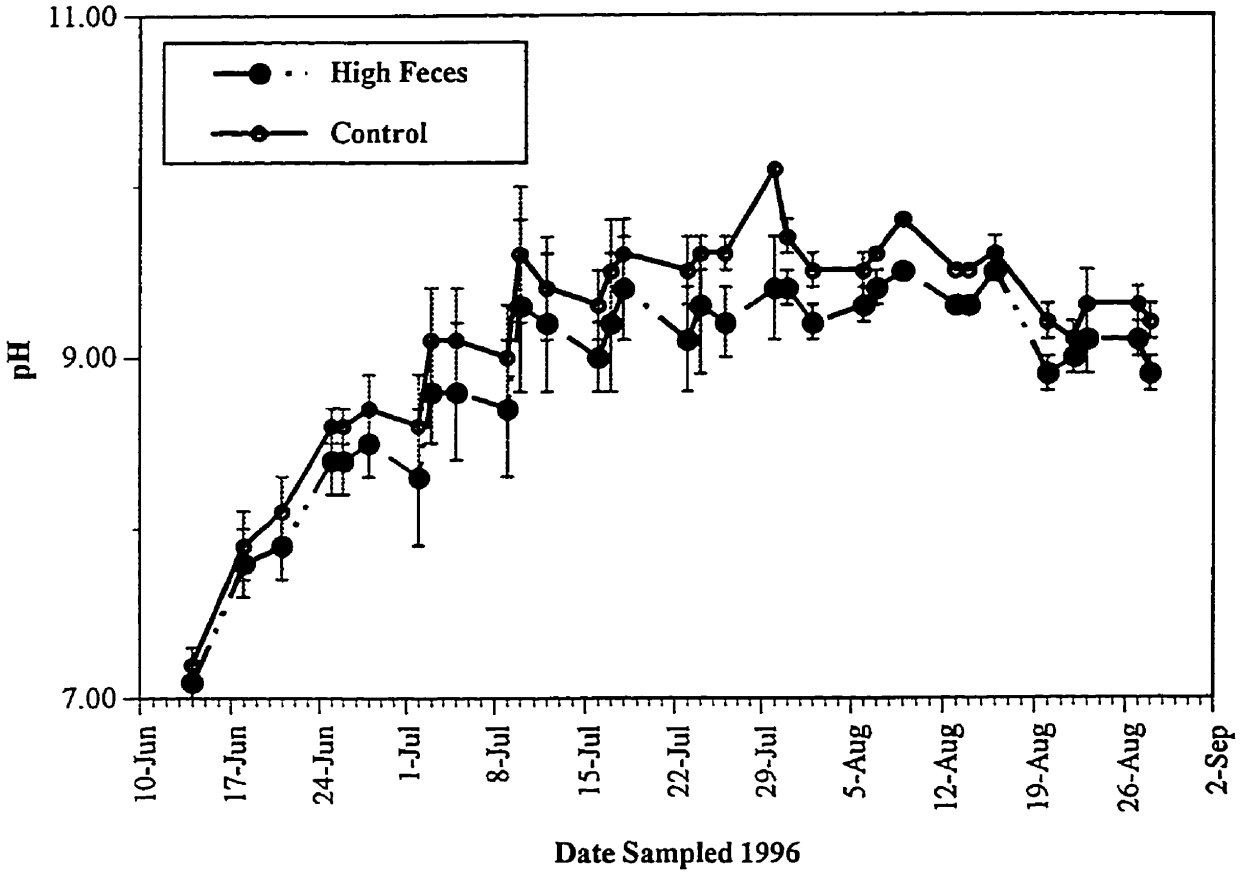

Figure 24. pH (± SE, n = 3) in the water column during a 12-week sampling period in control (open circles) and high feces load (closed circles) enclosures, 1996. Feces additions began on 5 July and continued once every week following the initial application. The final addition was made on 23 August.

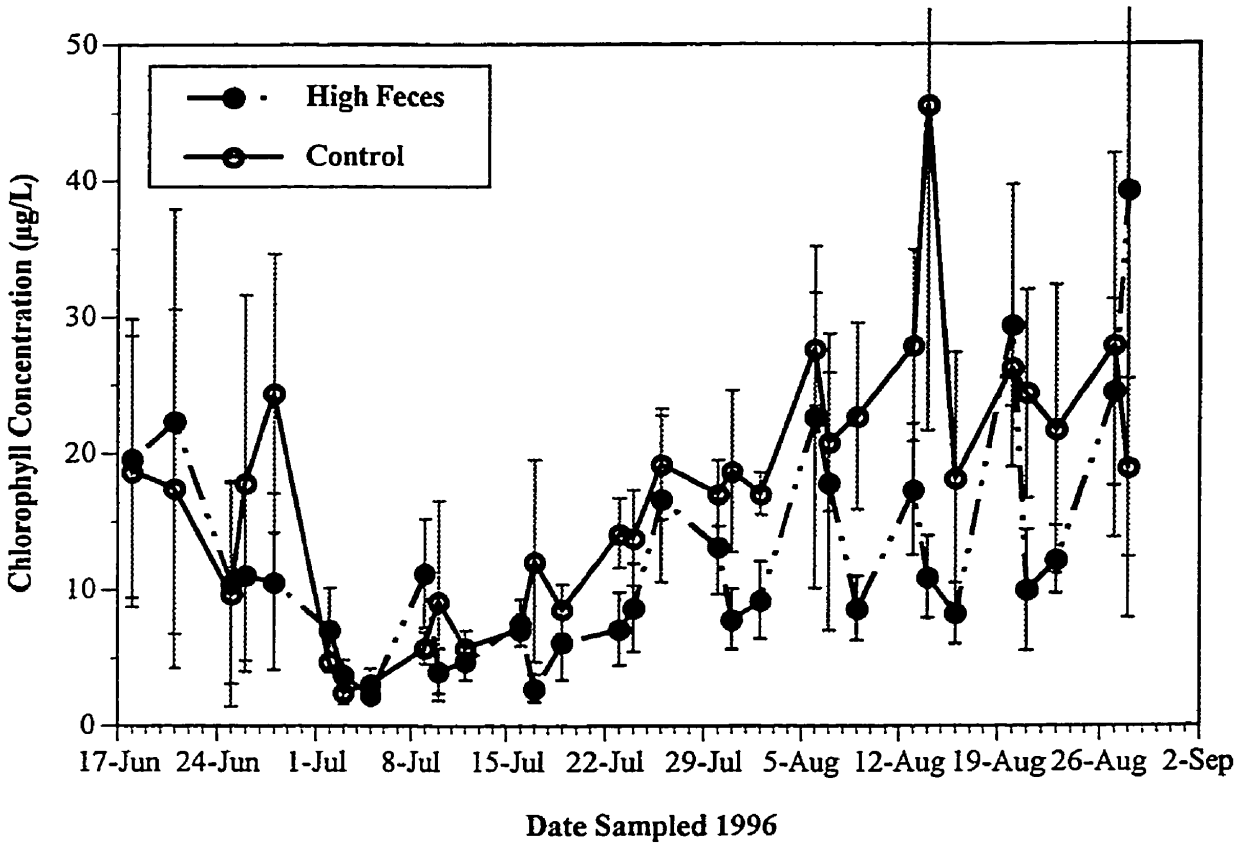

Figure 25. Phytoplankton chlorophyll concentration (µg/L ± SE, n = 3) during an 11-week sampling period in control (open circles) and high feces load (closed circles) enclosures, 1996. Feces additions began on 5 July and continued once every week following the initial application. The final addition was made on 23 August.

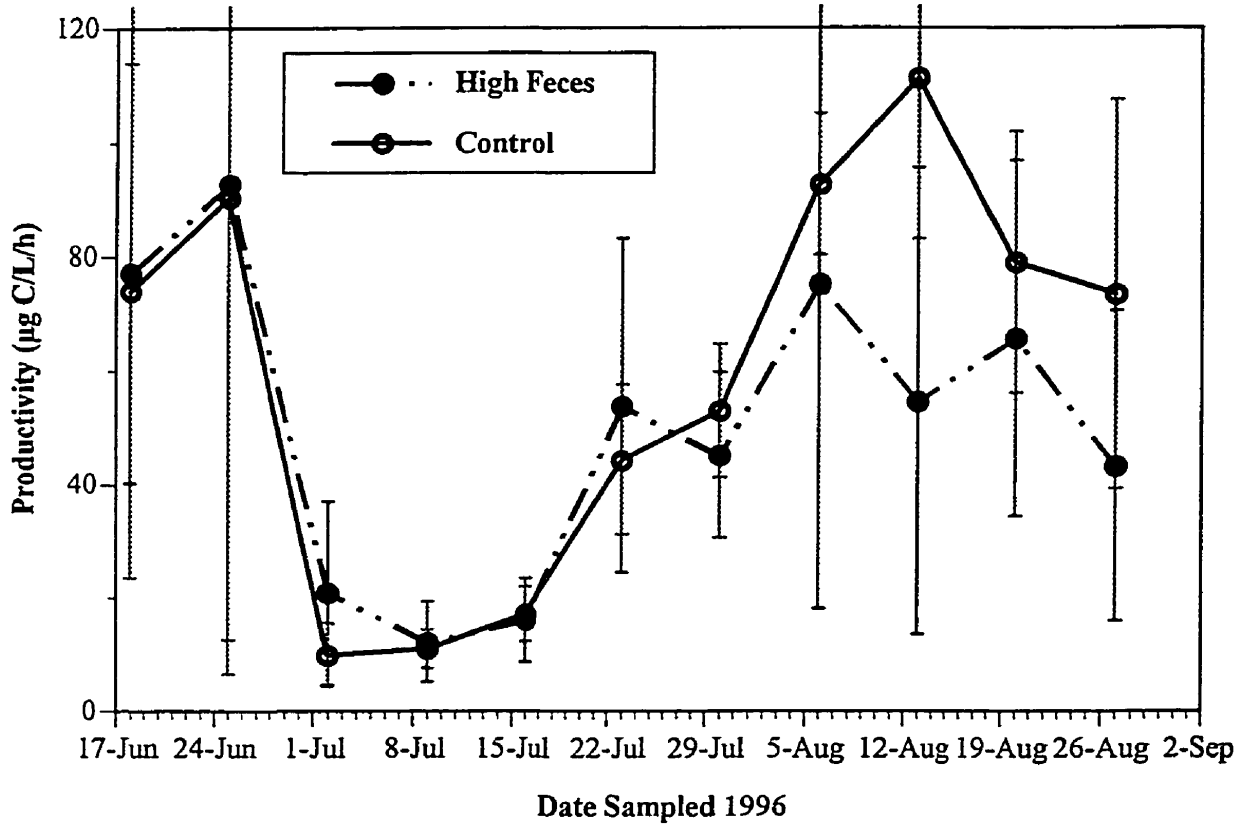

Figure 26. Phytoplankton photosynthetic rate (µgC/L/h ± SE, n = 3) during an 11-week sampling period in control (open circles) and high feces load (closed circles) enclosures, 1996. Feces additions began on 5 July and continued once every week following the intial application. The final addition was made on 23 August.

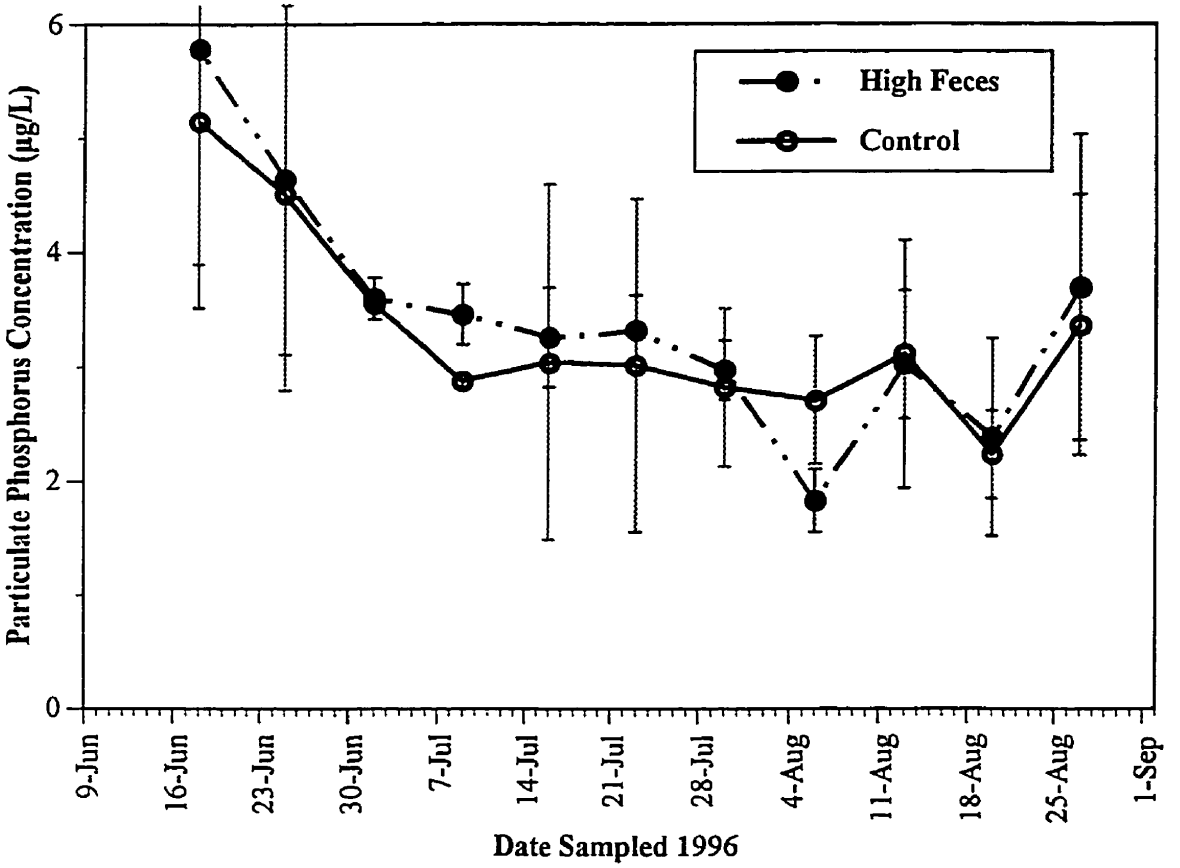

Figure 27. Phytoplankton particulate P concentration (µg/L ± SE, n = 3) during an 11-week sampling period in control (open circles) and high feces load (closed circles) enclosures, 1996. Feces additions began on 5 July and continued once every week following the initial application. The final addition was made on 23 August.

Table 4. Mean (range in parentheses) of biological data measured for periphyton, epipelon, sediment, macrophyte, epiphyton and invertebrates for experimental enclosures (1996). None of the treatments varied significantly ($p>0.05$).

Parameter	High Feces Load	Control
Periphyton		
Chlorophyll ($\mu g/cm^2$)	1.65 (0.36 - 3.11)	1.64 (0.31 - 3.78)
Photosynthesis ($\mu gC/cm^2/h$)	2.18 (0.94 - 3.10)	1.76 (0.60 - 2.38)
Particulate P ($\mu c/cm^2$)	0.27 (0.05 - 0.97)	0.10 (0.04 - 0.35)
Epipelon		
Chlorophyll ($\mu g/cm^2$)	0.08 (0.05 - 0.17)	0.07 (0.05 - 0.11)
Photosynthesis ($\mu gC/cm^2/h$)	0.04 (0.02 - 0.06)	0.04 (0.02 - 0.07)
Sediment		
Particulate P ($\mu g/gdw$)	166.17 (101.49 - 227.44	167.58 (106.68 - 228.20)
Macrophyte		
Particulate P ($\mu g/gdw$)	573.23 (315.60 - 1053.93)	571.05 (308.05 - 1026.31)
Epiphyton		
Chlorophyll ($\mu g/gdw$)	182.97 (39.48 - 396.64)	138.72 (81.56 - 225.68)
Invertebrates		
Particulate P ($\mu g/gdw$)	564.04 (417.24 - 697.76)	749.73 (469.74 - 1032.31)

two weeks. Periphyton chlorophyll concentrations increased in both the feces load and control treatments from late July until the end of the experiment and no significant difference with respect to treatment were detected. Photosynthesis was higher in the feces load treatment than the control from late July through to mid-August, but again, there were no significant differences in photosynthesis between treatments on any date. Periphyton particulate P remained at constant levels (~ 0.35 $\mu g/cm^2$) in the control treatment throughout the experiment. Particulate P concentrations in the feces treatment increased steadily from 0.05 $\mu g/cm^2 \pm$ 0.02 on 25 June to 0.97 $\mu g/cm^2 \pm$ 1.26 on 18 July and then declined rapidly to 0.027 $\mu g/cm^2$ $\pm$ 0.005 on 26 July. Throughout August, particulate P levels remained at a constant concentration in the feces load enclosures (~ 0.25 $\mu g/cm^2$). There were no significant differences between treatments.

Epipelon

Epipelon chlorophyll concentrations did not differ with treatment until late, when concentrations, in response to feces loading, were higher in feces load treatment than in the controls. Epipelon photosynthesis decreased with time in both treatments. Feces addition had no significant effect ($p > 0.05$) on either epipelon biomass and productivity.

Sediment

Feces addition had no significant effect ($p > 0.05$) on sediment particulate P.

Macrophyte

Macrophyte particulate P concentrations in both treatments followed the same trend over time as sediment particulate P concentrations, with a peak in mid-July. In the feces load treatment values increased from 521.01 $\mu g/g \pm$ 22.29 in mid-June to 1053.93 $\mu g/g \pm$ 177.46 in mid-July, while in the control treatment values increased from 396.96 $\mu g/g \pm$ 81.87 to 1026.31 $\mu g/g \pm$ 284.29. Particulate P levels declined to their lowest levels by mid-August in both the feces load (315.60 $\mu g/g \pm$ 14.81) and control (308.05 $\mu g/g \pm$ 86.05) treatments. Macrophyte particulate P concentrations did not differ significantly between treatments.

Epiphyton

Epiphyton biomass varied over time, but there were no significant differences due to treatment.

Invertebrates

After treatment commenced, invertebrate particulate P concentrations were generally higher in the controls that in response to the feces loading throughout the experiment. Differences between treatments were not significant.

5. DISCUSSION

5.1 Year 1 (1995)

Biomass

Seasonal and experimental factors both contributed to determining which of the four algal assemblages, all expressed in proportionate terms (mg/m^2 wetland area), predominated in experimental enclosures (Table 5). The results obtained were different in the high, low and control treatments. There was a shift from phytoplankton dominance in the control and low feces enclosures, starting in the beginning of June to periphyton dominance through July to mid-August. After 13 August, periphyton was displaced by phytoplankton which remained the dominant assemblage until the end of the experiment. I attribute this shift to macrophyte development and macrophyte decomposition.

With the development of macrophytes in the enclosures in late June, competition for nutrients between phytoplankton and macrophytes occurred and macrophytes were competitively superior to phytoplankton. Other studies found similar patterns. Meijer *et al.* (1990) examined changes in water quality that resulted after they experimentally reduced the total fish stock in two shallow lakes in The Netherlands by 70 to 85%. The growth of submerged macrophytes increased after the fish reduction. Coinciding with the increase in macrophytes was decreased algal abundance and dissolved N, and increased water transparency. They inferred that the decrease in algal abundance was partly due to the development of the submerged macrophytes, and macrophytes out-competed algae for N. A similar study found that planktivorous fish removal was responsible for increased macrophyte growth in the shallow Lake Zwemlust, The Netherlands (Ozimek *et al.* 1990). Increased macrophyte abundance resulted in N-limitation and decreased phytoplankton biomass; N-limitation by macrophytes was confirmed by bioassay experiments in the laboratory.

Coupled with macrophyte development was an increase in colonizable surface area for epiphytic algae. I used acrylic rods as artificial substrata in these experiments from which I estimated epiphytic (periphyton) algal biomass, productivity and particulate P. I assumed

Table 5. Mean algal biomass (mg chlorophyll-a per m^2 wetland area) in control, high feces and low feces treatments in Delta Marsh 1995 (range in parentheses). Comparative data from the Marsh Ecology Wetland Research Program (MERP), collected in Delta Marsh from 1985 through 1986, are summarized from Robinson *et al.* (1997a). In MERP epiphyton samples were collected from artificial substrata, which I refer to as periphyton, while no biomass measurements were collected from algae on natural substrata, which I refer to as epiphyton. Metaphyton did not develop in my study.

Assemblage	Control	Low Feces	High Feces	MERP
Epipelon	1 (<0.4 - 2)	0.8 (0.4 - 1)	0.8 (0.3 - 1.3)	4 (<1 - 17.5)
Epiphyton	1 (0.2 - 2)	1 (0.6 - 2)	2 (0.2 - 8)	not measured
Phytoplankton	6 (0.8 - 19)	10 (1 - 30)	10 (3 - 28)	7 (<1 - 39)
Periphyton	5 (0.2 - 16)	10 (<0.2 - 31)	13 (0.4 - 41)	67 (6 - 182)
Metaphyton	N/A	N/A	N/A	530 (123 - 1,309)

the values for the parameters that I measured for periphytic algae were close estimates to those of epiphytic algae because the rods were placed in the enclosures at the time of macrophyte emergence, as suggested by Hooper and Robinson (1976). However, biomass was consistently higher on the rods than on the macrophytes. For example, mean concentration of epiphyton chlorophyll in the control was 1 mg/m^2, whereas periphyton chlorophyll was 5 mg/m^2. The reason for this difference will be examined in a later section. Howard-Williams (1981) demonstrated that the epiphytic alga, *Cladophora* (at times loosely attached to my rods), absorbed ^{32}P 8.1 times faster than the macrophyte, *Potamageton*. This suggests that epiphytes can compete effectively for nutrients with developing macrophytes and, therefore, it was probably the later development of macrophytes and epiphytes that resulted in observed decrease of phytoplankton in the control and low feces treatment.

Periphyton biomass decreased and phytoplankton biomass increased in August, corresponding to a decrease in macrophyte biomass with the onset of senescence. The shift observed late in the sampling season in the low feces treatment and the control may be attributed to a release of nutrients from decaying macrophytes. Landers (1982) tested the effects of senescence by *Myriophyllum spicatum* on the nutrient and chlorophyll-a levels in Lake Monroe, Indiana using *in situ* open-bottomed enclosures. Decomposing macrophytes were responsible for 2.2% N and 17.9% P of the total non-point sources entering the lake yearly. This increase in nutrients to the surrounding waters as the result of macrophyte senescence contributed to a significant increase in phytoplankton chlorophyll. Murkin *et al.* (1989) reasoned that raised water levels in Delta Marsh would remove existing submersed plant litter and release bound nutrients into the surrounding waters upon their decomposition. They found that litter from all macrophyte species studied showed significant losses of N and P within the first 48 hours after litter bags were laid on the substratum surface, approximately 75 cm deep. The Hardstem Bulrush (*Scirpus lacustris glaucus*) continued to leach nutrients after two years of flooding. They suggested that submerged macrophytes, with small amounts of non-labile structural material, decomposed readily, releasing nutrients

which, in turn, may support phytoplankton growth.

Phytoplankton and periphyton biomass responded most prominently to feces additions (Table 5). Mean phytoplankton biomass increased from 6 mg/m^2 in the control to 10 mg/m^2 in the low and high feces treatments, while mean periphyton biomass increased from 5 mg/m^2 in the control to 10 mg/m^2 in the low feces treatment and to 13 mg/m^2 in the high feces treatment. Phytoplankton chlorophyll per m^2 of wetland area (Table 5) increased after the first feces application in the high treatment, yet decreased the following week and remained similar to levels measured in the controls. Because macrophytes had not yet developed, there may have been no competition for nutrients so the nutrients released from the first feces addition were assimilated by the phytoplankton. Perhaps the greatest response was observed after the second addition in the high feces treatment in the periphyton and epiphyton biomass. I suggest that it was the combination of macrophyte senescence and nutrient addition that caused increases in the two algal assemblages. For example, at the time of the second nutrient addition, *Cladophora* surrounded the rods in the high and low feces enclosures.

Epipelon biomass was unaffected by any treatment. Epipelon biomass was highest at the beginning of the experiment when macrophytes had yet to establish and sediment surfaces tended not to be shaded. As the macrophyte canopy became more dense, less light was able to reach the substratum and epipelon biomass decreased. This is supported by low turbidity values in the control treatment (~ 1 NTU) at the same time that epipelon biomass peaked in the control (~ 2 mg/m^2). Lack of effects of external nutrient loading on epipelon has been observed by others. For example, Murkin *et al.* (1991) found that epipelon biomass in a poorly vegetated site at Narcisse Marsh, MB was higher than in a vegetated site. In another experiment, Murkin *et al.* (1994) added inorganic N and P to a wetland at Long Lake, MB and observed no significant differences in epipelon biomass between the manipulated and unmanipulated enclosures even though there was an increase in the other algal communities after fertilization. This suggests that epipelon did not respond to the addition of either inorganic or organic nutrients to the water column.

Metaphyton mats, which flourished with nutrient enrichment in experiments by McDougal *et al.* (1997) and others (Gabor *et al.* 1994; Murkin *et al.* 1994), were not observed in this study. Perhaps, as suggested by Gabor *et al.* (1994) for experiments involving organic enrichment by ground alfalfa, nutrients were released slowly into the wetland and were quickly assimilated by other plant communities. Metaphyton probably did not develop in this experiment, like that of the alfalfa treatments, because epiphytes did not flourish with the added nutrients to yield metaphyton.

Biomass-normalized photosynthesis

Biomass-normalized photosynthesis was calculated to assess algal responses to feces additions. It is the rate of C assimilated per unit chlorophyll (Robinson *et al.* 1997b). I proposed that the biomass-normalized photosynthesis would increase in response to feces additions where high values imply that algal cells are more efficient at using C when they are replete with nutrients provided by the feces. In 1995, there was little variation in the biomass-normalized photosynthesis between treatments for the three algal assemblages measured (Table 6). Goldsborough and Robinson (1996) discuss variation in the photosynthetic-irradiance relationship for the benthic algae of wetlands and suggest that part of the variation is due to the three-dimensional growth observed in assemblages such as epiphyton. They observed that, at times, there is an inverse correlation between biomass and biomass-normalized photosynthesis such that as biomass of epiphyton increases, self-shading and nutrient limitation occur in the layers most closely associated with the substratum. Müller (1996) found that self-shading did occur in dense periphytic layers when chlorophyll concentrations were more than 6 $\mu g/cm^2$. Under these conditions, the chlorophyll-specific rate of photosynthesis (P^B) decreased due to the dense layering of epiphytes which caused intensive shading. Even though periphytic chlorophyll values in all treatments never exceeded 6 $\mu g/cm^2$ (a maximum value of 2.5 $\mu g/cm^2$ was observed after the second nutrient addition in the high feces treatment), I suggest that self-shading was possibly a factor that affected biomass-normalized photosynthesis. Phytoplankton had the highest overall biomass-

Table 6. Mean algal biomass-normalized photosynthesis (μgC/μgChl-a/h) in control, high feces and low feces load treatments in Delta Marsh 1995 (range in parentheses). Comparative data from the Marsh Ecology Wetland Research Program (MERP), collected in Delta Marsh from 1985 through 1986, are summarized from Robinson *et al.* (1997b). In MERP epiphyton samples were collected from artificial substrata, which I refer to as periphyton. Metaphyton did not develop in my study.

Assemblage	Control	Low Feces	High Feces	MERP
Epipelon	1.0 (<0.5 - 2)	0.8 (0.5 - 1)	0.6 <0.5 - 1	2.3 (0.3 - 5)
Phytoplankton	4.9 (1 - 8)	3.7 (<2 - 5)	4.0 (1 - 9)	7.2 (0.2 - 23)
Periphyton	4.8 (1 - 19)	4.3 (<1 - 15)	4.5 (<1 - 19)	2.4 (0.1 - 17)
Metaphyton	N/A	N/A	N/A	1.1 (0.1 - 11)

normalized photosynthesis in the control after increased biomass was observed in the periphyton community (Table 6), suggesting that phytoplankton may assimilate C more efficiently than periphyton, possibly due to its increased density and subsequent self-shading. With the addition of waterfowl feces, biomass-normalized photosynthesis in periphyton increased, which may be due to increased nutrient availability. It appears that the seasonal trend of higher biomass-normalized photosynthesis in the phytoplankton, observed in the control, is still present in the feces-loaded enclosures, but the "gap" between the biomass-normalized photosynthesis of phytoplankton and periphyton narrowed. Epipelon biomass-normalized photosynthesis values were the lowest of the three algal assemblages and were not affected by feces loading (Table 6). Again, I propose that less light was able to reach the substrate as the macrophyte canopy became more dense so epipelon was unable to assimilate C efficiently.

Particulate Phosphorus

PP (mg/m^2 wetland area) in the three assemblages was affected by nutrient enrichment where the highest PP values were observed in the high feces treatments (Table 7). Phytoplankton had the highest mean PP concentration throughout the experiment, followed by periphyton and then epiphyton in each of the treatments. The seasonal trend of PP, as observed in the control, had phytoplankton values higher than periphyton values. Phytoplankton control PP concentrations varied with time with no consistent temporal trend. The control periphyton PP increased with time, until it peaked in early July, where it decreased until the end of the experiment. I propose that with the development of macrophytes and their associated epiphytes, there was increased competition for nutrients and the assemblage that was favored was the one better able to utilize the nutrients available to it.

5.2 Year 2 (1996)

Biomass

The seasonal trend observed in the control was similar to that observed in 1995 where there was a shift in algal dominance from phytoplankton, observed early in the season, to

Table 7. Mean algal particulate phosphorus (mg per m^2 wetland area) in control, high feces and low feces load treatments in Delta Marsh 1995 (range in parentheses).

Assemblage	Control	Low Feces	High Feces
Epiphyton	0.1 (0.002 - 0.2)	0.1 (0.02 - 0.27)	0.2 (0.01 - 0.4)
Phytoplankton	1.2 (0.4 - 3.7)	1.8 (0.5 - 7.9)	2.5 (0.5 - 6.5)
Periphyton	0.4 (0.01 - 1.2)	0.7 (0.02 - 2.5)	0.8 (0.01 - 2.6)

periphyton, beginning to increase mid-July and dominate late July. Again, I attribute this shift in dominance to macrophyte development which resulted in increased colonizable surface area and competition for available nutrients. In 1996, I did not see a shift back to phytoplankton dominance later in the season; however, phytoplankton biomass values did increase in late July with maximum biomass at the onset of macrophyte senescence after 11 August. Periphyton biomass increased steadily in August suggesting that it was able utilize the nutrients leached from the decaying macrophytes.

Of the four algal assemblages measured, the addition of waterfowl feces affected only periphyton (Table 8). Before feces loading (5 July), periphyton biomass levels in the control and feces treatment were similar. Trends between the treatments were similar, yet biomass increased in the feces treatment above levels observed in the control. I suggest that this increase in periphyton in the feces treatment was due to nutrients released from the feces into the surrounding waters which were made available for uptake.

Epipelon biomass increased with the addition of feces. I suspect that shading of the sediments was greater in the controls because macrophyte biomass was higher in the controls than in the feces treatment throughout the experiment. However, the magnitude of the difference was not sufficiently large to be statistically significant.

Biomass-normalized photosynthesis

Phytoplankton had the highest mean biomass-normalized photosynthesis in both the controls and feces treatment (Table 9), yet values in the controls were higher than in the manipulated enclosures. Biomass-normalized photosynthesis in the control reached its maximum value during the second week of sampling and its lowest value by the third week. From weeks 4 through 9, biomass-normalized photosynthesis increased and then decreased during the last two weeks of sampling. The trend in the control enclosures was the opposite, which suggests that as periphyton biomass increased, as observed above, self-shading occurred and the periphyton became inefficient at assimilating C. When the two assemblages were compared in the feces treatment, there appeared to be an overall trend where biomass-

Table 8. Mean algal biomass (mg chlorophyll-a per m^2 wetland area) in control, high feces and low feces treatments in Delta Marsh 1996 (range in parentheses). Comparative data from the Marsh Ecology Wetland Research Program (MERP), collected in Delta Marsh from 1985 through 1986, are summarized from Robinson *et al.* (1997a). In MERP epiphyton samples were collected from artificial substrata, which I refer to as periphyton, while no biomass measurements were collected from algae on natural substrata, which I refer to as epiphyton. Metaphyton did not develop in my study.

Assemblage	Control	Feces Addition	MERP
Epipelon	1 (<0.5 - 1)	1 (<0.5 - 2)	4 (<1 - 17.5)
Epiphyton	11 (<5 - 25)	10 (<2 - 25)	not measured
Phytoplankton	13 (4 - 22)	12 (6 - 21)	7 (<1 - 39)
Periphyton	32 (2 - 108)	36 (<1 - 88)	67 (6 - 182)
Metaphyton	N/A	N/A	530 (123 - 1,309)

Table 9. Mean algal biomass-normalized photosynthesis (μgC/μgChl-a/h) in control and feces load treatments in Delta Marsh 1996 (range in parentheses). Comparative data from the Marsh Ecology Wetland Research Program (MERP), collected in Delta Marsh from 1985 through 1986, are summarized from Robinson *et al.* (1997b). In MERP epiphyton samples were collected from artificial substrata, which I refer to as periphyton, while no biomass measurements were collected from algae on natural substrata, which I refer to as epiphyton. Metaphyton did not develop in my study.

Assemblage	Control	Feces Addition	MERP
Epipelon	0.5 (<0.5 - 1)	0.5 (<0.5 - 1)	2.3 (0.3 - 5)
Phytoplankton	3.2 (2 - 6)	3.0 (1 - 6)	7.2 (0.2 - 23)
Periphyton	2.3 (<1 - 5)	1.6 (<1 - 3)	2.4 (0.1 - 17)
Metaphyton	N/A	N/A	1.1 (0.1 - 11)

normalized photosynthesis decreased with time with feces additions and, on average, phytoplankton values were higher. It appeared that nutrient enrichment lessened the effect of self-shading, perhaps by increasing nutrient availability to deeply buried epiphytic layers near the substratum that were most effected by self-shading. Epipelon biomass-normalized photosynthesis values were the lowest of the three algal assemblages and were not affected by feces loading. I suggest that decreased light availability limited the C assimilation efficiency of epipelon.

Particulate Phosphorus

Phytoplankton PP per m^2 of wetland was not affected by feces loading (Table 10). Phytoplankton PP values in the feces treatment at the beginning of the experiment prior to loading were higher than the controls. Through the experiment, the trends observed in the controls and feces treatment mirrored one another with the feces load PP values higher than the controls yet there is no increased separation between the treatments with feces loading. This suggests that nutrient enrichment from the feces additions did not occur. I suggest that phytoplankton was not the primary recipient of increased nutrient supply because PP concentration in phytoplankton per m^2 of wetland area did not increase. Periphyton PP did increase with nutrient loading (Table 10) which, coupled with the observed increase in biomass, suggests periphyton was able to utilize the nutrients released from the feces.

5.3 Summary

Total mean algal biomass was higher in Year 2 than in Year 1. For example, total algal biomass in the control treatments increased from 13 mg/m^2 in 1995 to 57 mg/m^2 in 1996. One possibility for higher algal biomass may be the difference in nutrient levels between the two years. In 1996 SRP and NH_3-N was approximately 3 and 4 times higher, respectively in the control enclosures than in 1995. Macrophyte biomass more than doubled in 1996 from 1995 in the control enclosures (35.4 g/m^2 to 89.8 g/m^2, respectively), which may provide an explanation for increased epiphyton biomass. Epiphyton biomass in the control increased from 1 mg/m^2 in 1995 to 11 mg/m^2 in 1996, possibly due to increased colonizable surface

Table 10. Mean algal particulate phosphorus (mg per m^2 wetland area) in control and feces load treatments in Delta Marsh 1996 (range in parentheses). Epiphyton particulate phosphorus was not measured in 1996.

Assemblage	Control	Feces Addition
Phytoplankton	2.8 (1.6 - 4.1)	2.9 (1.4 - 4.8)
Periphyton	1.5 (0.2 - 5.4)	2.9 (0.1 - 5.7)

area as macrophytes developed.

Biomass-normalized photosynthesis was lower in all the algal assemblages in 1996 than compared to 1995 which may be due to increased macrophyte canopy and subsequent lower light levels. This difference cannot be explained by a reduction in the subsurface light field in 1996 because, as stated above, light extinction was lower in the second year of this study. With regards to the periphytic algal assemblage, biomass increased dramatically from 5 mg/ m^2 in 1995 to 32 mg/m^2 in 1996 in the control treatment and from 13 mg/m^2 in 1995 to 36 mg/m^2 in 1996 in the high feces treatment. I suggest that increased biomass in the periphytic assemblage lead to increased self-shading and therefore this may be a possible explanation its decreased biomass-normalized photosynthesis in 1996.

When the control and high feces datasets are compared between 1995 and 1996, one sees there is an overall increase in PP levels in the controls. In 1995 there was an increase in phytoplankton PP in the high feces treatment, while in 1996 there was not. A possible explanation for may be due to the pulse addition in 1995 versus the press addition in 1996. Phytoplankton may have been able to utilize the nutrients in the pulse addition because there was a higher concentration of PP added, therefore "more to go around" and competition with developing periphyton was not as great. The second addition appears to have half the PP content as the first and therefore I suggest that the phytoplankton were unable to out-compete the periphyton for nutrients and this is why there is no increase in PP after the second addition in the phytoplankton. In 1996, loading was applied every week beginning on 5 July when periphyton started to establish and periphyton was able to out-compete phytoplankton for the nutrients with each addition.

Researchers have suggested that nutrient enrichment with inorganic nutrients can stimulate plant and algal growth in wetlands (Gabor *et al.* 1994; Murkin *et al.*. 1994; Craft *et al.* 1995; McDougal *et al.* 1997). Other studies involving nutrients released from organic sources, such as sewage effluent, have observed an increase in wetland productivity (Richardson and Schwegler 1986; Kadlec and Bevis 1990). Inorganic nutrients are released from the feces of

aquatic birds into surrounding waters (Baxter and Fairweather 1994; Manny *et al.* 1994; Marion *et al.* 1994). I hypothesized that the biomass and productivity of the macrophyte and algal communities of Delta Marsh enclosures would be affected by feces addition, yet it appears that, in both years of the study, neither assemblage responded according to predictions.

There are some indications that abiotic factors, primarily nutrient inputs, ultimately determine the productivity of a system (Dillon and Rigler 1974; Schindler 1978). although other evidence points to the role of the consumer in influencing ecosystem structure and productivity (McQueen *et al.* 1990; Sarnelle 1992). Based on my experiments, it appears that primary production is regulated by a complex interaction of both abiotic and biotic factors (Gophen 1990; Rosemond *et al.* 1993; Kjeldsen 1996). Some of the factors which influence macrophyte and algal production are nutrients, light and grazing. Therefore, I propose, based on previous research, that it was one or more of these factors that resulted in the observed lack of response by algae and macrophytes to feces additions.

Contrary to my predictions, wetland algae manipulated in these experiments did not respond to nutrients liberated from waterfowl feces in a consistent way. Because this finding contradicts the "conventional wisdom" that waterfowl make substantial, important contributions to the nutrient requirements of algae and plants (Gere and Andrikovics 1992; Manny *et al.* 1994; Marion *et al.* 1994), it is an interesting and noteworthy finding for which I sought some explanation. I formulated several hypothesis and, in the sections that follow, I address each in turn. Since these hypothesis were developed *a postiori*, data collected for this thesis necessarily cannot fully address their likely importance. Proper evaluation is left for subsequent studies.

Hypothesis 1:

Nutrients in added waterfowl feces were not released sufficiently quickly to benefit algae

Nutrients are released from waterfowl feces (Gere and Andrikovics 1992; Manny *et al.* 1994; Marion *et al.* 1994) and they are known to increase algal biomass in lakes (Manny *et al.* 1994), so perhaps no algal response was observed because nutrients remained bound to

the fecal particles as they sank to the bottom sediments. Feces loads added experimentally to my experimental enclosures were in substantially higher concentration than those occurring naturally in Delta Marsh. The natural feces loading to Delta Marsh by Canada geese was calculated from measurements of bird density and defecation rates, and mass and chemical composition of the feces. The density of waterfowl in Delta Marsh is ~ 1 bird/ha (Dr. Bob Jones, Manitoba Natural Resources, Winnipeg, MB, personal communication to C. Pettigrew). Manny *et al.* (1994) measured defecation rates of Canada geese on Wintergreen Lake, Michigan and determined that geese defecate 1.96 droppings/bird/hr during the day, and 0.37 droppings/bird/hr at night. Therefore, assuming a 12-hour daylight period, a goose defecates about 28 times/day. Manny *et al.* (1994) also determined the average dry weight of one goose dropping to be 1.17 g dry weight or 7.29 g wet weight (based on my estimate of 80.9% water content). Therefore, given 28 droppings/bird/day and 0.0001 bird/m^2 in Delta Marsh, the natural daily loading rate is 0.0204 g/m^2/day wet weight. In 1995, the nutrient additions applied over nine weeks represented a hypothetical natural loading of 1.28 g/m^2 wet weight, as compared to the actual experimental loading to each of the high feces enclosures of 488.9 g/m^2 wet weight (the low feces enclosure values were one-tenth of this level). In 1996, the total experimental loading was the same as in 1995 but it was added over an 8-week period so the total hypothetical natural loading would have been approximately 1.14 g/m^2 wet weight.

The total natural loading rate of N and P after 9 weeks would have been 0.0014 g/m^2 N and 0.0034 g/m^2 P while the total experimental loading on N and P in 1995 in the high and low feces enclosures was 2.73 g/m^2 N, 1.57 g/m^2 P and 0.273 g/m^2 N, 0.157 g/m^2 P, respectively. The total natural loading rate of N and P after 8 weeks would have been 0.0011 g/m^2 N and 0.0027 g/m^2 P while the total experimental loading of N and P in 1996 for the enclosures that received the duckling feces slurry was 5.87 g/m^2 N and 1.95 g/m^2 P. From the numbers calculated above, I added approximately the same total inorganic P load as applied by McDougal *et al.* (1997), yet I did not observe a significant increase in epiphyton

and metaphyton biomass and, in fact, metaphyton did not develop during the experiment.

It is apparent that the applications of waterfowl feces in my experiments exceeded those that would have occurred naturally, so perhaps the problem was not that there was insufficient nutrients to stimulate growth, but rather that nutrients were not released quickly enough to benefit algae. The results from the aquarium experiments, however, suggest that this is not the case for nutrients were released immediately upon addition. It is clear that there was an immediate release of SRP and NH_3-N within the first 24 hours of the feces additions. The release of NO_3-N, however, was delayed in experiments #1 and #3 for at least 40 hours and, in experiment #2, NO_3-N was not released during the experiment. In 1995, the enclosure NO_3-N values fluctuated and were low, never exceeding 0.4 mg/L and did not appear to be affected by the addition of feces. Two significantly sharp increases ($p < 0.05$) were observed in NH_3-N and SRP concentrations after the two feces additions in the load enclosures. In 1996, the NO_3-N values were low and there was only one date where the concentration was detectable and this occurred in the controls. NH_3-N and SRP concentrations increased above the control concentrations after the first application of feces on 5 July and remained higher than the control values throughout the experiment. These results refute the possibility that nutrients are not released from the feces quickly, for they were detected in the water column immediately after addition to the enclosures.

Hypothesis 2:

Ammonia was released from waterfowl feces in sufficient quantities to cause direct toxicity, thereby reducing rather than stimulating algal biomass

Ammonia was the major form of inorganic N occurring after feces additions, commonly reaching concentrations > 0.6 mg/L in 1995 and > 0.02 mg/L in 1996. Although ammonia is the primary form of N used by algae, it is toxic when in high concentrations (Wetzel 1983). Niederlehner and Cairns (1990) tested the effects of six ammonia concentrations (0 to 137.7 mg/L) on the biomass of periphyton in laboratory test tanks. They found that periphyton biomass was significantly lower than the controls when ammonia concentrations were ≥

0.011 mg/L. Hürlimann and Schanz (1993) found that exposure of periphyton in artificial channels to 5.1 and 9.3 mg/L NH_4^+-N over an 80-day period in the winter lowered biomass as compared to that in control channels. They suggested that these "toxic" levels in the winter would be observed in the summer if 0.5 mg/L NH_4^+-N (or 0.006 mg/L NH_3-N) were added to natural water.

The above studies suggest that if ammonia toxicity had occurred during this study, the periphyton values in the feces enclosures would be significantly lower than the controls. In 1995 the ammonia values peaked 7 hours after each feces application in both the high and low load treatments. During this time, when the ammonia values were maximum (1.035 and 0.671 mg/L, respectively) the periphyton chlorophyll values increased. In 1996, ammonia levels in the feces treatment were above the "toxic" levels found by Niederlehner and Cairns (1990) and Hürlimann and Schanz (1993) throughout the experiment and were always higher than the control values after feces applications began on 5 July. The periphyton chlorophyll concentrations, however, did not appear to respond to the increased levels of NH_3-N and, in fact, the periphyton values were higher in the feces treatment than in the control when the NH_3-N concentrations were the highest on 23 and 27 August. These results refute the possibility that ammonia toxicity was responsible for the lack of response to the feces additions for in both years because there was no significant ($p > 0.05$) decrease in periphyton biomass with increase in NH_3-N concentrations.

Hypothesis 3:

Algae and/or plants luxury consumed liberated nutrients without growing

Algae are known to consume nutrients in excess of their immediate metabolic needs (luxury consumption), so it is theoretically possible that they could take up added nutrients without a corresponding increase in biomass or productivity. Pickering *et al.* (1993) found that the seaweed, *Gracilaria chilensis*, achieved its maximum growth if a high ammonium concentration (up to 150 μM) was pulsed into N-depleted sea water once every 7 days. Growth continued when the N source was depleted, suggesting that plants can take up N in

excess (luxury consume) and store it until it is required, and continue to grow in the nutrient-limited medium. Steward and Ornes (1975) found that there was an increase in nutrient uptake when enclosed stands of *Cladium jamaicense* were enriched with N, P and K, but no increase in growth was observed. They suggested that natural levels of these nutrients were enough to sustain growth and that this wetland in the southern Everglades, was not nutrient-limited. Therefore, the plants luxury consumed the added nutrients and stored them as a reserve until ambient nutrient levels dropped below required amounts.

In 1995, TP increased in the water column of the high feces treatment and remained above levels in the low feces and control treatments throughout the experiment. As well, TP values increased after the first feces load in 1996 above levels in the controls and remained so until the end of the experiment. This suggests that P was available for uptake, yet in both years there was no significant increase in PP levels in the algal and macrophyte communities, suggesting that P was not luxury consumed and, therefore, neither aided nor limited growth.

Hypothesis 4:

Feces were depleted in N, relative to P as compared to the ambient N:P ratio in Delta Marsh, suggesting that feces provided insufficient quantities of the growth-limiting nutrient for algae

Inorganic P and N concentrations often determine whether a system will shift from a less productive state to a more productive state (Wetzel 1983) and, therefore, the limitation of one of these elements may have been responsible for the lack of response to added feces, if the feces were depleted in either N or P. Schindler (1974) demonstrated the stimulatory effects of P, N and C on Lake 226 in the Experimental Lakes Area, ON. Lake 226 was divided into two basins where both basins received equal additions of N and C while only one received a P addition. The basin which received the three elements became highly eutrophic where algal biomass increased while the basin which received only N and C remained unchanged. This demonstrates the effect P had on controlling production.

P was probably not a limiting factor in the enclosure experiment because TP values

increased in the water column in the treatment enclosures after feces additions above the levels in the control treatment throughout the experiments. Lake productivity is eutrophic when total P concentrations are between 30 and 100 µg/L, (Wetzel 1983). P levels in the high feces enclosures were above 100 µg/L following treatment in both years.

Vymazal *et al.* (1994) tested the effects of P and N additions on periphyton growth, composition and biomass nutrient content in three different plant communities using experimental plots in the South Florida Everglades. Highest values of periphyton biomass were obtained with high P concentration, and medium and high N and P concentration treatments. The lowest biomass was observed in the treatments that received only N. These results suggest that P was the limiting nutrient; however, it is important to note that a combination of N and P resulted in significantly higher periphyton biomass. Strauss *et al.* (1994) also observed the highest chlorophyll *a* concentrations in enclosures in a Kansas farm pond that received N and P in combination, suggesting that phytoplankton were "co-limited" by these two nutrients.

The foregoing leads me to suspect that the marsh may be N-limited. Relative to the Redfield ratio (1958) of the molar concentration of total N (sum of TKN and NO_3-NO_2) to total P (TP), if a value ≤ 16 is obtained, a system is N-limited while if values are > 16, the system is P-limited. Healey and Hendzel (1980) showed that P-deficiency in freshwater phytoplankton occurs as the N/P molar loading ratio exceeds 10. Therefore, it should follow that an N-deficiency occurs when there is a decrease in the N:P loading. In 1995, the ratio between total N and total P varied in the three treatments, showing no trends during the experiment with no significance between treatments on any of the sampling dates. However, the ratio fell below 16 on three separate sampling dates in at least one treatment, indicating N-limitation. TN:TP was 14.55 ± 1.07 in the low nutrient load treatment on 16 June; in the control treatment on 7 July TN:TP was 7.96 ± 6.74, while on 25 August the TN:TP ratio in high nutrient load and control treatments were 6.83 ± 3.10 and 14.32 ± 5.38, respectively.

In 1996, TN:TP in the water column declined with each nutrient addition, shifting the

system away from P-limitation towards N-limitation. TN:TP increased in both treatments at the beginning of the experiment, prior to nutrient additions. The ratio decreased sharply after the first feces addition in both treatments and, by mid-July, the values for the treatments started to diverge; the pattern of the trends, however, remained the same. TN:TP decreased with time in the treatments in early August but levels were N-limited (<16) in the enclosures which received the nutrients. The controls remained P-limited (>16) throughout the experiment until the last sampling date (28 August) where levels were 14.47 ± 0.25. I suggest that it is this change in the resource ratio upon the addition of the waterfowl feces which may have caused the wetland to be depleted in N, relative to P.

Hypothesis 5:

Algae were light-limited, not nutrient-limited, so additions of nutrient did not stimulate growth

There was no significant difference in the light extinction coefficient of any treatments in both years although it decreased with time in all treatments, probably due to shading caused by the increase in macrophyte abundance. The increase in macrophyte abundance, coupled with the removal of fish and the presence of the enclosure curtains, reduced the resuspension of bottom sediments, producing a decrease in turbidity of the water column. A decline in turbidity probably allowed increased light to penetrate the water column and likely an increase in transparency, more so than what would be observed outside the enclosures.

Müller (1996) found that periphytic algae associated with *Phragmites* in the littoral zone of Lake Belau, North Germany was not limited by light, even in cases of dense shading. She suspected that the communities adapted to low light intensities with changes in community structure. As well, Robinson *et al.* (1997b) tested the effects of water-level manipulations in large (5.5 - 7.7 ha) mesocosms in Delta Marsh and found that the ambient light levels in the marsh were well above I_k (saturating irradiance value) for wetland algae. Therefore, it appears unlikely that algae in Delta Marsh are light-limited.

Hypothesis 6:

Fecal nutrients were not available for algal uptake because they were rapidly and irreversibly sequestered in the sediments

Nutrients entering a wetland may be absorbed by biota, such as macrophytes, or sequestered in the sediments (Steward and Ornes 1975; Kadlec 1994). Wetland sediments contain abundant nutrients (Jansson *et al.* 1994), and they are known to have high assimilative capacity for N and P (Walbridge and Struthers 1993; Jansson *et al.* 1994; Paludan and Jensen 1995) so feces and the associated nutrients, particularly those in particulate form, might be rapidly and permanently adsorbed, thereby rendering them unavailable for algal assimilation. Murkin *et al.* (1991) compared two marshes in the Interlake region of MB; Narcisse Marsh received no known external nutrient input whereas Cruise Marsh received external nutrient input from a cattle feedlot. They found that Cruise Marsh had higher levels of N and P, increased epiphyte and phytoplankton biomass and greater invertebrate abundance than Narcisse Marsh. From data interpolated from Murkin *et al.* (1991), Goldsborough and Robinson (1996) determined that the N:P of Narcisse and Cruise marshes were 126 and 27, respectively, indicating severe P-limitation at the Narcisse site. They suggested that, even when N and P entered the Narcisse site, they were rapidly removed from the water column and deposited in the sediments, unavailable for algal uptake.

The aquarium experiments conducted in 1995 support the hypothesis that inorganic nutrients were released from waterfowl feces. Subsequent to the release of the fecal nutrients, I hypothesized that, in the presence of marsh sediment, nutrient concentration in the water column would decrease as they became bound to the sediment particles. In the aquarium with sediments, SRP concentration increased to approximately 0.6 mg/L within less than 20 hours after the feces addition, while in the corresponding aquarium without sediments, SRP concentrations increased to approximately 1.8 mg/L. The control aquarium without sediments had undetectable amounts of SRP throughout the rest of the experiment, while the control aquarium with sediments had a constant SRP concentration approximately 0.1 mg/L. I suspect

that this may be the reason for the gradual increase in SRP concentration with time in the feces-treated aquarium with sediments as compared to the feces-treated aquarium without sediments, where nutrients may have slowly released from the sediments as the experiment proceeded.

Hypothesis 7:

Feces additions did stimulate algal production, but the increase was entirely transferred to consumers so an increase in grazers with treatment mitigated the algal response

Considerable research has been conducted on the role of invertebrates in regulating algal growth when nutrients are not a limiting factor (Murkin *et al.* 1991; Gabor *et al.* 1994; Strauss *et al.* 1994). Campeau *et al.* (1994) used enclosures in the Interlake region of MB to test two hypothesis, one of which was to determine if algae are a food source to invertebrates. They found that when enclosures were enriched with inorganic N and P, phytoplankton and epiphyton biomass increased significantly above levels in unfertilized enclosures. Subsequent to this increase in biomass was a significant increase in the number of cladocerans, copepods and ostracods. Kjeldsen (1996) found that stones which had previously been immersed in insecticide had significantly higher algal biomass than stones which had not been treated with the insecticide in Gelbaek stream, Denmark. She also found that there was a significantly higher density of *Ancylus fluviatilis* on the untreated stones confirming that algal biomass was regulated by invertebrate grazing.

In an experiment conducted in enclosures at Delta Marsh, Hann and Goldsborough (1997) examined the microinvertebrate communities after press and pulse additions of inorganic N and P. They found that there was no significant difference between treatments concerning cladoceran abundance in the water column; however, cladoceran abundance increased after a phytoplankton bloom such that algal biomass was kept low throughout the experiment. Cladocerans associated with artificial substrata increased after the press additions until mid-July, while following the application of each nutrient pulse, cladoceran abundance increased, keeping the periphyton biomass down. Hann and Goldsborough (1997) attributed this

difference in periphyton biomass to size-selective herbivory. They suggest that, as periphyton biomass increased in the press treatment, cladocerans grazed on the smaller algal cells colonizing the artificial substrata, which allowed the filamentous green algae (*Cladophora*) to increase under the pressed nutrient regime. These results support the impact grazers have on controlling algal dominance.

As the evidence above suggests, the lack of algal response in my study may be due, in part, to the top-down, regulating forces of zooplankton herbivory. For example, in an experiment conducted in enclosures at Delta Marsh concurrent with mine, Pettigrew *et al.* (1998) examined the microinvertebrate communities after the pulsed additions in 1995. They found there was no significant difference between treatments concerning cladoceran abundance in the water column; however trends indicate there was an increase in cladoceran abundance after the first feces addition in one of the high feces load enclosures (#1). This increase may have caused decreased algal abundance after the first addition. Algal biomass remained low through the duration of the experiment while cladoceran abundance increased substantially. During my experiment in 1995 I observed increased phytoplankton biomass after the first feces addition in the high feces treatment, but it did not increase in either treatment after the second addition. Perhaps invertebrates in the water column were able to take advantage of the increased biomass and graze down the phytoplankton, thereby keeping phytoplankton biomass low even when nutrients were available after the second addition. Epiphyton chlorophyll increased one week after the second feces addition in the high load treatment in 1995, while invertebrate particulate P, of those grazers associated with macrophytes, increased in this treatment three weeks after the addition, perhaps a response to the increased food source.

In 1996, phytoplankton biomass was highest in both treatments before the weekly feces additions but, perhaps as in Pettigrew et al. (1998) invertebrates in the water column increased such that phytoplankton was maintained at a constant concentration during the rest of the experiment. Epiphyton chlorophyll increased after the first feces application in the high

feces treatment but it decreased the following week. Concurrent with the decreased epiphytic biomass was increased invertebrate particulate P, again perhaps muting the algal response. There is no corresponding invertebrate data in 1996.

6. CONCLUSION

Natural feces loading rates by the waterfowl inhabiting the Delta Marsh during a nine-week period would have equaled approximately 1.28 g/m^2 wet weight, while the amounts added to the high feces enclosures each comprised a total load of 488.9 g/m^2 wet weight. Contrary to my hypothesis, there was no significant change in the biomass and productivity of the submersed macrophytes and algal communities by waterfowl feces loading even when loading greatly exceeded estimated natural values. I was unable to shift the system from the prevailing epiphyte-dominated state to a phytoplankton-dominated state with pulsed or weekly additions of waterfowl feces, contrary to earlier enrichment experiments with inorganic nutrients (McDougal *et al.*. 1997). I propose that my inability to shift the system was attributed to one or more factors that, in combination, interacted to regulate primary production. Feces were depleted in N, relative to P, so when added to an N-limited system, the feces additions did not lead to a growth response. Therefore, I suspect that natural feces inputs over an eight- to nine-week period to Delta Marsh probably do not substantially alter nutrient cycling. Top-down control of invertebrate grazers may have regulated the algal response whereby increased algal biomass may have lead to increased invertebrate abundance and subsequent depression of the algal communities. Nutrients released from the feces may have been adsorbed rapidly and deposited in the sediments upon application and, therefore, were unavailable for assimilation by the algal components of the marsh.

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8. APPENDIX A

8.1 Year 1 (1995)

8.1.1 Physical Data

Table A1. Mean (range in parentheses) of physical parameters from experimental enclosures, none of which varied significantly ($p>0.05$) with treatment.

Parameter	High Feces	Low Feces	Control
Vertical attenuation coefficient (n/cm)	-0.067 (-0.122 - -0.017)	-0.068 (-0.140 - -0.024)	-0.076 (-0.169 - -0.019)
Macrophyte biomass (g/m^2)	24.3 (4.4 - 43.8)	31.8 (4.4 - 68.7)	35.4 (5.9 - 66.8)

8.1.2 Chemical Data

Table A2. Mean (range in parentheses) of chemical parameters from experimental enclosures, none of which varied significantly ($p>0.05$) with treatment.

Parameter	High Feces	Low Feces	Control
Dissolved oxygen at 10cm (mg/L)	14.3 (7.2 - 19.4)	13.8 (7.6 - 18.8)	13.7 (7.8 - 20.0)
Titratable alkalinity (mg/L)	208.3 (181.8 - 237.6)	179.1 (123.7 - 237.2)	160.4 (114.3 - 223.1)
pH	9.3 (8.2 - 10.2)	9.4 (8.0 - 10.4)	9.5 (8.1 - 10.4)

8.2 Year 2 (1996)

8.2.1 Physical Data

Table A3. Mean (range in parentheses) of physical parameters from experimental enclosures, none of which varied significantly ($p>0.05$) with treatment.

Parameter	High Feces	Control
Turbidity (NTU)	1.7 (0.8 - 2.9)	1.6 (0.9 - 2.5)
Vertical attenuation coefficient (n/cm)	-0.045 (-0.110 - -0.017)	-0.041 (-0.098 - -0.016)
Macrophyte biomass (g/m^2)	66.2 (28.4 - 101.0)	89.8 (41.0 - 127.8)

8.2.2 Chemical Data

Table A4. Mean (range in parentheses) of chemical parameters from experimental enclosures, none of which varied significantly ($p>0.05$) with treatment.

Parameter	High Feces	Control
Dissolved oxygen at 10cm (mg/L)	8.0 (6.1 - 10.1)	8.2 (6.0 - 9.8)
Dissolved oxygen at 50cm (mg/L)	4.5 (1.1 - 8.2)	4.7 (2.0 - 8.0)
Nitrate-nitrite (mg/L)	0.012 (0.005 - 0.027)	0.011 (0.005 - 0.029)
Silicon (mg/L)	2.2 (0.2 - 4.3)	2.4 (0.2 - 4.3)
Titratable alkalinity (mg/L)	213.1 (192.4 - 257.4)	191.9 (162.9 - 257.4)