The Effects of Common Carp (*Cyprinus carpio L.*) on Water Quality, Algae and Submerged Vegetation in Delta Marsh, Manitoba

by

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Abstract

Common Carp, (*Cyprinus carpio)*, have long been associated with the degradation of wetlands worldwide. Through their feeding activities they resuspend sediments leading to reductions in the abundance and diversity of submerged macrophytes, and the alteration of water chemistry which can lead to the phytoplankton-dominated state. This study took in Delta Marsh, a freshwater coastal wetland of Lake Manitoba, in Manitoba, Canada. It was the second part of a four-year study in which baseline data were collected in 2001 from ten ponds (1-13 ha) with varying degrees of connectivity to the main marsh and carp-accessibility. I continued to monitor a subset of the control and altered ponds two and three years following their alteration (2003 and 2004); I included new ponds, including one large open bay (20.3 ha). The overall four-year study has shown that the presence of carp is at least partially responsible for the turbid, phytoplankton-dominated state that exists in Delta Marsh, and that carp abundance is an important factor. Ponds previously isolated then exposed to carp activity, particularly in the spring when they were gathered at high densities, shifted to the turbid, phytoplankton-dominated state with few macrophytes, and the removal of carp from ponds led to the clear-water state, though not necessarily an abundance of macrophytes. Due to the complexity of natural ecosystems, the effects of carp were not as predictable as smaller-scale studies would suggest. In my study, water quality, submerged vegetation biomass and algal growth varied both temporally and spatially in carp-accessible and carp-free ponds. Nutrient deficiency among periphyton assemblages was hypothesized to

be alleviated by the presence of carp. Using nutrient diffusing substrata, I found that nutrient deficiencies varied from year to year among carp-free and carp-accessible ponds. In 2003 the hypothesis was supported, however, in 2004 two of the carp-free ponds exhibited no-nutrient limitations to periphyton assemblages while N and P co-limitation became prevalent in one carp-accessible pond. Parameters over which there was no control, such as the spatial and temporal distribution of carp, their density within a pond, water depth and unquantified top-down effects, including zooplankton grazing, may have contributed to the variability of the results.

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Dedication

To my mother who taught me to have faith in myself and to persevere no matter how rough the road.

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Introduction

There exists in the scientific literature and personal accounts worldwide, convincing evidence that the introduction of the Common Carp, (*Cyprinus carpio*) (hence forward referred to as “carp”), has been detrimental to the healthy function of wetlands and shallow lakes. Once clear-water, macrophyte-dominated systems providing shelter, breeding grounds and nourishment to invertebrates, fish and waterfowl have, with the presence of carp, shifted to systems characterized by phytoplankton-dominated turbid waters, few macrophytes and subsequent decreases in biodiversity (e.g., King et al. 1997; Zambrano et al. 1999; Khan 2003; Miller and Crowl 2006; Hnatiuk 2006).

Small scale enclosure studies and exclusion studies have confirmed and identified the manner in which carp may contribute to the turbid, phytoplankton-dominated state in wetlands and shallow lakes (e.g., Roberts et al. 1995; Breukelaar et al. 1998; Lougheed et al. 2001; Badiou 2005; Chumchal 2005). Experiments conducted in mesocosms are beneficial in that they provide the researcher with the benefits of control, replicability and high level of statistical confidence (Bloesch et al. 1988; Carpenter 1996; Schindler 1998). However, Schindler (1998) warns that they lack all of the trophic levels and functions of a real ecosystem, some of which could be essential to the understanding of how carp impact natural ecosystems. Dangers include basing results upon artifacts of the design and sometimes the structure of the mesocosm itself which can introduce changes to basic functions such as chemical and algal dynamics and

organism behaviour (Bloesch et al. 1988). Schindler (1998) goes on to cite experiments at sub-system and whole ecosystem levels in which results were very different. Badiou (2005) compared small enclosure experiments to those performed at a larger mesocosm scale and discovered that in the case of some parameters the results were exaggerated in the smaller enclosures. While providing basic understanding of ecosystem processes, there exists the danger that these experiments are not representative of the natural ecosystems they seek to characterize (Dunham and Beaupre 1998). Hnatiuk (2006) undertook a whole ecosystem level study on the effects of carp in the coastal wetland, Delta Marsh, MB. She found ponds to which carp had access tended to be turbid and phytoplankton-dominated when compared to carp-free ponds which were clear and macrophyte-dominated. However, she noted a significant degree of local variation both temporally and spatially in the magnitude of their effects on the biomass of submerged vegetation, algae and water column nutrients in a subset of ponds within Delta Marsh.

Objectives

In this study, I performed a survey of ponds across, Delta Marsh, a large coastal wetland (18, 500 ha) in south-central Manitoba where carp have been present in abundance for more than fifty years (Wrubleski 1998). I compared ponds with and without access to the influences of carp in a natural environment, without the benefit of true replication and control of mitigating factors, to determine how results from mesocosm experiments apply to real world scenarios. I have

continued Hnatiuk's (2006) work, by comparing water column nutrients, submerged macrophyte abundance and algal abundance in the carp-accessible and carp-free ponds of Delta Marsh. Additionally, I examined the status of the bio-manipulated ponds in Hnatiuk's (2006) study two and three years after the ponds had been rendered accessible or inaccessible to carp by means of blasting of a channel connecting it to the main marsh or by installation of screens or dikes to prevent carp access. I also included in the study the use of nutrient diffusing substrata (NDS) to determine N and P limitation to algae within ponds by measuring the growth response of periphyton in response to nutrients provided. In theory, if either nitrogen or phosphorus is growth limiting, algal growth on the substratum enriched with N and/or P should be significantly greater than on the control.

Hypotheses

Hypothesis: Water clarity

Ponds to which carp have access will exhibit higher turbidity due to elevated water column concentrations of suspended particles and greater abundance of phytoplankton than ponds to which carp do not have access.

Hypothesis: Water column nutrient concentrations

Ponds to which carp have access will have higher water column concentrations of N and P compared to carp-free ponds due to the disruption by carp of

sediments, releasing nutrient rich sediment porewater, and nutrient excretion by carp.

Hypothesis: Algae

Ponds to which carp have access will have higher concentrations of periphyton per unit of available substratum and phytoplankton relative to carp-free ponds due to an expected increase in available nutrients associated with carp presence.

Hypothesis: Submerged macrophytes

I expect the biomass and species diversity of submerged macrophytes to be reduced in carp-accessible ponds compared to carp-free ponds. Reductions in macrophyte biomass and diversity is expected as a result of reduced light availability due to elevated water column concentrations of suspended solids, phytoplankton and epiphyton associated with their presence, and physical damage, such as uprooting while carp are feeding.

Hypothesis: Nutrient limitation

In ponds open to the main marsh where adult carp have access, I expect that neither N nor P will be limiting to the growth of periphyton, as the resuspension of the sediments and subsequent nutrient release or inputs of nutrients by excretion by carp should provide ample N and P for periphyton growth. In sites to which carp do not have access, I expect periphyton to be either N or P limited or N and P co-limited as there will be no bioturbation of the sediments and no carp to add

nutrients via excretion, in addition to abundant submergent and emergent macrophytes to compete for nutrients.

Literature Review

Importance of Wetlands in Manitoba

Wetlands are valuable habitats which contribute many valuable functions. Among them are their ability to help protect the “health” of lakes and oceans by removing excess N, P and suspended sediments from the water that flows through them from agricultural run off by means of a number of physical, chemical and biological processes (van der Valk 1989; Mayer et al. 1999). Wetlands can be highly effective nitrogen sinks (van der Valk 1989). In the Lake Waco Wetland, Texas, nitrate concentrations were found to have been reduced by more than 90% in the first half kilometer from the inflow (Scott et al. 2008). Nitrogen is removed from the water column mainly through denitrification, but dissimalatory nitrate reduction to ammonia, volatilization and assimilation by plants and algae are also important (van der Valk 1989; Tomaszek et al. 1997, Bachand and Horne 1999; Whitmore and Hamilton 2005; Scott et al. 2008). Phosphorus is removed from the water column by means of sedimentation, co-precipitation of calcium carbonate with soluble reactive phosphorus and uptake by aquatic vegetation and their associated periphyton (van der Valk et al. 1979; Kadlec and Knight 1996; Dierberg et al. 2002; Gu 2008). The presence of shallow, well-vegetated wetlands reduce the flow velocity of water entering the system, allowing sediments to settle (Murkin 1998). Settling of suspended particles increases the penetration of photosynthetically active radiation (PAR) by creating clearer water important for the growth and function of submerged macrophytes. It

also serves to remove nutrients bound to the suspended particles and can remove pollutants, such as metals and organic chemicals (Kadlec and Knight 1996). Wetlands also serve to mediate flood peaks and storm flows, regulate stream flow and act as ground water recharge and discharge sites (Carter et al. 1979; Novitzki 1979; Murkin 1998; LaBaugh et al. 1998).

The high productivity of coastal marshes and their diversity of structural habitat attract and support populations of a variety of species of invertebrates, amphibians, fish and waterfowl which use marshes to feed, and/or reproduce and rear young (Janusz and O'Connor 1985; Stephenson 1990; Kiers and Hann, 1995; Brazner et al. 1997). Studies on coastal wetlands of Lake Winnipeg, Lake Manitoba and the Laurentian Great Lakes have shown communities of fish consisting of upwards of 25 species (Janusz and O'Connor 1985; Stephenson 1990; Jude and Pappas 1992; Brazner and Beals 1997; Brazner 1997; Parks 2006). The high productivity, high species diversity and complex architectural structure of healthy coastal wetlands also attract migrating and breeding waterfowl (Prince et al. 1992; Mallory et al. 1994; Murkin et al. 1997).

Worldwide, more than half of all wetlands have been altered, degraded or lost in the last two hundred years, due in large part to human activity (O'Connell 2003). Many wetlands have been filled or drained in order to increase the area of arable land for human habitation and use. In Manitoba, marshes and shallow open water make up 2.5% (13,532 km^2) and 1.3 % (6,855 km^2), respectively, of the total area of the province. While they are found throughout the province, they are

concentrated in the southern and central regions (Halsey et al. 1997). According to Ducks Unlimited Canada (2009), 6 ha of wetlands are lost every day in southwestern Manitoba. Annually, 2,185 ha are drained in the southwest part of the province. It is estimated that this drainage emits over 1,200 tonnes of carbon dioxide into the atmosphere daily and contributes an additional 6.2 tonnes of P annually to downstream flows, which contributes to water quality problems such as algae blooms in Manitoba lakes and streams (Ducks Unlimited Canada 2009) as well as downstream erosion and flooding. Water level regulation of the lakes for hydroelectric development and other reasons can damage coastal wetlands by adversely altering water regimes. Water level fluctuations are necessary for maintaining the floral and faunal diversity and health of freshwater coastal wetlands by keeping them in a perpetual state of disturbance (Murkin et al. 1997; Keddy and Fraser 2000; Wilcox and Nichols 2008). Additionally, excessive sedimentation as a result of erosion due to deforestation, poor agricultural practices in the watershed, eutrophication, as a result of high nutrient inputs from point sources, and agricultural run-off can result in the simplification of aquatic food webs and impairment of basic wetland functions related to water quality improvement by promoting a turbid, phytoplankton-dominated state (Gleason and Euliss 1998).

Currently, the health of the two largest coastal wetlands in Manitoba is in decline. Netley-Libau (250 km^2), at the south end of Lake Winnipeg, no longer functions as a healthy wetland due to the stabilization of water levels, and the alteration of the Red River's flow through the wetland. This has resulted in the increase of

open water areas and the decline of macrophyte abundance (Grosshans et al. 2004). Macrophytes are important for maintaining floral and faunal diversity as well as their ability to remove nutrients from the river water. The health of Delta Marsh (185 km^2), at the south end of Lake Manitoba, has been in decline due to water level stabilization and the introduction of invasive species . Over the last 40 years, waterfowl populations, area of macrophytes and islands have been in decline, in addition to a dramatic increase in water column turbidity (Ould 1980; Bond 1996, Goldsborough and Wrubleski 2001;).

The introduction of exotic species is detrimental to the diversity of native species and the healthy function of wetlands. Currently, wetlands in Manitoba are threatened by purple loosestrife (*Lythrum salicaria*), and flowering rush (*Butomus umbellatus*) (Dupont 2008). If left unchecked these species have the potential to outcompete native flora in Manitoba wetlands, reducing the diversity of fauna dependant upon the native floral communities. Introduced fauna also pose a threat to Manitoba wetlands. Initially introduced as a food fish, the long term ecological impact of Common Carp (*Cyprinus carpio*) in North American waters was not considered. Evidence of their propensity to damage wetlands was first noticed within twenty years of their first introductions (McCrimmon 1968). At high densities, carp can damage submerged macrophyte beds and promote a turbid, phytoplankton-dominated state through bioturbation of wetland sediments during spawning and feeding activity. The subsequent lack of aquatic vegetation results in fewer spawning sites for native fish and a lack of refugia for larval fish, as well as reducing the availability of aquatic invertebrate prey (Engel 1985; Cooper

1987; Hann 1995; Sandilands 2000; Williams et al. 2002). Waterfowl are also negatively impacted by reductions in biomass and diversity of aquatic vegetation, which results in less nesting material, food resources and cover (Cahoon 1953; King and Hunt 1967; Goldsborough and Wrubleski 2001; Haas 2007)

Natural History of Common Carp (Cyprinus carpio)

Common Carp (*Cyprinus carpio*) are one of the largest members of the minnow family, Cyprinidae. They have a robust and laterally compressed body with average length reported between 38 and 47 cm, reaching maximum reported lengths in Manitoba of 108 cm (Scott and Crossman 1998; Stewart and Watkinson 2004).

Originating in Eurasia (Balon 1995), carp have been used as a subsistence fish since the time of the Roman Empire and were distributed across Europe during the Middle Ages (Hoffmann 1994). Carp were first introduced to North America in the 1870s by private parties and the U.S. Fish Commission with the intention of culturing the species for use as an affordable food source in the face of declining native fish populations (McCrimmon 1968). Today carp can be commonly found throughout North America. In Manitoba they are found mainly in the south and central regions and due in part to habitat alteration as a result of the construction of dams and reservoirs for hydroelectric development, can be found as far north as the Churchill River System (Badiou and Goldsborough 2006).

The same qualities that carp were prized for in the early days of aquaculture are those that made the carp successful as an invasive species, facilitating their spread and persistence. The carp is an extremely hardy fish. They are tolerant of a wide temperature range (1.7°C to 38°C), with optimal growth occurring between 10°C and 25°C, and can weather rapid temperature fluctuations (Scott and Crossman 1998). They can tolerate elevated salinity levels as high as 176 mM for three months, and are found in the coastal areas of the northern Caspian Sea (Lam and Sharma 1985; Martem'anov 1996) and high turbidity levels (upper lethal limit of 165,000 ppm) (Bardach et al. 1972; Alabaster and Lloyd 1980). In addition to physiological tolerance to low oxygen conditions (~ 2 mg/L O_2, below which they showed a significant reduction in feeding rate) (McCrimmon 1968; Zhou et al. 2001; Fraser et al. 2006), they also have behavioral methods of surviving hypoxia. Gehrke and Harris (1994) observed carp gulping air at the surface of hypoxic water associated with cyanobacterial blooms in Australia. For these reasons the carp can survive and proliferate in a wide range of habitats such as large lakes and reservoirs, various types of wetlands, large slow moving rivers and fast flowing streams (Panek 1987).

To maintain a viable population carp have two habitat requirements. Highly productive, shallow water habitats with muddy or sandy bottoms and an abundance of aquatic macrophytes are necessary, which provide an abundance of prey items for both adult and juvenile carp, in addition to protection for their young (Ottis and Weber 1982; Panek 1987). Carp also require waters deep enough to provide refuge when conditions in the shallow habitats of wetlands

become unfavorable. This may occur in response to anoxia, extreme temperatures, a dwindling supply of prey items or to avoid being trapped in waters that may freeze to the sediment in the winter (McCrimmon 1968; Johnsen and Hasler 1977; Ottis and Weber 1982). In a telemetry study at Delta Marsh, MB., tagged carp would frequently leave the marsh for Lake Manitoba and return for varying periods of time throughout the summer months, though the reasons for these movements were not identified (Wrubleski unpublished report 2000).

Generally carp enter shallow waters, usually wetlands, shortly after the ice melts and begin spawning at 17°C. Maximum spawning activity occurs between 19°C and 23°C and ceases above 28°C (Swee and McCrimmon 1966). Although the majority of the spawn occurs in the spring, carp have the potential to spawn two or more times throughout the summer (Scott and Crossman 1998). In Delta Marsh, MB. they have been observed spawning from late-May to late-July (personal observation) and as late as early-August (Badiou 2005).

Carp are among the most prolific of freshwater fishes (Swain 1979). Fecundity measurements of carp were recorded at 50,000 to 100,000 eggs in females ranging in fork length from 400 to 500 mm (Stewart and Watkinson 2004) and over two million eggs in a female measuring 851 mm from Lake St. Lawrence, Ontario (Swee and MCrimmon 1966). Swee and McCrimmon (1966) report fertilization rates in Lake St. Lawrence, Ontario, estimated at 90% based on observation of egg masses attached to aquatic vegetation. Hatch time (three to six days) and growth rate vary according to water temperature. Young of the year

(YOY) carp grow rapidly relative to other species of fish, reaching lengths of 190 mm during the first growing season in Ontario waters (McCrimmon 1968). In Delta Marsh, MB., YOY carp were recorded in August with a fork length of 120 mm (Badiou 2005). The fast growth rate and presence of large serrated spines of YOY carp mean they are available to predators such as northern pike (*Esox lucius*) and pelicans for only a short period of time. Their superior sense of hearing relative to other fish and the behavioural adaptations of carp YOY, such as hiding amongst macrophytes and burrowing in wetland sediments, help to ensure their survival (Lagler et al. 1962).

Carp are opportunistic omnivores consuming a wide variety of organisms depending on their availability (Panek 1987). At less than two centimeters the diet of YOY carp consists mainly of microcrustacea (Adzhimuradov 1972; Scott and Crossman 1998; Khan et al. 2003). As they increase in size, benthic prey items come to dominate their diet (Sigler 1958; Scott and Crossman 1998; Khan et al. 2003). As adults, they feed mainly on chironomid larvae, tubificids, larger zooplankton (Panek 1987). They have also been found to consume molluscs, detritus and infrequently soft plant materials, and even fish eggs (Crivelli 1981; Scott and Crossman 1998; Garcia-Berthough 2001). To obtain benthic invertebrates, they suck up pond sediment, as deep as 10 centimeters if necessary, forcibly ejecting it into the water column while filtering out food items (Panek 1987).

Effects of carp on turbidity and suspended solids

Carp can increase water column turbidity both directly and indirectly. In the act of spawning and feeding they disturb sediments, suspending inorganic solids (Roberts et al. 1995, Angeler et al. 2002; Parkos III et al. 2003; Badiou 2005; Hnatiuk 2006), and algal cells which have settled on the sediment surface (Roozen et al. 2007). Nutrients released from disturbed sediments and by waste excretion stimulate phytoplankton growth thereby increasing turbidity (Meijer et al. 1990; Qin and Threlkeld 1990; King et al. 1997; Williams et al. 2002; Badiou 2005). Exclusion of carp from wetlands, shallow lakes and reservoirs usually resulted in significant decreases in water column turbidity and the concentration of suspended solids (Schrage and Downing 2004; Hnatiuk 2006). In Coote's Paradise, Ontario, a 40% reduction in turbidity was observed following carp exclusion (Lougheed et al. 2004) while in Laurel Lake Reservoir, Ontario, ISS in the water column was reduced by as much as 45% even in the absence of vegetation (Barton et al. 2000).

The magnitude of the effects of carp on turbidity and TSS is dependant upon the density/biomass of carp present in a system. Enclosure and mesocosm studies have shown that the concentration of total suspended solids increases linearly with increasing biomass of carp (Meijer et al. 1990; Breukelaar et al. 1994; Lougheed et al. 1998; Badiou 2005). However, Zambrano et al. (2001) and Badiou (2005) found that TSS increased substantially once a critical carp density was exceeded (>300 kg/ha carp in mesocosms), at which point carp were

thought to increase their foraging effort in response to a diminishing food supply (Zambrano and Hinjosa 1999). In a natural ecosystem, carp are not confined to a specific area and the high densities necessary to cause substantial increases in suspended solids may be a temporary and/or transient phenomenon. They may move elsewhere where prey items are more readily available. For example, carp tend to congregate at high densities in the spring during the spawning season after which they disperse (Lougheed et al. 1998; Angeler et al. 2002; Hnatiuk 2006). In the carp-accessible ponds of Delta Marsh, Hnatiuk (2006) found turbidity and TSS to be higher in carp-accessible ponds in the spring, when adult carp congregated at high densities to spawn.

The presence of abundant submerged macrophytes can enhance transparency of the water column, even in the presence of carp. Roberts et al. (1995) found that although carp increased turbidity, the magnitude of the increase was reduced where macrophytes were present. In Delta Marsh, both Badiou (2005) and Hnatiuk (2006) found this to be the case. Badiou (2005) found that in a large wetland cell (5 - 7 ha) stocked with 1200 kg/ha carp, an abundance of macrophytes persisted in the pond, effectively suppressing TSS. He suspected that an abundance of benthic prey items in the pond may have prevented extensive damage to the macrophytes. Similarly, Hnatiuk (2006) found low TSS and turbidity in one carp-accessible pond with an abundant growth of submerged macrophytes, compared to ponds that were not accessible to carp. Scheffer (1999) provides an extensive review of the literature on the mechanisms by which macrophytes suppress turbidity and TSS. Submerged macrophytes can

suppress the growth of phytoplankton through a combination of shading, competition for nutrients (directly, or by the periphyton associated with aquatic marcrophytes), exudation of allelopathic chemicals toxic to algae and by harboring an abundance of phytoplankton grazing invertebrates. Additionally they promote an increase of sinking losses of suspended solids, both organic and inorganic. Submerged macrophytes also act as barriers against wind-induced resuspension of the sediments.

The amount of sand, silt, clay and organic matter in the sediments of ponds and other experimental systems also influence the degree to which carp can affect water column turbidity (Crivelli 1983; King et al. 1997; Scheffer 1998). Fine sediments like clay and organic matter will suspend easily upon disturbance and remain in the water column longer whereas larger particles settle out quickly (Scheffer 1998). Where substrates consist mainly of sand, the water column will remain clear despite the presence of carp (Scheffer 1998). Dieter (1990) found this to be true of two shallow lakes in the Sand Lake National Wildlife Refuge in South Dakota, where the lake with predominantly silt sediments exhibited greater turbidity and ISS than did the lake with sediment of a sand-silt mixture. Hnatiuk (2006) noted that ponds in east of Delta Marsh tended to have harder substrates compared to those on the west end of the marsh and as a result tended to be clearer. In an enclosure study in a wetland in central Spain, Angeler et al. (2002) found that ISS was no greater in enclosures stocked with ~ 6000 kg/ha carp than in the controls. Though sediment analysis was not done, they suspected that the sediment in their enclosures was resistant to resuspension.

Benthivorous fish, like carp, have been shown to cause instability of sediments and increase their susceptibility to resuspension by wind through the removal of submerged macrophytes and continual disturbance. In Lake Wolderwijd, Netherlands, TSS increased dramatically with wind speed when carp were present (Scheffer et al. 2003). In laboratory experiments simulating the disturbance to the sediments that carp would incur, (Scheffer et al. 2003) found that the disturbance of approximately 2% of the surface area was sufficient to reduce erosion resistance of the sediments to a level comparable to that of unconsolidated sediments. Once carp were removed no significant relationship was found between wind and TSS concentrations. Only a brief period of quiescence was required to increase erosion resistance of the sediments above a critical point through physical settling and formation of the protective crust of benthic algae, bacteria and other microorganisms. The crust effectively prevented sediment resuspension by even relatively strong wave action (Scheffer et al. 2003). However, the likelihood of this occurring is dependant upon the available fetch of the water body. In a study of two shallow lakes (mean depth 0.6-1m), with few submerged macrophytes and low biomasses of carp (0-92 kg/ha carp), in Sand Lake National Wildlife Refuge, South Dakota, Dieter (1990) found that the open areas of the lakes (>1km fetch) were prone to wind-induced sediment resuspension (ISS and turbidity), while areas protected by interspersed water and emergent vegetation were less affected. In a study of water level effects on the boreal wetlands of northern Manitoba, Watchorn (2010) found that sediment resuspension tended to occur at approximately 40 cm. Hnatiuk (2006)

found a weak correlation between water depth and inorganic suspended solids in the ponds of Delta Marsh, suggesting the possibility of wind-induced resuspension of the sediments even in the absence of carp.

Effects of carp on water column nutrients

Carp have been found to increase nutrient concentrations in the water column by means of excretion (Lamarra 1975; Nuttall and Richardson 1991), release of porewater nutrients during sediment resuspension (King and Hunt 1967; Andersson et al. 1978; Cline et al. 1994; Mayer et al. 1999; Angeler 2002) and by enhancement of remineralization rates (Shormann and Cotner 1997). Badiou (2005) calculated that carp at densities of 200 kg/ha could contribute 0.16 $mg/m^2/d$ total reactive phosphorus (TRP) and 1.73 $mg/m^2/d$ ammonia-N and estimated increases of 31% N and 42 % internal loading in Delta Marsh. Persson (1997) and Braband et al. (1990) found that P excretion from benthivorous fish could match or exceed the phosphorus loading from external sources depending on the time of year, underscoring the importance of benthivourous fish in phosphorus cycling of lakes.

Numerous studies have shown that total phosphorus (TP) generally increases in the presence of carp (Andersson et al., 1978; Keen and Gagliari, 1981; Breukelaar et al. 1994; Shormann and Cotner 1997; King et al. 1997; Scheffer 1998; Lougheed et al. 1998, Angeler et al. 2002) and that TP increases with increasing biomass of carp (Chumchal et al. 2005). In an enclosure study in Coote's Paradise, it was found that TP concentrations did not increase linearly

with increasing biomass but peaked at intermediate densities (approx 600 kg/ha) (Lougheed et al. 1998). Upon removal of 75 % of benthivorous fish from Ventura Marsh, Iowa, P concentrations decreased despite relatively high external loading (Schrage and Downing 2004). TP also decreased in the shallow eutrophic wetland-type lake, Lake Major, Hungary, following the removal of > 60% of carp and roach (Tatrai et al. 2005). Conversely, Lougheed and Chow-Fraser (2001) found that upon exclusion of carp from enclosures in Coote's Paradise, no significant decrease in TP occurred. Similarly, Hnatiuk (2006) found there to be no significant difference in TP concentrations between carp-accessible ponds and carp-free ponds in Delta Marsh, nor were changes observed when access of carp to the ponds was altered by means of screens or dikes preventing their access or by creation of a channel to allow their access. She offered no explanation.

The relationship between total reactive phosphorus (TRP) in the water column and the presence of carp is controversial in the literature. Total reactive phosphorus may not change (Cline et al. 1994; Angeler et al. 2002), or even decrease with increasing densities/biomass of carp (Keen and Gagliardi 1981; Breukelaar et al. 1994; Shormann and Cotner 1997; Lougheed et al. 1998). These results are suspected to be due to rapid adsorption of P to sediment surfaces or by rapid assimilation by algae (Keen and Gagliardi 1981; Cline et al. 1994). The increase of oxygen to the sediments by benthic invertebrates or by sediment resuspension through bioturbation by benthivorous fish increases the P binding potential of the sediments (Scheffer 1998). The likelihood of adsorption is

influenced by the type of substrate. P binds more readily to clay than to sand. If the concentration of soluble reactive phosphorus (SRP) adsorbed to the particles is less than that of the water column the sediment particles can act as a sink. If the sediment particles are already saturated with P, they may become a source. In the latter case one might expect to see an increase in reactive P in the presence of benthivorous fish, particularly when one takes into consideration additions due to excretion. In a mesocosm experiment Badiou (2005) found that TRP increased as a function of carp stocking density, but was not significant until reaching carp biomasses between 300 and 600 kg/ha. He suggested there is a critical biomass below which the amount of sediment resuspended is sufficient to remove any additional dissolved phosphorus added to the water column as a result of excretion or disruption of the sediment-water interface. Additionally, phosphorus release from the sediment is also influenced by other characteristics of the sediment such as iron, aluminum, organic and TP content, and oxygenation, which can vary among systems (Lougheed et al. 1998).

Unlike P, N is removed from the water column mainly through denitrification and uptake by autotrophs. This reduction is greatest in shallow systems, especially with long retention times and where productivity is high (Toet et al. 2005). While the sediment buffer is less relevant for N than for P, ammonia can be bound to sediments by benthic algae and bacteria on sediment particles (Howard-Williams 1985). The forms of interest in most studies, are total nitrogen (TN) and total inorganic nitrogen (TIN) which consists of two main components: ammonium and nitrate.

As for TRP, the effects of carp additions or removals into experimental systems on water column N are controversial. In an enclosure (0.36 ha) study in Fort Worth, Texas, Chumchal et al. (2005) found that concentrations of TN increased with increasing carp biomass (0 - 475 kg/ha). Angeler et al. (2002) found higher concentrations of TN in enclosures (1 m diameter) stocked with 5500 – 6500 kg/ha biomass of carp relative to controls, in central Spain. Few other studies have reported TN concentrations. Where some small enclosure studies (25 – 50 m^2) in Canada have shown that ammonia-N increased linearly with carp biomass (Lougheed et al. 1998; Badiou 2005). Angeler et al. (2002) found that TIN was not affected by the presence of high densities of carp, a result they attributed to rapid uptake by autotrophs. In the natural ponds of Delta Marsh, MB., Hnatiuk (2006) found that, on average, there were no differences in the concentrations of TN and TIN between carp-accessible and carp-free ponds. Badiou (2006) found that in 5-7 ha wetland cells, approximating the natural conditions found in the Delta Marsh, MB., ammonia-N increased minimally with carp biomass until critical density of carp was reached (> 300 kg/ha). Specific references to nitrate concentrations were rarely reported in nutrient studies. However, where they were reported no significant relationships to carp presence/biomass/density were found (Lougheed et al. 1998; Zambrano et al. 1999; Schrage and Downing 2004).

The effects of carp to water column N and P may be difficult to ascertain in natural systems due to the dynamic nature of the nutrient cycle. Algal and bacterial communities quickly sequester available nutrients. The reported

increases in nutrients are often interpreted as an increase of algal abundance commonly associated with the presence of benthivorous fish. For example, Brett and Stuart (1998) found that sediment resuspension in shallow lakes of the Otago region in New Zealand increased chorophyll *a* concentrations by relieving N deficiency. Similarly, in a study involving Smallmouth Buffalo (*Ictiobus bubalus*) in an oxbow lake in Texas, Shormann and Cotner (1997) concluded that the re-mineralization rate of ammonium through sediment resuspension was enhanced based upon increased phytoplankton blooms. A study of the effects of the removal of planktivorous and benthivorous fish (e.g. *Abramis brama)* from a small lake in the Netherlands, revealed the importance of phytoplankton as a nutrient sink. In the year following bio-manipulation the authors found water column dissolved N and P were extremely high (about 90% of N and P present) as a result of zooplankton grazing which suppressed phytoplankton growth. The year prior to bio-manipulation 44% of N and 47% of P were stored in phytoplankton and 23% N and 44% P were present in dissolved form in the water column. Of course, algae is not the only organism which sequesters water column nutrients for growth. Heterotrophic bacteria are also a key component forming the basis of aquatic ecosystems (Loreau 2001), controlling nutrient cycling. While their relationship can be described as commensalism, wherin the bacteria benefit from the algae's exudates, under nutrient poor conditions they become competitors, and have been found to be superior competitors for P than algae (eg. Bratbak and Thingstad 1985; Jansson 1993; Joint et al. 2002).

Effects of carp on algae

Studies have shown that where benthivorous fish such as carp were present, both phytoplankton and periphyton growth were enhanced in response to increases in available nutrients by their disturbance of the sediment or excretion (Anderson et al. 1978; Phillips et al. 1978; Sand-Jensen 1983; Qin and Threlkeld 1990; Breukelaar et al. 1994; Roberts et al. 1995; King et al. 1997; Zambrano et al. 1999; Sidorkewicj et al. 1999; Angeler et al. 2002; Williams et al. 2002; Badiou 2005). In experiments in the Netherlands and in North America focusing on response of phytoplankton growth to varied biomasses of carp, it was found that the relationship can be linear with increasing biomass of fish resulting in increasing concentrations of phytoplankton chlorophyll *a* (King et al. 1997; Breukelaar et al. 1994; Chumchal et al. 2005; Badiou 2005). In the natural environment of Delta Marsh, MB., Hnatiuk (2006) found that the greatest concentrations of phytoplankton occurred in the spring concurrent with the spawning period of carp, which is when adult carp are found in greatest densities. However, in her study, while she found that phytoplankton chlorophyll *a* concentrations were generally higher in carp-accessible ponds relative to ponds to which carp did not have access, she noted a high degree of variation among carp-accessible ponds, one of which supported very little phytoplankton at all. Similarly, in a study examining the relationship between carp density and phytoplankton growth in a Lake Ontario coastal marsh, Lougheed et al. (1998) found there to be no relationship. In enclosures stocked with 700 kg/ha carp, epiphytic chlorophyll *a* increased from 1100 to 3000 μg/g (dry weight) in Little

Mere, U.K. (Williams et al. 2002). In turbid habitats impacted by sediment loading/resuspension, periphyton can thrive in part because of enhanced access to nutrients from close association with suspended sediments (Burkholder and Cuker 1991). Yet, in Delta Marsh, Hnatiuk (2006) found no detectable changes in epiphyton and periphyton growth when carp were introduced or excluded from a pond. Similarly, no differences were found between carp-accessible and carp-free ponds.

The degree to which benthivorous fish affect phytoplankton growth can vary due to macrophyte presence and light limitation. Several studies have shown that extensive submerged macrophyte beds can suppress phytoplankton production (Scheffer et al. 1994; Scheffer 1998; Parkos III et al. 2003; Badiou 2006). Hnatiuk (2006) referred to significant variation in the carp-accessible ponds of Delta Marsh, from abundant to minimal, similar to that of isolated ponds, finding that the clearer ponds tended to have an abundance of submerged macrophytes. Alternatively, in a stocking study of large wetland cells (5-7 ha), Badiou (2005) suggested that exceptionally high concentrations of dissolved organic carbon may limit phytoplankton growth by limiting the amount of light available. He also found that in mesocosms (5 x 5 m) in which nutrients were added, there may be a limit to the abundance of phytoplankton growth as a result of severe light limitation resulting from the combination of increased inorganic suspended solids and phytoplankton induced turbidity. Light limitation may also depress the growth of epiphyton. Hnatiuk (2006) suggested that this may explain why she found no differences in periphyton/epiphyton growth between carp-accessible and carp-

free ponds. In Australian billabongs, Robertson et al. (1997) reported a decrease in periphyton abundance at high carp densities surmising that light limitation and nutrient limitation, resulting from competition with phytoplankton, may have been responsible.

Grazing pressure by aquatic invertebrates may also reduce the abundance of phytoplankton and epiphyton predicted in the presence of benthivorous fish. There is convincing evidence that zooplankton grazing can greatly reduce the concentrations of phytoplankton, even when benthivorous fish are present (van Donk et al. 1993; Chow-Fraser 2005). However, many studies have shown that carp alter the community of zooplankton such that the abundance of larger, more efficient grazers is depressed, resulting in a community dominated by less efficient grazers, and so phytoplankton concentrations may not be affected at all (Williams et al. 2002). Zooplankton communities are altered either directly, via selective consumption of the larger species (Richardson et al, 1990; Williams et al. 2002; Khan 2003), or indirectly, through increased turbidity negatively affecting the efficiency of zooplankton to graze phytoplankton as resuspended sediment particles damage the filter apparatus of some species (Kirk and Gilbert 1990; Richardson et al. 1990; Angeler et al. 2002). Although macro-invertebrates are known to have a significant grazing effect on epiphyton (Bronmark and Weisner 1992), Williams et al. (2002) found in their work that the grazing was negligible as the abundance of epiphyton and macro-invertebrates increased simultaneously.

Other considerations have been put forward in interpreting algal data in ecosystem level studies. It has been demonstrated that sediment resuspension can increase chlorophyll a concentrations, normally used to quantify phytoplankton, by entraining algal cells from the sediment-water interface into the water column (Stahl-Dalbenko and Hansson 2002; Roozen 2007). Additionally, Sidorkewicj et al. (1999) warned that increases in periphyton biomass can be deceiving as fine inorganic sediments can make up a large component of the periphyton.

Effects of carp on submerged vegetation

The presence of carp has long been associated with the decline of the biomass and diversity of submerged macrophytes in shallow lakes and wetlands where they have been introduced. As early as the 1890s, shortly after their introduction into North America, people began to disapprove of the species, noting damage to the natural waterways in which they had been introduced (McCrimmon 1968). Cahn (1929) reported elimination of all aquatic vegetation over a thirteen year period in a mud bottomed lake in Wisconsin. Utah Lake, Utah, currently supports only *Stuckenia pectinata*, where, prior to their introduction in 1886, a wide diversity of submergent macrophytes were known to exist (Miller and Crowl 2006). Coote's Paradise, Ontario, supported more than ten species of macrophytes in 1948, and less than five in 1995 (Lougheed et al. 1998). In Delta Marsh, submerged macrophyte biomass has decreased substantially following the introduction of carp around 1970 and stabilizing of water levels on the

adjacent Lake Manitoba with the construction of the Fairford Dam in 1961 (Wrubleski 1998; Batt, 2000). The decline of submerged macrophytes due in part to benthivorous fish is not limited to North America, but has also been observed and studied in Australia and Europe (e.g., Roberts et al. 1995; King et al. 1997; Meijer and Hosper 1997; Tatrai et al. 2005).

Numerous studies have shown that carp negatively affect the biomass and diversity of aquatic macrophytes (Kolterman 1990; Lougheed et al. 1998; Zambrano et al. 1999; Williams et al. 2002; Miller and Crowl 2006; Hnatiuk 2006). In enclosure studies the loss in biomass of submerged macrophytes was found to be positively correlated to the increasing biomass of carp (Robel 1961; Crivelli, 1983), though Williams et al. (2002) found that density of carp is more important than biomass. In the wetlands of the Great Lakes Basin and ponds at Delta Marsh, submerged macrophytes dominated where carp were not found, however, macrophyte-dominated systems were not always carp-free (Lougheed et al. 1998; Hnatiuk 2006). Both authors proposed that low density/biomass of carp may allow the continued presence of macrophytes in these wetlands. Results from studies examining the effects of carp biomass on macrophyte abundance in eutrophic Mexican ponds, suggest there is a critical biomass of carp that will cause a catastrophic shift from the macrophyte-dominated to the phytoplankton-dominated state in eutrophic wetlands (Zambrano and Hinojosa 1999; Zambrano et al. 1999; Zambrano et al. 2001). In Australian studies, this biomass was thought to be approximately 450 kg/ha (Fletcher et al. 1985). As noted earlier in the section on turbidity and suspended solids, Zambrano (2001)

hypothesized that above a certain threshold of density, carp will increase their foraging efforts to obtain diminishing prey items, thereby increasing the potential for physical damage to aquatic macrophytes and increasing turbidity enough to shade out most species. Once macrophytes are eliminated, the sediments may become susceptible to wind-induced sediment resuspension, further promoting the phytoplankton-dominated state, through the internal cycling of nutrients (Ryding 1985; Søndergaard et al. 1992).

The mechanisms behind the negative relationship between carp and submerged aquatic vegetation is both direct and indirect. Carp have been found to cause direct physical damage in the act of foraging in the benthic substrata resulting in the uprooting of aquatic vegetation and, although rare, direct consumption (Tryon 1954; Robel 1961; King and Hunt 1967; Kolterman 1990; Lougheed et al. 1998; Sidorkewicj et al. 1999; Miller and Provenza 2007). In the spring, when carp gather to spawn in shallow lakes and wetlands, seedlings are most susceptible as carp densities are high during this time, resulting in a greater likelihood of direct physical damage and indirect damage through shading and smothering (King and Hunt 1967; Crivelli 1983; Sidorkewicj et al. 1999). Indirectly, decreases in light availability as a result of high turbidity (e.g. suspended sediments) associated with high carp density, has been shown to negatively impact the growth of several submerged macrophyte species. Increases in inorganic suspended solids associated with carp feeding and spawning activities causes shading and the re-settlement of winnowed sediment that can smother young plants (Meijer et al. 1990; Wright and Phillips 1992). Sediment disturbance and

excretion of wastes can increase the amount of available nutrients in the water column, stimulating an increase in algal production leading to higher turbidity and reduction in light (Roberts et al. 1995; Zambrano et al. 1999; Badiou 2005). Given a high nutrient load, submerged macrophytes can be suppressed due to shading by epiphytes even prior to effects of phytoplankton shading (Phillips et al. 1978; Sidorkewicj et al. 1999; Williams et al. 2002). Shading can result in the stunting or prevention of the growth of submerged macrophytes (Sidorkewickj et al. 1999; Miller and Crowl 2006). In a survey of 19 wetlands in the Great Lakes Basin, less than five species of submerged macrophytes were found in wetlands with turbidities exceeding 20 NTU, whereas wetlands with lower turbidity had a higher density and diversity of macrophyte species (>7) (Lougheed et al. 1998). A comparison of carp-free and carp-accessible ponds of Delta Marsh also showed that where turbidity was high, few species of macrophytes were found (Hnatiuk 2006). In Utah Lake and in some coastal wetlands of the Great Lakes at very high turbidities, only *S. pectinata* may be found growing (Lougheed et al. 1998; Miller and Crowl 2006).

Phytoplankton and epiphyton compete with macrophytes for carbon dioxide as well as light (Sand-Jensen 1977; Phillips et al. 1978; Sand-Jensen 1983). Attached epiphyton can create high O_2 and pH regimes that are unfavorable to macrophytes (Simpson and Eaton 1986).

Numerous studies have shown that the removal of carp from a wetland or shallow lake, results in clearer waters, which allows for greater biomass and

diversity of species of submerged macrophytes. Following the removal of carp, submerged macrophyte taxa doubled in diversity in a number of shallow lakes and wetlands (Lougheed et al. 1998; Schrage and Downing 2004; Chow-Fraser 2005; Hnatiuk 2006; van de Haterd and Ter Heerdt 2007). Lundholm and Simser (1999) reported a dramatic resurgence of macrophyte species following the reduction of carp biomass from 700 kg/ha to 50 kg/ha from Cootes Paradise, Ontario, but emphasize that they grew mainly from vegetative structures buried beneath the sediment. Where once macrophytes only occurred along the periphery of a eutrophic wetland in Iowa, they expanded dramatically following the removal of carp (Schrage and Downing 2004). A similar event occurred in a screened pond in Delta Marsh, MB. (Hnatiuk 2006). Badiou (2005) found that increasing biomass of carp did not result in significant decreases in submerged macrophyte biomass, but did slow their growth. He attributed this finding to light penetration which, while reduced, was still sufficient to enable macrophyte growth.

Susceptibility to carp disturbance, direct and indirect, is species specific. Unlike many species of submerged macrophytes, *Stuckenia pectinata* is capable of persisting at high turbidities where high densities of carp are found (Lougheed et al. 1998; Jeppesen et al. 1998; Badiou 2005; Miller and Crowl 2006; Hnatiuk 2006). Its growth habit of forming a canopy of foliage near the water surface may be a key factor in its ability to tolerate turbid waters (Kantrud 1990). *S. pecitinata* is also resistant to herbivory by carp (Miller and Provenza 2007). However, while they may persist, their biomass is reduced in the presence of carp, particularly in

shallow, windswept areas. This is likely due to intense shading, physical damage by carp and/or wave action (Anderson 1978; Zambrano and Hinojosa 1999; Miller and Crowl 2006; Badiou 2006). *Myriophyllum sibiricum* and *Ceratophyllum demersum* are somewhat persistent in the presence of carp and are often among the first to re-establish after improvements to water clarity (King and Hunt 1967; Roberts et al. 1995; Drenner et al. 1998; Lougheed et al. 1998, 2001; Chow-Fraser 2005). *C. demersum* does not root in the sediments and so is less likely to be affected by physical damage by carp feeding habits than some other species of macrophytes, and is structurally resistant to herbivory by carp (Lahring 2003; Miller and Provenza 2007). Nevertheless, it does seem to be more sensitive to turbidity than *S. pectinata*. In Utah Lake, *C. demersum* was extirpated following the introduction of carp in 1888, likely due to the reportedly very high turbidity of the lake, in which only *S. pectinata* remained (Miller and Provenza 2007). Charophytes are particularly susceptible to the presence of benthivorous fish. Roberts et al. (1995) noted that while other macrophytes remained relatively unaffected, *Chara* sp. had disappeared within eight days of being exposed to carp at 450 kg/ha, in a pond in New South Wales, Australia. Drenner et al. (1998) and Hnatiuk (2006) noted that charophytes were always absent in ponds to which carp had access. In the Netherlands, the decline of benthivorous fish (carp and bream) was associated with increases in *Chara* sp. biomass/density in Lake Maarseveen I and in Lake Veluwe (Ten Winkel and Meulemans 1984; Lammens et al. 2004). Exclusion of carp from small mesocosms in Delta Marsh led to a three-fold increase in the standing crop of *Chara* sp. (Evelsizer and Turner 2006).

Though likely attributed to the sensitivity of the species to light conditions, they have also been shown to be directly consumed by carp (King and Hunt 1967; Miller 2004).

In Utah Lake, Utah, reductions in macrophyte abundance in the presence of carp was exacerbated, and that *S. pectinata* abundance did not recover as quickly to the exclusion of carp from mesocosms in a bay exposed to high winds relative to the wind sheltered bay (Miller and Crowl 2006). In open-water areas, high wave energy can cause constant reburial of propagules of even the more tolerant species (Sager et al.1998). The diversity and rate of regeneration of submerged macrophytes following the removal of carp is influenced by the abundance of propugles of aquatic macrophyte species (van der Valk and Davis 1978; Lundholm and Simser 1999; Evelsizer and Turner 2006).

Methods

Site Description

This study took place in Delta Marsh, a moderately brackish marsh located along the southern shore of Lake Manitoba (50° 11’ N, 98° 19’ W) (Figure 1). Spanning approximately 18,500 ha it is one of the largest lacustrine wetlands in North America. Bordered by agricultural land to the south, and the beach ridge of Lake Manitoba to the north, it is divided into two sections, the western and eastern halves, by the Assiniboine River Diversion. The marsh is connected to Lake Manitoba by four narrow channels: Cram Creek and Deep Creek in the western portion of the marsh and Clandeboye Channel and Delta Channel in the east. These channels allow for continuous water exchange between the marsh and the adjoining lake during ice-free periods by way of spring run-off and wind-induced seiching of the lake water which results in water flowing into or out of the marsh depending on wind direction, strength and duration (Wrubleski 1998; Batt 2000). Water levels in the open and connected areas of the marsh have been known to vary (~ 0.5 m) over time due to the influence of wind driven seiches in the lake (Goldsborough, pers comm.).

The barrier-beach protected marsh consists of a complex of narrow channels, large wind-swept open water areas, bays and isolated ponds ranging from less than 1 m to 3 m in depth (Parks 2006). Both the clear-water, macrophyte-dominated state as well as the turbid, phytoplankton-dominated state, as described by Scheffer et al. (1993), exist within the marsh complex. Ponds,

channels and larger bays which are connected to the main complex tend to lack abundant submerged vegetation and are turbid and phytoplankton-dominated. Isolated ponds tend to be characterized as having clear waters and are dominated by submerged macrophytes (Goldsborough 1994 & 2000; Evelsizer 2001; Hnatiuk 2006). In the eastern section of the marsh, in connected waterways, blooms of the cyanobacteria, *Aphanizomenon flos-aquae,* are a common occurrence during the summer months (Goldsborough, personal communication). Water quality parameters from six sites in the west marsh are summarized by Goldsborough (1994) and in ten sites spanning the east and west sides of the marsh by Hnatiuk (2006). Information of the geology and soil composition of Delta Marsh can be found in Teller and Last (1981) and climate data can be found online at Environment Canada.

Emergent species dominating shorelines in Delta Marsh include species of cattail (*Typha latifolia, T. angustifolia* and *Typha* X *glauca*), and hardstem bulrush (*Schoenoplectus acutus* var. *acutus*). At slightly higher elevations whitetop (*Scolochloa festucacea*), sedges (*Carex* spp.) and common reed grass (*Phragmites australis*) are common (Shay et al. 1999; Batt 2000). Common submerged macrophyte species include sago pondweed (*Stuckenia pectinata*), water milfoil (*Myriophyllum sibiricum*), sheathed pondweed (*Stuckenia vaginatus*), hornwort (*Certophyllum demersum*), common bladderwort (*Utricularia macrorhiza*), Richardson's pondweed (*Potamogeton richardsonii*), horned pondweed (*Zannichellia palustris*), wigeon grass (*Ruppia cirrhosa*), flat stem pondweed (*Potamogeton zosteriformis*) and Eurasion watermilfoil (*Myriophyllum*

spicatum) (Anderson and Jones 1976; Sandilands 2000). *Chara* sp. was also found (Hnatiuk 2006).

Twenty-five species of fish, including rough, prey and commercially important fish species, as well as the invasive species carp (*Cyprinus carpio*), have been found in Delta Marsh (summarized by Parks 2006). Several species of fish use the marsh for the spawning and nursery habitat it provides, including commercially important fish species such as Yellow Perch (*Perca flavescens*), Northern Pike (*Esox lucius*) and White Sucker (*Catostomus commersonii*) (Parks 2006).

Study Ponds

Study ponds were selected based on a number of criteria. Pairs were chosen each consisting of one carp-accessible pond which was connected to the main marsh and one which was inaccessible to carp, either by isolation or by a screen barrier. Included in this study were five ponds examined in Hnatiuk's (2006) work which examined the effects of carp on nutrients, algal and submerged vegetation growth. In 2001, baseline data were collected and in the spring of 2002 the accessibility of carp to six of the ten ponds in her study was altered, by means of diking, screening or the creation of a channel allowing access. In this study, I included two ponds to which carp access was prevented (one screened, one diked), two ponds which were naturally isolated in the original study and one which was made accessible to adult carp. The close proximity of the ponds in each pair to one another ensured minimal variation in abiotic characteristics and local climate, in addition to minimizing the amount of time required to sample the

ponds. In 2003, three pairs of ponds were included in the study; one pair on the west side of the Assiniboine Diversion and two on the east side (Table 1). A fourth pair was added in 2004 from the east marsh and one additional pond described below.

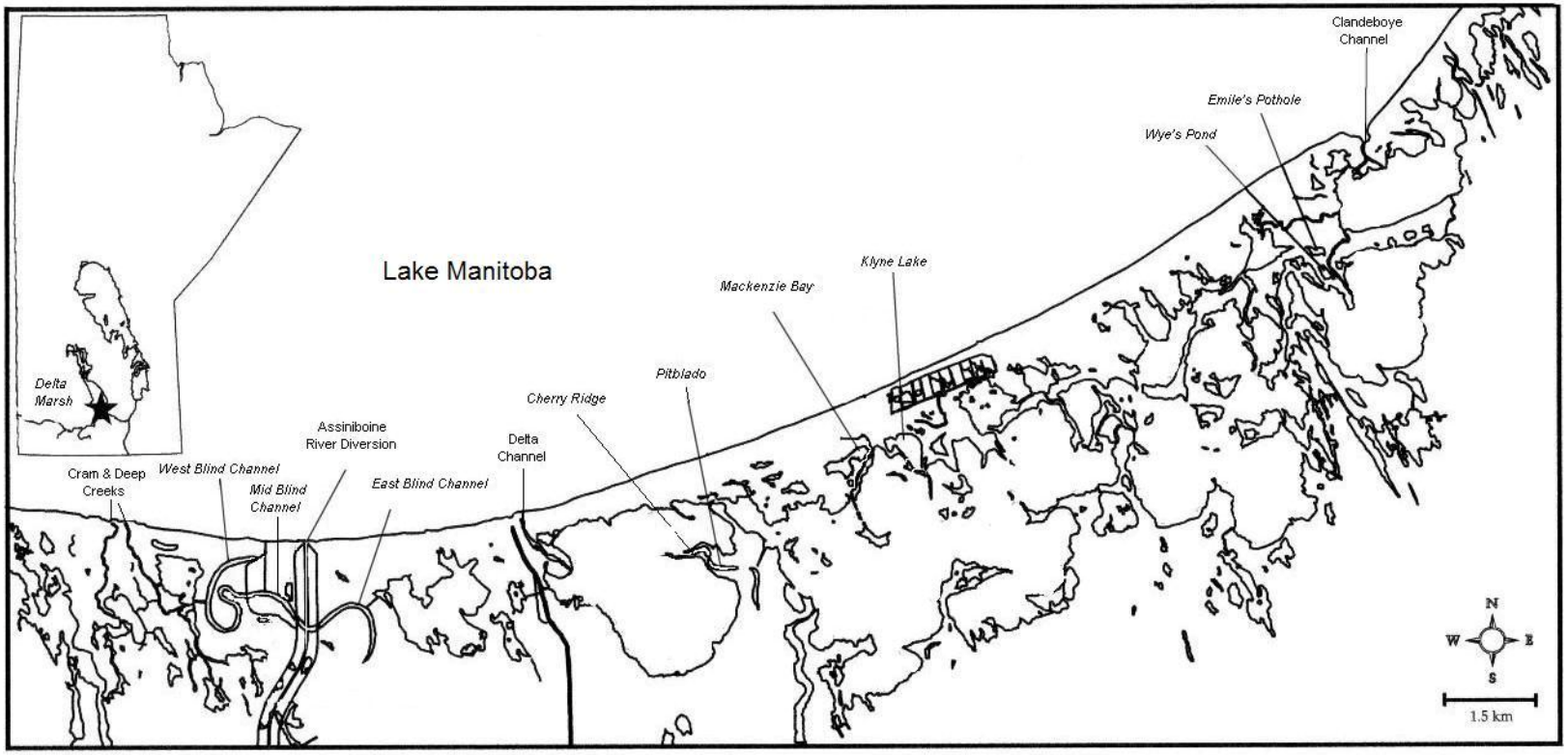

Figure 1. Delta Marsh complex highlighting the four channels allowing water exchange with Lake Manitoba, MB, Canada and the ponds used in this study (in italics).

Table 1. Geographic co-ordinates of the center of the ponds in this study, their connection status to the main marsh, open water area (ha), orientation of longest axis and years studied. * only submerged vegetation sampled.

Pond Name	Latitude	Longitude	Connection Carp accessibility	Open Water Area (ha)	Orientation of Longest Axis	Year Studied	
Cherry Ridge	50˚10'56	98˚16'30	Connected/accessible	3.0	E-W	2003	2004
Klyne Lake	50˚11'52	98˚13'22	Connected/accessible	20.3	N-S	2003	2004
West Blind Channel	50˚10'35	98˚23'21	Connected/accessible	12.4	E-W	2003	2004
Wye's Pond	50˚13'28	98˚07'10	Connected/accessible	3.0	N-S	*	2004
Pitblado	50˚10'46	98˚16'16	Isolated/inaccessible	3.1	E-W	2003	2004
Mackenzie Bay	50˚11'48	98˚14'10	Isolated/inaccessible	11.9	E-W	2003	2004
Mid-Blind Channel	50˚10'32	98˚22'44	Screened/inaccessible by adult carp	5.9	E-W	2003	2004
Emile's Pothole	50˚13'41	98˚07'17	Isolated/inaccessible	2.7	N-S	*	2004
East Blind Channel	50˚10'22	98˚21'54	temporary connectedness	8.1	E-W	-	2004

Located on the west side of the Assiniboine River Diversion, West Blind Channel and Mid-Blind Channel were sampled in both 2003 and 2004 (Figure 1). West Blind Channel was directly connected to the main marsh via a single channel eight meters wide and 185 meters long which permitted access to feeding and breeding carp each spring. Separated by a gravel road, West and Mid-Blind Channel were connected by three culverts; two were 75 cm in diameter and one was 90 cm in diameter. Adult carp were excluded from the Mid-Blind Channel by two overlapping steel grates of 1.5 cm diameter bars spaced 5 cm apart held in place over the westernmost opening of the culverts by collars supporting a steel frame (small: 75 x 82.5 cm; large: 90 x 97.5 cm) during the open water season (Figure 2). The screens were initially installed as part of a carp exclusion study in April 2002, and have remained in place since their installation (Hnatiuk 2006; Goldsborough, pers. comm.). East Blind Channel was added in 2004 as it was assumed that it had been inaccessible to carp for many years, thus adding a carp-free pond to the aforementioned pair. However, in the spring of 2004 the narrow channel, normally blocked to Lake Manitoba, was temporarily opened in an extreme storm event permitting access by spawning white suckers, caught in this study. While carp were seen in the adjacent pond, Center Marsh, (Bortoluzzi, personal communication) they were neither seen nor caught in East Blind Channel in this study.

Figure 2. The largest of the three screens separating Mid-Blind Channel from West Blind Channel, preventing carp from accessing Mid-Blind Channel in Delta Marsh, MB.

Cherry Ridge and Pitblado were located along the southern edge of the east marsh nearest to agricultural land (Figure 1). Prior to the spring of 2002, Pitblado was connected to the main marsh via Cherry Ridge. In the spring of 2002, the construction of a sandbag dyke effectively isolated Pitblado from the main marsh and prevented access by adult carp thereafter (Hnatiuk 2006). Cherry Ridge was connected to the main marsh via a naturally formed channel approximately 5 meters across. In 2003, low water conditions forced a stop to sampling in Pitblado three weeks prior to the end of the sampling season (Figure 3).

Figure 3. Pitblado pond, Delta Marsh, MB viewed from the southeastern corner of the pond August 13, 2003.

Klyne Lake and Mackenzie Bay were situated in the central area of the east marsh within a kilometer of the beach ridge to the north (Figure 1). Klyne Lake was the largest of the study sites (Table 1). It was connected to the main marsh and accessible to carp via three channels; one to the southeast (20 m wide) and two to the south (2 m wide and 7 m wide). Mackenzie Bay was isolated in 2003 and 2004 and was inaccessible to carp throughout the study period. The most easterly pair of study ponds were Wye's Pond and Emile's Pothole (Figure 1). Prior to the spring of 2002, both ponds were isolated from the marsh by naturally formed dikes. However, In 2002, Wye's Pond was connected to the main marsh via a single channel (30 m long and 3 m wide) excavated in June 2002 to provide a connection to the main marsh and allow carp access to the pond (Hnatiuk 2006).

Sampling and Analysis Procedures

All ponds were accessed with and samples taken from a canoe. Care was taken to avoid disturbing sediments and contamination of samples. In 2003, ponds were sampled on a weekly basis from the second week of May to the second week of August. A single set of environmental data and water samples were collected from a permanent sampling site centrally located within each pond. The frequency of sampling was reduced in 2004 to once every two weeks to accommodate the increase in the number of ponds included in the study. In 2004, environmental data and water samples were collected at three permanent

sampling sites within each pond along its longest axis: one central and one on either side (Figures 4-7).

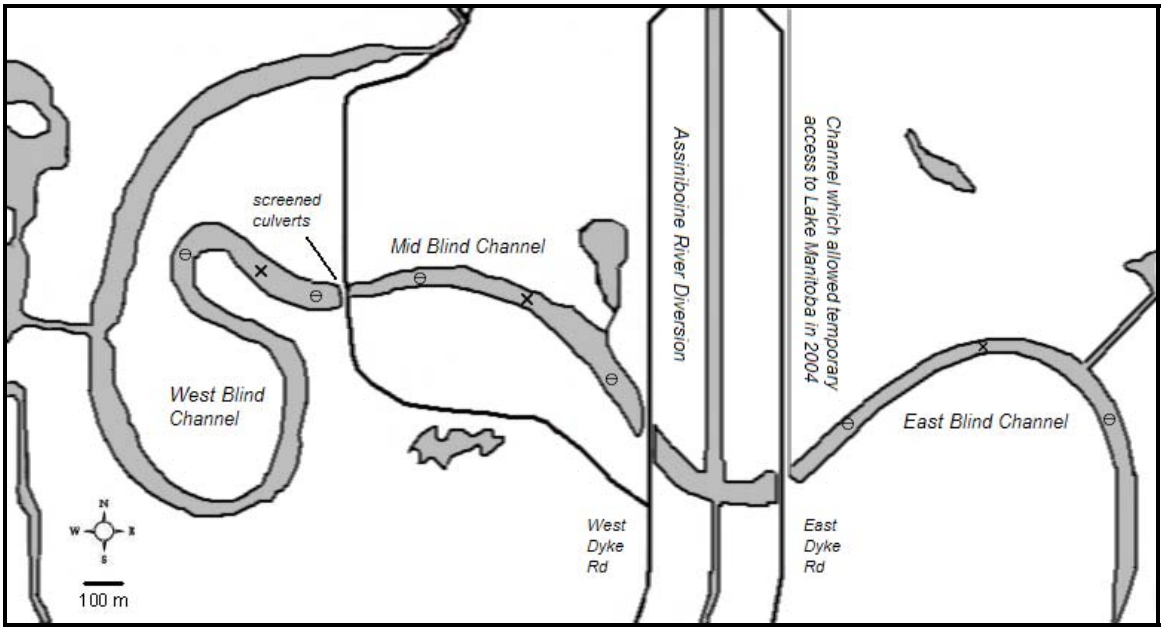

Figure 4. Schematic of West Blind Channel, Mid-Blind Channel and East Blind Channel, Delta Marsh, MB showing the permanent water sampling sites of 2003 (x) and 2004 (⊖ & x) and locations of the nutrient-diffusing substrata apparati (x).

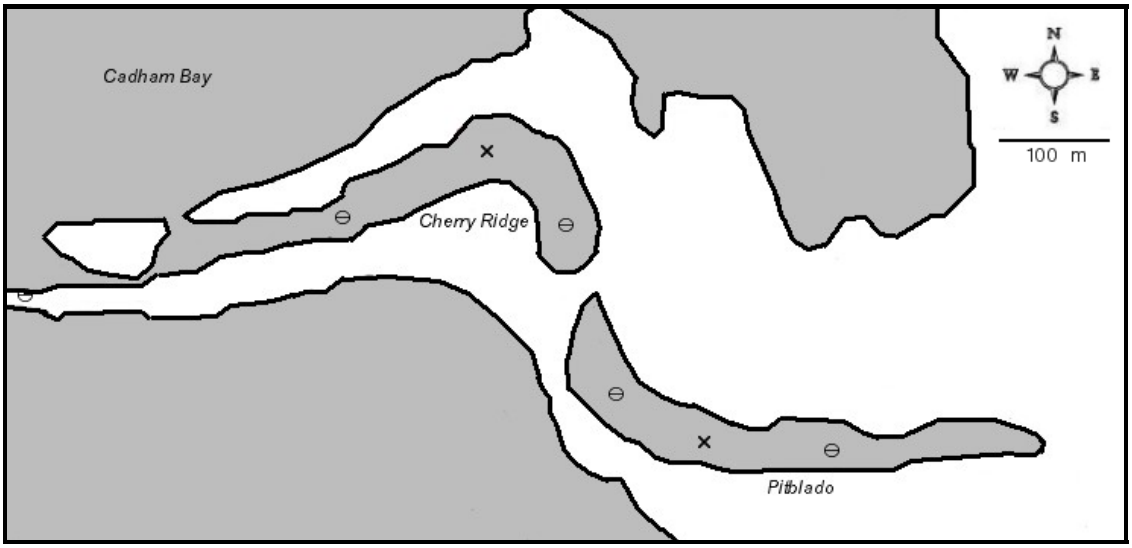

Figure 5. Schematic of Cherry Ridge and Pitblado, Delta Marsh, MB showing the permanent water sampling sites of 2003 (x) and 2004 (⊖ & x) and locations of the nutrient-diffusing substrata apparati (x).

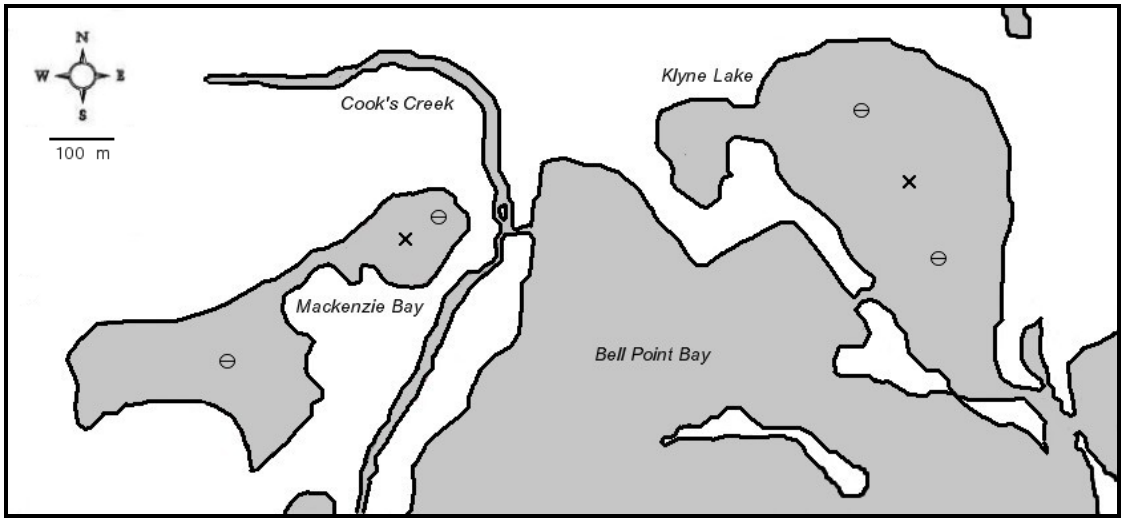

Figure 6. Schematic of Klyne Lake and Mackenzie Bay, Delta Marsh, MB showing the permanent water sampling sites of 2003 (x) and 2004 (⊖ & x) and locations of the nutrient-diffusing substrata apparati (x).

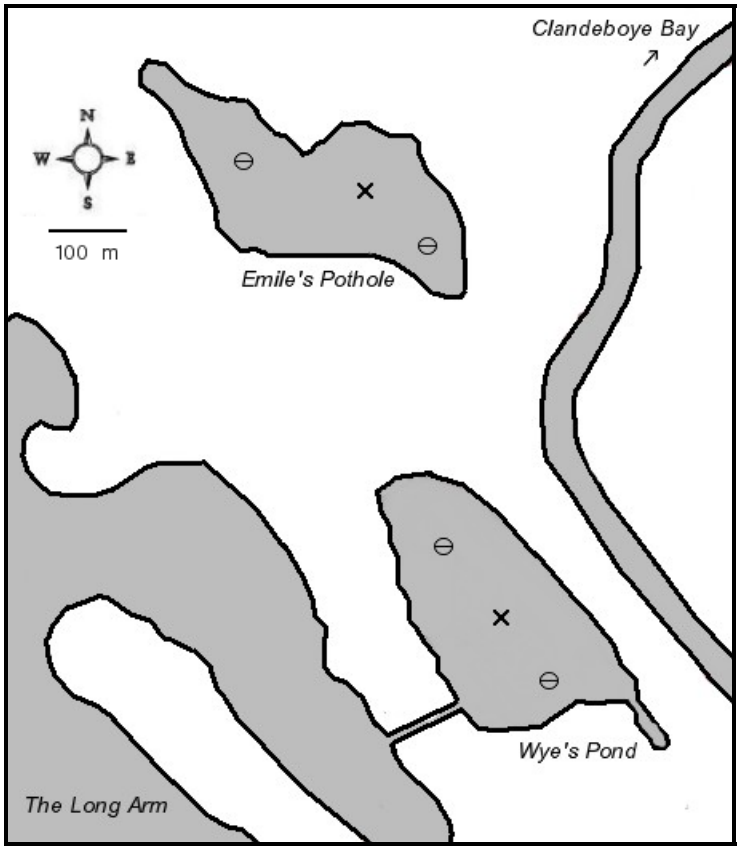

Figure 7. Schematic of Emile's Pothole and Wye's Pond, Delta Marsh, MB showing the permanent water sampling sites in 2004 (⊖ & x) and locations of the nutrient-diffusing substrata apparati (x).

A number of parameters were recorded on site. Water temperature at the mid-point of the water column and near the sediment surface were recorded (YSI Model 30 conductivity meter). The water temperature reported in the results is the mean of the two. Average air temperature, average and maximum wind speed (km/hr) and direction (N, S, E, W, SW etc.) were measured using a Kestrel held 1.5 meters from the water surface into the wind for one minute. Comments regarding a visual description of the water color and clarity, percent cloud cover and notes as to activity of carp and other animals as well as debris were recorded at this time.

Photosynthetically active radiation (PAR) was measured using a LI 1000, LI COR Datalogger, to measure the amount of incident light at the water surface using a flat light sensor and another flat sensor (2003) or a spherical sensor (2004) to record the amount of light just above and below the surface and every ten centimeters down to the sediment surface. Where metaphyton covered a sampling site it was moved aside to allow enough room to employ the apparatus. In 2004, the values given by the surface sensor were divided by the surface reading to account for varying incident light conditions. In 2003, surface readings were not recorded and the depth readings were divided by the reading at 10 cm of depth. I strove to ensure that readings were taken during periods in which the ambient light was consistent (i.e. no cloud movement). Euphotic zone depth was calculated using only those depth readings at or below 10 cm from the water

surface where submersion was certain. At least three measurements were used to calculate the euphotic zone depth.

Secchi depth (centimeters) was recorded. The disk was always lowered on the leeward side of the canoe to reduce variation due to wave action and on the shaded side to avoid surface reflection of sunlight.

Water Chemistry

Integrated water column samples were obtained by lowering a clear plastic tube, 2.5 inches in diameter, vertically into the water column to a depth near to the sediment surface but not so close as to disturb the sediment surface, to avoid contamination of the water sample, and plugged with a plastic ball at the top to create a vacuum. The contents were emptied into a plastic tub (triple rinsed with site water) then poured into a uniquely labeled acid washed one liter plastic bottle (triple rinsed with site water), filled to the top to exclude air and stored in a cooler with an ice pack. All samples were returned as soon as possible to the laboratory at the Delta Marsh Field Station and stored in a refrigerator at 4˚C until such time as the chemical analyses could be performed, usually no longer than two hours later. Components such as total reactive phosphorus and ammonia-N were the first to be analyzed due to their time-sensitive nature. All water quality components were analyzed within the recommended time (APHA 1998).

The following water samples were analyzed at the onsite laboratory at the Delta Marsh Field Station. Unfiltered sample water, lightly shaken to ensure mixed

water, was analyzed for turbidity (Hach 2100A turbidimeter), pH (Corning ion analyzer 250 pH meter), alkalinity (acid titration), ammonia-N (μg/L) (hypochlorite method), total reactive phosphorus (μg/L) (acid molybdate-antimony method) followed by colorimetric analysis using an Ultrospec 400 UV/visible light spectrophotometer, dissolved inorganic carbon (mg/L) and phytoplankton chlorophyll *a* (μg/L) (Stainton et al. 1977; Marker et al. 1980; APHA 1998). Total nitrogen (μg/L) (persulfate method) and total phosphorus (μg/L) (the PosVer 3 with acid persulfate digestion method) were determined using analysis kits from Hach (APHA 1998; Hach Company 1997), followed by colorimetric analysis using a Ultrospec 400 UV/visible light spectrophotometer. Total P and N were defined as the soluble and particulate organic and inorganic pools of P and N, respectively, not including large organisms such as fish. Total reactive P (TRP) consisted of the soluble and particulate forms of P that reacted in the molybdenum-blue test, and mostly consisted of inorganic forms of the nutrient. Soluble reactive P (SRP), which consists only of soluble inorganic P, was not measured in this study although occasional analyses of individual samples usually found little difference between SRP and TRP.

A filtered water sample (Whatman GF/C, 42.5 mm filter under vacuum) was collected in a 20 mL glass vial and kept frozen for analysis in the following fall. One vial was used for analysis by ion chromatography using a (Dionex®) Dionex DX500ic system with a PRPX100 column (dimensions 150 x 4.1 mm, 10 um) and 1 mM phenol; 4 mM $NaHCO_3$ buffered to pH 10.1 as the eluent. The electrochemical detector was used to determine conductivity and peak areas

were compared to external standard curves to quantify nitrate-N (μg/L), chloride (mg/L) and sulfate (mg/L).

Total suspended solid (TSS) concentration (mg/L) was determined by filtering sample water through a pre-weighed and dried Whatman GF/C 42.5 mm filter, under vacuum. Where possible, 200 mL of sample water was filtered, however, in some cases the suspended matter in the sample did not allow for full volume filtration and less was used (i.e., minimum 40 mL). The filter was dried at 105˚C for 24 hours to remove water and weighed. Subtraction of the dry filter weight (g) from the total weight (g) provided the TSS. The same filter was then burned at 550˚C for one hour to burn off organic matter and reweighed. Inorganic suspended solid (ISS) concentration was determined by subtracting the weight of the pre-dried filter from the total weight. The organic component determined by subtracting the ISS from the TSS.

Juvenile carp and other small fish

Two Beamish nets (Beamish 1973) were placed randomly around the noon hour with one wing extending from the shore for a period of 24 hours. Nets were removed at about the same time the following day and their contents were recorded. All fish were identified to species, enumerated and returned alive to the pond. If the nets contained too many fish to feasibly count each individual fish, they were sub-sampled and the numbers estimated. In this case, one scoop (1/2 liter) of fish was identified and their numbers recorded. This process was

repeated three times after which all subsequent scoopfuls were counted, recorded and returned to the pond. The mean number of fish per scoop was calculated and then multiplied by the number of scoops in the sample.

Adult carp

A number of attempts to estimate the density of adult carp in the ponds were made and failed. Gill netting was attempted in 2003. Numbers of fish caught did not reflect my visual estimates of carp on a given sampling day. I chose instead to make note of the numbers of carp I was able to see upon each visit to a site. A circuit was made of each pond once per week in 2003 and bi-weekly in 2004. In 2004, additional visits were made to the ponds in some of the “off weeks” to collect nutrient-diffusing substrata (NDS) or do vegetation surveys. Estimates were provided for these weeks as well. Numbers were either direct counts or estimates to give an impression of the relative numbers of carp using each pond. Unless they were moving, carp were difficult to spot. For this reason I periodically hit the floor of the canoe with a paddle which caused the fish in the immediate vicinity to move, making their presence detectible by means of distinctive swirls of sediment indicating the sudden movement of an individual adult and other signs such as a wake on the water surface and the agitation of emergent vegetation along the shoreline during spawning events. Spawning activity was also recorded where evident. Ponds were visited on two consecutive days each week. At times the number of carp would vary considerably from less than ten on day one to over 100 the following day. To simplify matters, I chose the larger

recorded estimate to use as an indicator of the numbers of carp using a pond in a given week.

Nutrient-Diffusing Substrata (NDS)

NDS have been found to be useful tools for determining nutrient limitation in periphyton communities over short time scales (15-60 days). This method has been used to study nutrient limitation to periphyton communities in wetlands (eg. Scott et al. 2005; Kolochuck 2008; Watchorn 2010), lakes (eg. Fairchild et al. 1985), streams (eg. Lowe et al. 1986, Winterbourn and Fegley 1989; Scott et al. 2009) and large rivers (Corkum 1996; Crimgeour and Chambers 1997).

The NDS in this study consisted of four treatments of 2 % agar infused with: 1) 0.05 mg/L N (from sodium nitrate $NaNO_3$), 2) 0.05 mg/L P (from K_2HP0_4), 3) 0.05 mg/L N and 0.05 mg/L P and 4) no nutrients added which served as the control. The dry chemicals (agar and nutrients) were mixed with de-ionized water in an Erlenmeyer flask and autoclaved at 121°C. The agar solution was then poured into sterilized 50 ml plastic centrifuge vials and capped with a sterilized porous silica frit 2.84 centimeters in diameter, matching the diameter of the vials. Prepared vials were kept cool in a refrigerator at 4°C and in a cooler with an icepack en route to each site. At the site three replicates of each treatment were placed in a 30 x 60 cm PVC frame. Each frame had three rows of four vials, each representing one of the four treatments. Vials were positioned at random in the first row. In the second and third row vials were arranged such that no treatment was in the same position in any of the three rows (Figure 8.). Each frame was

supported in the water by floats (pool noodles covered in duct tape to prevent UV deterioration and damage by wildlife) on either side running its length such that the vials were held horizontally in the water column at ten centimeters below the water surface (Figure 9), a depth to which light would rarely be growth limiting (Bortoluzzi thesis in prep.). A third float, in the shape of a ring to which the frame was attached by fifty centimeters of line, secured the frame in place to a pole lodged in the sediment. This allowed the apparatus to move into the path of least resistance when the winds shifted ensuring the silica frits were always downwind and protected from wave action. A single NDS frame was deployed in each pond of the study in a centrally located permanent sampling site, with the exception of Mackenzie Bay which was difficult to navigate due to dense growth of submerged vegetation in 2003. In this case the NDS apparatus was placed in the center of the eastern most section of the pond. NDS were deployed in each pond four consecutive times over the sampling period, from May to August. Studies by Bortoluzzi (Appendix 1), in a controlled environment have shown that nutrients were released initially rapid and exponential but continued to be released over a 45 day period. Other studies have also shown that N and P diffusion rates, though high at first, remained relatively constant for a period of up to 4 weeks ensuring enough nutrients in the vials to last in a short term study (eg. Tank and Dodds 2003; Bernhardt and Likens 2004; Von Schiller et al. 2007; Scott et al. 2009). In my study the NDS remained in the ponds for approximately three weeks (Table 2 and 3). On site, each silica frit was removed by squeezing the tube with pliers to avoid contact with the frit and placed in a uniquely labeled

amber glass jar. The jar was placed into a cooler containing an ice pack to keep it cool during transport to the laboratory the same day. Spent vials were replaced in situ with prepared vials of nutrient infused agar with their silica frits using the aforementioned method. The amber glass jars containing the used frits were placed in a freezer at the earliest opportunity for a minimum of 24 hours. The jars were then removed from the freezer and spiked with 10 mL of 90 % methanol after which they were placed in a dark drawer for a further 24 hours. The resulting methanol extract was then analyzed for chlorophyll *a* and pheophytin by the same methods used for phytoplankton and calculated in $\mu g/cm^2$ based on the surface area of the silica frit. Although it is well known that the growth of individual algal species can be limited only by a single nutrient at one time, assemblages of species may be comprised of species that are limited by different nutrients. Consequently, it is possible for such assemblages to be simultaneously co-limited by nitrogen and phosphorus, or by other combinations of factors (eg. Fairchild 1985: Armitage 2006). Additionally, by focusing on chlorophyll a, heterotrophs such as bacteria and fungi are not included here.

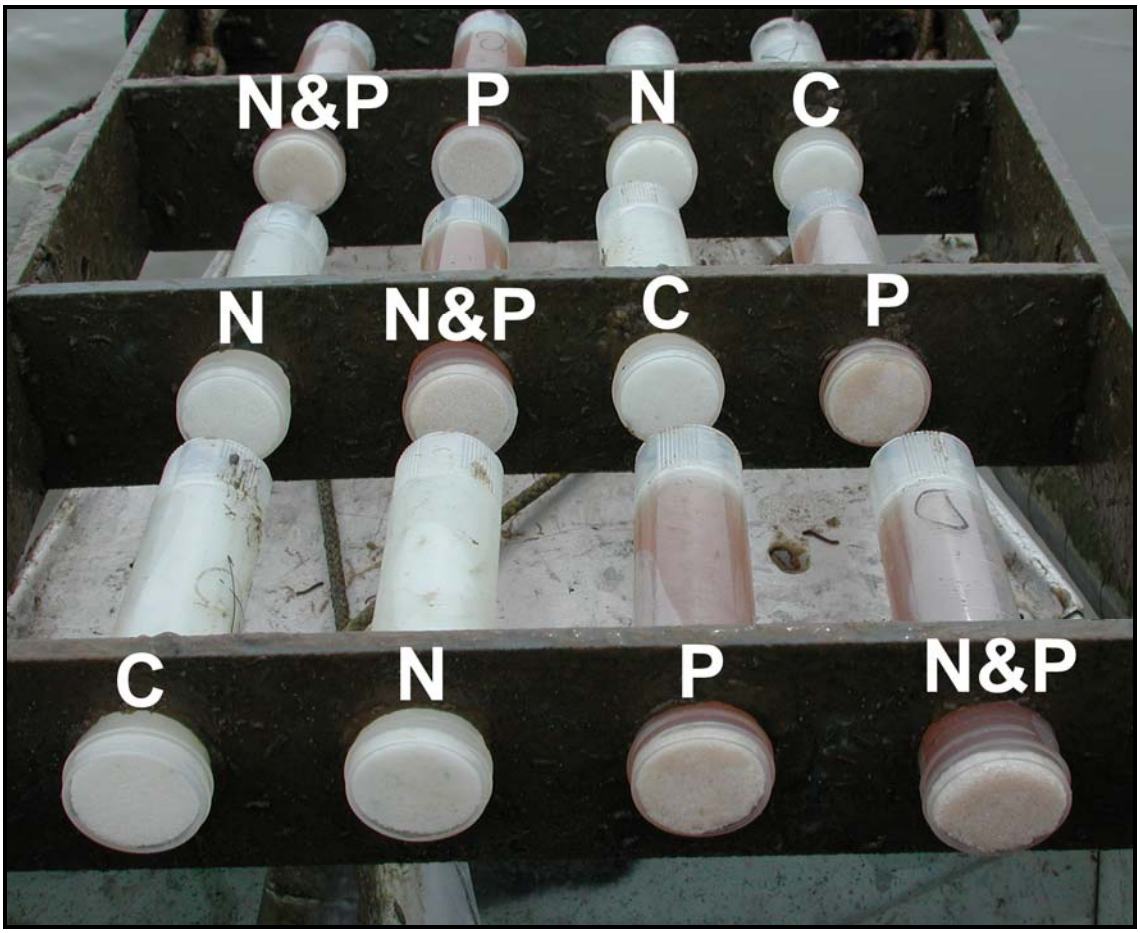

Figure 8. Example of an NDS frame containing new vials of agar infused with 0.05 mg/L nitrogen (N), 0.05 mg/L phosphorus (P), 0.05 mg/L nitrogen and phosphorus (N&P) and no nutrients (C).

Figure 9. NDS apparatus deployed in Mackenzie Bay, Delta Marsh, MB. The ring encircles a pole secured in the sediments of the pond, allowing the frame to align with the wind direction thus minimizing possible damage to the frit surfaces due to wave action which are oriented downwind.

Table 2. Set and pull dates of nutrient-diffusing substrata (NDS) apparati in carp-accessible ponds in 2003 and 2004, Delta Marsh, MB. The dash indicates that no NDS apparati were deployed.

	Cherry Ridge		Klyne Lake		West Blind Channel		Wye's Pond	
	2003	2004	2003	2004	2003	2004	2003	2004
set 1	May 27 Jun 17	May 26 June 14	May 28 Jun 18	May 24 Jun 14	Jun 05 Jun 25	May 18 Jun 09	-	May 18 Jun 09
set 2	Jun 17 Jul 08	Jun 14 Jul 05	Jun 19 Jul 09	Jun 14 Jul 05	Jun 25 Jul 09	Jun 09 Jun 30	-	Jun 09 Jun 30
set 3	Jul 08 Jul 29	Jul 05 Jul 26	Jun 09 Jul 29	Jul 05 Jul 26	Jul 09 Jul 30	Jun 30 Jul 22	-	Jun 30 Jul 22
set 4	Jul 29 Aug 18	Jul 26 Aug 16	Jul 29 Aug 18	Jul 26 Aug 16	Jul 30 Aug 18	Jul 22 Aug 17	-	Jul 22 Aug 17

Table 3. Set and pull dates of nutrient-diffusing substrata (NDS) apparati in carp-free ponds in 2003 and 2004, Delta Marsh, MB. The dash indicates that no NDS apparati were deployed.

	Pitblado		Mackenzie Bay		Mid-Blind Channel		East Blind Channel		Emile's Pothole	
	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004
set 1	May 27 Jun 17	May 26 Jun 14	May 28 Jun 18	May 24 Jun 14	May 28 Jun 18	May 18 Jun 09	-	May 18 Jun 09	-	May 18 Jun 09
set 2	Jun 17 Jul 08	Jun 14 Jul 05	Jun 19 Jul 09	Jun 14 Jul 05	Jun 18 Jul 09	Jun 09 Jun 30	-	Jun 09 Jun 30	-	Jun 09 Jun 30
set 3	Jul 08 Jul 29	Jul 05 Jul 26	Jun 09 Jul 29	Jul 05 Jul 26	Jul 09 Jul 30	Jun 30 Jul 22	-	Jun 30 Jul 22	-	Jun 30 Jul 22
set 4	Jul 29 Aug 18	Jul 26 Aug 16	Jul 29 Aug 18	Jul 26 Aug 16	Jul 30 Aug 18	Jul 22 Aug 17	-	Jul 22 Aug 17	-	Jul 22 Aug 17

Sediment analyses

Surface sediment samples were collected from three points in each pond along its longest axis. A plastic tube was pushed into the sediment to a depth of at least 10 cm and plugged at the top to create a vacuum. The tube was then raised out of the water and a plunger inserted into the bottom of the tube to push the water and sediment to the top. The top two centimeters were then removed and placed into a small plastic container which was sealed, transported back to the lab and stored in a refrigerator at 4˚C until they could be analyzed (days for organic content and weeks for texture analysis).

To determine the organic and inorganic components of the sediments each sample was stirred by hand using a metal rod and 10 ml of soil was removed and placed in a pre-dried and weighed ceramic crucible. The wet weight (g) was recorded prior to drying at 100˚C for 24 hours and weighed again. The sample was burned at 550˚C for one hour and weighed again. The inorganic component in the sample was calculated by subtracting the weight of the crucible from the total weight after the 100˚C burn. The organic component was calculated by subtracting the total weight after the 550˚C burn from the total weight after the 100˚C burn. This procedure was repeated three times for each sample, totaling nine per pond to obtain and average. The average organic and inorganic component was used in the results.

Soil texture was determined using the Bouyoucos hydrometer method (Buoyoucos 1936). Chemical dispersion was used to determine soil texture by particle size analysis. Calgon (sodium hexametaphosphate) was used as the dispersing agent. Fifty grams of dried and ground sediment was mixed with 125 mL of Calgon solution. Distilled water was added to make 1000 mL of solution. The column of solution was gently inverted 30 times (or for one minute) and replaced on the counter and a measurement taken using a hydrometer. Two hours later another hydrometer reading was taken. The contents of the column were then safely disposed of. The percentage of sand, silt and clay were then calculated using the densities given by the hydrometer readings.

Submerged Vegetation

Submerged vegetation was sampled in early August 2003 and late July 2004 using a plastic cylinder 1.80 meters in circumference or 57.3 cm in diameter. Samples were taken from five randomly selected locations within each pond. The water depth was recorded and all above-ground plant matter (roots were removed) within the confines of the tub was removed using a rake or by hand, bagged, labeled and stored at 4˚C. To obtain dry weight per species the vegetation in each bag was sorted by species and dried at 100˚C for 48 hours and weighed to grams. The average grams per square meter of each species were then calculated for each pond. In 2004, we sampled vegetation four times per pond, once in mid May, June, July and August in order to get a sense of the progression of aquatic macrophyte growth over the season. Metaphyton was

collected in the process of collecting the submerged macrophytes as above. Since its collection was unavoidable I decided to dry and weigh it as well.

Data Analyses

The sampling season was divided, for both 2003 and 2004, into three consecutive four week periods which corresponded to general shifts in the abundance of adult carp recorded in both years. The three periods were independent, roughly including; 1) the last week in May up to and including the third week in June, 2) the fourth week in June up to and including the third week in July, and 3) the fourth week in July up to and including the second week in August. Univariate statistics were performed using JMPin 8.0.1 (SAS Institute Inc.). All data were log10(x+1) transformed (pH was not transformed) prior to analysis. Analysis of variance (one-way ANOVA) was used to determine significant differences in the means of the variables between carp-accessible and carp-free ponds in a particular time period by pooling the data collected within the specified time period within each treatment group. To determine if there was a change over time in any one variable, analysis of variance was used (one-way ANOVA) followed by Tukey-Kramer HSD to test for differences of the means for each time period in a single year. To determine if the mean of a particular variable had changed significantly among carp-accessible or carp-free ponds from 2003 and 2004, seasonal means of the combined data from each treatment group were calculated and compared using one-way ANOVA. Correlations between variables were determined using simple linear regression.

In order to determine nutrient limitation to periphyton from the nutrient diffusing substrata, the mean algal growth (chlorophyll *a*) on each treatment was calculated. The four possible outcomes were; 1) no significant response; 2) N-limitation; 3) P-limitation; and 4) N and P co-limitation). Using JMP IN 8.0.1 statistical software, one-way ANOVA combined with Dunnett's method was used to determine if the mean algal growth (log10(x+1) transformed) on any of the treatments differed. When the mean algal growth on a treatment was found to be significantly greater than the control it was considered to be the limiting nutrient in the water column for the duration of the set. Where the mean algal growth response of two treatments differed significantly from the control, Tukey-Kramer HSD was employed to determine if there was a significant difference between these two treatments. If they differed significantly the treatment with the greater mean algal growth response was deemed the limiting nutrient or combination of nutrients. If the mean algal growth response on the N or P treatment and the N and P combined treatment did not differ significantly, the limiting nutrient was deemed to be N or P. Differences in algal growth response on the control treatments of the NDS were also compared between ponds. A one-way ANOVA was used for pair-wise comparisons, using Tukey-Kramer HSD to determine which means were significantly different from the others.

Principal components analysis (PCA) was conducted to determine the overall relationship between the ponds studied with respect to the parameters measured. PCA was run in R using the PRINCOM (covariance distance matrix). The ordination bi-plot diagrams were created using Adobe Illustrator CS4

software. This analysis was performed using the set means of eight variables for each of the ponds in each of the two years (TP, TRP, TN, ammonia-N, nitrate-N, sulfate, DIC and pH), having excluded highly correlated variables from the analysis. Data were divided into four consecutive sets which corresponded to the dates during which the NDS were in the water. For example, NDS set one in Cherry Ridge, 2003 was in place from May 27 to 17 June 17, therefore variable means were calculated using all data collected within two days of the set (May 25 to June 19). NDS set 2 of the same pond and year was in place June 17 to July 08. Variable means were calculated in the same manner as above using all data collected from June 15 to July 10. The overlap was necessary to include data encompassing the full period of the NDS set. The mean was then calculated for each set, of which there were four, for each pond (excluding East Blind Channel) and input into the PCA. For each pond the points in space were then connected by an arrow to show a continuum in time. NDS-derived nutrient limitations for each pond representing each of the four time periods were then superimposed onto the ordination bi-plot.

Results

Carp Presence

Visual estimates of the numbers of carp in carp-accessible ponds throughout the sampling season of 2003 and 2004 revealed that adult carp tended to congregate in large numbers in late May and June (Table 4). In 2004, carp were observed in all the ponds from May through August, with the exception of Wye's Pond in which they were not seen after the first week of August. By contrast, in 2003, adult carp were rarely observed in the carp-accessible ponds after the first week in July and then only in small numbers. Spawning behaviour was observed in the first week of June in all three carp-accessible ponds and again in the third week of June in Klyne Lake in 2003. In 2004, spawning behaviour was observed only in Klyne Lake and West Blind Channel beginning in the first week of June in Klyne Lake and again in the last week of July, and in the last week of June in West Blind Channel. Although spawning was not observed in Cherry Ridge or Wye's Pond in 2004, young of the year (YOY) carp were found in all carp-accessible ponds. YOY began to appear in Beamish traps in the last week of June in 2003 and after July 12 in 2004 (Table 5). In 2003 the abundance of YOY peaked in the first two weeks of July and peaked two weeks later in 2004. YOY were also found in 2003 and 2004 in relatively small numbers in Mid-Blind Channel, the only pond which retained a connection to the main marsh, but to which there was no access to adult carp (Table 5).

Table 4. Visual estimates and counts of adult carp, *C. carpio,* during sampling periods (weeks) in carp-accessible ponds of Delta Marsh in 2003 and 2004. Ponds in which adult carp were not seen are not included here. CR=Cherry Ridge; KL = Klyne Lake; WBC= West Blind Channel; W = Wye's Pond. **C. carpio* observed exhibiting spawning activity. † carp present in Cadham Bay to which Cherry Ridge is connected. The dash indicates no sample taken.

	2003			2004			
week	CR	KL	WBC	CR	KL	WBC	W
1	6	20	20	6	10	6	-
2	0	15	10	10	-	-	3
3	7	8	20	-	100s*	100s	-
4	20*	20*	1*	6	-	-	7
5	1	100s	100s	-	50	50	-
6	0	15*	3	3	-	100s	3
7	0	0	0	-	20	100*	-
8	5	4	2	8	5	-	3
9	0	3	0	-	1	4	-
10	0	3	4	3	-	-	3
11	0	20	0	-	30*	3	-
12	0	0	0	3	-	-	7
13	0†	0	0	-	1	0	0
14	0	0	0	5	9	-	0

mid May----------mid June----------mid July----------mid August

Table 5. Mean and standard deviation (in brackets) of young of the year carp, *C. carpio*, caught in trap nets during each sampling period in 2003 and 2004 and standardized to the open water area of the ponds. Only those ponds in which young of the year carp were found are presented here. CR = Cherry Ridge; KL = Klyne Lake; WBC = West Blind Channel; W = Wye's Pond; MBC = Mid-Blind Channel (carp-free/screened). The dash indicates no sample taken.

	2003				2004				
week #	CR	KL	WBC	MBC	CR	KL	WBC	W	MBC
1	0	0	0	0	-	0	0	-	0
2	0	0	0	0	0	-	-	0	-
3	0	0	0	0	-	0	0	-	0
4	0	0	0	0	0	-	-	0	-
5	0	0	0	0	-	0	0	-	0
6	0	0	0	0	0	-	-	0	-
7	72 (100)	3 (1)	2 (2)	0	-	0	0	-	0
8	22 (16)	17 (6)	70 (99)	<1 (<1)	0	-	-	0	-
9	328 (168)	83 (23)	35 (13)	2 (1)	-	3 (4)	0	-	0
10	130 (167)	11 (1)	23 (15)	0	99 (160)	-	-	89 (94)	-
11	80 (88)	13 (4)	25 (22)	<1 (<1)	-	128 (101)	22 (23)	-	<1 (<1)
12	11 (10)	7 (6)	10 (7)	4 (2)	1306 (898)	-	-	202 (125)	-
13	13 (16)	7 (4)	18 (21)	<1 (<1)	-	178 (55)	7 (3)	-	0
14	0	3 (1)	7 (3)	<1 (<1)	-	-	-	-	-

mid May ---- Mid June ---- Mid July ---- mid August

Effects of carp on water clarity

Water clarity was generally poorer in carp-accessible ponds relative to carp-free ponds when adult carp were present. Total suspended solids (TSS) and inorganic suspended solids (ISS) were significantly greater in carp-accessible ponds compared to ponds to which carp did not have access from mid-May to mid-June in 2003 and from mid-May to mid-July in 2004 (Figures 10 and 11). In both years the elevated levels of TSS and ISS were concurrent with the presence of abundant adult carp (Table 4). The water column in carp-accessible ponds remained significantly more turbid than carp-free ponds throughout the summer of both years (Figure 12). In 2004, the euphotic zone depth was significantly shallower in carp-accessible ponds than in carp-free ponds from mid-May to mid-July (Figure 13). Generally, there was sufficient photosynthetically active radiation reaching the sediment surface (> 1 % of incident PAR) to permit the growth of submerged macrophytes in all ponds throughout the sampling period. However, in Klyne Lake, on several occasions there was less than 1 % of the surface irradiance at the sediment surface. Concentrations of TSS and OSS were positively correlated in both 2003 ($r^2 = 0.82$, $p < 0.0001$) and 2004 ($r^2 = 0.96$, $p < 0.0001$). TSS and ISS were positively correlated in 2004 ($r^2 = 0.81$, $p < 0.0001$), but not in 2003. Turbidity was weakly positively correlated with TSS ($r^2 = 0.74$, $p < 0.0001$) and ISS ($r^2 = 0.69$, $p < 0.0001$) in 2004, and was not correlated with the other water clarity variables in 2003. The euphotic zone depth was negatively correlated to turbidity, but weakly ($r^2 = 0.67$, $p < 0.0001$) and only in 2004.

A seasonal trend in water column TSS and was evident in carp-accessible ponds in 2004 and was equivocal in 2003. In 2004, water column TSS and ISS decreased in carp-accessible ponds from a mean of 71 ± 19 mg/L TSS and 35 ± 13 mg/L ISS in mid-May to mid-June to 37 ± 23 mg/L TSS and 8 ± 7 mg/L ISS in mid-July to mid-August (p = 0.0417 and p = 0.0036, respectively). In 2003, a seasonal trend was not observed when the data from the three carp-accessible ponds were pooled. However, in Cherry Ridge, where carp were seen infrequently in 2003, TSS and ISS were low ranging from means of 21 - 19 NTU, 26 - 19 mg/L TSS; and 6 - 5 mg/L ISS and there was sufficient light available for plant growth throughout the summer comparable to that in carp-accessible ponds (Figure 13). In West Blind Channel, adult carp were abundant from mid-May to mid-June and water clarity was poor during this period; 30 NTU, 59 mg/L TSS, and 21 mg/L ISS. Nevertheless, there was always sufficient photosynthetically active radiation (>1 % of surface irradiance) reaching the sediment surface to allow for the growth of submerged macrophytes (Figure 13). From mid-June to mid-August the water column in West Blind Channel became increasingly clearer with means of 17 NTU, 18 mg/L TSS, and 3 mg/L ISS by mid-July to mid-August. Conversely, Klyne Lake remained turbid for the majority of the summer, and PAR did not reach the sediment surface on two occasions in June and July (Figure 13). Mean turbidity, TSS and ISS in the early, middle and late summer, in Klyne Lake, ranged from 30 - 33 NTU, 44 - 48 mg/L TSS, and 10 - 12 mg/L ISS (* with the exclusion of the data collected from July 07, 2003).

The outlier in the mid-June to mid-July block in carp-accessible ponds was due to an abrupt decrease in water clarity in Klyne Lake on July 7, 2003, at which time the water was milky in appearance. All parameters relating to water clarity confirm that this was likely the result of a real phenomenon. ISS was recorded at 250 mg/L (65 % of the TSS), 135 mg/L OSS and a turbidity of 97 NTU, the highest readings recorded all summer. Secchi depth and euphotic zone depths were the lowest recorded that summer at 8 cm and 19 cm, respectively. It is unlikely that carp were responsible for this event alone, as few carp were observed in the area at the time. This event may have been the result of a bacterial bloom associated with the breakdown of algae following the deterioration of a prolific phytoplankton bloom which occurred in Klyne Lake on June 18, 2003. Even with the removal of the outlier no significant differences in suspended solids or turbidity were found between carp-accessible and carp-free ponds.

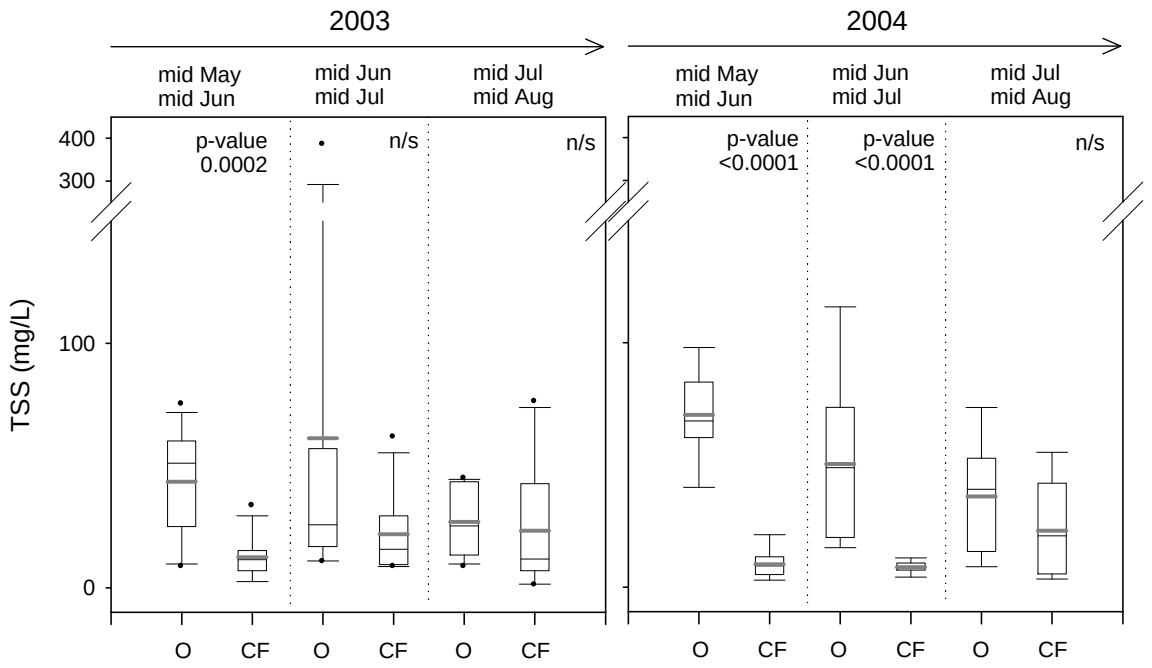

Figure 10. Mean total suspended solids (TSS) (mg/L) among carp-accessible (O) and carp-free ponds (CF) in 2003 and 2004. The data used in the derivation of the means for each of the three time periods are independent between successive time intervals. Mid-May to mid-June = weeks 2 - 5; mid-June to mid-July = weeks 6 - 9; mid-June to mid-August = weeks 10 - 13. The shaded horizontal line represents the mean of the means. The solid horizontal line represents the median of the means.

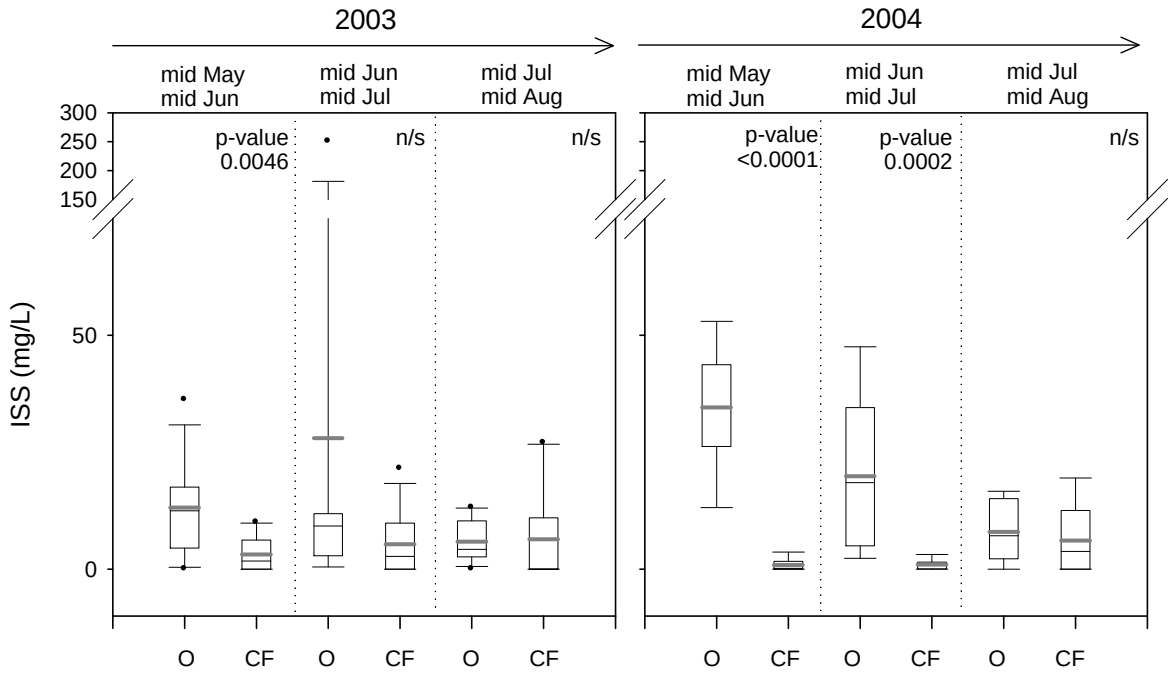

Figure 11. Mean inorganic suspended solids (ISS) (mg/L) among carp-accessible (O) and carp-free ponds (CF) in 2003 and 2004 The data used in the derivation of the means for each of the three time periods are independent between successive time intervals. Mid-May to mid-June = weeks 2 - 5; mid-June to mid-July = weeks 6 - 9; mid-June to mid-August = weeks 10 - 13.

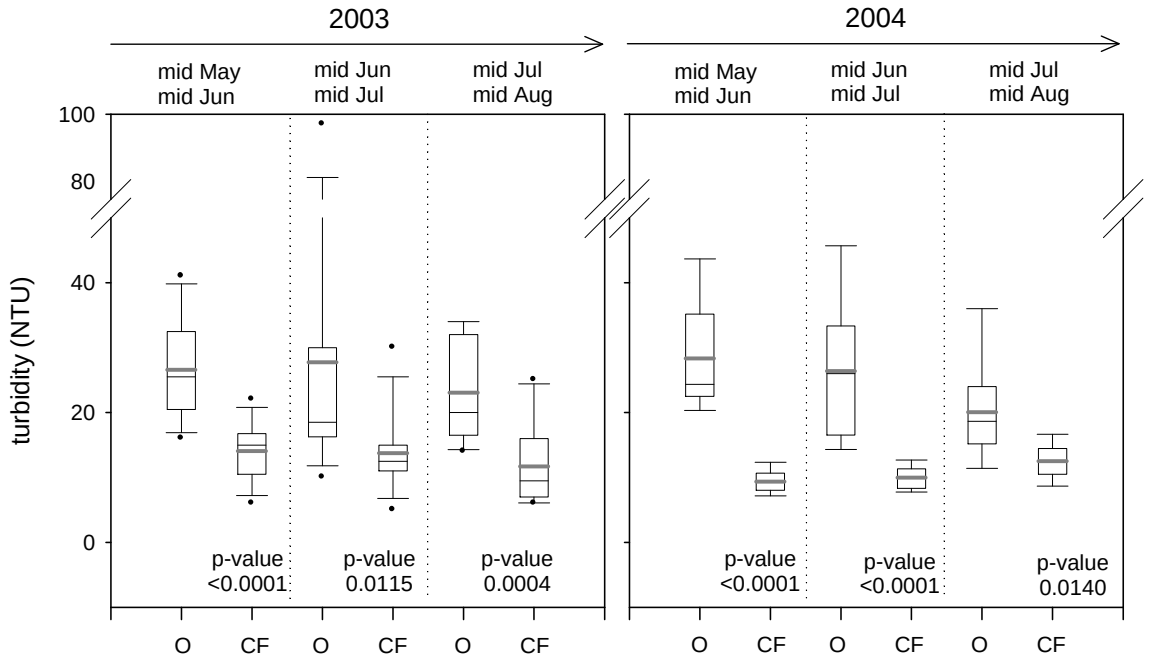

Figure 12. Mean water column turbidity (NTU) among carp-accessible (O) and carp-free ponds (CF) in 2003 and 2004. The data used in the derivation of the means for each of the three time periods are independent between successive time intervals. Mid-May to mid-June = weeks 2 - 5; mid-June to mid-July = weeks 6 - 9; mid-June to mid-August = weeks 10 - 13.

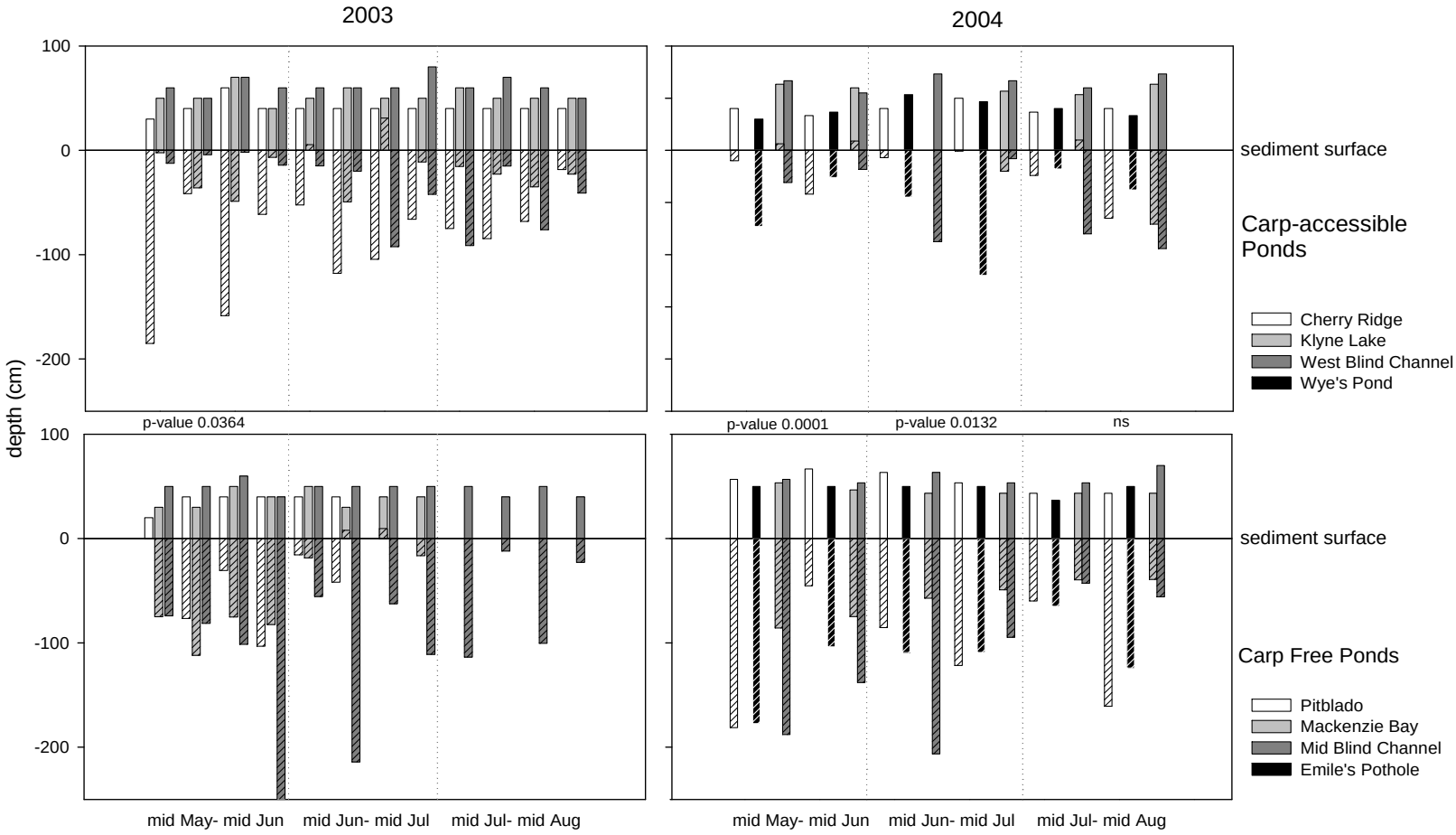

Figure 13. Water depths (solid bars above 0 cm) (cm) and corresponding to potential euphotic zone depths (cross hatched) (cm below water surface), the depth to which 1% of the surface irradiation would extend, in carp-accessible and carp-free ponds in 2003 and 2004.

Effects of carp on pH and DIC

In 2003, dissolved inorganic carbon (DIC) concentrations in the water column were significantly lower in carp-accessible ponds compared to carp-free ponds, particularly from mid-June to mid-August ($p = 0.0173$ and 0.0438, respectively). The pH of the water column was significantly greater in carp-free ponds compared to carp-accessible ponds from mid-June to mid-August 2003 and became increasingly disparate over time ($p = 0.0125$ mid-June to mid-July and $p < 0.0001$ mid-July to mid-August). These differences were not seen in 2004. Simple linear regressions revealed no correlations of DIC or pH to any other variables examined in this study.

Effects of carp on specific conductance, chloride and sulfate

Specific conductance of the water column and concentrations of chloride and sulfate were significantly higher in carp-free ponds relative to carp-accessible ponds, in both years, with the exception of sulfate in mid-June to mid-July in 2004 (Figure 14, 15 and 16). Specific conductance, chloride and sulfate concentrations increased gradually with significant differences between the spring and late summer ($p < 0.0001$, $p = 0.0005$ and $p = 0.0007$, respectively) in carp-free ponds in 2003, but not in 2004. Of note is the wide variation in sulfate and chloride among ponds in 2004. West Blind Channel had the highest seasonal mean concentration of sulfate (465 ± 75 mg/L) compared to other carp-accessible ponds (seasonal mean range 176 ± 31 mg/L in Cherry Ridge and 255 ± 41 mg/L in Wye's Pond). Among carp-free ponds, Mid-Blind Channel and

Pitblado had the highest concentrations of sulfate (seasonal mean 761 ± 94 mg/L and 535 ± 89 mg/L, respectively) compared to 330 ± 45 mg/L and 246 ± 21 in the other ponds. Pitblado also had the highest seasonal mean chloride concentration (1064 ± 106 mg/L) among carp-free ponds whose seasonal means ranged from 451 ± 57 mg/L in Emile's Pothole to 622 ± 63 mg/L in Mackenzie Bay.

In 2003, water depth was significantly deeper in carp-accessible ponds compared to carp-free ponds though was not significantly different between 2003 and 2004 (Figure 17). In both 2003 and 2004, water column chloride and sulfate were positively correlated (r^2 = 0.80 and 0.81, respectively; $p < 0.0001$). Chloride and specific conductance were positively correlated in 2004 (r^2 = 0.88; $p < 0.0001$). Water depth was not correlated with specific conductance, chloride and sulfate concentrations.

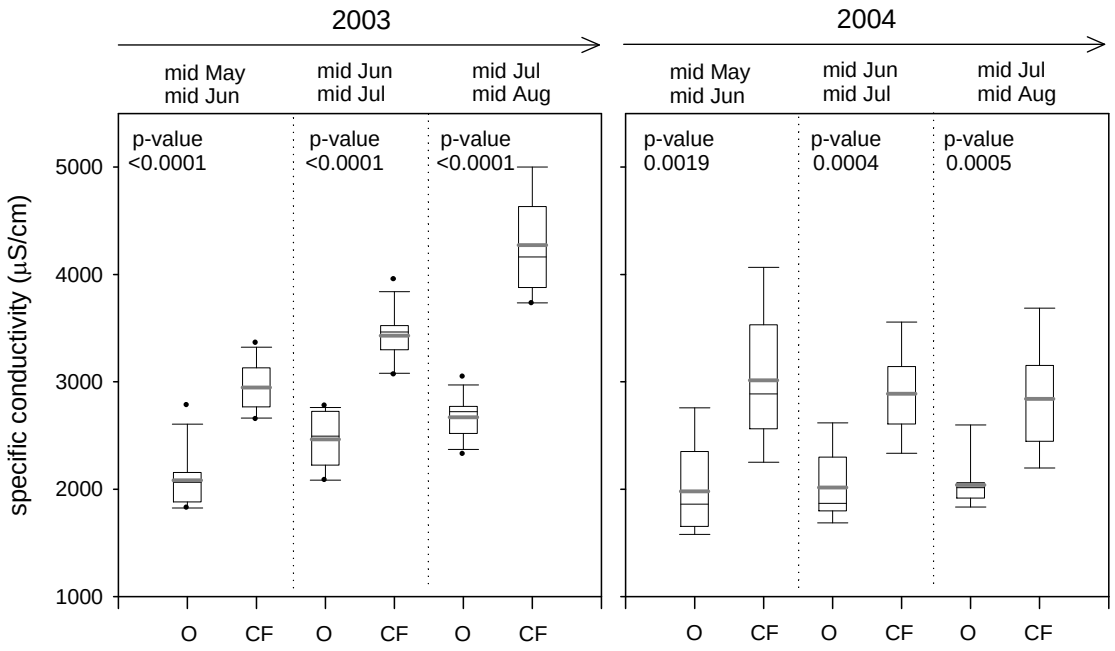

Figure 14. Mean specific conductance (µS/cm) among carp-accessible (O) and carp-free ponds (CF) in 2003 and 2004. The data used in the derivation of the means for each of the three time periods are independent between successive time intervals. Mid-May to mid-June = weeks 2 - 5; mid-June to mid-July = weeks 6 - 9; mid-June to mid-August = weeks 10 - 13.

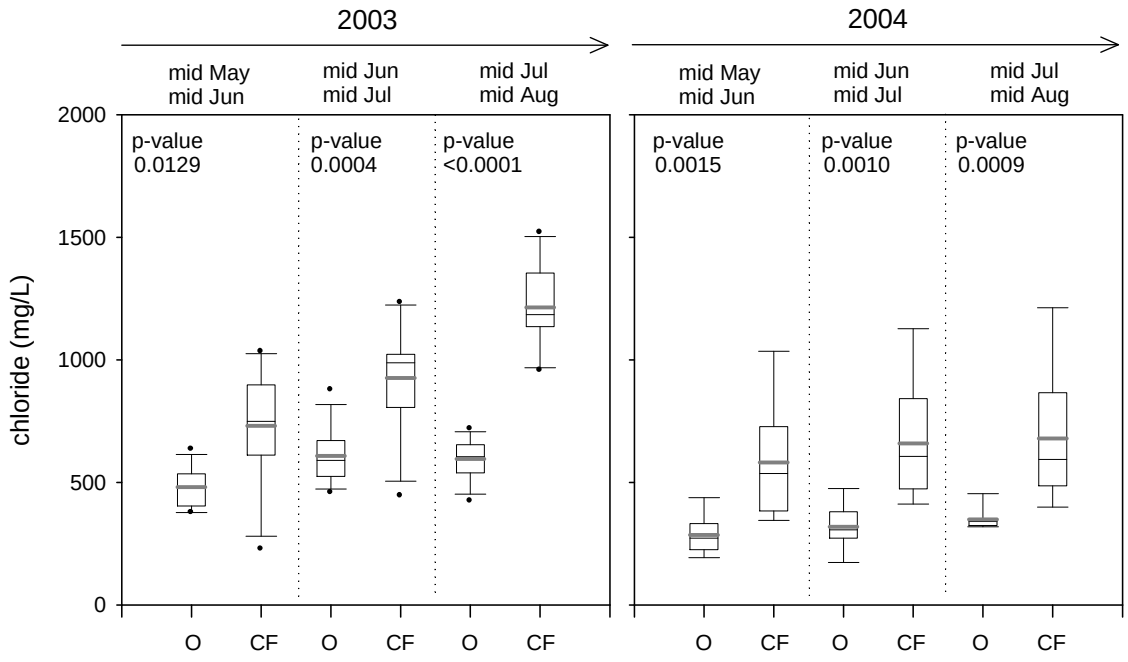

Figure 15. Mean water column chloride concentration (mg/L) in carp-accessible (O) and carp-free ponds (CF) in 2003 and 2004. The data used in the derivation of the means for each of the three time periods are independent between successive time intervals. Mid-May to mid-June = weeks 2 - 5; mid-June to mid-July = weeks 6 - 9; mid-June to mid-August = weeks 10 - 13.

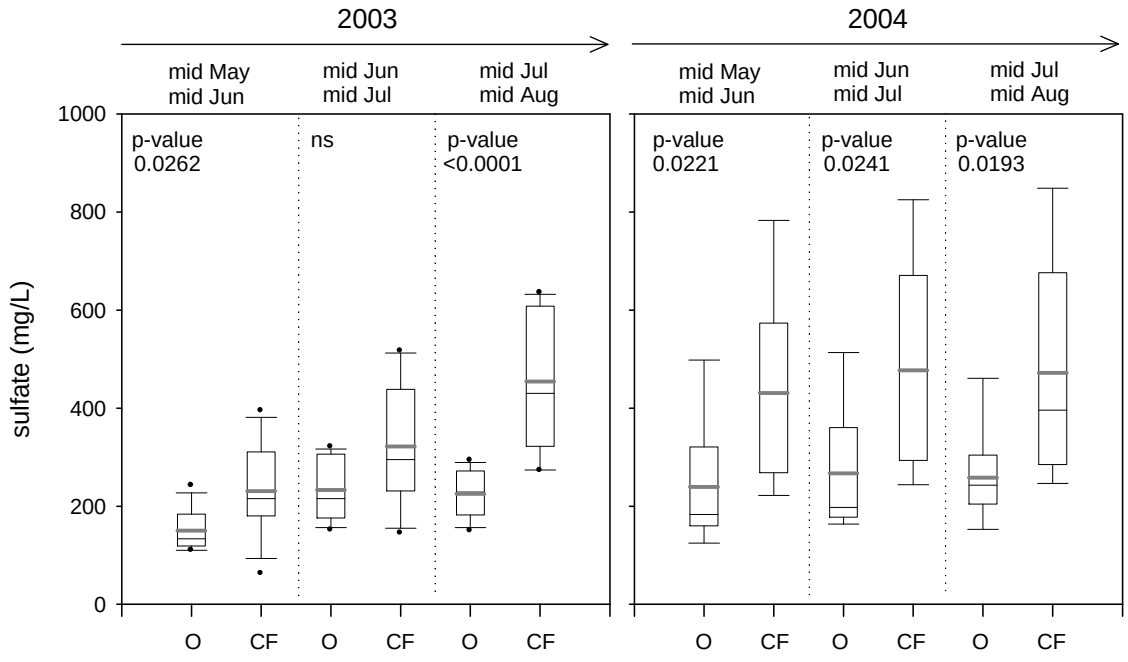

Figure 16. Mean water column sulfate concentration (mg/L) among carp-accessible (O) and carp-free ponds (CF) in 2003 and 2004. The data used in the derivation of the means for each of the three time periods are independent between successive time intervals. Mid-May to mid-June = weeks 2 - 5; mid-June to mid-July = weeks 6 - 9; mid-June to mid-August = weeks 10 - 13.

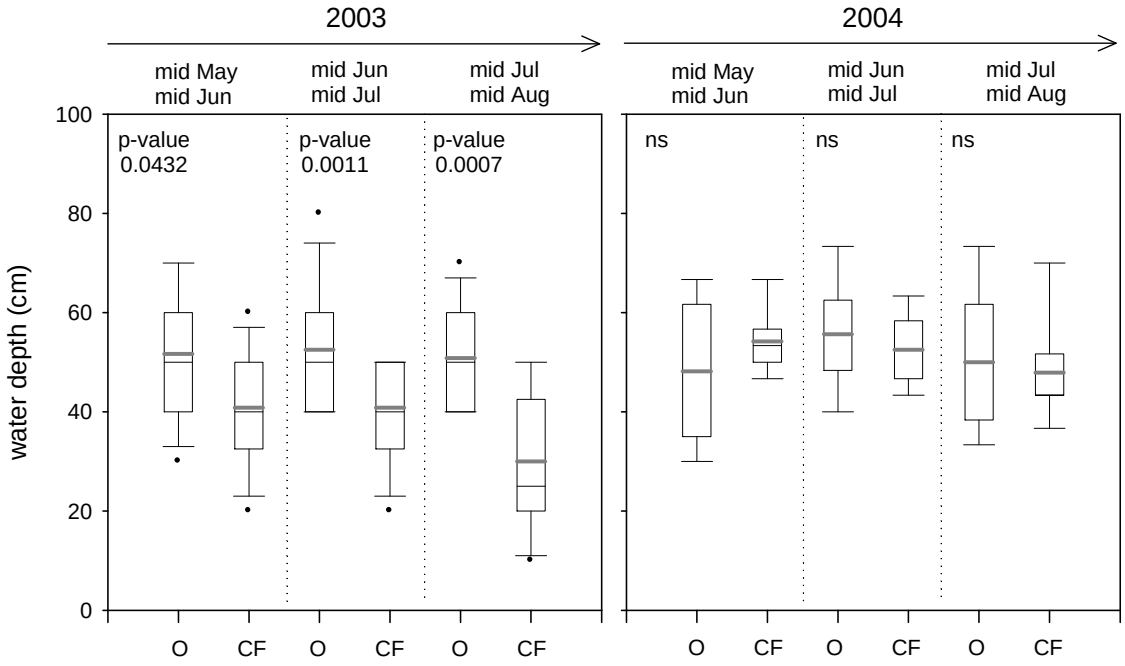

Figure 17. Mean water depth (cm) in carp-accessible (O) and carp-free ponds (CF) in 2003 and 2004. The data used in the derivation of the means for each of the three time periods are independent between successive time intervals. Mid-May to mid-June = weeks 2 - 5; mid-June to mid-July = weeks 6 - 9; mid-June to mid-August = weeks 10 - 13.

Effects of carp on water column nutrients

In 2003, carp-accessible ponds tended to have higher water column concentrations of ammonia-N, TRP and TP compared to carp-free ponds (Figure 18). The degree of the difference became more pronounced as the season progressed. Total phosphorus (TP) and total reactive phosphorus (TRP) concentrations were significantly greater in carp-accessible ponds relative to carp-free ponds from mid-June to mid-August in 2003 (Figure 19 and 20). Ammonia-N was significantly greater in carp-accessible ponds than in carp-free ponds throughout the summer in 2003 (Figure 21). Although TRP concentration seems high relative to other systems, it is comparable to Hnatiuk's (2006) findings. No statistically significant seasonal trend was found when the data from all three carp-accessible ponds were pooled, comparing the mean concentration of nutrients in carp-accessible and carp-free ponds over three consecutive time blocks; mid-May to mid-June, mid-June to mid-July and mid-July to mid-August. However, a seasonal trend was observed in two of the three carp-accessible ponds which exhibited high concentrations of ammonia-N and TRP in the latter part of the summer. In Cherry Ridge and West Blind Channel, TRP and ammonia-N concentrations increased substantially from around the time the adult carp were no longer frequently seen in the ponds in early June to mid-August (Figure 22). In Cherry Ridge mean TRP and ammonia-N concentrations increased from 304 μg/L TRP and 1005 μg/L ammonia-N in the spring to 1062 μg/L TRP and 2343 μg/L in mid-July to mid-August. In West Blind Channel, TRP concentrations fluctuated extensively with means of 36 μg/L in the spring, 453

μg/L mid-summer and 503 μg/L from mid-July to mid-August. By contrast, in Klyne Lake, water column TRP and ammonia-N remained low and relatively stable throughout the sampling period ranging from 35 μg/L TRP and 178 μg/L ammonia-N in the spring to 144 μg/L TRP and 52 μg/L in the late summer. This difference in the nutrient concentrations in carp-accessible ponds can be seen in the PCA ordination bi-plot which shows nutrient concentrations in Klyne Lake were similar to those of the carp-free ponds (Figure 18). Total N and nitrate-N were not important in defining the difference between ponds in 2003. However, in carp-free ponds a seasonal trend in water column nitrate-N was observed with mean concentrations rising from the spring (810 ± 267 μg/L) to the late summer (1360 ± 262 μg/L nitrate-N) (p = 0.0004).

In 2004, carp-accessible ponds and carp-free ponds did not separate out in the PCA based on ammonia-N and TRP as they did in 2003 (Figure 23). Neither TRP nor ammonia-N concentrations were significantly different between carp-accessible and carp-free ponds throughout the sampling season (Figure 20 and 21). Instead, the majority of the variation in nutrient concentrations occurred within individual ponds over time (Figure 23). Two of the four carp-accessible ponds were low in TRP and ammonia-N in May, increased in June, decreased again in July and increased substantially by August. In Wye's Pond (carp-accessible), the trend was opposite in that ammonia-N and TRP increased from mid-June to mid-July and decreased by August. In Mackenzie Bay, a carp-free pond, there was a peak in the water column concentrations of ammonia-N and TRP in the spring and mid summer that was much higher than compared to all

other carp-free ponds in both years (Figure 22). Ammonia-N was on average 1519 μg/L in the spring and 1931 μg/L in mid summer compared to means of 118 μg/L and 65 μg/L in the other carp-free ponds in 2004. TRP concentrations in Mackenzie Bay were on average 329 μg/L in the spring and 548 μg/L mid summer compared to means of 29 μg/L and 30 μg/L in the other carp-free ponds. This peak did not occur in any of the carp-free ponds in 2003.

Generally, carp-accessible and carp-free ponds differed in terms of TN, TP and nitrate-N water column concentrations in 2004. Three of the four carp-accessible ponds tended to be higher in water column TP and lower in TN and nitrate-N than the carp-free ponds (Figure 23). As a group, TP was significantly greater in carp-accessible ponds in the spring of 2004 compared to carp-free ponds (Figure 19). TN was significantly greater in carp-free ponds from mid May to mid July, whereas and nitrate-N was significantly greater in carp-free ponds from mid-June to mid-August (Figure 24 and 25). A significant increase in nitrate-N concentration was also observed in carp-free ponds in 2004 from the spring to the late summer (mean 1465 ± 473 μg/L; $p = 0.0413$). Of the carp-accessible ponds in 2004, West Blind Channel was unique in that water column nutrients were low compared to other carp-accessible ponds and were comparable to that of Mid-Blind Channel, the carp-free pond to which it shared a connection (Figure 23).

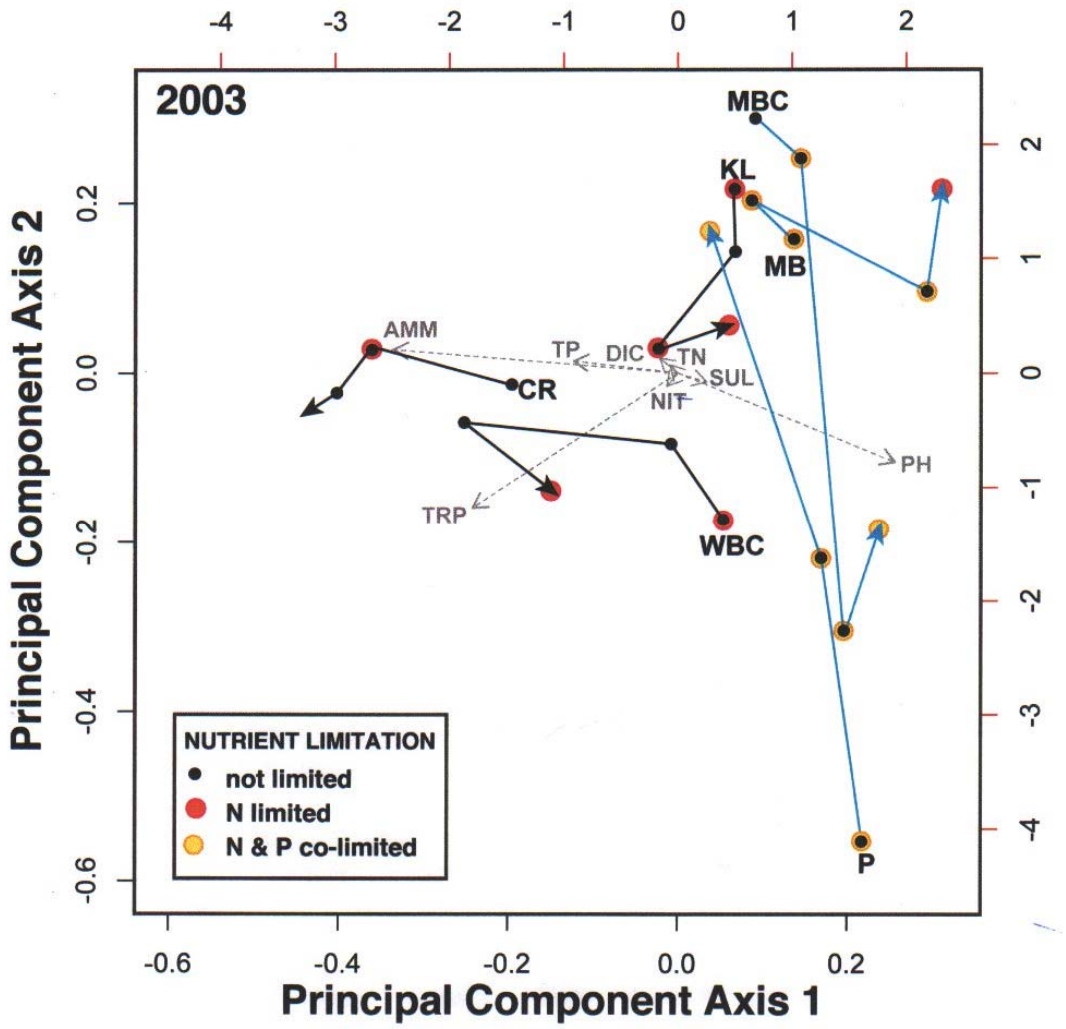

Figure. 18. PCA ordination time series model depicting seasonal water nutrient dynamics within six ponds sampled in 2003 in Delta Marsh, Manitoba, Canada. Percent variance explained by the first two principal ordination axes is 78.1% and 15.1% respectively. Solid vectors correspond to temporal change within each pond; late May to early August 2003 (solid circles = sample points, arrow = last reading taking at the end of the season). Blue vectors = carp-free pond ponds; black vectors = carp-accessible ponds. Dashed vectors correspond to the 8 fresh water environmental descriptors (eigenvectors): AMM = ammonia-N, TRP = total reactive phosphorus, TP = total phosphorus, DIC = Dissolved inorganic carbon, TN = total nitrogen, SUL = sulfate, NIT = nitrate, PH = water pH. All water variables were log transformed (log10(X±1)) except pH. PCA was run in R using the PRINCOM (covariance distance matrix). Nutrient limitations determined from bio-assays are indicated on the diagram; yellow circles indicate the pond was N&P co-limited; red circles indicate N-limitation; and no circle indicates the pond was not limited by N or P. KL = Klyne Lake; CR = Cherry Ridge; WBC = West Blind Channel; MB = Mackenzie Bay; P = Pitblado; MBC = Mid-Blind Channel. Pitblado was sampled only during the first three periods.

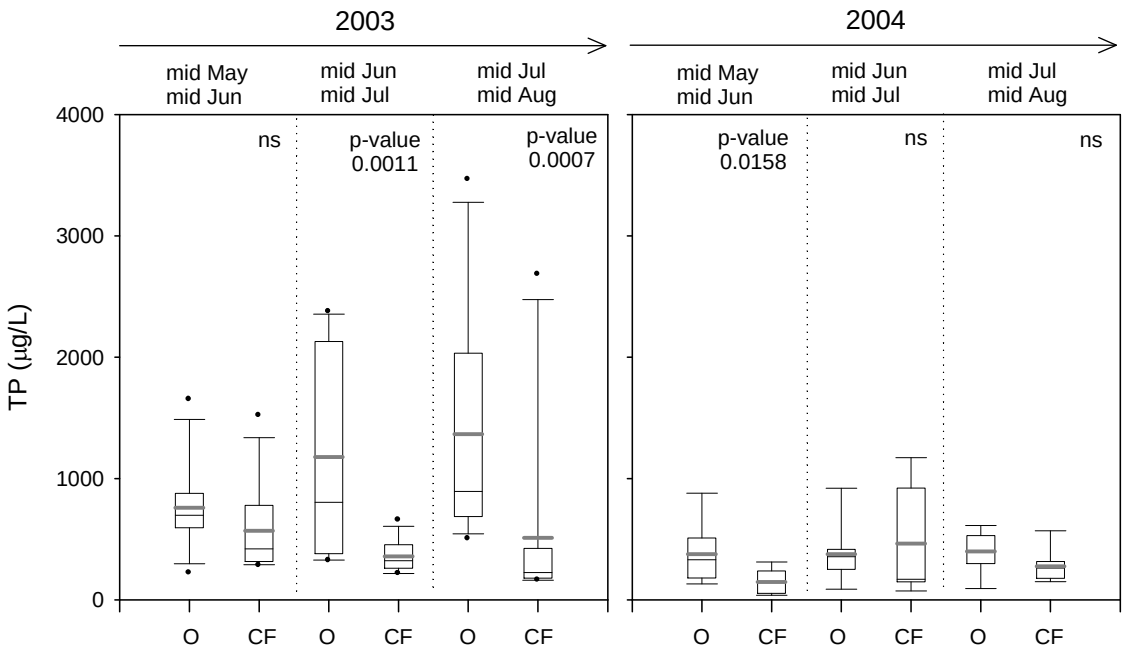

Figure 19. Total P (TP) (µg/L) in carp-accessible (O) and carp-free ponds (CF) in 2003 and 2004. The data used in the derivation of the means for each of the three time periods are independent between successive time intervals. Mid-May to mid-June = weeks 2 - 5; mid-June to mid-July = weeks 6 - 9; mid-June to mid-August = weeks 10 - 13.

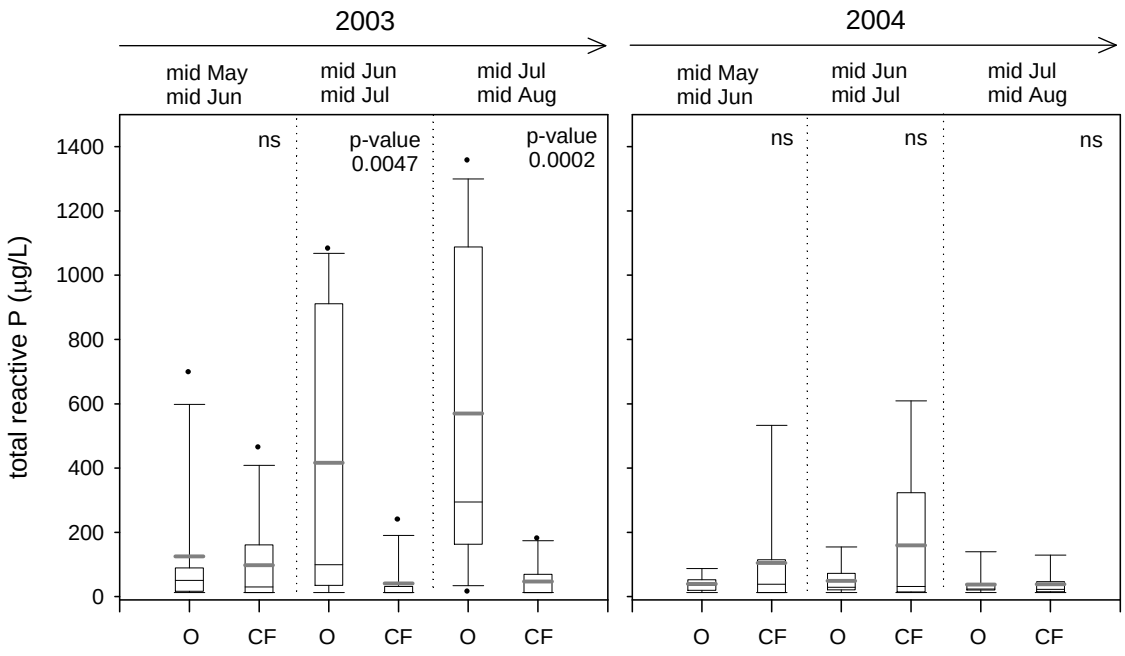

Figure 20. Total reactive P (TRP) (µg/L) in carp-accessible (O) and carp-free ponds (CF) in 2003 and 2004. The data used in the derivation of the means for each of the three time periods are independent between successive time intervals. Mid-May to mid-June = weeks 2 - 5; mid-June to mid-July = weeks 6 - 9; mid-June to mid-August = weeks 10 - 13.

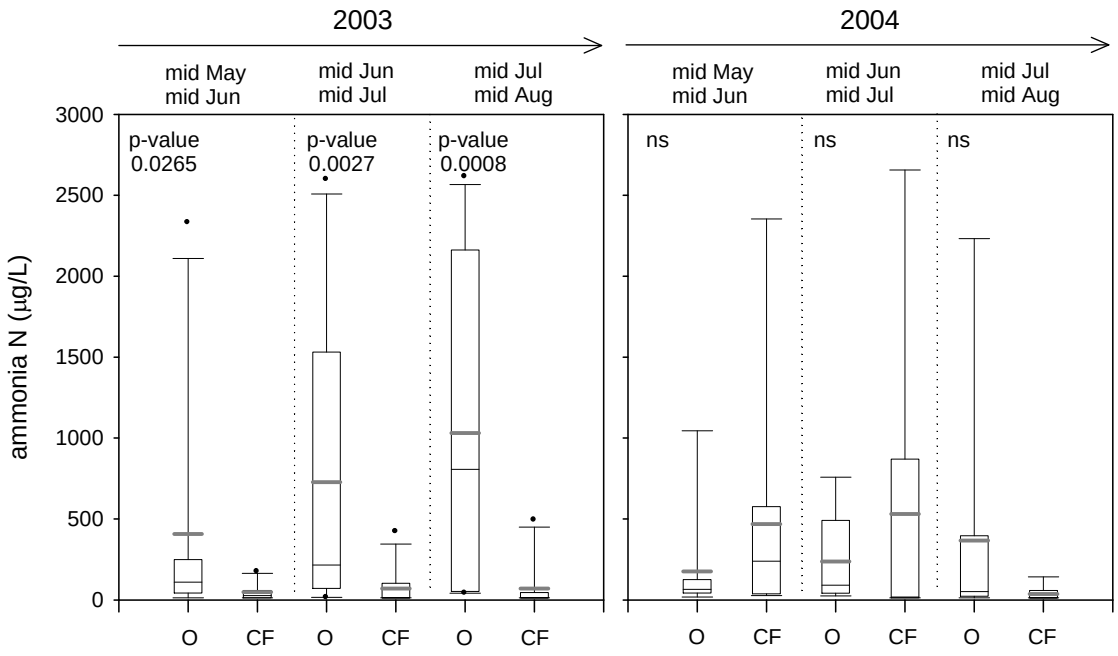

Figure 21. Ammonia-N (μg/L) in carp-accessible (O) and carp-free ponds (CF) in 2003 and 2004. The data used in the derivation of the means for each of the three time periods are independent between successive time intervals. Mid-May to mid-June = weeks 2 - 5; mid-June to mid-July = weeks 6 - 9; mid-June to mid-August = weeks 10 - 13.

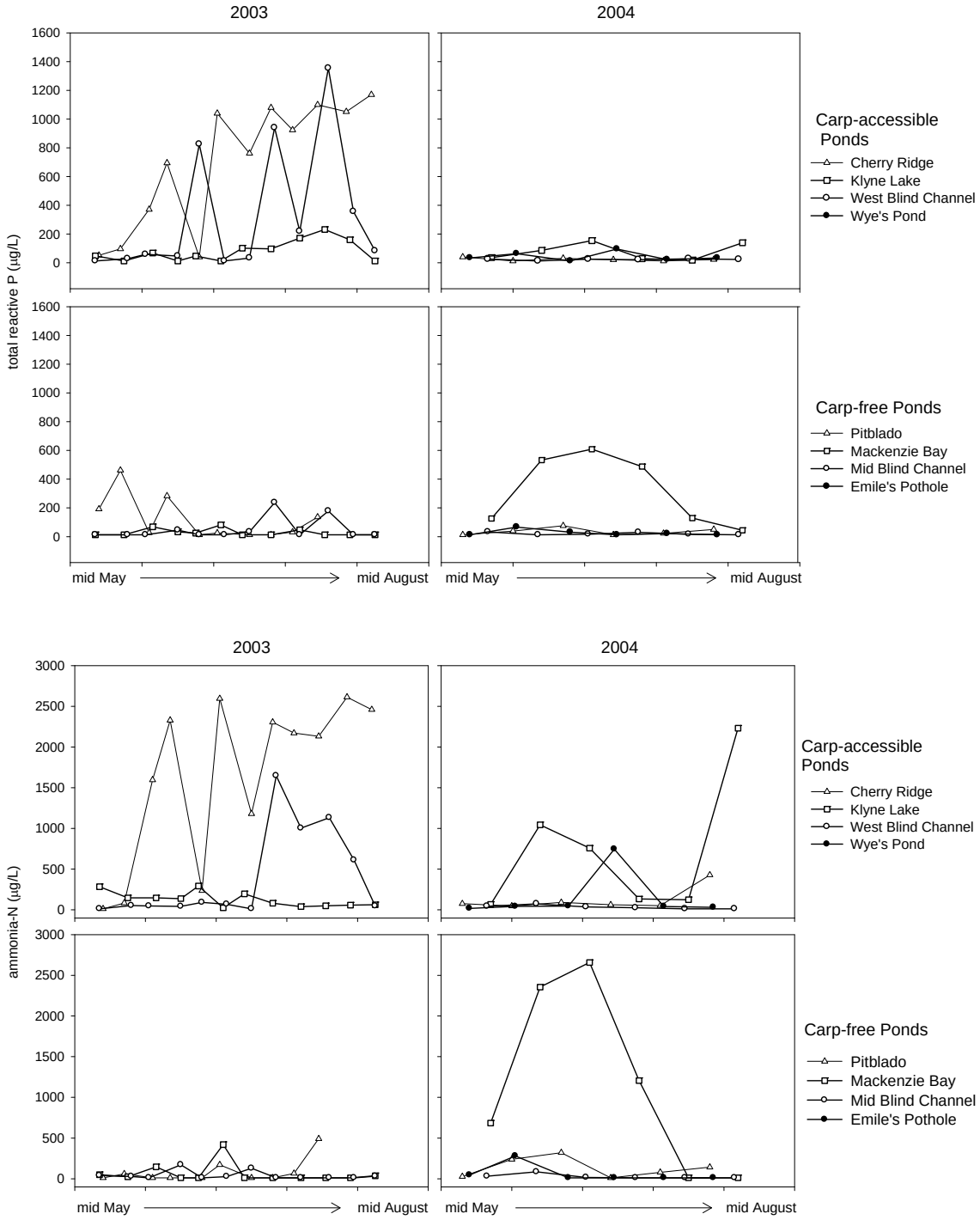

Figure 22. Total reactive phosphorus (TRP) (µg/L) and ammonia-N concentrations (µg/L) in the water column of carp-accessible and carp-free ponds of Delta Marsh, MB, at each sampling event in 2003 and 2004.

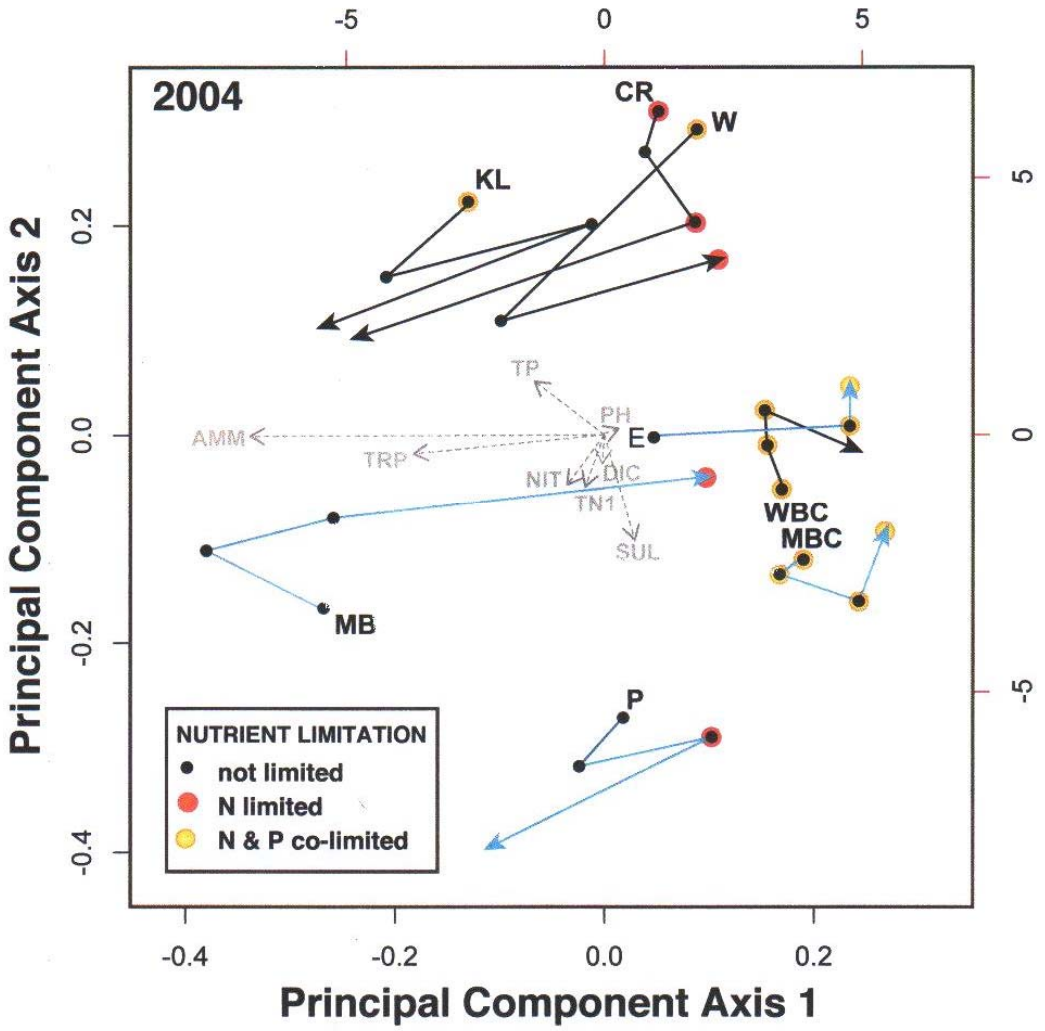

Figure 23. PCA ordination time series model depicting seasonal water nutrient dynamics within ponds sampled in 2004 in Delta Marsh, Manitoba, Canada. Percent variance explained by the first two principal ordination axes is 77.8% and 9.43% respectively. Solid vectors correspond to temporal change within each pond; late May to early August 2004 (solid circles = sample points, arrow = last reading taking at the end of the season). Blue vectors = carp-free pond ponds; black vectors = carp-accessible ponds. Dashed vectors correspond to the 8 fresh water environmental descriptors (eigenvectors): AMM = ammonia-N, TRP = total reactive phosphorus, TP = total phosphorus, DIC = dissolved inorganic carbon, TN = total nitrogen, SUL = sulfate, NIT = nitrate , PH = water pH. All water variables were log transformed (log10(X±1)) except pH. PCA was run in R using the PRINCOM (covariance distance matrix). Nutrient limitations determined from bio-assays are indicated on the diagram; yellow circles indicate the pond was N&P co-limited; red circles indicate N-limitation; and no circle indicates the pond was not limited by N or P. KL = Klyne Lake; CR = Cherry Ridge; WBC = West Blind Channel; MB = Mackenzie Bay; P = Pitblado; MBC = Mid-Blind Channel. Pitblado was sampled only during the first three periods.

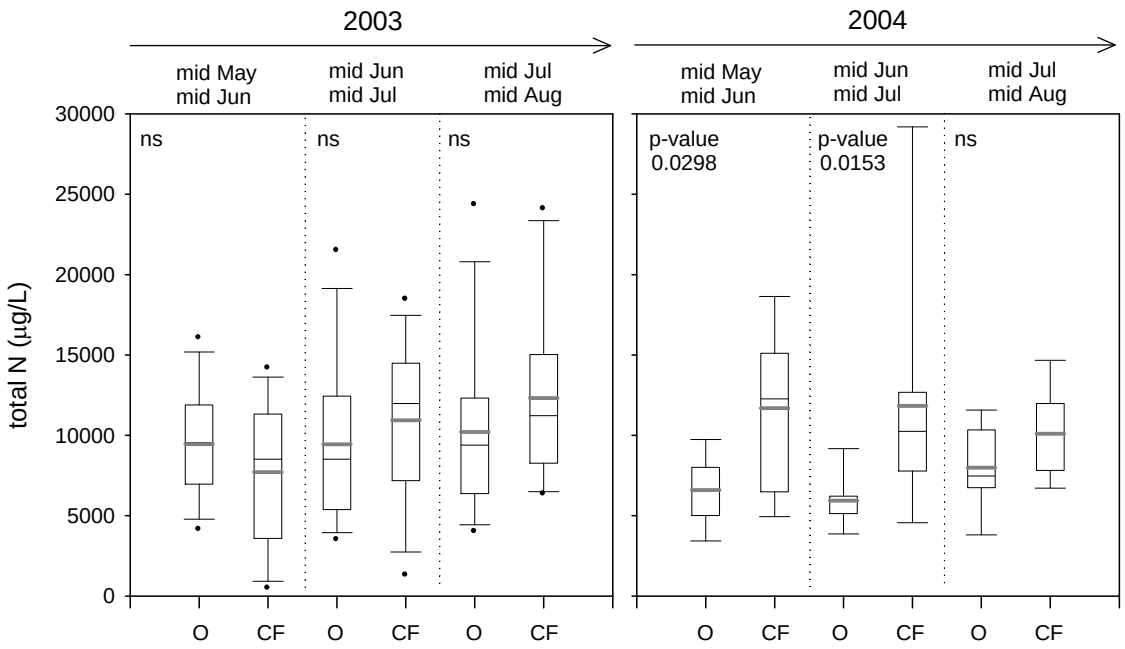

Figure 24. Total N (TN) (µg/L) in carp-accessible (O) and carp-free ponds (CF) in 2003 and 2004. The data used in the derivation of the means for each of the three time periods are independent between successive time intervals. Mid-May to mid-June = weeks 2 - 5; mid-June to mid-July = weeks 6 - 9; mid-June to mid-August = weeks 10 - 13.

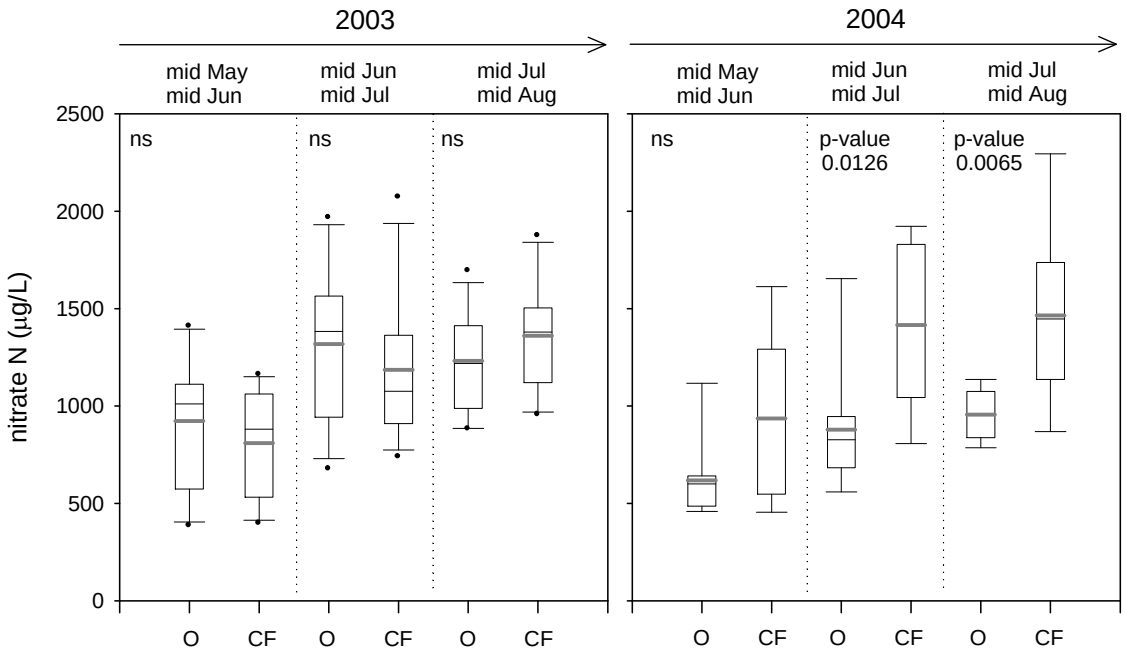

Figure 25. Nitrate-N (μg/L) in carp-accessible (O) and carp-free ponds (CF) in 2003 and 2004. The data used in the derivation of the means for each of the three time periods are independent between successive time intervals. Mid-May to mid-June = weeks 2 - 5; mid-June to mid-July = weeks 6 - 9; mid-June to mid-August = weeks 10 - 13.

Effects of carp on algae and organic suspended solids

Phytoplankton abundance, as measured by chlorophyll *a*, and the concentration of water column organic suspended solids (OSS) were significantly greater in carp-accessible ponds compared to carp-free ponds, particularly early in the summer. Phytoplankton abundance and OSS were significantly greater in carp-accessible ponds in mid-May to mid-June in 2003 and mid-May to mid-July in 2004 (Figure 26 and 27). No statistically significant seasonal trend was found with respect to either phytoplankton abundance or OSS in either year. However, in 2003, there appeared to be a seasonal trend in two of the three carp-accessible ponds. Concentrations of chlorophyll *a* and OSS in Cherry Ridge were reduced from 53 ± 55 μg/L chlorophyll *a* and 19 ± 12 mg/L OSS in mid-May to an average of 16 ± 8 μg/L chlorophyll *a*, 12 ± 6 mg/L OSS from mid-June to mid-August, comparable to that in carp-free ponds (mean range 18 ± 4 μg/L to 48 ± 33 μg/L chlorophyll *a*, 8 ± 3 to 24 ± 16 mg/L OSS). A similar pattern was evident in West Blind Channel, though elevated concentrations of phytoplankton (chlorophyll *a*) and OSS persisted through to July. By contrast, in Klyne Lake, mean chlorophyll *a* and OSS was 152 ± 111 μg/L and 47 ± 37 mg/L, respectively, from mid-June to mid-August, and did not change significantly from the spring. Phytoplankton (chlorophyll *a*) and OSS were not correlated in 2003, though they were positively so in 2004 ($r^2 = 0.72$, $p < 0.0001$).

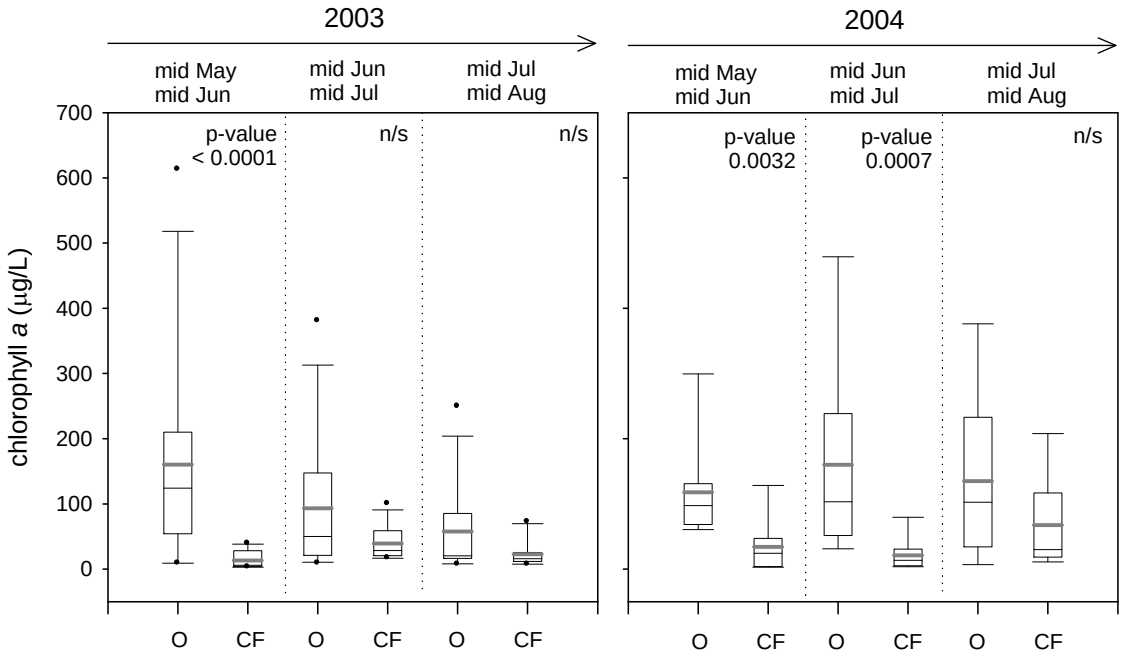

Figure 26. Phytoplankton abundance as measured by chlorophyll *a* (µg/L) in carp-accessible (O) and carp-free ponds (CF) in 2003 and 2004. The data used in the derivation of the means for each of the three time periods are independent between successive time intervals. Mid-May to mid-June = weeks 2 - 5; mid-June to mid-July = weeks 6 - 9; mid-June to mid-August = weeks 10 - 13.

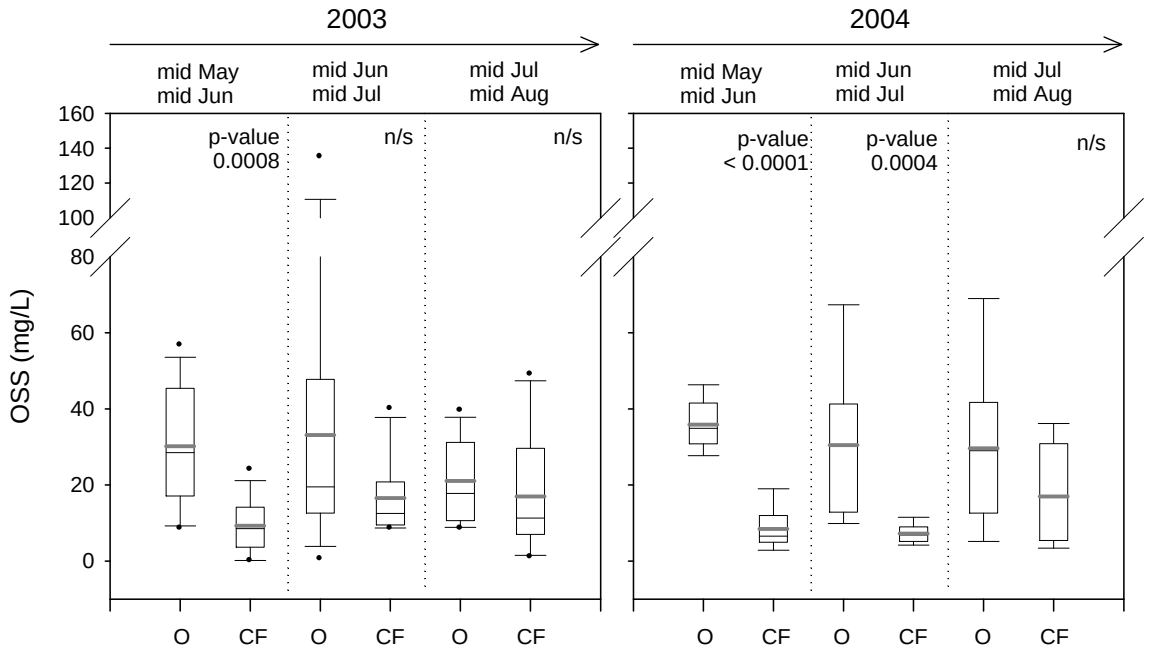

Figure 27. Organic suspended solids (mg/L) in carp-accessible (O) and carp-free ponds (CF) in 2003 and 2004. The data used in the derivation of the means for each of the three time periods are independent between successive time intervals. Mid-May to mid-June = weeks 2 - 5; mid-June to mid-July = weeks 6 - 9; mid-June to mid-August = weeks 10 - 13.

Generally, periphyton grew more abundantly on the NDS controls in carp-accessible ponds than in carp-free ponds in 2003 (Figure 28). Mean chlorophyll *a* growth in sets from mid-June to mid-August in carp-accessible ponds (means ranging from 7.6 to 16.5 $\mu g/cm^2$), were all significantly higher than in carp-free ponds (means range: 0.9 to 1.2 $\mu g/cm^2$) ($p < 0.0001$ in sets 2 and 3 and $p = 0.0081$ in set 4). Periphyton growth in late-May to mid-June in carp-free and carp-accessible ponds was not significantly different. During this period in Mid-Blind Channel (carp-free), mean chlorophyll *a* growth was higher (14.3 $\mu g/cm^2$) than in the other carp-free ponds (0.7 and 0.4 $\mu g/cm^2$) and comparable to periphyton abundance in carp-accessible ponds (Figure 28). During the same period, West Blind Channel (carp-accessible) had the least periphyton growth (2.2 $\mu g/cm^2$) relative to the other carp-accessible ponds in that period (7.6 and 16.3 $\mu g/cm^2$).

Periphyton growth on the NDS controls in carp-accessible and carp-free ponds did not differ significantly in 2004 and shifts in periphyton abundance occurred in some of the ponds from 2003 to 2004. carp-free ponds in which very little periphyton grew on the control in 2003 had significantly more growth in 2004 (Figure 30). In Pitblado, mean periphyton chlorophyll *a* ranged from 0.4 to 0.9 $\mu g/cm^2$ (seasonal mean 0.6 $\mu g/cm^2$) in 2003 and 4 to 14.3 $\mu g/cm^2$ (seasonal mean 8.5 $\mu g/cm^2$) in 2004. Periphytic algal growth on the controls also increased in Mackenzie Bay from 0.7 to 1.6 $\mu g/cm^2$ (seasonal mean 1.3 ug/cm^2) in 2003 to 4.1 to 22.9 $\mu g/ cm^2$ (seasonal mean 10.1 $\mu g/cm^2$) in 2004. In the carp-accessible

pond, West Blind Channel, less periphytic algae grew on the control in 2003 (range = 2.2 to19.6 μg/cm^2; seasonal mean 9.1 μg/ cm^2) than in 2004 (range = 1.02 to 2.5 μg/ cm^2; seasonal mean = 2.3 μg/cm^2). Periphytic algal growth on the controls in Klyne Lake and Mid-Blind Channel did not change significantly between 2003 and 2004. Simple linear regression revealed no correlation between the abundance of periphyton and the mean water column concentrations of TRP (r^2 = 0.3), ammonia-N (r^2 = 0.5) or nitrate-N (r^2 = 0.1) during the corresponding 3-week sets.

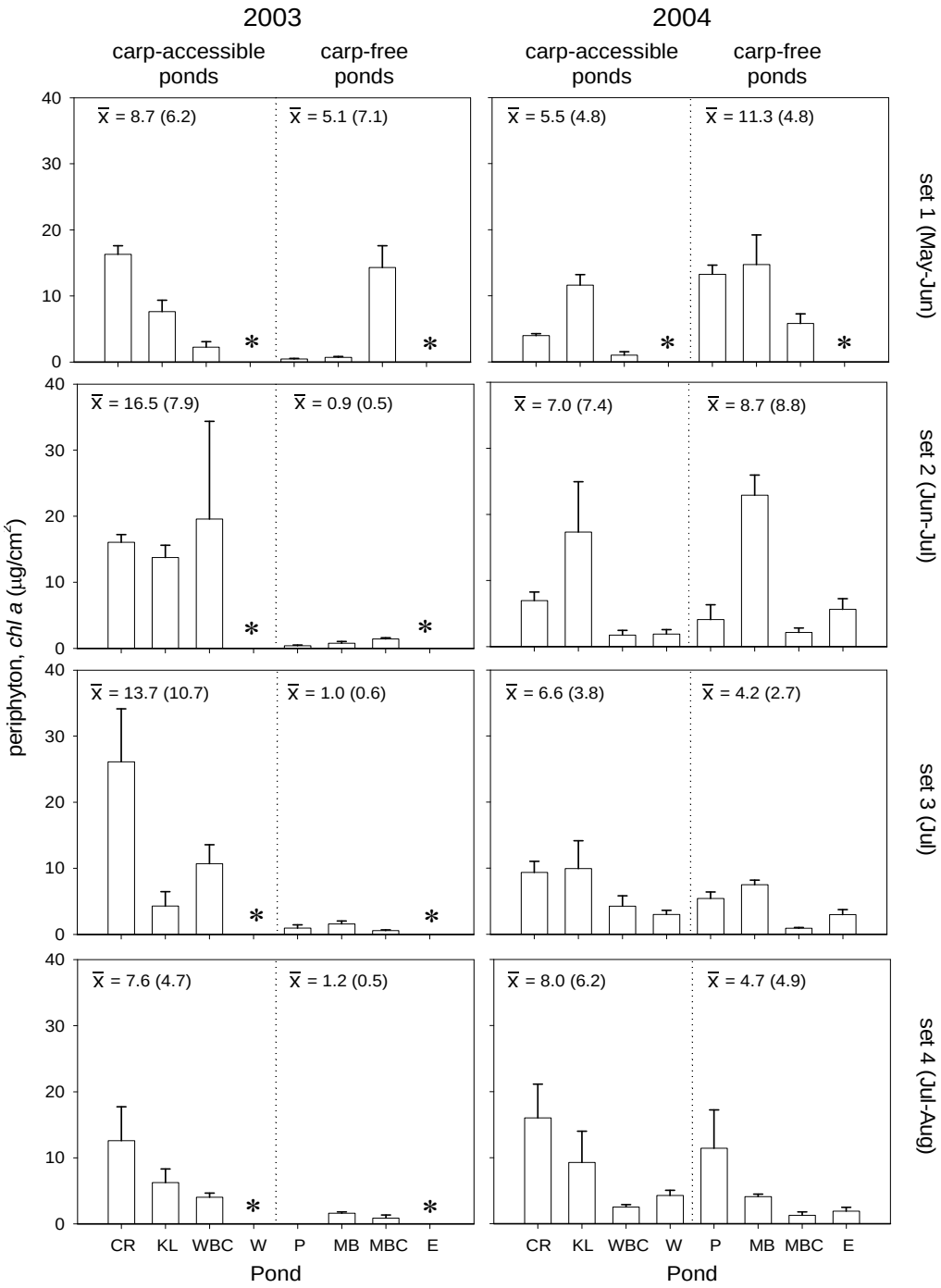

Figure 28. Mean periphyton growth (µg/cm^2) on control treatments of NDS apparati in individual carp-accessible and carp-free ponds of 2003 and 2004 organized by set. carp-accessible ponds (CR - Cherry Ridge; KL - Klyne Lake; WBC - West Blind Channel; W - Wye's Pond). carp-free ponds (P - Pitblado; MB - Mackenzie Bay; MBC - Mid-Blind Channel; E – Emile's Pothole). * indicates no sample taken.

Effects of carp on submerged macrophytes

Though not significantly different as a group, individually most carp-accessible ponds tended to have a low biomass of submerged macrophytes relative to most carp-free ponds in 2003 and 2004 (Figure 29). Biomass of submerged macrophytes in Cherry Ridge, Klyne Lake and West Blind Channel ranged from 0.4 ± 0.3 g/m^2 to 13.2 ± 13.8 g/m^2, (mean 14.5 ± 28.2 g/m^2) in 2003. The biomass of submerged macrophytes in Wye's Pond, consisting entirely of *Stuckenia* sp., was 42 ± 46.8 g/m^2 in 2003. With Wye's Pond included, the mean biomass of carp-accessible ponds was 14.5 ± 19.2 g/m^2. Where vegetation did occur in carp-accessible ponds it was found in small dispersed patches. carp-free ponds also showed a wide range in the abundance of submerged macrophtyes ranging from 2 ± 2.8 g/m^2 in Pitblado to 55.7 ± 50.1 g/m^2 in Mackenzie Bay (mean = 26.1 ± 24.9 g/m^2) in 2003. In 2004, submerged macrophytes was 0 to 7.4 ± 11.2 g/m^2 (mean = 2.4 ± 3 g/m^2) in carp-accessible ponds and 0.26 ± 35 g/m^2 to 34.3 ± 61.4 g/m^2 (mean = 21.5 ± 15.2 g/m^2) in carp-free ponds.

Fewer species of submerged macrophytes were found in carp-accessible ponds relative to carp-free ponds (Table 6). *Stuckenia* sp. was present in all ponds in both years. Where carp-free ponds included as many as six species, carp-accessible ponds had no more than three. *Utricularia macrorhiza* was found only in two carp-free ponds, Pitblado and Emile's Pothole in 2004. It was also

found in East Blind Channel. *Chara* sp. was found only in Pitblado 2004 and in Mid-Blind Channel. *Ceratophyllum demersum* was found in only four ponds, three of which only in small amounts, whereas it was dominant in East Blind Channel. *Myriophyllum sibiricum* was found in most carp-free ponds and in West Blind Channel in small amounts in 2003 and was especially dense in Mackenzie Bay in 2003.

Although not measured in 2003, dense mats of filamentous algae were present in Pitblado and Mackenzie Bay covering about ninety percent of the ponds' surface area (Figure 30 and 31). In 2004, the mats were less dense and found only in patches throughout both ponds. Nevertheless, it accounted for 9 - 81 g/m^2 (mean = 32 ± 34 g/m^2) in Pitblado in 2004 and in one sample in Mackenzie Bay (196 g/m^2, mean = 39 ± 88 g/m^2). Other forms of filamentous algae were also present in other carp-free ponds. This unidentified algae grew close to the sediment surface also in mats. Mid-Blind Channel had 0 - 149 g/m^2 (mean = 42 ± 65 g/m^2) more than the dry weight of the submerged macrophytes collected in the same survey, and in Emile's there was 0 to 20 g/m^2 (mean = 5.5 ± 8.4 g/m^2), about a quarter that of the submerged macrophytes collected.

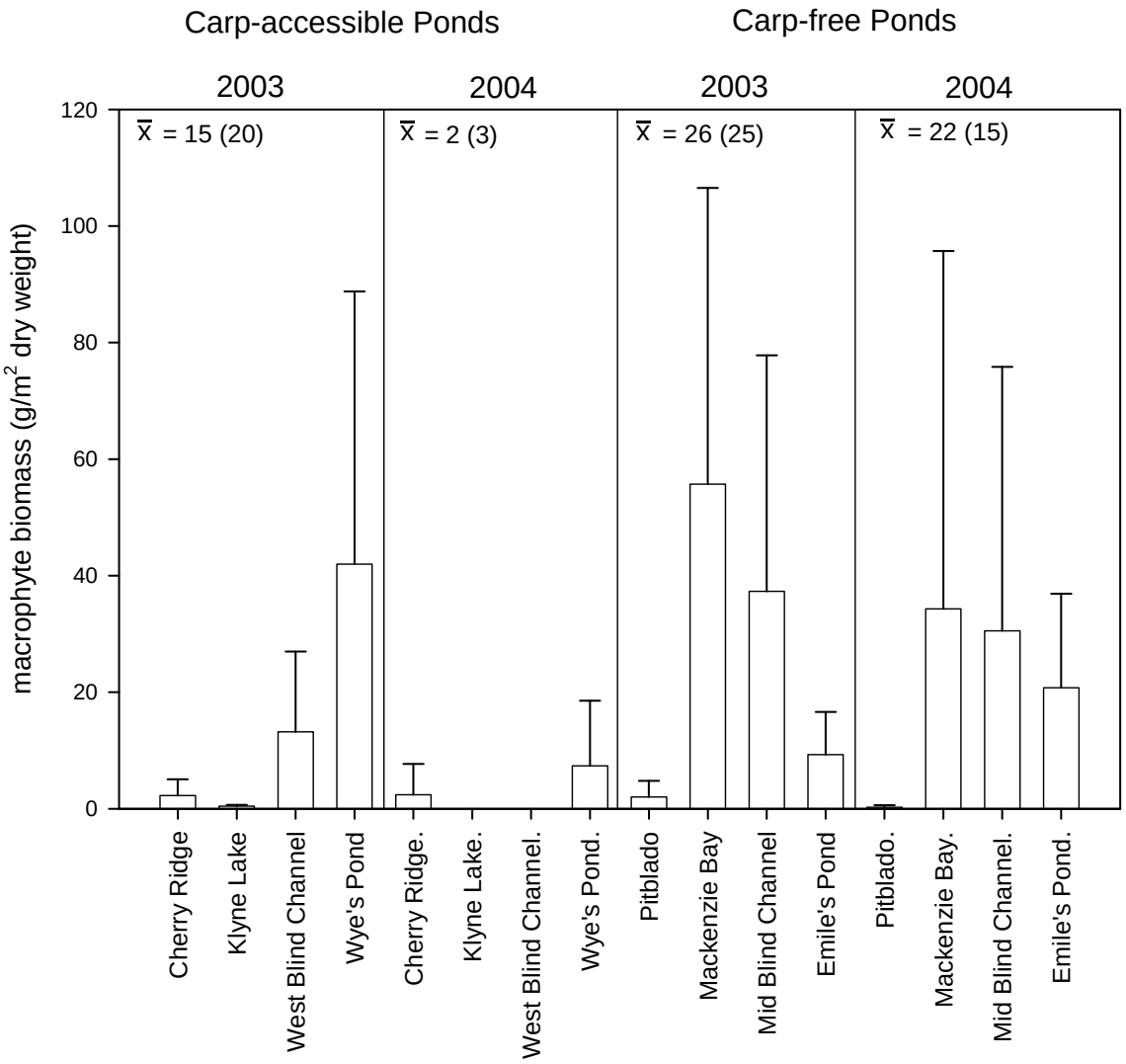

Figure 29. Mean dry biomass of submerged macrophytes (g/m^2) in individual carp-accessible and carp-free ponds from samples collected in late July to early August 2003 and 2004. Standard deviation in brackets.

Table 6. Submerged macrophyte taxa found within study ponds in 2003 and 2004 (Delta Marsh, MB.), including mean dry weight per unit area (g/m2) and standard deviation in brackets. The * indicates taxa which were seen to be present in the ponds but not collected in the macrophyte surveys.

Species	Carp-accessible Ponds								carp-free Ponds								
	Cherry Ridge		Klyne Lake		West Blind Channel		Wye's Pond		Pitblado		Mackenzie Bay		Mid-Blind Channel		Emile's Pothole		East Blind Channel
	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004	2003	2004	2004
Stuckenia sp.	1.96 (2.49)	2.37 (5.31)	0.4 (0.3)	*	5.83 (13.0)	*	41 (46.8)	7.4 (11.2)	2 (2.8)	0.1 (0.1)	0.1 (0.2)	22.1 (49.3)	31.3 (40.4)	21.9 (48.7)	6.8 (9.1)	4.7 (5.9)	1.7 (3.8)
Ceratophyllum demersum	0.05 (0.10)									0.1 (0.1)				*			25.6 (26.6)
Utricularia macrorhiza										*						1.1 (1.8)	0.5 (1)
Myriophyllum sibiricum					2.1 (4.7)					*	55.6 (50.8)	12.2 (16.7)	5.8 (12.6)	8.6 (12)			
Najas flexilis					5.3 (11.4)			0.01 (0.03)		0.1 (0.1)							
Chara sp.										0.1 (0.2)			0.1 (0.2)	*			
Bryophyte													0.2 (0.4)	*	0.4 (0.7)	15 (16.2)	
All taxa mean biomass (g/m2)	2.23 (2.84)	2.37 (5.31)	0.4 (0.3)	0	13.2 (13.8)	0	42 (46.8)	7.4 (11.2)	2.02 (2.76)	0.3 (0.4)	55.7 (50.8)	34.3 (61.4)	37.3 (40.5)	30.5 (45.3)	9.3 (7.3)	20.8 (16.1)	27.8 (27.8)

Figure 30. Dense growth of metaphyton in Pitblado, Delta Marsh, MB., July 2003.

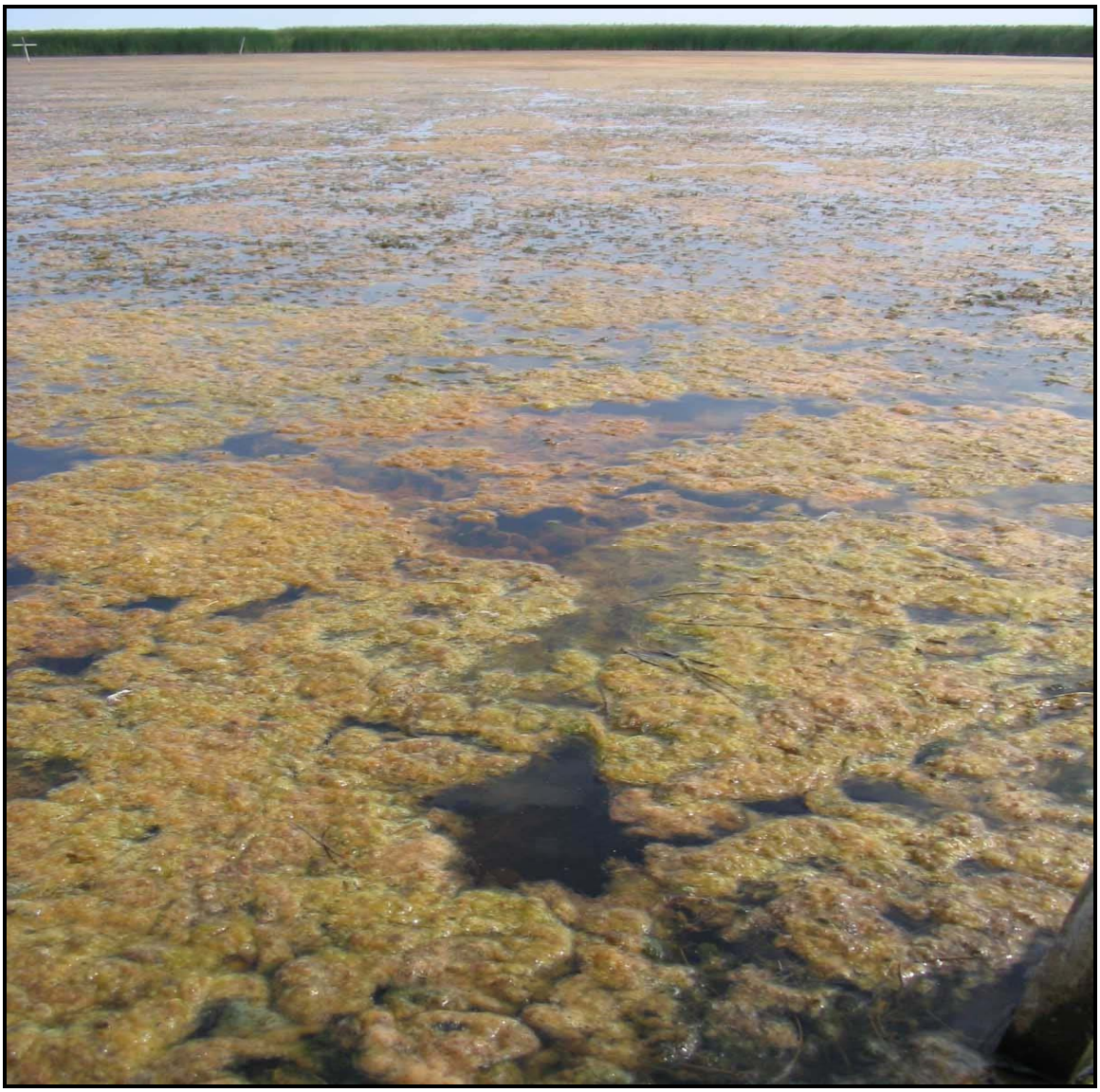

Figure 31. Dense growth of metaphyton in Mackenzie Bay, Delta Marsh, MB., August 2003.

Substrate Characteristics

Although not significant, sediment composition in carp-free ponds differed from carp-accessible ponds in that carp-free ponds had proportionally less sand compared to carp-accessible ponds ($p = 0.0549$) and more silt ($p = 0.0735$) (Figure 32). Percent organic matter of the substrates of carp-accessible and carp-free ponds did not differ significantly (Figure 33). Note that a subset of the ponds were sampled for percent organic matter, Wye's Pond and Emile's Pothole were not included. The highest mean percentage of organic matter was in the substrates of Cherry Ridge, a carp-accessible pond. The lowest, at 15 percent organic matter, was in the screened carp-free pond, Mid-Blind Channel. The other carp-accessible ponds had between 17 and 18 percent organic matter, while carp-free ponds had between of 21 and 27 percent organic matter.

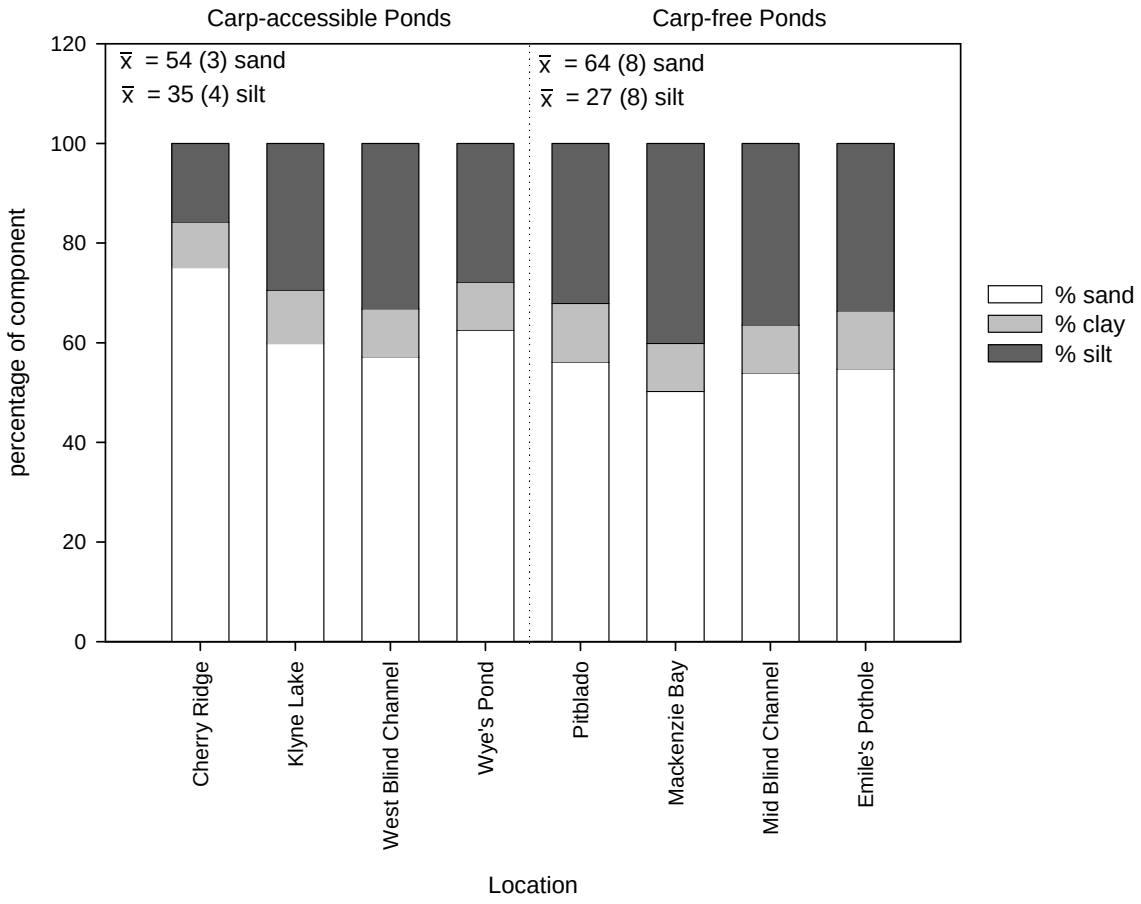

Figure 32. Ratio of inorganic components of pond sediments in Delta Marsh, MB, 2004.

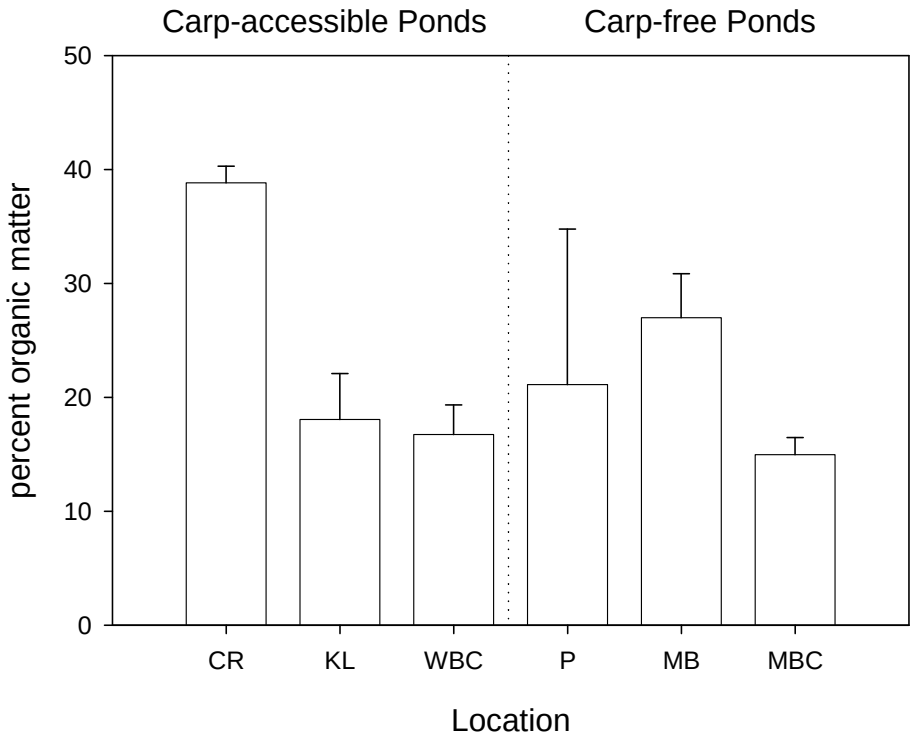

Figure 33. Percent organic matter in upper two centimeters of pond substrates, Delta Marsh, MB, 2004. CR = Cherry Ridge, KL = Klyne Lake, WBC = West Blind Channel, P = Pitblado, MB = Mackenzie Bay, MBC = Mid-Blind Channel, E = East Blind Channel

An Atypical Pond

East Blind Channel was kept separate in the analyses of this study for a number of reasons. Although a few carp were seen in an adjacent and connected pond, Center Marsh (Bortoluzzi, personal communication), they were neither seen nor caught during my study. As such, I could not be certain that carp had used the pond during the sampling period. In addition it was unlike all other ponds, carp-accessible or carp-free, in that it had exceptionally high concentrations of TRP and TP, particularly in sets 2-3 (June through July) and among the lowest concentrations of TIN (ammonia-N and nitrate-N) and TN (Table 7). Combined these resulted in the lowest N:P ratios using either total or inorganic forms of N and P to calculate the ratio of all ponds, it was clearly N-limited according to these ratios (Table 7). Like most carp-free ponds, in East Blind Channel phytoplankton (chlorophyll *a*) was not abundant. The water remained clear throughout the sampling season with among the lowest concentrations of suspended solids and turbidity readings, and there was always sufficient light reaching the sediment surface to permit macrophyte growth. It had among the lowest pH, specific conductivity, chloride and sulfate concentrations (Table 7). It was also the deepest of all the ponds at 82 ± 7 cm compared to the next deepest, West Blind Channel at 65 ± 7 cm. Although it did not have the greatest mean density of submerged macrophytes among the ponds in the study (Table 7), it was comparable to other carp-free ponds, except that the community was dominated by *Ceratophylum demersum* (Table 6).

Table 7. Seasonal means and range of values of 18 parameters in East Blind Channel compared to the ponds of Delta Marsh, used in this study in 2004.

		East Blind Channel	**Other ponds (n=8)**
parameter	units	Mean (min – max)	Mean (min - max)
TP	μg/L	2,428 (281 – 3,554)	343 (38 – 1,171)
TRP	μg/L	1061 (618 – 1,215)	71 (<25 – 609)
TN	μg/L	7,594 (1,974 – 19,464)	9,423 (3,426 – 29,189)
ammonia-N	μg/L	59 (<25 – 295)	339 (<25 – 2656)
nitrate-N	μg/L	638 (393 – 971)	1,063 (455 – 2,294)
TIN:TRP	–	<1 (<1 – 20)	43 (6 – 155)
TN:TP	–	12 (<1 – 69)	45 (8 – 280)
pH	–	8.1 (7.8 – 8.5)	8.5 (7.8 – 9.5)
dissolved inorganic carbon	mg/L	76 (57 – 94)	86 (50 – 146)
specific conductance	μS	1,086 (878 – 1,273)	2,486 (1,573 – 4,067)
sulfate	mg/L	83 (50 – 116)	362 (124 – 848)
chloride	mg/L	101 (56 – 137)	487 (173 – 1,212)
turbidity	NTU	8 (5 – 13)	18 (6 – 56)
TSS	mg/L	2 (1 – 3)	32 (23 – 122)
OSS	mg/L	2 (1 – 3)	20 (3 – 69)
ISS	mg/L	<1 (0 – <1)	12 (0 – 73)
phytoplankton (*chl a*)	μg/L	10 (6 – 18)	81 (3 – 479)
Mean biomass submerged vegetation	g/m^2 dry weight	28	12 (0 – 34)

Effects of carp on nutrient limitation within ponds

There appeared to be a clear relationship between nutrient limitation as determined by NDS assays to periphyton and the accessibility of ponds to carp in 2003, but not in 2004 (Figure 34); however, there was no clear seasonal pattern (Table 5). In general N and P co-limitation of periphyton occurred exclusively in carp-free ponds in 2003, comprising 73 % of all the NDS sets over the summer. By contrast, N and P co-limitation occurred in 40 % of the NDS sets in both carp-accessible and carp-free ponds in 2004. The two connected ponds, West Blind Channel (carp-accessible) and Mid-Blind Channel (carp-free) were limited by both N and P throughout the sampling period in 2004 (Figure 23). N and P co-limitation also occurred in spring in the carp-accessible ponds, Klyne Lake and Wye's Pond, and in the latter half of the summer in Emile's Pothole (carp-free). N-limitation of periphyton was more common in carp-accessible ponds than in carp-free ponds (50 % vs. 9 % of the NDS sets) in 2003. N-limitation occurred in only two NDS sets among the carp-free ponds: in June in Mid-Blind Channel and in August in Mackenzie Bay. In 2004 N-limitation was less common in carp-accessible ponds than in 2003 (20 % vs. 50 % of the NDS sets), occurring in two of the four sets in Cherry Ridge, at the end of the summer in Wye's Pond. The lack of nutrient limitation to periphyton was more common in carp-accessible ponds in 2003 (50% vs. 18%) occurring at various times throughout the sampling period in the individual ponds. In 2004 the lack nutrient limitation was common in both carp-accessible and carp-free ponds (40 % and 47 % of the NDS sets, respectively). While it occurred mainly in the early portion of the summer in

carp-free ponds, in carp-accessible ponds it tended to occur from mid-June to mid-August.

There was no clear relationship between nutrient limitation of periphyton and mean water column nutrient concentrations in this study. Principal component analysis of the nutrient limitations of periphyton in relation to corresponding nutrient concentrations in the water column of the ponds showed that where periphyton was co-limited by N and P the water column tended to be low in concentrations of all forms of N and P, particularly ammonia-N in 2003 (Figure 18). However, in 2004 there was at least one instance (Klyne Lake in May/June) in which TP was high (Figure 23). N-limitation seemed to correspond to low levels of ammonia-N and TRP, in 2004, but not in 2003 where water column nutrients of N and P were both high and low (Figure 18 and 23). No nutrient limitation of periphyton seemed to correspond with higher amounts of nutrients in the water column as they are mainly gathered at the left hand side of the ordination bi-plot (Figures 18 and 23).

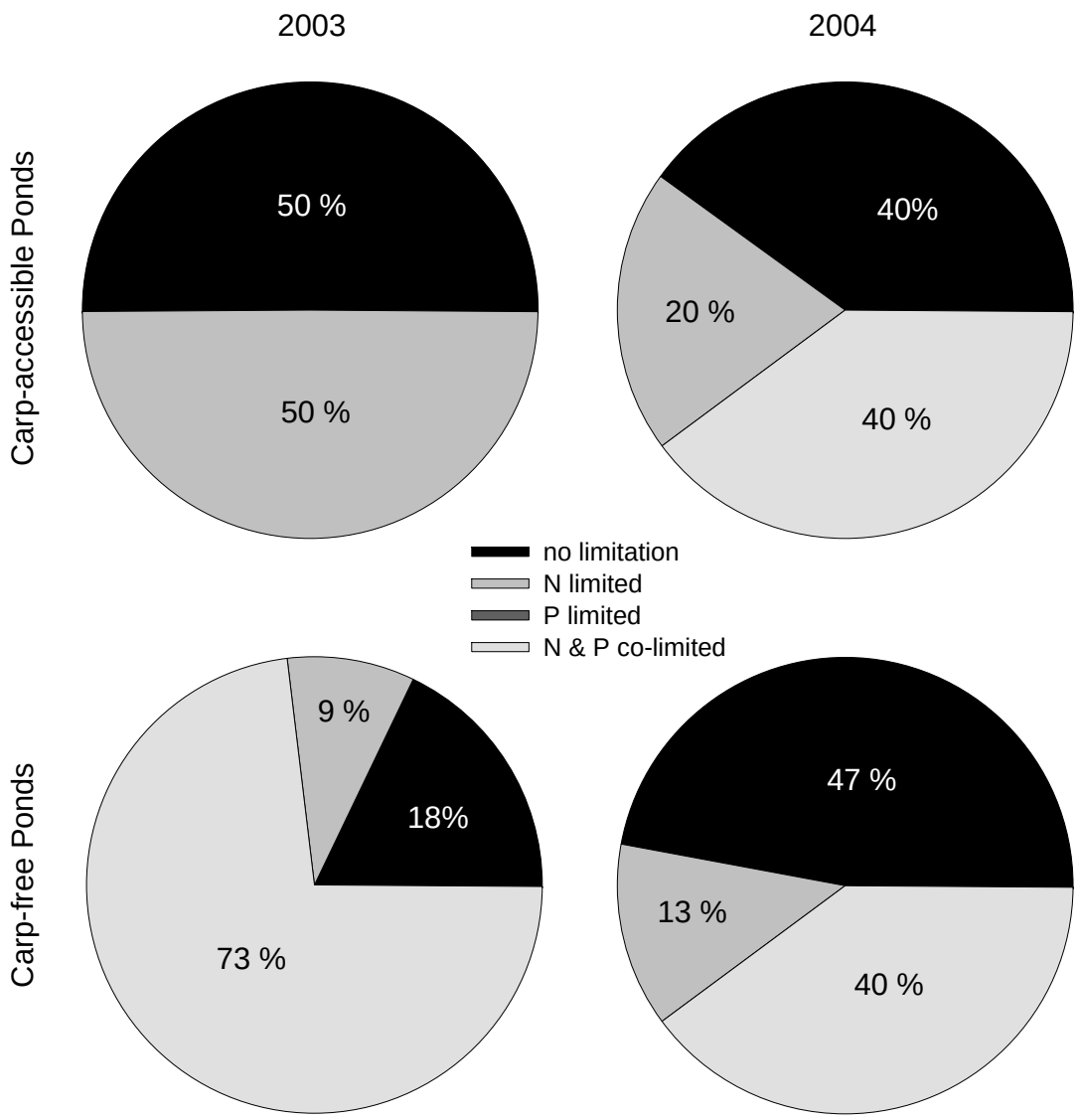

Figure 34. Percentage of sets in carp-accessible and carp-free-ponds limited by nitrogen (N), phosphorus (P), nitrogen and phosphorus (N and P) co-limited or not limited by either N or P in 2003 and 2004. There were four consecutive NDS sets per pond over the sampling season with the exception of Wye's Pond and Emile's Pothole which each had three sets in 2004; totaling 12 NDS sets in carp-accessible and 12 NDS sets in carp-free ponds in 2003 and 15 NDS sets each in carp-accessible and carp-free ponds of Delta Marsh, MB in 2004.

Table 8. N and P limitation of periphyton (as per NDS assays) in four consecutive three week sets over the sampling season (May to August) in carp-accessible and carp-free ponds in Delta Marsh, MB., 2003 and 2004. The dash indicates that the NDS apparatus was not deployed in the pond.

	Pond	Year	Spring	----------	--------→	Autumn
Carp-accessible	Cherry Ridge	2003	O	N	O	O
	Klyne Lake	2003	N	O	N	N
	West Blind Channel	2003	N	O	O	N
	Cherry Ridge	2004	N	O	N	O
	Klyne Lake	2004	N&P	O	O	O
	West Blind Channel	2004	N&P	N&P	N&P	N&P
	Wye's Pond	2004	-	N&P	O	N
Carp-free	Pitblado	2003	N&P	N&P	N&P	-
	Mackenzie Bay	2003	N&P	N&P	N&P	O
	Mid-Blind Channel	2003	O	N	N&P	N&P
	Pitblado	2004	O	O	N	O
	Mackenzie Bay	2004	O	O	O	N
	Mid-Blind Channel	2004	N&P	N&P	N&P	N&P
	Emile's Pothole	2004	-	O	N&P	N&P
Atypical Pond	East Blind Channel	2004	N	N&P	N	N

Mean TN:TP molar ratios corresponding to the time in which the NDS were deployed within carp-accessible ponds were significantly lower compared to carp-free ponds in both 2003 and 2004 ($p < 0.0001$ and $p < 0.0001$ respectively) (Figure 35). As a group carp-accessible ponds in 2003 exhibited TN:TP ratios closer to the Redfield Ratio of 16:1 (mean = 28 ± 11) than carp-free ponds (mean = 74 ± 28), becoming increasingly lower as the season progressed (Figure 35). In 2004, the mean TN:TP ratio among carp-accessible ponds was higher than in 2003 at 56 ± 28 compared to 2003 and lower than carp-free ponds of 2004 (mean = 134 ± 70). N-limitation was evident in Cherry Ridge in 2003.

Molar ratios of TIN:TRP were generally lower in carp-accessible ponds compared to carp-free ponds in 2003 (Figure 35). The difference was significant only in 2003 ($p = 0.0056$) where the mean TIN:TRP ratio was 120 ± 54 in carp-free ponds compared to 55 ± 48 in carp-accessible ponds. TIN:TRP varied considerably within the treatment groups (carp-accessible and carp-free) in both years. In 2003, Cherry Ridge (carp-accessible), the pond water was limited by N for the latter half of the summer. Klyne Lake tended to have higher TIN:TRP ratios as compared to the other ponds in 2003 but not in 2004. N-limitation was evident in Cherry Ridge in the latter half of the summer in 2003, and in Mackenzie Bay in 2004.

No significant differences were observed among the nutrient limitations of periphyton when comparing their corresponding mean chemical N:P (total and

inorganic) ratios per set in 2003 and 2004, using a oneway ANOVA. Superimposing NDS-derived nutrient limitations on corresponding individual N:P molar ratio set means in each pond emphasizes the absence of a relationship between molar N:P ratios and nutrient limitations to periphyton (Figure 35). On a superficial level the results from the NDS and TN:TP seem to agree, carp-accessible ponds in 2003 were indeed either N-limited or not limited. The NDS indicated that the majority of carp-free ponds in 2003 were N and P co-limited. This is supported in part by the elevated set means of TN:TP. In 2004 the NDS suggest carp-accessible and carp-free ponds were N and P co-limited about half the time, with a few N-limited. However, upon closer inspection the NDS-derived nutrient limitations did not match up to individual set means of TN:TP (Figure 35). Examples include: 1) Cherry Ridge 2003 where the set means of TIN:TRP from July and August (NDS sets 3 and 4) indicated that the ponds were N-limited (8 ± <0.9), yet the NDS indicated no nutrient limitation, and 2) Cherry Ridge 2004 NDS set 3 (July), was clearly N-limited according to the NDS results, yet the total and inorganic nutrient molar ratios were well above the 16:1 ratio (138 ± 81 and 101 ± 65).

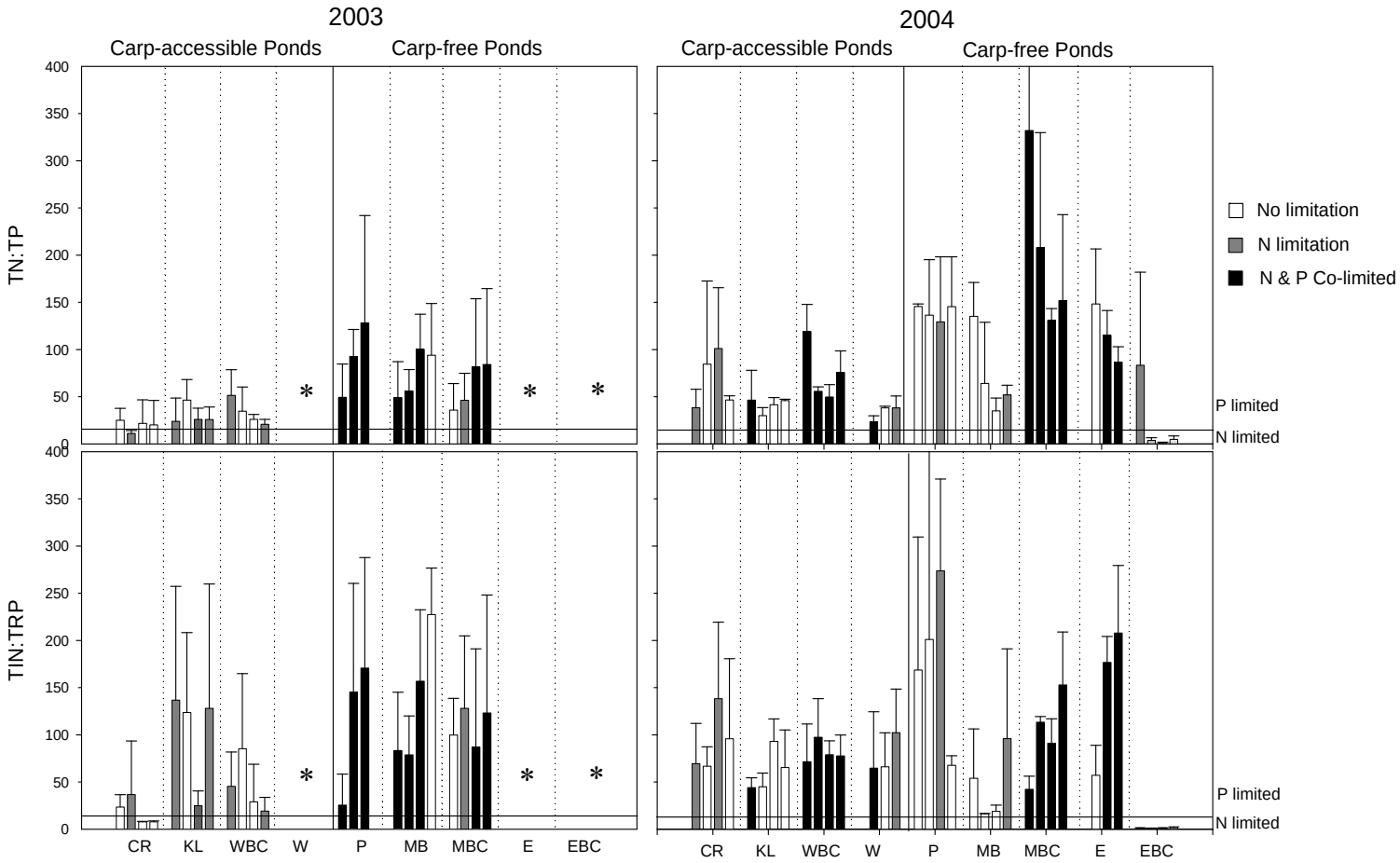

Figure 35. Mean N:P molar ratios corresponding to set periods of the NDS using total nitrogen and phosphorus (TN:TP) and inorganic nitrogen and total reactive phosphorus (TIN:TRP) in carp-accessible and carp-free ponds of Delta Marsh, MB In 2003 and 2004. Superimposed on the individual sets per pond are the NDS derived nutrient limitations. CR = Cherry Ridge, KL = Klyne Lake, WBC = West Blind Channel, W = Wye's, P = Pitblado, MB = Mackenzie Bay, MBC = Mid-Blind Channel, E = Emile's and EBC = East Blind Channel. * indicates no sample take

There were a number of significant differences among the seasonal means of biotic and abiotic parameters of the carp-accessible and carp-free ponds between 2003 and 2004 (Table 9 and 10). The water temperature in both carp-accessible and carp-free ponds was greater in 2003 than in 2004 by 4°C and 5°C, respectively. The specific conductance of the water column and the concentration of chloride were greater in 2003 than in 2004 and the concentration of sulfate was lower in carp-free ponds alone. The water column of carp-free ponds was also shallower in 2003, differing by 18 cm (seasonal mean). The concentration of ammonia-N in carp-free ponds was greater in 2004 than in 2003, by virtue of Mackenzie Bay which exhibited high ammonia-N throughout most of the summer relative to the other carp-free ponds in the study in 2004. Among carp-accessible ponds concentrations of P (total and reactive) and nitrate-N in the water column were significantly greater in 2004 compared to 2003. This is especially true of TRP which was very high two of the three carp-accessible ponds in 2003.

Overall, the 2003 growing season was warmer and drier than in 2004 (Figure 36 and 37). The seasonal average mean daily temperature, average daily maximum temperature and average daily minimum temperature was 3.7°C , 4.6°C and 2.9°C greater, respectively than in 2004. From May to August of 2004, 278.4 mm of precipitation fell compared to 195.6 mm in 2003, a difference of 84 mm overall.

May, July and August all received less than half amount of rain in 2003 than in 2004. June of 2003 was the exception with 98 mm of precipitation compared to 27.4 mm in 2004. Approximately half the total precipitation for the 2003 sampling season fell in the month of June, during several small events and two larger events of 30.2 mm on June 06 and 18.6 mm June 25.

Table 9. Summary of variables in which the seasonal means were significantly different between 2003 and 2004 in carp-accessible ponds of Delta Marsh, MB. Only data from ponds that were studied in both 2003 and 2004 were used in the analysis (Cherry Ridge, Klyne Lake and West Blind Channel). Comparisons were made using a one-way ANOVA, with level of significance $p < 0.05$.

CARP-ACCESSIBLE PONDS						seasonal mean (standard deviation)	
variable	unit				*p-value*	2003	2004
water temperature	°C	2003	➤	2004	0.0038	22 (3)	18 (5)
specific conductance	μS	2003	➤	2004	0.0040	2425 (327)	2070 (387)
chloride	mg/L	2003	➤	2004	<0.0001	582 (125)	334 (75)
dissolved inorganic carbon	mg/L	2003	➤	2004	0.0006	97 (18)	75 (16)
nitrate-N	μg/L	2003	➤	2004	0.0018	1159 (320)	841 (294)
total P	μg/L	2003	➤	2004	<0.0001	1083 (747)	371 (239)
total reactive P	μg/L	2003	➤	2004	0.0138	336 (450)	41 (42)

Table 10. Summary of variables in which the seasonal mean were significantly different between 2003 and 2004 in carp-free ponds of Delta Marsh, MB. Only data from ponds that were studied in both 2003 and 2004 were used in the analysis (Pitblado, Mackenzie Bay and Mid-Blind Channel). Comparisons were made using a one-way ANOVA, with level of significance $p < 0.05$.

CARP-FREE PONDS						seasonal mean (standard deviation)	
variable	unit				*p-value*	2003	2004
water temperature	°C	2003	➤	2004	0.0012	23 (3)	18 (4)
depth of water column	cm	2003	➤	2004	<0.0001	35 (10)	53 (9)
specific conductance	μS	2003	➤	2004	0.0131	3569 (608)	3095 (488)
chloride	mg/L	2003	➤	2004	0.0048	961 (248	710 (266)
sulfate	mg/L	2003	➤	2004	0.0026	341 (145)	528 (201)
dissolved inorganic carbon	mg/L	2003	➤	2004	0.0135	85 (21)	103 (19)
ammonia-N	μg/L	2003	➤	2004	0.0365	54 (102)	440 (813)

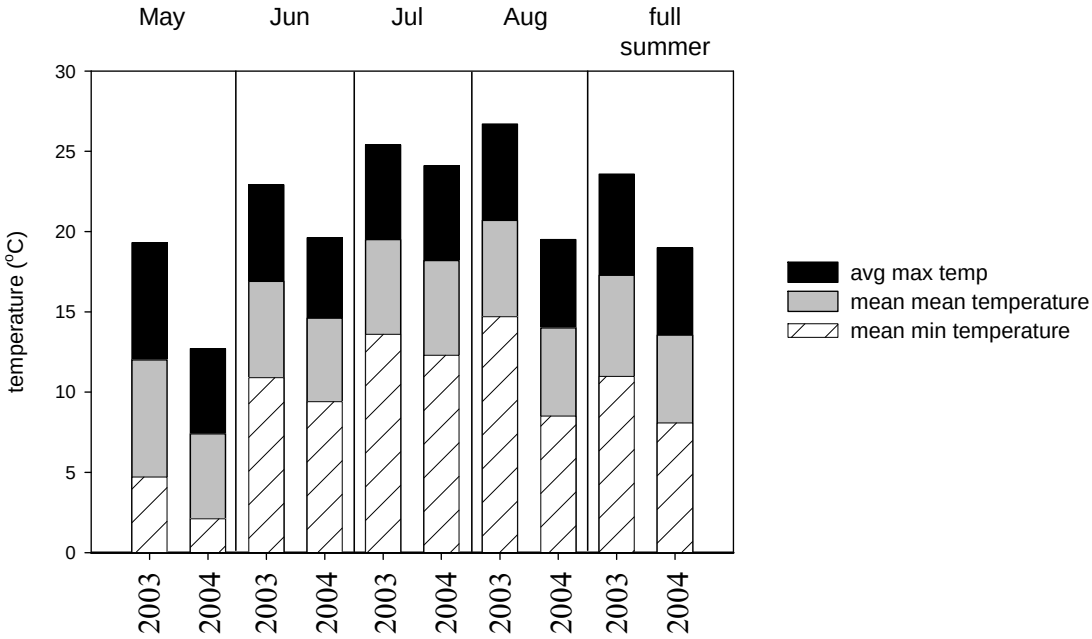

Figure 36. Mean maximum, mean and minimum temperatures per month and for the full summer of 2003 and 2004, Delta Marsh, MB.

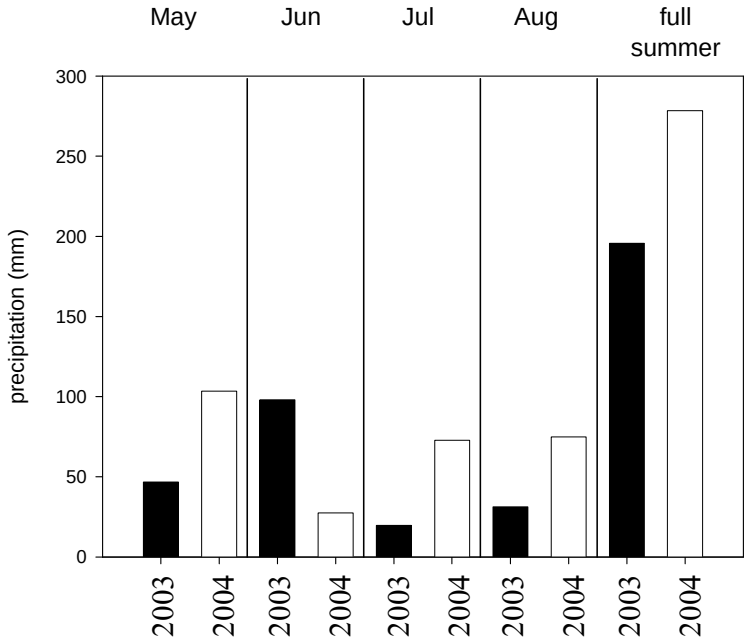

Figure 37.Total precipitation per month (mm) and for the full summer of 2003 and 2004, Delta Marsh, MB.

Discussion

My study was an extension of Hnatiuk's (2006) research, in that some of the ponds studied here were used in her original study. Here is presented a discussion of the state of carp-accessible and carp-free ponds in both studies in addition to changes that occurred two and three years following alteration of the carp-accessibility of Wye's Pond, Pitblado and Mid-Blind Channel.

Effects of carp on water clarity: turbidity, total suspended solids, phytoplankton abundance

I hypothesized that water column turbidity would be greater in ponds to which carp had access compared to ponds in which carp did not have access. Through the act of feeding and spawning by carp, sediments would be suspended in the water column resulting in increased ISS concentrations where carp were present. Additionally, OSS would also increase either through the entrainment of sediment associated algae into the water column or in the form of phytoplankton blooms which would grow in response to nutrients released from the disturbed sediments or by waste excretion.

The results of my study support the hypothesis that where carp were present turbidity, TSS and phytoplankton concentrations were greater than in carp-free ponds. Similar to Hnatiuk's (2006) findings, with few exceptions, turbidity, the concentration of TSS and phytoplankton abundance were greater and calculated photic zone depths were shallower in ponds accessible to carp. Like Hnatiuk

(2006), I found that water column TSS and ISS were greatest in the spring in carp-accessible ponds. Unlike Hnatiuk's findings in which phytoplankton also showed a seasonal trend, I found that, with two exceptions in 2003, turbidity, OSS and phytoplankton abundance did not decrease with declining carp abundance towards the latter half of the summer in carp-accessible ponds.

This study provides evidence in agreement with mesocosm studies that the magnitude of the effects of carp on phytoplankton, turbidity and concentrations of suspended solids within the ponds may be dependant upon the density/biomass of carp (e.g., Bruekellar et al. 1994; Badiou 2005). Removal of carp from Mid-Blind Channel in the spring of 2002 resulted in increased water column clarity, including a reduction in phytoplankton abundance (Hnatiuk 2006). This state was maintained in 2003 and 2004. In the spring of 2002, a channel was created permitting carp to access South Mackenzie Bay. Prior to channel creation, South Mackenzie Bay was macrophyte-dominated and the water column was clear (Hnatiuk 2006). In 2002, water column turbidity, TSS and phytoplankton abundance increased substantially, and the plants disappeared. Conversely, upon connection of Wye's Pond to the main marsh, turbidity, TSS and phytoplankton abundance, as measured by chlorophyll *a* did not increase in response to carp-accessibility in the first year. Hnatiuk (2006) proposed the lack of carp effect in the year of the pond's alteration was due to unintended circumstances of carp accessibility to the pond. Specifically, carp were frequently seen in the pond in the baseline year due to temporary access caused by high water levels. This may have resulted in higher turbidity and phytoplankton

abundance than would be expected in a truly isolated pond. Additionally, the connection of Wye's Pond to the main marsh was delayed, having occurred in mid-June of 2002. As a result, adult carp were not present during the peak spawning period and were observed in the pond infrequently thereafter. Unlike circumstances in Wye's Pond, carp were found in large numbers in South Mackenzie Bay, particularly in the spring when they were spawning (Hnatiuk 2006). Although no changes were observed in 2003 in Wye's Pond, after two years of being accessible to carp, turbidity, total suspended solids and the abundance of phytoplankton were greater in Wye's Pond in 2004 compared to the first two years of the study. This suggests that in order for carp to have a significant impact on water clarity it is important that they are present in the spring during spawning season when they congregate in high densities. In most of the carp-accessible ponds in my study, water clarity was less than in the carp-free ponds and phytoplankton concentrations greater. In these ponds, carp were frequently seen throughout the majority of the summer. At Cherry Ridge, however, turbidity, TSS (both organic and inorganic), calculated photic zone depth and phytoplankton abundance were comparable to that of isolated ponds throughout the mid-summer months of 2003. Carp used the pond infrequently and in small numbers until the beginning of July, after which they were not observed. Similarly, in West Blind Channel higher concentrations of TSS and phytoplankton occurred in the spring when carp were present in their greatest numbers, declining in the latter half of the summer when carp were rarely seen in the pond.

Abundant macrophytes in carp-accessible ponds can mitigate the effect of carp on turbidity by reducing the amount of suspended sediment and phytoplankton in the water column. Phytoplankton abundance in the water column may be suppressed either through the reduction of suspended sediments facilitating nutrient release or by direct competition for nutrients (Roberts et al. 1995). An abundance of submerged macrophytes grew in North School Bay, Delta Marsh, in 2001 and 2002, despite the presence of carp (Hnatiuk 2006). In this pond, phytoplankton abundance, turbidity and ISS concentrations were comparable to those in carp-free ponds and lowest among carp-accessible ponds in Hnatiuk's (2006) study. Similarly, Badiou (2005) also found that where submerged macrophytes were abundant, phytoplankton growth as well as turbidity were suppressed in a large wetland cell (5 - 7 ha), stocked with 1200 kg/ha of carp.

The response of phytoplankton to carp-induced nutrient loading may not be apparent due to top-down effects. Studies have found that grazing pressure by zooplankton can suppress chlorophyll *a* concentrations in the presence of high concentrations of nutrients, even in the presence of carp (Parkos III et al. 2003; Khan 2003; Coops and Havens 2005). Unlike other carp-accessible ponds in 2003 and 2004, in which phytoplankton concentrations remained elevated throughout the summer months, phytoplankton concentrations in Cherry Ridge and West Blind Channel were low, particularly from mid-summer on, similar to that of carp-free ponds. Submerged macrophytes were not abundant and therefore could not have acted to suppress phytoplankton growth. Furthermore, available nutrients were abundant in these ponds in 2003 and readily available

for assimilation by phytoplankton. I propose that abundant zooplankton observed in the ponds during this period may have played a key role in the suppression of phytoplankton growth and subsequent clearing of the water column.

Sediment resuspension by wind may be important in the deterioration of water clarity when water levels in wetlands are low, whether or not carp are present. In a recent study researching the effects of water level fluctuations in a boreal wetland in Manitoba, Watchorn (2010) found that wind-induced sediment resuspension was likely to occur at approximately 40 cm in a boreal wetland in Manitoba. In this study, high levels of turbidity and inorganic suspended solids were observed in the water column of three carp-free ponds. In all three cases the water level was 30 cm or less when the elevated turbidity levels and TSS were observed. In Section 5, the greatest turbidity was observed in the spring and autumn of 2002 when macrophytes were either becoming established or in the process of deteriorating (Hnatiuk 2006). Once water levels had dropped below 30 cm in Mackenzie Bay and Pitblado, ISS and OSS increased and the calculated photic zone depth decreased to levels comparable to those in carp-accessible ponds. This occurred despite the presence of thick mats of metaphyton covering the majority of the ponds, which should have protected the sediment surface. Elevated concentrations of OSS may have been a result of the suspension of sediment-associated algae or decaying metaphyton at the time of sampling or detachment of algae from metaphytic mats. Elevated levels of ISS may have been the result of wind-induced sediment resuspension.

The textural composition the sediments where carp are present is an important consideration when interpreting experimental results of the effects of carp on water quality in wetlands (Crivelli 1983; King et al. 1997; Scheffer 1998). Fine sediments like clay and organic matter will suspend easily upon disturbance and remain in the water column while larger particles settle quickly (Scheffer 1998). Where substrates consist mainly of sand, the water column will remain clear despite the presence of carp. Hnatiuk (2006) noted that ponds in the eastern portion of Delta Marsh tend to have harder, more compacted substrates compared to those of the western marsh. She proposed that the clarity of the ponds in the east relative to those in the west was as a result of these soils. I found no significant differences in sediment composition (proportion of sand, silt, clay and organic matter) with respect to their geographic position within the greater Delta Marsh. However, I did find that there tended to be proportionally more sand and less silt in carp-accessible ponds than in carp-free ponds. This may be a result of carp- and wind-induced resuspension of the sediments where silt would remain in the water column for a longer period of time once resuspended.

Effects of carp on water column nutrients

My hypothesis that carp-accessible ponds would have more N and P in the water column than carp-free ponds in Delta Marsh was not supported, though some evidence suggests that the possibility should not be discounted entirely. This hypothesis was based on numerous studies which have shown that carp can

increase N and P in the water column, as a result of sediment resuspension and/or excretion, and that this relationship is often linear with increasing biomass of carp (e.g. Richardson et al. 1990; Lougheed et al. 1998; Angeler et al. 2002; Khan et al. 2003; Badiou 2005). With few exceptions, no significant differences and no seasonal trends in water column N or P concentrations were found among ponds in Delta Marsh. This was the case regardless of connectivity or accessibility to adult carp or changes in accessibility of adult carp to the ponds (Hnatiuk 2006). Similary, studies either removing or introducing carp into a natural system have shown that increases in nutrient concentrations were not always evident (King et al. 1997; Drenner et al. 1998; Lougheed and Chow-Fraser 2001; Hnatiuk 2006). These different outcomes in the literature may be the result of the complexity of natural systems. Factors other than carp, such as rapid uptake by autotrophs, denitrification, microbial uptake and binding to suspended sediment may remove detectable nutrients from the water column. As such, the evidence observed in mesocosm and aquaria experiments supporting the hypothesis that carp are responsible for increases of nutrients in the water column is not necessarily apparent in natural systems.

In the overall four-year study (2001 - 2004), there was some evidence that carp density did affect water column nutrient concentrations. The connection of South Mackenzie Bay to the main marsh in the spring of 2002 rendered the pond accessible to adult carp. A substantial increase of TP and TN was observed in the year in which carp had access as compared to the previous year in which it was carp-free (Hnatiuk 2006). Similar increases were not observed in Wye's

Pond either in the year of its connection in the spring of 2002 (Hnatiuk 2006) or three years later. Unlike South Mackenzie Bay where adult carp were observed in large numbers early in the season, carp were rarely seen in Wye's Pond throughout 2002, nor were they present in great numbers throughout 2004. Badiou (2005) noted that in large wetland cells (5 - 7 ha), which approximated the conditions in Delta Marsh, concentrations of ammonia-N and SRP did increase where carp were present but only at high carp densities of >600 kg/ha. Below this critical density, rapid adsorption to suspended sediments of soluble P, rapid uptake by autotrophs of available nutrients, and/or extensive rates of denitrification have been proposed as likely causative factors in the discrepancy with results from small scale studies (Badiou 2005). Although the density of carp in the ponds was not measured, it is possible that carp were present in South Mackenzie Bay in sufficient densities to allow for increases in nutrients, which because of rapid nutrient uptake by autotrophs or adsorption to suspended sediments was observed in their total fractions, but not in terms of TRP and TIN.

The presence of phytoplankton and suspended sediments, or other factors, in experimental ponds may have masked the increases in water column nutrients expected where carp are present. Nutrients are quickly taken up by phytoplankton or are adsorbed to resuspended sediments and subsequently settle out of the water column. The consumption of nutrients by bacteria in the water column may also have played a role as they are known to be efficient nutrient users and superior competitors to algae in the uptake of P (Currie and Kalff 1984; Kirchman 1994; Joint et al. 2002). Where comparisons of carp-

accessible and carp-inaccessible ponds showed no significant differences in Hnatiuk's (2006) study as well as in my own, the carp-accessible ponds of 2003 were an exception. When adult carp were present they stirred up sediments in the ponds, as evidenced by elevated levels of ISS, observable nutrient concentrations were low and phytoplankton concentrations were elevated. However, once adult carp densities had decreased, water column concentrations of ammonia-N, TP and TRP in Cherry Ridge and West Blind Channel were very high relative to Klyne Lake and all carp-accessible ponds in 2004. The period in which the nutrients were elevated in both ponds corresponded to periods when phytoplankton chlorophyll *a* concentrations were low in both ponds, comparable to concentrations in carp-free ponds. As zooplankton were seen to be abundant during these periods (pers. observation), it is possible that grazing pressure suppressed phytoplankton growth, thereby preventing nutrient uptake. Since adult carp were rarely seen at this time and the concentration of ISS was low, it follows that suspended sediments were not present to adsorb nutrients that may have been added to the water column through excretion by the young of the year carp. Conversely, carp were present in Klyne Lake until late July in 2003 and the pond exhibited greater concentrations of phytoplankton, ISS and lower concentrations of nutrients compared to Cherry Ridge and West Blind Channel. Also, carp-accessible ponds in 2004 exhibited similar characteristics as those of Klyne Lake in 2003, and no significant differences in P or ammonia-N between carp-accessible and carp-free ponds were observed, although nitrate-N and TN were greater in carp-accessible ponds.

Carp activity was obviously not the sole determinant of nutrient concentrations in the water column. Contrary to the hypothesis that carp exclusion should result in decreases in nutrients in the water column, N and P increased following isolation of Pitblado in the spring of 2002. TN in the pond was greater in the years in which it was isolated than when the pond was carp-accessible. In 2003, the concentration of TRP was higher than in all other years, primarily in the spring. TP also fluctuated between years with the highest seasonal mean concentration in 2003. Additionally, carp-free Mackenzie Bay was unique among all other ponds in 2004, in that there was a strong peak in water column TRP and ammonia-N concentrations throughout the mid-summer months. This peak resulted in a seasonal mean of TRP and ammonia-N greater than those of the other carp-free ponds and carp-accessible ponds that year. This event may be explained by the die-off of the abundant metaphyton present the year before, returning nutrients to the system. However, the same did not occur in Pitblado, which was also thick with metaphyton in 2003, and very little in 2004. As in Pitlbado, TN and TP concentrations in Mackenzie Bay increased slightly from 2001 to 2004. Similarly, water column nutrients, such as nitrate-N, and P were significantly higher in carp-accessible ponds in 2003 than in 2004. While the absence of phytoplankton and submerged macrophytes may explain the high levels of P among carp-accessible ponds in 2003, the overall reduction of seasonal mean nitrate-N from 2003 to 2004 is unexplained.

Effects of carp on the abundance of *periphyton*

I hypothesized that periphyton as measured by chlorophyll *a* on control NDS treatments would be more abundant in ponds to which carp had access, in response to increases in available nutrients via excretion and sediment disturbance. This hypothesis was supported equivocally. Periphytic algal growth in ponds to which carp had access was greater than in their carp-free counterparts in 2003. However, in 2004, periphyton growth on the control treatments in two of the carp-free ponds (Pitblado and Mackenzie Bay) was greater than in 2003, and comparable to levels found in carp-accessible ponds of 2003. Similarly, the abundance of periphyton in the carp-accessible ponds, Cherry Ridge and West Blind Channel, had decreased from 2003 to 2004.

The presence of other algal groups, like phytoplankton and metaphyton, may have been a factor influencing the growth of periphyton in the ponds. Although the presence of abundant phytoplankton has been attributed to carp presence, the presence of metaphyton in carp-free ponds may be attributable to the isolated nature of the ponds and that they had been flooded two years prior in 2001. In the case of Cherry Ridge and West Blind Channel, the decrease in the abundance of periphyton from 2003 to 2004 may have been the result of competition with phytoplankton for nutrients, as phytoplankton abundance was low and water column nutrients high in 2003 compared to 2004. It may also have been a result of lack of light due to poorer water clarity in 2004 compared to 2003. Pitblado and Mackenzie Bay were choked with metaphytic algae

throughout the summer months of 2003. The metaphyton in the ponds may have been competing for nutrients and almost certainly reduced the availability of light to the periphyton on the frit surfaces resulting in lower concentrations of periphyton on the control NDS treatments. Once the metaphyton was gone in 2004, periphyton grew in abundance, lending support to the proposed role of metaphyton. Similar to the carp-accessible ponds, water column nutrients were high in Mackenzie Bay in 2004 compared to 2003, likely a result the decaying metaphyton of the previous year and a subsequent lack of competition for nutrients as the metaphyton was no longer as abundant. However, water column nutrients in Pitblado did not increase as they did in Mackenzie Bay. This suggests that had the metaphyton not been present in the carp-free ponds in 2003, periphyton growth may have been greater than it was and the differences in periphyton growth between carp-accessible and carp-free ponds may not have been significant. Unlike my study, Hnatiuk (2006) found no difference in the abundance of epiphyton growing on cattail stems between isolated and connected sites, only differences in the seasonal trends. Also, no seasonal or carp-accessibility effects on the growth of periphyton on artificial substrata were found (Hnatiuk 2006). By contrast, periphyton growth on the NDS controls in Klyne Lake was similar in 2003 and 2004, reflecting the relative consistency of nutrient concentrations and other parameters between years. As in the case of phytoplankton, the pond's large size and orientation to prevailing winds may have resulted in wind-induced sediment resuspension, possibly providing a more

stable efflux of nutrients to the water column. In order to better understand the dynamics of periphyton growth in Delta Marsh, further research is needed.

Effects of carp on submerged macrophyte biomass and diversity

The majority of the results of my study, in conjunction with those of Hnatiuk (2006), support the hypothesis that carp presence has a negative effect on the biomass and diversity of submerged macrophytes. Hnatiuk (2006) reported increases in submerged macrophyte biomass in the year following the diking/screening of previously carp-accessible ponds and decreases in the biomass of submerged macrophytes in the year of the connection of previously isolated ponds. Like Hnatiuk's (2006) study, with few exceptions, I found that connected ponds tended to have lower submerged macrophyte biomass relative to carp-free ponds.

The relative abundance of carp using a pond has been shown to have to negatively impacted macrophyte biomass and diversity in the ponds of Delta Marsh. Hnatiuk (2006) noted that although carp were frequently seen in North School Bay, the water remained clear and supported an abundance of *Ceratophyllum demersum,* as well as four other species, including *Utricularia macrorhiza*. She suggested that the presence of macrophytes may have prevented a shift to the turbid, phytoplankton-dominated state typical of carp-accessible ponds. Indeed, other studies in Hungary and the Netherlands have found that the presence of vegetation above 30% coverage of a shallow lake or wetland is important to secure clear-water conditions (e.g. Jeppesen et al. 1994;

Scheffer et al. 1994; Tatrai et al. 2009). She also noted that carp congregated in the shallow areas of the pond near the periphery and did not appear to use the entire pond. Perhaps their limited distribution within the pond explains the persistence of macrophytes within the pond.

The lack of carp in a pond at the height of the spawning season, when they are generally present in high densities, may also result in greater than expected diversity of species present in a typical carp-accessible water body. In 2002, Wye's Pond was connected to the main marsh by the excavation of a channel permitting access to adult carp (Hnatiuk 2006). The connection of the pond occurred in mid-June and may have missed the height of the spawning period when the majority of the carp damage was likely to occur (Hnatiuk 2006). Turbidity was low in this pond and although the biomass of the macrophytes had decreased in 2002, a number of species were found within the pond including *Stuckenia pectinata*, *C. demersum, U. macrorhiza* and bryophytes at the time of the vegetation survey in August (Hnatiuk 2006). In 2003, the pond was connected all summer, yet the biomass of submerged macrophytes had increased to pre-connection levels but consisted soley of *S. pectinata.* Although water clarity parameters were not collected in 2003, the loss of diversity may be explained by the likely presence of carp in sufficient numbers to reduce light conditions to levels unfavorable to the establishment of other species, thereby releasing *S. pectinata* from competition. In 2004, adult carp were present at low densities in the pond throughout the open water season, and YOY carp were found within the pond suggesting that spawning activity had occurred. Turbidity in

2004 had increased substantially relative to 2001 and 2002 levels. *S. pectinata* was again dominant but macrophyte biomass had decreased substantially to levels comparable to the average carp-accessible pond.

My study shows that, in the long term, connectivity and water depth in carp-free ponds may be important in maintaining a macrophyte-dominated state with a diverse assemblage of species. Regardless of the method used to prevent access by carp, the biomass of submerged macrophytes had increased in the year following the ponds' alteration (Hnatiuk 2006). In the screened pond, Mid-Blind Channel, the increased biomass of submerged macrophytes observed in 2002 (Hnatiuk 2006) was maintained in 2003 and 2004. The number of species in Mid-Blind Channel also increased in 2003, with the presence of *Chara* sp. a prime indicator that the pond had recovered from the turbid state. Conversely, the biomass of submerged macrophytes in Pitblado was lower in the second and third year following isolation than in most carp-accessible ponds. Isolation of a pond may result in the growth of abundant metaphyton, common to eutrophic systems (Hillebrand 1983) and known to occur in protected areas of northern prairie wetlands, particularly following a year or two of flooding (Gurney and Robinson 1987, Hosseini 1989). The abundance of filamentous algae in Pitblado in 2003 may have affected the biomass and diversity of macrophytes within the pond, by creating a light limited environment through shading or through nutrient competition. In 2003, only *S. pectinata* was found within the pond, whereas in 2002 Hnatiuk (2006) reported the presence of *S. pectinata*, *C. demersum* and *U. macrorhiza*. In 2004 the abundance of the filamentous algae was much reduced,

found only in patches throughout Pitblado and six species of macrophytes were found, including the light sensitive *Chara* sp., *Myriophyllum sibiricum*, *U. macrorhiza* and *C. demersum*, albeit in trace amounts. Unlike Pitblado, *M. sibiricum* was abundant and was the dominant species in Mackenzie Bay despite the presence of the thick mats of metaphyton present within the pond. The persistence of *M. sibiricum* suggests it is tolerant to the presence of metaphyton. *M. sibiricum* was not found in Pitblado prior to 2004. Since Pitblado had been a carp-accessible pond prior to the spring of 2002 (Hnatiuk 2006) and Mackenzie Bay had been isolated for a much longer period of time, it is conceivable that *M. sibiricum* was low in the seed/propagule bank in Pitblado and required the appropriate conditions to become established. In 2003, water levels were at their lowest in isolated ponds from 2001 to 2004. Although Section 5 pond, Delta Marsh, MB, was screened in the spring of 2002 and submerged biomass had increased that summer, diversity did not increase as it did in Mid-Blind Channel (Hnatiuk 2006). Only *S. pectinata* grew in Section 5 in 2002, likely a result of high levels of turbidity and inorganic suspended solids recorded that summer (Hnatiuk 2006). The turbid water was likely a result of extremely low water depths facilitating wind-induced sediment resuspension in the pond (Watchorn 2010). In 2003, the water level in Section 5 was lower than in 2002, and much of the pond had grown in with emergent species. Conversely, the biomass of submerged macrophytes had decreased substantially in the isolated pond Emile's Pothole in 2003 despite a dense growth of submerged macrophytes (mainly *S. pectinata*) in 2002 (Hnatiuk 2006). Although water quality data and water depth were not

collected from this pond in 2003 it is possible that wind-induced sediment resuspension may have played a role here as metaphyton was not present.

The presence and absence of specific submerged macrophyte species is indicative of the extent of the effects of carp on water clarity. *S. pectinata* is known to tolerate the presence of carp due to its resistance to being uprooted and ability to grow under low light conditions brought on by increased turbidity (King and Hunt 1967; Lougheed et al. 2001). Consistent with this observation it was present in all ponds in 2003 and 2004, as well as in 2001 and 2002 (Hnatiuk 2006). *C. demersum* and *M. sibiricum* have also been reported to tolerate low light conditions. They are, however, not as tolerant of high turbidity, as *S. pectinata* was the first species to grow in response to a moderate clearing of the water column as shown in Cootes Paradise, ON, where turbidity had decreased as a result of the suppression of phytoplankton by grazing *Daphnia* sp. (Coops and Havens 2005). The presence of *C. demersum* in the carp-accessible ponds of Cherry Ridge (2003), North School Bay (2002) and Wye's Pond (2002) and *M. sibiricum* in West Blind Channel (2003) and North School Bay in (2002) supports this observation. In each of these ponds, water column turbidity levels were lower in comparison to other carp-accessible ponds where these species were not found. Similarly, upon isolation of Mid-Blind Channel and Pitblado, *C. demersum* had reappeared following isolation and subsequent water column clearing. *Chara* sp. and *U. macrorhiza* were found only in carp-free ponds. These species are known to be intolerant of turbid waters. The presence of charophytes in particular is considered a potential indicator species as they grow only in ponds to which

carp are present at very low densities or not at all (King and Hunt 1967; Roberts et al. 1995; Drenner et al. 1998; Hnatiuk 2006).

Effects of carp on pH and DIC

Carp presence or absence did not consistently affect pH and DIC in the water column of the experimental ponds. The amount of photosynthetic activity within ponds can be inferred from pH and water column DIC concentration. As photosynthetic activity increases, so too does pH. DIC acts as a buffer in the system effectively stabilizing changes in pH while DIC decreases as carbon is consumed in photosynthesis. In 2003, pH was higher and DIC lower in the carp-free ponds compared to carp-accessible ponds, but no significant differences were observed in 2004. In 2003, extensive metaphyton mats were found in Pitblado and Mackenzie Bay, and were likely responsible for the high pH and low DIC. Metaphyton only occurred in these two ponds in a single year, so its presence is not likely in direct response to carp presence or absence but rather to other unmeasured causes such as external inputs of nutrients.

Effects of carp on specific conductance, chloride and sulfate

As per my hypothesis, specific conductance, chloride and sulfate were all greater in carp-free ponds compared to carp-accessible ponds. Although they were not correlated with water column depth, they nevertheless increased with declining water levels in the carp-free ponds of 2003 and subtly in the carp-accessible ponds. By contrast, in 2004, water levels remained relatively stable, as did the

specific conductance, and concentrations of chloride and sulfate in carp-free ponds as well as carp-accessible ponds. The major differences between carp-accessible and carp-free ponds was their connection to the main marsh. With the exception of Mid-Blind Channel, carp-free ponds were surrounded by a dike and unable to exchange water freely with the rest of the marsh, whereas all carp-accessible ponds were always connected and the water could be diluted by the constant inflow and outflow of water from the marsh to the lake. However, there did appear to be another factor, perhaps a nearby saline source which caused conductivity to be greater in some ponds. For example, West Blind Channel, which shares a connection with Mid-Blind Channel, had higher conductivity than all other carp-accessible ponds, perhaps by virtue of its connection to Mid-Blind Channel. Also, Pitblado (diked) had exceptionally high conductivity and chloride concentrations relative to other carp-free ponds, though Cherry Ridge, historically connected to Pitblado and separated by a dike since 2002, did not. However, unlike chloride and specific conductance, sulfate concentrations increased in carp-free ponds from 2003 to 2004 and were particularly high in Pitblado, West and Mid-Blind Channel. A recent study in southwest Michigan examined the role of certain sulfur oxidizing bacteria in removing nitrate from aquatic systems by using nitrate to oxidize sulfide and elemental S to sulfate and in the process produce either N_2 through denitrification or ammonium through nitrate reduction to ammonium (DNRA) (Burgin and Hamilton 2008). This process has been shown to be an important component in the removal of nitrate in wetland sediments in southwest Michigan, accounting for as much as 25 - 40 percent of

overall nitrate removal (Burgin and Hamilton 2008). However, in the Lake Waco Wetland in Texas, DNRA was considered to be of minor importance relative to denitrification (Scott et al. 2008). In this study, however, there was no correlation between water column nitrate, sulfate and ammonia-N.

Effects of carp on nutrient limitation

My hypothesis that no nutrient limitation to periphyton would occur in carp-accessible ponds was not supported by this study. I found instead that nutrient limitation to periphyton varied among ponds and changed within a season and between years. In 2003, carp-accessible ponds were either N-limited or limited by neither N nor P and carp-free ponds were most often limited by a combination of N and P. N-limitation in carp-accessible ponds makes sense as P is known to remain in a system, either trapped in the sediments or assimilated by autotrophs rendering it susceptible to long term internal cycling, compared to N which is lost quickly through denitrification. In 2004, however, N and P co-limitation became more prevalent in carp-accessible ponds. In this case it was limited mainly to West Blind Channel, the only carp-accessible pond on the west side of the Assiniboine Diversion, and the only one in the study directly connected to a screened pond which was in a macrophyte-dominated state, Mid-Blind Channel. Since Mid-Blind Channel was also N and P co-limited throughout the 2004 growing season, it is possible that the water in West Blind Channel may have been pushed into Mid-Blind Channel when the water levels rose due to north winds pushing water into the marsh from the lake. There nutrients may have

been removed by submerged macrophytes before draining back into West Blind Channel when the winds shifted to the south and the water was pushed back out into Lake Manitoba. It is possible that the connection with the macrophyte dominated pond had a positive effect on the nutrient conditions of West Blind Channel in 2004 when water levels were high enough for water to flow freely between Mid and West Blind Channel. On the east side of the Assiniboine Diversion carp-free ponds that were N and P co-limited in 2003 were mainly limited by neither N nor P in 2004. In these ponds metaphyton was abundant in 2003 and may have sequestered most of the available water column nutrients. Through its decomposition the following year and its absence in the ponds, sufficient nutrients may have been supplied/available to offset nutrient limitation. Assessment of nutrient limitation by examination of molar ratios of N and P also showed that the water column of carp-accessible ponds tended to have low N:P ratios, particularly in 2003. However, N-limitation (below the Redfield Ratio of 16:1) was uncommon. Carp-free ponds by comparison tended to have higher molar ratios of TN:TP suggesting that they were, for the most part not N-limited in either 2003 or 2004. This too is in general agreement with the results from the NDS. However, it was noteworthy that assessments of nutrient limitation of the water column of the ponds based on molar ratios of N and P did not correspond well with nutrient limitation to periphyton using the NDS on a set by set basis. In a survey of nutrient limitations of farm ponds across southern Manitoba, Kolochuck (2008) also found that NDS-derived nutrient limitations did not correspond to N:P molar ratios of the ponds in his study. Bioassays such as NDS

provide researchers with insight into the relative availability of N and P over a three-week deployment period which takes into account high rates of biological turnover that can quickly make nutrients available. By contrast N:P ratios reflect a "snap-shot" of what is left in the environment at one-time water samples. For example, Dodds (2003) warned that low dissolved nutrient levels (SRP < 0.1 mg/L and DIN <1mg/L) can be deceiving as they are static and do not take into account high rates of biological turnover rates, misleading researchers as to the true nutrient limitation within a water body. As such, a single water sample cannot be relied upon to determine nutrient limitation to algae. My study, as well as Kolochuck's (2008), has shown that results from NDS should be interpreted with caution. An understanding of the species of algae present in a periphytic community is important to interpretations of overall growth in response to a bioassay. Individual species within a single community can have different nutrient needs, growth rate and morphology, which can contribute to a variation in the community assemblages of periphyton between sites (Healey and Hendzel 1979; Rhee and Gotham 1980; Fairchild et al. 1985; Francoeur 2001; Armitage 2006; Scott et al. 2009). Some members within a community could even be capable of N fixation (Scott et al. 2009). Kolochuck (2008) warned that it is also possible that the species composition of a periphyton community on NDS may vary when the treatment concentrations remain the same but ambient nutrient concentrations in each water body are different. Potential shading and alteration of the local chemical environment or competition for inorganic nutrients due to the presence of metaphyton, periphyton, fungi or bacteria growing on the frames and

invertebrate grazing may also affect the growth response of periphyton on a bioassay. For example, at some sites the NDS frame; including the frits, were sometimes found covered in filamentous algae that could potentially result in either shading of the surface of the frits upon which the periphyton would grow or have created a microclimate of chemical conditions not representative of the water column at the site, resulting in misleading results (Figure 38). In carp-accessible ponds, the NDS frames were sometimes found covered in a film of periphyton infused with mud which might also cause light limitation to the algae on the frits (Titus et al. 2004). Despite efforts to clean frames of the NDS apparati upon each visit, the algae on the frames would in some cases grow back between cleanings. Additionally, there was the possibility of mechanical damage to the periphyton on the bioassays. The cleaning of the frames presented a problem in that filamentous algae attached to the surface of the frit could potentially be ripped off resulting in a bare section upon which new algae could grow. Additionally, the potential for grazing of periphytic algae by invertebrates (Allanson 1973; Cattaneo 1983; Cuker 1983; Bronmark 1992) may suppress the amount of periphyton growth on the NDS. In ponds exposed to carp I would sometimes find frames covered in a slick of what appeared to be periphyton infused with clay/mud, along with chironomid larvae, which are known to graze on epiphtyon (Mason and Bryant 1975). Whether or not they may have impacted the results of this experiment is unknown. There is at least one example that suggests it is a possibility as algae was conspicuously absent in patches on the frits (Figure 39). Although a number of studies have reported a positive

relationship between periphyton/epiphyton growth and density of chironomids (Winterbourn 1990; Mundie et al. 1991; Williams et al. 2002; Miller and Crowl 2006;), Williams et al. (2002) found that chironomids did not significantly affect the amount of epiphyton which grew in response to the presence of benthivorous fish, in the UK.

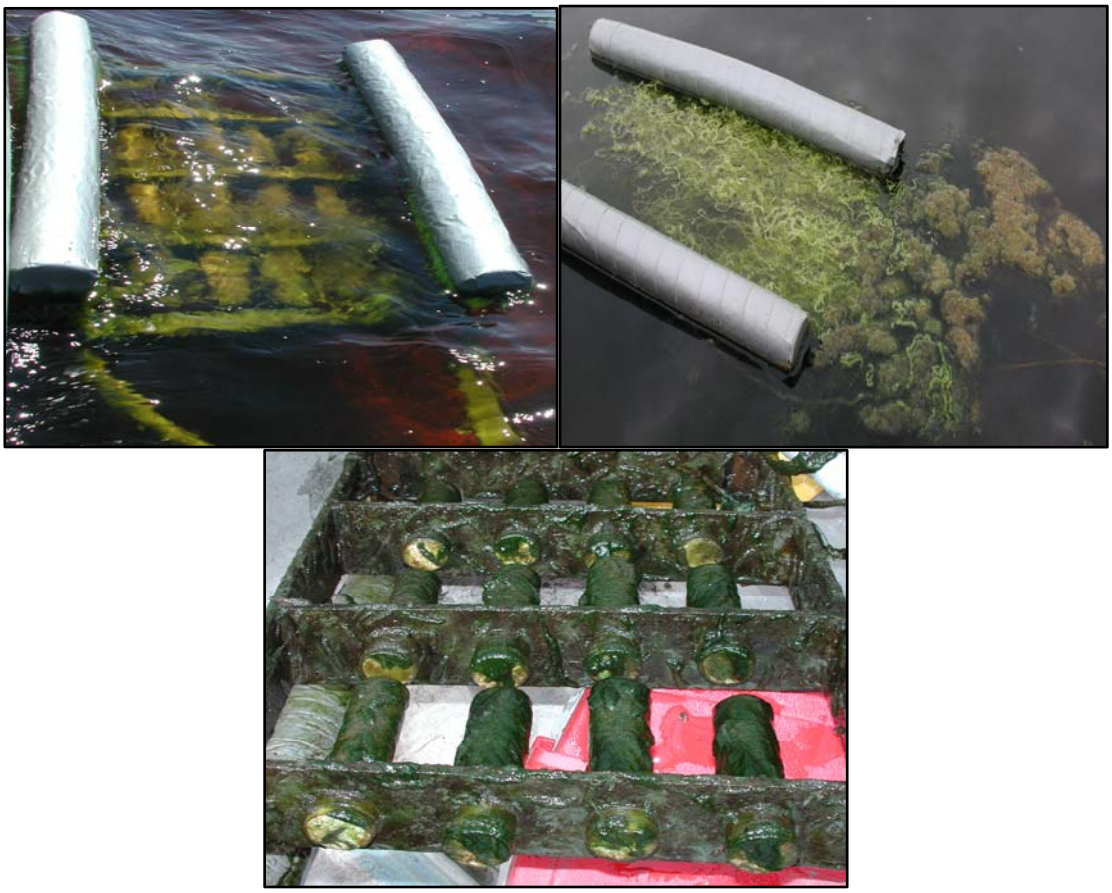

Figure 38. Nutrient diffusing substrata apparati covered by filamentous algae which grew in the space of seven days.

Figure 39. NDS apparati showing algal growth, infused with clay, the presence of chiromid larvae and evidence of invertebrate grazing in Cherry Ridge, August 05, 2003 and West Blind Channel July 16, 2003.

To supplement the findings of the N:P molar ratio and the NDS it may be beneficial to take into consideration the community of algae growing within the pond. For example, the presence of known N-fixing cyanobacteria in the water column is an indicator of the N-limitation within the water column, and can support or refute the findings by either NDS or molar ratios of N and P. N-fixing cyanobacteria are known to outcompete non-N-fixing cyanobacteria and chlorophytes when N:P ratios are low, though Barica et al. (1980) notes that they will not always occur. In this study, blooms of the N-fixing cyanobacteria *Aphanizomenon flos-aquae* were present in Klyne Lake and Cherry Ridge throughout most of both summers, Wye's Pond in 2004, and in all open water areas in the east marsh. Its presence supports the N-limitation observed by using the total N:P ratios, that were not observed using the NDS. However, these blooms were not evident on the west side of the marsh in West Blind Channel (carp-accessible) or in East Blind Channel, despite a tendency toward N-limitation. *Gloeotrichia* sp., another cyanotbacterial taxon known to occur in N-limited environments, was found on occasion growing on the NDS frame in Mid-Blind Channel, which during the period in which it was present was found to be N-limited by the NDS bioassay and at least intermittently by the inorganic molar ratio of N and P.

East Blind Channel: An Atypical Pond

East Blind Channel was kept separate in the analyses of this study by virtue of some unique properties that would have affected the outcome of the analyses.

Although a few carp were seen in an adjacent pond, Center Marsh (Bortoluzzi, personal communication), they were neither seen nor caught at this site for the duration of my study, so I could not be certain that carp had used the pond during the sampling period. Unlike all other ponds, it had exceptionally high concentrations of TRP and TP and among the lowest concentrations of ammonia-N and nitrate-N and total N. Consequently this site had the lowest N:P ratios using either total or inorganic forms of nitrogen and phosphorus to calculate the ratio of all ponds. Like most carp-free ponds, East Blind Channel had very low concentrations of phytoplankton (chl *a*), total suspended solids and turbidity, and sufficient light reached the sediment surface to allow for the growth of submerged macrophytes. It had among the lowest pH, specific conductivity, chloride and sulfate. It was also the deepest of all the ponds. Although it did not have the greatest mean density of submerged macrophytes it was comparable to other carp free ponds except that the community was dominated by *C. demersum*, much as North School Bay was in 2002.

The unique chemical properties of the water column in East Blind Channel suggested it was influenced by factors different from those affecting ponds in the east and west portion of Delta Marsh. Unlike all other ponds in my study, East Blind Channel was situated in the Center Marsh. It was connected to the east marsh via Center Marsh and School Bay, by means of a narrow drain which runs beneath highway 240 separating the center marsh from the east marsh. It was bounded to the north by the sandy beach ridge separating the marsh from Lake Manitoba and by agricultural land to the south and on the west by the Assiniboine

River Diversion. There is a small channel extending from East Blind Channel to the lake which was usually blocked by sand, but a storm event late in May of 2004 forced the channel open allowing for an influx of spawning white suckers and possibly carp. Precipitation and runoff from agricultural land to the south is likely the main source of water to the East Blind Channel as water levels remained high and relatively even all summer. As such the retention time of the water is likely to be long.

Conceivably, the high P concentrations may have been due, in part, to leaking septic tanks associated with the cottages populating the beach ridge and fertilizer applications on the adjacent agricultural land which drains into Center Marsh. If carp were present they were not of sufficient biomass or density to effect a reduction of the submerged macrophyte density, which in turn may have suppressed phytoplankton growth. Denitrification is recognized to be the main means by which nitrogen is removed from the water column in wetlands (Scott et al. 2008). Since the water in East Blind Channel may have a long retention time due to its restricted connection to the main marsh, this may help to explain the low levels of total and inorganic nitrogen in the East Blind Channel. Further study of the sources of nutrients and nutrient dynamics within this pond is required.

Summary and Conclusion

Revisiting the Hypotheses

My hypothesis that water clarity would be poorer in ponds to which carp had access was supported in this study. When and where carp were present, water column concentrations of TSS, ISS, OSS and phytoplankton abundance were higher and the euphotic zone depth shallower when compared to carp-free ponds. However, where water column TSS and ISS showed a seasonal trend in which they decreased in concentration roughly concurrent with declining densities of adult carp in the ponds, OSS, phytoplankton and turbidity did not, suggesting there may been a lag effect.

My hypothesis that the water column nutrients TN, ammonia-N, nitrate-N, TP and TRP would be greater in carp-accessible ponds than in carp-free ponds was supported equivocally. In 2003, ammonia-N, TP and TRP were present in greater concentrations in two of the three carp-accessible ponds relative to all other ponds in the study. However, the elevated concentrations were concurrent with low phytoplankton abundance. This suggests that algal populations may assimilate nutrients quickly or they may be removed from the system in some other way (eg. bacterial uptake), hence the lack of available water column nutrients, higher TP and greater abundance of algae in most carp-accessible ponds. In 2004, ammonia-N and TRP did not differ significantly between carp-accessible and carp-free ponds though the highest concentrations of these were found in one of the carp-free ponds. Nitrate-N and TN were not significantly

greater among carp-free ponds in 2003, though they were for most of the summer in 2004.

My hypothesis that submerged macrophytes would be greater in ponds to which carp did not have access, compared to carp-accessible ponds, was supported. Most of the carp-accessible ponds in this study had very little or no submerged vegetation and what vegetation did occur was represented mainly by species tolerant to turbid water. However, while the biomass and diversity of submerged vegetation was greater in carp-free ponds, one of the ponds, Pitblado, supported very little submerged vegetation biomass. In 2003 the pond was covered with metaphyton which may have affected plant growth through competition for nutrients and light as only *Stuckenia pectinata* was found within the pond. In 2004, the metaphyton died off and several macrophyte species were present, though in small quantities.

My hypothesis that periphyton would be present in greater abundance in carp-accessible ponds relative to carp-free ponds was supported equivocally. In 2003, periphyton concentrations on the NDS controls were indeed greater in carp-accessible ponds compared to carp-free ponds. However, in 2004, there was a shift in periphyton abundance in two carp-free ponds and two carp-accessible ponds which was related to the amount of metaphyton or phytoplankton in the ponds at the time of sampling. My research suggested that the presence of either of these two forms of algae in the ponds seemed to out-compete periphyton for nutrients and/or light, since periphyton grew in abundance when water column

nutrients were present in high concentrations and the two forms of algae were in low abundance. Although the presence of carp seemed to be responsible for an abundance of phytoplankton in a pond, the presence of metaphyton in a pond seemed to be related to the isolated condition of a pond following a season of flooding.

My hypothesis that no nutrient limitation to periphyton would occur in carp-accessible ponds was not entirely supported by this study. I found instead that nutrient limitation to periphyton varied among ponds and changed within a season and between years and depended upon conditions within individual ponds. In 2003, carp-accessible ponds were either N-limited or not limited by either N or P and carp-free ponds were most often limited by a combination of N and P. In 2004, however, N and P co-limitation became more prevalent in carp-accessible ponds. In this case it was limited mainly to West Blind Channel, the only carp-accessible pond on the west side of the Assiniboine Diversion. Mid-Blind Channel, the screened pond which shared a connection with West Blind Channel, was also N and P co-limited throughout the sampling period. This suggested that the sharing of the water with the submerged-macrophyte rich Mid-Blind Channel, made possible by higher water levels in 2004, may have had an effect on reducing available nutrients in West Blind Channel. On the east side of the Assiniboine Diversion carp-free ponds that were N and P co-limited in 2003 were mainly limited by neither N nor P in 2004. This suggests that the metaphyton abundant in both those ponds in 2003 may have taken up most of the available water column nutrients.

My study, along with those of Badiou (2005) and Hnatiuk (2006), reinforce Schindler's (1998) view that whereas mesocosm experiments allow for the isolation and study of individual factors important to the basic understanding needed to conduct ecosystem-level experiments, the results cannot be readily extrapolated to a natural ecosystem which are by nature more complex. Badiou (2005) found that the effects of carp were more pronounced in small mesocosms (5 x 5 m) than in large wetland cells (5 - 7 ha), which most closely represented the natural ecosystem of the surrounding marsh. Similarly, at the ecosystem level, Hnatiuk (2006) and I found that the effects of carp were not as predictable as smaller scale studies would suggest. In particular, water quality, submerged vegetation biomass and algal growth varied both temporally and spatially in both carp-accessible and carp-free ponds. Parameters over which there was no control, such as the spatial and temporal distribution of carp, their density within a pond, water depth and unquantified top-down effects, including zooplankton grazing, may have contributed to the variability of the results. Nevertheless, in the overall four-year study of carp in Delta Marsh, Hnatiuk's (2006) work and my own have shown that the presence of carp is at least partially responsible for the turbid, phytoplankton-dominated state that exists in the connected waterways of Delta Marsh, and that carp abundance is an important factor. Ponds previously isolated then exposed to carp activity, particularly in the spring when they were gathered at high densities, shifted to the turbid, phytoplankton-dominated state with few macrophtyes, and the removal of carp from a pond led to the clear-water state, though not necessarily an abundance of macrophytes. For example, in

some of the isolated ponds, mats of metaphyton grew after a high water year, preventing macrophytes from establishing, with the exception of *M. sibiricum*. We also found that removal of carp did not always result in the clear-water state. In the screened pond, Section 5 pond, water levels were shallow enough to render the pond susceptible to wind-induced sediment resuspension during a potentially critical period prior to the establishment of a sufficient coverage of submerged macrophtyes (i.e. spring), resulting in turbid waters (Hnatiuk 2006).

Implications for the Restoration of Delta Marsh

In October of 2009, the Province of Manitoba announced that it would participate in a restoration initiative of Manitoba's two largest freshwater coastal wetlands, Netley-Libau and Delta Marsh. This initiative is guided by a working group led by Manitoba Water Stewardship and with representatives from Ducks Unlimited Canada, the University of Manitoba, Environment Canada, the International Institute for Sustainable Development, the Nature Conservancy of Canada and Manitoba Conservation. Currently, the health of Lake Winnipeg and Lake Manitoba is threatened by eutrophication. Restoration of these fresh water coastal wetlands to the macrophyte-dominated state is an important step to 1) restore and maintain the health of Manitoba's two largest freshwater lakes, through the removal of nutrients from the Lake Winnipeg's major water source, Assiniboine River and from agricultural runoff into Lake Manitoba and 2) restore them as centers of diversity for flora and fauna. Plans for Delta Marsh include the installation of screens at the four channels connecting the Delta Marsh to the

adjacent Lake Manitoba in an effort to rehabilitate the marsh by excluding carp (Ducks Unlimited 2009).

Research from around the world and in Delta Marsh itself has shown that reductions in the abundance of carp can facilitate a shift from a current turbid phytoplankton-dominated state to the healthy clear-water macrophyte-dominated state (e.g. Schrage and Downing 2004; Lougheed et al. 2001; Badiou 2005; Hnatiuk 2006; Tatrai 2009). Our research has shown that in wind-sheltered ponds and channels to which carp do not have access, the restoration to the macrophyte-dominated state can be achieved within two years and can be sustained for at least three years (2002 – 2004). Smaller ponds and channels relatively protected from the wind, more typical of the west side of the marsh, would likely achieve the clear-water, macrophyte-dominated state within a year or two, provided the depth of the ponds is sufficient to avoid wind-induced sediment resuspension. The isolation, by means of a screen, of Mid-Blind Channel before the onset of the carp's spawning season, resulted in an increase in the biomass of submerged macrophytes that same summer, supporting a greater density and diversity of plants (Hnatiuk 2006), invertebrates and fish (Parks 2006). In the years following the treatment it remained so and was frequently seen to be a favored pond for waterfowl and muskrat use (Goldsborough, personal communication). Cherry Ridge and West Blind Channel were also protected from the wind and were found to have relatively clear water, particularly in July and August after the carp had spawned. Despite the clearer waters, however, submerged macrophytes did not become established. This may

have been a result of too short a period in which to become established (July – August).

The coverage of submerged macrophytes has been shown to be on of the most important factors in achieving and maintaining the clear-water state, the other being the reduction of nutrient inputs (Tatrai et al. 2009). Re-colonization of macrophytes may be a slow process taking several years, or may not happen at all in the larger open wind-swept bays of Delta Marsh. Continued wind-induced sediment resuspension, high wave energy and the erosion of the propagule/seed bank from prolonged wind and carp activity, can result in a delayed recovery time in the wind-swept bays (Sager et al. 1998; Coops and Havens 2005; Miller and Crowl 2006; van de Haterd and Ter Heerdt 2007). In the absence of sediment-disturbing carp, a period of quiescence long enough in which the sediment is left undisturbed is required to allow for the consolidation of the sediments to a critical point such that the sediments are resistant to strong winds (Scheffer et al. 2003). Once this critical consolidation of sediments is reached, macrophytes can re-colonize, further stabilizing the sediments and leading to the preferred clear-water, macrophyte-dominant state. Jeppensen et al. (1994) estimated that a minimum of 30% of a shallow lake's area must be covered by submerged vegetation to secure clear-water conditions in the longer term. However, Tatrai et al. (2009) warn that this shift may not be permanent as vegetation may die back as a result of internal P loading from a mobile pool accumulated in the sediment. They suggest that submerged macrophytes accumulate P in the sediments, and that by increasing the abundance of organic matter, over time it results in

anaerobic conditions that enhance P release (Sondergaard et al. 2007). When TN and TP are both high, the risk of loss of submerged macrophytes as a result of a phytoplankton bloom is high (Jeppesen et al. 2007; Tatrai 2009). Climate may also have a large impact on the water clarity of shallow lakes as inter-annual water temperature variation may affect the seasonal development of submerged plants and the long term maintenance of the biotic community structure (Hargeby et al. 2004; Tatrai 2009).

Recommendations to researchers

1. In this study NDS were used to compliment the water quality data collected to aid in the determination of nutrient limitation within the study ponds. I propose a study be done to determine the effectiveness of using NDS at Delta Marsh incorporating the following suggestions:

    a. Placement of NDS into a series of mesocosms or aquaria with known N:P ratios, and without grazers, would be useful in determining the predictability or accuracy of the NDS method and aid in the interpretation of NDS results.

    b. Identification of algal taxa growing on the frits of the NDS would clarify the nutrient limitation within ponds as nutrient requirements vary within and between species.

c. In connected ponds, where carp were present, it was not unusual to find chironomids on the frit surfaces. In at least one case frits were collected with small patches devoid of periphyton, presumably as a result of grazing. It would be informative to determine if inverebrates graze equally on all treatments. Methods, such as the infusion of insecticides in the agar, should be devised to prevent grazing pressure from altering the results.

d. Periphyton and metaphyton growing on the frames may alter the microhabitat in the vicinity of the NDS vials by nutrient uptake, pH changes, and shading. The extent to which these growths may effect the growth of periphyton on the frits should be determined.

e. The best method for keeping the NDS frame clean of periphyton and metaphyton and other debris is essential. Cleaning the frames risks dislodging periphyton growing on the frits in response to the treatments.

2. Nutrient-limitation studies should be complimented through the identification of algal taxa growing within a study pond. Identifying the community of algae present in a water body may prove more useful than a direct examination of nutrients. For example though Mid-Blind Channel was not deemed to be nitrogen limited either by examination of N:P ratios or by nutrient diffusing substrata, *Gloeotrichia* sp., a nitrogen-fixing cyanobacterium was found growing on the NDS frame in this study.

3. In light of the aforementioned installation of screens at the four creeks separating Delta Marsh from Lake Manitoba to prevent access by the majority of carp, baseline data should be taken from ponds both isolated and connected and particularly of the large wind swept bays on the east side of the marsh. This should be followed up by a monitoring program in the two years following the installation of the screens. In connected ponds in particular monitoring should occur every five years after the second year since rehabilitation of the large wind swept bays is likely to take more time.

    a. Sediment composition analyses (sand, silt, clay and organic matter) across the marsh would prove useful in predicting the rate at which the marsh could return to the macrophyte dominated state.

    b. Susceptibility of ponds to wind-induced sediment resuspension is a key factor in the rate of rehabilitation of wetlands. Detailed records of the fetches in open water areas of Delta Marsh and the wind speeds at which sediments resuspend in relation to water depth are necessary. Sediment traps could be used to determine sedimentation rates in open water areas where carp are present. Placed in a grid pattern in a large pond, with half the pond fenced along the axis parallel to the prevailing winds to exclude carp may help to determine whether carp or wind have the greater effect on sediment resuspension.

c. Seed and propagule bank inventories of a number of ponds in the east and west marsh are necessary in order to predict the likelihood of rehabilitation of the ponds and open water areas of Delta Marsh. A study exploring re-seeding of a variety of species would be useful in those areas of the marsh in which the seed bank is low.

4. Hnatiuk (2006) and other unpublished studies (Goldsborough, personal communication) have shown that the center marsh area in Delta Marsh is worthy of further study. While East Blind Channel was clear and macrophyte dominated, Center Marsh, the pond to which it is connected has been described as being turbid and phytoplankton-dominated. To the east, closest to the connection to the east marsh, North School Bay was clear water-macrophyte dominated despite the presence of carp (Hnatiuk 2006). In addition, while North School Bay did not stand out from other ponds outside of the center marsh area in terms of nutrient concentrations and other water quality parameters (Hnatiuk 2006), East Blind Channel did, having the highest water column concentrations of P and among the lowest concentrations of N, despite all ponds of the center marsh being connected. A study examining sources of N and P incorporating a grid system across center marsh may help to identify sources, particularly before, during and after cottage season and rain events. This would involve detailed records on cottage septic tank usage, precipitation and run-off data. Since phosphorus concentrations tend to be unusually high and nitrogen concentrations unusually low in East Blind Channel, research

should be done to determine how denitrification rates and internal recycling of phosphorus may be different from the surrounding marsh.

5. I recommend an in-depth study monitoring the seasonal movements of a number of carp within the marsh in order to determine habitat usage, particularly in the open water areas. This may be in the form of surgically implanted transmitters with stationary receivers triangulating the position of marked individuals over one summer season. Hnatiuk (2006) suggested that carp did not use the open water bays. Since none of her or Parks' (2006) study ponds included the wide open bays typical of the east side of the marsh complex, this conclusion must have been reached based on bi-weekly visual observations to and from the sampling sites. I would argue that the conclusion is not substantiated as visual observations are not a reliable indicator of carp habitat usage. The waters in open bays are windswept and turbid rendering positive identification of carp difficult. The large open water bays of Delta Marsh are characteristically turbid and phytoplankton dominated, a state known to occur in highly eutrophic waters and most particularly in the presence of carp in conjunction with wind induced resuspension. If carp only used these areas as thoroughfares to the smaller protected connected ponds then it is conceivable that consolidation of the sediments should have occurred in the absence of disturbances such as those caused by bioturbation through feeding. As Scheffer (2003) points out, all that is required is a brief period of quiescence for the sediments to consolidate enough to be able to

withstand even relatively high wind action in the absence of bioturbation. I propose that this would occur over the winter months and simply “passing by” should not perpetuate the turbid phytoplankton dominated state.

6. To date no study has been done to obtain an estimation of the density of carp using Delta Marsh. Although Badiou (2004) predicted it may be as much as 400 kg/ha carp, my research as well as Hnatiuk’s suggests this may not be the case throughout the marsh. This may be possible if a variety of areas of the marsh were blocked off temporarily and a mark recapture or catch per unit effort study was performed on a monthly basis to determine seasonal variation. Since we found carp to be very difficult to catch using gill nets, perhaps another method such as electrofishing could be used.

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Appendix 1.

NDS Time Lapse Experiment (Tara Bortoluzzi PhD Candidate, University of Manitoba)

"Nutrient diffusion rates from the clay pot NDS and silica disk micro-NDS were determined via laboratory experiments as described by Fairchild *et al*. (1985). NDS vials were immersed in 500 ml of distilled water in the laboratory. Samples were taken at the start of the experiment, once every 24 hours for 4 days, and then every second day for 45 days. The samples were analyzed for TRP (PO_4-P) and nitrate+nitrite (NO_3+NO_2-N) using standard methods as described above for water samples (Stainton *et al.* 1977, APHA 1992). The experiments indicated that all NDS treatments diffused nutrients throughout a 45-day period, and the diffusion rate decreased as a negative exponential as found similarly by Pringle and Bowers (1984), Fairchild et al. (1985), and Gibeau and Miller (1989). Overall, the mean diffusion rates of NO_3 and PO_4 from the micro and pot NDS were similar, with diffusion rates of 42 and 33 µmol/cm^2/day, respectively for NO_3, and of 3.5 and 2.2 µmol/cm^2/day, respectively for PO_4. No nitrogen or phosphorus was detected diffusing from the control substrata."