Ecological impacts of an exotic benthivorous fish in wetlands: A comparison between common carp (*Cyprinus carpio* L.) additions in large experimental wetlands and small mesocosms in Delta Marsh, Manitoba

By

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A Thesis Submitted to the Faculty of Graduate Studies
In Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

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Abstract

I examined the impacts of an exotic benthivorous fish, the common carp (Cyprinus carpio L.), in large (5-7 ha) experimental wetlands and in small (5 x 5 m) mesocosms located in Delta Marsh, Manitoba, Canada. In addition to following the impacts of common carp on water quality, sedimentation, and submerged macrophyte biomass, the impacts of common carp on phytoplankton, zooplankton, benthic invertebrates, and forage fish populations in the small mesocosms were intensively studied. As carp are often the dominant fish species found in degraded aquatic systems, the interaction between nutrient loading and carp, and the resulting impacts on important biotic and abiotic components were investigated through the small mesocosm experiments.

In both the large experimental wetland cells and the small mesocosms common carp significantly increased turbidity and suspended solid concentrations, sedimentation rates, chlorophyll a concentrations, and reduced submerged macrophyte biomass and light penetration. These results indicate that carp can significantly affect water quality and nutrient cycling in wetlands and lakes of Manitoba, even at relatively conservative densities. However, carp only induced a shift to the turbid state in the small mesocosm experiments. Failure to shift the large wetland cells to the phytoplankton dominated state was likely due to high DOC concentrations and submerged macrophyte biomass in these large ponds, which reduced the ability of the common carp to increase phytoplankton biomass.

At high densities of common carp in the fertilized enclosures, phytoplankton biomass was greatly reduced relative to the no carp and low carp treatments. My

results contradict the belief that carp interact synergistically with nutrient loading to enhance phytoplankton biomass, and imply that there is likely a threshold carp density above which phytoplankton biomass is reduced regardless of nutrient supply due to light limitation resulting from carp induced turbidity.

Although phytoplankton biomass was reduced in fertilized enclosures at high carp biomass, the overall effect of carp was to increase phytoplankton biomass. Carp also altered the composition of the phytoplankton community. Additionally, carp significantly increased zooplankton density, reduced benthic invertebrate and forage fish populations, and dependant on the treatment altered the community structure of the zooplankton and benthic invertebrates.

Scaling up my results from the large experimental wetland cells indicated that at 400 kg.ha, a density likely to in Delta Marsh, nutrient loading from carp would be equivalent to 66% of internal phosphorus loading in the marsh. Furthermore, a common carp biomass of 200 kg.ha in Lake Manitoba, which is similar to the biomass found in other large shallow lakes, would contribute approximately the same amount of nitrogen, and double the amount of phosphorus to Lake Manitoba, relative to the combined loading from the major tributaries entering the lake.

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1.0 Introduction

Delta Marsh, on Lake Manitoba is one of North America's largest wetlands covering an area of approximately 18,500 hectares. Over the last 40 years the marsh has become more turbid than in previous times. This is usually indicative of marsh degradation and eutrophication. A model for shallow lakes and wetlands proposed by Scheffer *et al.* (1993) hypothesizes the existence of macrophyte-dominated (clear) or phytoplankton-dominated (turbid) states over a wide range of nutrient concentrations. Transitions from one state to the other require a trigger mechanism or disturbance. In Delta Marsh, it is thought that the shift from a relatively clear state that existed prior to the 1960s to the current turbid state was caused by loss of submerged macrophyte cover that, in turn, was caused by the proliferation of common carp (*Cyprinus carpio*).

Common carp were introduced into Manitoba as early as 1886 as a food source for settlers; neverthless, they only appeared in the south end of Lake Manitoba in 1947 (Atton 1959). Common carp have been observed in Delta Marsh since 1952, and they migrate each year from the lake to the marsh soon after ice breakup in the spring (Hachbaum & Ward 1964). Benthivorous fish such as common carp can have profound effects on marsh turbidity by disturbing sediments while foraging and spawning. Additionally, common carp are known to uproot submerged macrophytes during spawning and accidentally consume them while foraging for benthic invertebrates. Sediment resuspension and excretion by common carp can increase water column nutrient concentrations, thereby causing phytoplankton to flourish. A

shading effect results from these blooms, further suppressing submerged macrophytes and creating an ecological feedback mechanism that perpetuates the turbid state. Common carp also physically disturb the sediment-water interface and the algae associated with the sediment, which play a major role in the stabilization of the bottom and the regulation of nutrient fluxes across the sediment-water interface. Finally, common carp feed on chironomids, which are the most abundant and widely distributed invertebrate group in prairie wetlands (Wrubleski 1987). By reducing the abundance of chironomids and facilitating phytoplankton dominance, common carp may lead to drastic changes in wetland food webs.

Although common carp have long been considered a nuisance in Delta Marsh, and are still considered so, anecdotal evidence from local fishers and landowners suggests that common carp were more numerous in the past. This evidence is further supported by the annual spring carp catch for Lake Manitoba where production has decreased over the last few decades even though the price of common carp has increased (Figure 1.1).

1.1 Objectives and Major Hypotheses

1.1.1 Project 1: Biomanipulation of large experimental wetlands (2000, 2001, and 2002)

Several studies using small enclosures or ponds (< 1 hectare) have shown that common carp can increase water column nutrient concentrations and turbidity through sediment resuspension (Andersson *et al.* 1978, Keen & Gagliardi 1981, King *et al.* 1997), and reduction of submerged macrophyte cover (Havens 1991, Breukelaar *et al.* 1994, Lougheed *et al.* 1998, Sager *et al.* 1998). However, there have been

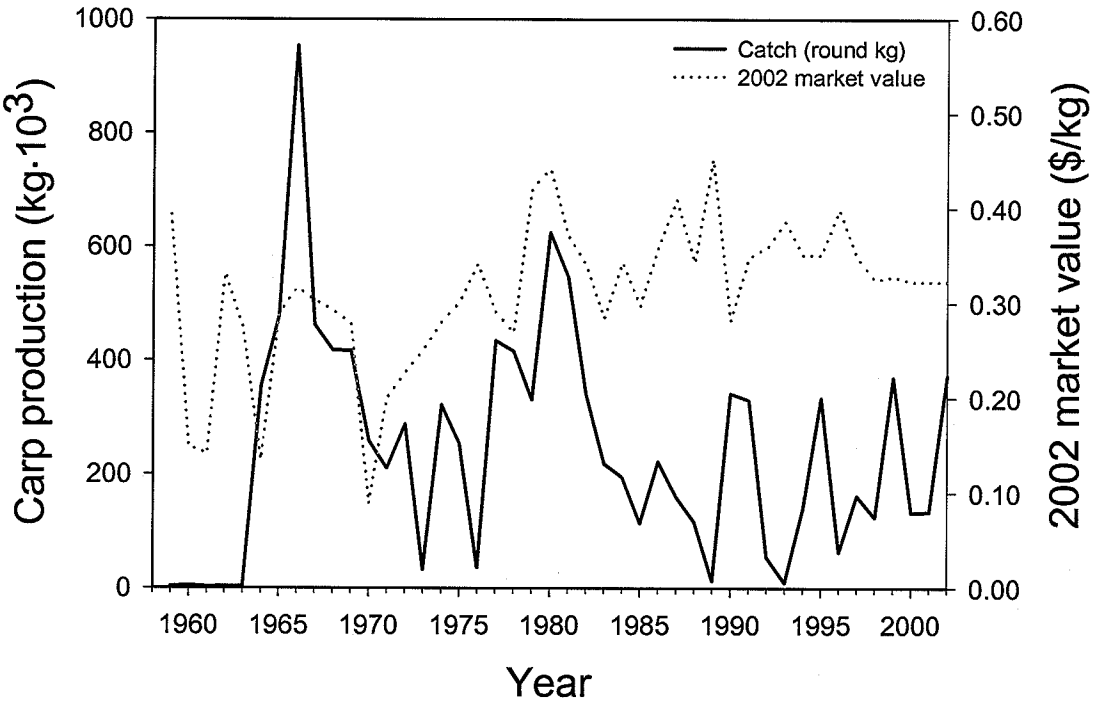

Figure 1.1. Production and market value (in 2002 dollars) of the spring carp fishery on Lake Manitoba (1958 – 2002). Common carp production data provided by Manitoba Conservation, Fisheries Branch.

relatively few experimental studies of common carp impacts in larger, more realistic sized wetlands. I will examine the direct and indirect ecological impacts of common carp on water column nutrient concentrations, suspended solids, sedimentation, and submersed macrophytes, as clear- state wetlands (5-7 hectares each) are shifted to a turbid state under varying densities of common carp. To my knowledge, no previous study has taken this type of whole ecosystem approach to examining the ecological impacts of common carp, at the scale proposed here. The four primary objectives of this experiment were as follows:

Objective 1.1. To quantify the effects of increasing common carp densities on water column nutrient concentrations.

Hypothesis 1.1. As carp densities increase, water column nutrient concentration will increase as a result of sediment resuspension and excretion.

Objective 1.2. To quantify the effects of increasing common carp densities on turbidity, suspended solids and submerged macrophyte biomass.

Hypothesis 1.2. Increasing densities of common carp will cause water column turbidity and concentrations of suspended solids to increase due to increased foraging activity of carp. Common carp will also directly reduce submerged macrophyte biomass through physical disturbance during feeding and spawning activities, and indirectly by increasing turbidity and suspended solids, thereby reducing light penetration.

Objective 1.3. To quantify changes in phytoplankton biomass under increasing densities of common carp.

Hypothesis 1.3. Phytoplankton biomass (measured as chlorophyll *a*) will increase with increasing densities of common carp due to increased nutrient loading from sediment resuspension and excretion.

Objective 1.4. To determine if common carp are able to trigger a switch from the clear macrophyte-dominated state to the turbid phytoplankton-dominated state.

Hypothesis 1.4. At a certain density, common carp will impair macrophyte growth and increase water column nutrient concentrations to the point where prolific phytoplankton blooms will occur, and will result in the loss of submerged macrophytes beds and the perpetuation of the turbid state.

These results will then be used to generate conservative estimates of the impacts common carp are having on Delta Marsh and adjacent Lake Manitoba.

1.1.2 Project 2: Biomanipulation and eutrophication of small experimental mesocosms (2002)

Most studies examining the impact of common carp on aquatic ecosystems have been conducted in small experimental mesocosms. For this reason, in addition to the experimental biomanipulation of large wetland cells, I also conducted experiments in small (5m x 5m) mesocosms to facilitate the comparison of the impacts of common carp amontg different geographic areas. This experiment will allow me to examine differential impacts of common carp in small scale experiments compared to those conducted in a

more realistic, whole ecosystem experiments. Additionally, the smaller and more homogenous environment associated with the enclosures, will allow me to more easily determine the impacts of common carp on the community structure and biomass of phytoplankton, and zoobenthos, as well as emerging chironomids.

Common carp are tolerant of low dissolved oxygen concentrations and are extremely tolerant of high turbidity levels (Cooper 1987). For this reason, common carp are often the most abundant fish in degraded aquatic systems where eutrophic conditions (i.e. high turbidity, high nutrients, and low light) afford them a competitive advantage over other fish that depend on their visual acuity to capture prey. Nevertheless, it is difficult to separate the effects of omnivorous fish such as the common carp from those associated with increased eutrophication, as both ultimately contribute to enhanced phytoplankton biomass which is the endpoint of choice for most scientific investigations of degraded aquatic ecosystems. Although the presence of common carp and nutrient loading have similar negative impacts on aquatic ecosystems, they may interact synergistically to increase phytoplankton biomass (Tryon 1954, Drenner *et al.* 1998).

The goals of this experiment, in addition to the goals already described for project 1, were as follows:

Objective 2.1. To determine if common carp interact synergistically with nutrient additions to increase phytoplankton biomass.

Hypothesis 2.1. Phytoplankton biomass in the presence of common carp and nutrient additions will be greater than the sum of the independent effects of carp and nutrients on algal biomass due to the fact that common carp will

maintain water column nutrient concentrations at higher levels, whereas nutrients may settle out and be sequestered in the sediments in the absence of common carp. As a result of enhanced phytoplankton biomass the shift from the clear to the turbid state will be more dramatic and occur earlier relative to treatments receiving only carp or nutrients.

Objective 2.2. To determine the impacts of common carp density and nutrient additions on the relative abundance of phytoplankton.

Hypothesis 2.2. Increasing turbidity and reduced light penetration as a result of common carp additions will favour phytoplankton groups adapted to low light conditions such as the cyanobacteria, which can regulate their buoyancy and position in the water column. Additionally, nutrient additions alone will favour algal groups well adapted to high nutrient environments such as the chlorophytes, whereas common carp and nutrient treatments will again favour cyanobacteria due to low light conditions.

Objective 2.3. To determine the impacts of common carp density and nutrient additions on the density and composition of the zooplankton community.

Hypothesis 2.3 Zooplankton densities will decrease with increasing densities of common carp as a result of elevated inorganic suspended solid concentrations, which can impair filter feeders, and the community composition will be altered.

Objective 2.4. To determine the impacts of common carp density and nutrient additions on the density of zoobenthos.

Hypothesis 2.4 Zoobenthos densities will decrease with increasing common carp densities due to predation from carp, but in enclosures receiving nutrient additions impacts of common carp may be dampened by higher phytoplankton biomass resulting in increased food resources for the zoobenthos.

Objective 2.5. To determine the impacts of common carp density and nutrient additions on total biomass and relative abundance of emerging chironomids (based on biomass).

Hypothesis 2.5. Total chironomid abundance will decrease as common carp density increases due to increased consumption. Additionally, the relative abundance of larger chironomid species will decrease as common carp density increases due to selective feeding by carp.

Objective 2.6. To compare the impacts of common carp in large wetland cells and small experimental mesocosms.

Hypothesis 2.6 The impacts of common carp will be much more pronounced in small enclosures relative to large wetland cells. Additionally, impacts will accumulate much more quickly in the small enclosures relative to the large wetland cells.

2.0 Literature Review

2.1 Wetlands

According to the National Wetlands Working Group (1988), a wetland is defined as land that is saturated with water long enough to promote wetland or aquatic processes as indicated by poorly drained soils, hydrophytic vegetation, and various kinds of biological activity that are adapted to a wet environment. Wetlands are critical components of the freshwater resources of North America and one of the components most vulnerable to changes imposed by industry, agriculture, and society in general (Murkin 1998). Historically, wetlands have been valued only for the space they occupy when drained or filled (Perry & Vanderklein 1996). It is only over the last two decades that wetlands have been recognized as vital ecosystems.

2.2 Wetland distribution and loss

Wetlands are estimated to cover between 7 to 9 million km^2 worldwide, or about 4 to 6 percent of the Earth's land surface (Mitsch & Gosselink 2000). Estimates suggest that more than half of the world's wetlands may have been altered, degraded or lost over the last two centuries (O'Connell 2003). In the province of Manitoba, wetlands cover 233,340 km^2 or 43% of the province (Halsey *et al.* 1997). Although a large portion of the surface area of Manitoba is covered by wetlands, peatlands concentrated in the boreal forest region of the province, particularly around the north basin of Lake Winnipeg, and in the Hudson Bay Lowlands region compose approximately 90% of all wetlands. For the most part, wetlands of these regions have been maintained in a relatively pristine and unaltered state due to the lack of human activity in these areas.

Although wetlands in northern Manitoba have remained relatively unaltered by human influences, the same cannot be said for those located in the southern portion of the province, particularly those in the prairie region. In the prairies, approximately 1.2 million hectares of wetlands have been converted to agricultural use (National Wetlands Working Group 1988). For example, a study by Hanuta (2001), comparing historical (pre-settlement) and modern wetland cover in 100 townships covering approximately 9400 km^2 within the Red River drainage basin in southern Manitoba, found that wetland cover decreased dramatically between the 1870's and 1995. In the 1870's, wetlands comprised 1098.0 km^2 or 11.7% of the total area within these 100 townships, compared to 14.5 km^2 (0.2%) in 1995. Wetland loss has also occurred, and still is occurring in the United States. In the lower 48 states more than 50% of the original wetlands have been lost to agricultural activities (Perry & Vanderklein 1996). Additionally, historic losses in the Great Lakes Basin have been estimated at 70% in the U.S. and 68% in Canada south of the Precambrian shield, with historic losses attributed primarily to agriculture drainage, and more recently, to development (Snell 1987). Many wetlands have been degraded by a variety of disturbances, including nonpoint source pollution, biomass removal, exotic species invasions, and hydrologic alterations (Detenbeck 1999).

Manitoba is home to two of the largest lacustrine lagoon marshes or delta marshes in North America. Delta Marsh located at the south end of Lake Manitoba covers approximately 150 km^2, while Netley-Libau Marsh on the Red River at Lake Winnipeg covers approximately 200 km^2 (National Wetlands Working Group 1988). Water levels on Lake Manitoba and Lake Winnipeg are artificially stabilized by hydro-electric power development causing the physical structure of these marshes to be altered, leading to the

loss of wetland habitat. This alteration can be seen in the number of water bodies comprising Netley Marsh: in 1960 before stabilization of water levels on Lake Winnipeg there were 50 individual waterbodies within the marsh, whereas in 1980 after stabilization of Lake Winnipeg water levels, the number had decreased to 17 (IBA 2004).

2.3 Wetland functions

Wetlands occur at the interface between terrestrial and aquatic ecosystems and provide a range of essential ecosystem functions that are often overlooked. Zones of enhanced elemental cycling, known as biogeochemical hot spots, often occur at interfaces between aquatic and terrestrial ecosystems (McClain *et al.* 2002). Additionally, the unique environment of wetlands and their role in elemental transformations means that their importance to global biogeochemistry is much greater than their proportional surface area on Earth would suggest (Schlesinger 1991).

Hydrologically, wetland ecosystems preform vital roles in the attenuation of flood peaks and storm flows, the regulation of stream flows, and groundwater recharge and discharge (Carter *et al.* 1979, Novitzki 1979, Murkin 1998, LaBaugh *et al.* 1998). Despite the recognized importance of the hydrologic regime to the structure and function of wetlands, it is often the component of wetland ecosystem research that is not nvestigated thoroughly (LaBaugh 1986).

In addition to their hydrologic importance, wetlands play a major role in mitigating the impacts of excessive nutrient and toxicant loads to aquatic ecosystems (Mayer *et al.* 1999). The location of wetlands at the interface between terrestrial and aquatic ecosystems affords them the ability to intercept large volumes of water in the form of

runoff from surrounding lands before it enters adjacent aquatic ecosystems. Once water enters a wetland it is exposed to various physical, chemical, and biological processes that inevitably alter its original chemical composition. These various processes enable most natural wetlands to act as nutrient traps, removing excess nitrogen and phosphorus from polluted water that flows through them. Denitrification is typically the dominant nitrogen removal process in wetlands (Tomaszek *et al.* 1997, Bachand & Horne 1999), whereas phosphorus is primarily removed through precipitation or sorption on organic matter and assimilation by vascular plants and algae (van der Valk *et al.* 1979, Dierberg *et al.* 2002). Although phosphorus can be removed through physical and/or biological mechanisms, long-term removal of phosphorus through physical processes such as sedimentation (particulate phosphorus) and sorption (soluble phosphorus) is far more effective relative to phosphorus assimilation by plants and algae which typically release most of their stored phosphorus to the water column upon decomposition (Kadlec & Knight 1996).

Another major function performed by wetland ecosystems is the removal of suspended sediments from water as it moves through a wetland. Shallow vegetated wetlands serve to reduce flow velocities and allow sediments to settle (Murkin 1998). Additionally, well-vegetated wetlands with extensive submerged macrophyte beds provide an enormous surface area for the sorption of suspended particles. Removing suspended solids from the water column increases the penetration of photosynthetically active radiation (PAR) and enhances the underwater light environment, that is vital to the functioning of primary producers in wetland ecosystems. In addition to clarifying the water column and retaining nutrients bound to suspended particles, the settling of suspended sediments in wetlands removes many pollutants, such as metals and organic

chemicals, that are associated with and partition strongly to suspended matter. (Kadlec & Knight 1996). However, excessive sedimentation, such as is common in wetlands adjacent to agricultural land, may alter aquatic food webs as well as basic wetland functions related to water quality improvement, nutrient cycling, and other biogenic processes that transform and sequester pollutants (Gleason & Euliss 1998)

As well as being hot spots of biogeochemical activity, wetlands are also hot spots of biodiversity. Wetland habitats are vital to many microorganisms (bacteria and fungi), plants, invertebrates, amphibians, reptiles, fish, waterfowl, and fur-bearing animals such as muskrat (*Ondatra zibethicus*) and nutria (*Myocastor coypus*) (Weller 1979, Tilton & Schwegler 1979, Flake 1979, Clark 1979).

2.4 Wetland fish communities

The importance of marshes for providing spawning and rearing habitat for sport and forage fish has long been recognized. Nevertheless, only a few fish tolerate harsh wetland conditions such as anoxia, winter-kill, and high summer temperatures (Batzer *et al.* 2000). Despite the harsh environmental conditions that occur in many North American wetlands, fish are an important component of wetland faunas (Snodgrass & Burger 2001).

When reviewing the literature of fishes of freshwater wetlands of North America, one quickly realizes that there are two distinct types of fish communities. The first community is associated with isolated wetlands and consists usually of small-bodied forage fish such as the fathead minnow (*Pimephales promela*) and brook stickleback (*Culaea inconstans*). In the prairie region of Manitoba, Lawler *et al.* (1974) found fathead minnows and brook sticklebacks in 10 – 20% of the wetlands. Probable reasons for the

success of fathead minnows and sticklebacks in wetlands include their tolerance to low dissolved oxygen, their high reproductive potential, and their tolerance to high concentrations of dissolved solids (Peterka 1989). Fathead minnows, in particular, can reach high densities in wetlands. In a study conducted by Duffy (1998) in four wetlands in South Dakota initial densities of fathead minnows in late May to early June ranged from 52,000 to 241,000 fish·ha^{-1}. Densities of fathead minnows and brook sticklebacks typically peak in late May and early June, and decrease throughout the remainder of the open-water season in temperate regions. Additionally, in isolated wetlands located in flood plains or situated in larger coastal wetlands, larger fish species tolerant of harsh wetland conditions such as common carp, northern pike, and bullheads can establish temporary populations after being introduced by flood events. A survey of farm dugouts, conducted by the Prairie Farmers Rehabilitation Association (PFRA) in southern Manitoba following the 1997 Red River flood found common carp had entered into many farm dugouts with the floodwaters (personal observation).

A second type of fish community is associated with freshwater coastal wetlands. Relative to fish populations in isolated wetlands, fish communities in coastal wetlands are much more diverse and productive due to the avalaibiltiy of deeper aquatic habitats to which fish can escape when conditions deteriorate in coastal wetlands. Although forage fish compose a large portion of the total fish biomass in coastal wetlands as in isolated wetlands, large fish entering from adjacent water bodies also contribute significantly to the total fish biomass. Nevertheless, most large fish are non-permanent residents of coastal wetlands, entering them only at certain times of day or seasons of year, to feed or spawn (Clark 1979). Previous studies on coastal wetlands of Lake Winnipeg, Lake

Manitoba, and the Laurentian Great Lakes indicate that these coastal wetland fish communities are often comprised of more than 25 species (Janusz & O'Connor 1985, Jude & Pappas 1992, Brazner & Beals 1997, Brazner 1997, and Wrubleski, D.A. unpublished data 2000). Additionally, coastal wetland fish communities are composed of piscivores, omnivores, planktivores, and benthivores, whereas isolated ponds are usually inhabited solely by planktivores.

Large coastal wetlands in temperate regions typically have two distinct open-water fish species compositions consisting of a spring spawning species assemblage and a summer feeding species assemblage (Janusz & O'Connor 1985). Studies conducted in Manitoba by Derksen & Gillies (1985) and Janusz & O'Connor (1985) found that wetland fish communities (adult) in spring (April – May) were dominated by spring spawners such as the northern pike (*Esox lucius*), white sucker (*Catostomus commersoni*), and yellow perch (*Perca flavescens*), while summer spawners such as the common carp (*Cyprinus carpio*) and bullheads (*Ameiurus* sp.) usually dominated the fish community in June and July. In a study of the Saskeram Marshes of the Saskatchewan River delta, Derksen & Gillies (1985) found large numbers of walleye (*Sander vitreum*) entered the marshes to spawn in certain years when a more suitable habitat was not available. Coastal wetlands of the Great Lakes tend to have a more diverse fish assemblage relative to coastal wetlands in Manitoba. On the other hand, a study by Jude & Pappas (1992) examining fish utilization of nine coastal wetlands of the Great Lakes found species composition of similar to those of coastal wetlands in Manitoba.

The extensive utilization of coastal wetlands by fish for reproduction, as well as the high diversity of the fish community, is probably related to high levels of primary

productivity of the marshes, and to the diversity of structural habitat (Stephenson 1990). In coastal wetlands, high levels of primary productivity provide fish with abundant food resources making them attractive nursery habitats. Additionally the structural diversity afforded by extensive expanses of emergent and submerged vegetation provides refugia for many small fish.

In a study designed to assess fish utilization of coastal marshes of Lake Ontario near Toronto, Stephenson (1990) found that 32 fish species, or 89% of all species, encountered utilized these marshes for some aspect of reproduction. Brazner *et al.* (2001) estimated forage fish movement between Bark Bay Slough (a lagoonal coastal wetland) and Bark Bay on Lake Superior, and concluded that there was a net emigration of 38,784 individuals from the slough to Lake Superior. They also concluded that if all Great Lakes coastal wetlands exported fish at the same level as the Bark Bay Slough, the lake-wide export of forage fish from coastal wetlands to Lake Superior would total approximately 38.5 million individuals. These studies clearly indicate that coastal wetlands contribute significantly to the production of forage fish.. Furthermore, the calculation by Brazner *et al.* (2001) likely underestimates substantially the contribution of coastal wetlands to forage fish production in Lake Superior due to the fact that Bark Bay Slough reaching depths of up to 30 m, resembles a lacustrine environment rather than a wetland environment. Additionally, the shear volume, depth and oligotrophic nature of Lake Superior limits the contribution of coastal wetlands to fish production in the lake itself. In other larget lakes, such as Lake Erie, Lake Winnipeg, and Lake Manitoba, that are relatively shallow (compared to other great lakes) with large surface areas, coastal wetlands likely contribute significantly more to forage fish production relative to

production from Bark Bay Slough. Unfortunately, there is no data available to support this assumption. Derksen & Gillies (1985) found that the shallow Saskeram Marshes of the Saskatchewan Rive delta, dominated by submerged macrophyte beds, produced approximately 90,000 northern pike between 1983 and 1984. Janusz & O'Connor (1985) found that large numbers of sauger, one of Manitoba's most economically important fish, migrated into the Netley-Libau Marsh on the southern shore of Lake Winnipeg in mid-summer to take advantage of the concentrated food resources, specifically young of the year yellow perch. Based on their study of the seasonal abundance of fish in Delta Marsh, Kiers & Hann (1995) concluded that the Delta Marsh on the southern shore of Lake Manitoba was used extensively for spawning and as an important area for rearing young-of-the-year fish of several species.

2.5 Importance of fish in nutrient cycling and the structuring of food-webs in wetlands and shallow lakes

Although it is widely accepted that wetlands are important fish habitat, the trophic importance of fish in wetland communities and their role in nutrient cycling within wetlands is understood poorly (Batzer 1998). One reason for the lack of knowledge is the relative complexity of wetland food webs compared to those of large deep lakes. The lack of knowledge also results from difficulties encountered during sampling. Wetland systems have, for the most part, profuse submersed macrophyte beds that make sampling fish populations very difficult (Dewey *et al.* 1989). Consequently, fish are often inadequately sampled.

Wetland fish communities can influence nutrient cycling directly and indirectly through several mechanisms. Fish can directly affect nutrient cycling by recycling

nutrients through excretion, sediment resuspension, and decomposition. Fish can also act as a storage compartment for nutrients. Additionally, fish can be important vectors in nutrient cycling, transferring nutrients and contaminants accumulated in coastal wetlands to the near shore and/or pelagic environments of their associated lakes. The transport of nutrients by fish between habitats or ecosystems is typically referred to as nutrient translocation (Kitchell *et al.* 1979).

Through the trophic cascade described by Carpenter *et al.* (1985) fish can change the structure of aquatic food webs through selective feeding, thereby indirectly altering nutrient cycling within aquatic ecosystems. Fish can also indirectly alter nutrient cycling by causing physico-chemical changes in the aquatic environment that promote various biogeochemical reactions important in nutrient cycling.

2.5.1 Nutrient cycling by fish: nitrogen excretion and its importance to phytoplankton

Virtually all discussions of fish-mediated nutrient cycling focus on the end products of nitrogen and phosphorus metabolism in fish. These elements are targeted because they are frequently limiting nutrients in aquatic ecosystems and may lead to nuisance algal blooms. Net retention of dietary nitrogen in fish is quantitatively similar to that of omnivorous birds and mammals (40-50%) with up to 60% of dietary nitrogen being excreted in soluble form (Cowey 1995) and available for uptake by phytoplankton. Ammonia is excreted primarily through the gills and is the major nitrogenous excretory product (Sayer & Davenport 1987) comprising approximately 80% of nitrogen excretion in most teleosts (Randall & Wright 1987).

Ammonia excretion rates vary greatly among fish species and are dependent on the state of the animal and environmental conditions (Randall & Wright 1987). Nitrogen excretion is the result of protein catabolism for energy production in fish. As such, nitrogen excretion rates increase with protein intake (Beamish & Thomas 1984). As expected, based on the previous statement, it has been demonstrated that ammonia excretion rates increase dramatically in fed fish relative to starved fish. Brett & Zala (1975) found that baseline ammonia excretion in sockeye salmon (*Oncorhynus nerka*) was 8.2 mg $N \cdot kg^{-1} \cdot hr^{-1}$ and rose to a sharp peak of 35 mg $N \cdot kg^{-1} \cdot hr^{-1}$ approximately four hours after being fed a maintenance ration. Similarly, Mather *et al.* (1995) found N excretion rates in recently fed bluegill (*Lepomis macrochirus*) and gizzard shad (*Dorosoma cepedianum*) ranged between 34.5 – 47.0 mg $N \cdot kg^{-1} \cdot hr^{-1}$, and 5.9 – 101.3 mg $N \cdot kg^{-1} \cdot hr^{-1}$ respectively. Additionally, a study by Alsop & Wood (1997) found that rainbow trout (*Oncorhynus mykiss*) fed to satiation excreted three times more ammonia than fish fed a maintenance ration, and 6 times more than starved fish. Other studies have demonstrated that nitrogen excretion in fish increases with temperature (Kieffer *et al.* 1998), decreases with increasing size within species (Kraft 1992, Mather *et al.* 1995), and increases in fish forced to feed out of phase with their natural regimes due to decreased efficiency in energy conversion (Gelineau *et al.* 1998).

Although ammonia is a major excretory product of aquatic animals, it is thought that this source is quantitatively minor in comparison to that generated by bacterial decomposition in most lakes (Wetzel 1983). Nevertheless, a review of nutrient cycling by freshwater animals by Vanni (2002) found that various fish species and assemblages were able to provide 5 to 49% of the N demand of primary producers through excretion.

2.5.2 Nutrient recycling by fish: phosphorus excretion and its importance to phytoplankton

Phosphorus is an essential element for all life forms, and unlike nitrogen and carbon that can enter aquatic systems through atmospheric fluxes, virtually all phosphorus in surface waters arrives in these systems through surface flows (Correll 1998). Relative to nitrogen, much less is known about the metabolism of P in fish (Cowey 1995). Similar to nitrogen, phosphorus excretion is positively related to dietary uptake of phosphorus (Nakashima & Leggett 1980a) and 85-95% of P excreted by fish is soluble reactive phosphorus that is available for phytoplankton growth (Brabrand *et al.* 1990). Various studies have concluded that fish can comprise approximately 40 – 75% of the total phosphorus in the pelagic regions of lakes (Kitchell *et al.* 1975, Nakashima & Leggett 1980a). Nevertheless, over the last few decades there has been considerable debate over the role of fish in phosphorus cycling in aquatic ecosystems.

An early study by Lamarra, in Kuska Pond, Minnesota,(1975) concluded that benthophagous fish populations at a density of 200 $kg \cdot ha^{-1}$ and a temperature of 22 °C could contribute 2.18 mg $P \cdot m^{-2} \cdot day^{-1}$, significantly increasing internal P loading and stimulating phytoplankton growth. Conversely, Kitchell *et al.* (1975) found that dietary P could not explain increments in body P in the bluegill sunfish (*Lepomis macrochirus*) and suggested that they supplemented their growth through active uptake of P from the water column. However, Nakashima & Leggett (1980a) found that growth of juvenile yellow perch was independent of dietary P levels within the range of P levels found in their prey, contrary to the findings of Kitchell *et al.* (1975). Additionally, Kitchell *et al.* (1975) calculated that bluegill sunfish only remineralized 0.33% of their body P content per day.

For this reason it has often been assumed that zooplankton such as *Daphnia pulex*, that can recycle between 35 and 60% of their total P content per day (Lehman 1980) are much more important in nutrient recycling relative to fish. Results of a study by Nakashima & Leggett (1980b) in Lake Memphremagog, Québec, found that P excretion by littoral fish communities supplied 0.11-0.33% of the requirements of the seston, whereas zooplankton supplied 12% of the daily seston P requirements. Based on these results the authors concluded that phosphorus excretion by fish was unimportant relative to seston P requirements. Contrary to this, Schindler (1992) found that P excretion by sockeye salmon explained 95% of the variation in chlorophyll *a* concentrations in mesocosms and that the zooplankton community had no significant effect on phytoplankton biomass. Furthermore, Kraft (1993) estimated that alewives (*Alosa pseudoharengus*) in Lake Michigan in the 1970s egested and excreted 12,000 tonnes of phosphorus, comparable in amount to the P regenerated through zooplankton in the off-shore epilimnion.

2.5.3 Nutrient recycling vs. translocation

Discrepancies regarding the importance of fish in phosphorus cycling, and nutrient cycling in general, are largely resolved when the overall feeding habits of the dominant fish species in aquatic systems are considered. Commenting on the conclusions of Nakashima & Leggett (1980b), which discounted Lamarra's (1975) findings that fish can contribute significantly to phosphorus cycling, Shapiro & Carlson (1982) argued that unlike planktivorous fish that can transform but not increase total P in the open water, benthivorous fish such as common carp and bullheads are not part of the open water food chain and can add new nutrients to the water column by excreting nutrients accumulated through the consumption of benthic prey. Due to this fact increased P loading from fish is

likely more important in shallow lakes and wetlands, that are well suited to support significant standing crops of benthivorous fish. Additionally, Shapiro & Carlson (1982) agreed with Nakashima & Leggett's (1980b) assessment that P excretion by fish is negligible compared to seston uptake, but that the importance of fish excretion in the P budget of lakes is more appropriately assessed relative to external P loading.

Comparing fish excretion to external nutrient loading in a shallow eutrophic lake, Persson (1997) found that P excretion from fish was of the same magnitude (110%) as the external loading, and that new P introduced by translocation through benthivorous fish constituted 27% of the external P load. Similarly, Brabrand *et al.* (1990) found that excretion by the roach (*Rutilus rutilus*) contributed P at approximately the same order of magnitude as the watershed between May and October, and that the P supply from fish was about double that of external loading between July and September when P loading from the watershed is low. These studies clearly indicate the importance of benthivorous fish in the P cycling of lakes.

2.5.4 Fish mediated nutrient translocation across ecosystem boundaries

In addition to translocating nutrients within a given system (i.e transfer of nutrients from sediment to water column), migrations of fish species can transfer nutrients across ecosystem boundaries (Kitchell *et al.* 1979). Most examples of fish mediated nutrient transfer between ecosystems stem from research on estuaries and coastal marine ecosystems. Laffaille *et al.* (1998) found that 50 tons of particulate organic matter (POM d.w.), consisting of 10.3 tons of organic carbon and 1.7 tons of nitrogen, is exported from the salt marshes of Mont Saint-Michel Bay to the adjacent coastal marine area through fish, accounting for up to 10% of the total POM output from the marshes depending on

the season. Additionally, Deegan (1993) calculated that gulf menhaden (*Brevoortia patronus*) exported approximately 3.1 g N and 0.9 g P·m^{-2} from a Louisiana estuary to the nearshore area of the Gulf of Mexico. These authors also estimated that N and P export by fish was equivalent to 5-10% of primary production in the estuarine area and of the same magnitude as passive export through water. Unfortunately there has been little research examining fish mediated transfer of nutrients between freshwater coastal wetlands and their associated lakes. One study conducted by Brazner *et al.* (2001) found that fish in Bark Bay Slough transferred a total of 1,376 g carbon, 335 g nitrogen, and 73 g phosphorus from the wetland to Lake Superior. However, Bark Bay Slough has a mean depth of approximately 20 m and as such is not representative of a true wetland where water depths are usually less than 2 metres. Fish mediated nutrient transfer is likely much more important in large shallow lakes with extensive shallow coastal wetlands.

2.5.5 Nutrient regeneration through decomposition of fish carrion

Although the earlier studies by Kitchell *et al.* (1975) and Nakashima & Leggett (1980b) claimed that P regeneration through excretion by fish was unimportant, both studies agreed that due to the large amounts of P bound in fish tissue, large mortality events could be a significant source of P to the water column of lakes. Nakashima & Leggett (1980b) calculated that the postspawning mortality of perch in Lake Memphremagog could contribute up to 20% of the external loading to the south basin in spring. In their study, Kitchell *et al.* (1975) estimated that decomposition of adult bluegill after postspawning mortality could remineralize 150 kg of P during late spring and early summer, substantially exceeding external loading. Nevertheless, to date most studies examining the importance of nutrient regeneration through decomposition have been

conducted on small salmon spawning streams. Richey *et al.* (1975) found that phosphate increased in Taylor Creek, California coinciding with the salmon run and that the decomposition of salmon accounted for the difference between upstream and downstream P concentrations. Bilby *et al.* (1995) found that nitrogen released by decomposing coho salmon (*Oncorhynchus kisutch*) contributed significantly to the nitrogen content at various trophic levels, ranging from approximately 17% in collector-gatherers to more than 30% in juvenile coho salmon. Studying the effects of fish carrion decomposition on the nutrient cycling in a freshwater marsh, Parmenter & Lamarra (1991) found that fish carcasses lost 95% of the original carcass N and 60% of carcass P. When one considers the harsh environmental conditions associated with shallow lakes and wetlands, such as summer kill and winter kill, it is obvious that decomposition of fish carcasses can be of particular importance in nutrient regeneration in these systems.

2.5.6 Indirect nutrient recycling by fish: the trophic cascade and size selective predation

Fish directly affected all previous nutrient cycling mechanisms discussed here. In addition fish can indirectly alter nutrient cycling through direct effects on prey assemblages and/or physical properties of ecosystems (Vanni 2002). The trophic cascade theory proposed by Carpenter *et al.* (1985) states that a rise in piscivore biomass brings decreased planktivore biomass, increased herbivore biomass, and decreased phytoplankton biomass. Conversely, reducing piscivore biomass should increase planktivore biomass, decrease herbivore biomass, and increase phytoplankton biomass. In wetlands and shallow lakes, planktivorous fish such as fathead minnows are abundant and promote turbid conditions, where algal biomass is dominated by cyanobacteria (Spencer & King 1984, Zimmer *et al.* 2001).

2.5.6.1 *Planktivorous fish:*

Most of the literature on the indirect effects of fish on nutrient cycling, have specifically focused on the importance of zooplanktivorous fish. In general, it has been demonstrated that increased populations of planktivorous fish can reduce large herbivorous zooplankton, and increase algal biomass (Andersson *et al.* 1978, Vanni & Layne 1997, Vanni *et al.* 1997, Attayde & Hansson 2001). For the most part it has been assumed that these increases in algal biomass were directly proportional to fish mediated reduction of grazing rates (Vanni & Layne 1997). Nevetheless, a meta-analysis conducted by Brett & Goldman (1996) of 54 separate studies that measured the response of zooplankton and phytoplankton to zooplanktivorous fish treatments concluded that phytoplankton biomass did not respond predictably to changes in zooplankton density. This suggests that other factors must be contributing to changes in algal biomass. In addition to reducing grazing pressure through predation, size selective prey consumption by planktivorous fish may affect nutrient recycling rates by the prey community (Kitchell *et al.* 1979) and alter nutrient availability for phytoplankton. Rates of P excretion, and nutrient flux rates in general, are inversely related to mean body size (Andersson *et al.* 1988), and by favouring smaller bodied zooplankton, planktivorous fish increase zooplankton mediated nutrient recycling.

2.5.6.2 *Omnivorous and benthivorous fish:*

Although it is clear that planktivorous fish can stimulate algal biomass in aquatic ecosystems, it has been hypothesized that their impacts are greater in oligotrophic relative to eutrophic systems (McQueen *et al.* 1986). According to Drenner *et al.* (1996) this hypothesis is based on the assumptions that: 1) direct reduction of herbivorous

zooplankton by fish is responsible for increased algal biomass, and 2) cyanobacteria which are resistant to zooplankton grazing are more abundant in eutrophic relative to oligotrophic lakes. Furthermore, the eutrophic pelagic (EP) trophic cascade model proposed by McQueen *et al.* (1986) predicts that as productivity increases, top-down control at lower trophic levels weakens and bottom-up control becomes more dominant. On the other hand, the impacts of omnivorous and benthivorous fish are predicted to be greater in eutrophic relative to oligotrophic systems (Drenner *et al.* 1996, Drenner *et al.* 1998) due to their ability to introduce new nutrients from the littoral region into the pelagic region, in addition to grazing zooplankton. Similar to the effects of planktivorous fish on zooplankton, omnivorous and benthivorous fish can alter the size structure of the macrobenthic community (Blumenshine *et al.* 2000), and increase nutrient recycling rates by selectively feeding on large organisms and releasing smaller organism from predation and competition for resources. Conversely, omnivorous and benthivorous fish may reduce P and N release from the sediment-water interface by consuming benthic organisms such as chironomids and tubificids, that are known to accelerate the transfer of nutrients from sediment to overlying water (Covich *et al.* 1999). Gardner *et al.* (1981) calculated that P excretion by benthic invertebrates could account for most P released from aerobic Lake Michigan sediments. Alternatively, through bioturbation, these organisms increase the depth to which oxygen can penetrate into the sediments and increase their ability to bind phosphate (Scheffer 1998). Due to this fact, reduction of benthic invertebrates may cause increased fluxes of nutrients from the sediments into the overlying waters due to reduced redox conditions. In freshwater wetlands, benthic invertebrates such as chironomids are particularly abundant (Wrubleski 1999), and

generally comprise the highest abundance and biomass in the benthos of many shallow aquatic systems (Wrubleski & Rosenberg 1990), indicating that omnivorous and benthivorous fish can strongly affect nutrient cycling in these systems.

2.5.7 Indirect nutrient recycling by fish: physicochemical effects

Additionally, fish can affect nutrient cycling by altering various physiochemical properties in aquatic ecosystems. For example, stimulating primary production in phytoplankton, whether it is through excretion or predation, increases water column pH which in turn increases the liberation rate of phosphorus from sediments through desorption (Andersen 1975). Additionally, Brabrand *et al.* (1984) found that fish consuming benthic organisms and sediments can introduce sediment derived iron into the pelagic region of lakes stimulating the growth of iron limited phytoplankton, which will increase nutrient uptake. Fish can also physically affect the exchange of nutrients between sediments and water by disrupting the sediment surface and releasing nutrients that accumulate in the interstitial porewaters into the water column. This is particularly important in eutrophic shallow lakes and wetlands, where porewaters can accumulate large quantities of dissolved P and N due to increased rates of decomposition in highly organic sediments (Mayer *et al.* 1999). Conversely, through bioturbation, fish can increase the penetration of oxygen into surface sediments, as do benthic invertebrates and increase the P binding potential of sediments.

Overall, it is evident that fish can play a major role in the cycling of nutrients in aquatic ecosystems, particularly those dominated by shallow littoral areas such as wetlands. In view of this fact, human activities that alter fish communities such as eutrophication and the introduction of exotic species can potentially alter nutrient cycling

in these systems. In the case of coastal wetlands, fish may even be capable of altering the natural role of these systems from sinks to sources of excess nutrients and contaminants.

2.6 Nonindigenous species in freshwater ecosystems

As indicated by fossil records, humans have been introducing species of plants and mammals for more than 10,000 years (Perry & Vanderklein 1996). Nevertheless, the rate of species introductions has increased dramatically with the development of global transportation, and the worldwide spread of nonindigenous species (NIS) is now considered one of the most serious conservation issues. According to the U.S .Congress (1993) the term nonindigenous refers to "the condition of a species being beyond its natural range or natural zone of potential dispersal; including all domesticated and feral species and all hybrids except for naturally occurring crosses between indigenous species". In the future, the spread of NIS will likely increase due to the expansion of global trade, which facilitates introduction of NIS to new regions as geographic barriers are bypassed. Levine & D'Antonio (2003) calculated that NIS would increase between 3 – 24% from 2000 to 2020 in the United States by coupling projected trade forecasts with various species-accumulation models.

According to Pimentel *et al.* (2000) there are approximately 50,000 nonindigenous species (aquatic and terrestrial) in the United States, which are responsible for economic and environmental damages totalling an estimated $137 billion per year. This number becomes particularly impressive when one considers the "tens" rule proposed by Williamson & Fitter (1996), which states that for a variety of NIS, 1 in 10 of those introduced will appear in the wild, 1 in 10 of those will become established, and that 1 in 10 of those established will become invasive. Based on this general statistical rule most

species introductions are unsuccessful and of those that do succeed most are benign. Although only a fraction of transfers are successful, the shear volume has caused many aquatic ecosystems to be replete with NIS. According to Ricciardi & MacIsaac (2000), the Great Lakes are inhabited by 145 NIS and this number is on the rise due to the dumping of ballast waters from Eurasia containing many NIS. Additionally, Cohen & Carlton (1998) counted 234 exotic species established in the San Francisco Bay and Delta, where NIS accounted for 40 to 100% of the common species, up to 97% of the total number of organisms, and up to 99% of the biomass in certain communities (benthos, brackish-water zooplankton and freshwater fish).

Many NIS are considered beneficial, at least to humans. Non-indigenous crops and livestock form the foundation of agriculture in the United States (U.S. Congress 1993) and Canada, and are vital to the economic prosperity of both countries. Other examples of introduced species and their usefulness or desirability to humans include iris (*Iris* spp.) used in horticulture, the European honey bee (*Apis mellifera*) used in apiculture, the soybean (*Glycine max*) used in cattle feed, the African clawed frog (*Xenopus laevis*) used in biomedical research, rainbow trout (*Oncorhynchus mykiss*) introduced for sportfishing, and the ring-necked pheasant (*Phasiannus colchicus*) and the chukar (*Alectoris chukar*) introduced for hunting (Baydack *et al.* 1999). Nevertheless, successful introductions of NIS can sometimes be catastrophic, as was the case in Lake Victoria where the introduction of the Nile perch (*Lates niloticus*) has been blamed for the decline in the diversity and biomass of cichlid fishes (Barel *et al.* 1985). Although the introduction of the Nile perch is generally viewed as a catastrophe by ecologists (Worthington 1989), some studies have argued that the impact of the Nile perch on endemic species in Lake

Victoria has been insignificant (Kudhongania *et al.* 1992) and that its introduction has greatly improved the economy of the region by increasing the total fishery yield nearly fourfold (Kitchell *et al.* 1997).

NIS can invade aquatic habitats through a variety of mechanisms. Some are purposefully introduced, some escape after import, and some enter accidentally (Ruesink & Parker 1995). According to Sakai *et al.* (2001), successful species invasions are composed of three stages consisting of: 1) the introduction of a species into a new habitat; 2) the initial colonization and establishment of a species; and 3) subsequent dispersal and secondary spread into new habitats. Although defining the important stages of an invasion is relatively easy, determining the factors that enhance the invasiveness of a species is particularly complex and likely varies between species and habitats. Intuitively, the successful establishment of a nonindigenous species is usually positively related to propagule pressure (Kolar & Lodge 2001). Simply stated, as the number of individuals introduced and the frequency of introduction events increases, the probability of a NIS becoming invasive also increases. However, in his pioneering work on biological invasions, Elton (1958) proposed that invasion success was determined by 1) characteristics of the invading species, and 2) features of the invaded habitat.

2.6.1 Impacts of NIS on aquatic ecosystems:

After being introduced to aquatic systems, NIS that become established can cause extensive ecological and economic damage through a variety of mechanisms. Simberloff (2002) suggested that the impacts of nonindigenous species could be classified into 6 broad categories consisting of: habitat change, competition, predation, herbivory, disease, and hybridization.

The alteration of aquatic habitats by NIS such as the zebra mussel (*Dreissena polymorpha*) has been widely documented. For example, through its superior filtering capacity, the zebra mussel can change aquatic ecosystems from a turbid state to a clear state by reducing the amount of suspended inorganic particles and phytoplankton in the water column. In the Kingston basin of Lake Ontario, the euphotic zone depth increased by approximately 5 m after the establishment of zebra mussels in the 1990s (Mills *et al.* 2003). Additionally, due its ability to reach high densities, the zebra mussel is known to change the physical structure of benthic environments by completely blanketing benthic substrates, thereby greatly increasing the surface area for colonization by benthic invertebrates.

In many cases, the success of NIS is dependant on their ability to out compete similar native species. One such species, Purple loosestrife (*Lithrium salicaria*) which has expanded rapidly in North America since its introduction in the early 1800s and now occupies more than 120,000 hectares of wetlands. Nagel & Griffin (2004) found that purple loosestrife assimilated 208% more carbon per unit energy invested in leaf biomass relative to two co-occurring native species in the Black Rock Forest, New York. This increase in photosynthetic energy-use efficiency may explain why purple loosestrife has been able to displace so many native wetland plant species in North America. In a study examining competition between the native Sacramento perch (*Archoplites interruptus*) and introduced bluegill (*Lepomis macrochirus*), Marchetti (1999) found that the Sacramento perch gained less weight when grown under food limiting conditions in the presence of bluegill, and suggested that competition may eventually lead to the extinction of Sacramento perch.

Predation by NIS can dramatically alter the species composition and functioning of aquatic ecosystems. The Nile perch, which was introduced in Lake Victoria, greatly reduced the abundance and eventually caused lakewide extirpation of most haplochromine stocks. Additionally, a study by Beisner *et al.* (2003) found that invasion of rainbow smelt (*Osmerus mordax* Mitchell) into two Wisconsin Lakes with dissimilar zooplankton communities dramatically altered these communities. By selectively feeding on larger zooplankton species in both lakes, rainbow smelt caused the zooplankton communities to become more similar to each other, with cyclopoid copepods becoming dominant.

Herbivory by NIS can also have dramatic and negative consequences for aquatic ecosystems. The grass carp (*Ctenopharyngodon idella*) was introduced into the U.S. in the 1960s (Dextrase & Coscarelli 1999), and since it's introduction it has been widely used to control aquatic vegetation. A review conducted by Cassani (1995) found that excessive stocking rates can lead to the complete eradication of vegetation in some systems, which in turn can have negative consequences for water quality, productivity, fish and invertebrate species composition, and waterfowl food resources. Pípalová (2002) found that even when stocked at a low density (29 $kg \cdot ha^{-1}$) in a small pond, grass carp significantly reduced total macrophyte biomass from 109 to 33 $g \cdot m^{-2}$. This low stocking density also had a dramatic effect on macrophyte community structure, where grass carp selectively eliminated filamentous algae, which in turn caused the macrophyte community to become dominated by less edible higher aquatic plants

In addition to the direct effects mentioned above, NIS may also adversely impact aquatic ecosystems indirectly through the introduction of pathogens that can potentially decimate vulnerable native species (Kiesecker *et al.* 2001). The grass carp are assumed to be responsible for the introduction of the Asian tapeworm (*Bothriocephalus opsarichthydis*), into North America, which has infected several native species and other exotics such as the common carp (McCann *et al.* 1996). A study by Dove & Ernst (1998) that examined the parasites associated with five exotic fish species, found that these fish were responsible for introducing four exotic species of monogenean flatworms to Australia. Furthermore, Kiesecker *et al.* (2001) found that mortality was significantly higher for embryos of the western toad (*Bufo boreas*) exposed to hatchery-reared rainbow trout (*Oncorhynchus mykiss*) infected with a pathogenic oomycete, *Saprolegnia ferax*, relative to those exposed to uninfected fish.

The direct impacts of habitat alteration, competition, predation, and herbivory on native species by NIS may be further compounded through hybridization between NIS and similar native species. Through hybridization, NIS can overwhelm and assimilate the native genotype (Huxel 1999) and possibly result in the genetic extinction of native flora and fauna (Rhymer & Simberloff 1996). In North America, the hybrid cattail (*Typha* x *glauca*), which resulted from hybridization between the native broad-leaf (*Typha latifolia*) and the exotic narrow-leaf (*Typha angustifolia*) cattails, has been spreading rapidly throughout wetlands in North America (Galatowitsch *et al.* 1999, Rahel 2002). The rapid spread of *Typha* x *glauca* is due to the fact that it possesses a combination of beneficial traits that it has derived from both parents, such as; the vigorous vegetative habit of *Typha latifolia* and *Typha angustifolia's* ability to colonize deeper habitats

(Waters & Shay 1990). Hybridization has been a problem for the genetic integrity of native fish populations across North America. In Arizona, the principle native trout species, Apache Trout (*Oncorhynchus gilae apache*), is listed as being endangered primarily due to competition and hybridization with introduced trout species (Brown *et al.* 2004).

Simberloff & Von Holle (1999) suggest that the invasion of one species may facilitate the invasion of future species through an invasional 'meltdown' process, whereby habitat alterations induced by the first nonindigenous species facilitates the invasion of a second. Invasional meltdown is likely responsible for the recent success of Ponto- Caspian invaders in the Great Lakes, where invasion of the zebra mussel appears to have facilitated the invasions of other species such as the round goby and *Echinogammarus* (Ricciardi & MacIsaac 2000). Furthermore, the interaction between introductions of NIS, extirpation of native species, and habitat alteration is believed to result in the biotic homogenization of aquatic ecosystems (Rahel 2002). In general, the biotic homogenization of an ecosystem results in reduced spatial diversity as endemic species are typically replaced with widespread exotic species (McKinney & Lockwood 1999). Rahel (2000) found that fish population in the United States have become more similar to one another due to introductions and that on average, pairs of states have 15.4 more species in common now compared to pre-European settlement communities.

Through one or more (and combinations) of the above mentioned mechanisms, biological invasions are responsible for more extinctions than any other factor, excluding human land use changes (D'Antonio & Vitousek 1992). Wilcove *et al.* (1998), found that habitat destruction endangered 85% of the imperilled species included in their study,

while competition or predation by nonindigenous species affected 49% of imperilled species. It is important to note that although habitat destruction is reducing species at a greater rate than NIS, it is much easier to restore degraded habitats than it is to control biological pollutants such as NIS that can reproduce, grow, and disperse once introduced successfully (Perry & Vanderklein 1996).

2.6.2 Characteristics of NIS invading aquatic habitats:

Since 1986, research on NIS has increased dramatically with much of it dedicated to determining whether there are common characteristics that facilitate a species becoming a NIS (Kolar & Lodge 2001). The idea that certain characteristics determined the invasive success of a species was brought to light when Baker (1965) defined the characteristics of the perfect weed. Summarizing these characteristics, Newsome & Noble (1986) stated that the ideal weed is a plastic perennial which will germinate in a wide range of conditions, grow quickly, flower early, is self-compatible, produces many seeds which will disperse widely, reproduces vegetatively and is a good competitor. Similarly, Ehrlich (1989) summarized that successful vertebrate invaders possessed the following attributes: 1) large native range, 2) abundant in original range, 3) high mobility, 4) broad diets, 5) short generation times, 6) ability to shift between r and K strategies, 7) high genetic variability, 8) social, 9) female able to colonize alone, 10) larger than most relatives, 11) associated with humans, and 12) able to function in a wide range of physical conditions. Nevertheless, all of the characteristics listed above are not required for a species to become invasive. Additionally, species possessing a subset of these characteristics do not necessarily become invasive. In general, the characteristics listed by Baker and Ehrlich are parallel to those of the r-strategists that are characterized by short life spans and high

reproductive output. Furthermore, closer examination of these traits reveals two broad categories consisting of those associated with life history traits, and those associated with phenotypic plasticity.

Currently there is some debate regarding which of the aforementioned categories is more important for predicting the spread of aquatic NIS. In a study comparing invasive and indigenous bivalves in North America, McMahon (2002) found that many aquatic invaders had poorer or equivalent physiological tolerance relative to similar native species, suggesting that life history traits (such as reproductive capacity and parental care) are more important than phenotypic plasticity in determining the success of invaders. Conversely, in a study comparing an introduced and a native cyprinid fish, Rosecchi *et al.* (2001) found that invasion success was determined by the ability to tolerate environmental changes through phenotypic plasticity, rather than from life-history traits pre-adapted to invasion. In all likelihood the importance of these categories to the success of aquatic invaders probably varies among plants, invertebrates, and vertebrates, and even within similar species. In summarizing the similarities in aquatic plant and fish invasions in Australia, Arthington & Mitchell (1986) concluded that success in the initial stages of biological invasions is dependent on reproductive capacity with most invasive plants and fish being opportunist r-strategists with high reproductive rates. Additionally, it is believed that some degree of preadaptation is essential for a NIS to successfully establish itself in a new environment (Sakai *et al.* 2001). Recent studies suggest that evolutionary genetics may determine whether an invasion succeeds by providing genetic substrate upon which natural selection could act (Lee 2002), allowing the introduced organism to adapt to its new environment. Species invasions offer some of

the best opportunities to study rapid evolution, however, the genetics of invasive species has received little attention relative to their ecology (Sakai *et al.* 2001).

2.6.3 Characteristics of freshwater habitats that promote invasions of NIS

Although species characteristics are paramount in determining the success of an invading NIS, characteristics of the habitat that they are invading are also important. One key characteristic that has long been hypothesized to influence the invasibility of a community is its diversity (Levine & D'Antonio 1999). Elton (1958) was the first to suggest that simple plant and animal communities lack stability, relative to diverse communities, and are therefore more vulnerable to invasions. This theory is the basis of the "biotic resistance" model (Ricciardi 2001), which predicts that the rate of establishment of new species in a system should decrease with time as new species are accumulated. Elton's theory was supported by Moyle (1986) who found that fish introductions in the western United States were more successful when introduced to waters with depauperate fish communities. Conversely, Levine (2000) found that the incidence of exotic plants was significantly greater on more diverse tussocks in a Californian riparian system. Furthermore, Ricciardi (2001) found that the invasion history of the Great Lakes was better explained by the invasional meltdown model, where invasions increase with increasing diversity, than by the biotic resistance model.

In addition to the diversity of a habitat, the level of anthropogenic habitat disturbance may also increase the invasiveness of NIS. Anthropogenic disturbances occur on much shorter time scales than the evolutionary responses of native species and therefore may select certain NIS with genetic traits that provide them with a competitive advantage over native species. Other factors, such as human induced global changes, particularly the

globalization of commerce, construction of dams and canals, urbanization and conversion of land to agriculture, climatic and atmospheric changes, and some practices of fisheries management (Kolar & Lodge 2000) can increase the potential for NIS invasions. A study by Ross *et al.* (2001) found that successful invasions of exotic and nonindigenous fish into river systems in northern Appalachia, were the result of changes to water and habitat quality related to anthropogenic and natural disturbances. Similarly, Meador *et al.* (2003) found that 18% of the fish taxa in 20 major river basins in the United States were introduced and that the richness of introduced fish species was related to factors such as increased human population density and increased water column concentrations of total nitrogen and phosphorus. Of all the introduced fish collected in this study, the common carp was the most frequently collected and occurred in 48.4% of the 157 sites studied.

Of the various types of aquatic ecosystems, wetlands are particularly susceptible to invasions by NIS due to their location at the land-water interface. Zedler & Kercher (2004), found that although <6% of the earth's land mass is wetland, 24% of the world's most invasive species are wetland species. Lavoie *et al.* (2003) found that exotic species comprised 13.7% of the vascular flora of the St. Lawrence River wetlands. The fact that wetlands can contain purely aquatic habitats and terrestrial habitats as well as a range of intermediate habitats alone increases the potential for invasions by NIS who can invade through the terrestrial or aquatic component of the wetland. Additionally, as discussed earlier, freshwater wetlands worldwide have undergone significant degradation due to anthropogenic activities and are therefore more susceptible to invasions by opportunistic species capable of out-competing native species.

2.7 The common carp (*Cyprinus carpio*): description and biology

2.7.1 Description

The common carp (*Cyprinus carpio*) is the largest cyprinid species and has a robust and laterally compressed body (Scott & Crossman 1973), large scales, an elongate dorsal fin, and spines at the leading edges of the dorsal and anal fins (Stewart & Watkinson 2004). Similar to other minnows the common carp has a Weberian apparatus, cycloid scales, pharyngeal teeth in the throat, and no teeth on the jaws (Panek 1987). Common carp also possess two pairs of barbells about the mouth, with the pair located posteriorly at the corners of the mouth being the larger of the two (Scott & Crossman 1973). Colouration can be quite variable but adults are typically olive-green dorsally, yellowish ventrally, and have fins that are often reddish. There are three distinct varieties of carp: 1) the wild scaled form; 2) the mirror carp with several rows of large scales; and 3) the leather carp, which is scaleless (Hinks 1943). The later two varieties are the result of domestication. Typically, only the wild form and mirror carp are found in Manitoban waters. However, Stewart & Watkinson (2004) reported that another variant of this species, the koi carp, can be found in the urban Winnipeg area as a result of the illegal release or escape of aquarium fish.

Common carp grow rapidly, and in Delta Marsh, Manitoba, Canada underyearlings can reach lengths in excess of 120 mm (fork length) by late August (Appendix A). Common carp can live for a maximum of approximately 20 years and the largest specimen caught in Manitoba measured 108 cm (Stewart & Watkinson 2004). Due to their fast growth rate and large serrated spines, common carp are only available as prey to piscivorous birds and fish for a short period of time.

Additionally, ostariophysan fishes including the common carp have an improved sense of hearing relative to other fish species due to a bony connection between the swim bladder and the ear known as the Weberian apparatus (Bond 1996). Volume changes in the swim bladder cause the Weberian apparatus to transmit pressure changes to the ear, allowing common carp to respond to a larger range of frequencies relative to other fish (Lagler *et al.* 1962). The acute sense of smell that common carp possess allow them to avoid predators by using an alarm response that is triggered when predators damage the skin of a fish, which then releases sensory chemicals into the water.

Furthermore, common carp are able to withstand a suite of environmental conditions that are typically detrimental to most fish species. Common carp have a broad temperature tolerance and can inhabit ice-covered lakes and survive for short periods at a temperature of 41°C (Panek 1987). Common carp are also tolerant of very low dissolved oxygen concentrations and have been observed gulping air at the surface of hypoxic waters associated with cyanobacterial blooms (Gehrke & Harris 1994).

2.7.2 Habitat

In North America, common carp occur 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). More importantly is their ability to invade and dominate in degraded aquatic ecosystems due to their tolerance of elevated levels of salinity (Lam and Sharma 1985) and turbidity (Buck 1956; Alabaster and Lloyd 1980), and hypoxic conditions (Zhou *et al.* 2000). According to McCrimmon (1968), common carp need two basic habitat requirements to maintain viable population in Canadian waters: a shallow marsh environment for spawning, and an area of deep water to which they can retreat

during winter. Common carp generally prefer shallow, weedy habitats with muddy or sandy bottoms where they can easily graze benthic prey items (Panek 1987). This is likely the main reason why common carp have not become well established in the Precambrian Shield region to the east of Lake Winnipeg, where lakes typically have rocky substrates. Additionally, common carp prefer warm shallow waters and rarely occur at depths greater than 30 m (Sigler 1958).

2.7.3 Seasonal movements

Seasonal movements by common carp in Manitoba are regulated by their habitat requirements for spawning and over-wintering. In spring, common carp inhabiting Manitoba lakes move into shallow littoral waters or adjacent marshes and wetlands with abundant submerged or flooded vegetation, which they use for spawning. Additionally, prior to spawning, there is a well-marked upstream movement of common carp in Manitoban rivers (Stewart & Watkinson 2004). This upstream migration can often be witnessed in the City of Winnipeg, where large schools of common carp can be observed as they move into the Seine River from the Red River in late spring or early summer.

After spawning, common carp remain in shallow waters with abundant submerged macrophyte cover for most of the summer. Ottis & Weber (1982) found that common carp in Lake Winnebago, Wisconsin spent most of the summer in 0.9 – 1.2 m of water and were usually associated with beds of pondweed. Although common carp typically remain in shallow littoral regions with abundant submerged macrophytes throughout the summer, there is mounting evidence that they are not as restricted in their movement as was originally thought. In a telemetry study conducted in Delta Marsh, Wrubleski (unpublished report 2000) found that common carp left the marsh on several occasions to

return to Lake Manitoba for short periods of time, usually returning within the same day. Furthermore, the number of days individual carp were tracked in the marsh in this study was quite variable, ranging from 12 to 77 days.

As fall approaches and temperatures begin to cool, carp leave the shallow waters they inhabit during the summer and migrate to deeper warmer waters where they overwinter (McCrimmon 1968). A telemetry study conducted in Lake Winnebago by Ottis & Weber (1982) found that the home ranges of radio tagged carp (n=19) were restricted to the deepest part of the lake and were about one-third of the size of summer home ranges. Similarly, Johnsen & Hasler (1977) found that carp populations aggregated in two deep-water areas in Lake Mendota, and that carp originating from different parts of the lake appeared to arrive at these sites with relative synchrony.

2.7.4 Reproductive biology and early life stages

In Manitoba, carp typically spawn in May and early June (Stewart & Watkinson 2004). As temperatures rise in the spring, large numbers of adult carp congregate in shallow waters with abundant submerged vegetation, where they eventually form smaller breeding clusters consisting of 1-3 females and 2-15 males (Scott & Crossman 1973). Spawning activity usually occurs at water depths less than 0.5m and consists of breeding clusters thrashing about violently over submerged macrophyte beds or along shorelines with emergent vegetation. During spawning, females release adhesive eggs (approximately 1 mm in diameter) that are scattered and attach to submerged vegetation (Stewart & Watkinson 2004).

According to Swee & McCrimmon (1966), common carp in Lake St. Lawrence, Ontario begin spawning at 17°C, with maximum spawning activity occurring between 19 and 23°C. Additionally, these authors found that spawning activity decreased at 26°C and ceased at 28°C. Although the common carp is generally assumed to be a spring spawner (Swain 1979), carp may spawn into late summer if temperatures permit (Scott & Crossman 1973). In Delta Marsh, Manitoba, it is not rare to see carp spawning as late as early August (personal observation). This is supported by the size variation in young-of-year (YOY) carp populations observed in the MERP cells in late August, where length ranged from 2.0 – 11.0 cm, and weight ranged from 0.2 to 23.9 g (Appendix A). The size of the smallest YOY carp observed on August 21 suggest that spawning occurred at least until late July or early August.

According to Swain (1979), carp are among the most prolific of freshwater fishes. In fact, it is believed that the generic name of carp was derived from a secondary name of Aphrodite, the goddess of love, due to their high fertility (Balon 1995). The high reproductive capacity of the common carp is due to its early sexual maturity, relatively long life, and ability to produce enormous quantities of eggs. Swee & McCrimmon (1966) found that fecundity varied enormously in carp specimens in Lake St. Lawrence, Ontario, and ranged from 36,000 eggs in an age IV fish (394 mm) to 2,208,000 eggs in an age XVI fish (851 mm). In areas where extensive spawning has occurred, egg densities may reach levels as high as 3000 eggs$\cdot m^{-2}$ of bottom (Panek 1987). The efficiency of natural fertilization was estimated by Swee & McCrimmon (1966) to be approximately 90% based on observations of egg masses attached to aquatic vegetation.

The time required for carp eggs to hatch varies substantially with temperature (Swain 1979). In Manitoba, hatching likely occurs within the same time frame (3 to 6 days) that has been reported for other northern populations of carp (Swee & McCrimmon 1966). At the time of hatching, fry average 5.0 to 5.5 mm in total length (Swain 1979). Once fry attain a total length of 6 mm they are able to attach to aquatic vegetation. At 7 mm the air bladder is filled with air, and at 8 mm the yolk sac has normally disappeared and the fry swim well and feed actively on plankton (McCrimmon 1968). Scales begin to form when juveniles attain lengths between 16-18 mm and are completed at lengths between 22-25 mm (Scott & Crossman 1973). Juvenile carp remain in shallow, well-vegetated sites, during the majority of their first growing season where they are sheltered from predators. Growth rates of juveniles depend on factors such as temperature and food availability, but carp in southern Ontario and Manitoba typically attain lengths between 130 and 190 mm during the first growing season (Scott & Crossman 1973).

2.7.5 Diet and trophic position

Carp are omnivorous fish that consume a wide variety of organisms and have highly specialized feeding structures that allow them to be very selective in the prey they consume. Studies by Sibbing (1988) and Sibbing *et al.* (1986) demonstrated that food handling and processing in the common carp consists of ten head movements that fulfil the following twelve feeding actions: 1) particulate feeding for intake; 2) particulate gulping for intake; 3) rinsing; 4) repositioning; 5) selective retention; 6) spitting (for selection); 7) gathering from the branchial sieve; 8) transport; 9) loading of the teeth; 10) crushing; 11) grinding; and; 12) deglutition.

In general, microcrustacea are the dominant food source for juvenile carp. Additionally, benthic invertebrates are always an important part of the diet of the common carp and increase in importance as carp increase in size. In two lakes in western Australia, Khan (2003) found that the diet of carp larvae <2 cm consisted entirely of cladocerans, and at lengths >2 cm they began to include benthic prey items. Similarly, in a study examining the food of carp in the Bear River Refuge in Utah, Sigler (1958) found that young-of-the-year carp fed almost exclusively on small crustaceans, with cladocerans and copepods occurring in 62% and 100% of the stomachs examined in the study. In this same study, Diptera, consisting mostly of larval chironomids, comprised between 40 and 87% of the stomach contents of adult carp, and crustaceans comprised between 1 and 17%.

In addition to the above mentioned soft tissue animal material, carp are able to incorporate molluscs and plant material into their diet due to the molarlike surfaces of their pharyngeal teeth which allow them to crush and grind hard surfaces. García-Berthou (2001) and Sigler (1958) found that plant material comprised greater than 10% of the stomach contents of adult carp. Additionally, Crivelli (1981) found that the stomachs of adult carp in the Camargue, in southern France, contained up to 1000 seeds. Marsden (1997) found that 77% of carp collected in summer in Lake Michigan contained zebra mussels. Additionally, the stomachs of a subset of the above mentioned carp contained a substantial amount of lake trout eggs, likely as a result of the fouling of cobble substrate by zebra mussels that prevented the eggs from settling into the interstitial spaces.

2.8 The common carp (*Cyprinus carpio*): history, distribution, and economic significance in Manitoba

The common carp (*Cyprinus carpio*) has one of the longest and richest histories of all freshwater fish species. According to Balon (1995) the wild ancestor of the common carp originated in the Asian watersheds of the Black, Caspian, and Aral seas, and dispersed east into Siberia and China and west as far as the Danube River. However the original range of the common carp is somewhat unclear due to transfers from the Danube River to Greece and Italy during the Roman Empire and its widespread culture by Christian monks throughout Europe in the Middle Ages (Panek 1987). The theory that Christian monks spread carp has been challenged by new anthropological evidence that suggests that carp were more likely transferred by peasant fishers who used them for subsistence and commercial purposes in Medieval Europe (Hoffmann 1994).

Today, thanks to the help of humans, the common carp enjoys a near worldwide distribution (Figure 2.1). In fact, according to the FAO Database on Introductions of Aquatic Species, the common carp is the most introduced species of fish (Table 2.1) and has been introduced to more than 100 countries, usually for aquaculture production. Due to the hardiness of this fish species, its use in aquaculture has increased dramatically since the mid 1980s (Figure 2.2). In 2000, worldwide aquaculture produced 2,682,543 metric tonnes of carp at a value of U.S. $2.8 billion (FIGIS 2005a). Of all fish species used in aquaculture, the common carp is the third most productive and valuable. Although aquaculture is the primary reason that the common carp was introduced to Europe, Asia, and the Middle East it is also a prized sport fish in many European

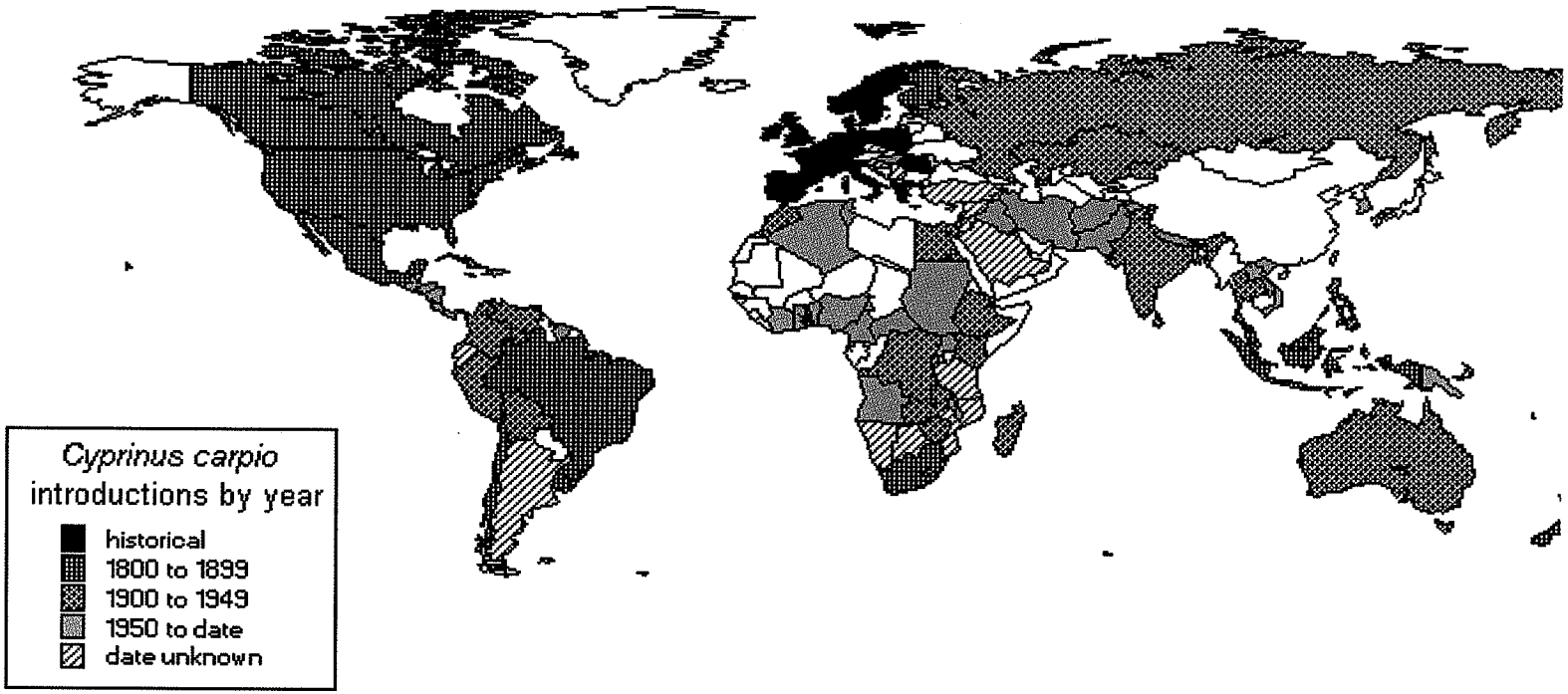

Figure 2.1. *Cyprinus carpio* introductions by year. Modified from the Database on Introductions of Aquatic Species (FIGIS 2005b)

countries such as France and England where they are commonly stocked in sport fishing ponds.

Common carp were first introduced into North America in 1872 when Julius A. Poppe imported a shipment of carp from Reinfeld, Germany, which he cultured in specially designed ponds on his farm in California (McCrimmon 1968). Seeing the success of Poppe, the U.S. Fish Commission began importing common carp from Germany in the late 1870s, with thousands of fish distributed to various U.S. states and Canadian provinces by the early 1880s. The purpose of most introductions of common carp into North America was to provide a stable food source. However, by 1897, introductions were halted due to growing public disapproval of the species (McCrimmon 1968).

The common carp was introduced intentionally to Manitoba, Canada, when fish from Minnesota were stocked in the Assiniboine River watershed southeast of Brandon in 1886 (Stewart & Watkinson 2004). These early attempts at introduction failed and common carp only became established after populations from the Northern U.S. entered the province through the Red River (Atton 1959). In fact, the common carp was largely unknown in Manitoba until 1938, when it was positively identified in the Red River near Lockport (Hinks 1943). Today, the common carp is ubiquitous in the southern and central regions of the province with the exception of the eastern portion of the province where the rocky substrates and clear deep waters typical of the Canadian Shield do not provide suitable habitat to support viable populations.

Table 2.1. List of the most introduced fish species. Modified form the FAO Database on Introductions of Aquatic Species (FAO 1997).

Scientific name	**Common name**	**Number of introductions**
Cyprinus carpio	Common carp	124
Oncorhynchus mykiss	Rainbow trout	99
Oreochromis mossambicus	Mozambique tilapia	92
Ctenopharyngodon idella	Grass carp	91
Oreochromis niloticus	Nile tilapia	80
Hypophthalmichthys molitrix	Silver carp	79
Gambusia affinis	Mosquitofish	67
Micropterus salmoides	Largemouth black bass	64
Hypophthalmichthys nobilis	Bighead carp	55
Carassius auratus	Goldfish	54

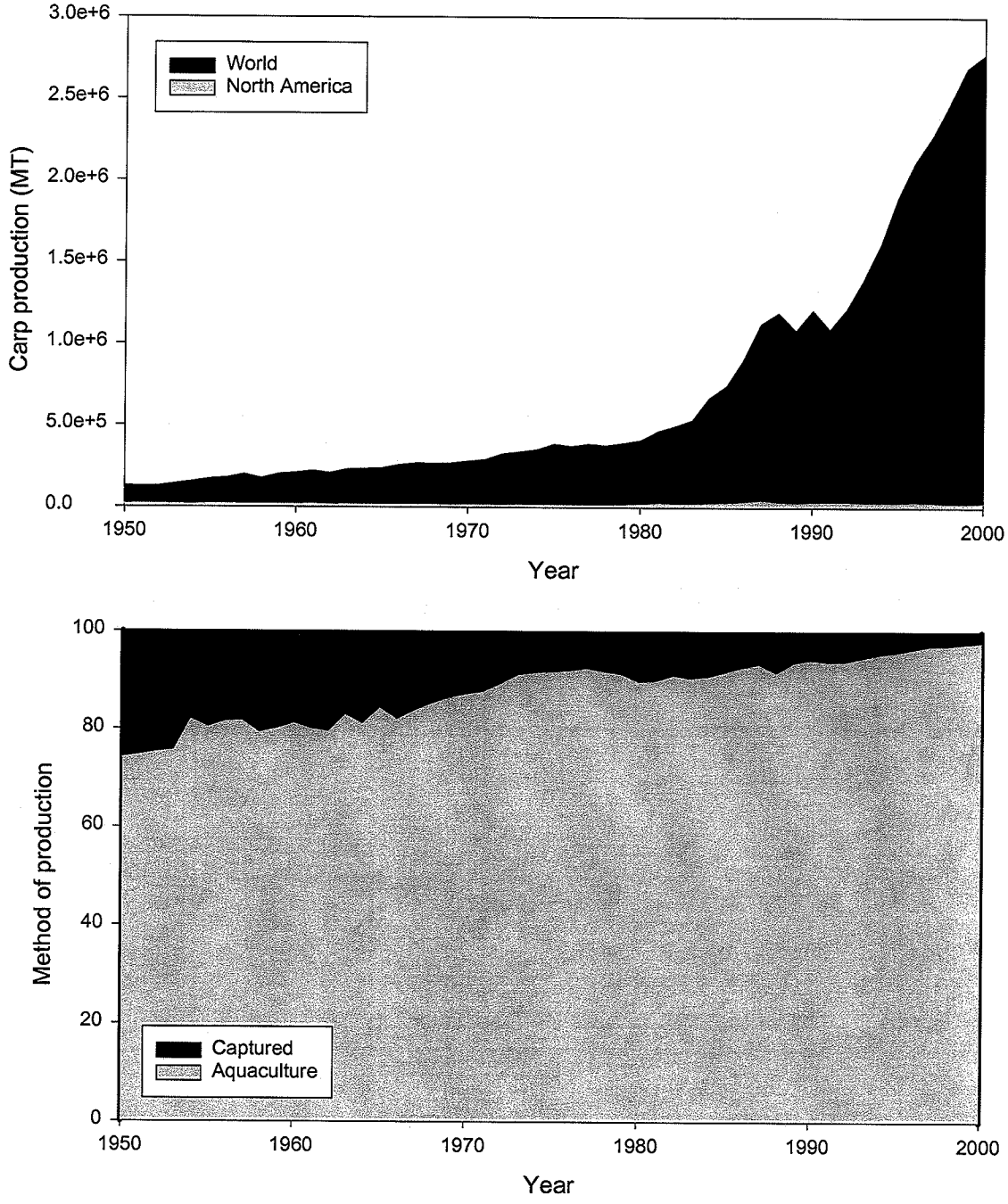

Figure 2.2. Global common carp production. Upper panel shows total global common carp production and North American common carp production (metric tons). Bottom panel shows the method of production used to obtain carp (taken from FIGIS 2005a).

Before 1940, common carp were found only in the waters of the Red River (Figure 2.3a). After invading the province from the south, common carp spread quickly throughout the Red and Assiniboine River watersheds and established themselves in the south basins of Lakes Winnipeg and Manitoba (Figure 2.3b). The greatest range expansion occurred between 1950 and 1970 when common carp were able to easily access the northern and western portions of the province after successfully invading Lake Winnipeg, Lake Manitoba, and Lake Winnipegosis, the largest lakes in the province (Figure 2.3c). Swain (1979) indicated that by 1976 the common carp was found in most large lakes and virtually all major river systems in Manitoba, with the exception of the Churchill River system.

A specimen collected from Split Lake (Figure 2.3d) in 1963 was considered to be the most northerly record for the distribution of common carp in the world (McCrimmon 1968). These original reports stated that common carp caught from Split Lake were very skinny and unhealthy. According to Atton (1959) cold summer temperatures prevented the common carp from invading the Churchill River system. Based on these facts, it was believed that the common carp would not become established in the northern portion of the Nelson River and would not invade the Churchill River system. However, as illustrated in Figure 2.3d, the common carp has migrated northward through the Nelson River system and, in the last decade, has become established in the Churchill River system according to common carp production data spanning the period of 1970 to 2004.

On the Nelson River system, common carp seem to have become established in Split Lake where commercial catches (3 – 74 kg per year) have been reported starting in 1996. Fish monitoring studies for the Limestone Generating Station (C. Barth, North/South

Figure 2.3. Range expansion of the common carp (*Cyprinus carpio*) in Manitoba A) prior to 1940, B) prior to 1950, C) prior to 1970, and D) prior to 2000. Carp distributions prior to 1970 were estimated based on date of first occurrences reported in Swain (1979), while the range expansion between 1970 and 2000 was estimated from common carp production data provided by Manitoba Conservation and the Freshwater Water Fish Marketing Corporation for the period of 1970 to 2000. Numbers in plate D indicate locations discussed in the text: 1) Split Lake, 2) Stephens Lake, 3) Limestone Generating Station, 4) Britton Lake, 5) Sisipuk Lake, 6) Guthrie Lake, 7) Highrock Lake, 8) Southern Indian Lake, 9) Loon Lake, 10) Churchill River Estuary, and 11) Nelson River Estuary.

Consultants Inc., personal communication), and the proposed Gull Generating Station (Pisiak et al., 2004, unpublished report) indicate that common carp have continued to migrate down the Nelson River system and can now be found in Stephens Lake and as far north as the forebay of the Limestone Generating Station (Figure 2.3d). Furthermore, the mean condition factor calculated for common carp between 620 and 730 mm in Delta Marsh on the south shore of Lake Manitoba was 1.82 ± 0.06 (N=29) (D.A. Wrubleski, 2000 unpublished data), lower than the mean condition factor of 2.11 ± 0.04 (N=3) calculated for common carp caught in the Burntwood River and Stephens Lakes in northern Manitoba during fish monitoring studies conducted by North/South Consultants (Holm and Remnant 2002, Pisiak et al., 2004, unpublished report). These results suggest that common carp have adapted to the habitat in the northern extent of the Nelson River system and are actually heavier than fish of the same length caught in the southern portion of the province.

More important than the northward expansion of common carp on the Nelson River system is the invasion of the Churchill River system in the last decade. Recent fisheries records provided by the Freshwater Fish Marketing Corporation for northern Manitoba indicate that the common carp is now established in and around the Churchill River system with commercial catches reported from Britton, Guthrie, Highrock, Loon, Sisipuk, and Southern Indian Lakes (Figure 2.3d). Commercial catches in these lakes were much higher (range 8 – 1,184 kg per year) relative to those reported from Split Lake on the Nelson River system. Common carp were likely introduced into the Churchill River system from the Saskatchewan River system, either by fishers using them as bait or by birds that may have transferred carp eggs from one system into the other.

Based on the fact that common carp were found in Split Lake as early as 1963, it is not surprising that they have continued to migrate northward through the Nelson River system. However, the fact that these fish appear to be as healthy, if not healthier (based on condition factor), than those from the south indicates that a change must have occurred to allow the establishment of healthy populations. The two basic habitat requirements necessary to sustain common carp populations are: 1) a shallow marsh environment with abundant aquatic vegetation for spawning and, 2) an area of deep water where common carp can overwinter (McCrimmon 1968). I hypothesize that the construction of the Kettle Generating Station in 1974 at the outlet of Stephens Lake on the Nelson River provided the necessary habitat requirements to sustain and allow the establishment of healthy populations of the common carp in Split Lake and Stephens Lake. Construction of this generating station increased the size of Stephens Lake by 242 km^2 and resulted in the flooding of 192 km^2 of land (Environment Canada / Fisheries and Oceans 1992b). This created an extensive area of shallow marsh-like habitat where common carp could spawn in summer. This was the case in Ontario where Swee & McCrimmon (1966) reported that Lake St. Lawrence near Cornwall, formed as the result of flooding during hydroelectric development on the St. Lawrence River, provided ideal spawning habitat for common carp. However, it was also noted that fluctuations in lake level associated with hydroelectric activities caused many of the eggs attached to vegetation to be exposed and destroyed. More importantly, the construction of the Kettle Generating Station, with a forebay head of 30 m (Environment Canada / Fisheries and Oceans 1992b), created a deep basin with warmer profundal waters to which common carp can escape during cold winter months.

The completion of the Churchill River Diversion in 1976 raised the water level in Southern Indian Lake by approximately 3 m and flooded 187 km^2 of surrounding land (Environment Canada / Fisheries and Oceans 1992b). Like the flooding experienced on Stephens Lake after the construction of the Kettle Generating Station, flooding on Southern Indian Lake would have also provided ideal spawning habitat for common carp. The extensive flooding on Southern Indian Lake increased shoreline erosion and drastically increased suspended sediment concentrations in the lake from 5 $mg \cdot L^{-1}$, pre-impoundment, to 30-50 $mg \cdot L^{-1}$, post-impoundment (Environment Canada / Fisheries and Oceans 1992a). This anthropogenic increase in suspended sediments would have conferred a competitive advantage to common carp, who can feed more efficiently relative to sight-feeders in highly turbid waters due to their superior olfactory senses (Panek 1987).

Additionally, water flows on the Churchill and Nelson River systems have been dramatically altered as a result of the Churchill River Diversion, which has diverted 80% of the flow from the Churchill River at Southern Indian Lake into the Nelson River system. Common carp are found in large slow moving rivers as well as fast flowing streams (Panek 1987). Due to the ability of common carp to inhabit waters of varying flow, the increased flow on the Nelson and decreased flow on the Churchill as well as the increased variability in flows in both systems as a result of hydroelectric development would also have conferred an advantage to the common carp relative to native fish who may be less tolerant of variations in flow regime.

Overall, it is not surprising that the common carp seems to be expanding and invading further into northern Manitoba in step with hydroelectric development, as many authors have demonstrated the link between anthropogenic habitat alteration and invasibility of ecosystems (Moyle & Light 1996, Keith & James 1999, Byers 2002). Furthermore, Keith & James (1999) showed a positive correlation between the number of reservoirs and the number of introduced species in North American drainages. Given that common carp has already been reported in subarctic regions (Lukin 1999) and is tolerant of a wide range of salinity levels (Lam & Sharma 1985) it is only a matter of time before the populations of common carp established on the Nelson and Churchill River systems reach the Churchill River and Nelson River estuaries.

Relative to other fish species such as walleye and lake whitefish, common carp are generally considered to be unimportant economically. However, since their establishment, there has been a long history of major commercial carp fisheries in Ontario and Manitoba (McCrimmon 1968). These fisheries appear to be especially productive in large shallow lakes with extensive coastal wetlands, such as Lake Erie in Ontario, and Lakes Manitoba, Winnipeg, and Winnipegosis in Manitoba. Over the last few decades as common carp have expanded their range in Manitoba many more carp fisheries have developed, with commercial catches (although irregular) reported as far North as Southern Indian Lake on the Churchill River system (Figure 2.4). Although there are numerous lakes reporting commercial harvests of common carp, total production for Manitoba is comprised almost entirely of catches from Dauphin Lake, Lake Manitoba, Lake Winnipeg, Lake Winnipegosis, and Lake St. Martin (Table 2.2). These fisheries appear to be the most productive in Canada, accounting for 33 to 98% of

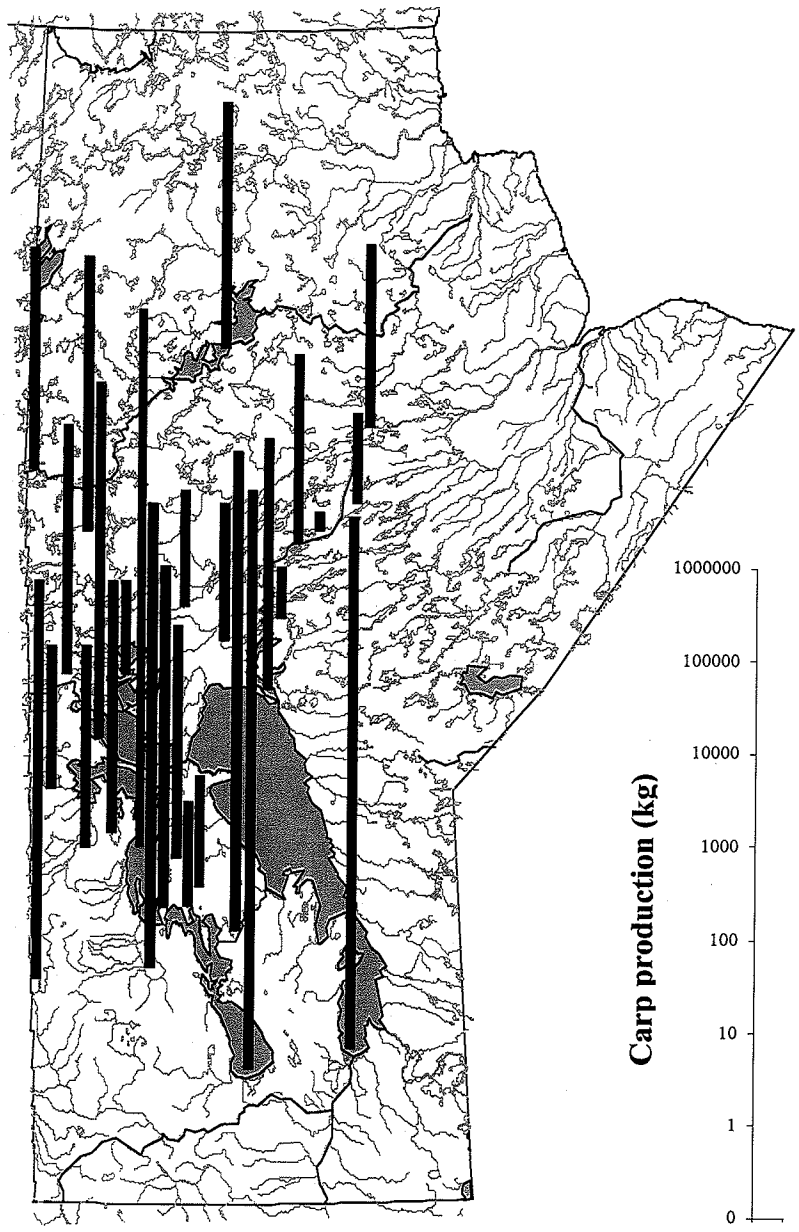

Figure 2.4. Location of the major carp fisheries in Manitoba. Bars represent the mean weight (kg) delivered annually between 1990 and 2003 (data provided by the Freshwater Fish Marketing Corporation).

total production between 1991 and 2001 (FIGIS 2005c; Freshwater Fish Marketing Corporation 2004, unpublished data). During this period, Lake Manitoba was always the largest producer of carp with the fishery worth an estimated $95,000 annually.

2.9 Impacts of the common carp (*Cyprinus carpio*) on freshwater ecosystems

The common carp can, directly and/or indirectly, negatively impact aquatic ecosystems by: 1) increasing total suspended solids, sedimentation and erosion; 2) increasing water column nutrient concentrations; 3) increasing the biomass and altering the community structure of phytoplankton; 4) decreasing submerged macrophyte abundance 5) decreasing large zooplankton; 6) decreasing benthic invertebrates; 7) reducing native fish diversity and abundance; 8) competing with waterfowl for food resources; and 9) by altering contaminant cycling.

2.9.1 Total suspended solids, sedimentation and erosion

The most notable impact of common carp in aquatic ecosystems is the increase in total suspended solid concentrations (particularly inorganic suspended solids) and water column turbidity, which are a direct result of their feeding and spawning activities that greatly disturb surface sediments. Additionally, by increasing water column nutrient concentrations, carp can indirectly increase total suspended solids concentrations and turbidity by increasing phytoplankton abundance (see section 2.9.3).

Many mesocosm studies examining the impacts of common carp on water quality have demonstrated that this species significantly increases suspended solids (and

Table 2.2. Total common carp capture production (Metric tonnes) for Canada, Manitoba, and the five major carp producing lakes in Manitoba. Data for Manitoba common carp production was provided by the Freshwater Fish Marketing Board, whereas total Canadian production was from FIGIS (2005c)

	Major carp fisheries in Manitoba							
Year	Lake Winnipeg ($kg \cdot 10^3$)	Lake Manitoba ($kg \cdot 10^3$)	Lake Winnipegosis ($kg \cdot 10^3$)	Lake St. Martin ($kg \cdot 10^3$)	Lake Dauphin ($kg \cdot 10^3$)	Manitoba Total ($kg \cdot 10^3$)	Canada Total ($kg \cdot 10^3$)	Carp production in MB as a percentage of total Canadian production
1991	25	189	77	0	1	318	801	40
1992	52	330	65	1	10	483	494	98
1993	7	28	36	1	14	87	222	39
1994	18	170	108	1	3	302	649	46
1995	25	195	53	2	6	288	619	47
1996	49	194	46	3	15	310	687	45
1997	98	178	77	33	4	392	543	72
1998	93	143	35	38	5	314	354	89
1999	13	140	49	38	0	241	741	33
2000	0	236	49	3	8	357	516	69
2001	88	162	58	16	12	335	506	66

turbidity), particularly the inorganic fraction (Roberts *et al.* 1995, Angeler *et al.* 2002, Parkos III *et al.* 2003). Studies at the mesocosm scale (Breukelaar *et al.* 1994,Lougheed *et al.* 1998) and the whole ecosystem scale (Meijer *et al.* 1989) have also found that suspended solid concentrations typically increase in a linear fashion with carp biomass. Conversely, Zambrano *et al.* (2001) suggested that carp only increase suspended solids substantially when a critical carp density is exceeded.

Although most studies have concluded that carp increase suspended solids, the range of impacts among studies is enormous. Parkos III *et al.* (2003) found that stocking carp at a density of 476 $kg \cdot ha^{-1}$ in 0.06 ha enclosures increased the mean suspended solid concentrations by more than 50 $mg \cdot L^{-1}$ over three months. Conversely, experiments conducted in central Spain, at carp densities ranging between 5,000 – 6,000 $kg \cdot ha^{-1}$ only increased mean suspended solid concentrations in enclosures by approximately 20 $mg \cdot L^{-1}$ (Angeler *et al.* 2002). The discrepancy in suspended solid concentrations between these studies is likely the result of the different sizes of carp and enclosures that were used.

Experiments where common carp have been excluded or removed from whole ecosystems have also concluded that common carp are responsible for increasing suspended solids (Lougheed *et al.* 2004, Schrage & Downing 2004). Lougheed *et al.* (2004) found that by excluding common carp from Cootes Paradise, turbidity was reduced by 40 and 60 percent at open-water and vegetated areas in the marsh, respectively. Enclosure studies conducted within the marsh prior to exclusion of the carp significantly increased total suspended solids, particularly the inorganic fraction (Lougheed *et al.* 1998). Similarly, Barton *et al.* (2000) found that eliminating the

common carp population in Laurel Lake Reservoir, Ontario, the fraction of inorganic sediments in the outflow was reduced by approximately 45%. Schrage & Downing (2004) also found that excluding common carp from Ventura Marsh in Iowa significantly reduced suspended solids. However, in this last study it was the organic suspended solids that were reduced, indicating that in some systems common carp may affect total suspended solids by resuspending inorganic suspended solids or by enhancing phytoplankton growth.

As a result of increasing suspended solids concentrations, common carp increase sedimentation rates in aquatic ecosystems. Richardson *et al.* (1990), Breukelaar *et al.* (1994), and Szumiec *et al.* (1995) found that particle settlement rates increased with increasing carp densities. As was the case for suspended solids, sedimentation rates can vary over a large range in the presence of common carp. Robertson *et al.* (1997) found that in a billabong on the floodplain of the Murrumbidgee River, Australia, with a common carp biomass of 1181 $kg \cdot ha^{-1}$, that sedimentation rates varied between 30 and 350 $g \cdot m^{-2}$ (d.w.). In a study conducted in enclosures, Breukelaar *et al.* (1994) found that a density of 100 $kg \cdot ha^{-1}$ of carp corresponded to a sedimentation rate of approximately 24 $g \cdot m^{-2}$ (d.w.). Using the regression equation provided by Breukelaar *et al.* (1994) and applying it to the carp density of 1181 $kg \cdot ha^{-1}$ reported in Robertson *et al.* (1997) I would expect to find a sedimentation rate of approximately 279 $g \cdot m^{-2}$ (d.w.) in the billabong. This calculated value is within the actual range of sedimentation recorded in the billabong and is similar to the mean sedimentation rate averaged over the study. Based on these results it appears that sedimentation rates are a more reliable predictor of common carp activity than to total suspended solids.

Benthivorous fish such as common carp may increase the erosion of surface sediments by reducing their resistance to wave resuspension. Scheffer *et al.* (2003) found that before fish were removed from Lake Wolderwijd in the Netherlands, suspended solid concentrations increased dramatically with wind speed. After the fish biomass had been reduced, there was no significant relationship between wind and suspended solid concentrations. In laboratory experiments where sediments were mechanically perturbed to simulate carp activity, Scheffer *et al.* (2003) found that disturbing approximately 2% of the surface area reduced erosion resistance of the sediments to a level comparable to those of unconsolidated sediments.

2.9.2 Water column nutrient concentrations

The common carp can increase water column nutrient concentrations directly through excretion (Lamarra 1975) or indirectly by disturbing surface sediments (Andersson *et al.* 1978, Cline *et al.* 1994) and enhancing remineralization rates of certain nutrients (Shormann & Cotner 1997). Conversely, by consuming benthic invertebrates, which are known to enhance the release of phosphorus from sediments, benthivorous fish such as the common carp may reduce loading of nutrients from the sediments to the water column (Scheffer 1998).

Although the extent to which fish affect water column nutrient concentrations through excretion has been debated for many years, it is widely accepted that benthivorous fish such, as the common carp, are more important relative to planktivorous fish, as they are capable of pumping nutrients stored in the benthos to the water column (Drenner *et al.* 1996, Drenner *et al.* 1998). Lamarra (1975) found that through excretion a common carp population of 200 $kg \cdot ha^{-1}$ contributed between 0.53 and 2.18 mg total $P \cdot m^{-2} \cdot d^{-1}$. Based on

excretion, rates reported by Nuttall & Richardson (1991), a common carp population of 200 $kg \cdot ha^{-1}$ would contribute 0.096 mg dissolved $P \cdot m^{-2} \cdot d^{-1}$ and 0.91 mg ammonia-$N \cdot m^{-2} \cdot d^{-1}$. However, this last study was based on a starvation regime, and therefore likely underestimates the nutrient loading attributed to excretion. Results, based on excretion experiments conducted at the Delta Marsh Field Station (Appendix B), found that common carp excreted phosphorus (measured as total reactive phosphorus) and ammonia-nitrogen at rates of 0.34 and 3.59 $mg \cdot kg^{-1} \cdot hr^{-1}$, respectively. At densities of 200 $kg \cdot ha^{-1}$, common carp in Delta Marsh would contribute 0.16 and 1.73 $mg \cdot m^{-2} \cdot d^{-1}$ of phosphorus and nitrogen. These loading rates are within the range of those based on excretion rates from Lamarra (1975) and Nuttall & Richardson (1991).

At densities of 200 $kg \cdot ha^{-1}$, common carp populations could offset nitrogen and phosphorus retention in wetlands by 1-24%, and 1-14%, based on nutrient excretion rates of common carp in Delta Marsh and nutrient retention rates of cold climate wetlands (constructed and natural) summarized by Mitsch & Gosselink (2000). Furthermore, common carp excretion would increase internal nitrogen and phosphorus loading in Delta Marsh by 31 and 42% based on background sediment nutrient fluxes in Delta Marsh reported by Goldsborough & Robinson (1985). However, I believe common carp densities in Delta Marsh are much greater than 200 $kg \cdot ha^{-1}$, and therefore the results above are conservative.

Although common carp are able to increase dissolved phosphorus concentrations through physiological processes, their feeding activities and subsequent resuspension of sediments may considerably reduce this fraction. Keen & Gagliardi (1981) found that

soluble reactive phosphorus (SRP) concentrations in enclosures with benthivorous fish and sediment were lower relative to concentrations in enclosures with only fish, and concluded that decreased SRP concentrations in the presence of fish and sediments were a result of sorption onto sediments. This process is also supported by the results of Lougheed *et al.* (1998) and Scheffer (1998), where total phosphorus (TP) concentrations increased in the presence of common carp but SRP did not, indicating that dissolved phosphorus was being sorbed to suspended sediments. Additionally, Andersson *et al.* (1978) found that sediments in enclosures with bream and roach (900 $kg \cdot ha^{-1}$) released 18 mg total $phosphorus \cdot m^{-2} \cdot d^{-1}$. Assuming that common carp have similar impacts to those of bream and roach, and based on the internal loading of total phosphorus through sediment resuspension reported by Andersson *et al.* (1978), at densities of 200 $kg \cdot ha^{-1}$, common carp would resuspend approximately 4.0 $mg \cdot m^{-2} \cdot d^{-1}$ of total phosphorus. In a shallow eutrophic lake in Denmark, Søndergaard *et al.* (1992) found that SRP-release rates in undisturbed sediments were between 4 and 12 $mg \cdot m^{-2} \cdot d^{-1}$ and that these rates increased to between 60 and 70 $mg \cdot m^{-2} \cdot d^{-1}$ after wind-induced resuspension increased suspended sediment concentrations by 42 $mg \cdot L^{-1}$. My experiments in small enclosures and large experimental wetland cells stocked with high densities of carp (1,200 – 1,700 $kg \cdot ha^{-1}$) demonstrate that common carp can have the same influence on suspended sediment concentrations as wind-resuspension and hence likely influence phosphorus loading to the same extent.

It appears that sediment resuspension contributes substantially more phosphorus relative to excretion. However, it is important to note that phosphorus loading through

excretion increases the soluble phosphorus fraction, that is immediately available to phytoplankton, while sediment resuspension increases the total or particulate bound fraction, which is not immediately available for phytoplankton growth.

2.9.3 Phytoplankton biomass and species composition

Omnivorous fish such as the common carp can enhance phytoplankton by reducing large herbivorous cladocerans (Andersson *et al.* 1978, Richardson *et al.* 1990, Lougheed *et al.* 1998, Schrage & Downing 2004) by entraining benthic algal cells into the water column (Karlson-Elfgren & Brunberg 2004), and by increasing nutrient loads to the water column through excretion (Brabrand *et al.* 1990, Qin & Threkeld 1990) and sediment resuspension (Havens 1991, Shormann & Cotner 1997, Brett & Stuart 1998). Excessive algal growth is a concern in aquatic ecosystems as it can lead to oxygen depletion and fish kills. Furthermore, by altering the physical and chemical environments in aquatic ecosystems, the common carp can also cause shifts in the phytoplankton community structure.

Summarizing the results from 29 published papers which examined the effects of omnivorous fish on phytoplankton, Drenner *et al.* (1996) found that in 90% of the studies omnivorous fish had a significant affect on phytoplankton. The majority of these studies where phytoplankton was significantly affected found that the presence of omnivorous fish (including the common carp) resulted in increased phytoplankton abundance, biomass, and primary productivity.

In experiments where common carp were added to enclosures Qin & Threkeld (1990) found that phytoplankton chlorophyll, biomass, and photosynthetic capacity were

increased regardless of the presence of sediments. This suggests that common carp were likely enhancing phytoplankton through excretion or by reducing large herbivorous cladocerans. Brabrand *et al.* (1990) found that phosphorus released from bream, perch, and roach was readily available for algal growth and increased the growth rate and total cell yield in cultures of *Selenastrum capricornutum*. These authors also calculated that phosphorous release from roach biomass in Lake Gjersjøen, Norway, between July and September was approximately double the external phosphorus load for this same period, and that fish excretion was likely important in sustaining phytoplankton populations during this period when serious phosphorus depletion occured. Similarly, Persson (1997) found that the combined excretion rates of bream and roach in Lake Finjasjön, Sweden contributed approximately 110 and 42% of the external and internal phosphorus load, respectively, and were likely an important nutrient source for phytoplankton.

Breukelaar *et al.* (1994) found that in the presence of benthivorous bream, chlorophyll *a* and total P were positively correlated with fish biomass and increased by 9.0 and 30 $\mu g \cdot L^{-1}$, respectively. However, the fact that orthophosphate was not correlated with fish biomass in this study indicates that phytoplankton was enhanced as a result of nutrient resuspension and not excretion as in the previously mentioned studies. Brett & Stuart (1998) also found that sediment resuspension in shallow lakes of the Otago region in New Zealand increased chlorophyll *a* concentrations by relieving nitrogen-deficiency. Similarly, Shormann & Cotner (1997) found that benthivorous smallmouth buffalo (*Ictiobus bubalus*) enhanced the remineralization rate of ammonium through sediment resuspension, and increased phytoplankton biomass levels.

In addition to increasing phytoplankton biomass, benthivorous fish such as the common carp can also alter the community structure of phytoplankton populations. In Australia, common carp are believed to be responsible for the increase in cyanobacterial blooms as a result of nutrient excretion, sediment resuspension, and the reduction of submerged macrophytes (Gehrke & Harris 1994). In an enclosure experiments conducted in Lake Trummen, southern Sweden, Andersson *et al.* (1978) found that cyanophytes (mostly *Microcystis* species) dominated the phytoplankton community in the presence of bream and roach, whereas the phytoplankton community in the fishless enclosure was comprised mostly of cryptomonads and a mix of small cyanophytes and diatoms. Total TP concentrations are positively correlated with the occurrence of cyanobacterial blooms (Downing *et al.* 2001) and likely explain the dominance of *Microcystis* in the enclosures with fish.

Through sediment resuspension, common carp increases turbidity and enhances cyanobacterial population, as carp are superior competitors for nutrients under light-limited conditions (Scheffer 1998). Additionally, Ståhl-Dalbenko & Hansson (2002) found that bioturbation by macroinvertebrates increased recruitment of cyanobacterial cells from lake sediments and, hence, common carp also likely enhance recruitment of cyanobacterial cells from the sediments. Some studies have also found that cyanobacteria (particularly mucilaginous genera such as *Microcystis*) may be stimulated by passage through fish guts (Kolmakov & Gladyshev 2003, Lewin *et al.* 2003). Common carp may also stimulate the occurrence of other algal classes such as diatoms. Kyeongsik *et al.* (1999) found that fish, nutrients, mixing, and sediments interacted significantly and caused major shifts in the structure of the phytoplankton community, with Cryptomonads

dominating in the unmixed, high nutrient treatment, *Synedra* (Bacillariophyceae) dominating in the high nutrient, high sediment treatment, and *Ulothrix* (Chlorophyceae) dominating in the mixed, high nutrient, low sediment treatment.

2.9.4 Submerged macrophyte abundance

Common carp have long been held accountable for reducing submerged macrophyte biomass and diversity in aquatic ecosystems. Cahn (1929) found that common carp completely eliminated submerged macrophytes in an artificial lake in Wisconsin. Schrage & Downing (2004) found that after removing common carp from a eutrophic wetland in Iowa, submerged macrophytes, which were only found within 5 m of shore when common carp were present, expanded dramatically and extended 60 m from shore in some areas. Additionally, the number of observed submerged macrophyte taxa doubled from three to six after the removal of common carp. Similarly, Lougheed *et al.* (1998) found that wetlands containing common carp had on average five or fewer species, compared to wetlands without common carp, which had ten or more submergent species. Although it is clear that common carp negatively affect submerged macrophyte biomass and diversity, the exact mechanism involved is unclear.

In Pymatuning Lake, Pennsylvania, Tryon (1954) found that mean submerged macrophyte biomass over a three year period was 3.9 $g \cdot m^{-2}$ in quadrats where common carp were excluded, compared to 1.4 $g \cdot m^{-2}$ in open quadrats. The authors concluded that physical disturbance of submerged macrophytes as a result of the rooting and splashing habits of common carp, and not increased turbidity, were responsible for the difference in biomass. Robel (1961) found a significant negative relationship in enclosures between carp stocking rates and submerged macrophyte biomass. Once again, reductions in

submergent biomass were attributed to physical disturbance as there was no significant relationship between stocking rate and turbidity. Kolterman (1990) found that large common carp (>1.5 kg), stocked at a density of 675 $kg \cdot ha^{-1}$ in enclosures reduced the biomass of sago pondweed by 85% over a two month period. Once again there was no significant relationship between turbidity and fish activity, hence sago pondweed biomass appeared to be reduced as a result of physical disturbance by common carp while foraging for benthic invertebrates.

Conversely, other studies have found that common carp reduce submerged macrophyte biomass through shading as a result of increased turbidity and epiphytic algal growth (Threinen & Helm 1954, Sidorkewicj *et al.* 1999, Williams *et al.* 2002). In Lake Koshkonong, southeastern Wisconsin, common carp increased turbidity levels and decreased submerged macrophyte biomass relative to an adjacent bay that was fenced off with chicken wire (Threinen & Helm 1954). This fenced bay had the highest submerged macrophyte density and diversity compared to all other bays within the lake. In small aquaria experiments, Sidorkewicj *et al.* (1999) found that in the presence of muddy substrates, one-year-old common carp (21.0 ± 1.3 g), increased turbidity by up to 329 NTU, and decreased the length and biomass of *Stuckenia pectinata* by 95 and 57%, respectively. Additionally, seedlings were completely eliminated from treatment aquaria. However, these authors found that the development of dense periphytic algal communities was also responsible for increased shading and decreased submerged macrophyte biomass. Similarly, Williams *et al.* (2002) found that submerged macrophyte biomass decreased from approximately 310 g in control enclosures to approximately 140 g in enclosures stocked with 700 $kg \cdot ha^{-1}$ of common carp, while epiphyton chlorophyll *a*

increased from approximately 1100 to 3000 $\mu g \cdot g^{-1}$ (dry macrophyte), concurrently. Based on these results the authors concluded that decreased macrophyte abundance in enclosures stocked with common carp resulted from increased epiphytic algal growth and subsequent reduction in light availability.

Although common carp generally are not herbivorous, it has been suggested that they may switch to herbivory when preferred food items are not available (Sibbing 1988). Sidorkewicj *et al.* (1999) concluded that direct consumption by common carp was partly responsible for the complete eradication of macrophytes in their experiments based on signs of direct grazing damage to many of the plants examined. Furthermore, King & Hunt (1967) found that in a Lake Erie marsh, common carp consumed large quantities of *chara*.

2.9.5 Zooplankton biomass and species composition

Many studies have found that zooplankton are an important component in the diet of the common carp, particularly in juveniles (Adzhimuradov 1972, Khan 2003). As common carp grow, zooplankton become less abundant in their diet because large common carp can no longer effectively retain zooplankton due to the increased mesh width of the branchial sieve (Sibbing 1988). However, zooplankton may still form a significant portion of the diet of adult common carp (Crivelli 1981, Khan 2003), and hence even adult common carp populations can regulate the biomass and community structure of zooplankton communities.

In a series of mesocosm experiments, Williams *et al.* (2002) found that the biomass of small zooplankton (i.e. *Bosmina long* and *Daphnia hyalina*) increased significantly as

rough fish biomass increased from 0 to 700 kg·ha^{-1}, while the opposite was true for large zooplankton. Similarly, Angeler *et al.* (2002) found that enclosures stocked with 5,000-6,000 kg·ha^{-1} of carp had increased abundances of rotifers and decreased abundances of copepods, nauplii, and cladocerans relative to control enclosures. Even at low densities of approximately 18 kg·ha^{-1}, Richardson *et al.* (1990) found that common carp significantly reduced *Ceriodaphnia*, a large slow moving cladoceran, while simultaneously increasing smaller zooplankton such as *Bosmina*, copepods, rotifers, and protozoa. Richardson *et al.* (1990), and Angeler *et al.* (2002) suggested that the change in the zooplankton community was not a direct result of predation from common carp, but resulted indirectly due to increased turbidity, increased nutrients, and increased algal production and biomass in the presence of common carp. Kirk (1991) found that suspended sediments significantly decreased the phytoplankton ingestion rates of five cladoceran species by 13-83% but did not affect those of three rotifer species. Suspended sediments can differentially inhibit cladocerans and not rotifers (Kirk and Gilbert 1990) and therefore may confer a competitive advantage to rotifer populations in the presence of common carp.

Large scale carp exclusion studies have also demonstrated that common carp can regulate zooplankton biomass and community structure. Lougheed & Chow-Fraser (2001) found that after excluding common carp from a turbid, eutrophic coastal marsh on Lake Ontario, species richness increased from 27 species to 40 species, and there was a notable increase in the occurrence of large-bodied cladocerans. Similarly, Schrage & Downing (2004) found that after excluding common carp in a eutrophic marsh in Iowa, larger cladocerans such *Daphnia* and *Ceriodaphnia* increased in abundance.

2.9.6 Benthic invertebrate biomass

Benthic invertebrates compose the majority of the diet of adult common carp, and as such, carp can significantly reduce the biomass of benthic invertebrates. Richardson *et al.* (1990) found that in enclosures stocked with common carp, Chironomidae, which were the most abundant benthic invertebrate, were suppressed. Similarly, Tatrai *et al.* (1994) found that total benthos biomass was significantly reduced in experimental ponds stocked with common carp, relative to control ponds. Additionally, Schrage & Downing (2004) found that after removal of common carp from a eutrophic marsh, the average benthos biomass increased from 22 to 116 $mg \cdot L^{-1}$ of sediment. Although common carp consume large numbers of larval chironomids, Batzer *et al.* (2000) found that excluding common carp from certain parts of a marsh did not result in chironomid population increases, as populations of chironomid competitors and predators were released from predation pressure in the absence of common carp.

In addition to regulating the biomass of benthos, common carp foraging can alter benthic invertebrate community structure. Richardson *et al.* (1990) found that common carp were selective and suppressed Tanypodinae (Chironomidae) relative to non-tanypodine chironomids. Wilcox & Hornbach (1991) found that in enclosures stocked with common carp, benthic invertebrate species diversity and richness were reduced, and that spatial and size distributions of the dominant taxa were altered. Interestingly, in this previous study, it appears that common carp reduced the smaller size classes of *Chironomus* spp. and *Bezzia* spp. rather than the larger size classes. Because common carp were not selecting the largest prey, as is expected of predators, the authors suggest that carp may have altered the benthic invertebrate community structure indirectly by

modifying and increasing the patchiness of the benthic habitat. This is supported by the fact that large chironomids such as *Chironomus plumosus* are able to burrow deeper into the sediments, relative to smaller chironomid species (Hruska 1961), and this may afford them some protection from the grazing activities of benthivores. Conversly, Schrage & Downing (2004) found that excluding common carp from a marsh resulted in an increase in the size of larval chironomids as a result of reduced predation from common carp. In natural and experimental ponds located in El Estado de Mexico near Mexico City, Hinojosa-Garro & Zambrano (2004) found that common carp significantly reduced the abundance of *Cambarellus montezumae*, a benthic crayfish, by depleting its habitat, namely submerged macrophytes and filamentous algae.

By affecting benthic invertebrates such as chironomids, which can regulate the microbial community of surficial sediments (Johnson *et al.* 1989), common carp may indirectly alter nutrient cycling. For example, Fukuhara & Sakamoto (1988) found that inorganic nitrogen release rate from sediment cores increased exponentially with the biomass of *Chironomus plumosus*. Similarly, Gallepp (1979) found that phosphorus release rates from sediments increased in a linear fashion with increasing densities of *Chironomus tentans* larvae. Gardner *et al.* (1981) concluded, based on phosphorus release rates from chirnomids and tubificids, that benthic invertebrate excretion could account for most of the P released from aerobic sediments in Lake Michigan. Although predation of benthic invertebrates by common carp may reduce nutrient release rates from the sediments, it may also concurrently enhance release rates due to the fact that benthic invertebrates such as chironomids enhance the penetration of oxygen into surficial

sediments and reduce the risk of anaerobic phosphorus release from the sediments (Scheffer 1998).

2.9.7 Waterfowl and fish populations

Chironomids are a very important food resource for waterfowl and wetland birds (Wrubleski 1999). Common carp have the ability to significantly reduce the biomass of larval and emerging chironomids, and therefore may reduce the success of waterfowl and other birds that depend on chironomids as a primary food source. Similarly, common carp reduce waterfowl food plants such as sago pondweed by increasing turbidity and physically damaging the plants while foraging (see section 2.9.4). At a Ramsar site near München, Southern Bavaria, fish ponds stocked with 500 common carp·ha^{-1} had fewer waterbirds (approximately 10 ha^{-1}) relative to ponds that remained fishless, that had approximately 300 waterbirds·ha^{-1} (Köhler *et al.* 1997).

The major mechanisms through which common carp may affect fish populations consist of: 1) direct competition with species utilizing the same food source, and 2) by increasing suspended solids. Common carp are omnivores and as such are able to exploit many different food sources, and therefore directly compete with many other species of fish. Common carp have a highly developed sensory system for detecting benthic prey items and are likely capable of out-competing native benthivores in many systems. In Saskatchewan it is believed that invasion of the common carp are responsible for the dramatic decrease in bigmouth buffalo (*Ictiobus cyprinellus* Valenciennes), which is soon to be listed as an endangered species in the province (Espie *et al.* 2002).

Although the diet of common carp overlaps with that of many other fish species, common carp likely have a greater effect on the health of fish through sediment resuspension and increased sedimentation rates. Reviewing the biological effects of fine sediment on lotic systems, Wood and Armitage (1997) stated that fine sediment adversely affects fisheries in the following five ways: (1) by adversely acting on fish and either reducing their rate of growth, reducing their tolerance to disease or killing them; (2) by reducing the quality of spawning habitat and hindering the development of fish eggs, larvae and juveniles; (3) by modifying the natural migration patterns of fish; (4) by reducing the abundance of food available to fish due to a reduction in light penetration, photosynthesis, primary production, and of habitat available for insectivore prey items; and (5) by affecting the efficiency of hunting in visual predators. Through the above mentioned mechanisms common carp can seriously affect fish species that are sensitive to turbidity, while at the same time they themselves arecapable of tolerating suspended sediment concentrations of 100 000 mg/L (Alabaster and Lloyd 1980).

2.9.8 Contaminant cycling

Various compounds such as polychlorobiphenyls (Moermond *et al.* 2004), pesticides (Tsuda *et al.* 1993; Tsuda *et al.* 1992), and metals (Sun and Jeng 1999) are known to accumulate in common carp. Additionally, through the bioturbation of contaminated sediments, common carp could increase the exposure and bioaccumulation of contaminants in planktonic organisms. However, (Wall *et al.* 1996) found that although common carp significantly increased cadmium concentrations in the water column through bioturbation, they also increased the binding capacity through sediment resuspension, and hence availability to planktonic organisms did not change. Sun and

Jeng 1999) found that common carp accumulated zinc to a greater extent relative to grass carp and tilapia and suggested that the digestive tract tissue of common carp is likely an important zinc reservoir. However, this same study found that this accumulated zinc could easily be released and therefore it appears that common carp could actively pump zinc accumulated in the sediments and benthic invertebrates back into the water column.

Due to their ability to accumulate a wide range of compounds, common carp are ideal biomonitors and have been used to detect the presence of pesticides (Gruber and Munn 1998; Neškovic *et al.* 1993), and wastewater effluent (Solé *et al.* 2003; Kosmala *et al.* 1998).

3.0 Methods

3.1 Study Site and Experimental Design

3.1.1 Project 1: Impacts of carp in large experimental wetland cells

3.1.1.1 Delta Marsh

Delta Marsh is one of the largest and most important freshwater wetlands in North America. It is a 18,500 ha freshwater lacustrine marsh (50°11′N, 98°23′W) located on the south shore of Lake Manitoba (Figure 3.1). The marsh was created between 2500 and 2000 years ago, when erosion and redistribution of the sandy deltaic sediments deposited by the Assiniboine River created the barrier beach that now separates the marsh to the south of the lake from the main lake (Teller & Last 1981). Prior to regulation, water levels in Delta Marsh fluctuated within an upper and lower range of 2.1 m (Murkin *et al.* 2000). However, in 1961 the Fairford Dam became operational and stabilized the water levels in Lake Manitoba within a range of 0.3m. Four emergent species form the major monodominant vegetation zones in the Delta Marsh: *Phragmites australis*, *Scolochloa festucacea*, *Typha glauca*, and *Schoenoplactus lacustris* spp. *glaucus* (Squires & van der Valk 1992), while submerged macrophytes are comprised primarily by *Stuckenia pectinatus*.

3.1.1.2 MERP Cell Study Site

For this study, I used five of ten experimental wetland cells that were constructed by Ducks Unlimited Canada and the Delta Waterfowl and Wetlands Research Station in 1979 for the Marsh Ecology Research Program, or MERP. The experimental wetland cells were created by diking ten contiguous (5-7 ha) sections of the Delta Marsh,

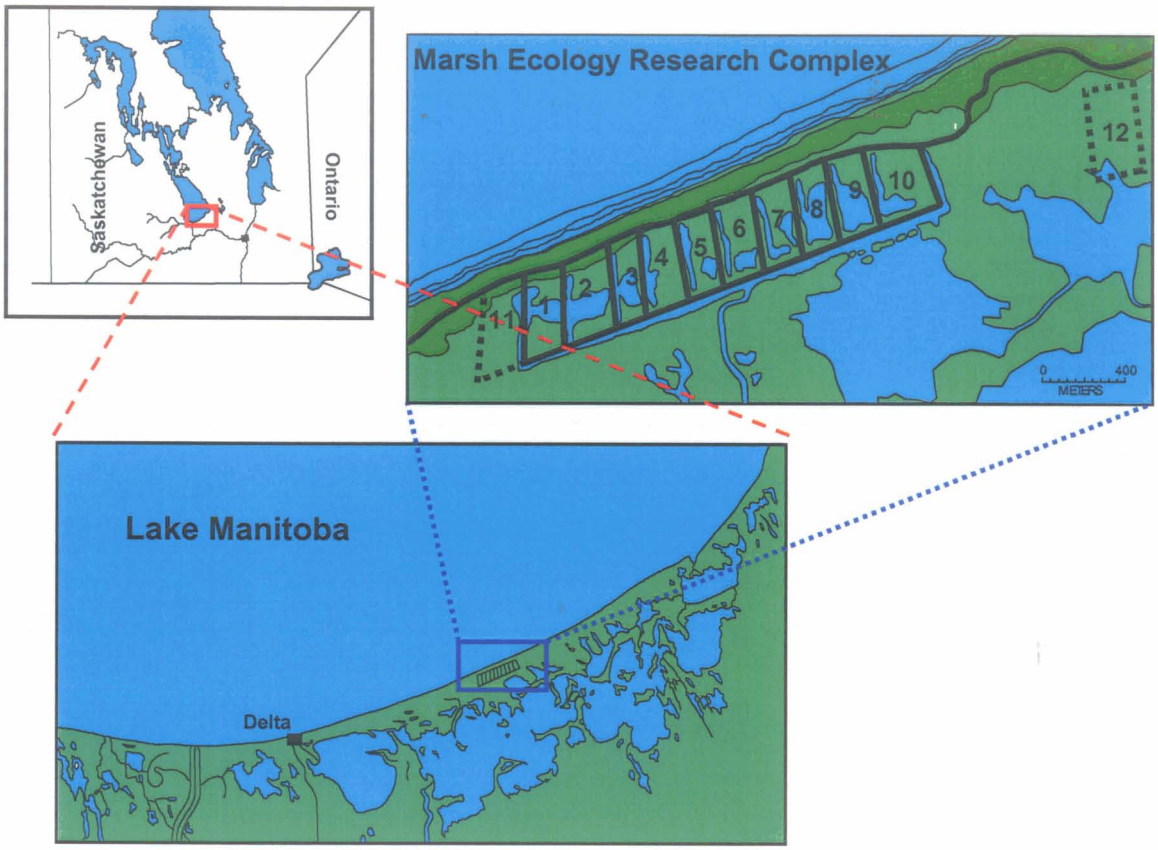

Figure 3.1. Location of the Marsh Ecology Research Program study area on the Delta Marsh, Manitoba. (Modified from *Murkin et al.* 2000).

which are numbered 1 – 10 from west to east (Figure 3.1). Material for the dikes was taken from borrow pits on the east side of all N-S dikes and on the south side of the south E-W dike (Kadlec 1983). Each cell was equipped with a water level control structure and electric pump to adjust and maintain water levels (Murkin & Kadlec 1986). The MERP site is located approximately 7 km east of the Delta Waterfowl and Wetlands Research Station.

MERP was a long-term experimental study of the wet-dry cycle in prairie wetlands (Murkin *et al.* 2000). The main subjects of study during MERP included the effects of water level fluctuations on algal biomass and productivity (Robinson *et al.* 1997a, Robinson *et al.* 1997b); plant (Squires & van der Valk 1992), vertebrate (Clark & Kroeker 1993) and invertebrate (Murkin & Kadlec 1986) ecology; nutrient dynamics (Kadlec 1986a); hydrology (Kadlec 1983) and water chemistry (Kadlec 1986b).

With the exception of cells two, four, and five, the MERP cells have not undergone any extensive manipulations nor have they been directly connected to the marsh through their control structures since the end of MERP in 1989. In the early 1990s cells two, four, and five were drawn down and burned for waterfowl management purposes (Grosshans 2001). Therefore, at the beginning of the current experiment in 2000, the ten experimental wetland cells had been in a stable state with regards to water level fluctuation for approximately eight years in cells two, four, and five; eleven years in cells one, six, nine, and ten; and for 15 years in cells three, seven, and eight.

The five experimental wetland cells used in this study (cells one, two, three, five, and six) have total surface areas ranging from 5 to 7 ha. However, open-water area among the

five experimental wetland cells varied from 0.6 to 3.2 ha. Major vegetation types occurring in the MERP cells during the current study were similar to those observed in 1980 and consisted mainly of whitetop (*Scholochloa festucacea*), cattail (*Typha* spp.), phragmites (*Phragmites australis*), hardstem bulrush (*Schoenoplactus acutus*), and open-water areas which contained predominantly sago pondweed (*Stuckenia pectinatus* L.) formerly known as *PotamogetonPectanatu* (Kadlec 1986b). Other types of submerged macrophytes such as *Ceratophyllum demersum* and *Utricularia macrorhiza* also occure in the MERP cells but only constituted a fraction of the biomass represented by sago pondweed.

The open-water season of 2000 was used to collect baseline data (i.e. water chemistry, sediment chemistry, and submerged macrophyte abundance) on each experimental wetland cell before applying the experimental treatments in 2001 and 2002. Relative to water levels in 2001 and 2002, water levels in 2000 were low. By the end of July in 2000 there were exposed mudflats in many of the experimental wetland cells. This created ideal habitat for returning waterfowl, which reduced the remaining submerged macrophyte community and greatly increased turbidity and nutrients in the water column. In general, excluding values from August when mudflats were exposed, water quality parameters were similar across all cells during the baseline monitoring year (Table 3.1). All experimental cells were devoid of large fish but did contain small populations of fathead minnows (*Promelas pimphales*) and brook stickleback (*Culaea inconstans*).

3.1.1.3 Experimental Stocking Design

As was the case during MERP, there were marked differences in the amount and depth of open water in the five cells to be used. Due to this fact, the experimental wetland

Table 3.1. Mean and standard error (n=4) of various water quality parameters measured during June and July in the MERP cells during the baseline-monitoring year (2000) prior to common carp additions. Note data for submerged macrophyte biomass were based on only 2 samples (one from June and one from July).

	Experimental wetland				
Parameter	Cell 1	Cell 2	Cell 3	Cell 5	Cell 6
Open-water area (ha)	1.32	3.22	0.71	2.39	0.62
Mean depth at sampling sites (cm)	54 ± 3	43 ± 2	59 ± 2	57 ± 1	58 ± 2
Dissolved oxygen ($mg \cdot L^{-1}$)	8.60 ± 0.02	8.72 ± 0.04	7.61 ± 0.25	4.77 ± 1.36	9.08 ± 0.73
pH (units)	9.25 ± 0.20	9.12 ± 0.21	8.76 ± 0.04	8.61 ± 0.05	8.78 ± 0.12
Conductivity ($\mu S \cdot cm^{-1}$)	3330 ± 67	4776 ± 107	3300 ± 126	4771 ± 96	3480 ± 197
Turbidity (NTU)	2.3 ± 0.4	3.5 ± 0.5	2.7 ± 0.5	2.9 ± 0.4	4.2 ± 0.3
TSS ($mg \cdot L^{-1}$)	8.0 ± 1.1	13.7 ± 3.1	6.9 ± 0.2	16.0 ± 3.4	4.8 ± 0.8
Chlorophyll a ($\mu g \cdot L^{-1}$)	2 ± 1	2 ± 1	1 ± 1	3 ± 1	<1
NH_3 ($\mu g \cdot L^{-1}$)	33 ± 25	62 ± 30	11 ± 2	74 ± 24	7 ± 2
TRP ($\mu g \cdot L^{-1}$)	10 ± 3	9 ± 4	3 ± 1	17 ± 4	6 ± 2
DOC ($mg \cdot L^{-1}$)	66.2 ± 3.1	89.6 ± 4.2	57.5 ± 3.6	91.3 ± 2.8	71.5 ± 6.3
Submerged macrophytes ($g \cdot m^{-2}$)	79 ± 43	34 ± 26	28 ± 25	69 ± 51	42 ± 15
Euphotic zone depth (cm)	126 ± 5	155 ± 11	164 ± 6	136 ± 2	154 ± 6

cells cannot, in a statistical sense, be considered replicates. Therefore, I opted to use a multivariate regression approach, where changes were related linearly to successively higher densities of common carp in unreplicated wetland cells. Additionally, I decided to stock the experimental cells based on the amount of open water they contained, with the highest density stocked in the cell with the least amount of open water and the lowest density stocked in the cell with the greatest amount of open-water. Although this eliminated all randomness from my experimental design, it would have been extremely difficult to catch the large number of live fish needed to implement any other stocking regime.

After monitoring the experimental wetland cells throughout the open-water season in 2000, common carp (*Cyprinus carpio*) were stocked in four cells in 2001 and again in 2002 at target densities of 150, 300, 600, and 1,200 $kg \cdot ha^{-1}$ live fish mass. The actual density of common carp in Delta Marsh is not known, however the range of densities I used spanned values reported in the literature and, presumably, the density in the surrounding marsh.

In 2001, all common carp stocked in the MERP cells were procured from a local fisher operating at the Delta Channel near the entrance to Cadham Bay. Common carp entering the channel passed through a series of funnel traps suspended from a bridge and were trapped in a large area of the channel surrounded by a large mesh net. Once caught, carp were kept in the penned-off section of the Delta Channel, where they remained until their fork length could be measured, following which, the length of each fish was recorded and assigned a weight based on a weight-length relationship (Figure 3.2) developed from common carp caught in Delta Marsh during the open-water period of

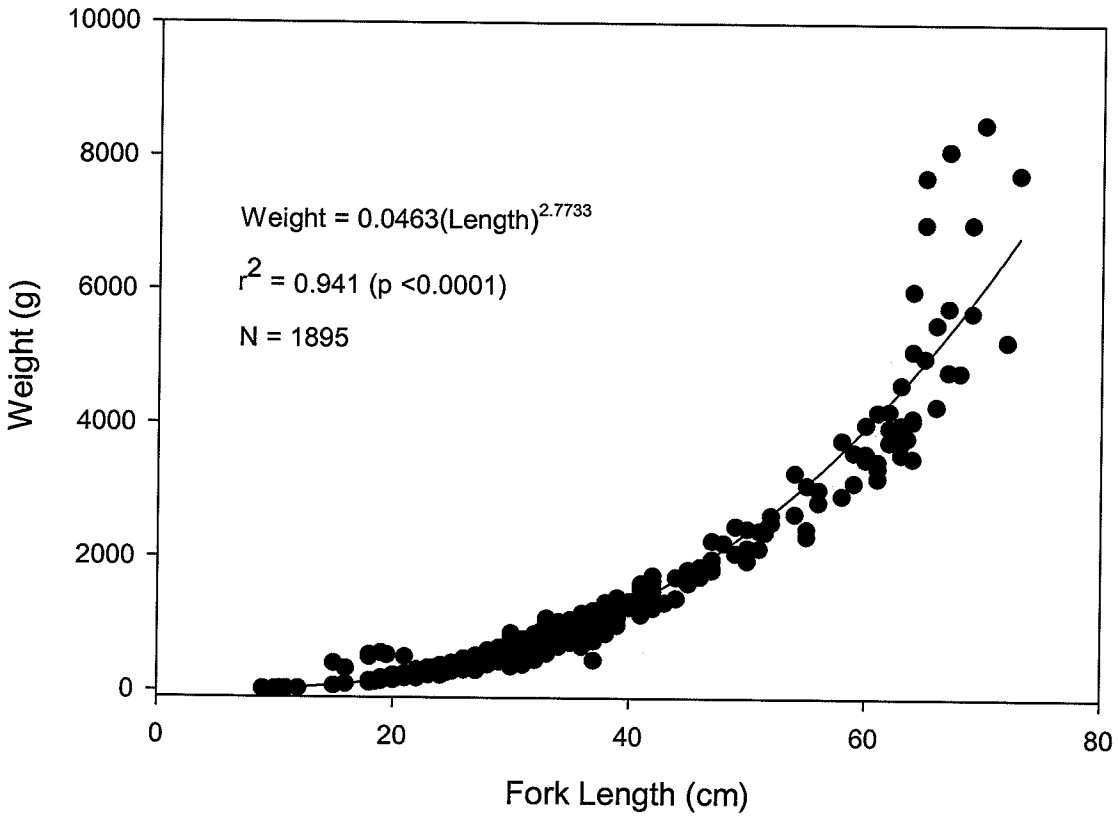

Figure 3.2. Length-weight relationship for common carp of Delta Marsh sampled during the open-water period in 1999 and 2000 (from Wrubleski, D.A. 2000, unpublished data) .

1999 and 2000. Carp were then loaded into a series of tubs ranging from 75 to 140 L filled with water from Delta Channel and transported to the MERP cells where they were released. Transportation time rarely exceeded 20 minutes. However, hot temperatures and a flat tire resulted in high mortality for one carp shipment. Approximately 85 fish died during transport and deployment into the cells causing actual carp densities to be less than the desired targets. All cells were stocked over a period of two days (May 11-12, 2001).

In 2002, common carp were once again procured from the local fisher operating at the Delta Channel. However, compared to 2001, the number of common carp entering the marsh through the Delta Channel decreased significantly. Due to this fact, I was forced to supplement the number of carp caught at the Delta Channel with common carp I collected from a culvert near the Delta Marsh Field Station (Figure 2.1) on the west side of them arsh. In total 57% of the 444 common carp caught in 2002 were from the Delta Channel with the remaining 43% mostly coming from Blind Channel. At this location, common carp would accumulate in a pool at a culvert. When this occurred, a small mesh purse seine was used to fence off the pool where common carp congregated. Fish were then removed using a standard dip net, their fork length measured, and transported to the MERP cells.

Summary statistics for common carp caught in 2001 and 2002 are provided in Table 3.2, and the length-frequency distributions are provided in Figure 3.3. Additionally, a summary of target densities and actual stocking densities of common carp ($kg \cdot ha^{-1}$) as well as the total number of common carp stocked in each cell in 2001 and 2002 are presented in Table 3.3.

Table 3.2. Descriptive statistics for length and weight of all common carp stocked in the MERP cells 2001 and 2002.

	2001	**2002**
Number of carp stocked	794	444
Mean length (cm ± SE)	51.7 (0.3)	61.4 (0.3)
Range	32 – 75	44 – 79
Mean weight (kg ± SE)	2.79 (0.05)	4.35 (0.06)
Range	0.69 – 7.34	1.67 – 8.48
Total biomass (kg)	2,216.35	1,930.24

Table 3.3. Target densities, number of common carp stocked, and actual density ($kg \cdot ha^{-1}$) of common carp.

MERP cell	target density ($kg \cdot ha^{-1}$)	2001		2002	
		no. of carp stocked	actual density ($kg \cdot ha^{-1}$)	no. of carp stocked	actual density ($kg \cdot ha^{-1}$)
Cell 1	0 (control)	-	-	-	-
Cell 2	150	162 (35)	150.4	100	151.4
Cell 3	600	155 (15)	576.5	95	629.3
Cell 5	300	248 (10)	271.4	59	96.6
Cell 6	1,200	229 (10)	886.7	190	1247.4

Note: Numbers in brackets indicate the number of carp that died during or shortly after stocking.

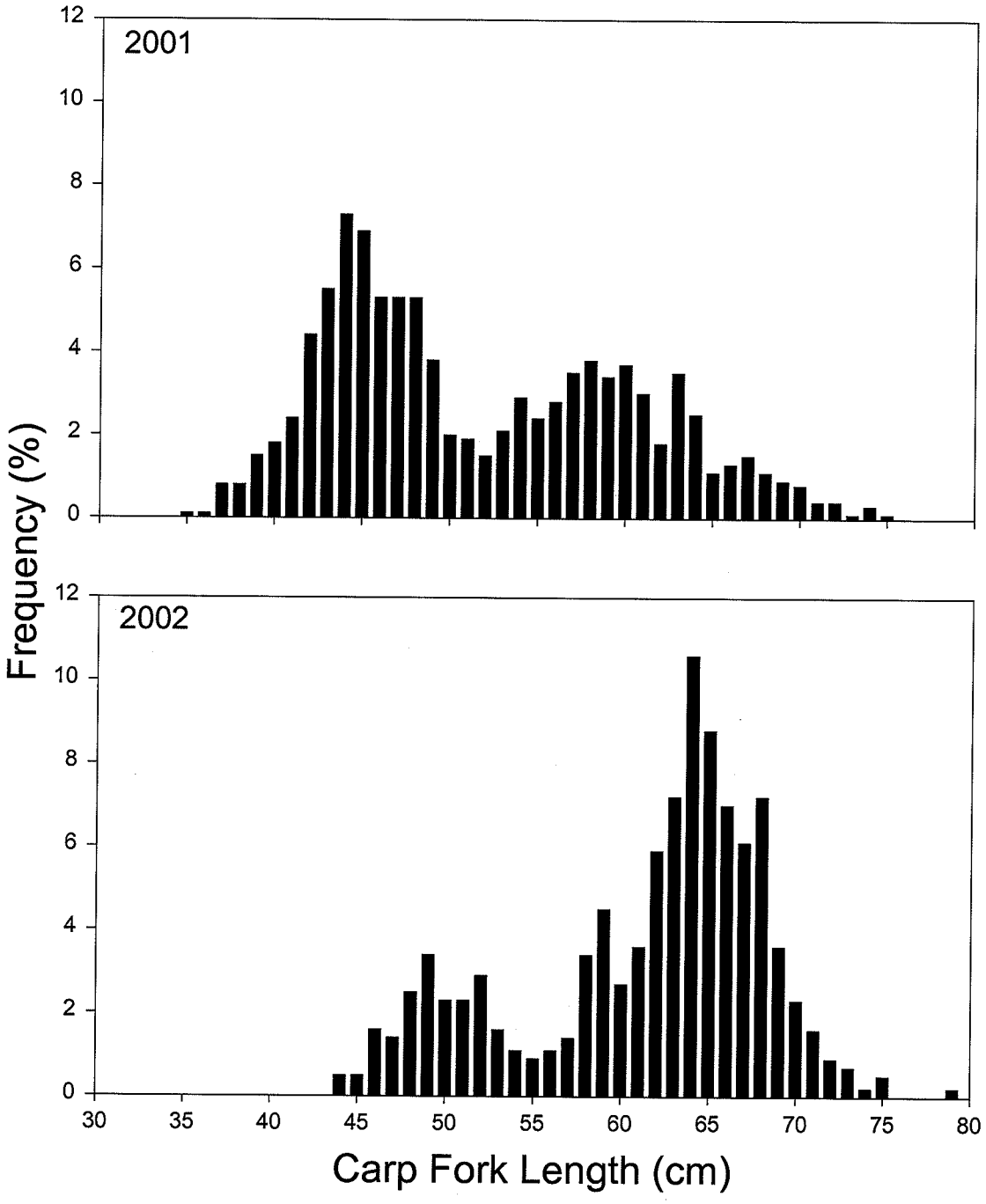

Figure 3.3. Length-frequency distribution of all adult common carp stocked in the MERP cells, 2001 and 2002.

3.1.2 Project 2: Impacts of carp in small experimental enclosures

3.1.2.1 Blind Channel

The study was conducted in Blind Channel, near the University of Manitoba's Delta Marsh Field Station (Figure 3.4). This is a shallow (~1m) flat bottom channel that is approximately 45 m wide. The shallow nature of this channel allows for the growth of submersed macrophytes, which consist almost entirely of sago pondweed (*Stuckenia pectinatus*) and coon tail (*Ceratophyllum demersum*). The early summer fish community of Blind Channel is composed primarily of fathead minnows (*Pimephales* promelas) followed by brook- and ninespined sticklebacks (*Culaea inconstans* and *Pungittius pungittius*), and spottail shiners (*Notropis hudsonias*), whereas the late summer fish community is comprised of yellow perch (*Perca flavescens*), bullheads (*Ictalurus ameluruss* and *Ictalurus nebulasus*), common carp (*Cyprinus carpio*), and white suckers (*Catostomus commersoni*) (Schneider 1983, Kiers & Hann 1995).

3.1.2.2 Experimental enclosures and treatments

Twelve floating enclosures (5m x 5m) were installed at the study site between 22 May and 31 May 2002 (Figure 3.4). Enclosures were constructed of plywood frames supported by high density foam floats. An impermeable polyethylene curtain (8 mil) was fastened to the inside perimeter of each enclosure. From this point, the curtains extended down through the water column and were embedded into the sediments (approximately 30 cm) using metal rebar inserted into folds created in the bottom of the curtains. Each enclosure enclosed a sediment surface area of 25 m^2. The average depth of the enclosures at the beginning of the experiment was 54 ± 1 cm, with an average volume of approximately 13.6 m^3. Once all enclosures were installed, small fish were removed

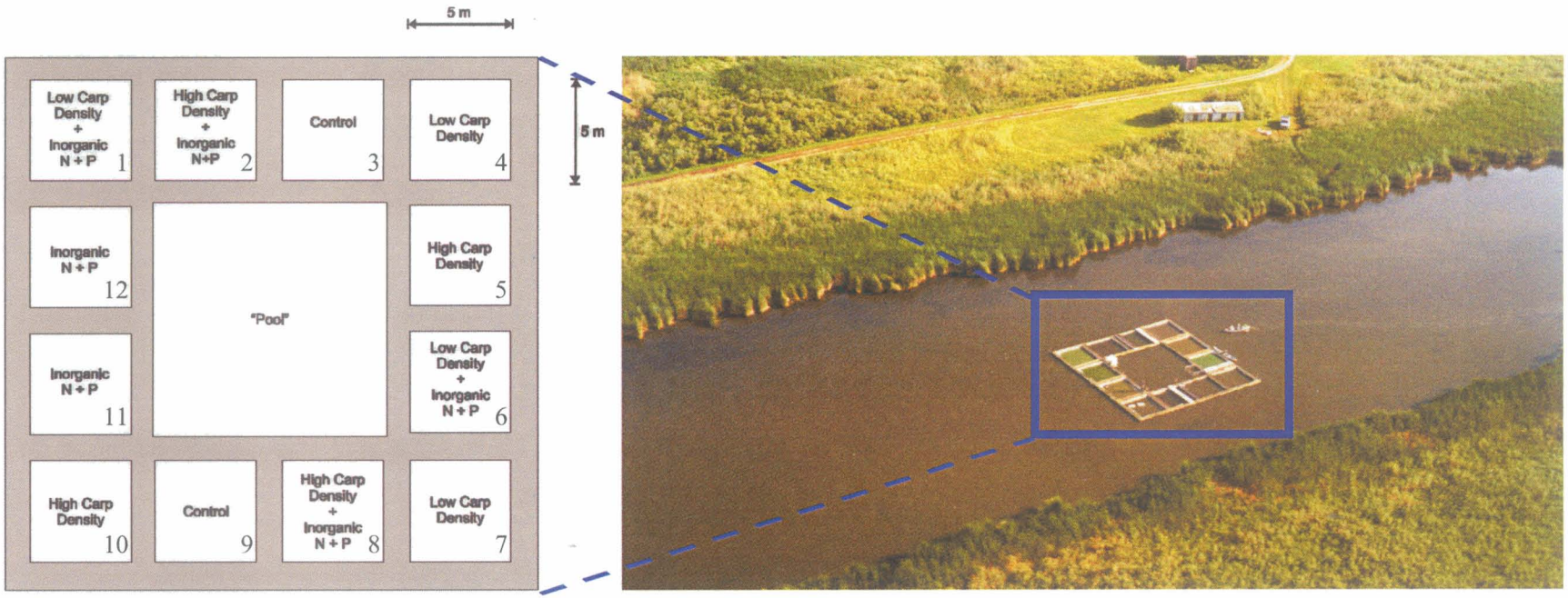

Figure 3.4. Aerial view and schematic diagram of the carp enclosure complex, located in the east end of Blind Channel, Delta Marsh, Manitoba, Canada, 2002. The treatments were 1) control, no fish and no nutrients (enclosures 6 and 12); 2) low carp density and no nutrient enrichment (enclosures 7 and 10); 3) high carp density and no nutrient enrichment (enclosures 1 and 8); (4) no carp and nutrient enrichment (enclosures 2 and 3); (5) low carp density and nutrient enrichment (enclosures 4 and 9); (6) high carp density and nutrient enrichment (enclosures 5 and 11).

using a purse seine on 4 June. However this did not remove larval fish that were present or any eggs that had been deposited on the curtain walls and submersed vegetation. Enclosures were allowed to recover from the disturbance of seining for a period of nine days before the experimental treatments began on 13 June. This was designated as the pre-treatment period.

The experiment followed a two by three factorial design with duplicate enclosures randomly assigned to each treatment. The treatments were (1) control, no fish and no nutrients (CON); (2) low carp density and no nutrient enrichment (LOW); (3) high carp density and no nutrient enrichment (HI); (4) no carp and nutrient enrichment (NP); (5) low carp density and nutrient enrichment (LOW-NP); (6) high carp density and nutrient enrichment (HI-NP).

On 13 June 2002, the LOW and LOW-NP enclosures were each stocked with one adult common carp while the HI and HI-NP enclosures were each stocked with two fish each. Length and weight of common carp stocked in each enclosure are presented in Table 3.4 along with calculated mean densities for each enclosure and each replicated treatment.

Nutrients were added every Monday, Wednesday, and Friday from 13 June to 19 August 2002 as a liquid mixture of sodium nitrate ($NaNO_3$) and sodium monophosphate, dibasic ($Na_2HPO_4 \cdot 2H_2O$). A total of 30 additions were made over a period of ten weeks. The ratio of N to P added was 8:1 by weight. This ratio is identical to those used in similar experiments conducted in enclosures at Delta Marsh, and simulates the flush of nutrients that occurs when exposed marsh sediments are reflooded. The total nutrient load

Table 3.4. Descriptive statistics for length and weight of all common carp stocked in mesocosms located in Blind Channel, Delta Marsh, Manitoba, 2002.

Treatment	Enclosure	Fish 1		Fish 2		Total
		Weight (kg)	Length (cm)	Weight (kg)	Length (cm)	Density ($kg \cdot ha^{-1}$)
LOW	7	1.5	43.0	na	na	600
LOW	10	1.5	45.0	na	Na	600
				average density for replicates		**600 ± 0**
LOW-NP	4	1.6	44.0	na	na	640
LOW-NP	9	1.8	46.0	na	na	720
				average density for replicates		**680 ± 40**
HI	1	1.7	46.0	1.7	46.5	1360
HI	8	1.9	46.5	2.4	54.0	1720
				average density for replicates		**1540 ± 180**
HI-NP	5	1.9	48.0	2.2	50.0	1640
HI-NP	11	1.5	43.0	1.8	46.0	1320
				average density for replicates		**1480 ± 160**

for the experiment was 22.0 $g \cdot m^{-2}$ N and 3.0 $g \cdot m^{-2}$ P. Nutrients were dissolved in 1L of distilled de-ionized water in the lab. Once at the enclosures, the nutrient solutions were mixed with 5L of enclosure water and distributed evenly over the enclosure surface.

3.1.3 Sampling and analysis

3.1.3.1 Water sampling: (Projects 1 & 2)

Depth-integrated water samples were collected weekly from the MERP cells (2000, 2001, and 2002) and the enclosures (2002) using an acrylic tube. During baseline monitoring of the MERP cells in 2000, one water sample was collected every second week from the centre of the largest open water area in each experimental cell, whereas in 2001 and 2002 samples were collected weekly from each cell. Water samples from the enclosures were collected from the centre of each enclosure using a walkway that could be suspended between opposite sides of the enclosure's floating frame. Additionally, to assess the diurnal fluctuations in water column nutrient concentrations water samples were collected from one replicate enclosure of each treatment at 6 hour intervals from 12:00 PM, 16 of July to 12:00 PM, 17 of July. All water samples were transported to the field lab in polypropylene bottles and stored in a refrigerator at 4°C until time of analysis. All nutrient constituents sensitive to rapid degradation were analyzed within four to six hours of being collected.

3.1.3.2 Water quality: (Projects 1 & 2)

All water samples were analyzed for pH, alkalinity (acid titration; (American Public Health Association (APHA) 1992)), and turbidity (Hach model 2100A turbidimeter). Water depth and surface temperature was measured weekly at all sites. Water samples were also analyzed for nutrients such as ammonia-N (NH_3) (hypochlorite method;

(Stainton *et al.* 1978)), nitrate/ite-N (NO_3/NO_2) (UV spectrophotometry; (American Public Health Association (APHA) 1992)), and total reactive P (TRP) (acid molybdate method; (Stainton *et al.* 1978)). Conductivity (YSI model 30 conductivity meter) and dissolved oxygen (YSI model 51 oxygen meter) were measured *in-situ* at approximately 15 cm below the water surface in the MERP cells and enclosures.

3.1.3.3 Water clarity: (Projects 1 & 2)

Light extinction profiles of photosynthetically active radiation (PAR) were created by measuring the % surface irradiance at 10 cm intervals throughout the water column using a Licor Li-1000 datalogger with a flat Licor Li-192SA submersible quantum sensor. Light extinction coefficients (K_d) and photic zone depths (Z_d) were calculated using the linear regression equations produced from the light extinction profiles.

All water samples were analyzed for total, organic, and inorganic suspended solids. Total suspended solids (TSS) were measured by passing a known volume of a well-mixed water sample through a pre-weighed glass microfibre filter (Whatman GF/C), which was dried at 103°C for a period of one hour and then weighed using a Sartorius balance. TSS was then calculated using the following formula:

$$TSS\ (mg \cdot L^{-1}) = ((A - B) \times 1000) / mL\ of\ sample\ filtered$$

where A is the weight of the filter + residue dried at 103°C and B is the original weight of the filter. After filters were dried and weighed to determine TSS they were placed in a muffle furnace at 550°C for a period of one hour to combust all organic residue on the filter. After one hour had passed the filters were removed from the furnace, allowed to

cool for five minutes, and then re-weighed. Organic suspended solids (OSS) and inorganic suspended solids (ISS) were then calculated using the following formulae:

$$OSS\ (mg{\cdot}L^{-1}) = ((A - C) \times 1000)/\ mL\ of\ sample\ filtered$$

and

$$ISS\ (mg{\cdot}L^{-1}) = ((B - C) \times 1000)/\ mL\ of\ sample\ filtered$$

where C is the weight of the filter + residue combusted at 550°C.

3.1.3.4 *Phytoplankton chlorophyll (Projects 1 & 2) biomass and relative abundance (Project 2)*

Chlorophyll *a* was used as a surrogate measure of phytoplankton biomass in projects 1 and 2. Water samples containing phytoplankton were filtered onto glass microfiber filters (Whatman GF/C), neutralized using two to three drops of saturated magnesium carbonate solution and frozen for a minimum of 24 hours to ensure the disruption of algal membranes prior to pigment extraction. After the filters were frozen, 5 mL of 90% methanol was added to the filters, which were then placed in the dark for 24 hours to allow the extraction of algal pigments. After determining the absorbance of the pigment extract spectrophotometrically at 665 and 750 nm before and after acidification with HCl, chlorophyll and phaeophytin ($\mu g{\cdot}L^{-1}$) concentration was calculated using the formulae of Marker *et al.*(1980).

Every two weeks in project 2, 20 mL sub-samples of the original integrated water column samples were preserved in glass vials for phytoplankton identification and enumeration (Note only samples collected on June 4, July 2, July 16, and August 13 were enumerated and used for statistical analysis). Samples were preserved with 2 mL's of

Lugol's iodine solution and 0.5 mL of formalin. Phytoplankton in a Palmer counting chamber (volume 100 μL) were identified and enumerated at a magnification of 400x with light microscopy using a Leitz Diaplan (Germany) microscope. A minimum of 200 algal cells were identified and enumerated in 20 fields in a linear transect along the centre of the Palmer cell. So as not to overlook large and rare phytoplankton species, samples were also enumerated and identified by scanning half of the Palmer chamber at a lower magnification (100X). Cell volumes were calculated by measuring cell dimensions and applying the standard geometric form which best described the algal taxon in question (Hillerbrand *et al.* 1999). A minimum of 10 cells was measured for each algal taxon.

3.1.3.5 Submerged macrophytes (Projects 1 & 2)

In project 1, submerged macrophyte samples were collected three times throughout the open-water season in 2000, 2001, and 2002. In project 2, submerged macrophytes were only sampled once in August towards the end of the experiment to avoid excessive disturbance in the small enclosures. Additionally, submerged macrophytes were sampled at three sites (that were selected based on depth; 20, 40, and 60 cm) in each experimental wetland on all dates in project 1, while nine samples were collected from each experimental enclosure in project 2. Submerged macrophytes were sampled by defining a sample area using a plastic open-ended barrel with a cross-sectional area of 0.24 m^2. All above-ground macrophyte biomass was harvested, identified, then dried at 105°C for 24 hours, and weighed to determine submerged macrophyte biomass expressed as $g \cdot m^{-2}$.

3.1.3.6 Sedimentation (Projects 1 & 2)

Sedimentation rates were determined by deploying sediment traps (Figure 3.5) at

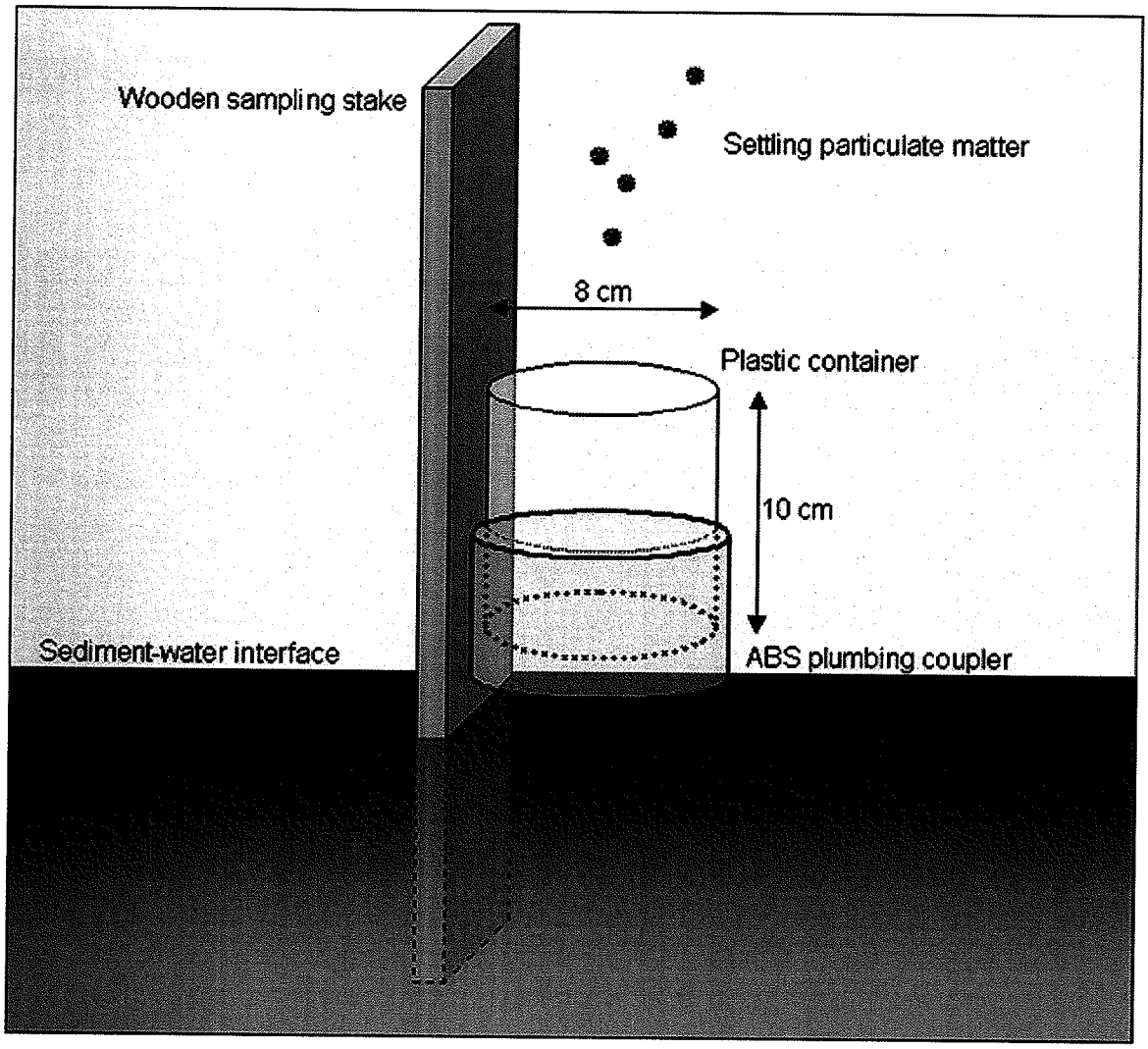

Figure 3.5. Diagram of shallow water sediment traps used to integrate the impacts of common carp on sedimentation rates in the MERP cells and Blind Channel experimental enclosures.

three random locations in each MERP cell and at one central location in the small experimental enclosures for a period of seven to ten days in 2002. Sediment traps consisted of a 500 mL wide-mouth plastic container (diameter 8 cm, height 10 cm) that sat in an ABS plumbing coupler attached to a wooden stake. The plastic container was anchored to the plumbing joint using thick elastic bands and standard S clips. The cross-sectional area of the opening for sediment traps was 50.3 cm^2 with a height/diameter ratio of 1.25. It has been shown that cylindrical traps with height/diameter ratio greater than to 5 (10 in turbulent systems) are the most appropriate instruments to correctly measure the downward settling flux of particulate matter (Banas *et al.* 2001). The proper height/diameter ratio is important to avoid resuspension of settled particulate matter from the sediment traps. However, this would require the use of a sediment trap that would be at least 25 cm in height given a minimum recommended diameter of 5 cm. A sediment trap this tall would ignore a substantial portion of the water column in shallow aquatic communities and would be more likely displaced by the activities of common carp. In light of these conflicts, I decided to ignore the recommended height/diameter ratio to capture sedimentation in a greater proportion of the water column. As the traps I used likely allowed significant resuspension under turbulent conditions, the resulting data are only used to compare relative impacts of common carp foraging activities on sedimentation.

Sediment traps were positioned by sinking the stake into the sediments until the bottom of the plumbing joint was at the sediment-water interface. Care was taken not to disturb the sediment-water interface during deployment of the sediment traps. At the end of the deployment period sediment traps were sealed with a plastic screw-on cap before

being removed so as to not lose any of the material in the trap. The plastic containers from each trap were then transported to the laboratory where the accumulated sediments were emptied into a large Erlenmeyer flask and brought to a volume of 1000 mL. The contents of the flask were then well mixed and volumes of the sediment slurry ranging from 25 to 200 mL were filtered on to triplicate pre-weighed glass microfibre filters (Whatman GF/C). Total settled particulate matter was then calculated using the same method used for calculating TSS with the exception that results were expressed on an areal basis ($g \cdot m^{-2}$) as opposed to a volume basis ($mg \cdot L^{-1}$).

3.1.3.7 Sediment sampling (Project 2)

Sediment samples were collected once every four weeks in all enclosures. Sediment samples were collected by gently inserting a clear acrylic tube (6.4 cm diameter) into the sediments. Inserting a stopper into the top of the tube created a vacuum seal that allowed the sediment core to be removed without losing material through the bottom. Once the sediment core was retrieved and before the stopper was removed, the portion of the acrylic tube containing the sediment was immediately placed on a core extruder. The top 1 cm of the sediment core was then sectioned off into a sample cup, placed on ice, and transported back to the laboratory were the sample was refrigerated.

3.1.3.8 Sediment chemistry (Project 2)

The Freshwater Institute Analytical Laboratory performed determination of total carbon, nitrogen, and phosphorus content in selected sediment samples. Carbon and nitrogen were determined using standard combustion methods, and phosphorus was measured by combustion, followed by hydrolysis and colorimetric analysis (Stainton *et al.* 1978).

3.1.3.9 Zooplankton density (Project 2)

Zooplankton density in the enclosures was assessed by randomly collecting three depth integrated water column samples (4 L) from each enclosure every two weeks. Water column samples were filtered through 53 μm mesh net to collect the zooplankton within the samples. Zooplankton were than categorized as Cladocera, Copepoda, Copepoda nauplii, or Rotifera. For each sample density was determined as the numenr of animals per litre.

3.1.3.10 Benthic invertebrate biomass and relative abundance (Project 2)

Adult Chironomidae were sampled using modified (LeSage & Harrison 1979) model 'week' traps that integrated emergence over a surface area of 0.5 m^2. In the small experimental enclosures in Blind Channel only one trap was placed in one replicate from each treatment. I chose to sample in this manner because the impact of carp on chironomid emergence was assumed to be much more pronounced than the impact, if any, of nutrient additions on emergence. In light of this assumption I pooled the results between enclosures with and without nutrient additions that had the same density of carp. Traps were sampled weekly from June 11 to August 20, 2002.

After removal from the traps, chironomids were preserved in glass vials (20mL) containing 70% ethanol. Adult chironomids were sorted and identified at a magnification of 40x using a Nikon SMZ-1B stereomicroscope. Species identification was based mainly on keys by Townes (1945), Roback (1970), Pinder (1978), and Oliver *et al.* (1981). Total and species-specific chironomid emergence was calculated by summing the number trapped over the entire sampling period and multiplying by 2 to give $no \cdot m^{-2}$. Biomass of emerging chironomids ($mg \cdot m^{-2} \cdot yr^{-1}$) was also calculated using length-weight regression

equations and species-specific mean body lengths provided in (Wrubleski & Rosenberg 1990).

In addition to adult chironomids, larval chironomids and tubificid oligochaeta inhabiting the surface sediments were sampled in the mesocosms. Duplicate benthic cores were taken from random locations within each enclosure on a weekly basis using an acrylic coring tube that was 6.9 cm in diameter. Each core sampled the invertebrates inhabiting the upper 7 cm of oxygenated surface sediments. Benthos samples were sieved through a 300-micron mesh that retained both micro- and macro-invertebrates. Benthos samples were preserved using 5 ml of 10% formalin. Once preserved, samples were sorted using a dissecting microscope and the invertebrates were removed and placed in a vial with 10% formalin.

3.1.3.11 Forage fish abundance (Project 2)

In Project 2, I attempted to remove the forage fish community from each enclosure before experimental manipulations began by seining each enclosure with a 7 m long box seine net with a mesh size of 3 mm (stretched). However, seining attempts only removed larger forage fish. Larval fish and eggs already present were not removed and populations of forage fish consisting mostly of shiners (*Notropis* spp) and fathead minnows (*Pimephales promelas*) developed within a couple of weeks. Instead of trying to remove the forage fish population at this point I opted to leave them in place so I could determine what impact common carp additions may have on the populations of native forage fish in Delta Marsh. At the end of the enclosure experiment the population of forage fish in each enclosure was estimated by seining each enclosure six times. After each seine, collected fish were counted and released outside of the enclosure complex so as to not be collected

in subsequent seining attempts. Population estimates of the total forage fish community were then determined based on declining catch rates associated with each successive seine haul. This method of population estimation is known as the "Depletion Method" and is used to estimate the size of a population from an equation developed by Ricker (1975) that represents the relationship between catch/effort (C/*f*) and cumulative catch (K):

$$C/f = a + q(K);$$

where:

a is the y-intercept of the regression equation, and

q is the slope of the regression equation.

The initial population (N_0) is estimated by substituting $C/f = 0$ into the equation and solving for *K*; at $C/f = 0$, $K = a/q = N_0$ (Schramm and Pugh 1997). Confidence limits (95%) for the depletion estimates were calculated using the equations provided in Neter *et al.* (1996). Population estimates were not derived on a species specific basis due to the fact the community in each enclosure was usually dominated by shiners with relatively small numbers of other forage fish common to Delta Marsh being detected.

3.2 Statistical analysis

3.2.1 Project 1

Impacts of common carp stocking density in 2001 and 2002 where determined by examining the rate of change in the mean open-water season values of various water quality parameters relative to those of the baseline monitoring year. Significant effects of

stocking density, experimental year, and their corresponding interaction were assessed using an ANCOVA-type model where the intercepts (via the "year" effect) and slopes (via the "density x year" effect) were allowed to vary by year. All ANCOVA-type models were run using the Statistical Analysis System (SAS 8.0) general linear models (GLM) procedure (SAS Institute Inc. 1985). Data that were not normally distributed, that was the case for most variables, were either $\log_{10}$ or $\log_{10}$ (X+1) transformed. Statistical significance of model effects were assessed via F-tests and models then reduced to contain only significant predictors. The effects of density on each water quality characteristic were estimated from appropriate linear combinations of the model parameters. Where linear relationships were investigated, simple linear regression analysis was used.

3.2.2 Project 2

Statistically significant ($P = 0.05$) effects of carp, nutrients, and their interactions on water quality in the enclosures were assessed using two-factor repeated measures ANOVA. As was the case in project 1, most data were not normally distributed and were either $\log_{10}$ or $\log_{10}$ (X+1) transformed. All repeated measures ANOVA's were conducted using PROC MIXED and the autoregressive (order 1) covariance structure, which has the desired property of correlations being larger for nearby times than far-apart times (Littell *et al.* 1996). Tukey's test was used for post hoc pairwise comparisons of means for significant effects.

For the biotic variables measured in the enclosures (phytoplankton biomass, zooplankton density, and benthic invertebrate density and emerging chironomid biomass), repeated measures ANOVA analysis could not be used due to the fact that this

analysis requires data to be spaced evenly over time. For this reason, these variables were compared using two-factor analysis of variance. As for the repeated measures analysis, Tukey's test was used for post hoc pairwise comparisons of means for significant effects.

4.0 Impacts of an exotic benthivorous fish, the common carp (*Cyprinus carpio*), on water quality, sedimentation, and submerged macrophytes in large experimental wetland cells

4.1 Results:

4.1.1 Water column nutrient concentrations

Mean open-water season TRP concentrations increased significantly with common carp biomass ($F_{1,6} = 20.06$, $p = 0.0042$) over those recorded during baseline monitoring in 2000. However, stocking density did not appear to have any noticeable effect on TRP concentrations in the cells with carp densities equal to or below 300 kg·ha^{-1} (Figure 4.1). In the cells with target densities of 600 and 1,200 kg·ha^{-1} TRP concentrations increased by 8 and 9 μg·L^{-1}, and by 14 and 40 μg·L^{-1} in 2001 and 2002, respectively. There was no significant density x year interaction ($F_{1,6} = 3.41$, $p = 0.1143$; Table 4.1). The lack of a significant density x year interaction effect indicates that the slopes of the linear relationships relating stocking density to changes in TRP concentrations for 2001 and 2002 were not significantly different from one another. However, the density effect was much more pronounced and significant in 2002, relative to 2001 (Table 4.2). Additionally, there was no significant year effect ($F_{1,6} = 0.16$, $p = 0.7031$; Table 4.1), indicating that the intercepts for the linear relationships relating concentration changes to stocking density in 2001 and 2002 were not significantly different.

The full model was reduced to retain density as the only significant predictor ($F_{1,8} = 22.12$, $p = 0.0015$) and therefore increases in TRP concentrations as a result of

Table 4.1. Results of ANCOVA-type analyses for differences in various water quality parameters among common carp treatment densities and between experimental years (2000-2002).

Variable	Source of variation	NDF	DDF	*F*-value	*p*-value
Total reactive phosphorus	density	1	6	20.06	0.0042
	year	1	6	0.16	0.7031
	year x density	1	6	3.41	0.1143
Ammonia-nitrogen	density	1	6	5.68	0.0545
	year	1	6	0.64	0.4529
	year x density	1	6	0.01	0.9312
Total suspended solids	density	1	6	60.95	0.0002
	year	1	6	0.17	0.6935
	year x density	1	6	14.78	0.0085
Inorganic suspended solids	density	1	6	44.94	0.0005
	year	1	6	2.91	0.1387
	year x density	1	6	19.40	0.0045
Organic suspended solids	density	1	6	50.65	0.0004
	year	1	6	0.03	0.8593
	year x density	1	6	8.32	0.0279
Phytoplankton chlorophyll	density	1	6	22.36	0.0032
	year	1	6	0.00	0.9808
	year x density	1	6	0.69	0.4366
Submerged macrophytes	density	1	6	1.95	0.2126
	year	1	6	4.91	0.0686
	year x density	1	6	0.30	0.6012
Photic depth	density	1	6	9.72	0.0206
	year	1	6	13.43	0.0105
	year x density	1	6	0.05	0.8351
Dissolved oxygen	density	1	6	59.96	0.0002
	year	1	6	1.11	0.3323
	year x density	1	6	5.89	0.0514

Table 4.2. Estimates of density effects (slope) in the full model for the 2001 and 2002 experimental stocking programs.

Variable	Density effect 2001	*P*-value	Density effect 2002	*P*-value
Total reactive phosphorus	0.01272	0.1592	0.03058	0.0015
Ammonia-nitrogen	0.05290	0.2110	0.05706	0.0745
Total suspended solids	0.01038	0.0520	0.03053	<0.0001
Inorganic suspended solids	0.00364	0.2100	0.01758	<0.0001
Organic suspended solids	0.00726	0.0416	0.01715	0.0001
Phytoplankton chlorophyll	0.01738	0.0146	0.01217	0.0146
Submerged macrophytes	-0.01713	0.6252	0.03954	0.1408
Photic depth	-0.01893	0.1269	-0.02176	0.0271
Dissolved oxygen	-0.00758	0.0008	-0.00396	0.0036

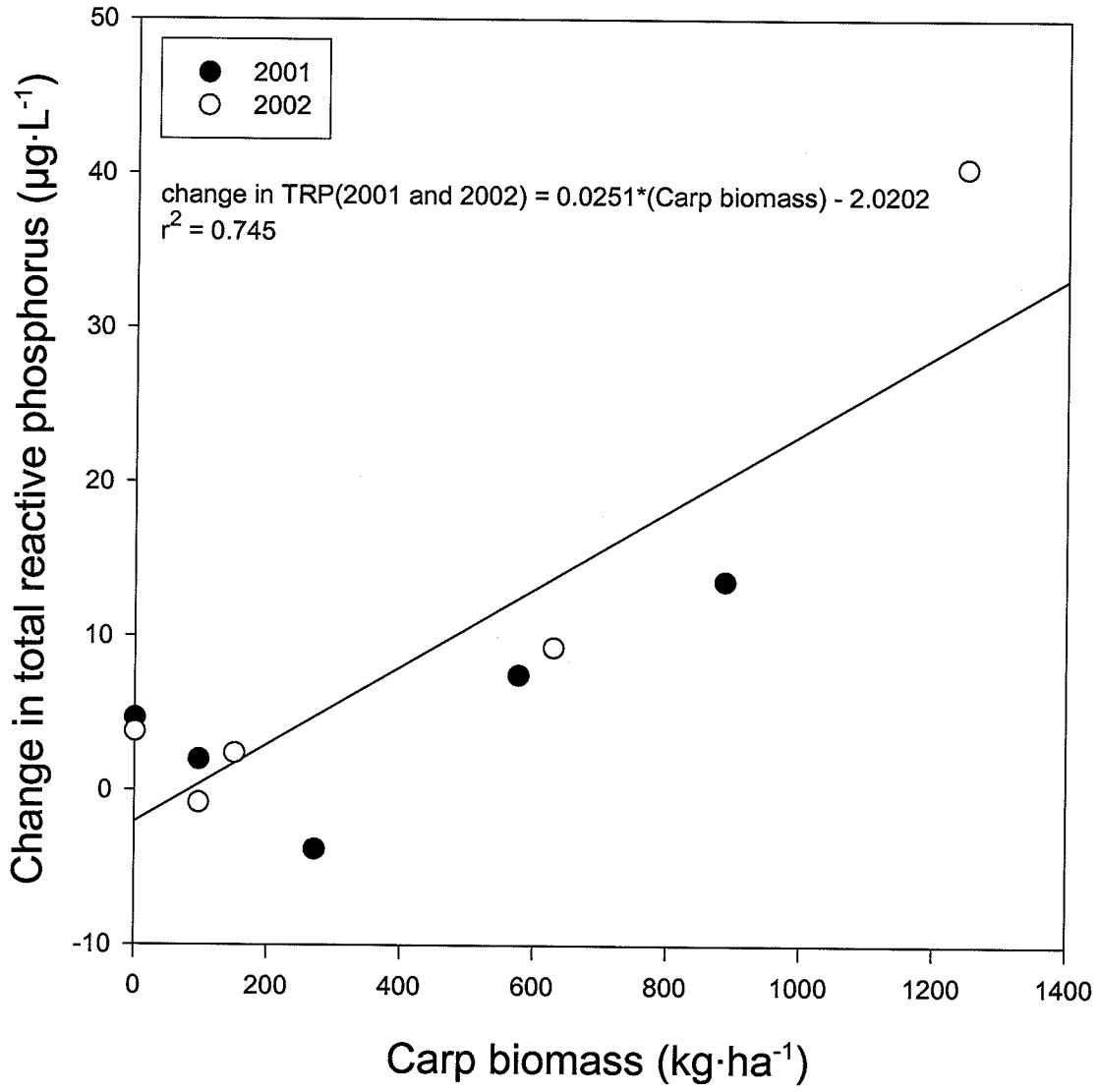

Figure 4.1. Relationship between the change in water column total reactive phosphorus ($\mu g \cdot L^{-1}$) concentrations and common carp biomass ($kg \cdot ha^{-1}$) between the baseline study year (2000) and two experimental stocking years (2001 and 2002).

increasing carp stocking densities in 2001 and 2002 could be predicted by a single linear equation (Figure 4.1). According to the reduced model, stocking density accounted for 75% of the variation in the changes in TRP concentrations above those in the baseline monitoring year.

Ammonia concentrations did not increase significantly with increasing common carp biomass in 2001 and 2002 over baseline concentrations in the full model ($F_{1,6} = 5.68$, $p = 0.0545$), and density effects were similar for both years (Table 4.2). However, when the model is reduced and the insignificant predictors of year and density x year are removed from the analysis, the density effect is significant ($F_{1,8} = 7.54$, $p = 0.0252$). Once again only one linear equation was required to predict the changes in ammonia concentrations in relation to carp stocking densities using the reduced model. However, unlike the equation for phosphorus, the equation for ammonia only accounted for 49% of the variation.

As was the case for TRP, in both 2001 and 2002 ammonia only increased above baseline concentrations at the two highest target stocking densities (600 and 1,200 $kg \cdot ha^{-1}$), and actually decreased substantially at the two lowest target stocking densities (150 and 300 $kg \cdot ha^{-1}$), relative to the control (Figure 4.2). In both 2001 and 2002, the increase in water column ammonia concentration in the cell stocked at a target density of 600 $kg \cdot ha^{-1}$ (28 and 67 $\mu g \cdot L^{-1}$) was greater than the increase in ammonia concentrations observed in the cell stocked at a target density of 1,200 $kg \cdot ha^{-1}$ (0 and 39 $\mu g \cdot L^{-1}$).

4.1.2 Suspended solids and phytoplankton chlorophyll

Concentrations of TSS ($F_{1,6} = 60.95$, $p = 0.0002$), ISS ($F_{1,6} = 44.94$, $p = 0.0005$), and

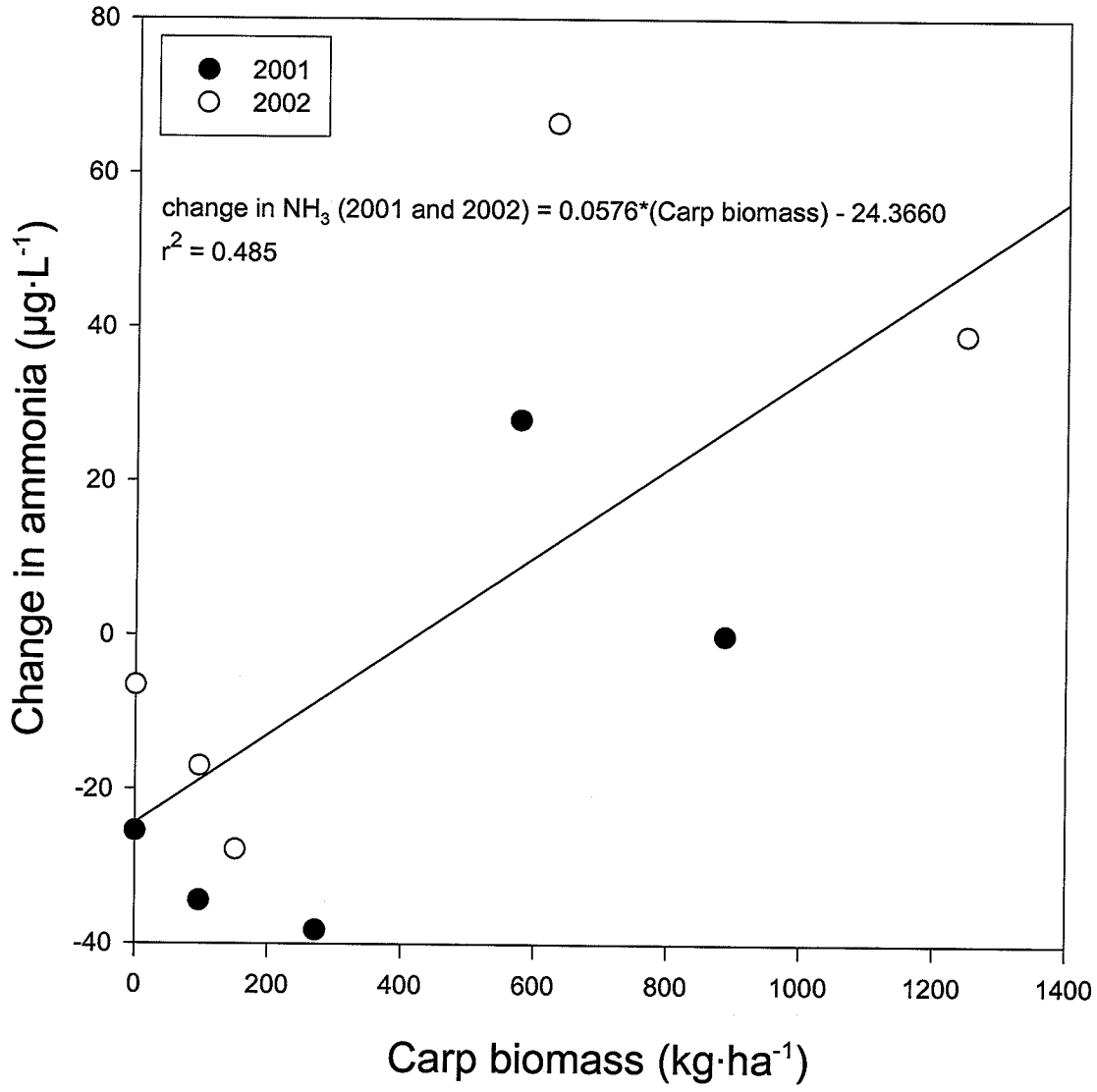

Figure 4.2. Relationship between the change in water column ammonia ($\mu g \cdot L^{-1}$) concentrations and common carp biomass ($kg \cdot ha^{-1}$) between the baseline study year (2000) and two experimental stocking years (2001 and 2002).

OSS ($F_{1,6}$ = 50.65, p = 0.0004), all increased significantly with carp biomass over concentrations recorded during baseline monitoring in 2000 (Table 4.1). Additionally, the year effect was insignificant while the density x year interaction effect was significant for all three parameters (Table 4.1).

ANCOVA-type models for TSS, ISS, and OSS were reduced to contain only the significant predictors of density (F1,7 = 70.41, p < 0.0001), (F1,7 = 40.45, p < 0.0004), (F1,7 = 60.48, p = 0.0001) and the density x year interaction (F1,7 = 39.62, p = 0.0004), (F1,7 = 16.25, p = 0.0050), (F1,7 = 21.52, p = 0.0024), respectively. The models explained 96, 92, and 94% of the variation in the changes in TSS, ISS, and OSS concentrations in 2001 and 2002 relative to those in the baseline monitoring year (Figures 4.3, 4.4, and 4.5).

Due to the fact there was a significant density x year interaction effects the reduced models required separate linear equations with the same intercept, but different slopes to predict the changes in suspended solid concentrations in 2001 and 2002. Linear equations generated by the reduced models for TSS (Figure 4.3), ISS (Figure 4.4), and OSS (Figure 4.5), indicated that the density effect was significant for all parameters in both years (Table 4.1) and that the density effect was much more pronounced in 2002, relative to the density effect in 2001 (Table 4.2).

Phytoplankton chlorophyll *a* concentrations increased significantly over baseline concentrations with carp stocking density ($F_{1,6}$ = 22.36, p = 0.0032; Table 4.1). However, there was no significant year effect or density x year interaction effect (Table 4.1), and density effects were similar in 2001 and 2002 (Table 4.2). As was the case for TRP, the

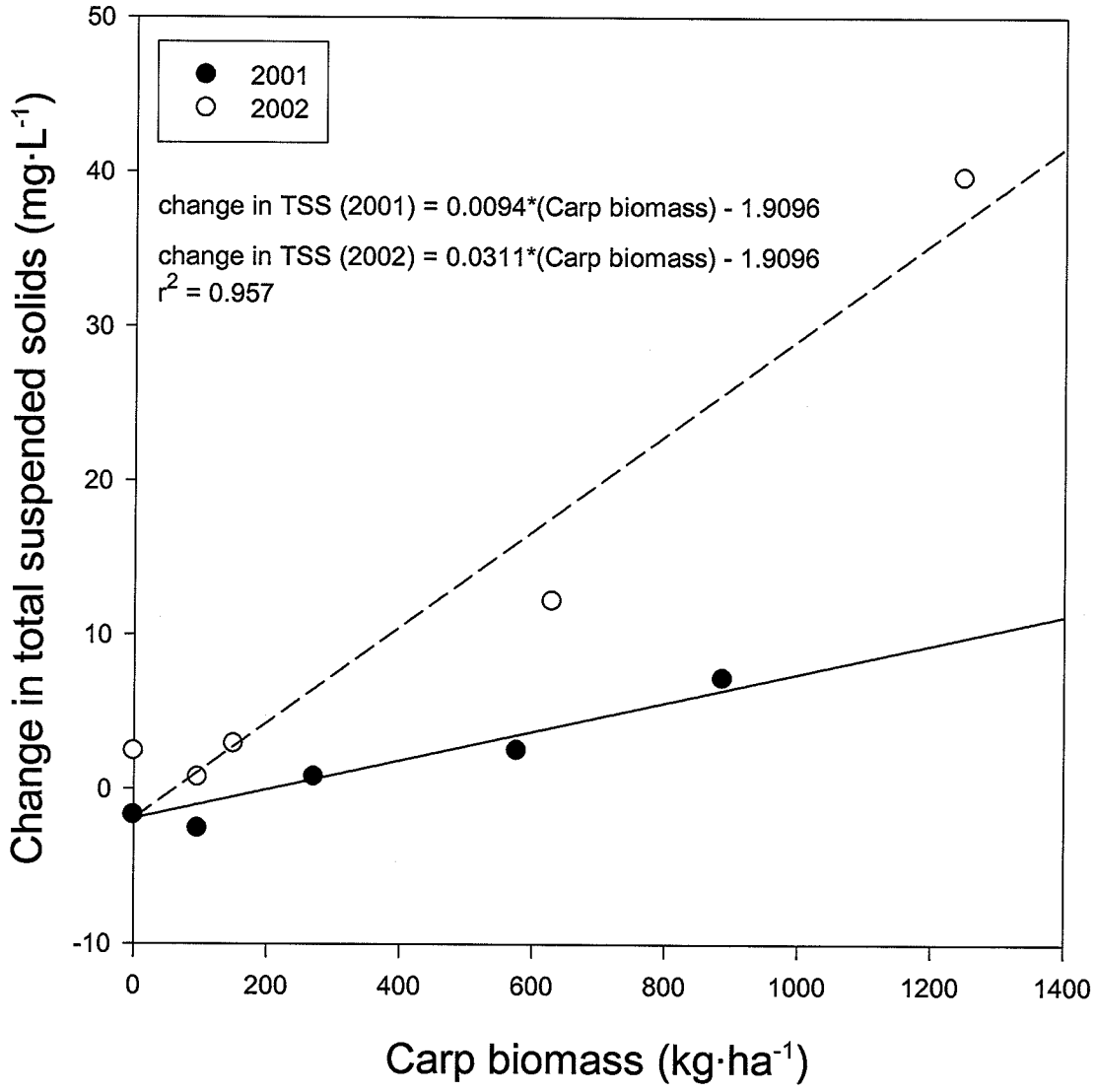

Figure 4.3. Relationship between the change in total suspended solid ($mg \cdot L^{-1}$) concentrations and common carp biomass ($kg \cdot ha^{-1}$) between the baseline study year (2000) and two experimental stocking years (2001 and 2002).

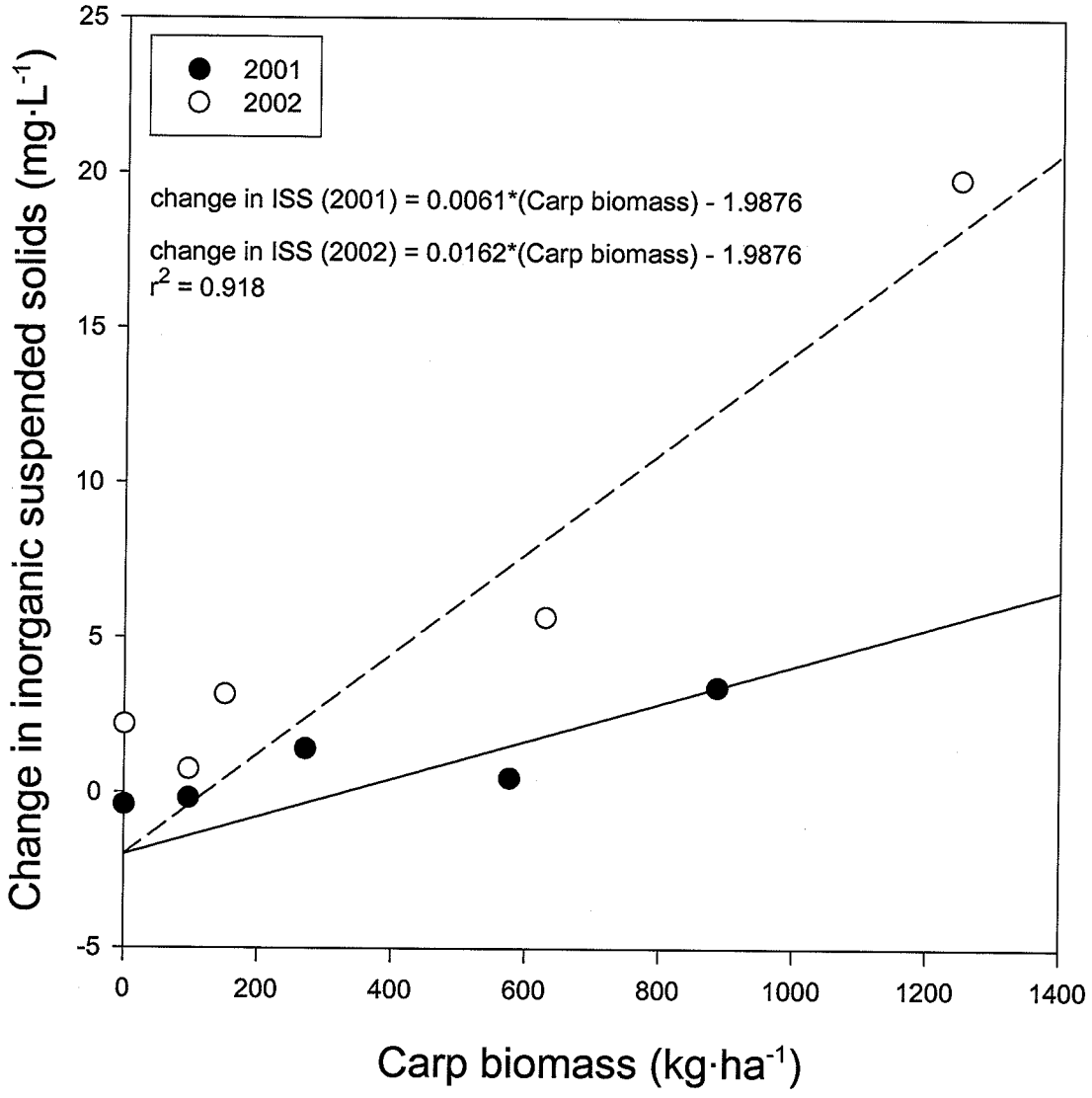

Figure 4.4. Relationship between the change in inorganic suspended solid ($mg \cdot L^{-1}$) concentrations and common carp biomass ($kg \cdot ha^{-1}$) between the baseline study year (2000) and two experimental stocking years (2001 and 2002).

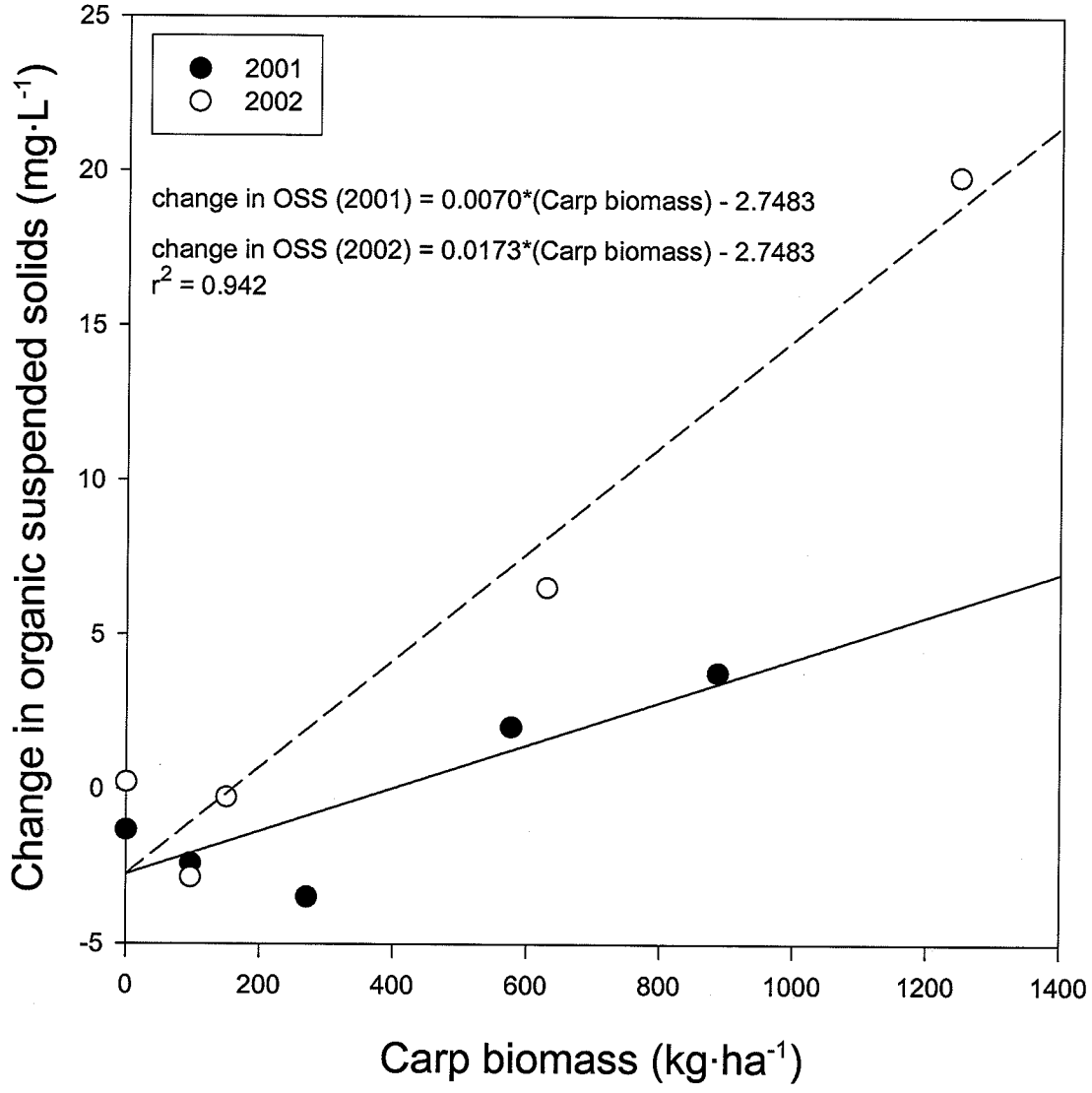

Figure 4.5. Relationship between the change in organic suspended solid ($mg \cdot L^{-1}$) concentrations and common carp biomass ($kg \cdot ha^{-1}$) between the baseline study year (2000) and two experimental stocking years (2001 and 2002).

full model for chlorophyll *a* was reduced to retain only density ($F_{1,8} = 23.40$, $p = 0.0013$) as a significant predictor, and required only one linear equation to predict changes in concentrations in relation to carp stocking densities in 2001 and 2002 (Figure 4.6). According to the reduced model, stocking density accounted for 75% of the variation in the changes in chlorophyll *a* concentrations in 2001 and 2002, relative to the baseline monitoring year.

4.1.3 Submersed macrophytes and light penetration

Common carp stocking density did not significantly affect submerged macrophyte biomass, and there was no significant year or density x year interaction effect (Table 4.1). Additionally, even after removing the insignificant year and density x year interaction effects, density remained insignificant as a predictor for changes in submerged macrophyte biomass. However, there were clear differences in trends between submerged macrophyte growth in 2001 and 2002 (Figure 4.7). Overall, submerged macrophyte biomass was lower in most treatment cells in 2001, relative to those observed in 2002. Although there was no statistically significant trend between carp density and submerged macrophyte biomass, there appeared to be a greater density effect in 2002 relative to 2001 (Table 4.2), and submerged macrophyte growth appeared to be suppressed with increasing stocking density.

Photic depth decreased significantly with carp stocking density ($F_{1,6} = 9.72$, $p = 0.0206$). Additionally, there was a significant year effect ($F_{1,6} = 13.43$, $p = 0.0105$), but no significant density x year interaction (i.e. no significant difference in slopes) effect ($F_{1,6} = 0.05$, $p = 0.8351$; Table 4.1). The ANCOVA-type model for photic depth was reduced to contain only the density effect and year effect as significant predictors. The equations for

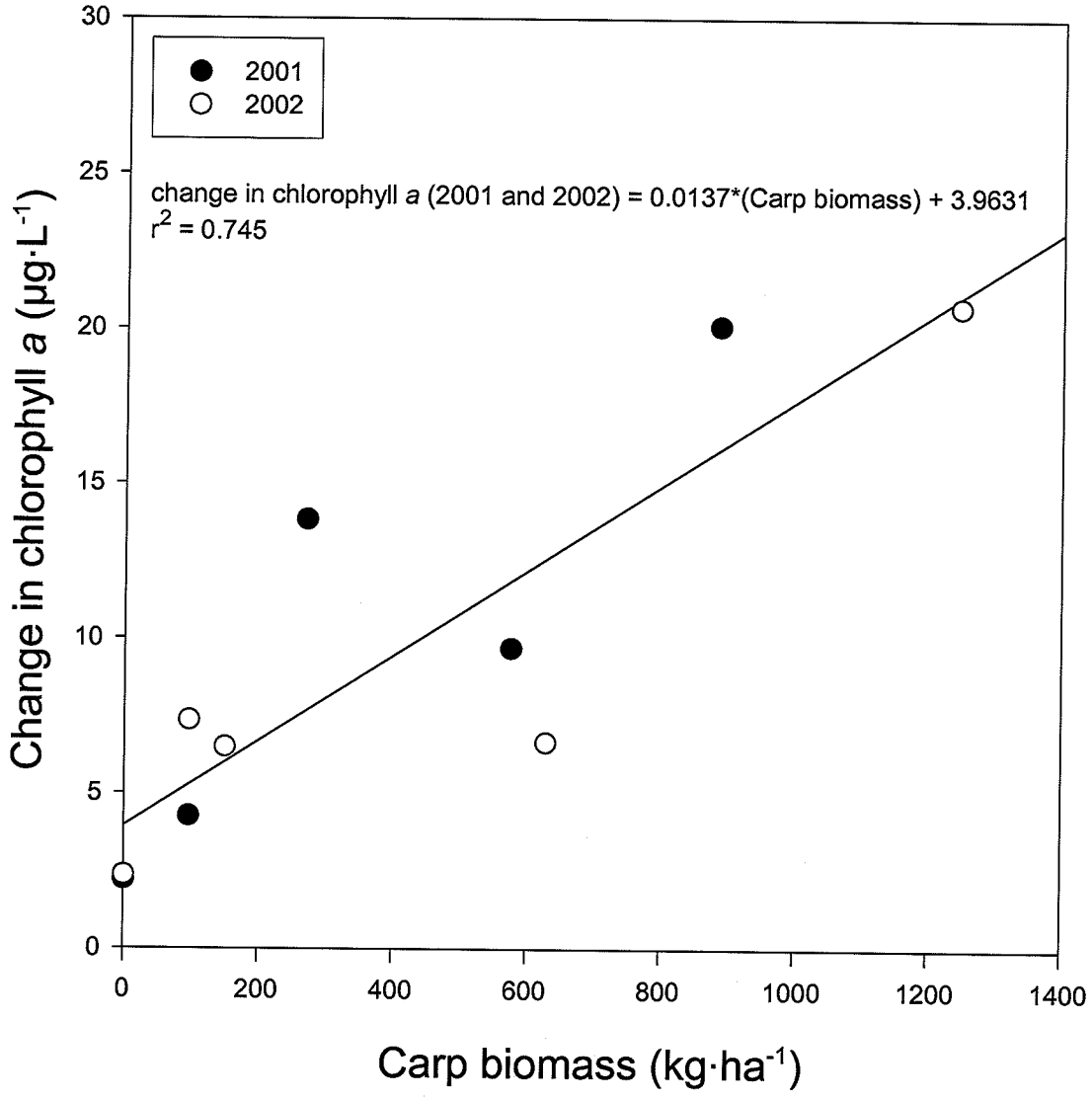

Figure 4.6. Relationship between the change in water column chlorophyll *a* ($\mu g \cdot L^{-1}$) concentrations and common carp biomass ($kg \cdot ha^{-1}$) between the baseline study year (2000) and two experimental stocking years (2001 and 2002).

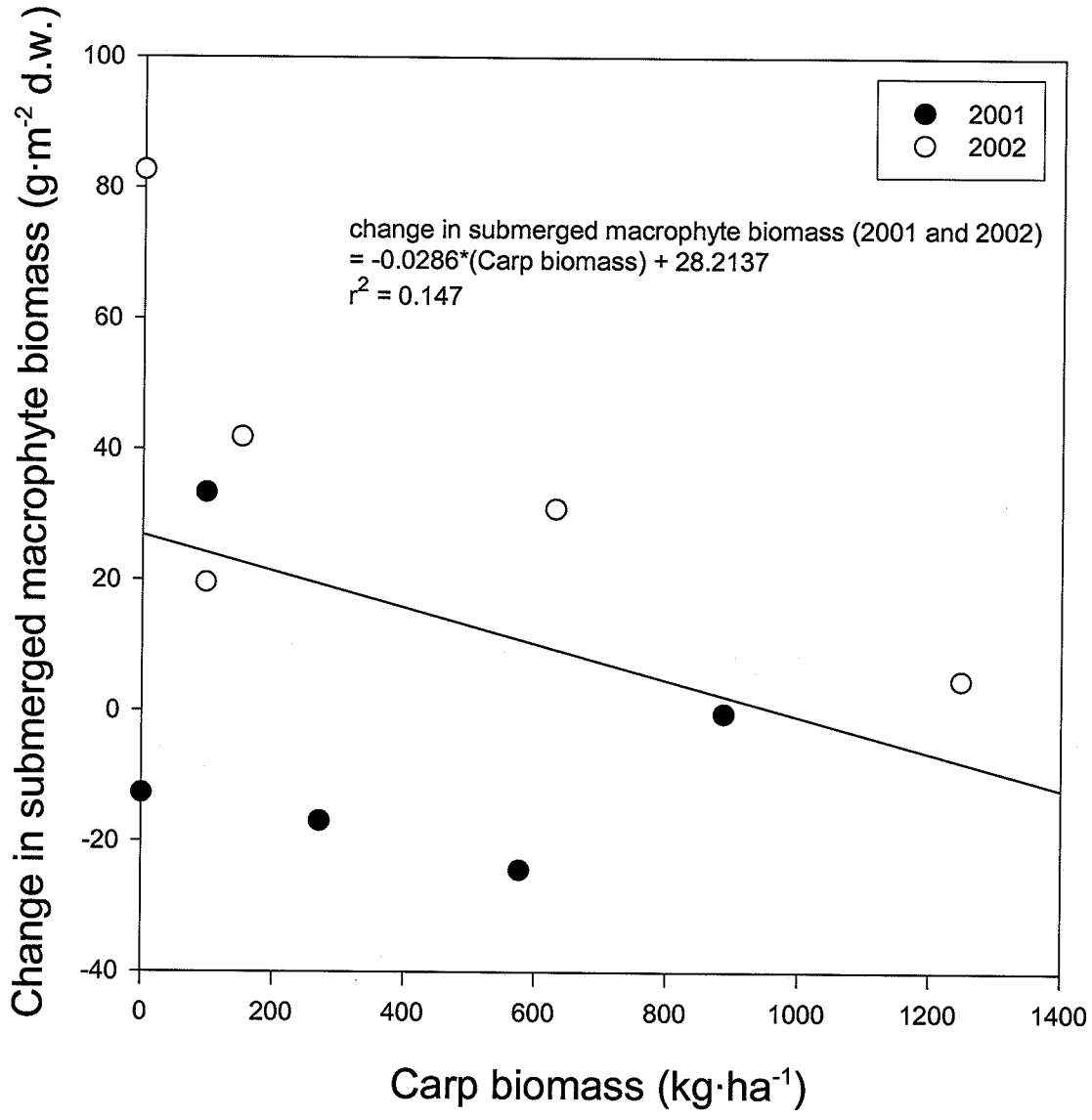

Figure 4.7. Relationship between the change in submerged macrophyte biomass ($g \cdot m^{-2}$ dry weight) and common carp biomass ($kg \cdot ha^{-1}$) between the baseline study year (2000) and two experimental stocking years (2001 and 2002).

the linear relationships relating change in photic depth to common carp density indicate that photic depth decreased in a linear fashion at a rate of -0.0208 cm per kg of common carp stocked in both 2001 and 2002, and that photic depth was reduced by approximately 25 cm across all stocking densities in 2001 relative to 2002 (Figure 4.8). The model explained 85% of the variation in the changes in photic depth in 2001 and 2002 relative to those in the baseline monitoring year.

4.1.4 Dissolved oxygen

Dissolved oxygen concentrations decreased significantly with increasing carp stocking density ($F_{1,6} = 59.96$, $p = 0.0002$; Table 4.1) in 2001 and 2002, relative to the baseline monitoring year. Additionally, the density effect in 2002 was almost double the density effect observed in 2001 (Table 4.2). There was no significant year effect or density x year interaction effect (Table 4.1), and therefore the full model was reduced to retain only density ($F_{1,8} = 33.30$, $p = 0.0004$) as a significant predictor, and required only one linear equation to predict changes in concentrations in relation to carp stocking densities in 2001 and 2002 (Figure 4.9). According to the reduced model, stocking density accounted for 81% of the variation in the changes in dissolved oxygen concentrations in 2001 and 2002.

4.1.5 Sedimentation

Sedimentation rates were only measured in July and August in the experimental wetland cells in 2002 and therefore the ANCOVA type analysis used for the previous parameters cannot be applied here. Instead sedimentation rates were analyzed using simple linear regression. In general, sedimentation rates increased with stocking density

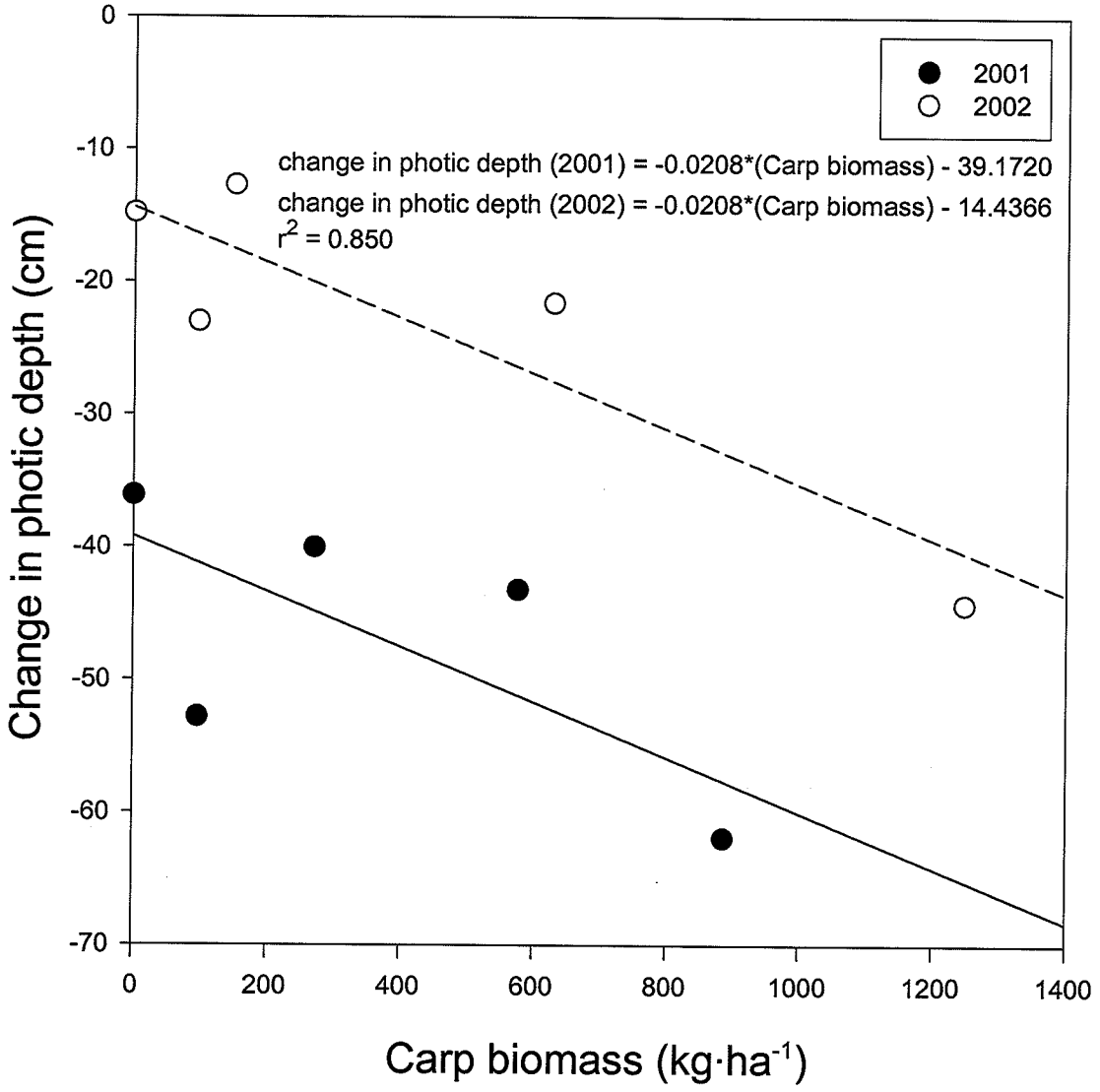

Figure 4.8. Relationship between the change in photic depth (cm) and common carp biomass ($kg \cdot ha^{-1}$) between the baseline study year (2000) and two experimental stocking years (2001 and 2002).

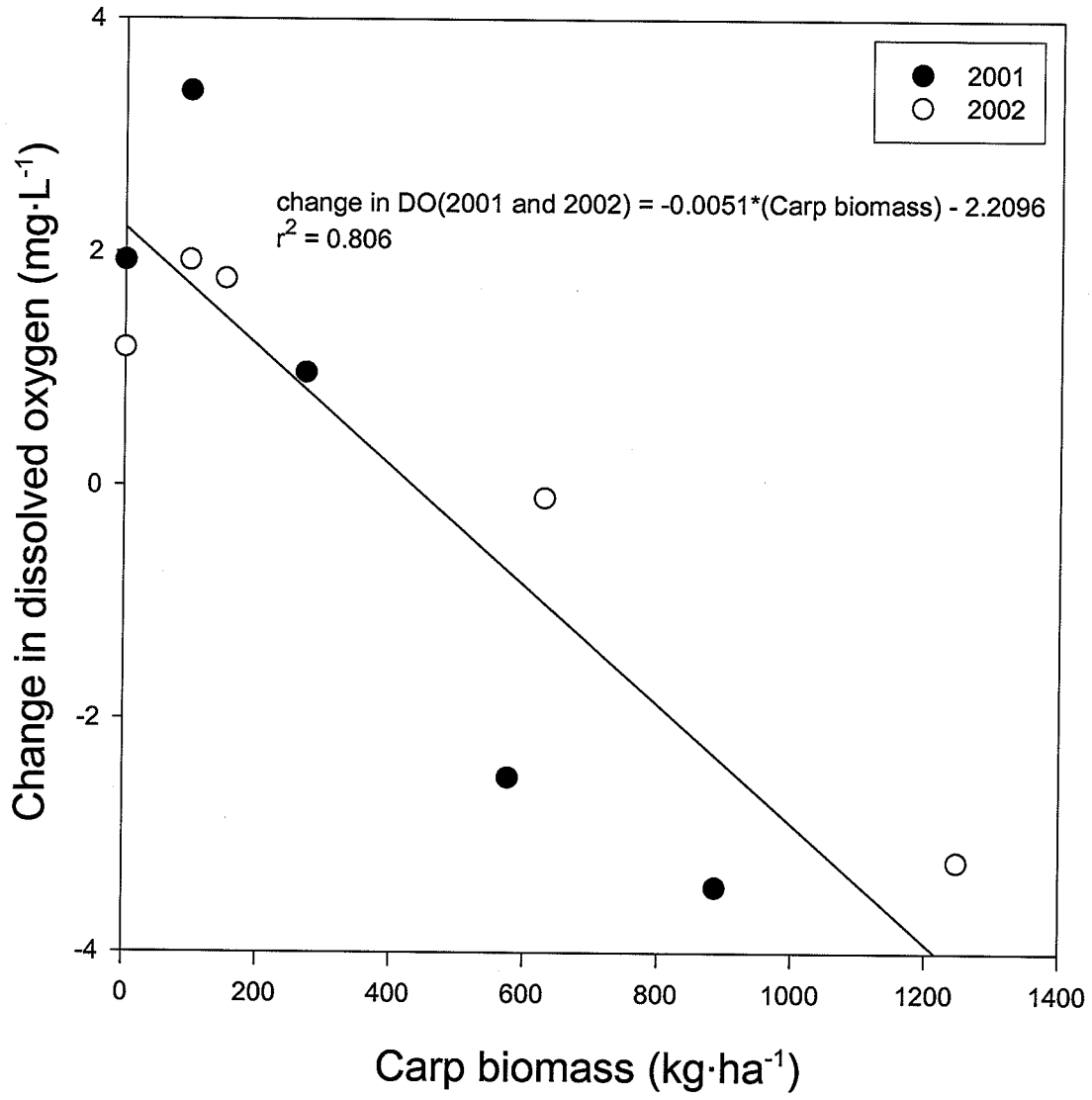

Figure 4.9. Relationship between the change in water column dissolved oxygen (mg·L^{-1}) concentrations and common carp biomass (kg·ha^{-1}) between the baseline study year (2000) and two experimental stocking years (2001 and 2002).

in both July and August (Figure 4.10). The relationship between sedimentation rate (averaged over July and August) and stocking density was significant ($p = 0.0001$), with stocking accounting for 99% of the variation in sedimentation rates (Figure 4.11). Sedimentation rates measured in August were higher than those in July (Figure 4.10).

Assuming sedimentation rates in the experimental cells (after subtracting background sedimentation rate from the control cell) are directly proportional to the amount of sediment resuspended, I calculated that common carp in the experimental cells resuspended between 37 and 361 kg of sediment per day. At this rate, the carp in the MERP cells would have resuspended between 1 and 10 metric tonnes of sediment over a 30 day period. Using the mass of sediment resuspended by common carp to predict water column loading of suspended solids over a one day period indicates that common carp would have contributed 18 $mg \cdot L^{-1} \cdot d^{-1}$ at the lowest carp density and 137 $mg \cdot L^{-1} \cdot d^{-1}$ at the highest density in 2002 (Table 4.3).

4.1.6 Predicted nutrient loading rates from excretion

Based on excretion experiments (Appendix B), nitrogen loading rates due to carp ranged between 4.3 and 32.1 $kg \cdot ha^{-1} \cdot yr^{-1}$, and between 1.6 and 19.3 $kg \cdot ha^{-1} \cdot yr^{-1}$ in 2001 and 2002, respectively. Phosphorus loading rates ranged between 0.41 and 3.02 $kg \cdot ha^{-1} \cdot yr^{-1}$, and between 0.14 and 1.75 $kg \cdot ha^{-1} \cdot yr^{-1}$ in 2001 and 2002, respectively. Individual loading rates calculated for each cell, as well as estimated cell volume, total number of common carp stocked, total mass of carp stocked, and average mass of carp stocked are presented in Table 4.3. Water column nutrient concentrations were predicted based on loading rates (from excretion) at day 30 after stocking occurred (corresponding

Table 4.3. Predicted impacts of common carp on total suspended solids, ammonia-nitrogen and total reactive phosphorus as a result of sediment resuspension and nutrient excretion from common carp in the MERP cells. TSS loading to the water column was calculated based on sedimentation rates and nutrient concentrations in the water column were predicted for 30 days after the MERP cells were stocked based on mass specific nutrient excretion rates.

Cell Target density ($kg \cdot ha^{-1}$)	Actual density ($kg \cdot ha^{-1}$)	Area (ha)	Volume (m^3)	Number of carp stocked	Average mass of individual carp stocked in cells (kg)	Predicted load of TSS to the water column ($mg \cdot L^{-1} \cdot d^{-1}$)	Predicted [NH_3-N] loading rate ($kg \cdot ha^{-1} \cdot yr^{-1}$)	Predicted [NH_3-N] 30 days after stocking ($\mu g \cdot L^{-1}$)	Predicted [TRP-P] loading rate ($kg \cdot ha^{-1} \cdot yr^{-1}$)	Predicted [TRP-P] 30 days after stocking ($\mu g \cdot L^{-1}$)
2001										
2 (150)	96.6	3.22	9,873	162	1.92	22	3.4	91	0.27	7
5 (300)	271.4	2.39	7,141	248	2.62	13	8.6	238	0.65	18
3 (600)	576.5	0.71	3,029	155	2.66	43	18.4	355	1.39	27
6 (1,200)	886.7	0.71	2,195	229	2.76	117	31.9	742	2.40	56
2002										
2 (150)	151.4	3.22	5,970	100	4.85	36	3.9	174	0.28	12
5 (300)	96.6	2.39	5,105	59	3.92	18	2.7	104	0.20	8
3 (600)	629.3	0.71	2,219	95	4.64	59	16.4	433	1.16	31
6 (1,200)	1,247.7	0.62	1,870	190	3.94	137	29.3	919	2.12	66

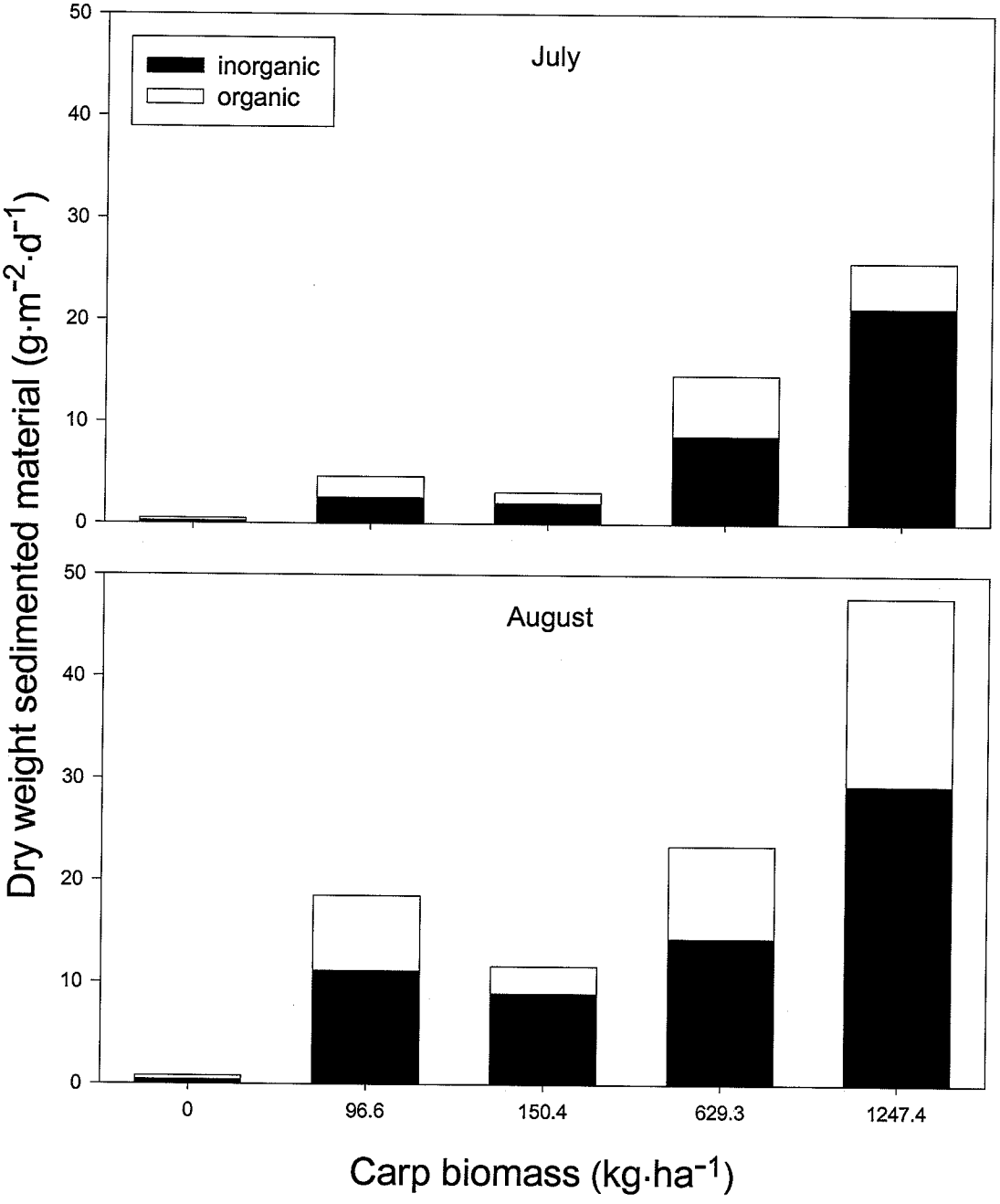

Figure 4.10. Sedimentations rates (organic and inorganic) measured in the MERP cells during the 2002 open-water season (July and August).

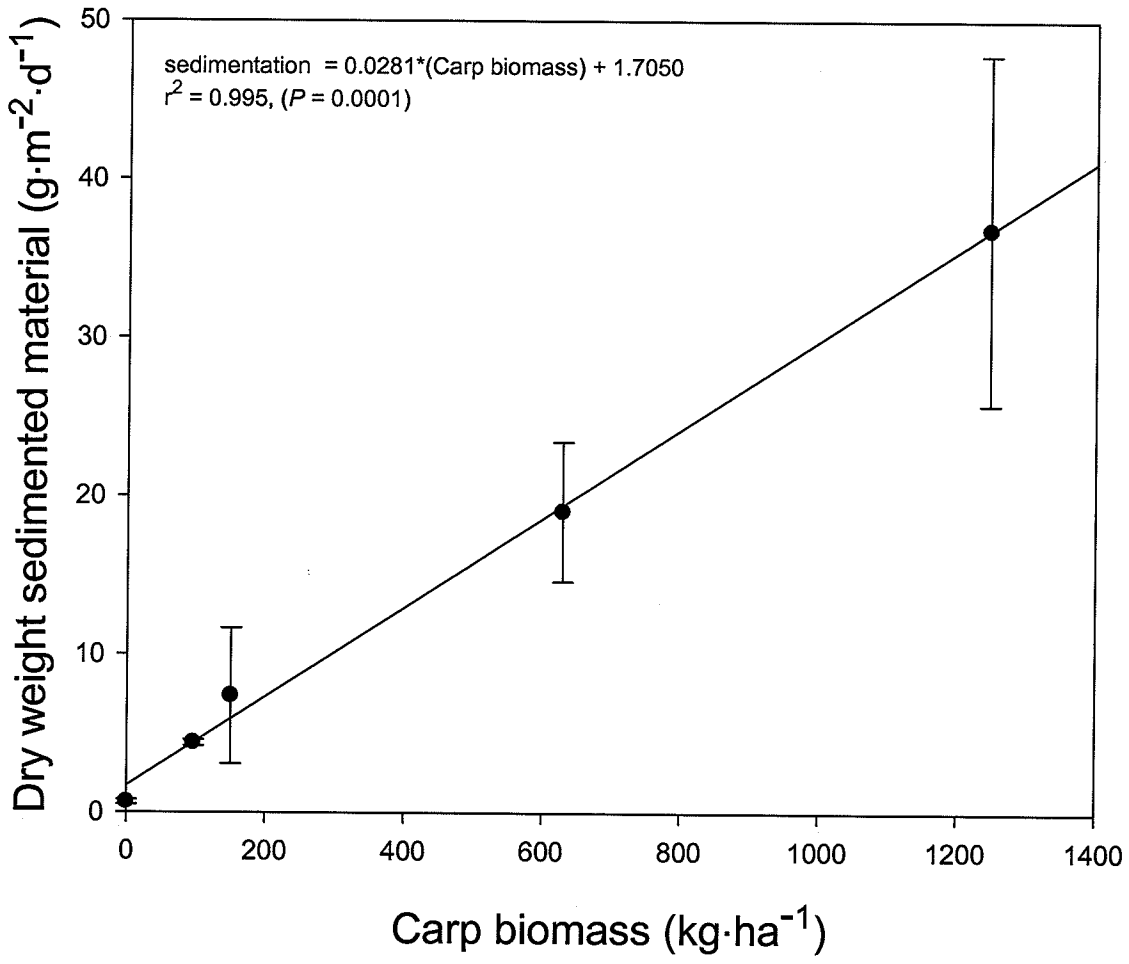

Figure 4.11 Relationship between average sedimentation rates measured in the MERP cells in 2002 and common carp biomass (kg·ha^{-1}).

approximately to the half-way point of each experimental season) and are also reported in Table 4.3. Water column nitrogen concentrations were predicted to increase between 71 and 459 $\mu g \cdot L^{-1}$, and between 27 and 365 $\mu g \cdot L^{-1}$, with increasing stocking density in 2001 and 2002, respectively. Water column phosphorus concentrations were predicted to increase between 7 and 43 $\mu g \cdot L^{-1}$, and between 2 and 33 $\mu g \cdot L^{-1}$, with increasing stocking density in 2001 and 2002, respectively. It is important to note that nutrient loading rates were calculated on an annual basis, which assumes that common carp are present all year and metabolically active. However, common carp are not present in the marsh in winter and are not metabolically active during the winter in the lake. Nevertheless, these loading rates allow us to compare the ability of carp to load nutrient relative to other sources.

4.1.7 Predicted impacts on Delta Marsh and Lake Manitoba

Currently there are no density estimates for common carp in Delta Marsh and therefore I cannot directly quantify the impacts that carp may have on this system. Common carp can reach biomasses in excess of 3000 $kg \cdot ha^{-1}$ (Koehn 2004), but in systems comparable to Delta Marsh, biomasses typically range between approximately 450 and 800 $kg \cdot ha^{-1}$ (Cooper 1987, Barton et al. 2000, Lougheed et al. 2004). To provide estimates of the impacts common carp have on Delta Marsh, I have conservatively estimated carp biomass for several scenarios in the marsh and in Lake Manitoba. For calculation purposes, I have estimated the marsh-wide biomass at 400 $kg \cdot ha^{-1}$, the localized common carp biomass during spawning season (in the marsh) at 1,200 kg.ha-1 and the lake-wide biomass at 200 $kg \cdot ha^{-1}$. Predicted changes in water quality parameters and nutrient loading rates are listed in Table 4.4 and were calculated using the estimated scenario-specific carp biomass and the linear equations generated from the MERP

Table 4.4. Predicted impacts of common carp on water quality variables (calculated from stocking experiments) and nutrient loading rates (calculated based on excretion experiments) in Delta Marsh and Lake Manitoba under various common carp biomass scenarios.

	Carp biomass for Delta Marsh and Lake Manitoba (estimated)		
Variable	400 ($kg \cdot ha^{-1}$) Marsh-wide average carp biomass during the open-water season	1,200 ($kg \cdot ha^{-1}$) Localized carp biomass at time of spawning season	200 ($kg \cdot ha^{-1}$) Lake-wide average carp biomass year-round
Water column concentrations			
Total reactive phosphorus ($\mu g \cdot L^{-1}$)	10	30	-
Ammonia-nitrogen ($\mu g \cdot L^{-1}$)	23	69	-
Total suspended solids ($mg \cdot L^{-1}$)	8	24	-
Inorganic suspended solids ($mg \cdot L^{-1}$)	4	13	-
Organic suspended solids ($mg \cdot L^{-1}$)	5	15	-
Chlorophyll *a* ($\mu g \cdot L^{-1}$)	5	16	-
Photic depth (cm)	-8	-25	-
Submerged macrophyte biomass ($g \cdot m^{-2}$)	-11	-34	-
Nutrient loading rates from excretion			
Ammonia-nitrogen ($kg \cdot ha^{-1} \cdot yr^{-1}$)	12.6	37.7	6.3
Total reactive phosphorus ($kg \cdot ha^{-1} \cdot yr^{-1}$)	1.18	3.54	0.59

stocking experiment. When there were two linear regression equations for one parameter, one for each experimental stocking year, the average of the two is presented. Nutrient loading estimates were generated assuming the average weight of common carp to be 2.76 kg (based on the average weight of carp caught in Delta Channel in 2001).

4.2 Discussion:

This study allowed me to determine the effects of an exotic benthivorous fish, the common carp, on water quality in large experimental wetlands representative of many of the smaller isolated ponds and connected bays within Delta Marsh. In general, the effects of common carp on water quality were similar to those encountered in systems undergoing cultural eutrophication. With increasing densities of common carp, water column nutrient concentrations, suspended solids, and chlorophyll *a* increased, while dissolved oxygen concentrations, submerged macrophyte density, and photic depth decreased.

4.2.1 Effects on water column nutrient concentrations

Water column nutrient concentrations increased linearly with carp biomass with total reactive phosphorus and ammonia-nitrogen concentrations increasing by approximately 2.5 and 5.8 $\mu g \cdot L^{-1}$ for each 100 $kg \cdot ha^{-1}$ of carp, respectively. Shormann & Cotner (1997) reported similar increases in ammonia concentrations in the presence of smallmouth buffalo (*Ictiobus bubalus*), a benthivorous fish and suggested that increased ammonia concentrations were the result of enhanced bacterial re-mineralization in the presence of suspended sediments.

Conversely, these authors did not find that soluble reactive phosphorus concentrations increased. Similarly, Cline *et al.* (1994) found that common carp did not significantly increase orthophosphate-phosphorus. Keen & Gagliardi (1981) found that a benthivorous fish, the brown bullhead (*Ameirus nebulosus*) increased soluble reactive phosphorus concentrations in aquaria filled with water, but not in aquaria with water and sediment. These authors concluded that although bullhead released large quantities of soluble reactive phosphorus through physiological processes, they reduced water column concentrations by resuspending sediments that bound with the phosphorus and subsequently transported it to the sediment-water interface.

The above-mentioned studies where phosphorus concentrations did not increase in the presence of benthivorous fish were conducted in small mesocosms (less than 6 m^2) and for the most part used much smaller fish compared to those used in my study. This may explain why these studies did not measure any significant change in soluble reactive phosphorus concentrations. Additionally, total reactive phosphorus concentrations in my study were only significantly enhanced at carp biomasses in excess of 600 $kg \cdot ha^{-1}$. This suggests that there may potentially be a critical biomass below which the amount of sediment resuspended by common carp is sufficient to remove any additional dissolved phosphorus added to the water column as a result of physiological processes or disruption of the sediment-water interface. My experiments in large wetland cells suggest that this critical biomass is between 300 and 600 $kg \cdot ha^{-1}$. Additionally, other important factors such as temperature, sediment oxygen demand, pH, and the quality of organic matter determine the rate at which nutrients are released and/or bound to the sediments. Any one or combination of these factors may explain why common carp enhanced phosphorus

concentrations in the water column in my experiment, while other studies have found no such increase.

Although water column nutrient concentrations increased with increasing carp biomass as hypothesized, these increases were much lower than the increases that were predicted based on excretion from common carp. However, predicted increases in phosphorus concentrations based on excretion were more similar to measured increases, relative to those for nitrogen. This is due to the fact that nitrogen is typically much more volatile relative to phosphorus. The most likely reason for the discrepancies between measured and predicted concentrations are the profuse submerged macrophyte beds that are capable of sequestering large quantities of nutrients. Additionally, with increasing carp biomass, dissolved nutrients in the water column would have been sequestered into algal cells and/or bound to suspended sediments and subsequently deposited at the sediment-water interface at an increasing rate.

4.2.2 Effects on suspended solids and phytoplankton chlorophyll

As would be expected, concentrations of suspended solids (inorganic and organic) and chlorophyll *a* all increased linearly with increasing carp biomass. Although total, inorganic, and organic suspended solids increased linearly with increasing carp biomass, the rate of increase varied between the two experimental years. In 2001, TSS, ISS, and OSS increased by approximately 0.9, 0.6, and 0.7 $mg \cdot L^{-1}$ for each 100 $kg \cdot ha^{-1}$ of carp stocked, respectively. In 2002, water levels in the MERP cells were approximately 0.20 m below those recorded in 2001 and water volumes in the MERP cells were reduced by approximately 27% (Badiou 2002, unpublished data). As a result of these lower water levels and reduced volumes, the rate of increase in total suspended solids (3.1 $mg \cdot L^{-1}$ per

100 kg·ha^{-1} of carp stocked) more than tripled, while the rates for inorganic (1.6 mg·L^{-1} per 100 kg·ha^{-1} of carp stocked) and organic (1.7 mg·L^{-1} per 100 kg·ha^{-1} of carp stocked) suspended solids more than doubled.

The increase in suspended solid concentration per 100 kg·ha^{-1} of carp biomass in the literature ranged from approximately 3.8 mg·L^{-1} per 100 kg·ha^{-1} of carp biomass in Dutch ponds and lakes (Meijer *et al.* 1989) to approximately 17 mg·L^{-1} per 100 kg·ha^{-1} of carp biomass in mesocosm (0.06 ha) experiments (Parkos III *et al.* 2003). Experiments conducted in small ponds (0.1 ha) by Breukelaar *et al.* (1994) yielded increases in suspended solid concentrations of approximately 8 mg·L^{-1} per 100 kg·ha^{-1} of carp biomass, intermediate to those in the previous two studies.

These results suggest that as the size of the experimental system decreases, carp resuspend more sediments per unit of mass. This increase in suspended solids with decreasing size of the experimental system may be due to the fact that common carp can easily overexploit benthic prey in small mesocosms and thus need to increase their foraging activity, resulting in increased levels of suspended solids. This hypothesis is similar to the one proposed by Zambrano *et al.* (2001) who suggest that shallow lakes may respond catastrophically to common carp when a critical density of common carp is exceeded. At this density benthic prey become overexploited and common carp increase their foraging activity dramatically causing a subsequent increase in suspended solid concentrations. Based on the model proposed by Zambrano *et al.* (2001), the effects of common carp on suspended solid concentrations would vary depending on the density of benthic prey. Increases in suspended solids per unit of carp biomass in my study were

very similar to those observed in ponds and lakes in the Netherlands, suggesting that my results resemble those measured in natural systems at large scales. Additionally, because chironomids are very abundant in Delta Marsh (MERP cells included), prey searching activity of common carp may be reduced which may also explain why the increases in suspended solid concentrations per unit carp biomass in my experiment was low relative to those from the studies mentioned above.

Phytoplankton chlorophyll *a* concentrations in the MERP cells increased by approximately 1.4 $\mu g \cdot L^{-1}$ per 100 $kg \cdot ha^{-1}$ of carp biomass. Additionally, unlike suspended solids, the rate at which chlorophyll *a* increased in response to increasing carp biomass did not differ between the two years when experimental stocking occurred. Many studies have found that chlorophyll *a* concentrations increase in the presence of benthivorous fish (Breukelaar *et al.* 1994, Roberts *et al.* 1995, King *et al.* 1997, Zambrano *et al.* 1999, Angeler *et al.* 2002). Similar to my results, Roberts *et al.* (1995) found that chlorophyll *a* concentrations increased at a rate of approximately 2.4 $\mu g \cdot L^{-1}$ per 100 $kg \cdot ha^{-1}$ of carp biomass, whereas Breukelaar *et al.* (1994) found that every 100 kg of $bream \cdot ha^{-1}$ caused an increase of 9 $\mu g \cdot L^{-1}$. The fact that chlorophyll *a* and water column nutrient concentrations increased linearly at a constant rate during both experimental years supports my hypothesis that common carp enhance phytoplankton biomass by increasing nutrient loading through sediment resuspension and excretion of benthically derived nutrients into the overlying water.

Although suspended solids and phytoplankton biomass (expressed as chlorophyll *a*) increased with carp biomass, none of the experimental treatments caused a catastrophic shift from the clear state to the turbid state.

4.2.3 Effects on submersed macrophytes and light penetration

Unlike most studies, my research did not find that common carp significantly reduced submerged macrophyte biomass. Although the impact of common carp on submerged macrophyte biomass was not significant, it appeared that for every 100 kg of carp·ha^{-1} stocked, submerged macrophyte biomass was reduced by approximately 2.9 g·m^{-2}. This decrease was particularly influenced by the effects of common carp on submerged macrophytes in 2002. However, this rate of decrease is much lower compared to the rate calculated by Robel (1961) where each 100 kg of carp·ha^{-1} stocked in enclosures resulted in a decrease in submerged macrophyte biomass of approximately 11.5 g·m^{-2}. Furthermore, Kolterman (1990) found that at densities of 675 kg·ha^{-1}, large common carp (1.5 – 3.0 kg) and small common carp (0.5 – 0.9 kg) reduced submerged macrophyte biomass in enclosures by approximately 184 and 114 g·m^{-2}, or 27 and 17 g·m^{-2} for every 100 kg of carp·ha^{-1} stocked, respectively.

The large effect of common carp on submerged macrophyte biomass observed by Robel (1961) and Kolterman (1990), relative to those observed in my study is likely due to the fact that these studies were conducted in small experimental enclosures where carp activity would be restricted to, and concentrated on, a delimited area. Additionally, large phytoplankton blooms that are often associated with the presence of high densities of benthivorous fish, and which lead to lower densities of submerged macrophyte biomass,

were never observed in the MERP cells. In fact, although submerged macrophytes appeared to be suppressed with increasing densities of common carp in 2002, the biomass of submerged macrophytes was higher in all MERP cells regardless of common carp biomass in 2002, relative to the baseline monitoring year. The high dissolved organic carbon concentration, and subsequent light limitation in the MERP cells is the most probable reason why increasing carp biomass did not switch the MERP cells from a clear macrophyte-dominated state to the turbid phytoplankton-dominated state. Furthermore, extensive submerged macrophyte beds, such as those present in most of the MERP cells throughout the course of the study, can suppress phytoplankton production (Scheffer *et al.* 1993, Scheffer 1998, Parkos III *et al.* 2003).

Based on the decreased photic depth in all MERP cells with stocked carp (2.1 cm per 100 kg of carp·ha^{-1}), I would have expected that macrophyte growth would have been reduced to a greater extent than I observed. However, even at the highest target stocking density of 1,200 kg·ha^{-1} where photic depth would have been reduced by approximately 25 cm, the entire water column and sediment surface in all the MERP cells would have remained within the euphotic zone. This may explain why submerged macrophyte growth was slowed, but biomass was not reduced with increasing densities of common carp.

4.2.4 Effects on dissolved oxygen concentrations

Dissolved oxygen concentrations in the MERP cells decreased at a rate of approximately 0.5 mg·L^{-1} per 100 kg·ha^{-1} of carp biomass. Similarly, Cline *et al.* (1994) found that common carp suppressed dissolved oxygen concentrations and Robertson *et al.* (1997) found that sediment oxygen demand was greater at higher densities of common

carp. The later study suggested that common carp had significant impacts on the microbial dynamics of the sediment. Common carp likely reduced water column dissolved oxygen concentrations in my experiment by resuspending sediments, which then increased bacterial production within the water column. This is supported by Wainright (1987) who found that resuspended marine sediments greatly enhanced production of heterotrophic microplankton. In the water column, resuspended particles have a larger surface area and are exposed to oxygen and other electron acceptors that allow these particles to support higher re-mineralization rates in the water column, relative to bottom sediments (Almroth 2002). As a result of enhanced microbial growth on these resuspended particles, water column respiration increases and dissolved oxygen concentrations decrease.

4.2.5 Effects on sedimentation

My results indicate that in 2002, every 100 $kg \cdot ha^{-1}$ of carp biomass increased sedimentation rates by 2.8 $g \cdot m^{-2}$. This sedimentation rate is much lower than reported by Breukelaar *et al.* (1994), where common carp increased sedimentation rates by 24 $g \cdot m^{-2}$ for every 100 $kg \cdot ha^{-1}$, almost on order of magnitude greater than the rate I observed. The smaller sedimentation rates measured in this study are likely due to the abundance of submerged macrophytes in the MERP cells. When submerged macrophytes are found in abundance in shallow lakes they have the ability to maintain the system in the clear state by reducing resuspension and sedimentation (Jeppesen *et al.* 1997, Scheffer 1998, Scheffer 1999). Additionally, Timms & Moss (1984) found that submerged macrophytes maintained the clear state by providing refuge for large cladocerans during the day, which enabled the zooplankton population to regulate phytoplankton biomass. Furthermore,

according to the catastrophic response model proposed by Zambrano *et al.* (2001), if benthic resources greatly exceeded the needs of the carp population stocked in the MERP cells, carp foraging activity and hence resuspension and sedimentation would be greatly reduced

4.2.6 Implications for the Delta Marsh and Lake Manitoba ecosystems

In general, my results suggest that common carp enhance the eutrophication process in both Delta Marsh and Lake Manitoba, but more so in Delta Marsh due to the fact that this system is shallower and would likely have higher densities of carp. Assuming the marsh-wide common carp biomass is approximately 400 $kg \cdot ha^{-1}$, total reactive phosphorus and ammonia concentrations would increase by 10 and 23 $\mu g \cdot L^{-1}$, respectively (Table 4.4). This increase is significant because an increase of 10 $\mu g \cdot L^{-1}$ has the ability to make a once clear system turbid (Smil 2000). Based on the total phosphorus trigger ranges for Canadian lakes and rivers (Environment Canada 2003), common carp densities of 400 $kg \cdot ha^{-1}$ could easily change the trophic status of most aquatic ecosystems.

At a marsh-wide biomass of 400 $kg \cdot ha^{-1}$, common carp would contribute 12.6 kg of ammonia-nitrogen$\cdot ha^{-1} \cdot yr^{-1}$ and 1.18 kg of total reactive phosphorus$\cdot ha^{-1} \cdot yr^{-1}$ through excretion. These loading rates are approaching the dangerous loading rates proposed by Vollenweider (1968) for total nitrogen (20 $kg \cdot ha^{-1} \cdot yr^{-1}$), and total phosphorus (1.3 $kg \cdot ha^{-1} \cdot yr^{-1}$) in water bodies with a mean depth of 5 m. Goldsborough & Robinson (1985) calculated that sediments from Blind Channel in Delta Marsh were responsible for internally loading phosphorus (measured as total reactive phosphorus) at a rate of 1.78

$kg \cdot ha^{-1} \cdot yr^{-1}$. Assuming this rate is constant throughout the marsh, phosphorus loading from common carp excretion would be equivalent to approximately 66% of internal loading. Furthermore, a lake-wide biomass of 200 $kg \cdot ha^{-1}$, common carp would contribute 6.28 kg of ammonia-nitrogen$\cdot ha^{-1} \cdot yr^{-1}$ and 0.59 kg of total reactive phosphorus$\cdot ha^{-1} \cdot yr^{-1}$ to Lake Manitoba through excretion (Table 4.4). The largest natural external sources of nutrients to Lake Manitoba are the Whitemud and Waterhen Rivers, which combine to add 6.44 kg of total nitrogen$\cdot ha^{-1} \cdot yr^{-1}$ and 0.22 kg of total phosphorus$\cdot ha^{-1} \cdot yr^{-1}$ (Jones & Armstrong 2001). Based on these rates, nitrogen loading from common carp excretion in Lake Manitoba (assuming a density of 200 $kg \cdot ha^{-1}$) would be similar to external loading from the two major tributaries, while phosphorus loading would be more than double that contributed by the major tributaries to Lake Manitoba. Similar to my results, other studies have also found that fish excretion can be just as important as external nutrient loading (Brabrand *et al.* 1990, Persson 1997).

In addition to their effects on water column nutrient concentrations and nutrient loading, common carp may also adversely affect fish populations in Delta Marsh by increasing suspended solid concentrations. According to the severity of ill effects model proposed by Newcombe & MacDonald (1991), the increase in suspended solids associated with a carp biomass of 400 $kg \cdot ha^{-1}$ (8 $mg \cdot L^{-1}$) would cause moderate physiological stress in fish assuming an exposure time of four weeks. This may explain why the relative abundance of walleye, one of the most economically important fish harvested commercially in Lake Manitoba, decreases significantly with increasing relative abundance of common carp (Figure 4.12).

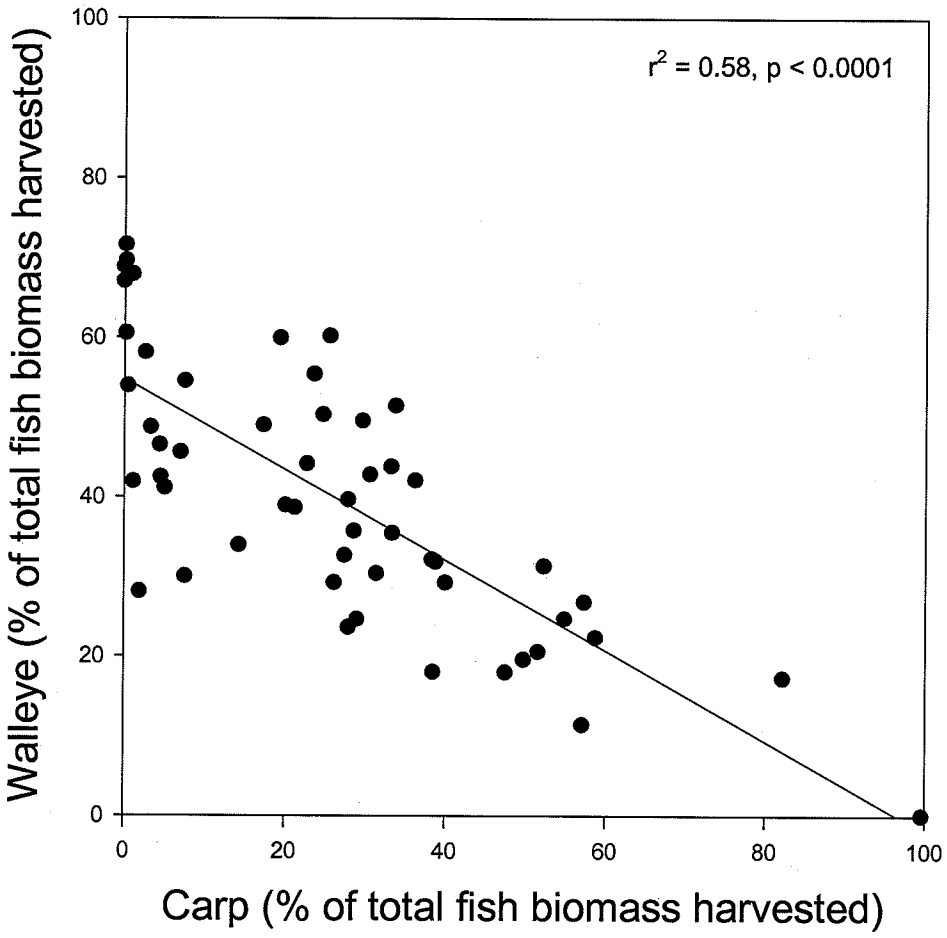

Figure 4.12. Relationship between relative abundance (calculated as % of total fish biomass harvested) of walleye and common carp in the Lake Manitoba commercial fishery, 1950-2004. Data provided by Manitoba Conservation, Fisheries Branch.

Although common carp had many of the effects I had hypothesized, such as increasing suspended solids, nutrients, and phytoplankton they did not trigger a dramatic switch from the clear macrophyte-dominated state to the turbid phytoplankton dominated-state. An equilibrium switch was likely avoided in my experimental wetlands due to the fact that submerged macrophytes were not reduced by carp, and high DOC concentration in the wetland cells prevented phytoplankton from flourishing. Additionally, the MERP cells have been isolated from the surrounding marsh for more than a decade and have not received much in the way of nutrient loading other than through precipitation. In light of this it is feasible that low nutrient levels in the MERP cells prevented carp form triggering a shift from the clear state to the turbid state.

5.0 Impacts of an exotic benthivorous fish, the common carp (*Cyprinus carpio*) on water quality, sediment chemistry and submerged macrophytes in small experimental mesocosms

5.1 Results:

5.1.1 Nutrient concentrations and ratios

In general, with the exception of NH_3, nutrient concentrations were similar between all experimental enclosures for the two week pre-treatment period (Figure 5.1, 5.2, and 5.3). The high NH_3 concentrations recorded during the pre-treatment period in the LOW treatment enclosure were the result of seining efforts, which resuspended sediments, that took place only a day before water samples were collected on June 11.

During the treatment period, carp ($F_{2,6} = 12.87$, $p = 0.0068$) and nutrient additions ($F_{1,6} = 242.93$, $p < 0.0001$; Table 5.1) significantly affected total reactive phosphorus concentrations in the experimental enclosures. Additionally carp x nutrient interactions significantly affected TRP concentrations ($F_{2,6} = 6.41$, $p = 0.0324$). Post-hoc analysis of enclosures not receiving nutrient additions revealed that TRP concentrations were significantly higher in the CON (68 $\mu g \cdot L^{-1}$) relative to the LOW (< 25 $\mu g \cdot L^{-1}$, $p = 0.02$) and HI (< 25 $\mu g \cdot L^{-1}$, $p = 0.0155$) treatments and that there was no difference in TRP between the LOW and HI treatments ($p = 0.9997$; Figure 5.1). Average TRP concentrations in enclosures receiving nutrient additions were 262, 267, and 175 $\mu g \cdot L^{-1}$ in the NP, LOW-NP, and HI-NP treatments, respectively. TRP concentrations were not

Table 5.1. Summary of results for repeated measures ANOVA for water quality parameters measured in the experimental enclosures.

* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, **** $p \leq 0.0001$, ns = not significant ($p \geq 0.05$).

		Between enclosures			Within enclosures			
Variable	N	Carp	Nutrients	Carp x Nutrients	Time	Time x Carp	Time x Nutrients	Time x Carp x Nutrients
TRP	2	**	****	*	****	*	****	**
NO_3	2	ns	**	ns	****	ns	****	*
NH_3	2	**	****	*	**	*	*	ns
DIN:TRP	2	*	****	ns	****	ns	***	*
DO	2	ns	****	ns	****	ns	*	ns
Chlorophyll *a*	2	ns	***	ns	*	ns	ns	ns
Turbidity	2	*	*	ns	*	*	**	ns
% surface irradiance at SWI	2	*	***	ns	***	ns	**	ns
TSS	2	**	**	*	****	ns	ns	ns
ISS	2	****	ns	*	****	**	*	ns
OSS	2	*	***	ns	****	ns	*	ns
Submerged macrophytes (% cover)	2	ns	ns	*	**	ns	ns	ns

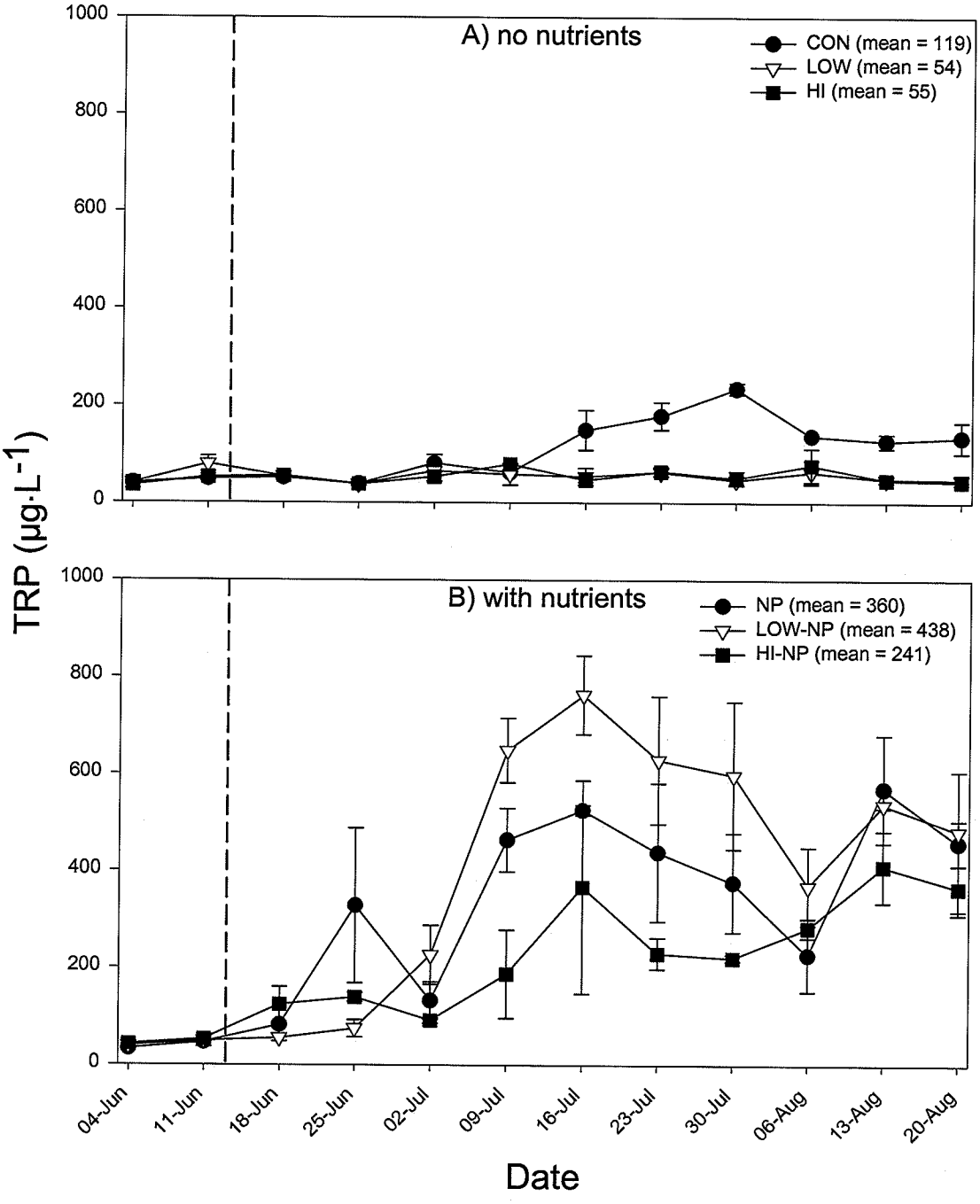

Figure 5.1. Total reactive phosphorus concentrations ($\mu g \cdot L^{-1}$; ±SE; n=2) in experimental enclosures without nutrient amendments (A) and enclosures receiving nutrient additions (B) stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions and the stocking of enclosures with carp on 13 June, 2002.

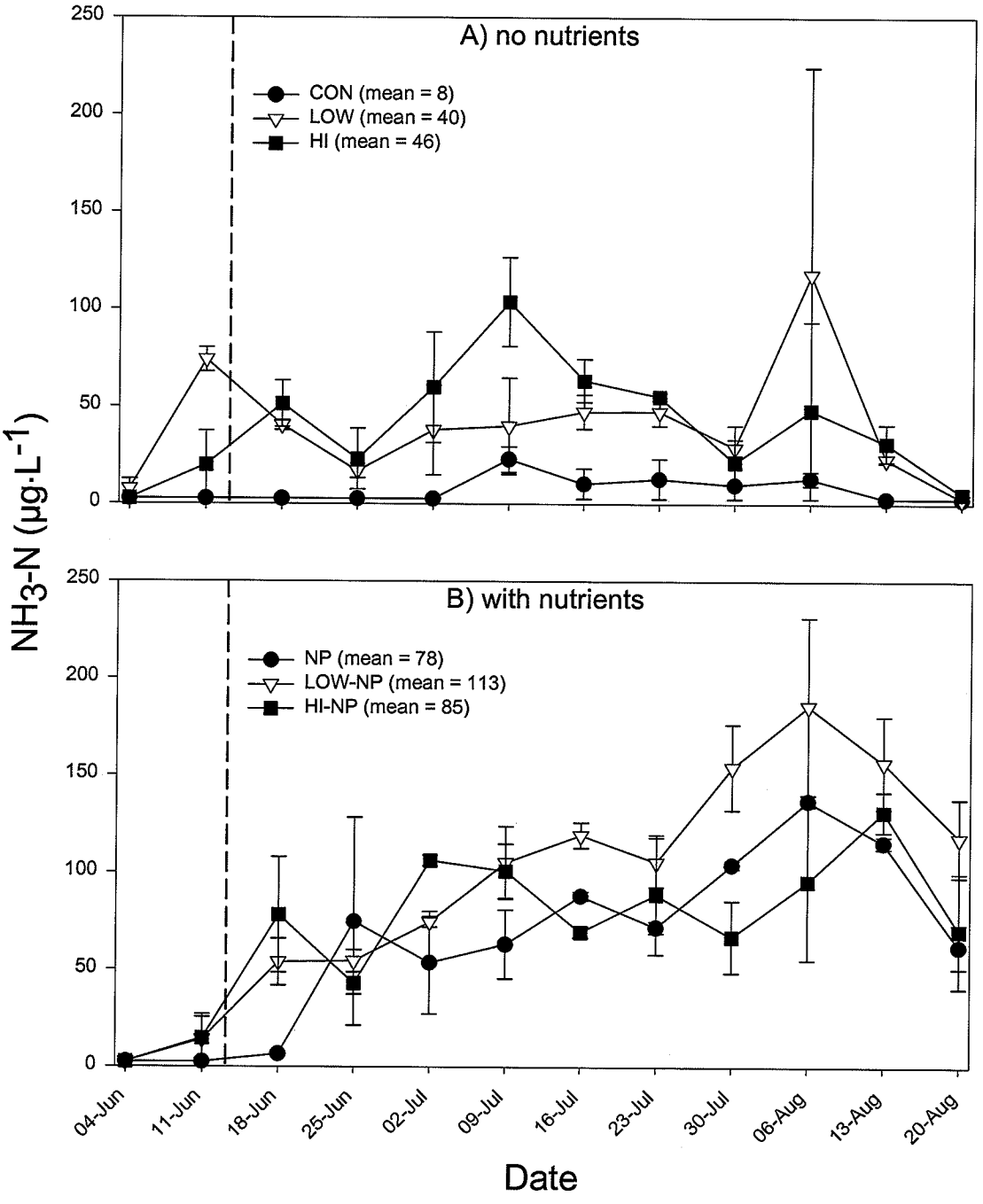

Figure 5.2. Ammonia-N concentrations ($\mu g \cdot L^{-1}$; ±SE; n=2) in experimental enclosures without nutrient amendments (A) and enclosures receiving nutrient additions (B) stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions and the stocking of enclosures with carp on 13 June, 2002.

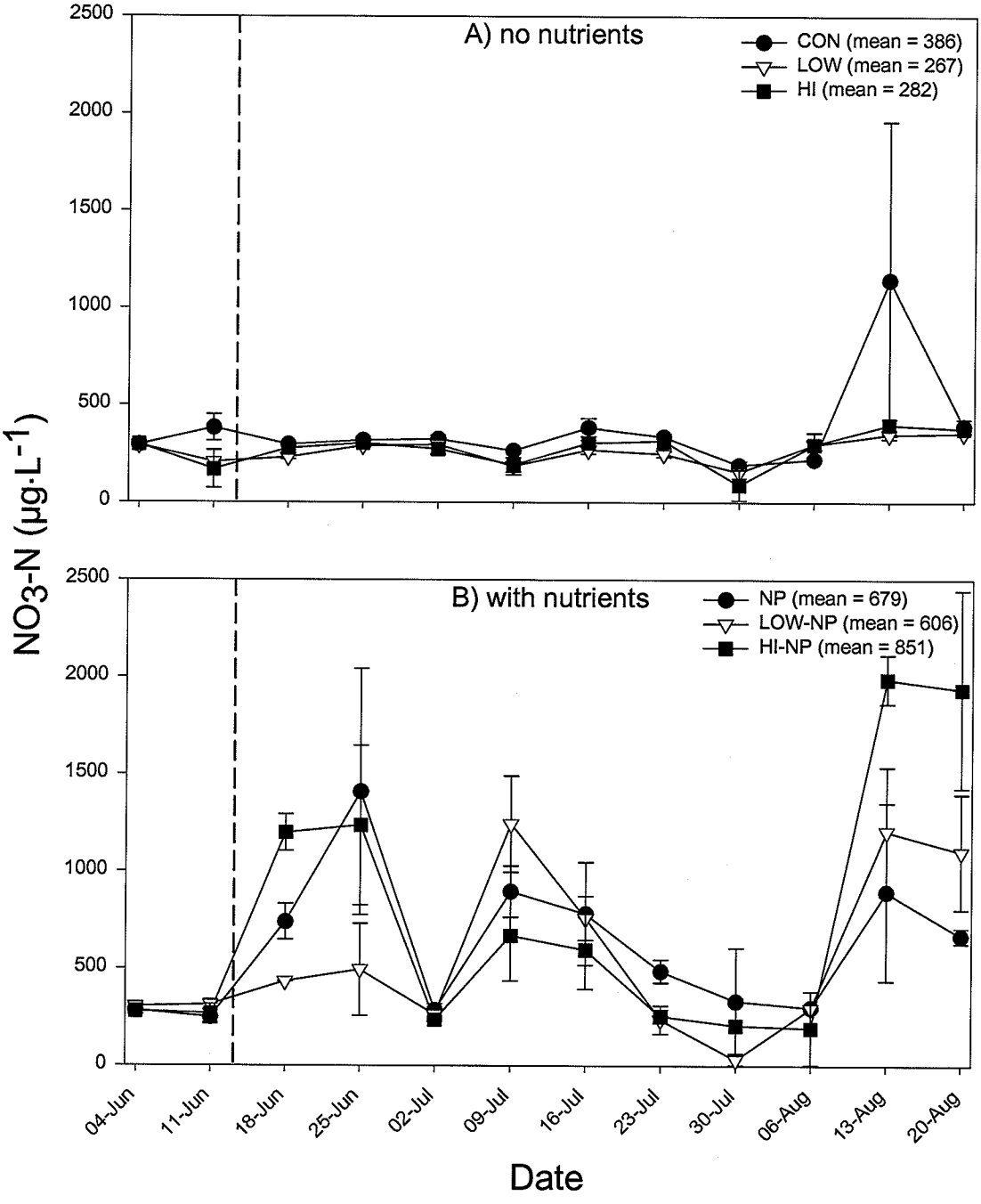

Figure 5.3. Nitrate-N concentrations ($\mu g \cdot L^{-1}$; ±SE; n=2) in experimental enclosures without nutrient amendments (A) and enclosures receiving nutrient additions (B) stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions and the stocking of enclosures with carp on 13 June, 2002.

significantly different between any combinations of the enclosures receiving nutrient additions.

NH_3 concentrations were significantly affected during the treatment period by carp ($F_{2,6} = 12.85$, $p = 0.0068$) and nutrient additions ($F_{1,6} = 82.81$, $p < 0.0001$; Table 5.1). Additionally, carp x nutrient interactions significantly affected NH_3 concentrations ($F_{2,6} = 5.28$, $p = 0.0476$). Concentrations in the LOW (49.8 $\mu g \cdot L^{-1}$, $p = 0.0302$) and HI treatments were significantly higher than the CON treatment (< 25 $\mu g \cdot L^{-1}$), but did not differ from one another ($p = 0.9441$). In enclosures receiving nutrient additions, NH_3 concentrations generally increased throughout the treatment period (Figure 5.2). Average NH_3 concentrations in enclosures receiving nutrient additions were 91.3 $\mu g \cdot L^{-1}$, 130.5 $\mu g \cdot L^{-1}$, and 105.1 $\mu g \cdot L^{-1}$ in the NP, LOW-NP, and HI-NP treatments, respectively. However, as was the case for TRP, differences were not statistically significant between any combinations of the enclosures receiving nutrient additions.

Unlike NH_3 and TRP, NO_3 concentrations were not significantly affected during the treatment period by carp ($F_{2,6} = 1.66$, $p = 0.2670$) and no significant carp x nutrient interactions were detected ($F_{2,6} = 0.41$, $p = 0.6826$). Conversely, nutrient additions significantly affected NO_3 concentrations ($F_{1,6} = 34.53$, $p = 0.0011$). NO_3 concentrations in enclosures not receiving nutrient additions were highest in the CON (457 $\mu g \cdot L^{-1}$), lowest in the LOW (390 $\mu g \cdot L^{-1}$), and intermediate in the HI (405 $\mu g \cdot L^{-1}$) treatments, but were not significantly different from one another. Unlike NH_3, NO_3 concentrations in enclosures receiving nutrient additions were quite variable over the course of the experiment (Figure 5.3). NO_3 concentrations averaged over the treatment period in

enclosures receiving nutrient additions were 693 $\mu g \cdot L^{-1}$, 579 $\mu g \cdot L^{-1}$, and 703 $\mu g \cdot L^{-1}$ in the NP, LOW-NP, and HI-NP treatments, respectively. As was the case for the other nutrient parameters, differences were not statistically significant for any combination of the enclosures receiving nutrient additions.

Molar ratios of dissolved inorganic nitrogen (DIN; measured as the sum of NO_3 and NH_3): total reactive phosphorus (TRP) differed significantly between carp treatments ($F_{2,6} = 10.48$, $p = 0.0110$) and nutrient treatments ($F_{1,6} = 104.61$, $p < 0.0001$; Table 5.1). No significant carp x nutrient interaction effects were detected for molar ratios of DIN:TRP ($F_{2,6} = 5.07$, $p = 0.0513$). Molar DIN:TRP ratios in enclosures not receiving nutrient additions were highest in the HI (10.9), lowest in the LOW (6.2), and intermediate in the CON (6.8) treatments, but were not significantly different from one another. Additionally, the trend in DIN:TRP was similar between these treatments with values declining consistently throughout most of the treatment period (Figure 5.4). Molar DIN:TRP ratios in enclosures receiving nutrient additions were quite variable over the course of the experiment, especially in enclosures stocked with carp (Figure 5.4). Additionally, molar DIN:TRP ratios averaged over the treatment period were higher in enclosures receiving nutrient additions and measured 16.0, 42.1, and 47.0 in the NP, LOW-NP, and HI-NP treatments, respectively. DIN:TRP ratios in enclosures receiving nutrient additions were significantly higher in the LOW-NP ($p = 0.0460$) and HI-NP ($p = 0.0285$) treatments relative to the NP treatment. However, there was no significant difference in DIN:TRP between the low carp and high carp treatments ($p = 0.9958$).

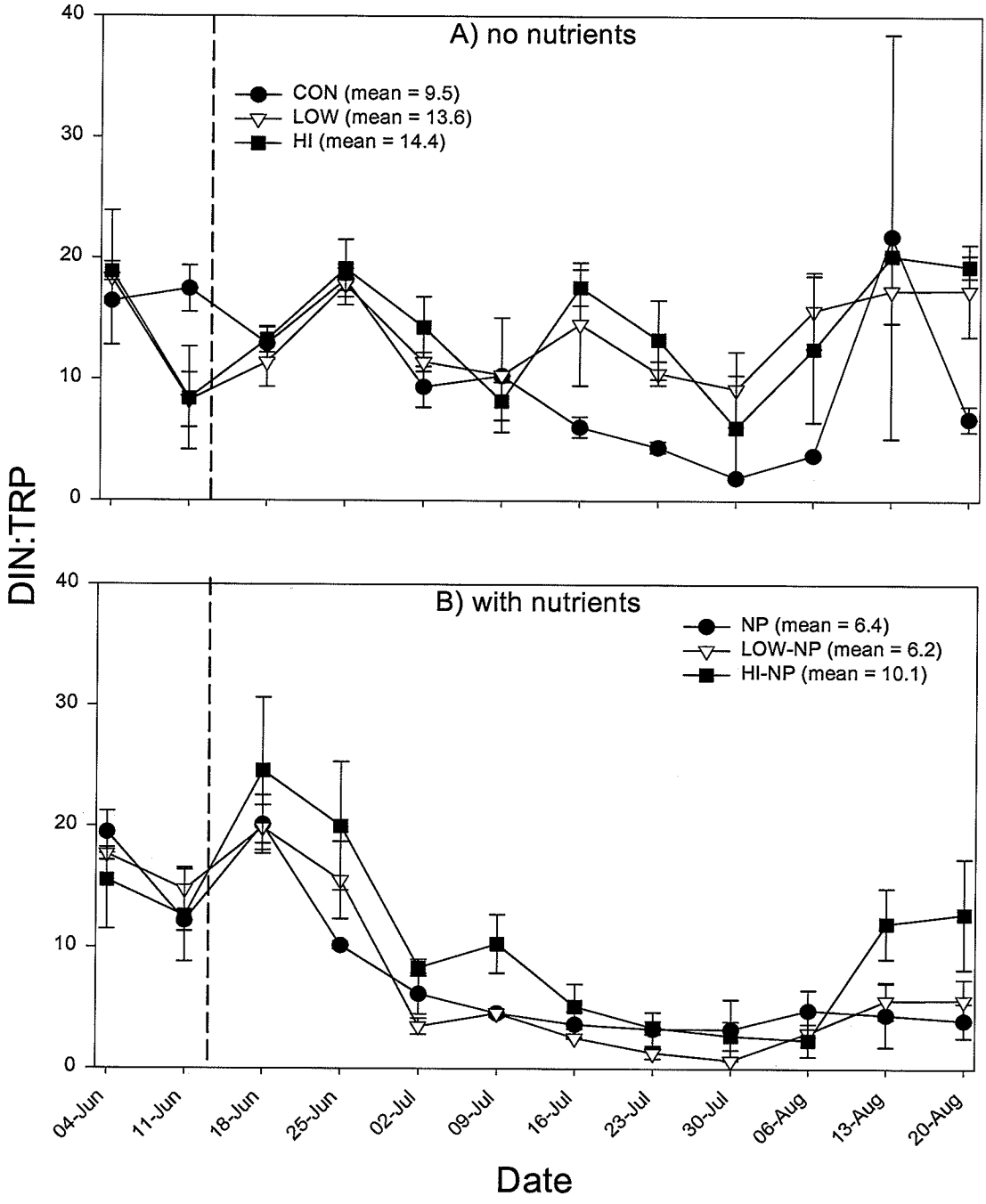

Figure 5.4. Molar DIN:TRP (±SE; n=2) in experimental enclosures without nutrient amendments (A) and enclosures receiving nutrient additions (B) stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions and the stocking of enclosures with carp on 13 June, 2002.

5.1.2 Diurnal changes in water column nutrient concentrations

No statistical analysis could be performed on diurnal samples due to the fact that I only sampled one replicate enclosure from each treatment. Nevertheless, water column nutrients exhibited significant diurnal fluctuations. In enclosures not receiving nutrient additions, dissolved oxygen concentrations were similar between enclosures with no carp, low carp, and high carp densities (Figure 5.5). DO concentrations peaked in the early evening (18:00 hour sample) and then decreased sharply to concentrations below 5 mg.L-1 in the morning (06:00 hour sample). DO trends observed in the enclosures receiving nutrient additions were generally similar to those observed in nutrient free enclosures with the exception that the diurnal fluctuation of DO concentrations in the nutrient enclosure without carp appeared to be dampened relative to nutrient enclosures with carp (Figure 5.5).

Nutrient concentrations in the enclosures not receiving nutrient additions did not appear to vary significantly over the course of a 24 hour period. Additionally, concentrations followed the same general trends that were observed in samples collected over the duration of the study. TRP concentration was much higher in the enclosure without carp (mean = 207 $\mu g \cdot L^{-1}$), relative to concentrations in the enclosures stocked at low (mean = 51 $\mu g \cdot L^{-1}$) and high (mean = 44 $\mu g \cdot L^{-1}$) carp densities (Figure 5.5). NH_3 concentrations increased with carp density, with mean concentrations of 26, 53, and 81 $\mu g \cdot L^{-1}$ calculated for the no carp, low carp, and high carp treatments, respectively. In the enclosures receiving nutrients, concentrations did fluctuate noticeably with time of day. TRP concentrations were negatively correlated with DO concentrations and were lowest at mid day and highest in early morning samples. Additionally, TRP concentrations were

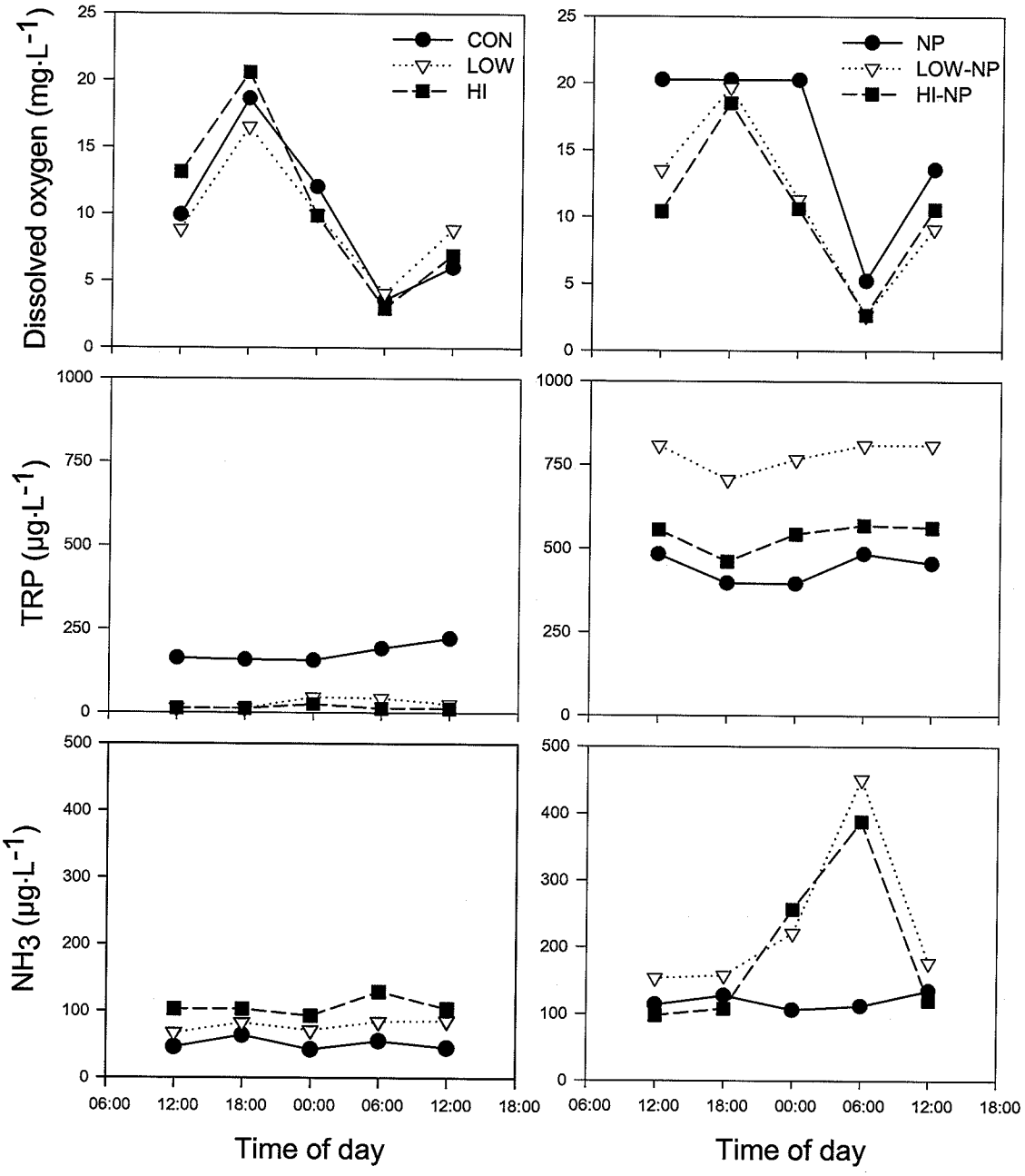

Figure 5.5. Diurnal changes in dissolved oxygen, total reactive phosphorus, and ammonia concentrations in experimental enclosures without nutrient amendments (CON, LOW, and HI) and enclosures receiving nutrient additions (NP, LOW-NP, and HI-NP) stocked with no carp, low carp, and high carp biomass.

higher in enclosures with carp, relative to the enclosure receiving only nutrients, but were not correlated to carp density. In the enclosure receiving nutrient additions only, NH_3 concentrations did not change significantly with time of day. Conversely, NH_3 concentrations increased by approximately 300 $\mu g \cdot L^{-1}$ in both the LOW-NP and HI-NP treatments, relative to the NP treatment. As was the case with TRP concentrations, although carp increased NH_3 concentrations relative to the enclosure receiving nutrient additions only, concentrations did not appear to be related to stocking density.

5.1.3 Turbidity, suspended solids, and phytoplankton chlorophyll *a*

Carp treatments ($F_{2,6} = 9.82$, $p = 0.0128$) and nutrient additions ($F_{1,6} = 12.76$, $p = 0.0117$; Table 5.1) both significantly increased turbidity in the enclosures (Figure 5.6). No significant carp x nutrient interactions were detected ($F_{2,6} = 3.24$, $p = 0.1113$). Mean turbidity during the treatment period in the enclosures not receiving nutrient additions was highest in the HI (40.7 NTU), lowest in the CON (13.8 NTU), and intermediate in the LOW (24.5) treatments. The HI treatment was significantly higher than the CON treatment ($p = 0.0325$) but was not significantly different from the LOW treatment ($p = 0.7755$). In the enclosures receiving nutrient additions, mean treatment period turbidity levels were 32.1, 57.7, and 40.9 NTU in the NP, LOW-NP, and HI-NP treatments, respectively. Although not statistically significant, mean treatment period turbidity was 18.3 and 33.2 NTU higher in the no carp and low carp treatments receiving nutrient additions relative to those not receiving nutrients while turbidity was similar for high carp treatments regardless of nutrient treatment. In general, turbidity increased throughout the treatment period (Figure 5.6) and was not statistically different for any combination of the enclosures receiving nutrient additions.

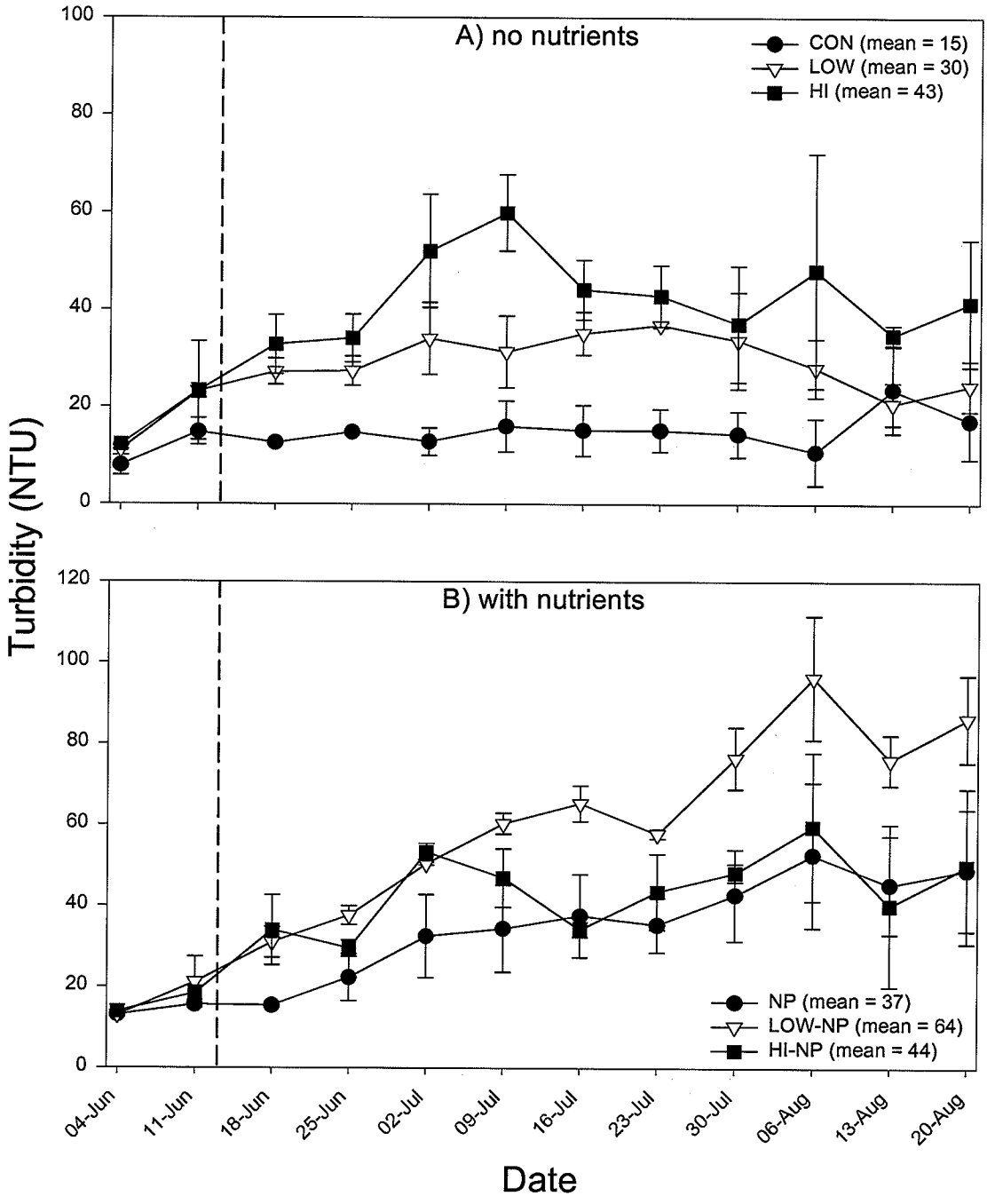

Figure 5.6. Turbidity (NTU; ±SE; n=2) in experimental enclosures without nutrient amendments (A) and enclosures receiving nutrient additions (B) stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions and the stocking of enclosures with carp on 13 June, 2002.

Total suspended solids increased significantly in response to carp ($F_{2,6} = 18.96$, $p = 0.0025$) and nutrient ($F_{1,6} = 27.66$, $p = 0.0019$; Table 5.1; Figure 5.7) treatments. Statistical analysis also revealed significant carp x nutrient interaction effects ($F_{2,6} = 5.52$, $p = 0.0436$). TSS concentrations were significantly higher in the LOW (mean = 52.0 mg.L-1; $p = 0.0225$) and HI (mean = 79.9 mg.L-1; $p = 0.0051$) treatments relative to the CON treatment (mean = 15.3 mg.L-1). However, TSS concentrations in the LOW and HI treatments were not significantly different from one another ($p = 0.5892$). Although not statistically significant there were clear differences in TSS concentrations over time between the LOW and HI treatments. In the HI treatment, TSS increased rapidly during the first four weeks following the start of the experiment to a maximum of 153.9 mg.L-1, a concentration more than 2.5 times greater than the concentration for the same date in the low carp-no nutrient enclosures (Figure 5.7). Unlike the rapid increase observed in the HI treatment enclosures, TSS concentrations in the LOW treatments increased at a slower rate but over a longer period of time, reaching a maximum of 85.5 mg.L-1 six weeks into the experiment (Figure 5.7). TSS was higher in enclosures receiving nutrient additions ($p = 0.0019$) compared to those not receiving nutrient additions, with mean treatment period TSS values in enclosures measuring 63.9, 101.8, and 101.3 mg.L-1 in the NP, LOW-NP, and HI-NP treatments, respectively. Although TSS in the LOW-NP and HI-NP treatments appears to be similar, and higher than the NP treatment, there was no statistical difference between any combination of the enclosures receiving nutrient additions. In general, TSS followed a similar trend in enclosures receiving nutrient additions, regardless of carp treatment, with concentrations increasing initially for the

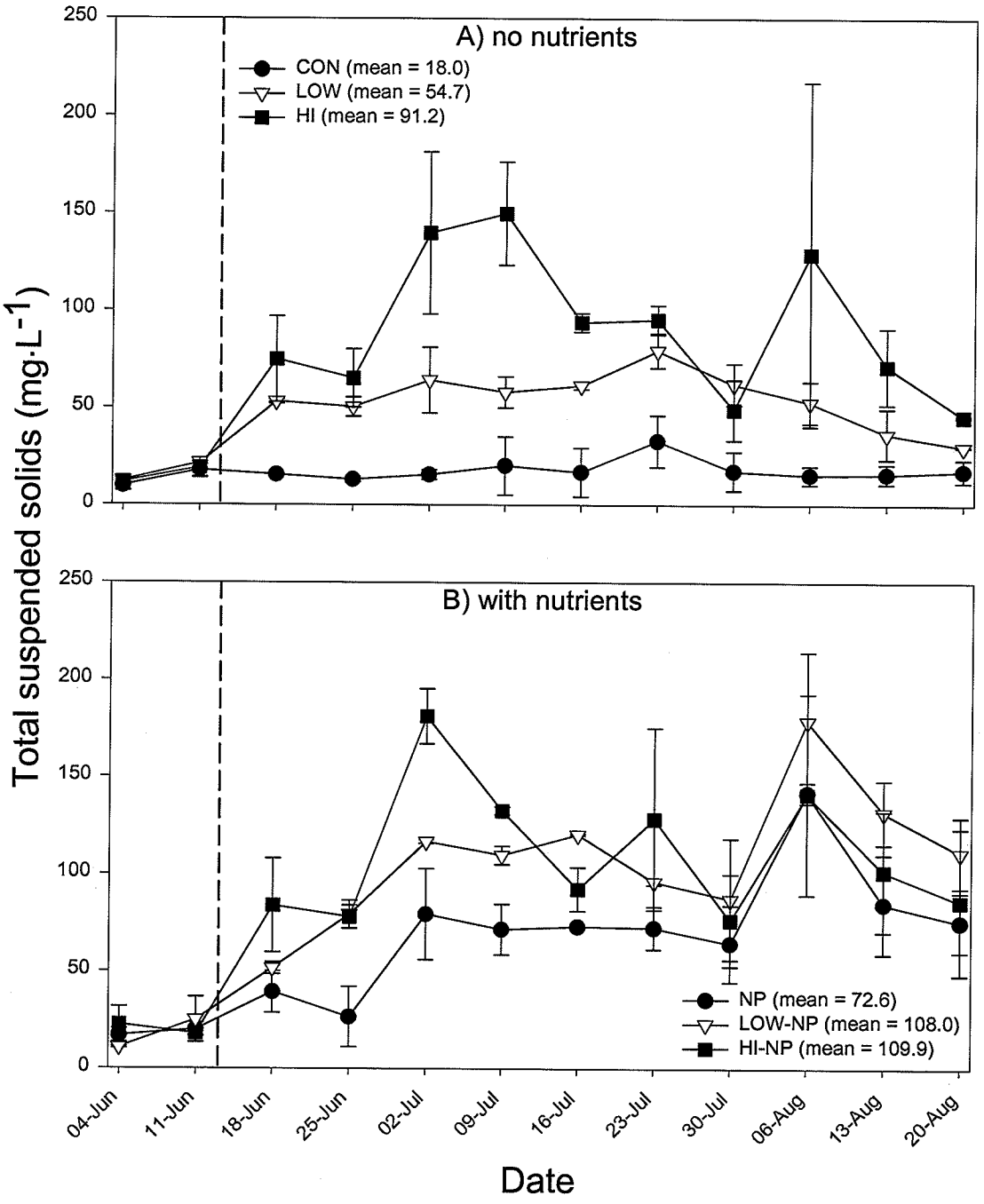

Figure 5.7. Total suspended solids ($mg \cdot L^{-1}$; ±SE; n=2) in experimental enclosures without nutrient amendments (A) and enclosures receiving nutrient additions (B) stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions and the stocking of enclosures with carp on 13 June, 2002.

first three weeks after which values were fairly stable for the remainder of the experiment (Figure 5.7).

The composition of TSS (inorganic suspended solids [ISS] vs. organic suspended solids [OSS]) varied noticeably with carp treatment in enclosures regardless of whether they were receiving nutrient additions or not. In general, the relative contribution of ISS increased, while that of OSS decreased with increasing carp biomass (Figure 5.8). Additionally, the contribution of ISS to TSS appeared to be more pronounced for enclosures not receiving nutrient additions. Inorganic suspended solids increased significantly in response to carp ($F_{2,6} = 87.04$, $p < 0.0001$), but not nutrient ($F_{1,6} = 0.00$, $p = 0.9673$; Table 5.1; Figure 5.9) treatments. Statistical analysis also revealed significant carp x nutrient interaction effects ($F_{2,6} = 8.61$, $p = 0.0172$). Mean treatment period ISS values in enclosures not receiving nutrient additions were 2.2, 19.8, and 39.8 mg.L-1 in the CON, LOW, and HI treatments, respectively. Inorganic suspended solids in the HI and LOW treatment enclosures were significantly higher than those in the CON treatment enclosures ($p = 0.0051$ and $p = 0.0225$) but were not statistically different from one another ($p = 0.5892$; Figure 5.9). In enclosures receiving nutrient additions, mean treatment period ISS measured 5.0, 10.2, and 34.2 mg.L-1 in the NP, LOW-NP, and HI-NP treatments, respectively. ISS was significantly higher in the HI-NP treatment relative to the NP ($p = 0.0025$) and LOW-NP ($p = 0.0252$) treatments. ISS in the LOW-NP and NP treatments were not significantly different from one another ($p = 0.2023$). Overall, trends in ISS were similar for a given carp treatment regardless whether or not the enclosures were receiving nutrients (Figure 5.9).

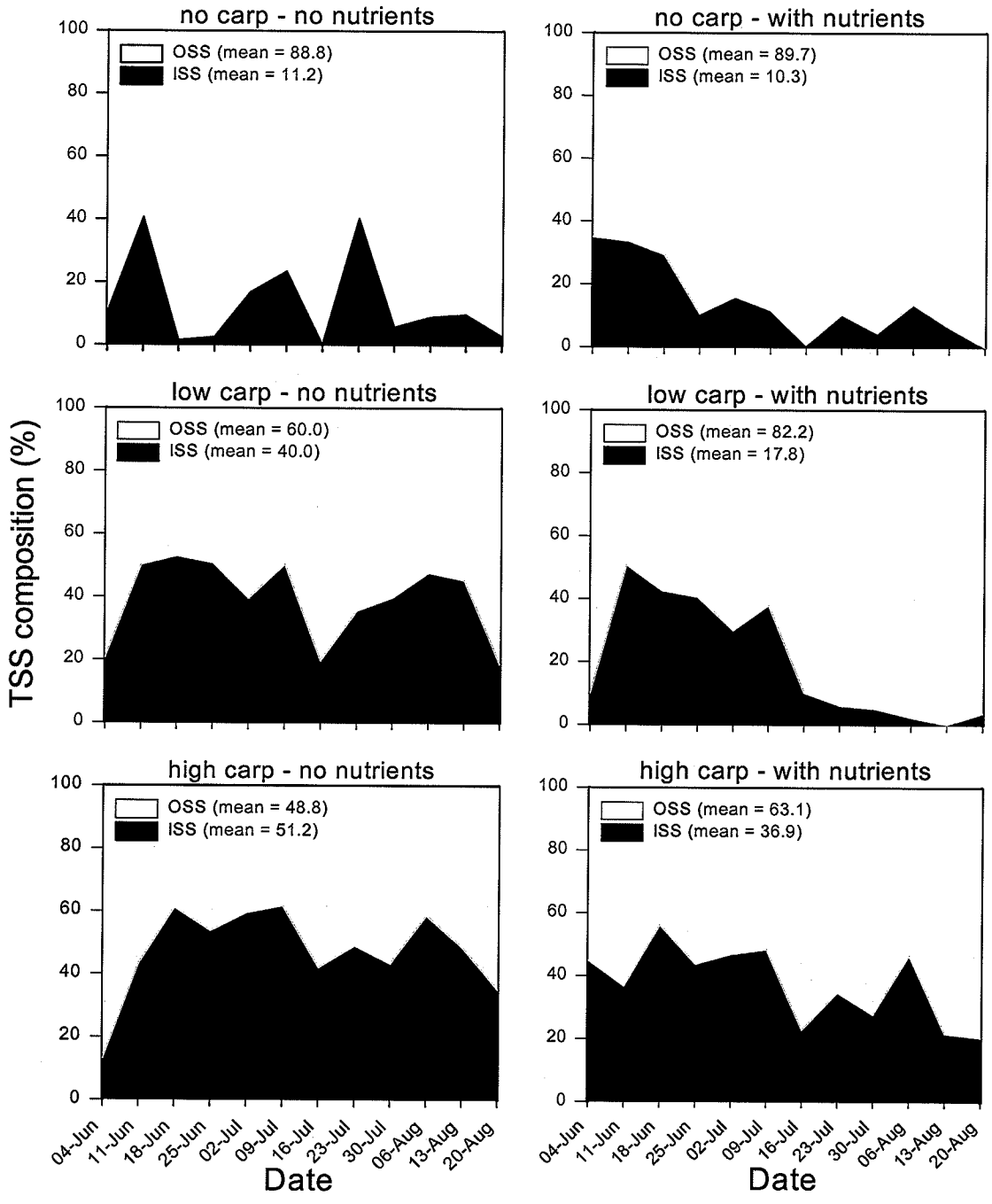

Figure 5.8. Composition of total suspended solids in experimental enclosures without nutrient amendments and enclosures receiving nutrient additions stocked with no carp, low carp, and high carp biomass.

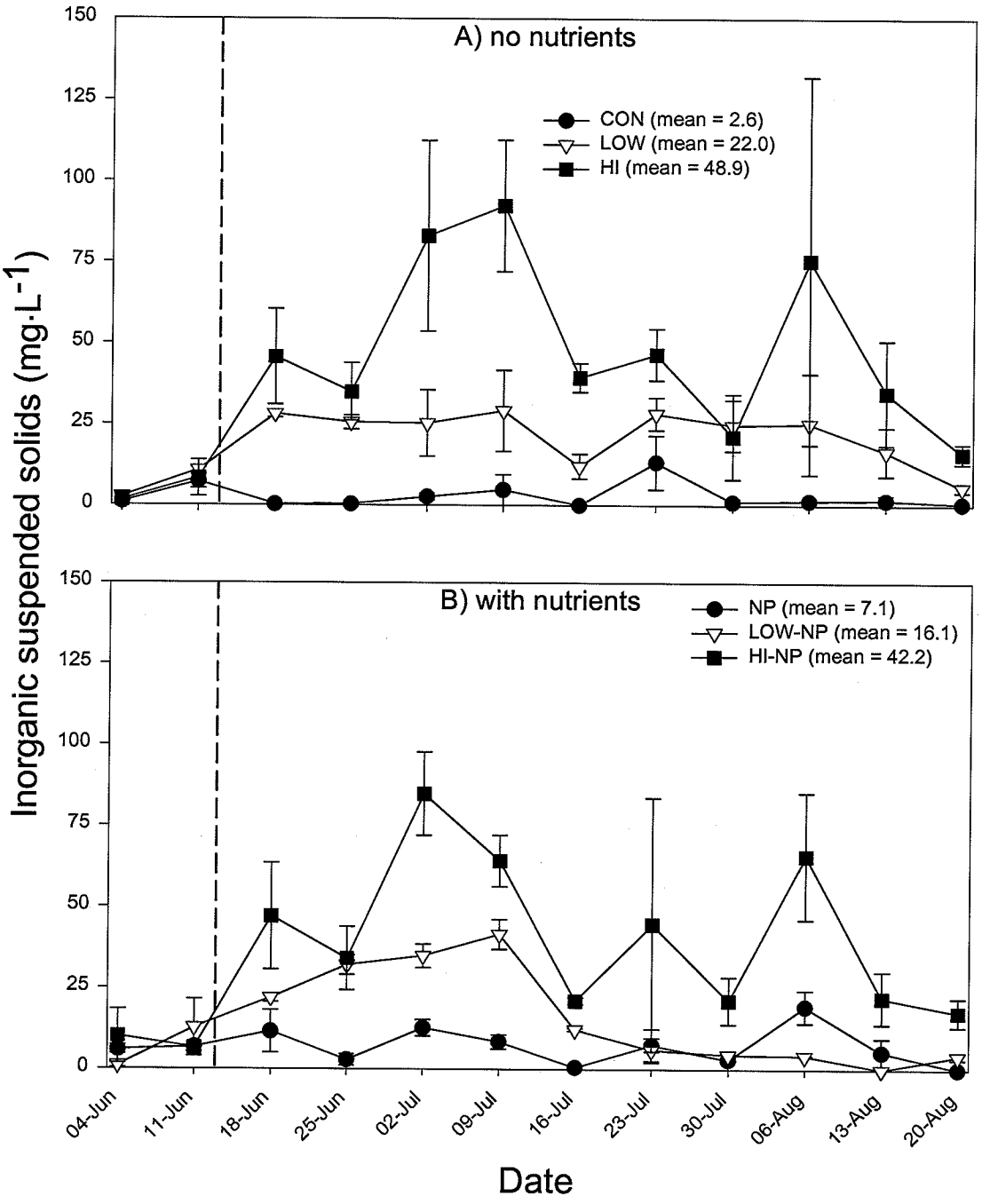

Figure 5.9. Inorganic suspended solids ($mg \cdot L^{-1}$; ±SE; n=2) in experimental enclosures without nutrient amendments (A) and enclosures receiving nutrient additions (B) stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions and the stocking of enclosures with carp on 13 June, 2002.

Organic suspended solids (OSS) increased significantly in response to carp ($F_{2,6}$ = 7.73, p < 0.0218) and nutrient ($F_{1,6}$ = 48.74, p = 0.0004; Table 5.1; Figure 5.10) treatments. Statistical analysis did not reveal any significant carp x nutrient interaction effects ($F_{2,6}$ = 4.26, p = 0.0704). Unlike ISS, trends in OSS were not similar between enclosures receiving and not receiving nutrients (Figure 5.10). In enclosures not receiving nutrient additions OSS in the LOW and HI treatments generally increased over the first five weeks of the experiment and then declined over the remaining five weeks. OSS in the CON treatment remained fairly consistent throughout the experiment (Figure 5.10). In enclosures receiving nutrient additions OSS in the NP and HI-NP treatments increased over the first three weeks of the experiment at which point they levelled off and remained consistent until the end of the experiment.

Conversely, OSS in the LOW-NP treatment appeared to increase steadily throughout the entire study period (Figure 5.10). Mean treatment period OSS values in enclosures not receiving nutrient additions were 13.8, 30.8, and 39.2 $mg \cdot L^{-1}$ in the CON, LOW, and HI treatments, respectively. OSS was significantly higher in the HI treatment relative to the CON treatment (p = 0.0316; Figure 5.10). OSS in the LOW treatment was not significantly different form the CON or HI treatments (p = 0.0931, and p = 0.8964). In enclosures receiving nutrient additions mean treatment period OSS measured 57.4, 81.7, and 61.6 $mg \cdot L^{-1}$ in the NP, LOW-NP, and HI-NP treatments respectively. Although OSS in the LOW-NP treatment appeared to be higher than those in the NP and HI-NP treatments, there was no statistical difference between any combination of the enclosures receiving nutrient additions.

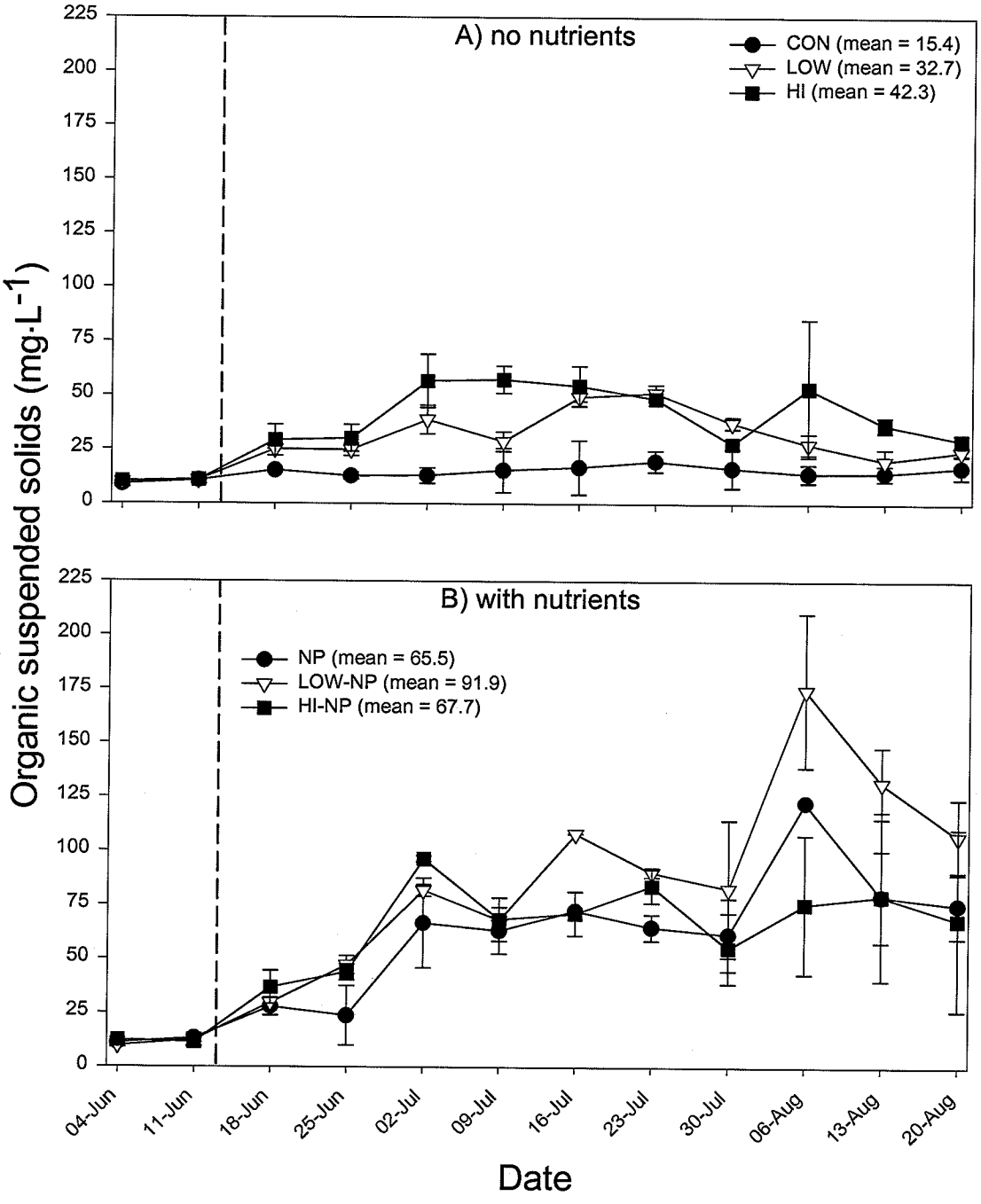

Figure 5.10. Organic suspended solids ($mg \cdot L^{-1}$; ±SE; n=2) in experimental enclosures without nutrient amendments (A) and enclosures receiving nutrient additions (B) stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions and the stocking of enclosures with carp on 13 June, 2002.

OSS were largely comprised of phytoplankton, as indicated by Figure 5.11, where fitting a power curve to the data yielded a significant positive relationship ($F_{1,142}$ = 381.6, $p < 0.0001$) in which chlorophyll a explained 73% of the variance in OSS concentrations. Similar to OSS, chlorophyll a increased significantly in response to carp ($F_{2,6} = 5.51$, $p < 0.0438$) and nutrient ($F_{1,6} = 53.82$, $p = 0.0003$; Table 5.1; Figure 5.12) treatments. Statistical analysis did not reveal any significant carp x nutrient interaction effects ($F_{2,6} = 3.70$, $p = 0.0896$). Trends in chlorophyll a concentrations were similar to those observed for OSS (Figure 5.10 and Figure 5.12). Mean treatment period chlorophyll a values in enclosures not receiving nutrient additions were 49, 94, and 130 μg.L-1 in the CON, LOW, and HI treatments, respectively. Chlorophyll a was significantly higher in the HI ($p = 0.0102$) and LOW ($p = 0.0201$) treatment relative to the CON treatment. Additionally, although not significantly different from one another ($p = 0.6188$), the mean treatment period chlorophyll a concentration in the HI treatment was almost 40 μg.L-1 above that of the LOW treatment. In enclosures receiving nutrient additions mean treatment period chlorophyll a concentrations measured 307, 407, and 268 μg.L-1 in the NP, LOW-NP, and HI-NP treatments respectively. As for OSS, although chlorophyll a in the LOW-NP treatment appeared to be higher than those in the NP and HI-NP treatments, there was no statistical difference between any combination of the enclosures receiving nutrient additions.

5.1.4 Sedimentation rates and sediment chemistry

Sedimentation rates were positively impacted by carp treatment during all three sampling periods (July 5-12, $F_{2,6} = 41.68$, $p = 0.0003$; July 16-23, $F_{2,6} = 34.63$, $p = 0.0005$; and August 13-20, $F_{2,6} = 9.83$, $p = 0.0128$; Table 5.2). Different from TSS, which

Table 5.2. Results of ANOVA's for sedimentation rates and change in sediment nutrient concentrations measured in experimental enclosures. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, ns = not significant ($p \geq 0.05$).

	Between enclosures		
Variable	Carp	Nutrients	Carp x Nutrients
Sedimentation (July 5-12)	***	ns	ns
Sedimentation (July 17-23)	***	ns	ns
Sedimentation (August 13-20)	*	ns	ns
Change in sediment [N]	ns	ns	ns
Change in sediment [P]	*	***	*

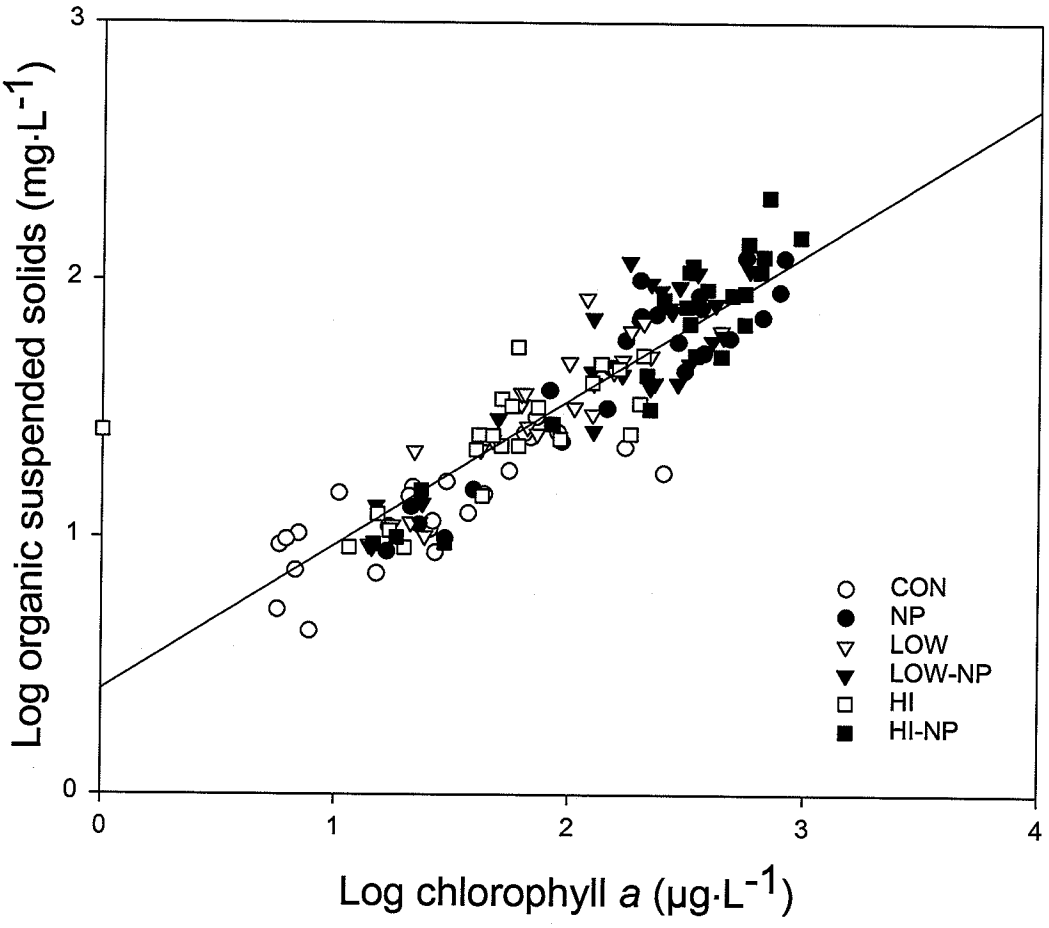

Figure 5.11. Relationship between organic suspended solids and phytoplankton chlorophyll *a* concentrations in experimental enclosures without nutrient amendments (open symbols) and enclosures receiving nutrient additions (closed symbols) stocked with no carp, low carp, and high carp biomass.

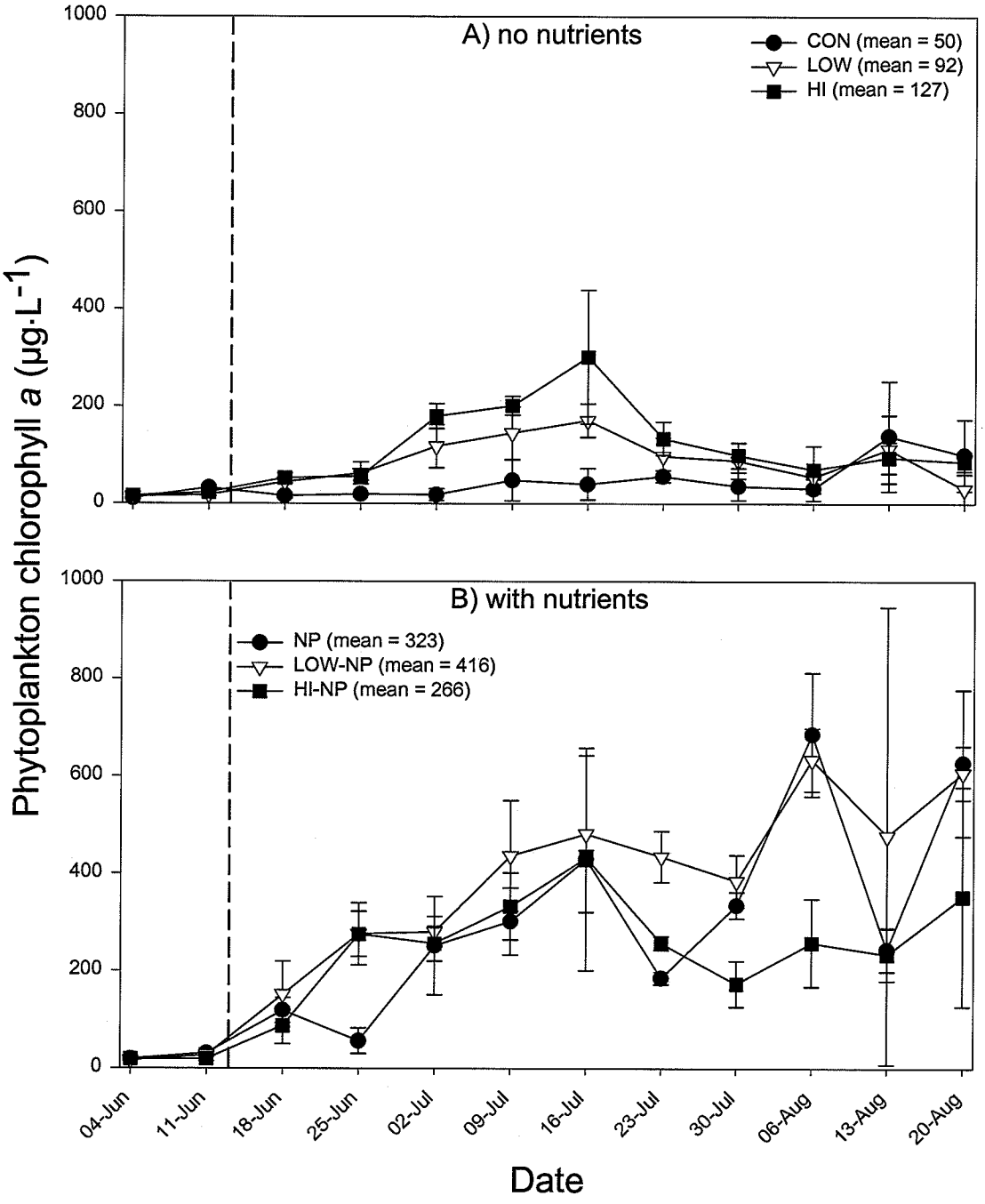

Figure 5.12. Phytoplankton chlorophyll *a* ($\mu g \cdot L^{-1}$; ±SE; n=2) in experimental enclosures without nutrient amendments (A) and enclosures receiving nutrient additions (B) stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions and the stocking of enclosures with carp on 13 June, 2002.

was mostly comprised of organic material in all treatments (Figure 5.8), the sediments that accumulated in sediment traps were largely inorganic in nature (range 64.1 – 82.3%; Figure 5.13). Sedimentation rates in enclosures not receiving nutrient additions ranged from 0.9 to 3.6, 44.7 to 84.6, and 86.5 to 207.9 $g \cdot m^{-2} \cdot d^{-1}$ in the CON, LOW, and HI treatments, respectively (Figure 5.13). During all three sampling periods sedimentation rates in the HI treatment was significantly higher than those in the CON treatment (July 5-12, $p = 0.0024$; July 16-23, $p = 0.0114$; and August 13-20, $p = 0.0363$). Similarly, sedimentation rates in the LOW treatment enclosures were significantly higher than those in the CON treatment enclosures for two of the three treatment periods (July 5-12, $p = 0.0131$; and July 16-23, $p = 0.0076$). Rates between the LOW and HI treatments were never significantly different from one another for any sampling period. In enclosures receiving nutrient additions, sedimentation rates ranged from 3.1 to 11.1, 5.0 to 136.4, and 50.6 to 286.5 $g \cdot m^{-2} \cdot d^{-1}$ in the NP, LOW-NP, and HI-NP treatments, respectively (Figure 5.13). With the exception of sedimentation rates in the LOW-NP treatment from the August 13-20 sampling period, rates were clearly higher in the LOW-NP and HI-NP treatments relative to the NP treatment. Sedimentation rates in the HI-NP treatment enclosures were significantly higher than those in the NP treatments for the July 5-12 ($p = 0.0201$) and July 16-23 sampling periods ($p = 0.0126$), but not the August 13-20 sampling period ($p = 0.4623$). Additionally, sedimentation rates in the LOW-NP treatment enclosures were only significantly higher than those in the NP treatments for one of the three treatment periods (July 5-12, $p = 0.0372$). As was the case for the no nutrient treatments, sedimentation rates between the LOW-NP and HI-NP treatments were never significantly different from one another for any sampling period. Although

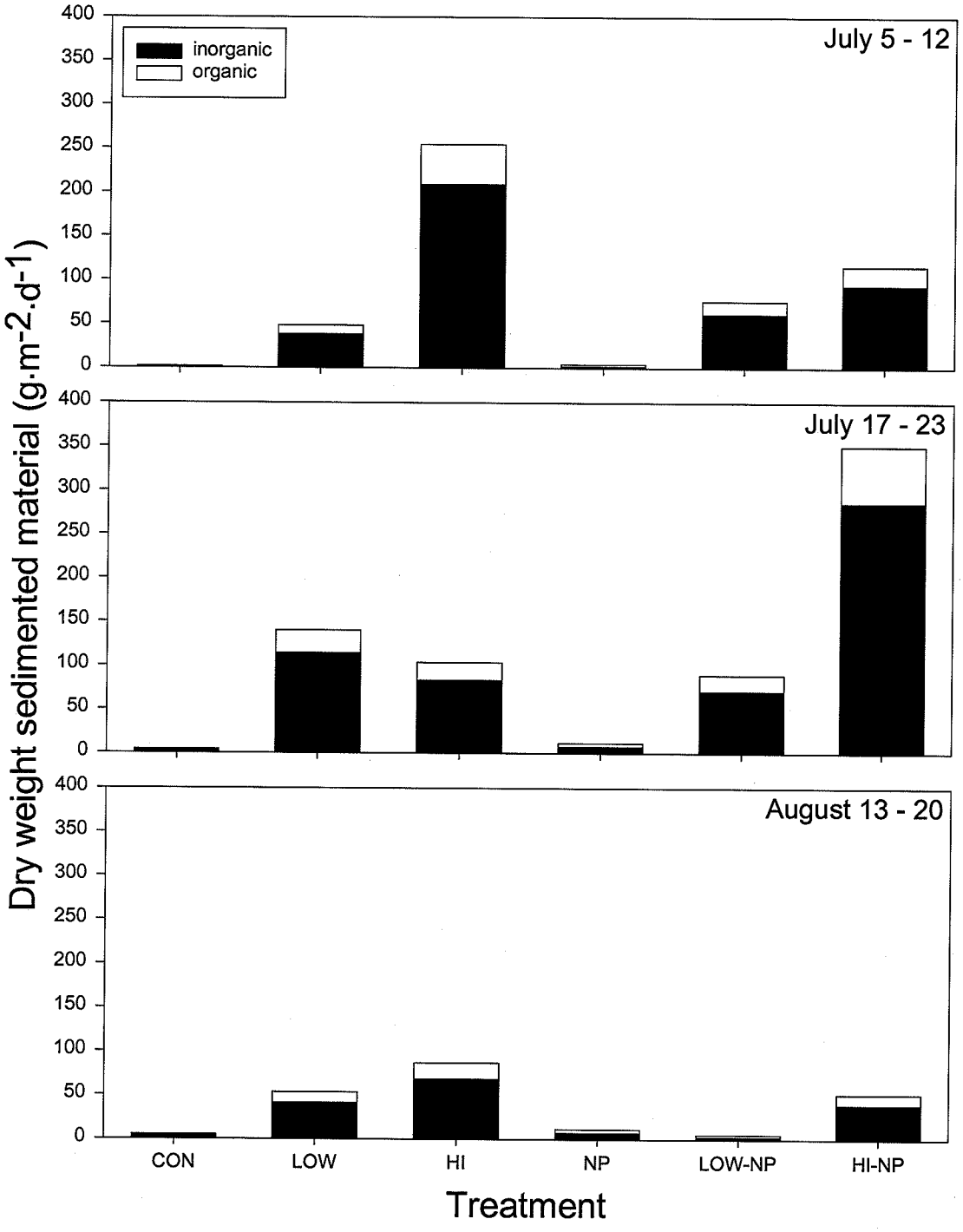

Figure 5.13. Sedimentation rates in experimental enclosures calculated from sediment traps deployed between July 5 – 12, July, July 16-23, and August 13-20 in Blind Channel, Delta Marsh.

ANOVA's did not always yield significant differences between the low and high carp treatments relative to no carp treatments linear regression analysis yielded a significant positive relationship ($F_{1,5} = 90.50$, $p = 0.0007$) between carp biomass and sedimentation rates averaged over the entire study period, explaining 96% of the variance (Figure 5.14).

Carp and nutrient treatments did not significantly change the concentration of nitrogen in surface sediments between the pre-manipulation period and post-manipulation period (Table 5.2; Figure 5.15). Mean sediment nitrogen ranged from 9.8 to 10.0 $mg \cdot g^{-1}$ in enclosure not receiving nutrient additions and from 10.0 to 10.5 $mg \cdot g^{-1}$ in enclosures receiving nutrient additions. Although not statistically significant, sediment nitrogen concentrations appear to decrease as carp density increases in enclosures not receiving nutrient additions (Figure 5.15). Sediment nitrogen concentrations increased noticeably in enclosures receiving nutrients, relative to the un-fertilized enclosures, but did not appear to be related to carp biomass. Sediment phosphorus concentrations changed significantly as a result of carp ($F_{2,6} = 6.80$, $p = 0.0287$), nutrients ($F_{1,6} = 55.29$, $p = 0.0003$), and their interaction ($F_{2,6} = 5.26$, $p = 0.0478$; Table 5.2).

Sediment phosphorus ranged from 0.97 to 1.04 $mg \cdot g^{-1}$ in enclosure not receiving nutrient additions and from 1.05 to 1.17 $mg \cdot g^{-1}$ in enclosures receiving nutrient additions. As was the case with sediment nitrogen, sediment phosphorus concentrations decreased with increasing carp biomass in the un-fertilized enclosures, while concentrations were always higher in the fertilized enclosures, but did not appear to change proportionally in response to carp biomass (Figure 5.15).

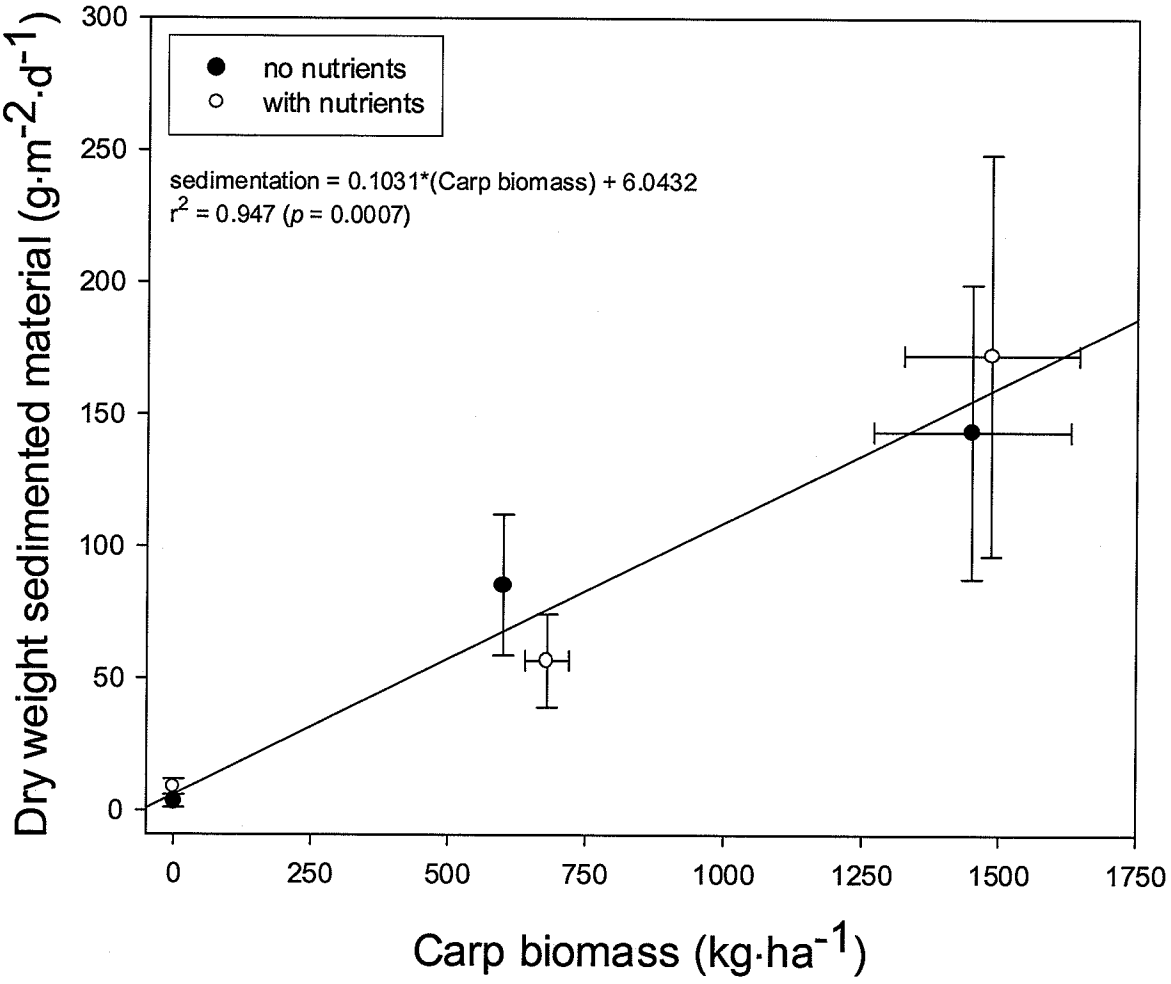

Figure 5.14. Relationship between dry weight sedimented material and carp biomass.

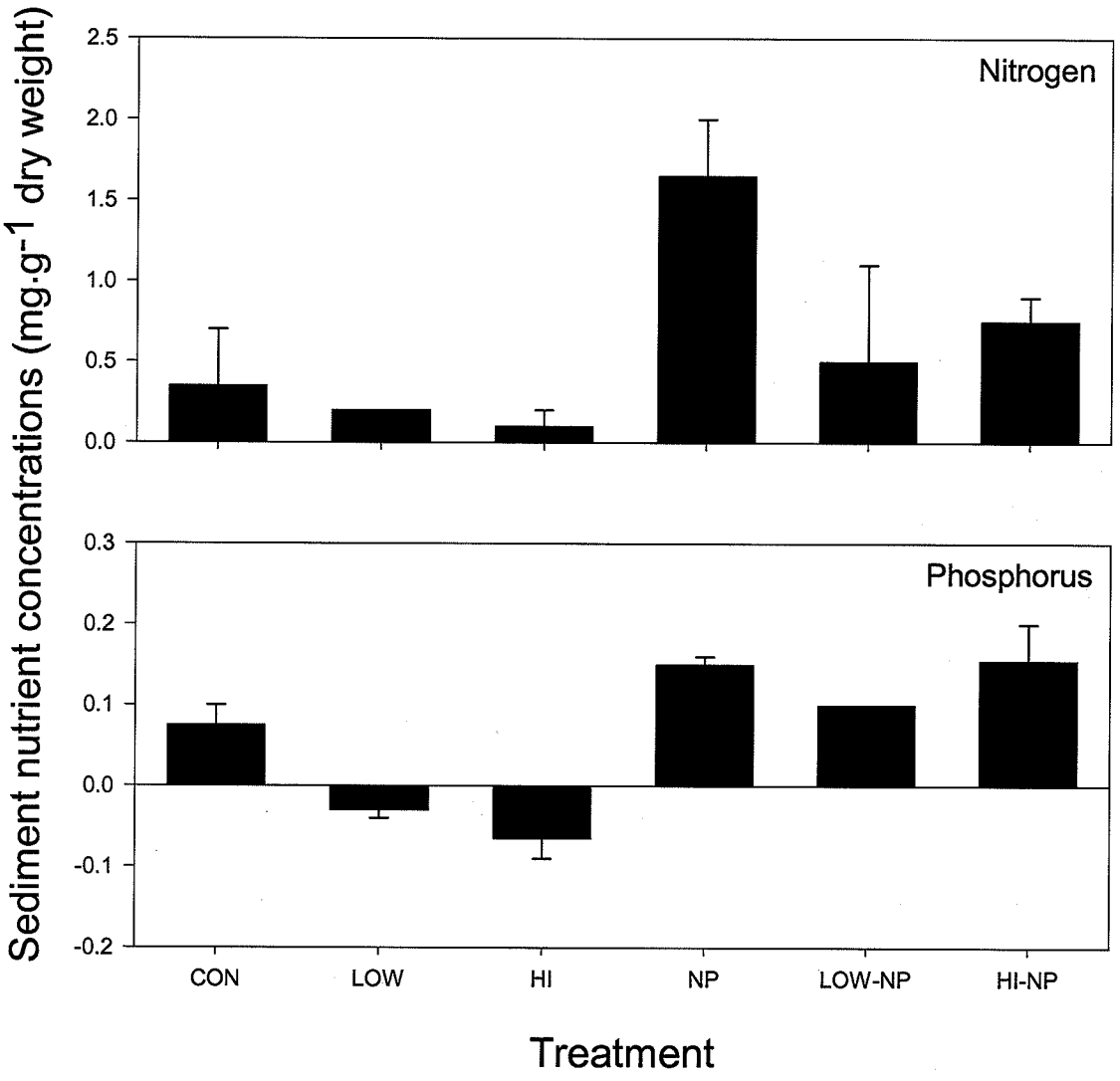

Figure 5.15. Change in sediment nutrient concentrations ($mg \cdot g^{-1}$ dry weight; ±SE; n=2) between the pre- and post-manipulation period in enclosures without nutrient amendments and enclosures receiving nutrient additions stocked with no carp, low carp, and high carp biomass.

5.1.5 Submersed macrophytes and light penetration

Submerged macrophyte biomass was not significantly affected by carp ($F_{2,6} = 2.02$, $p = 0.2134$) or nutrient ($F_{1,6} = 3.04$, $p = 0.1320$) treatments, nor by carp x nutrient treatment interactions ($F_{2,6} = 0.50$, $p = 0.6306$; Figure 5.16). Submerged macrophyte biomass (dry weight) measured at the end of the treatment period in enclosures not receiving nutrient additions was 78.7, 9.2, and 0.8 $g \cdot m^{-2}$ in the CON, LOW, and HI treatments, respectively (Figure 5.16). Biomass was significantly lower in the HI ($p = 0.0308$) but not the LOW ($p = 0.1088$) treatments relative to the CON treatment. In enclosures receiving nutrient additions submerged macrophyte biomass measured 3.6, 3.7, and 1.1 $g \cdot m^{-2}$ in the NP, LOW-NP, and HI-NP treatments, respectively. There was no statistical difference in submerged macrophyte biomass between any combination of the enclosures receiving nutrient additions.

Percent cover of submerged macrophytes was not significantly affected by carp ($F_{2,6} = 3.90$, $p = 0.0821$) or nutrient ($F_{1,6} = 4.17$, $p = 0.0873$) treatments, but was affected by carp x nutrient treatment interactions ($F_{2,6} = 5.42$, $p = 0.0453$; Table 5.1). In enclosure not receiving nutrient additions, only the HI treatment had a significantly lower areal coverage of submerged macrophytes, relative to the CON treatment ($p = 0.0437$; Figure 5.17). Although not statistically significant, submerged macrophyte cover in the LOW treatment was lower throughout most of the experiment relative to the HI treatment, and was somewhat higher relative the CON treatment towards the end of the experiment (Figure 5.17). There was no statistical difference in the percent cover of submerged macrophyte between any combination of the enclosures receiving nutrient additions.

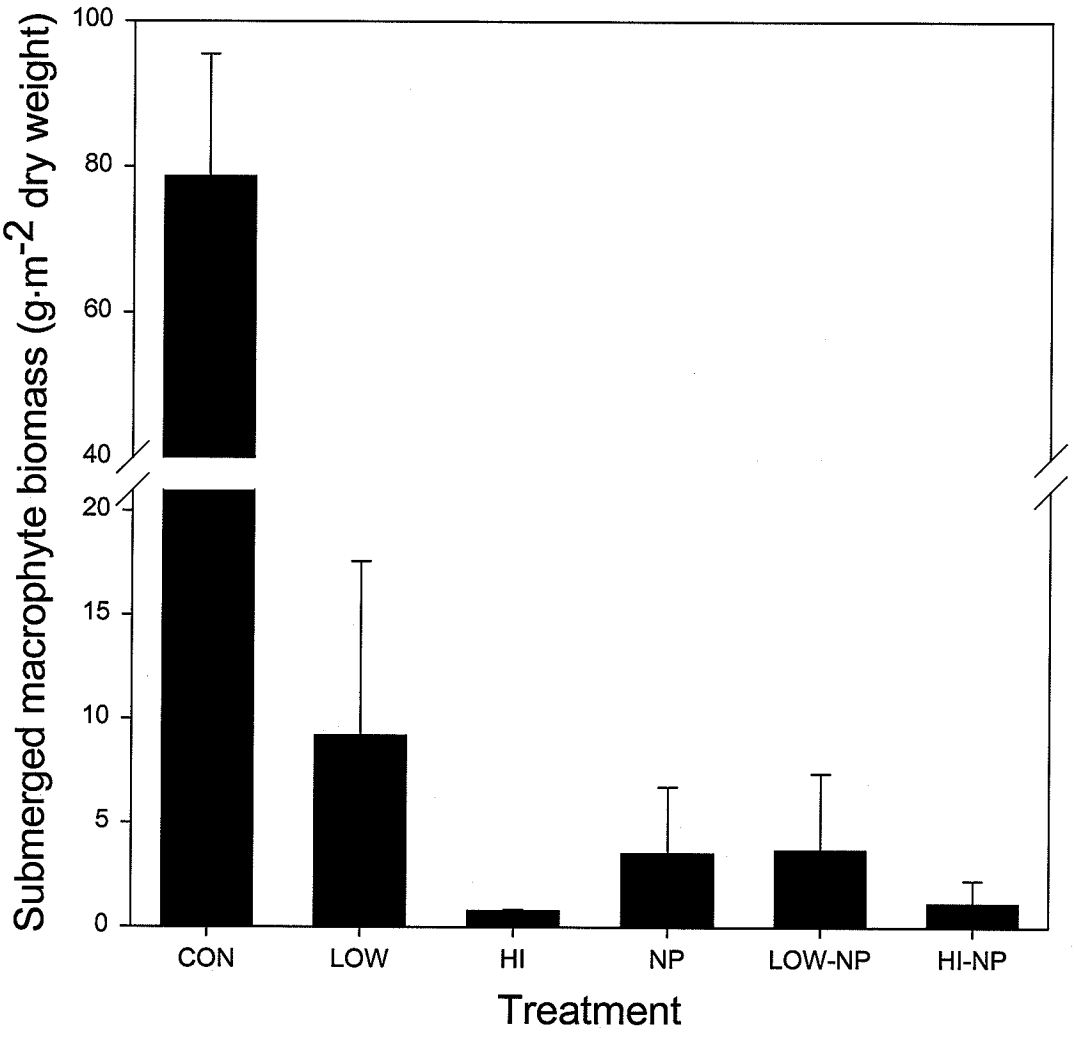

Figure 5.16. Submerged macrophyte biomass ($g \cdot m^{-2}$ d.w.; ±SE; n=2) in experimental enclosures without nutrient amendments and enclosures receiving nutrient additions (N+P) stocked with no carp, low carp, and high carp biomass. Macrophytes were harvested at the end of the experiment on August 20, 2002.

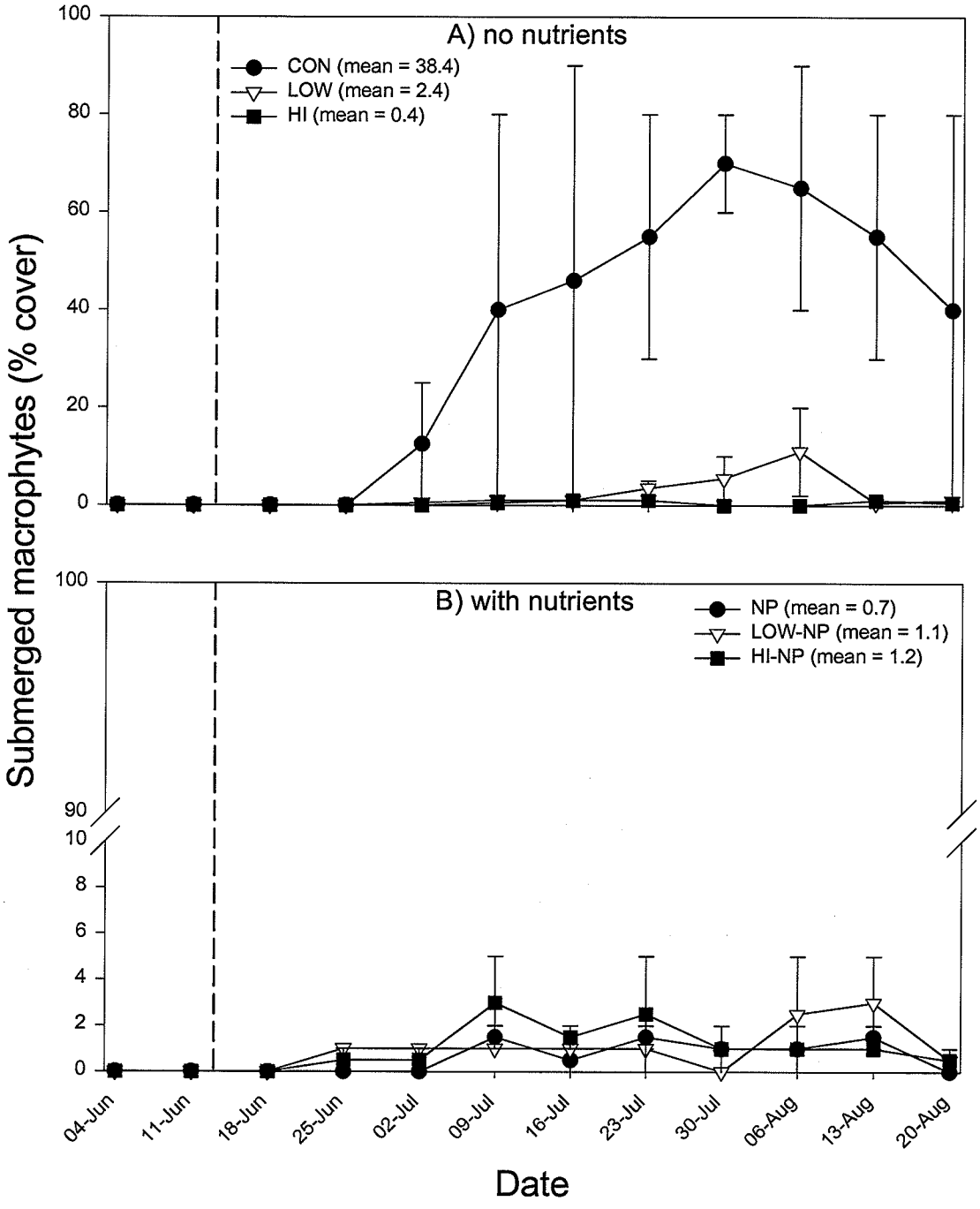

Figure 5.17. Submerged macrophytes (% cover; ±SE; n=2) in experimental enclosures without nutrient amendments (A) and enclosures receiving nutrient additions (B) stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions and the stocking of enclosures with carp on 13 June, 2002.

Light penetration, which was measured as the percent of surface irradiance reaching the sediment-water interface in the experimental enclosures, was significantly reduced by carp ($F_{2,6} = 10.53, p = 0.0109$) and nutrient ($F_{1,6} = 41.87, p = 0.0006$) treatments, but was unaffected by carp x nutrient treatment interactions ($F_{2,6} = 2.28, p = 0.1838$; Table 5.1). In general, light penetration decreased throughout the treatment period in all treatments (Figure 5.18). Mean % surface irradiance at the sediment-water interface in enclosures not receiving nutrient additions was 18.8, 5.1, and 3.1 % in the CON, LOW, and HI treatments, respectively. Light penetration was significantly greater in the CON treatment relative to the HI treatment ($p = 0.0336$), but was not significantly different between the CON and LOW treatments ($p = 0.0884$) or between the LOW and HI treatments ($p = 0.9303$). In enclosures receiving nutrient additions, mean % surface irradiance at the sediment-water interface was 3.7, 0.9, and 0.8 % in the NP, LOW-NP, and HI-NP treatments, respectively. There was no statistical difference in light penetration between any combination of the enclosures receiving nutrient additions.

5.1.6 Other water quality parameters

Dissolved oxygen (Figure 5.19), and pH (Figure 5.20) were significantly higher in enclosures receiving nutrients ($F_{1,6} = 84.09, p < 0.0001$; $F_{1,6} = 63.21, p = 0.0002$) relative to enclosures not receiving nutrient additions. Conversely, conductivity (Figure 5.21) was lower in enclosures receiving nutrient additions ($F_{1,6} = 30.15, p = 0.0015$), relative to enclosures not receiving nutrient additions. All three parameters were unaffected by carp treatment ($F_{2,6} = 2.31, p = 0.1799$; $F_{2,6} = 4.03, p = 0.0778$; $F_{1,6} = 0.64, p = 0.5596$). Additionally, statistical analysis detected a significant carp x nutrient interaction for conductivity ($F_{2,6} = 5.40, p = 0.0455$). With the exception of the LOW-NP treatment,

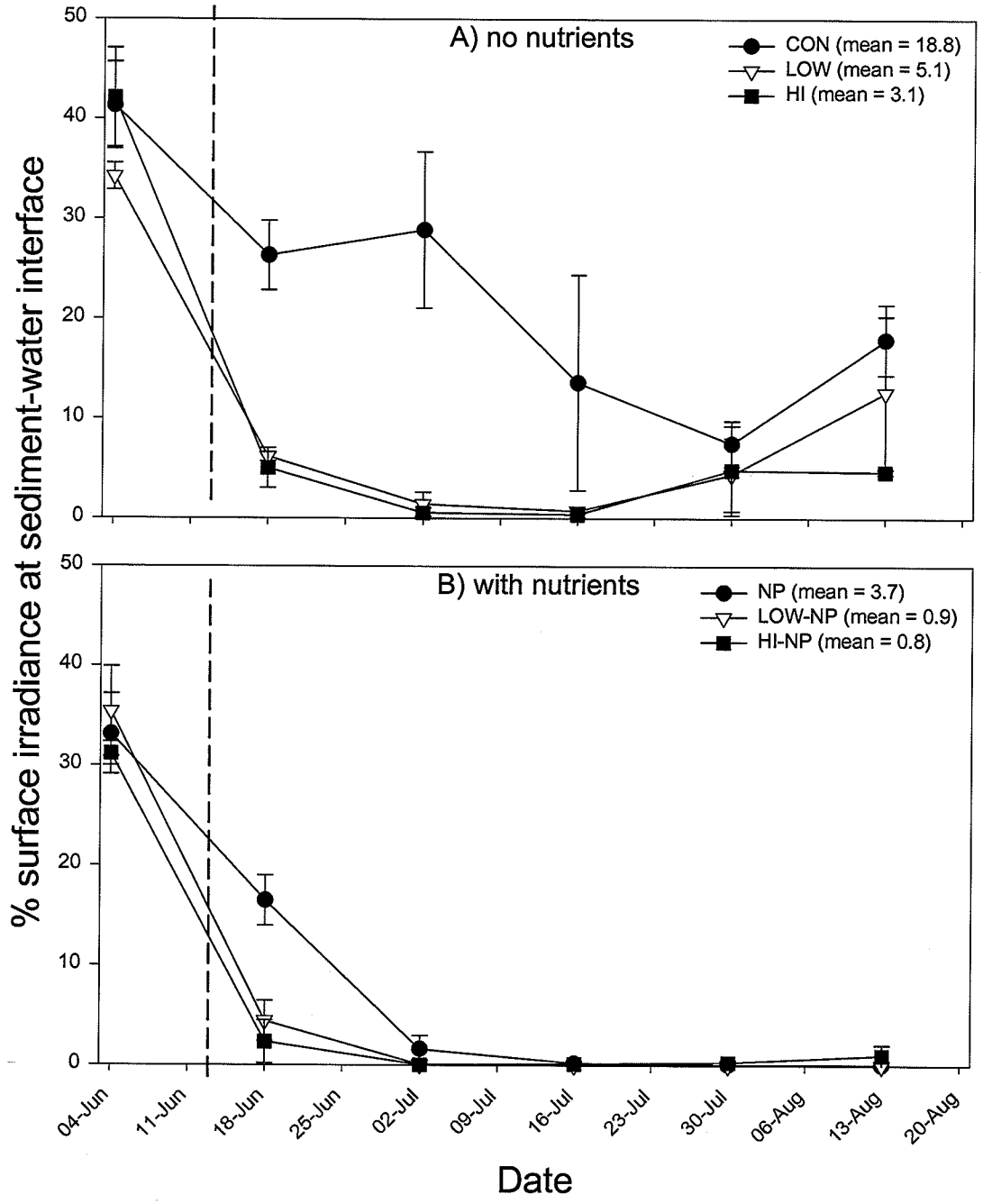

Figure 5.18. Percent (%) surface irradiance reaching the sediment-water interface (%; ±SE; n=2) in experimental enclosures without nutrient amendments (A) and enclosures receiving nutrient additions (B) stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions and the stocking of enclosures with carp on 13 June, 2002.

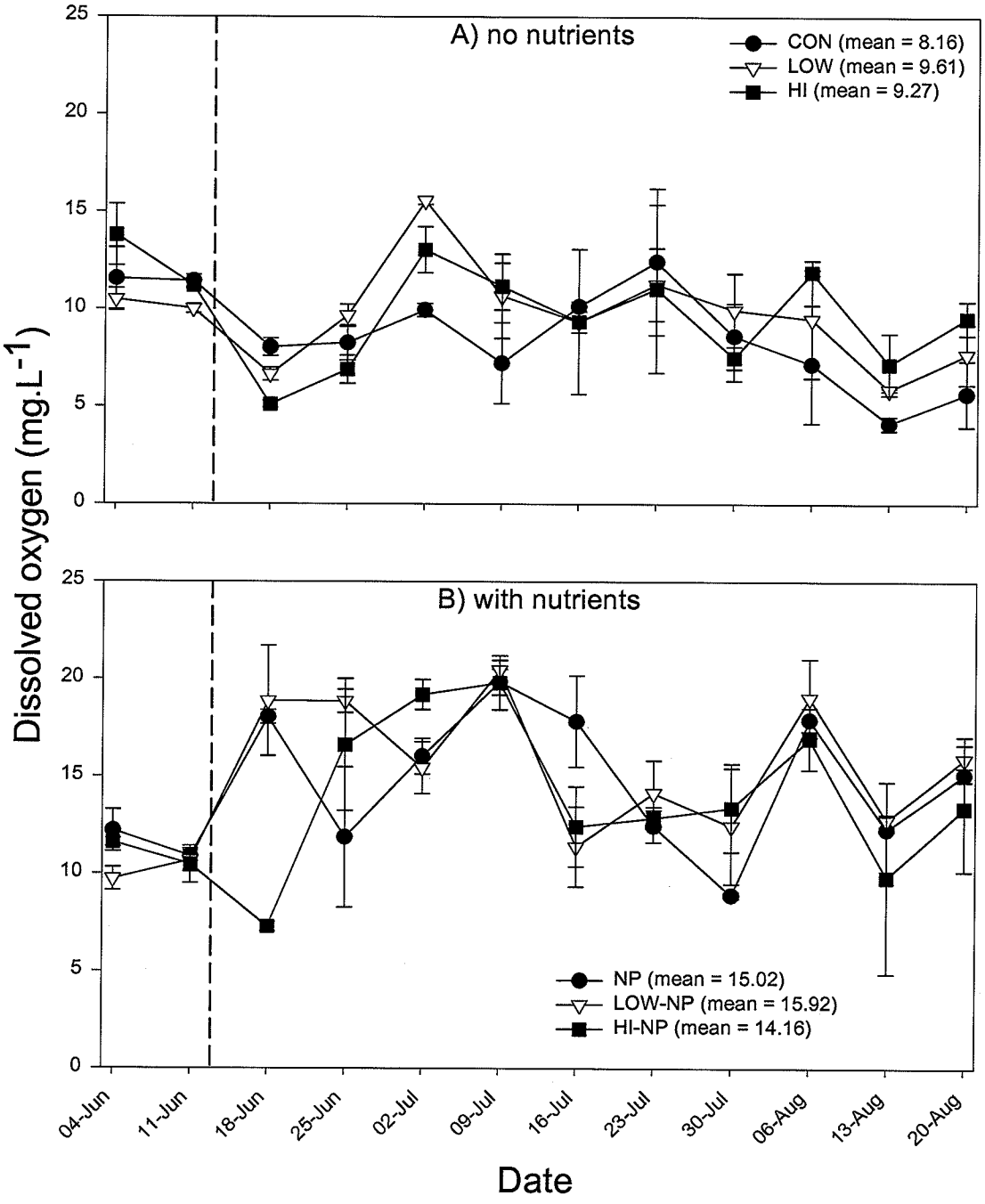

Figure 5.19. Dissolved oxygen concentrations ($mg \cdot L^{-1}$; ±SE; n=2) in experimental enclosures without nutrient amendments (A) and enclosures receiving nutrient additions (B) stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions and the stocking of enclosures with carp on 13 June, 2002.

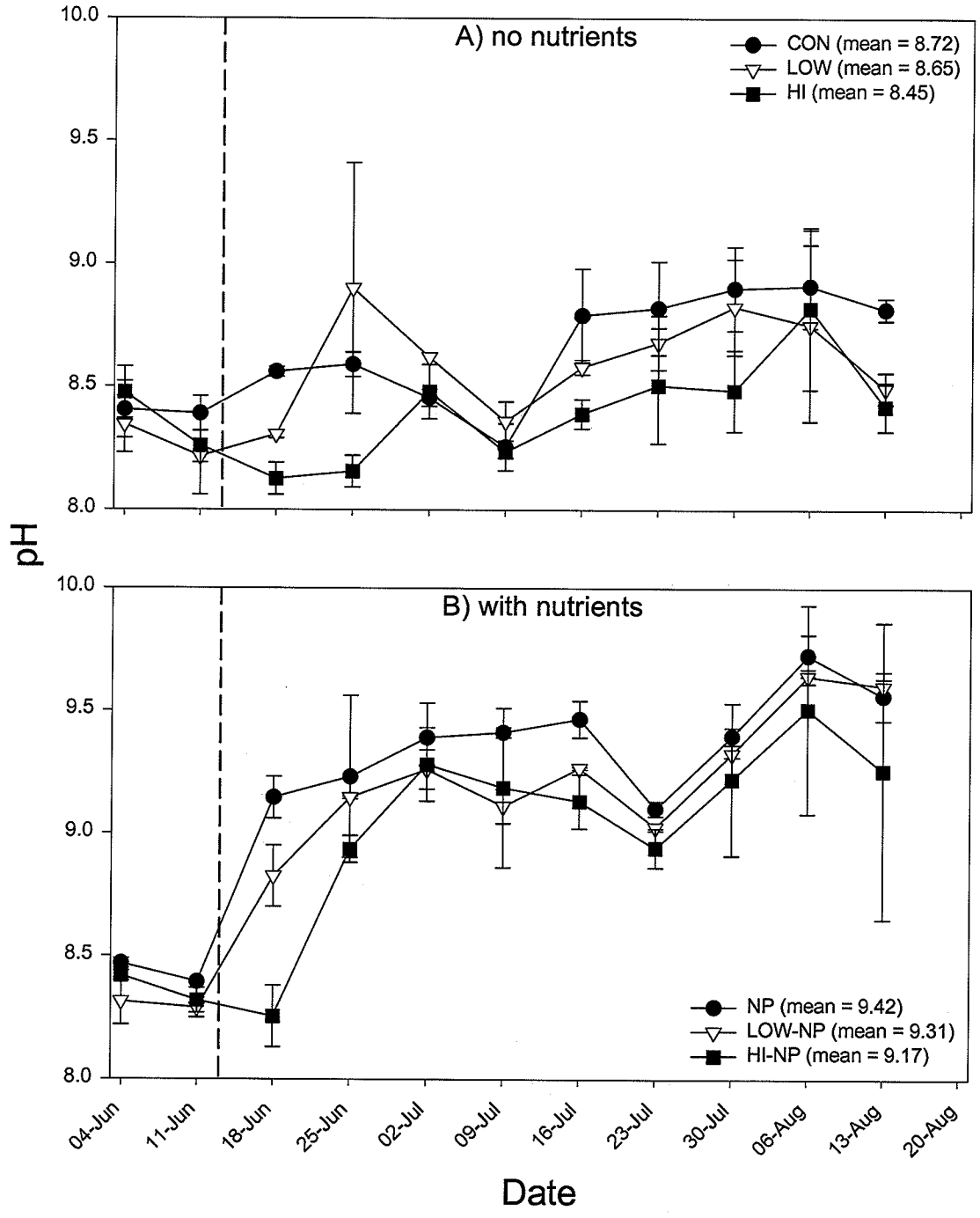

Figure 5.20. pH (pH units; ±SE; n=2) in experimental enclosures without nutrient amendments (A) and enclosures receiving nutrient additions (B) stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions and the stocking of enclosures with carp on 13 June, 2002.

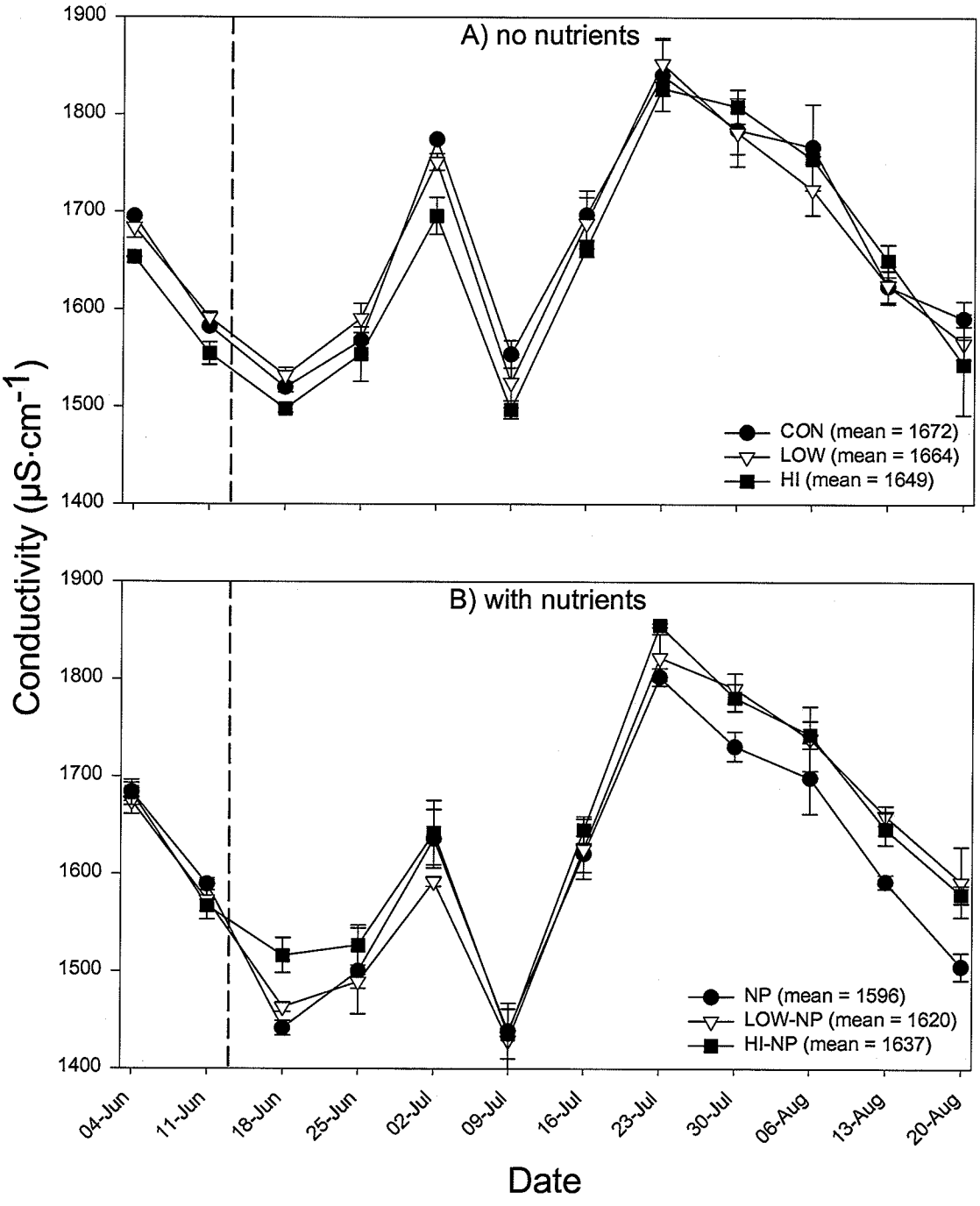

Figure 5.21. Conductivity ($\mu S \cdot cm^{-1}$; ±SE; n=2) in experimental enclosures without nutrient amendments (A) and enclosures receiving nutrient additions (B) stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions and the stocking of enclosures with carp on 13 June, 2002.

mean treatment period DO concentration increased with increasing carp density (Figure 5.19). Conversely, pH appeared to decrease with increasing carp density in enclosures whether or not they were receiving nutrient additions (Figure 5.20). There were no apparent trends in conductivity related to stocking density and although conductivity was significantly lower in enclosures receiving nutrient additions, all treatments followed a similar trend throughout the treatment period (Figure 5.21).

5.1.7 Multivariate analysis

Principal component analysis revealed clear differences between the various experimental treatments with the first three components explaining 79.5% of the total variance in water quality parameters (Table 5.3, Figure 5.22). Although more than 10 water quality parameters were monitored over the entire treatment period, variables that measured the same information as other variables were deemed redundant and excluded from the analysis (i.e. total dissolved phosphorus and nitrogen were not included but total reactive phosphorus, ammonia, and nitrate were included). PCA axis 1 explained 45% of the total variation between treatments and generally separated the "with nutrient" treatments from the "no nutrient" treatments. Organic suspended solids and % surface irradiance at the sediment-water interface explained 86 and 84% of the variance in treatment scores on axis 1, respectively (Table 5.3). Virtually all treatments at all times where nutrients were added were situated to the left of axis 1 and positively correlated to OSS, whereas almost all treatments at all times situated to the right of axis 1 and positively correlated with light penetration consisted of no nutrient treatments. PCA axis 2 explains 19% of the total variation between treatments and generally separated the various carp treatments from one another. Inorganic suspended solids and submerged

Table 5.3. Explained variances (%) for the three first principal components (PC) of the principal component analysis conducted on various water chemistry parameters monitored during the experiment.

	PC1	**PC2**	**PC3**
Organic suspended solids	86.0	3.1	3.3
Light penetration	83.9	4.2	2.8
NH_3	73.8	5.3	4.9
PH	63.1	20.1	0.0
TRP	57.2	30.1	0.1
Dissolved oxygen	53.7	0.0	1.2
NO_3	14.0	6.3	52.9
Submersed macrophyte cover	12.4	46.8	10.2
Inorganic suspended solids	2.2	71.4	2.7
Conductivity	0.0	5.1	78.8
Mean	44.6	19.2	15.7

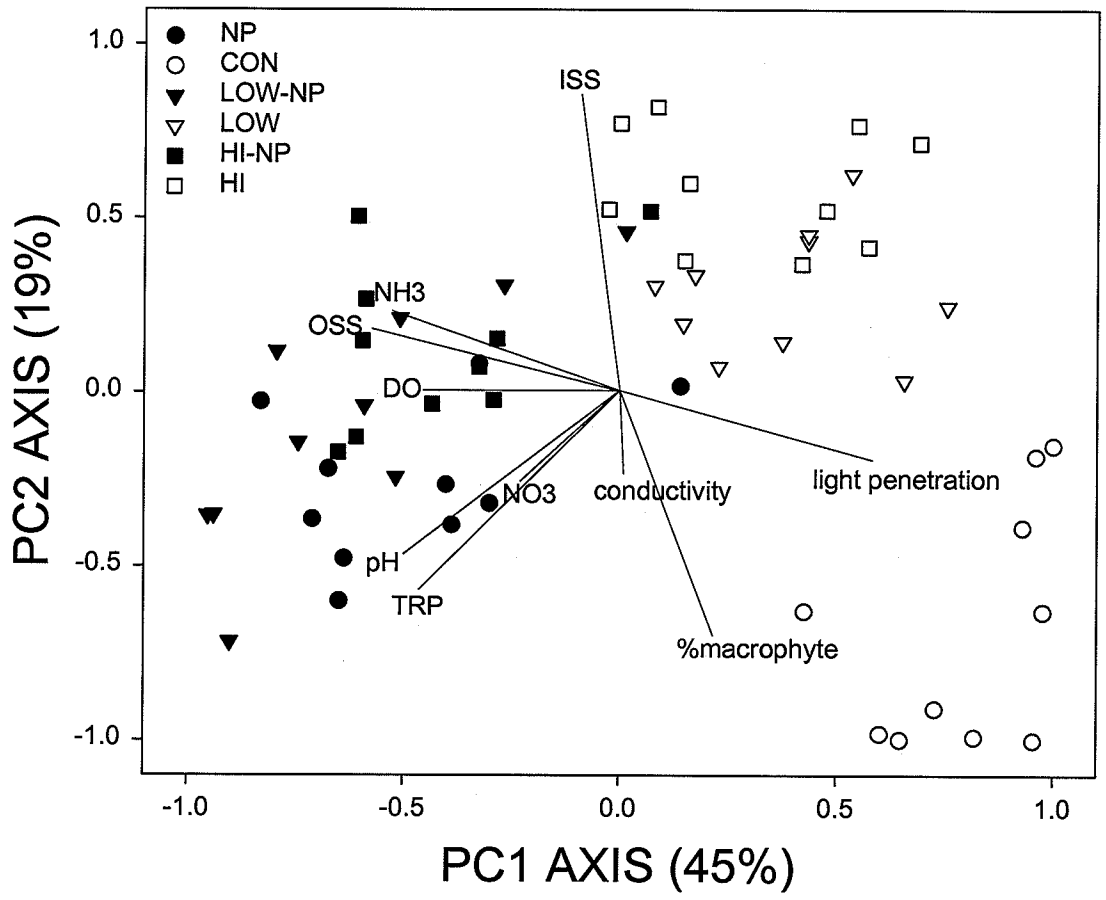

Figure 5.22. Principal component analysis of 10 water quality parameters measured throughout the treatment period in experimental enclosures without nutrient amendments and enclosures receiving nutrient additions stocked with no carp, low carp, and high carp biomass.

macrophyte cover explained 71 and 47% of the variance in treatment scores on axis 2, respectively (Table 5.3). CON treatments were positioned in the lower right quadrant and associated with increased light penetration and submerged macrophyte cover (Figure 5.22). HI and LOW treatments on all dates were positioned in the upper right quadrant and were associated with high levels of ISS and low pH and TRP. Carp treatments were not as clearly separated in enclosures receiving nutrient additions (left side of PC1) as they were for enclosures not receiving nutrient additions (right side of PC1). For the most part, NP and LOW-NP treatments were positioned in the lower left quadrant and associated with increased OSS, TRP, and pH. HI-NP treatments were mostly positioned in the upper left quadrant and as for the NP and LOW-NP treatments were primarily associated with increased ISS. However, unlike the NP and LOW-NP treatments, the HI-NP treatment scores were associated with increased ammonia (Figure 5.22).

5.2 Discussion:

Overall, mesocosm experiments demonstrated that the presence of carp had significant implications for water quality. Carp effects in enclosures not receiving nutrient additions were similar to those without carp but receiving nutrients, indicating that the presence of carp generally mimics the effects of eutrophication. This same pattern of eutrophication in the presence of benthivorous fish was also found by Andersson et al. (1978). One of the main goals of this experiment was to identify if carp interact synergistically with nutrient loading to increase dissolved nutrient concentrations in the water column, exacerbating the effects of eutrophication. Unfortunately, the nutrient addition regime that was applied to the enclosures appeared to saturate the experimental systems, making it difficult to detect any significant carp effect over the

effects of the nutrient additions themselves. However, there were some significant carp x nutrient treatment interaction effects. Overall, all experimental treatments in my study resulted in a dramatic increase in turbidity, relative to the control enclosures indicating that, at least in mesocosm experiments, carp can result in a switch from the clear macrophyte-dominated state to the turbid phytoplankton-dominated state.

5.2.1 Impacts of carp, fertilization and their interactions on water column and sediment nutrient concentrations

Benthivorous fish such as the common carp may increase water column nutrient concentrations by releasing nutrient rich porewaters through their feeding activities, by resuspending nutrient rich sediments, and by excreting nutrients acquired from benthic prey items. Excretion experiments I conducted (Appendix B) indicated that the carp stocked in the enclosures released between 0.49 to 0.59 $mg \cdot kg^{-1} \cdot hr^{-1}$ of TRP and 5.15 to 6.14 $mg \cdot kg^{-1} \cdot hr^{-1}$ of NH_3 and should have increased TRP and NH_3 concentrations in low carp density enclosures by approximately 49 $\mu g \cdot L^{-1}$ and 506 $\mu g \cdot L^{-1}$ by day 30 of the experiment, respectively. At high densities, nutrient excretion by carp should have increased TRP and NH_3 concentrations in the enclosures by approximately 99 $\mu g \cdot L^{-1}$ and 1035 $\mu g \cdot L^{-1}$ by day 30 of the experiment, respectively.

I did not determine the flux of phosphorus entering the water column from resuspended sediments, but assumed that rates were similar to those reported by Reddy *et al.* (2002) and Fisher & Wood (2004), where fluxes ranged between 0.004 to 0.013 $mg \cdot kg^{-1} \cdot hr^{-1}$, much smaller than the calculated input from carp excretion. Additionally, a previous study conducted in a shallow pond within Delta Marsh by Goldsborough & Robinson (1985) reported a sediment nutrient flux for total reactive phosphorus of 0.49

$mg \cdot m^{-2} \cdot d^{-1}$. Assuming this rate is similar to that in the Blind Channel, TRP flux from the enclosure sediments would have increased the concentration in the water column by approximately 30 $\mu g \cdot L^{-1}$ by day 30 of the experiment, similar to, but lower than the loading attributed to low carp densities. Goldsborough & Robinson (1985) also reported a sediment nutrient flux rate for ammonia of 4.63 $mg \cdot m^{-2} \cdot d^{-1}$. Once again, assuming this rate is similar to that in the Blind Channel, ammonia flux from the enclosure sediments would have increased the concentration in the water column by approximately 280 $\mu g \cdot L^{-1}$ by day 30 of the experiment, much lower than the loading attributed to low carp densities.

Nevertheless, the interstitial water of sediments in the Blind Channel are rich in dissolved phosphorus and nitrogen with TRP and NH_3 reaching concentrations of approximately 1.5 and 5.0 $mg \cdot L^{-1}$ at a depth of 15 centimetres (Bourne 2000). Therefore, the initial release of nutrient rich porewaters by the addition and subsequent foraging activity of carp likely increased nutrient levels in the water column substantially over background fluxes. These nutrient rich porewaters also explain the high ammonia concentrations that occurred in a few of the enclosures during the pre-treatment period as a result of seining that took place in certain enclosures just prior to the start of the experiment.

Based on the aforementioned mechanisms, I hypothesized that both TRP and NH_3 concentrations would increase in the presence of carp. Contrary to what I hypothesized, TRP was significantly higher in the CON treatment relative to the LOW ($p = 0.0200$) and HI ($p = 0.0155$) treatments indicating that carp did not increase water column TRP

concentrations in the un-fertilized enclosures. Other studies examining the effects of benthivorous fish on water quality have also found that various measures of dissolved phosphorus concentrations did not increase in the presence of benthivores (Keen & Gagliardi 1981, Qin & Threkeld 1990, Breukelaar *et al.* 1994, King *et al.* 1997, Shormann & Cotner 1997). In their paper examining the effects of brown bullheads on water quality, Keen & Gagliardi (1981) suggest that benthivores release dissolved phosphorus through excretion and by disturbing the sediment-water interface, but that this soluble fraction is quickly sorbed to suspended sediments generated through benthivore activity and removed through sedimentation. Lougheed *et al.* (1998) also found that TP concentrations increased in the presence of carp but SRP did not, indicating that dissolved phosphorus was being sorbed to suspended sediments. In the oxic conditions of the water column, phosphates have a high affinity for absorbing to suspended sediments containing iron oxides, and are subsequently transported to the sediments (Almroth 2002), possibly explaining why TP increases in the presence of carp but not SRP or TRP.

In my study, sediment phosphorus concentrations decreased noticeably (although not significantly) with increasing carp density. This decrease in sediment phosphorus is likely the result of increased mineralization of organic matter and the subsequent release of phosphorus from sediments, which is enhanced when benthivores expose bottom sediments to higher oxygen concentrations in the water column (Søndergaard *et al.* 1992). Based on the decrease in sediment phosphorus concentrations in the LOW and HI treatments relative to the control, water column phosphorus concentrations should have increased by approximately 4.97 and 6.78 $mg \cdot L^{-1}$, respectively. However, I never

detected any significant increase in TRP concentrations. Lower water-column TRP levels in the presence of carp relative to the control in the un-fertilized enclosures can be explained by a combination of two mechanisms. First any phosphorus released due to carp activity, whether it be through resuspension or excretion, is being rapidly consumed and converted into particulate phosphorus within algal cells. Secondly, any remaining dissolved P is likely sorbed to the sediments resuspended by carp. The fact that TRP remained constant throughout the treatment period in the LOW and HI treatments, while OSS and chlorophyll *a* representing algal biomass increased supports my claim that the phosphorus released in the un-fertilized enclosures as a result of carp activities is rapidly being sequestered in the phytoplankton.

As would be expected, in the fertilized enclosures, water column TRP concentrations generally increased throughout the experiment. However, given the amount of phosphorus added to the enclosures, water column concentrations remained low at all three carp densities for the first three weeks after the start of nutrient additions. This time-lag before additions affected water column phosphorus concentrations is likely due to phosphorus limitation of the phytoplankton. Over this same time period phytoplankton chlorophyll *a* increased dramatically at all carp densities to concentrations in excess of 200 $\mu g \cdot L^{-1}$. This indicates that luxury consumption by the phytoplankton is taking place, resulting in the un-coupling of nutrient supply and algal growth. Similar trends have been noted for other experiments conducted in Delta Marsh (Kiers-North 2000).

Carp appeared to increase water column concentrations of TRP in the LOW-NP, and decrease TRP in the HI-NP treatments, relative to the enclosures receiving only nutrient additions (NP). This is contrary to my hypothesis that water column nutrient

concentrations would increase with increasing densities of carp. Perhaps by resuspending a greater volume of sediment, more phosphorus in the HI-NP treatments is being bound, and therefore is not included in the TRP fraction. Furthermore, due to the increased sedimentation rates, larger quantities of phosphorus are being transferred from the water column to the sediment-water interface in the HI-NP treatment. This is supported by the fact that in the fertilized treatments, sediment phosphorus concentrations in the NP and HI-NP treatments were similar to one another and higher compared to the LOW-NP treatment indicating that more phosphorus was being transferred to the sediment-water interface. As was the case for the un-fertilized treatments, the higher TRP concentrations observed in the NP treatment relative to the HI-NP treatment is due to the fact that a larger fraction of dissolved phosphorus is being sorbed to suspended sediments in the HI-NP treatment, which subsequently lowers the TRP concentration.

Sediment nutrient concentrations indicate that approximately 62.5, 20.8, and 66.6% of the phosphorus added through fertilization was stored in the surface sediments for the NP, LOW-NP, and HI-NP, treatments respectively. Based on the percentage of added P that accumulated in the sediments water column concentrations should have increased by 2.04, 4.30, and 1.81 $\mu g \cdot L^{-1}$ in the NP, LOW-NP, and HI-NP treatments. Using these predicted concentrations and subtracting the mean open-water TRP concentrations, I estimate that approximately 17.7, 10.2, and 13.3% of the phosphorus added remained in dissolved form (as measured by TRP) in the NP, LOW-NP, and HI-NP treatments respectively, with the remaining phosphorus either bound to suspended sediment or sequestered in algal cells. It is important to note here that I assumed that no P would be liberated through sediment resuspension in the fertilized enclosures as a result of nutrient

additions, which would have dramatically increased water column concentrations above the equilibrium phosphorus concentration (EPC). EPC is the concentration at which no desorption or adsorption from sediments or suspended sediments occur. James & Barko (2004) found that sediments from Lake Pepin had an EPC of 0.155 $mg \cdot L^{-1}$, and Perkins & Underwood (2001) found a maximum EPC of 0.2 $mg \cdot L^{-1}$ in a eutrophic reservoir. These EPC values are below the mean TRP concentrations measured in all fertilized enclosures, indicating that suspended sediments would have been acting as a net sink for dissolved phosphorus.

Unlike TRP, NH_3 concentrations increased with increasing densities carp in un-fertilized enclosures as I had hypothesized (Table 5.1, Figure 5.2). Increases in NH_3 concentrations are a result of the combination of excretion through carp and the release of interstitial waters. Additionally, Shormann & Cotner (1997) found that carp enhanced ammonia mineralization and suggested that this increase was the result of larger numbers of bacteria being associated with resuspended sediments. Similarly, Wainright (1987) found that remineralization rates were stimulated by sediment resuspension due the fact that suspended sediments became more densely packed with bacteria relative to those at the sediment-water interface. Additionally, once resuspended through the foraging activities of carp, organic matter may degrade more rapidly due to the well mixed and oxic conditions in the water column relative to the sediments (Wainright & Hopkinson Jr. 1997).

In the fertilized enclosures NH_3 generally appeared to increase in a linear fashion over the course of the experiment and was unaffected by the presence of carp. However the

concentrations of NH_3 only account for a small fraction of the nitrogen added to the enclosures. Even summing NH_3 and NO_3 does not account for a significant fraction of the nitrogen added to the enclosures. In fact although there were considerable concentrations of NH_3 and NO_3 measured in the water column, sediment N concentrations, indicate that 147% of the N added to the NP enclosure was deposited at the sediment-water interface. Initially this does not seem to make sense, however, looking at the TRP:DIN ratios it is apparent that phytoplankton would have been nitrogen limited. This in turn would have allowed nitrogen-fixing cyanobacteria to flourish, which would have transferred atmospheric nitrogen to the sediments as cells settled out of the water column. Although it appears that carp did not influence water column NH_3 concentrations over the course of the experiment in the fertilized enclosures, the diurnal experiment indicated that carp significantly enhanced ammonia concentrations between 6 PM and 6 AM relative to concentrations in the fertilized enclosures without carp. However, increases in NH_3 did not differ between the LOW-NP and HI-NP treatments.

5.2.2 Impacts of carp, fertilization and their interactions on turbidity, suspended solids, and phytoplankton chlorophyll *a*

In the un-fertilized enclosures, common carp increased turbidity, suspended solids (total, inorganic, and organic) and phytoplankton chlorophyll *a* and increases appeared to be proportional to carp biomass, as predicted. Many other studies have also found that benthivorous fish significantly increase turbidity and suspended solids (Lougheed *et al.* 1998, Angeler *et al.* 2002, Parkos III *et al.* 2003) and phytoplankton chlorophyll *a* (Qin & Threkeld 1990, Richardson *et al.* 1990, Breukelaar *et al.* 1994, Angeler *et al.* 2002). Conversely, Parkos III *et al.* (2003) found that carp significantly increased suspended solids and turbidity, but did not enhance chlorophyll *a* concentrations. In the un-fertilized

enclosures carp increased mean TSS concentrations by approximately 37 and 73 $mg \cdot L^{-1}$, in the LOW and HI treatments, respectively. Based on these results I calculated that TSS increased at a rate of 6.1, and 4.8 $mg \cdot L^{-1}$·for every100 kg of carp stocked in the LOW and HI treatments, respectively. These rates compare favourably with those of Meijer (1989) and Breukelaar *et al.* (1994), who calculated rates of increase in TSS of 3.8 and 6.3 $mg \cdot L^{-1}$·for every 100 kg of carp stocked, respectively.

The lower rate of increase in TSS calculated for the HI treatment is likely the result of light limitation induced by the high inorganic suspended solid concentrations, which in turn prevent increases in the organic fraction of TSS by reducing phytoplankton productivity. This is supported by the rates of increase calculated for chlorophyll *a* concentrations, which were higher in the LOW treatment (7 $\mu g \cdot L^{-1}$·for every 100 kg of carp stocked), relative to the HI treatment (5 $\mu g \cdot L^{-1}$·for every 100 kg of carp stocked). These rates are similar to, but slightly lower compared to the rate calculated by Breukelaar *et al.* (1994) where chlorophyll *a* increased by 9 $\mu g \cdot L^{-1}$·for every 100 kg of bream stocked.

In the fertilized enclosures, inorganic suspended solid concentrations responded to increases in carp biomass in much the same way as in un-fertilized enclosures, increasing with carp biomass. However, organic suspended solids and phytoplankton chlorophyll *a* concentrations were much higher in the LOW-NP treatment relative to the NP and HI-NP treatment. This contradicts my hypothesis that carp and nutrients would interact synergistically to increase phytoplankton productivity, and that these increases would be proportional to the biomass of carp stocked. A study by Kyeongsik *et al.* (1999) found

that algal biomass was enhanced by mixing and nutrient additions, but impaired by increased suspended sediments. Furthermore these authors found that mixing and nutrient additions interacted synergistically, increasing phytoplankton biomass by more than the sum of these two factors. Conversely, a combination of mixing and sediment increased algal biomass less than expected. Based on this study it is likely that in my experiment, phytoplankton chlorophyll a and OSS were enhanced as a result of carp maintaining the added nutrients in suspension. This effect was particularly pronounced in the LOW-NP treatment where mixing maintained nutrients in the water column but did not generate enough suspended sediment to limit light. Conversely, in the NP and HI-NP treatments most of the added nutrients did not remain in the water column but for different reasons. In the NP treatment, the absence of carp allowed most of the nutrients added to the enclosures to be transferred to the sediment water interface, and therefore was not available to the phytoplankton. Conversely, in the HI-NP treatment, the high concentration of inorganic suspended solids generated by carp activity likely limited light, and scavenged dissolved nutrients from the water column at a greater rate compared to the LOW-NP treatment, thereby reducing phytoplankton biomass.

5.2.3 Impacts of carp, fertilization and their interactions on sedimentation rates

Sedimentation rates did not differ between un-fertilized and fertilized enclosures regardless of stocking density. Using the regression relationship presented in Figure 5.14 I calculated that a sedimentation rate of approximately 10 $g \cdot m^{-2} \cdot$(dry weight) for every 100 kg of carp stocked. This rate is noticeably lower than the rates calculated by Breukelaar *et al.* (1994) (46 $g \cdot m^{-2}$ per 100 kg stocked) and the common carp (24 $g \cdot m^{-2}$ per

100 kg stocked). However, even at a rate of 10 $g \cdot m^{-2}$ per 100 kg of carp, a carp density of 400 $kg \cdot ha^{-1}$ would resuspended approximately 257.8 g of sediment into the water column. On a volume basis this would be the equivalent of adding approximately 77 mg of $sediment \cdot L^{-1}$ in my enclosures. Using the severity of ill effects (SEV) model proposed by Newcombe & Jensen (1996) for freshwater non-salmonid fish, this level of exposure to sediments over a four week period yields an SEV score of 10 which corresponds to lethal responses in fish (0- 20% mortality) and moderate to severe habitat degradation.

5.2.4 Submersed macrophytes and light penetration

Although submerged macrophyte biomass was not significantly different between treatments, linear regression analysis revealed that submerged macrophyte biomass measured at the end of the experiment was significantly positively correlated ($p = 0.0005$) to the mean percent surface irradiance reaching the sediment-water interface, which explained approximately 95% of the variation in submerged macrophyte biomass. This correlation indicates that carp do not reduce submerged macrophyte biomass through physical damage or consumption, but rather through light limitation. This was also supported by the principal component analysis I conducted, where the second axis which explained 19% of the overall variation, was essentially a gradient between % submerged macrophyte cover and inorganic suspended solid concentrations. Furthermore, the addition of nutrients appears to reduce submerged macrophyte biomass to levels between those of low and high carp densities alone.

Lougheed *et al.* (1998) found that the number of submerged macrophyte species declined significantly above an apparent threshold of 20 NTU. My results suggest that the

same is true for submerged macrophyte biomass. In the control treatment enclosures where the mean turbidity was 15 NTU, submerged macrophyte biomass measured at the end of the experiment was approximately 79 $g \cdot m^{-2}$ (dry weight). However, doubling the mean turbidity measured in the control, as was the case in the LOW treatment, resulted in submerged macrophyte biomass more than eight times lower than those measured in the control enclosures.

Overall, my enclosure experiments demonstrated that carp generally impact aquatic ecosystems in much the same way as eutrophication. Additionally, my experiments demonstrated that carp can trigger a shift from the clear, macrophyte dominated state to a turbid, phytoplankton-dominated state, and that this switch likely occurs at a carp biomass less than 600 $kg \cdot ha^{-1}$. Furthermore my results suggest that the model proposed by Drenner *et al.* (1996) and Drenner *et al.* (1998) which predicts that carp interact synergistically with nutrient loading to increase phytoplankton biomass needs to be modified to incorporate the effects of severe light-limiting conditions that result at high carp biomass.

6.0 Impacts of an exotic benthivorous fish, the common carp (*Cyprinus carpio*), and nutrient additions on planktonic and benthic communities in small experimental mesocosms

6.1 Results:

6.1.1 Phytoplankton biomass and composition

Over the course of the experiment, carp ($F_{2,30} = 5.42$, $p = 0.0098$), nutrients ($F_{1,30} = 55.00$, $p < 0.0001$), and carp x nutrient interactions ($F_{2,30} = 13.74$, $p < 0.0001$; Table 6.1) significantly increased total phytoplankton biomass in the experimental enclosures. Of the seven major algal classes that were identified, Cyanophyceae and Chlorophyceae biomass were significantly increased by nutrients ($F_{1,30} = 32.05$, $p < 0.0001$; $F_{1,30} = 11.76$, $p = 0.0018$), and carp x nutrient interactions ($F_{2,30} = 5.44$, $p = 0.0097$; $F_{2,30} = 7.14$, $p = 0.0029$), while Bacillariophyceae biomass increased as a function of carp ($F_{2,30} = 5.26$, $p = 0.0110$), and Chrysophyceae biomass increased as a function of carp ($F_{2,30} = 11.85$, $p = 0.0002$), and nutrients ($F_{1,30} = 8.19$, $p = 0.0076$). The biomass of all other algal classes (Cryptophyceae, Euglenophyceae, and Dinophyceae) was un-affected by the experimental treatments (Table 6.1).

Post-hoc analysis of the un-fertilized treatments revealed that mean total phytoplankton biomass was significantly higher in the HI (98,465 $mg \cdot m^{-3}$, $p < 0.0001$), and LOW treatments (41,536 $mg \cdot m^{-3}$, $p = 0.0090$) relative to the CON treatment (10, 859 $mg \cdot m^{-3}$), and that there was no difference in total phytoplankton biomass between the LOW and HI treatments ($p = 0.3887$; Table 6.2 and Figure 6.1). Mean total

Table 6.1. Results of ANOVA's for phytoplankton biomass, zooplankton density, benthic invertebrate density, and emerging chironomid biomass measured in experimental enclosures. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, ns = not significant ($P \geq 0.05$).

	Between enclosures		
Variable	Carp	Nutrients	Carp x Nutrients
Phytoplankton biomass			
Total phytoplankton	**	***	***
Cyanophyceae	ns	***	**
Bacillariophyceae	*	ns	Ns
Chlorophyceae	ns	**	**
Chrysophyceae	**	**	Ns
Cryptophyceae	ns	ns	Ns
Euglenophyceae	ns	ns	Ns
Dinophyceae	ns	ns	Ns
Zooplankton density			
Total zooplankton	**	ns	Ns
Rotifer	**	ns	Ns
Nauplii	ns	ns	Ns
Cladocerans	*	***	Ns
Copepods	ns	*	Ns
Benthic invertebrate density			
Oligochaete	*	ns	Ns
Chironomidae	***	ns	Ns
Chironomini	***	ns	Ns
Tanytarsini	***	ns	Ns
Emerging chironomid biomass			
Chironomidae	***	n/a	n/a
Chironomini	**	n/a	n/a
Tanypodinae	***	n/a	n/a
Tanytarsini	***	n/a	n/a
Orthocladinae	ns	n/a	n/a
Forage fish density	ns	**	*

Table 6.2. Mean phytoplankton biomass, total and class, (mg m^{-3} ± SE) in experimental enclosures stocked with no carp (CON), low carp (LOW), and high carp densities (HI), and in enclosures receiving nutrient additions stocked with no carp (NP), low carp (LOW-NP), and high carp densities (HI-NP). Treatments with the same letters within a row are not significantly different from each other.

Phytoplankton biomass (mg m^{-3})	N	Treatment					
		CON	LOW	HI	NP	LOW-NP	HI-NP
All classes	2	10,859±4,250 (a)	41,536±8,625 (b)	98,465±34,632 (b,c)	214,408±32,116 (b,c)	225,529±33,110 (c)	108,186±22,573 (b,c)
Cyanophyceae	2	3,216±2,271 (a)	14,011±4,366 (a,b)	19,924±3,672 (b,c)	158,392±52,325 (b,c)	190,696±49,163 (c)	63,985±37,866 (b,c)
Bacillariophyceae	2	2,519±1,567 (a)	6,708±721 (a,b)	74,545±32,735 (b)	19,589±16,625 (a,b)	23,004±17,017 (a,b)	18,960±9,473 (a,b)
Chlorophyceae	2	4,366±564 (a)	8,883±3,606 (a,b)	2,625±171 (a,c)	28,512±9,059 (b)	5,031±1,772 (a,b)	16,639±8,205 (b,c)
Chrysophyceae	2	47±2 (a)	776±375 (b)	512±93 (b)	826±331 (b)	3,216±1,310 (b)	1,557±1,191 (b)
Cryptophyceae	2	457±265 (a)	5,889±3,289 (a)	374±189 (a)	5,262±4,425 (a)	1,737±1,285 (a)	4,091±1,146 (a)
Euglenophyceae	2	150±143 (a)	3,784±1,378 (a)	302±164 (a)	293±116 (a)	863±756 (a)	825±560 (a)
Dinophyceae	2	105±74 (a)	1,486±1,271 (a)	184±92 (a)	1,534±662 (a)	983±930 (a)	2,430±973 (a)

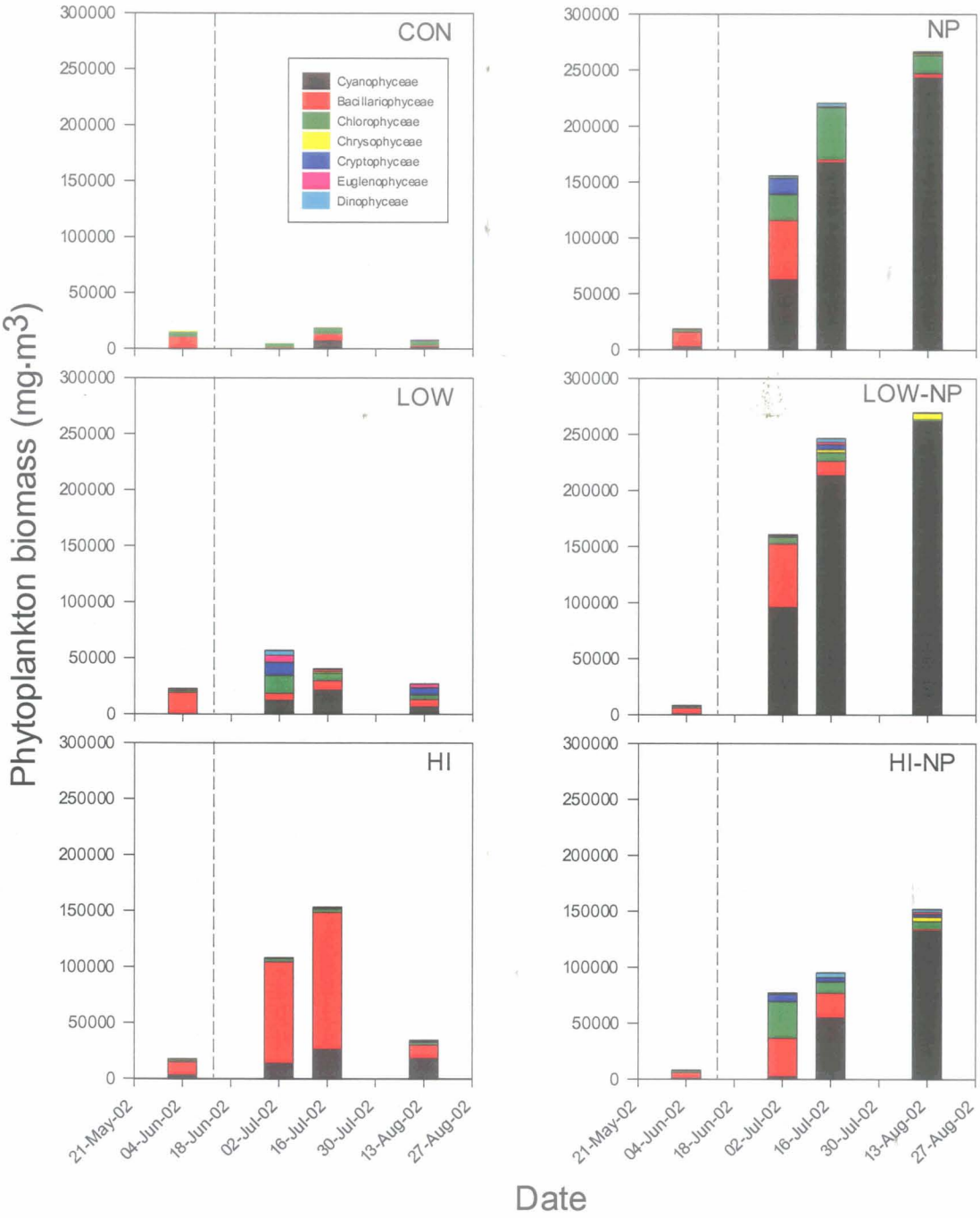

Figure 6.1. Phytoplankton biomass ($mg \cdot m^{-3}$; n=2) in experimental enclosures without nutrient amendments (CON, LOW, and HI) and enclosures receiving nutrient additions (NP, LOW-NP, and HI-NP) stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions and the stocking of enclosures with carp on 13 June, 2002.

phytoplankton biomass in enclosures receiving nutrient additions were 214,408, 225,529, and 108,186 $mg \cdot m^{-3}$ in the NP, LOW-NP, and HI-NP treatments, respectively. Algal biomass was not significantly different between any combination of the enclosures receiving nutrient additions. Compared to the un-fertilized enclosures, phytoplankton biomass in the fertilized enclosures increased more rapidly and attained greater levels, with the exception of the HI-NP treatment where algal biomass responded in a similar fashion as observed in the HI treatment (Figure 6.1).

In the un-fertilized enclosures, the biomass of the various algal classes was fairly evenly distributed in the CON and LOW treatments, and no single taxa consistently dominated. Conversely, in the HI treatments, as algal biomass increased, the Bacillariophyceae clearly became the dominant algal class, followed by the cyanophytes (Figure 6.1). The Bacillariophyceae were largely comprised of *Synedra nana* and *Nitzschia subacicularis*, whereas the cyanophytes were consisted mostly of *Planktothrix suspensa* and *Aphanizomenon flos-aquae*. In the fertilized enclosures, cyanophytes dominated the algal biomass throughout most of the experiment. By August 13, cyanophytes accounted for more than 80% of the algal biomass in all three treatments and were comprised mostly of *Planktothrix suspensa*, followed by *Pseudoanabeana* sp. Although phytoplankton biomass was dominated by the Cyanophyceae in the fertilized treatments, the first samples collected from these enclosures after the beginning of fertilization and stocking with carp were often dominated by smaller species such as *Scenedemus opoliensis* (Chlorophyceae), *Cryptomonas* sp. (Cryptophyceae), and *Nitzschia subacicularis* (Bacillariophyceae).

6.1.2 Zooplankton abundance

Rotifers comprised more than 95% of the mean number of zooplankton enumerated over the course of the experiment in each treatment, and hence accounted for most of the variation in total zooplankton numbers (Table 6.3). Total zooplankton and rotifer density averaged over the treatment period, increased significantly as a result of carp additions ($F_{2,54} = 6.36$, $p = 0.0033$ and $F_{2,54} = 5.83$, $p = 0.0051$), but were un-affected by nutrient additions ($F_{1,54} = 0.61$, $p = 0.4375$ and $F_{1,54} = 0.43$, $p = 0.5138$) or carp x nutrient interactions ($F_{2,54} = 0.76$, $p = 0.4745$ and $F_{2,54} = 0.58$, $p = 0.5607$; Table 6.1). Additionally, cladocerans were significantly increased by carp ($F_{2,54} = 4.63$, $p = 0.0139$), but decreased by nutrients ($F_{1,54} = 18.30$, $p < 0.0001$), while copepod density increased as a function of nutrients ($F_{1,54} = 6.36$, $p = 0.0147$).

Post-hoc analysis revealed that total zooplankton and rotifer densities increased significantly in the low ($p = 0.0101$ and $p = 0.0143$) and high ($p = 0.0076$ and $p = 0.0111$) carp density treatments, relative to the treatments without carp (Table 6.3). However, mean total zooplankton and rotifer densities were not significantly different between treatments with low and high carp densities ($p = 0.9945$ and $p = 0.9953$). Additionally, cladocerans increased significantly in the high carp density treatments ($p = 0.0181$) relative to the no carp treatments. No similar increase occurred in the treatment enclosures stocked with low densities of carp.

6.1.3 Benthic macroinvertebrates

6.1.3.1 Oligochaete and larval chironomid density

The density of oligochaetes and larval chironomids decreased significantly in response to carp ($F_{2,42} = 4.53$, $p = 0.0165$ and $F_{2,42} = 21.83$, $p < 0.0001$), but were un-

Table 6.3. Mean zooplankton density (animals L^{-1} ± SE) in experimental enclosures stocked with no carp (CON), low carp (LOW), and high carp densities (HI), and in enclosures receiving nutrient additions stocked with no carp (NP), low carp (LOW-NP), and high carp densities (HI-NP). Treatments with the same letters within a row are not significantly different from each other.

Zooplankton density (animals L-1)	N	Treatment					
		CON	LOW	HI	NP	LOW-NP	HI-NP
Total zooplankton	2	6,665±3,171 (a,c)	28,839±7,576 (a,c)	14,823±2,664 (a,c)	27,746±10,699 (a,c)	33,722±21,164 (a,c)	55,669±4,639 (b,c)
Rotifers	2	6,340±3,145 (a)	28,430±7,708 (a)	14,340±2,605 (a)	27,333±10,728 (a)	32,858±21,587 (a)	55,214±4,691 (a)
Nauplii	2	198.3±27.9 (a)	253.7±67.8 (a)	213.1±22.5 (a)	266.2±42.5 (a)	685.2±407.2 (a)	242.0±9.6 (a)
Cladocerans	2	53.7±22.8 (a,b)	50.3±18.8 (b)	115.1±24.5 (a,c)	3.4±2.4 (b,c)	1.9±0.0003 (a)	37.6±28.0 (a,b)
Copepods	2	78.0±24.3 (a)	104.9±46.3 (a,b)	154.5±12.9 (a,b)	144.4±15.5 (a,b)	176.5±16.2 (b)	175.8±14.9 (a,b)

affected by nutrients ($F_{1,42}$ = 0.19, p = 0.6647 and $F_{1,42}$ = 0.81, p = 0.3730) or the interaction between carp and nutrients ($F_{2,42}$ = 1.76, p = 0.1852 and $F_{2,42}$ = 2.30, p = 0.1128; Table 6.1 and Figure 6.2 and 6.3). Similarly, the two chironomid tribes, Chironomini and Tanytarsini, which comprised the bulk of larval chironomids in my samples, decreased significantly in response to carp ($F_{2,42}$ = 19.90, $p < 0.0001$ and $F_{2,42}$ = 23.20, $p < 0.0001$). Post-hoc analysis revealed that oligochaete density was significantly reduced at high carp densities (p = 0.0125), but not at low densities (p = 0.4441) relative to those observed in the carpless treatments (Table 6.4). Total larval chironomid density was significantly reduced at high carp densities ($p < 0.0001$), and at low densities ($p < 0.0001$) relative to densities observed in the carpless treatments, but did not differ significantly from each other (p = 0.5690). This was also the case for the Chironomini and Tanytarsini tribes.

6.1.3.2 *Biomass and composition of emerging chironomids*

Similar to larval chironomid density, the mean biomass of adult chironomids that emerged during the experiment was significantly reduced by carp ($F_{2,57}$ = 8.46, p = 0.0006; Table 6.1 and Figure 6.4). The effects of nutrients and the interaction between carp and nutrients could not be assessed as emerging chironomids were only sampled in one replicate from each treatment, and then pooled according to density of carp stocked. With the exception of the Orthocladinae which were never abundant, the mean biomass of the Chironomidae, Tanypodinae, and Tanytarsini were all significantly reduced by carp ($F_{2,57}$ = 7.07, p = 0.0018, $F_{2,57}$ = 16.72, $p < 0.0001$, and $F_{2,57}$ = 7.95, p = 0.0009). Additionally, post-hoc analysis revealed that total mean chironomid biomass, and the mean biomass of the Tanypodinae and Tanytarsinii were significantly lower at high and

Table 6.4. Mean benthic invertebrate density (animals·m^{-2} ± SE) in experimental enclosures stocked with no carp (CON), low carp (LOW), and high carp densities (HI), and in enclosures receiving nutrient additions stocked with no carp (NP), low carp (LOW-NP), and high car densities (HI-NP). Treatments with the same letters within a row are not significantly different from each other.

Benthic invertebrate density (animals m-2)	N	Treatment					
		CON	LOW	HI	NP	LOW-NP	HI-NP
Oligochaete	2	635.0±233.3 (a,b)	223.9±60.5 (b,c)	119.5±55.0 (c)	324.7±228.1 (b,c)	273.9±82.4 (b,c)	182.5±63.5 (b,c)
Chironomidae	2	72.4±0.5 (a)	8.7±2.3 (b,c)	5.0±0.7 (b)	35.3±15.9 (a,c)	7.4±0.7 (b,c)	5.0±1.0 (b,c)
Chironomini	2	43.8±1.7 (a)	7.0±1.7 (b,c)	2.5±0.2 (b)	22.1±11.0 (a,c)	4.8±0.2 (b,c)	2.7±0.7 (b,c)
Tanytarsini	2	28.6±2.2 (a)	1.7±0.7 (b)	2.5±0.5 (b,c)	13.2±4.8 (a,c)	2.5±0.8 (b,c)	2.3±0.3 (b,c)

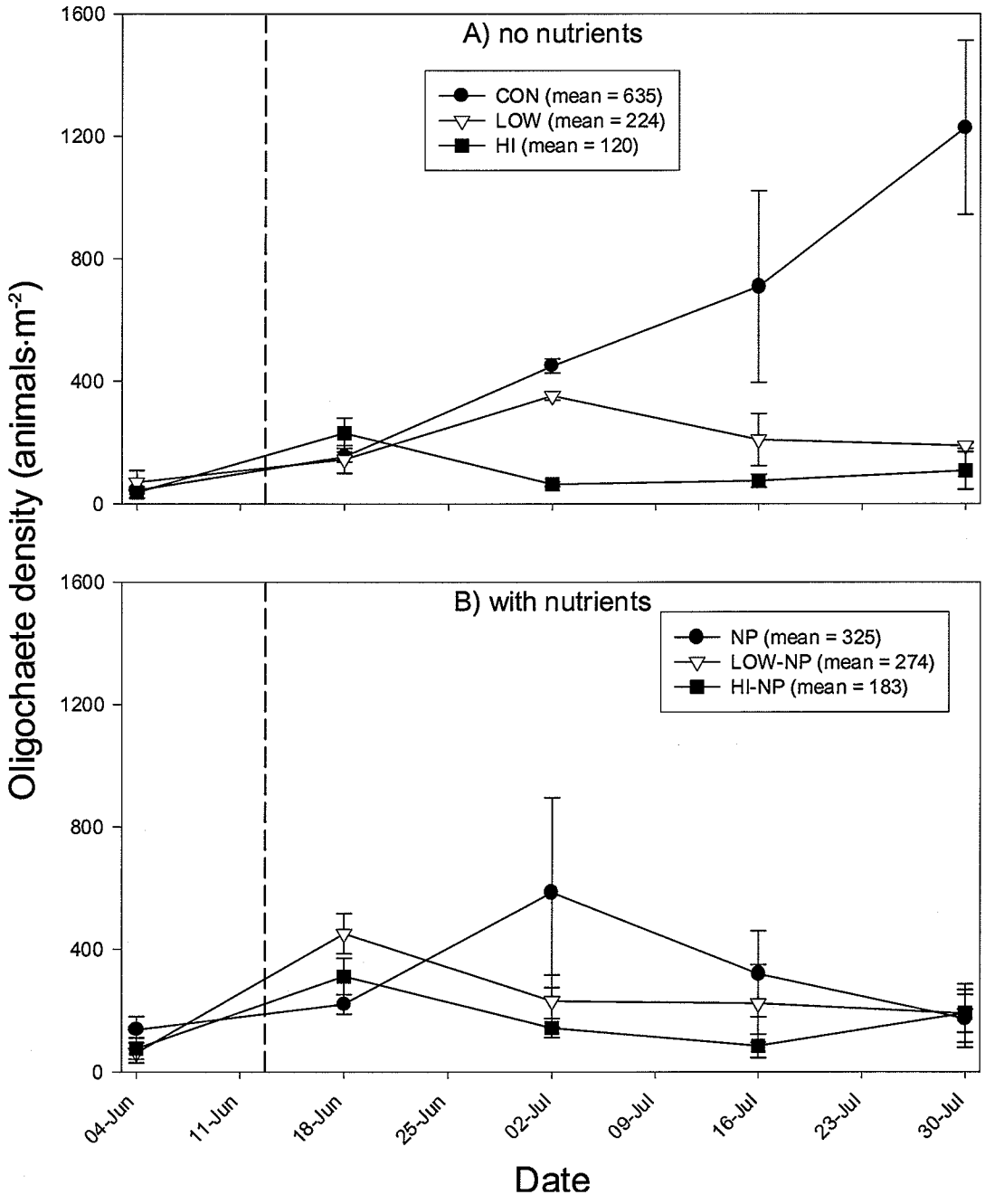

Figure 6.2. Temporal trends in mean oligochaete density (animals·m^{-2}; ±SE; n=2) in enclosures without nutrient amendments (A) and enclosures receiving nutrient additions (B) and stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions and the stocking of enclosures with carp on 13 June, 2002.

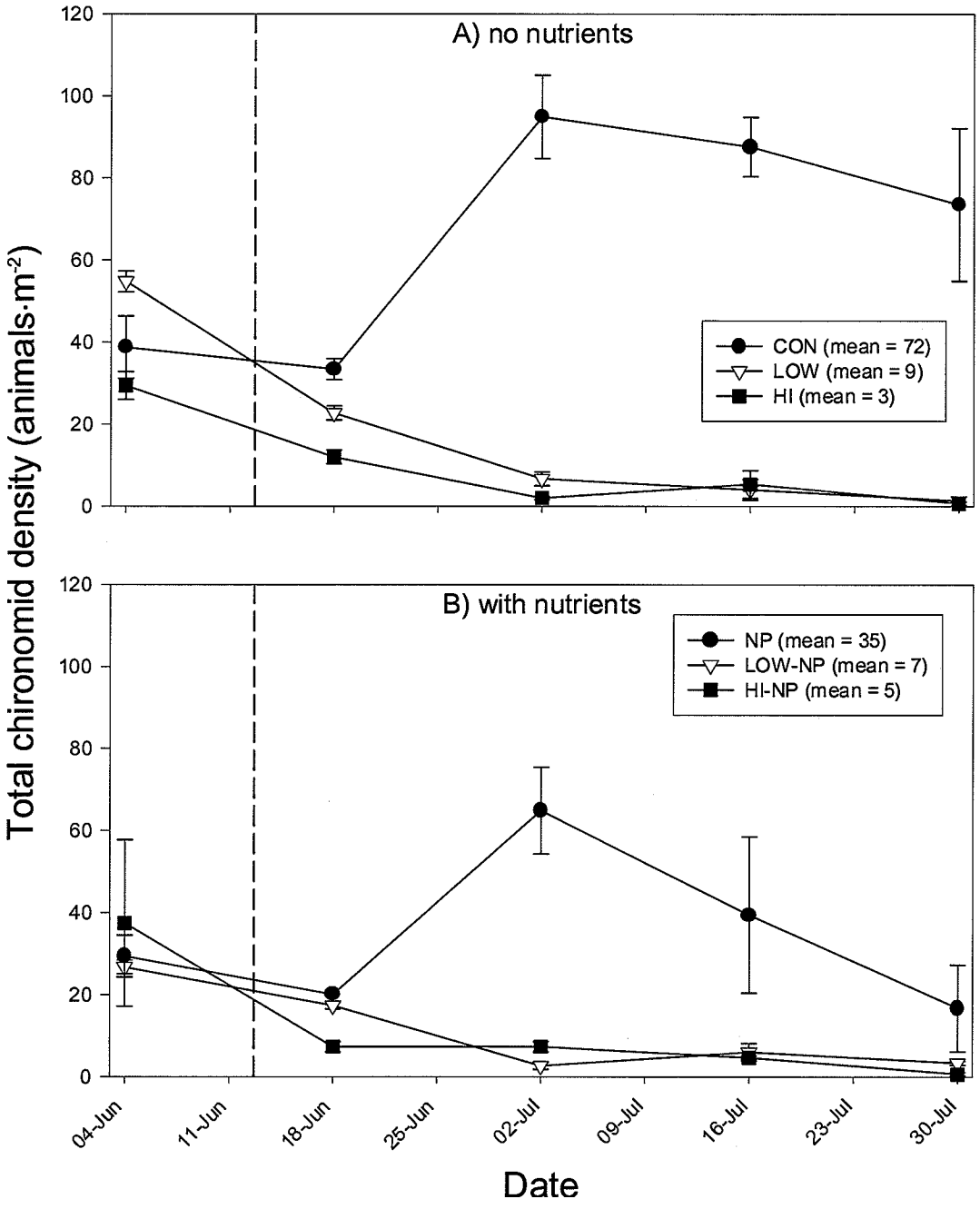

Figure 6.3. Temporal trends in mean chironomid density (animals·m^{-2}; ±SE; n=2) in enclosures without nutrient amendments (A) and enclosures receiving nutrient additions (B) and stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions and the stocking of enclosures with carp on 13 June, 2002.

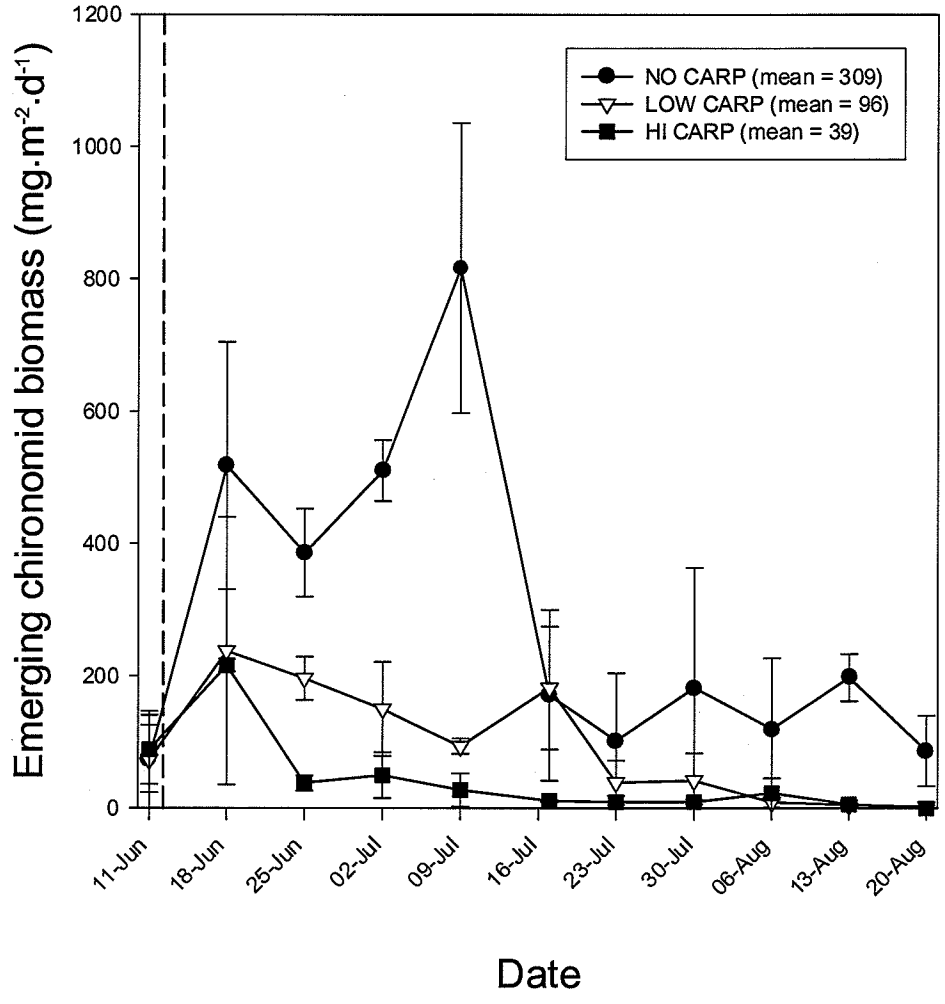

Figure 6.4. Temporal trend in emerging chironomid biomass ($mg \cdot m^{-2} \cdot d^{-1}$; ±SE; n=2) in experimental enclosures stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the stocking of enclosures with carp on 13 June, 2002.

low carp densities, relative to the enclosures without carp, while Chironomidae emerging biomass was only significantly reduced at high carp densities (Table 6.5).

In addition to reducing the biomass of emerging chironomids, carp also appeared to influence the overall composition of the chironomid community. Emerging biomass was largely composed of chironomini at all levels of carp (Figure 6.5). This major taxa consisted mostly of *Chironomus plumosus*. In the absence of carp, the Tanypodinae, consisting mostly of *Tanypus punctipennis*, and the Tanytarsini also comprised a significant portion of the emerging biomass and were generally present throughout the experiment. Conversely, the biomass of these two groups was greatly reduced in the presence of carp, and were virtually completely eliminated at low carp densities four weeks after stocking, and at high carp densities two weeks after stocking (Figure 6.5).

6.1.4 Forage fish populations

Although it was not my intention to include forage fish in the study, seining prior to the beginning of the experiment failed to remove the larval fish that were present. Instead of continuously seining the enclosures, which would have interfered with many of the water quality variables I was monitoring, I decided to leave the forage fish in place. Depletion estimates of the forage fish population size were conducted in each enclosure at the end of the experiment. The abundance of forage fish in the enclosures was not significantly affected by carp ($F_{2,6} = 3.86$, $p = 0.0837$), but was significantly affected by nutrients ($F_{1,6} = 24.07$, $p = 0.0027$) and the interaction between carp and nutrients ($F_{2,6} = 6.93$, $p = 0.0276$; Table 6.1). In the un-fertilized enclosures populations were estimated to be 2528±261, 793±130, 34±8 fish per enclosure in the CON, LOW, and HI treatments, respectively. Although not statistically significant, it is apparent that carp greatly reduced

Table 6.5. Mean biomass of the four major chironomid taxa ($\mu g \cdot m^{-2} \cdot d^{-1}$ ± SE) emerging in experimental enclosures stocked with no carp, low carp, and high carp biomass. Note: only one replicate from each treatment was sampled for emerging chironomid biomass and hence the effect of nutrient additions on emerging biomass cannot be assessed statistically. Treatments with the same letters within a row are not significantly different from each other.

Taxonomic group		Treatment		
	N	CON	LOW	HI
Total chironomids	2	308.9±59.7 (a)	95.5±47.6 (b)	39.0±10.0 (b)
Chironomini	2	253.7±21.2 (a)	83.3±45.1 (a,b)	35.7±8.2 (b)
Tanypodinae	2	42.4±29.3 (a)	10.5±2.1 (b)	3.0±2.0 (b)
Tanytarsini	2	11.8±8.4 (a)	1.2±0.1 (b)	0.0±0.0 (b)
Orthocladinae	2	1.0±0.8 (a)	0.6±0.4 (a)	0.2±0.1 (a)

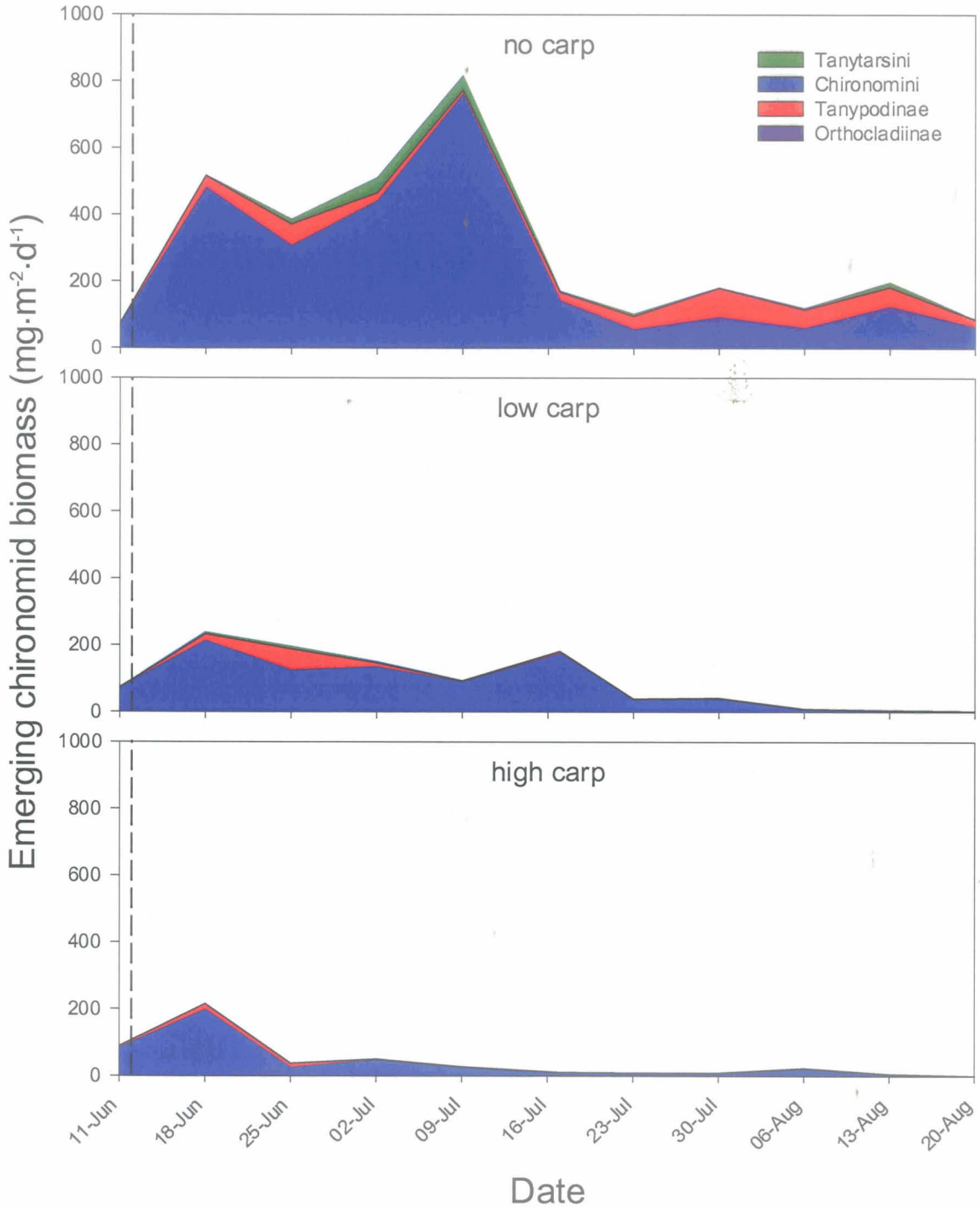

Figure 6.5. Temporal trends in biomass ($mg \cdot m^{-2} \cdot d^{-1}$; ±SE; n=2) and composition of the four major chironomid taxa emerging in enclosures stocked with no carp, low carp, and high carp biomass. Vertical dashed line indicates the start of nutrient additions on 13 June, 2002.

the number of forage fish in the enclosures, and that this decrease was proportional to the biomass of carp stocked. In the fertilized enclosures populations were estimated to be 28±15, 17±1, 97±89 fish per enclosure in the NP, LOW-NP, and HI-NP treatments, respectively.

6.2 Discussion:

6.2.1 Impacts of carp, fertilization and their interactions on phytoplankton biomass and composition

My results clearly indicated that phytoplankton biomass increased with increasing carp densities in the un-fertilized enclosures. Enhancement of phytoplankton biomass was likely the result of increased nutrient availability as a result of carp excretion and sediment resuspension. Andersson *et al.* (1978) found that similar increases in phytoplankton biomass for enclosures stocked with bream and roach at densities similar to those used in my study. Furthermore, Qin & Threkeld (1990) also found that carp enhanced phytoplankton populations, and that this increase occurred whether or not carp had access to sediments, indicating that carp were stimulating phytoplankton growth through physiological processes, such as nutrient excretion. Various other studies have found that dissolved phosphorus concentrations can actually be reduced by benthivorous fish due to scavenging of dissolved phosphorus from the water column by increased sedimentation rates (Keen & Gagliardi 1981, Shormann & Cotner 1997), while many other studies have found that carp significantly increase total phosphorus concentrations (Andersson *et al.* 1978, Shormann & Cotner 1997, Lougheed *et al.* 1998, Angeler *et al.* 2002). Furthermore it has been demonstrated that in addition to reducing nutrient limitation, sediment resuspension can increase phytoplankton biomass by entraining algal

cells from the sediment-water interface into the water column (Head *et al.* 1999, Ståhl-Dalbenko & Hansson 2002). Whether it is through resuspension or physiological processes, it is apparent that carp can significantly enhance algal biomass, and lead to nuisance blooms.

As expected, phytoplankton biomass increased dramatically within enclosures receiving nutrient additions, with the exception of the HI-NP treatment where algal biomass was similar to the biomass recorded in the un-fertilized enclosure stocked with the same density of carp. In the LOW-NP treatment algal biomass appeared to be somewhat higher relative to the NP treatment, likely due to added nutrients being maintained in the water column and therefore available to the phytoplankton as a result of carp induced turbulence. Conversely, mean algal biomass averaged over the course of the experiment in the HI-NP treatment was noticeably lower relative to both NP and LOW-NP treatment, and was similar to the mean biomass calculated for the HI treatment. Based on these results, it appears that at high densities carp can reduce the stimulating effect of nutrients on phytoplankton biomass. This observation has serious implications given the fact that models proposed by Drenner *et al.* (1998) and Drenner *et al.* (1996) suggest that omnivorous fish, such as the common carp, interact synergistically with nutrient loading to increase phytoplankton biomass. These models predict that as nutrient loading increases the impacts of omnivorous fish are multiplied, and likewise low nutrient loading in the presence of omnivorous fish can increase phytoplankton biomass to levels typically attained only at high nutrient loading rates.

My results suggest that there is a threshold biomass above which increases in omnivore or benthivore biomass is no longer capable of interacting synergistically with

nutrient loading, and in fact reduce the influence of nutrients all together, likely as a result of severe light limitation resulting from the combination of increased inorganic suspended solids and phytoplankton-induced turbidity.

Carp also significantly altered the composition of the phytoplankton community. In un-fertilized enclosures, phytoplankton biomass was rarely dominated by a particular algal class or species. However at high carp densities phytoplankton biomass was largely dominated by *Synedra* sp. and *Nitzschia* sp. of the Bacillariophyceae. *Synedra* species are typically planktonic, while *Nitzschia* species are usually benthic in nature. Kyeongsik *et al.* (1999) found that *Synedra* was stimulated by mixing, sediment additions, and nutrient additions. Additionally, Brett & Stuart (1998) found that sediment resuspension could dramatically alter phytoplankton community structure in the water column by entraining benthic algae such as *Nitzschia* species into the water column. This last study also found that after mixing, benthic/meroplanktic genera, such as *Nitzschia*, dominated the phytoplankton community and comprised between 60 and 90% of total phytoplankton numbers. These studies suggest that the dominance of *Synedra* and *Nitzschia* in the un-fertilized high carp density treatment is a result of sediment resuspension which entrains *Nitzschia* cells into the water column and releases *Synedra* from competition due to their ability to thrive in turbulent, light-limited environments. Although *Planktothrix* sp. was also common in the HI treatment it never dominated due to the nutrient poor conditions in the un-fertilized enclosures which would have favoured *Nitzschia* and *Synedra* due to their faster growth rates.

It has been widely cited that when the N:P ratio is low, as was the case in the fertilized enclosures (see section 5.1.1) cyanobacteria such as *Anabaena* and

Aphanizomenon, which can fix atmospheric nitrogen, should dominate (Scheffer *et al.* 1997). However, although cyanobacteria were dominant in the fertilized enclosures they were comprised mostly of *Planktothrix* sp. Additionally, this genus was dominant regardless of carp density. Jensen *et al.* (1994) also found that heterocystous cyanobacteria were not dominant at low TN:TP ratios, but were dominant at low TP (<0.25 mg$\cdot$L^{-1}), while nonheterocystous forms were dominant at TP concentrations between 0.25 and 0.8 mg$\cdot$L^{-1}. Phosphorus concentrations observed in the enclosures correspond well with the dominance of a nonheterocystous cyanobacteria such as *Planktothrix*. Species from this genus are superior competitors in low light situations due to the ability to regulate their position in the water column, possibly explaining there dominance in the fertilized enclosures. Furthermore, *Planktothrix* species are capable of promoting low light conditions by generating a greater amount of turbidity per unit of phosphorus relative to other algae (Scheffer *et al.* 1997). However, this statement seems to contradict the observed decline in the biomass of *Planktothrix* in the HI-NP treatment. One possible explanation for the reduction in *Planktothrix* biomass in the HI-NP treatment is that carp may have reduced water column stability to a point where cyanobacterial growth would have been hindered. This is supported by the findings of Zhang & Prepas (1996), who found that cyanobacteria preferred stable water columns, whereas diatoms were dominant at low water column stability. In addition to explaining the reduction in *Planktothrix* biomass in the HI-NP treatment, reduction in water column stability with increasing carp biomass would also explain the dominance of the Bacillariophyceae at high carp densities in the un-fertilized enclosures, where nutrient concentrations were low.

6.2.2 Impacts of carp, fertilization and their interactions on zooplankton density

Similar to other studies, I found that carp significantly increased the density of rotifers (Qin & Threkeld 1990, Richardson *et al.* 1990, Angeler *et al.* 2002). Contrary to these studies where carp were found to reduce the density of cladocerans, my results indicate that carp increased cladoceran density. The increased density of rotifers in carp treatments is explained by the fact that sediments resuspended by carp inhibit cladoceran populations, but not rotifer populations, thereby favouring rotifer populations (Kirk & Gilbert 1990). This difference in response to suspended sediments arises from the enhanced ability of rotifers to feed selectively, relative to large and small cladocerans (Kirk 1991). The concurrent increase in cladoceran densities with increasing densities of carp is explained by the fact that as carp biomass increased, forage fish populations decreased as a result of larval mortality due to increased sedimentation, which released cladocerans from predation at high carp densities. However, nutrient additions appeared to exert much more control over cladocerans and copepod density, relative to carp. Although carp increased total zooplankton densities, which consisted mostly of rotifers, it is likely that zooplankton biomass was reduced in the presence of carp due to the shift to these small zooplankton forms. A similar increase in density, with subsequent decline in biomass was found by Angeler *et al.* (2002).

6.2.3 Benthic macroinvertebrates

This study supports the results of numerous other studies, which have found that the density of benthic invertebrates was dramatically reduced by common carp (Hruska 1961, Richardson *et al.* 1990, Wilcox & Hornbach 1991, Riera *et al.* 1991, Tatrai *et al.* 1994, Parkos III *et al.* 2003). Although it has been stated that carp prefer Chironomidae and

Oligochaeta (Richardson *et al.* 1990), I found that although the density of Oligochaeta was greater than that of Chironomidae, carp reduced larval chironomids to a greater extent compared to oligochaetes. Additionally, there was no difference in predation between the Chironomini and the Tanytarsini. Furthermore, reductions in larval chironomids corresponded with reductions in emerging adult biomass, indicating that emerging adults were directly regulated through predation of larvae. Unlike predatory fish that depend on visual cues to detect prey, benthivorous fish such as the common carp rely on taste and texture to locate prey (Richardson *et al.* 1990). This is supported by the fact that large chironomid species such as *Chironomus plumosus*, which dominated the biomass, were not reduced at a faster rate than the Tanypodinae and Tanytarsini, which are much smaller. *Chironomus plumosus* is also capable of penetrating deep into the sediments relative to most chironomid species (Hruska 1961). This ability may confer a competitive advantage to this species relative to smaller species such as *Tanypus punctipennis*, which prefer to remain associated with surface sediments where they can move easily and there is an abundant supply of algal cells for consumption (Wrubleski & Rosenberg 1990). Many studies have found that benthic invertebrates such as chironomids play an important role in nutrient cycling (Gardner *et al.* 1981, Covich *et al.* 1999, Hudson *et al.* 1999), and hence reduction through predation by carp could significantly alter nutrient cycling within aquatic ecosystems. Furthermore, based on the dramatic reductions in benthic invertebrates caused by carp in my experiments it is easy to see how carp potentially translocate substantial amounts of nutrients sequestered within the benthic invertebrate community to the water column.

7.0 Conclusions and recommendations

7.1 Hypotheses revisited

Overall, the majority of my hypotheses from Project 1 (effects of carp in large experimental wetland cells) were supported (Table 7.1 – hypotheses 1.1 – 1.4). My results demonstrated clearly that carp significantly increased water column nutrient concentrations, suspended solid concentrations, turbidity, and chlorophyll *a* concentrations. However, my hypothesis that carp would shift the wetland cells from a clear macrophyte-dominated state to a turbid, phytoplankton-dominated state was not supported. A catastrophic shift to the turbid state was likely avoided due to the fact that, although submerged macrophyte growth appeared to decrease with increasing densities of carp, overall submerged macrophyte biomass was greater in the two experimental years when carp were stocked relative to the baseline year. However, increasing densities of carp did appear to reduce submerged macrophyte growth relative to the control cell (although not significantly).

A shift to the turbid state may have been avoided due to the fact that although phytoplankton biomass increased with carp biomass, mean chlorophyll *a* concentrations were usually below 10 $\mu g \cdot L^{-1}$ (25 $\mu g \cdot L^{-1}$ in cells stocked with carp at a density of 1,200 $kg \cdot ha^{-1}$), and never reached levels at which the phytoplankton could have limited the light environment for submerged macrophyte growth. Furthermore, DOC concentrations in the large wetland cells were very high (range 58 – 91 $mg \cdot L^{-1}$) relative to most freshwater systems and would have limited light and therefore phytoplankton biomass. This, combined with the inability of carp to effectively reduce submerged macrophyte biomass

Table 7.1. List of hypotheses for Project 1 and 2 and whether or not results supported these hypotheses. Note: Hypotheses for Project 1 were also assumed to hold true for Project 2.

Hypotheses	Supported (Yes/No)
Hypothesis 1.1. As carp densities increase, water column nutrient concentration will increase as a result of sediment resuspension and excretion.	Yes
Hypothesis 1.2. Increasing densities of carp will cause water column turbidity and concentrations of suspended solids to increase, and submerged macrophyte biomass to decrease due to increased foraging activity of carp.	Yes (partially)
Hypothesis 1.3. Phytoplankton biomass (measured as chlorophyll *a*) will increase with increasing densities of carp due to increased nutrient loading from sediment resuspension and excretion.	Yes
Hypothesis 1.4. At a certain density, carp will impair macrophyte growth and increase water column nutrient concentrations to the point where prolific phytoplankton blooms will occur and result in a switch to the turbid state.	No
Hypothesis 2.1. Phytoplankton biomass in the presence of carp and nutrient additions will be greater than the sum of the independent effects of carp and nutrients on algal biomass. As a result of enhanced phytoplankton biomass, the shift from the clear to the turbid state will be more dramatic and occur earlier relative to treatments receiving only carp or nutrients	No
Hypothesis 2.2. Increasing turbidity and reduced light penetration as a result of carp additions will favour phytoplankton groups adapted for low light conditions such as the cyanobacteria, which can regulate their buoyancy and position in the water column. Additionally, nutrient additions alone will favour algal groups well adapted to high nutrient environments such as the chlorophytes, whereas carp and nutrient treatments will again favour cyanobacteria due to low light conditions.	Yes
Hypothesis 2.3. Zooplankton densities will decrease with increasing carp densities, and community composition will be altered.	No
Hypothesis 2.4. Zoobenthos densities will decrease with increasing carp densities, however in enclosures receiving nutrient additions impacts of carp may be dampened as a result of higher phytoplankton biomass, and hence food resources for the zoobenthos to feed upon.	Yes
Hypothesis 2.5. Total chironomid abundance will decrease as carp density increases due to increased consumption. Additionally, the relative abundance of larger chironomid species will decrease as density increases due to selective feeding by carp.	Yes (partially)
Hypothesis 2.6. The impacts of carp will be much more pronounced in the small enclosures relative to the large wetland cells. Additionally, impacts will accumulate much more quickly in the small enclosures relative to the large wetland cells.	Yes

explains why a catastrophic shift to the turbid state was never triggered at any biomass of carp.

As was the case in Project 1, most of the hypotheses specific to Project 2 (effects of carp in small mesocosms) were supported (Table 7.1 – hypotheses 2.1-2.6). For the most part, the hypotheses from Project 1 were also supported by the results from the small mesocosm experiments. However, my hypothesis that carp would increase dissolved nutrient concentrations in the water column (hypothesis 1.1) was only partially supported by the small mesocosm experiment. As expected, in un-fertilized enclosures, ammonia concentrations increased with carp biomass. However, the highest concentrations of total reactive phosphorus occurred in the control enclosure. Although total reactive phosphorus concentrations did not increase, phytoplankton biomass and chlorophyll *a* concentrations increased significantly with carp biomass. My results indicate that carp were either supplying phosphorus to the phytoplankton in a suspended particulate form and/or that phytoplankton were severely phosphorus limited and any dissolved phosphorus entering the water column as a result of carp was rapidly sequestered into algal cells. Sediment phosphorus concentrations decreased with increasing carp biomass, indicating that carp were contributing significant amounts of particulate phosphorus to the water column. Therefore, it appears that sediment resuspension by carp was an important source of phosphorus for phytoplankton.

In addition to the above-mentioned hypotheses, hypotheses specific to project 2 were also supported for the most part. Small mesocosm experiments clearly demonstrated that carp increased phytoplankton biomass and altered the phytoplankton community structure by favouring phytoplankton species tolerant of low-light conditions. My results

also demonstrated clearly that carp dramatically reduced benthic invertebrate densities. However, my results did not indicate that carp were selectively feeding on larger chironomid species as I had expected. This is likely due to the fact that, *Chironomus plumosus*, which dominated that emerging biomass of adult chironomids, is capable of burrowing deep into the sediments, where it can find shelter from carp. Additionally, my hypothesis regarding the effects of carp on zooplankton density was not supported as carp actually increased the density of zooplankton. Zooplankton density was comprised almost entirely of rotifers who are tolerant of high inorganic suspended solid concentrations. Although zooplankton density increased, it is likely that zooplankton biomass decreased because rotifers are much smaller than most cladocerans.

My hypothesis that carp would interact synergistically with nutrient loading in small mesocosms to increase phytoplankton biomass, as proposed in the models by Drenner *et al.* (1998) and Drenner *et al.* (1996) was not supported. In fertilized enclosures, I found that phytoplankton biomass in the high carp biomass treatments were substantially lower relative to the biomass in the low carp and no carp biomass treatments. Furthermore, phytoplankton biomass in the fertilized enclosures with high carp biomass were similar to those of the un-fertilized enclosures with high carp biomass, indicating that at high carp biomass, the stimulatory effects of nutrient loading on phytoplankton biomass are cancelled out by the light-limiting conditions created by carp. Based on my results I propose a new model explaining the interaction between carp and nutrient loading. Similar to the models proposed by Drenner *et al.* (1998) and Drenner *et al.* (1996), my model predicts that increasing omnivore biomass will increase phytoplankton biomass at an accelerated rate in the presence of high nutrient loading relative to low nutrient

loading. However, my model predicts that at some critical carp biomass (the biomass where the light limiting conditions induced by carp begin to reduce the stimulatory effects of nutrient loading), the synergistic interaction between carp and nutrient loading begins to un-couple due to the very low-light conditions associated with high carp biomass (Figure 7.1).

Results from the large experimental cells suggest that a biomass of approximately 400 $kg \cdot ha^{-1}$ in the wetlands can significantly reduce water quality, by increasing nutrient concentrations and suspended solids concentrations, and reducing dissolved oxygen concentrations. Additionally, it was calculated that at a biomass of 200 $kg \cdot ha^{-1}$, nutrient loading as a result of excretion from carp was similar to external nutrient loading to Lake Manitoba. Clearly carp can significantly impact aquatic ecosystems.

7.2 Comparisons between impacts of carp in large wetland cells vs. small mesocosms

Due to the fact that the large wetland cells and small mesocosms were chemically different from one another, it is difficult to assess whether the size of the experimental system affected the degree to which carp influenced water quality variables. However, total suspended solid concentrations and sedimentation rates were similar in the control treatments regardless of the size of the experimental system, therefore I can assess how enclosure size and carp interact to influence these variables.

Increases in mean TSS associated with the two levels of carp biomass in the small mesocosms were two to four times greater than those observed in the large wetland cells stocked at the same biomass. Similarly, the regressions between carp biomass and

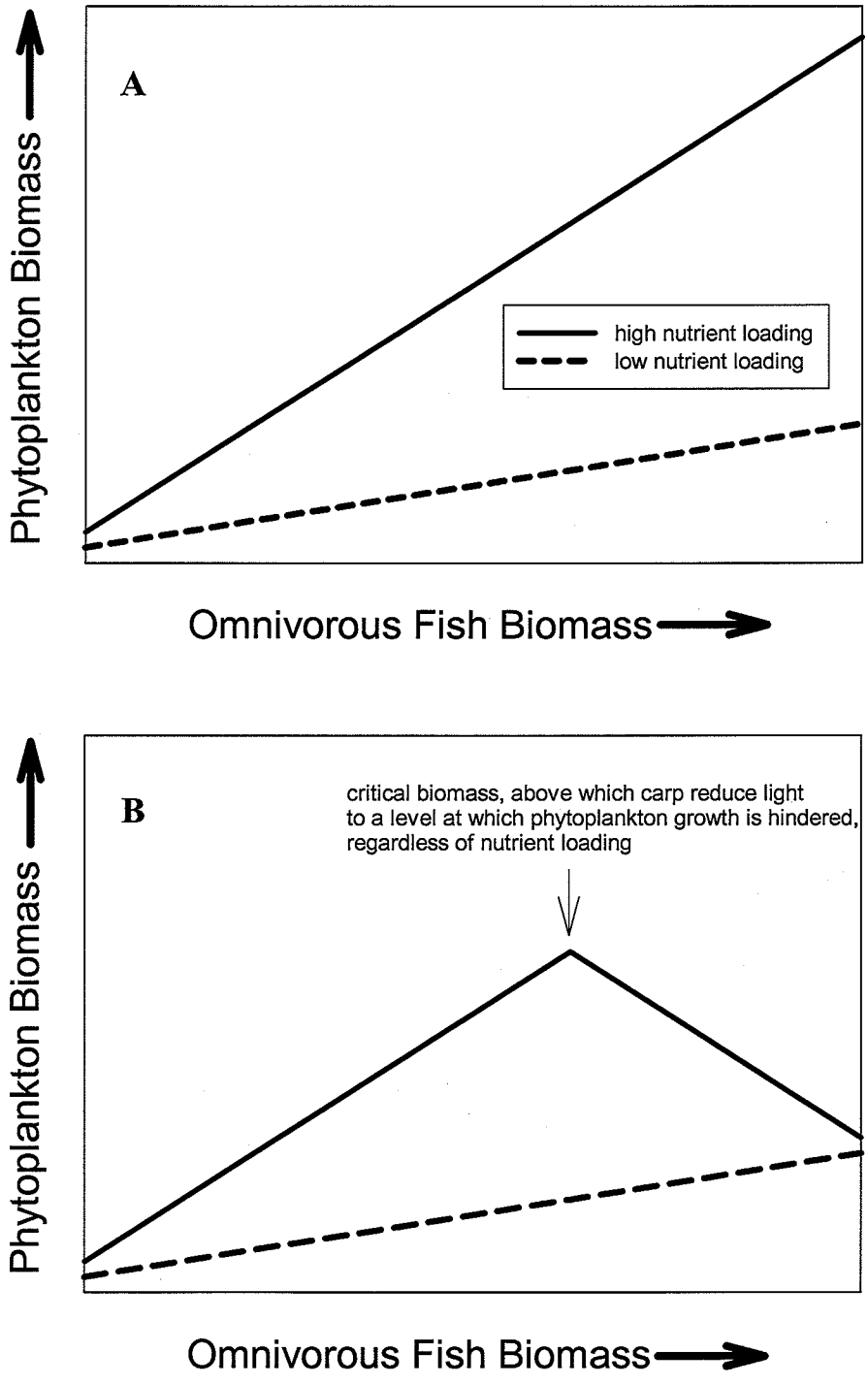

Figure 7.1. Hypothesized synergistic interaction between nutrient loading and omnivorous fish as proposed by Drenner *et al.* (1998) (A) and modified interaction as a result of light limitation cause by some critical biomass of carp (B).

sedimentation rates for large wetland cells (Figure 4.11) and small mesocosms (Figure 5.14) indicated that the rate of increase in sedimentation with increasing carp biomass in the small enclosures was approximately four times greater than the rate for the large cells.

I had hypothesized that carp effects (Hypothesis 2.6) would be magnified in small enclosures relative to large experimental wetland cells, and my results for TSS and sedimentation seem to support this claim. The large experimental wetland cells were likely better at buffering against the impacts of carp activity, relative to the mesocosms, due to their profuse submersed and emergent macrophyte beds which can limit sediment resuspension. This is supported by comparing results from August 2002, where mean submerged macrophyte biomass was 234 $g \cdot m^{-2}$ in the large experimental wetland cell without carp and 47 $g \cdot m^{-2}$ in the small mesocosm enclosures without carp. Turbidity increases exponentially as vegetation coverage decreases (Scheffer 1993), and therefore I suggest that differences in suspended solids and sedimentation rates observed between the large wetland cells and small mesocosms are the result of differences in submerged macrophyte biomass and not size of the experimental system studied.

7.3 Management and future research recommendations

Globally, eutrophication is the largest problem facing freshwater ecosystems, and is particularly damaging in shallow aquatic systems. For the most part, increased cultural eutrophication has been caused by increased nutrient loading, derived from a variety of point and non-point sources of pollution. Although eutrophication resulting in the loss of submerged macrophytes and a shift to the turbid-phytoplankton state is caused by increased nutrient loading, it has often been stated that reductions in external nutrient

loading alone do not allow restoration of the once clear, macrophyte-dominated state (Janse 1997; Scheffer 1990; Sammalkorpi 2000). Scheffer (1990) suggested that biomanipulation, as an additional measure to reductions in nutrient loading, can significantly increase the effectiveness of restoration measures. However, in a review of 18 lakes in the Netherlands, significant improvements in water clarity were only observed after >75% fish reduction (Meijer *et al.* 1999).

Currently, the Province of Manitoba is investigating various scenarios to reduce nutrient loading to Lake Winnipeg in an attempt to improve water quality within the lake. The province has also committed to the partial de-regulation of Lake Manitoba as a measure to restore the health of Delta Marsh and restore water quality within Lake Manitoba. In light of the fact that carp are a dominant fish in both Lake Winnipeg and Lake Manitoba and their associated coastal marshes, it is possible that the above mentioned restoration attempts will be unsuccessful. Based on these facts I have the following recommendations for resource managers and researchers:

7.3.1 Resource managers

1. An intensive investigation should be undertaken to quantify the biomass of carp in Manitoba lakes, with particular emphasis on Lake Winnipeg, Lake Manitoba, and Lake of the Prairies, where carp appear to be particularly abundant. Without accurate estimates of carp density it is impossible to know the true extent to which carp are influencing the health of these systems.

2. Telemetric surveys of carp should be conducted on a series of lakes to determine where carp are overwintering. Due to the fact that carp tend to

congregate in one location during the winter, this information would allow managers to determine where to direct reduction efforts.

3. Once densities of common carp have been determined for various water bodies, and their over-wintering sites have been identified, potential methods of reduction should be investigated, and a method or combination of methods should only be accepted if greater than 75% reduction in population size can be achieved.

7.3.2 Researchers

1. Studies examining the interaction of carp (at densities typical of lakes in Manitoba) with a range of nutrient loading rates known and/or expected to occur in Manitoban watersheds should be investigated to determine how carp may affect restoration attempts through reduction of nutrient loads. This would include determining the critical biomass at which carp negate the stimulatory effects of nutrient loading.

2. Sediments are usually where contaminants such as metals and pesticides accumulate. Due to this fact the impact of carp-induced sediment resuspension on contaminant concentrations and persistence needs to be thoroughly investigated.

3. Given the preliminary information on the northward expansion of the common carp, lakes in northern Manitoba should be monitored periodically to verify if viable populations are becoming established in the north. Furthermore, if carp are found to be invading northern lakes, I suggest a multi-year study be

conducted. This study would examine the differences between northern lakes which are being invaded by carp relative to those that are still carp free. Following carp populations in newly invaded systems over time would allow us to determine at what population size and how long after initial invasion the effects of carp begin to impact aquatic ecosystems.

7.3.3 Public

1. For the most part, the general public is unaware that the common carp is an exotic fish species and that its spread has serious consequences for aquatic ecosystems. Therefore, I would recommend that information plaques be designed and deployed at target areas such as high traffic river walks in the city of Winnipeg. These panels would inform the public that the common carp is an exotic species as well as provide a description of the effects carp can have on aquatic ecosystems and native species. Additionally, these information panels would also warn against using the species as a bait fish to reduce the chances of introduction into additional water bodies.

2. Although carp are thought of as a rough and undersirable fish species in Manitoba, and Canada in general, they are a highly prized recreational species in many parts of Europe. In light of this fact, this species should and could be promoted locally as a viable sport fishing species. This could be accomplished through a series of annual carp fishing tournaments that would be held on various lakes and rivers where carp are known to be abuandant. These events would stimulate the local economy and increase recreational fishing pressure

on carp. Furthermore a portion of the proceeds would be used for carp research and management programs.

3. Many carp are caught along riverways within the city of Winnipeg and are typically returned to the water body in question due to their undesirable nature. Similar to the program currently employed at Lake of the Prairies, the city of Winnipeg could install receptacles at popular recreational fishing locations within the city where carp would be discarded. This material could then be composted and used by the city or sold to the public.

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9.0 Appendix A: Young-of-the-year carp length-weight relationship

Periodically throughout the course of the experiments conducted in the MERP cells in 2001 and 2002 young-of-the-year carp were sampled using Beamish traps deployed over a 24-hour period to construct a length-weight relationship specifically for YOY carp in Delta Marsh, and Lake Manitoba. Additionally, based on the size of the young-of-the-year carp caught in Beamish traps, I was able to assess whether carp were spawning all at once or if there were multiple spawning events.

Table A1. Length and weight data for young-of-the-year common carp gathered in the MERPcells during the summers of 2001 and 2002. Specific cells and dates were recorded for carp sampled in 2002 only.

Location	Date	Length (cm)	Weight (g)
Merp C6	Jul-9-2002	2.2	0.2
Merp C6	Jul-9-2002	2.3	0.2
Merp C6	Jul-9-2002	2.5	0.3
Merp C6	Jul-9-2002	2.0	0.1
Merp C6	Jul-9-2002	1.6	0.1
Merp C6	Jul-9-2002	2.4	0.2
Merp C6	Jul-9-2002	2.5	0.3
Merp C6	Jul-9-2002	1.5	0.1
Merp C3	Jul-10-2002	3.6	1.1
Merp C3	Jul-10-2002	2.1	0.2
Merp C3	Jul-10-2002	3.5	0.8
Merp C3	Jul-10-2002	4.1	1.3
Merp C3	Jul-10-2002	2.7	0.4
Merp C3	Jul-10-2002	3.3	0.6
Merp C3	Jul-10-2002	3.0	0.5
Merp C3	Jul-10-2002	3.4	0.7
Merp C2	Jul-11-2002	5.0	2.8
Merp C2	Jul-11-2002	4.4	1.6
Merp C2	Jul-11-2002	4.5	2.0
Merp C2	Jul-11-2002	4.6	2.0
Merp C2	Jul-11-2002	4.8	2.1
Merp C2	Jul-11-2002	4.5	1.8
Merp C2	Jul-11-2002	4.4	1.6
Merp C2	Jul-11-2002	4.5	1.6
Merp C2	Jul-11-2002	3.4	0.7
Merp C2	Jul-11-2002	2.0	0.1
Merp C6	Jul-16&17-2002	2.1	0.2
Merp C6	Jul-16&17-2002	2.1	0.1
Merp C6	Jul-16&17-2002	2.3	0.2
Merp C6	Jul-16&17-2002	2.4	0.2
Merp C6	Jul-16&17-2002	2.5	0.2
Merp C6	Jul-16&17-2002	2.5	0.2
Merp C6	Jul-16&17-2002	2.5	0.3
Merp C6	Jul-16&17-2002	2.6	0.3
Merp C6	Jul-16&17-2002	3.3	0.6
Merp C6	Jul-16&17-2002	3.5	0.8
Merp C6	Jul-16&17-2002	3.5	0.7
Merp C6	Jul-16&17-2002	3.7	1.1
Merp C6	Jul-16&17-2002	3.7	0.9
Merp C6	Jul-16&17-2002	3.7	0.9
Merp C6	Jul-16&17-2002	4.0	1.3
Merp C6	Jul-16&17-2002	4.1	1.3
Merp C6	Jul-16&17-2002	4.3	1.4
Merp C6	Jul-16&17-2002	4.3	1.3
Merp C6	Jul-16&17-2002	4.5	1.7
Merp C6	Jul-16&17-2002	4.5	1.5
Merp C6	Jul-16&17-2002	4.5	1.7
Merp C6	Jul-16&17-2002	4.5	1.6
Merp C6	Jul-16&17-2002	4.5	1.8
Merp C6	Jul-16&17-2002	4.5	1.6
Merp C6	Jul-16&17-2002	4.6	1.8
Merp C6	Jul-16&17-2002	4.8	2.2
Merp C6	Jul-16&17-2002	4.8	2.0
Merp C6	Jul-16&17-2002	5.0	2.3
Merp C6	Jul-16&17-2002	5.0	2.5
Merp C6	Jul-16&17-2002	5.1	2.8
Merp C6	Jul-16&17-2002	5.2	2.7
Merp C6	Jul-16&17-2002	5.4	3.6
Merp C3	Jul-23-2002	7.8	8.4
Merp C3	Jul-23-2002	7.0	6.5
Merp C3	Jul-23-2002	5.0	2.5
Merp C3	Jul-23-2002	3.1	0.9
Merp C3	Jul-23-2002	8.2	10.6
Merp C3	Jul-23-2002	8.3	10.7
Merp C3	Jul-23-2002	7.1	8.0
Merp C3	Jul-23-2002	2.2	0.1
Merp C3	Jul-24-2002	8.4	10.9
Merp C3	Jul-24-2002	7.0	6.6
Merp C3	Jul-24-2002	5.3	3.0
Merp C3	Jul-24-2002	9.4	16.7
Merp C3	Jul-24-2002	8.6	12.6
Merp C3	Jul-24-2002	3.5	0.8
Merp C3	Jul-24-2002	4.0	1.2
Merp C3	Jul-24-2002	2.6	0.3
Merp C3	Jul-24-2002	5.6	3.5
Merp C3	Jul-25-2002	8.6	14.1
Merp C3	Jul-25-2002	5.5	3.6
Merp C3	Jul-25-2002	5.5	3.4
Merp C3	Jul-25-2002	2.3	0.2
Merp C3	Jul-25-2002	1.3	0.0
Merp C2	Jul-31-2002	5.7	3.1
Merp C2	Jul-31-2002	5.1	2.3
Merp C2	Jul-31-2002	2.2	0.1
Merp C2	Jul-31-2002	7.0	6.8
Merp C2	Jul-31-2002	8.0	9.6
Merp C2	Jul-31-2002	3.4	0.7
Merp C2	Jul-31-2002	5.6	3.3
Merp C2	Jul-31-2002	5.1	2.5
Merp C2	Jul-31-2002	3.2	0.6
Merp C2	Jul-31-2002	5.0	2.1
Merp C2	Jul-31-2002	5.4	2.9
Merp C2	Jul-31-2002	3.6	0.7
Merp C2	Jul-31-2002	4.8	1.9
Merp C2	Jul-31-2002	3.8	0.8
Merp C2	Jul-31-2002	4.0	1.1
Merp C2	Jul-31-2002	3.4	0.6
Merp C2	Jul-31-2002	3.5	0.8
Merp C6	Aug-2-2002	8.2	9.9
Merp C6	Aug-2-2002	5.4	2.9
Merp C6	Aug-2-2002	3.1	0.5
Merp C6	Aug-2-2002	6.5	5.0
Merp C6	Aug-7-2002	9.0	14.7
Merp C6	Aug-7-2002	7.1	6.8
Merp C6	Aug-7-2002	2.6	0.4
Merp C5	Aug-13-2002	6.6	5.1
Merp C5	Aug-13-2002	4.3	1.4
Merp C5	Aug-13-2002	4.5	1.5
Merp C5	Aug-13-2002	3.5	0.7
Merp C5	Aug-13-2002	2.4	0.2
Merp C5	Aug-14-2002	6.2	3.9
Merp C5	Aug-14-2002	1.9	0.1
Merp C5	Aug-14-2002	2.1	0.2
Merp C5	Aug-14-2002	2.1	0.2
Merp C5	Aug-14-2002	2.8	0.5
Merp C3	Aug-15-2002	9.5	14.7
Merp C3	Aug-15-2002	3.0	0.5
Merp C3	Aug-15-2002	2.2	0.2
Merp C3	Aug-15-2002	9.2	14.2
Merp C3	Aug-15-2002	10.8	23.5
Merp C3	Aug-15-2002	2.7	0.3
Merp C3	Aug-15-2002	5.3	2.7
Merp C3	Aug-15-2002	9.1	13.0
Merp C3	Aug-15-2002	5.6	3.1
Merp C2	Aug-21-2002	6.4	4.2
Merp C2	Aug-21-2002	6.3	4.1
Merp C2	Aug-21-2002	6.6	4.6
Merp C2	Aug-21-2002	6.6	5.5
Merp C2	Aug-21-2002	2.8	0.3
Merp C2	Aug-21-2002	4.1	1.3
Merp C2	Aug-21-2002	5.0	2.0
Merp C2	Aug-21-2002	3.3	0.6
Merp C2	Aug-21-2002	3.9	0.9
Merp C2	Aug-21-2002	3.0	0.4
Merp C2	Aug-21-2002	2.8	0.4
Merp C3	Aug-21-2002	2.8	0.3
Merp C3	Aug-21-2002	10.8	23.9
Merp C3	Aug-21-2002	7.5	8.2
Merp C3	Aug-21-2002	10.2	19.9
Merp C3	Aug-21-2002	2.2	0.3
Merp C3	Aug-21-2002	11.0	23.2
Merp C3	Aug-21-2002	3.7	1.0
Merp C3	Aug-21-2002	2.8	0.4
Merp C3	Aug-21-2002	2.0	0.2
Merp C6	Aug-21-2002	2.7	0.4
Merp C6	Aug-21-2002	2.7	0.4
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Merp C6	Aug-21-2002	8.0	9.1
Merp C6	Aug-21-2002	2.4	0.2
Merp C6	Aug-21-2002	9.2	14.1
Merp C6	Aug-21-2002	8.9	12.4
Merp C6	Aug-21-2002	8.9	12.1
Merp C6	Aug-21-2002	2.7	0.4
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Merp Cells	summer 2001	2.1	0.3
Merp Cells	summer 2001	2.2	0.2
Merp Cells	summer 2001	2.3	0.2
Merp Cells	summer 2001	2.5	0.5
Merp Cells	summer 2001	2.5	0.4
Merp Cells	summer 2001	2.7	0.3
Merp Cells	summer 2001	2.8	0.5
Merp Cells	summer 2001	2.9	0.5
Merp Cells	summer 2001	3.7	0.9
Merp Cells	summer 2001	4.0	1.2
Merp Cells	summer 2001	4.5	2.0
Merp Cells	summer 2001	4.5	1.8
Merp Cells	summer 2001	4.7	2.2
Merp Cells	summer 2001	4.8	2.3
Merp Cells	summer 2001	4.9	2.4
Merp Cells	summer 2001	4.9	2.3
Merp Cells	summer 2001	5.0	2.9
Merp Cells	summer 2001	5.1	3.3
Merp Cells	summer 2001	5.2	3.0
Merp Cells	summer 2001	5.4	3.1
Merp Cells	summer 2001	5.5	4.4
Merp Cells	summer 2001	5.5	3.4
Merp Cells	summer 2001	5.6	4.0
Merp Cells	summer 2001	6.0	5.0
Merp Cells	summer 2001	6.0	4.5
Merp Cells	summer 2001	6.0	3.9
Merp Cells	summer 2001	6.2	5.0
Merp Cells	summer 2001	6.3	5.4
Merp Cells	summer 2001	6.5	5.5
Merp Cells	summer 2001	6.5	5.9
Merp Cells	summer 2001	6.5	6.0
Merp Cells	summer 2001	6.7	6.3
Merp Cells	summer 2001	6.7	5.9
Merp Cells	summer 2001	6.8	6.7
Merp Cells	summer 2001	6.8	6.6
Merp Cells	summer 2001	6.8	6.8
Merp Cells	summer 2001	7.0	7.6
Merp Cells	summer 2001	7.0	7.5
Merp Cells	summer 2001	7.0	8.3
Merp Cells	summer 2001	7.1	7.8
Merp Cells	summer 2001	7.2	7.5
Merp Cells	summer 2001	7.2	8.0
Merp Cells	summer 2001	7.2	7.5
Merp Cells	summer 2001	7.5	9.3
Merp Cells	summer 2001	7.5	9.6
Merp Cells	summer 2001	7.7	10.9
Merp Cells	summer 2001	8.0	11.5
Merp Cells	summer 2001	8.2	12.0
Merp Cells	summer 2001	8.5	14.6
Merp Cells	summer 2001	8.5	13.3
Merp Cells	summer 2001	8.5	12.5
Merp Cells	summer 2001	8.5	13.1
Merp Cells	summer 2001	8.5	12.5
Merp Cells	summer 2001	9.0	16.0
Merp Cells	summer 2001	9.0	14.3
Merp Cells	summer 2001	9.2	17.3
Merp Cells	summer 2001	9.2	16.2
Merp Cells	summer 2001	9.9	20.0
Merp Cells	summer 2001	10.2	24.5
Merp Cells	summer 2001	10.3	22.6
Merp Cells	summer 2001	10.5	26.4
Merp Cells	summer 2001	10.5	26.2
Merp Cells	summer 2001	11.0	29.9
Merp Cells	summer 2001	12.5	44.5
Merp Cells	summer 2001	13.2	46.0

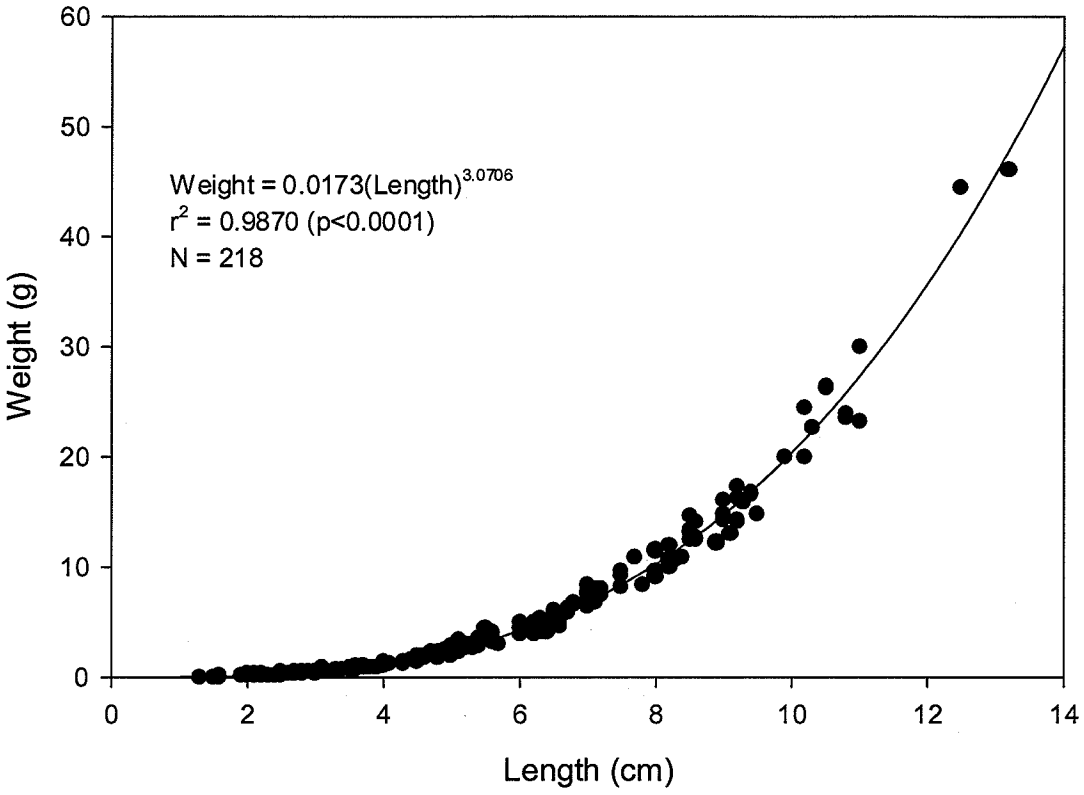

Figure A1. Length-weight relationship for young-of-the-year carp sampled in the MERP cells during the 2001 and 2002 open-water season.

10.0 Appendix B: Carp nutrient excretion experiments

To estimate the nutrient loading resulting from carp additions in the MERP cells I conducted a series of nutrient excretion experiments in 2002.

10.1 Methods

Nutrient excretion experiments were conducted between July and August 2002 using individual adult and juvenile carp. In total, experiments were conducted on 21 individual carp that ranged in size from 6 to 62 cm (fork length), and from 4.38 to 4450 g. Adult carp were captured using various fishing methods such as gillnets and or dip-netting in areas where adult carp tended to congregate. Juvenile carp were captured using Beamish traps. Collections occurred between 1030 and 1400 h. All carp were held in filtered lake water for one hour before being used in excretion experiments. This holding time was chosen based on the results of Lamarra (1975), who found that carp excreted nutrients at abnormally high rates during the first hour of captivity. After the acclimation period young-of-the-year carp (< 30 g wet weight) were placed in Erlenmeyer flasks ranging in size from 1 to 3.5 L. Adult and juvenile carp (>100 g wet weight) were placed in large plastic tubs (60 L capacity). All experimental flasks were filled with filtered lake water while the large plastic tubs were filled with raw lake water.

Immediately after being placed in the experimental flask or tubs, an initial water sample (125 mL) was collected. Subsequent water samples were collected at 1 and 2 hours after the beginning of the experiment at which time dissolved oxygen

concentrations were also measured using a YSI model 52 dissolved oxygen meter. All water samples were analyzed for ammonia nitrogen and total reactive phosphorus using the methods described in Section 3.1.5. When excretion experiments were conducted using large fish in large tubs, water samples were also collected from fish-free control tubs to insure that the containers did not influence nutrient concentrations. Gross excretion of ammonia-nitrogen and total reactive phosphorus was calculated as the difference in concentrations measured at the end of the excretion experiments (after 2 hours) relative to the initial concentrations. As in the study by Mather *et al.* (1995), cumulative gross excretion was divided by the mass of the experimental carp and time to obtain excretion rates expressed as milligrams of ammonia-nitrogen or total reactive phosphorus per kilogram wet mass per hour. Expressing the excretion rates in this way allowed all excretion data to be compared regardless of fish biomass and the volume of water used in the experiments. Aeration was not used over the course of the excretion experiments as carp are known to thrive in low oxygen environments. Of the 23 individual experiments conducted, dissolved oxygen concentrations were only reduced to levels below 3 $mg \cdot L^{-1}$ in seven of the experiments. However, at no time did any of the carp in the experiments appear agitated and increased ventilation rates were never observed. After each excretion experiment carp were released into Lake Manitoba. Water temperatures used in the experiments varied substantially, so all excretion rates were corrected to 20°C using the temperature correction factor for converting respiratory rates provided in Winberg (1956).

10.2 Results and Discussion

NH_3-N excretion in carp ranged between 2.4 and 30.5 $mg \cdot kg^{-1} \cdot h^{-1}$, and TRP excretion rates ranged between 0.08 and 5.75 $mg \cdot kg^{-1} \cdot h^{-1}$ (Table B1). The relationships relating mass specific excretion rates of NH_3-N and TRP to the wet weight of carp indicate that smaller fish excreted more nitrogen and phosphorus per unit biomass relative to larger fish. The mass specific phosphorus excretion rates were comparable to those measured in carp by Lamarra (1975), and nitrogen excretion rates were similar to those of other omnivorous fish such as gizzard shad (Schaus *et al.* 1997).

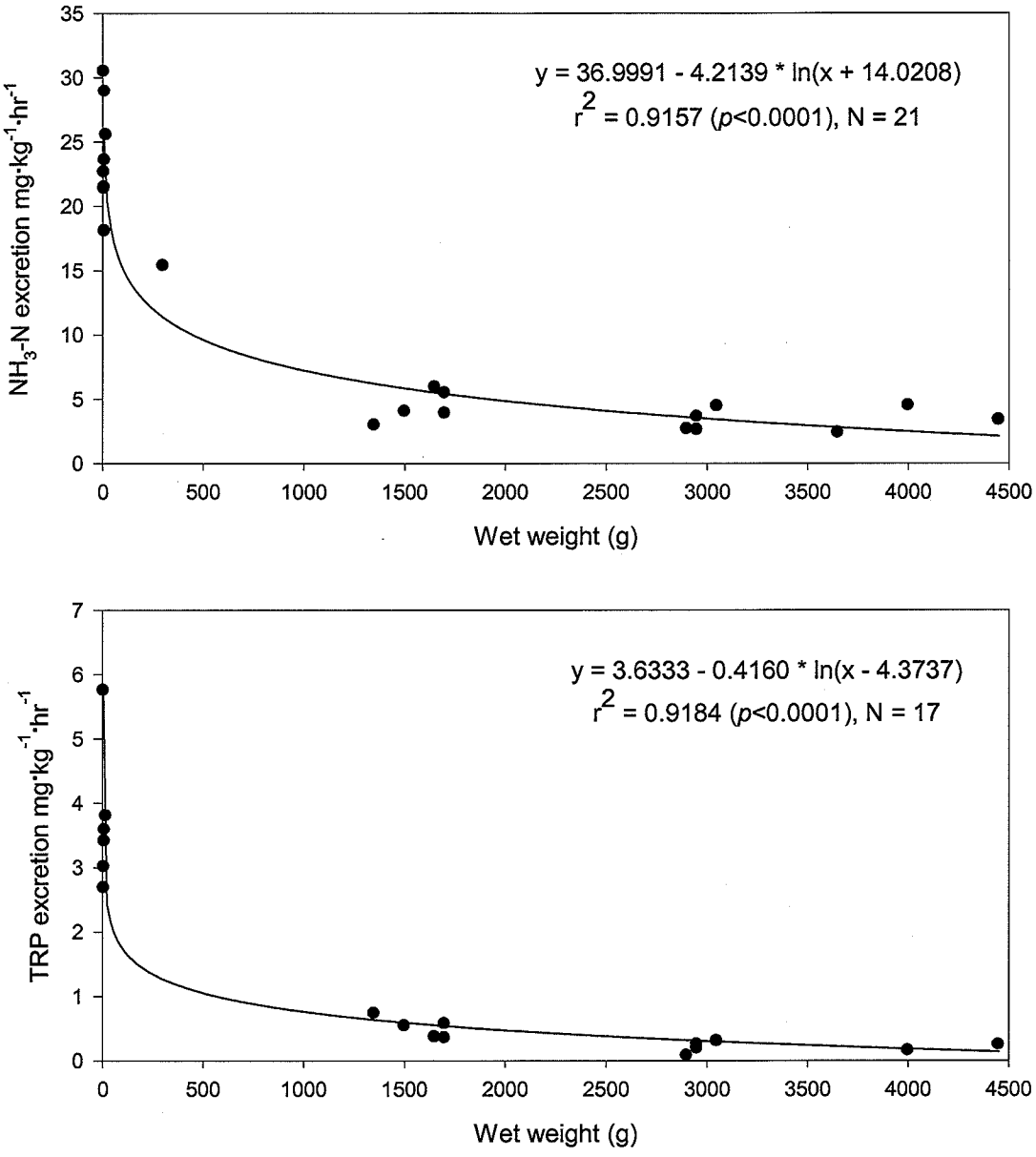

Figure B1. Ammonia and total reactive phosphorus excretion curves for carp collected in 2002

Table B1. Oxygen consumption and nutrient excretion results, corrected to 20°C, for individual carp tested in 2002.

Date	Initial volume (L)	Length (cm)	Weight (g)	Average temperature (°C)	q (correction factor)	O_2 consumption (mg/kg/hr @ 20 °C)	NH3-N excretion rate (mg/kg/hr @ 20 °C)	TRP-P excretion rate (mg/kg/hr @ 20 °C)
13-Aug-02	0.925	6.0	4.38	19.1	1.090	380	30.5	5.75
13-Aug-02	0.925	6.5	5.00	19.0	1.090	330	22.7	2.69
13-Aug-02	0.925	6.9	5.85	19.0	1.090	451	21.4	3.02
31-Jul-02	1.575	7.5	6.87	23.5	0.717	321	21.5	analytical error
13-Aug-02	0.925	7.7	9.13	19.1	1.090	350	28.9	3.59
31-Jul-02	1.575	7.9	8.51	23.5	0.779	287	23.6	analytical error
11-Jul-02	1.575	8.0	8.98	22.5	0.779	252	18.1	3.42
11-Jul-02	3.075	10.6	15.40	22.3	0.847	285	25.6	3.81
28-Aug-02	51.925	25.5	300	15.3	1.570	336	15.4	analytical error
26-Aug-02	51.925	43	1500	15.0	1.570	111	4.1	0.54
28-Aug-02	51.925	43	1350	15.8	1.433	141	3.0	0.73
31-Jul-02	51.925	46	1700	14.5	1.740	126	3.9	0.58
26-Aug-02	51.925	46	1650	15.1	1.570	142	5.9	0.37
31-Jul-02	51.925	47	1700	14.4	1.740	142	5.5	0.35
14-Aug-02	51.925	55	2950	16.6	1.310	104	2.6	0.25
14-Aug-02	51.925	55	2950	16.7	1.310	110	3.6	0.19
27-Aug-02	51.925	56	3050	15.9	1.433	132	4.5	0.30
14-Aug-02	51.925	56	2900	16.5	1.310	101	2.7	0.08
8-Aug-02	51.925	57	3650	18.1	1.200	31	2.4	2.15
8-Aug-02	51.925	62	4000	18.4	1.200	76	4.5	0.16
8-Aug-02	51.925	62	4450	18.8	1.090	63	3.4	0.24

*analytical errors occurred when blanks were higher than samples