A STUDY OF WATER QUALITY, ZOOPLANKTON AND MACROPHYTES IN WETLANDS OF THE CANADIAN GREAT LAKES BASIN: IMPLICATIONS FOR THE RESTORATION OF COOTES PARADISE MARSH.

By

VANESSA L. LOUGHEED, B.Sc.

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AUTHOR: Vanessa L. Lougheed, B.Sc. (McMaster University)

SUPERVISOR: Dr. Patricia Chow-Fraser

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GENERAL ABSTRACT

The overall objective of this study was to provide information on the ecology of coastal wetlands of the Great Lakes. Very little is known regarding the ecology of these highly productive and unique ecosystems. In particular, the aim was to assess the restoration of Cootes Paradise Marsh (via carp exclusion) by looking at zooplankton and how they are affected by water quality and habitat structure. Sixty additional marshes in the Great Lakes basin were visited to assess the quality of Cootes Paradise relative to these wetlands and to provide wetland managers throughout the basin with a large database with which to compare the restoration and degradation of other threatened marsh habitats.

This study describes how aquatic macrophytes and lower trophic levels are affected by water and sediment quality and how wetland quality is influenced by 2 major anthropogenic stressors: land-use and carp. Ultimately, an index (WZI) was developed using the zooplankton community as indicators to aid in the assessment of wetland quality. Because the database we used to develop the index included wetlands from all four Canadian Great Lakes, including a diverse range of wetland quality, wetland types and geomorphological settings, it should be widely applicable across the Great Lakes basin.

Detailed comparisons of water quality, macrophyte and zooplankton communities showed that there were significant improvements in wetland quality observed in shallow and protected areas of Cootes Paradise Marsh following carp exclusion; however, open and exposed sites remained unchanged and the quality of this coastal marsh was low to moderate relative to high quality marshes existing elsewhere in the Great Lakes basin. Carp exclusion alone was not responsible for these observed changes, and therefore, further remedial actions will be required to increase the functional capacity of this degraded coastal wetland.

PREFACE

The following Ph.D. thesis consists of manuscripts that are published or will be submitted for publication in peer-reviewed journals. Chapters 1 and 2 have been published in The Canadian Journal of Fisheries and Aquatic Sciences. The remaining chapters are being prepared for submission to peer reviewed scientific journals.

The following are the proper citations for these papers, including co-authorship. Besides my supervisor, Dr. Patricia Chow-Fraser, Chapters 2 and 5 were also co-authored by Barb Crosbie (M.Sc.). I wrote all these manuscripts; however, I extracted information on land use and macrophyte distributions for one-third (22 out of 62) of the wetlands covered in these 2 chapters from B. Crosbie's M.Sc. thesis (Crosbie 1997; McMaster University, Dept. of Biology).

Lougheed, V.L. and P. Chow-Fraser. (1998) Factors that regulate the zooplankton community structure of a turbid, hypereutrophic Great Lakes wetland. Can. J. Fish. Aquat. Sci. 55: 150-161.

Lougheed, V.L., B. Crosbie and P. Chow-Fraser. (1998) Predictions on the effect of carp exclusion on water quality, zooplankton and submergent macrophytes in a Great Lakes wetland. Can. J. Fish. Aquat. Sci. 55: 1189-1197.

Lougheed, V.L. and P. Chow-Fraser. Spatial variability in the response of lower trophic levels after biomanipulation in a freshwater marsh.

Lougheed, V.L., B. Crosbie and P. Chow-Fraser. Role of natural environmental variability and anthropogenic stressors in structuring the macrophyte community in 62 marshes across the Great Lakes basin.

Lougheed, V.L. and P. Chow-Fraser. Development and use of a zooplankton index to monitor wetland quality in the Great Lakes basin.

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Finally, I'd like to thank Chad & Chewie for always listening, the "Bank of Mom" for financial support, Don for always making too much breakfast, the fish lab for always eating lunch and Cootes Paradise for always being there (43°N, 79°W).

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GENERAL INTRODUCTION

Wetlands

In Canada, wetlands have been defined as:

> "land that is saturated with water long enough to promote wetland or aquatic processes as indicated by poorly drained soils, hydrophytic (i.e. water-loving) vegetation, and various kinds of biological activity which are adapted to a wet environment (National Wetlands Working Group 1988)."

There are a multitude of similar definitions in the literature (see Tiner 1999). All definitions are equally general by virtue of the great diversity of wetland types (e.g. prairie pothole marshes, Great Lakes coastal marshes, boreal bogs and fens, arctic muskegs, wet meadows, evergreen swamps, coastal salt marshes) with highly variable hydrologies and plant communities.

Hydrology is the most important factor determining the type of wetland formed, as well as the abiotic and biotic characteristics of the wetland. In particular, it influences plant species composition, primary productivity, erosion and deposition of sediment, export of organic material and nutrient cycling (see reviews by Keough et al. 1999; Sharitz and Batzer 1999). For example, soil chemistry changes as rising water levels change soils from oxic to anoxic. When waterlogged soils become anoxic, chemical reduction increases the availability of nutrients in the soil such as nitrogen (through denitrification) and phosphorus (through hydrolysis of ferric and aluminum phosphates) (Sharitz and Batzer 1999).

The structural characteristics of the plant community are also highly influenced by hydrology and can be described by general vegetation zones (Figure i-1) extending from the upland boundary lakeward to depths of approximately 2 meters. More obligate hydrophytic species such as submergent and emergent macrophytes dominate permanently and semi-permanently flooded areas, while landward areas contain facultative species that occur in both wetlands and non-wetlands (i.e. trees and shrubs). Natural seasonal and year-to-year fluctuations in water level help to maintain the structural and species diversity of the plant community and are a defining characteristic of wetland environments (Minc 1997; Sharitz and Batzer 1999).

Permanently, semi-permanently and seasonally flooded areas such as marshes and swamps are the wettest wetland environments. Marshes are dominated by non-woody emergent aquatic plants (grow with stems partly in and partly out of the water), with interspersed areas of submersed and floating-leaf vegetation in deeper water. These vegetation types thrive on more extreme water level fluctuations. Swamps are dominated by woody plants (i.e. trees and shrubs) and are often flooded for at least part of the year. Conversely, saturated and seasonally saturated wetlands such as bogs and fens may have little evidence of standing water, but the water table is at or near the land surface for much of the growing season. Bogs are characterized by the build-up and decomposition of plant material forming a floating mat of peat, with evergreen trees and shrubs often growing in more landward areas. Fens are also peatlands, found in more nutrient-rich areas, that contain herbaceous emergent vegetation and some shrubs (Niering 1989; Tiner 1999).

The primary differences between wetlands and more open water environments are: the occurrence of water level fluctuations (including periodic drying), lower rates of decomposition, higher rates of primary production and the dominance of primary productivity by aquatic vegetation as opposed to algae. In flowing water environments, wetlands provide areas of reduced flow rate which has important consequences for sediment attenuation and chemical gradients. Furthermore, wetlands are generally shallow environments that do not stratify and that freeze to the bottom in winter (Sharitz and Batzer 1999).

Freshwater wetlands occur across a range of hydrogeomorphic conditions (Sharitz and Batzer 1999) and can be divided into 3 broad classes (riverine, lacustrine and palustrine) depending on flow characteristics and residence time. Riverine wetlands are located along flowing water channels (i.e. rivers and streams). Their inflows and thus water levels are highly influenced by variable precipitation within their drainage basin. Lacustrine wetlands are usually found within lakes, and therefore tend to be less affected by flowing water. They often contain lakeward areas of deeper water. Palustrine wetlands are often found upland of riverine and lacustrine wetlands, and are protected from riverine and lacustrine processes such as flow rate and wave action. In the Great Lakes there are also wetlands classified as 'estuarine' and 'connecting channels' which generally are affected to differing degrees by both riverine and lacustrine processes (Minc 1997; Chow-Fraser and Albert 1999).

Wetlands are valuable ecosystems that provide a variety of important ecological functions such as protection from wave action and flood waters, as well as sediment attenuation and nutrient uptake. This functional capacity is highly dependent on the structural diversity and percent cover of aquatic vegetation. The presence of aquatic macrophytes reduces the flow velocity of water entering the wetland, thereby allowing the deposition of sediment. This can improve clarity and removes nutrient- and contaminant-laden sediment from the water column. Aquatic vegetation may also reduce nutrient levels directly via uptake for growth. Wetlands are also areas of exceptional biodiversity that provide habitat for a variety of terrestrial and aquatic organisms and provide excellent opportunities for research, education and recreation (Maynard and Wilcox 1997).

The Great Lakes and their coastal wetlands

The Laurentian Great Lakes basin spans nine degrees latitude and nineteen degrees longitude (1200 km from west to east) and lies within 1 Canadian province and 8 U.S. states (Figure i-2). The Great Lakes contain 20% of the earth's freshwater and are among the world's 12 largest lakes. As such, they contain many habitats unique to the world including Great Lakes coastal wetlands. Although all part of the same watershed, each Great Lake has unique features related to differences in latitude, population, land use, residence time, depth and bedrock (Table i-1).

Because of this geographical expanse, the Great Lakes consist of diverse physical environments, variable with respect to both climate and geomorphology (Smith et al. 1991; Minc 1997). Regional differences have important consequences for human settlement and land use patterns, with the most productive agricultural land and larger urban centers occurring south of the 46th parallel (Environment Canada and U.S. Environmental Protection Agency 1995). The largest populations and greatest proportions of agricultural land are found in L. Erie, L. Michigan and L. Ontario basins (Table i-1), while the upper lakes (L. Huron and L. Superior) have substantially smaller populations and less human development.

The Great Lakes are only about 10, 000 years old, their present-day physiography and soils sculpted by the retreat of the Wisconsin glacier. The upper lakes and St. Lawrence river are underlain by the Canadian Shield, consisting of Precambrian igneous and metamorphic rocks. The southern portion of the Great Lakes was submerged beneath shallow seas during the Paleozoic period, and consequently this area is composed of sedimentary rocks such as shale, limestone, sandstone and dolomite.

The distinct geomorphic characters of the Great Lakes shoreline, including substrate, soils, slope and drainage condition, are responsible for generating a variety of unique wetland types and distinguish Great Lakes coastal wetlands from more inland systems (Chow-Fraser and Albert 1999). In the upper lakes there tends to be fewer riverine and embayed wetlands, and a greater number of wetlands exposed to the lake (Smith et al. 1991) because the older, igneous and metamorphic bedrock in L. Superior and Georgian Bay (L. Huron) results in a deeper and more exposed shoreline. Conversely, the soft sedimentary rock underlying the lower lakes provides expansive areas of shallow water and fine-textured substrates favorable to marsh development (Minc 1997). Coastal wetlands generally are formed where shoreline geomorphic characteristics provide protection from wind and wave action: behind barrier beaches, protective sand bars and man-made dikes, and in bays, river-mouths and flooded river deltas. Open shoreline wetlands, formed by fringes of aquatic plants that are tolerant to wave energy, also form in more exposed locations (Maynard and Wilcox 1997). Each of these wetland hydrogeomorphic types theoretically can develop distinct ecosystem properties and biotic communities (Keough et al. 1999).

Hydrologically, Great Lakes coastal wetlands are influenced by large-lake processes such as such as wind and wave action, as well as both seasonal and long-term fluctuations in water level (Maynard and Wilcox 1997; Keough et al. 1999). Plant communities are very dynamic in coastal marshes because they experience extreme water level fluctuations. In low water years, macrophyte species intolerant of drying (i.e. submergents) are replaced by emergent species germinating from seeds, while in high water years dominant emergents like cattails (*Typha* spp.), which might otherwise form monocultures, are replaced by submergents and floating-leaf taxa (Keddy and Reznicek 1986) (Figure i-3). These fluctuations in Great Lakes water levels tend to cycle over an 8-10 year cycle (e.g. Chow-Fraser 1999). Fluctuations over the longer term help determine the upland boundary of the marsh, while shorter term fluctuations such as seiches determine the nature of the communities in the active zone. Marshes are the most common type of Great Lakes coastal wetland, because their diversity of vegetation thrives on the water level fluctuations that occur in the Great Lakes (Keddy and Reznicek 1986; Smith et al. 1991); however, the upper lakes contain a substantial proportion of swamp and fen habitats in palustrine zones or protected bays (Smith et al. 1991).

U.S. versus Canadian shoreline

Across the Great Lakes landscape, there are a great variety of geomorphological characteristics and consequently, substantial among- and within-lake variety of wetland hydrogeomorphic site types. Because of this variability and because of the Canadian focus of this thesis, there are some key differences worth mentioning between U.S. and Canadian shorelines. In particular, by not sampling the U.S. shoreline we have missed sampling diked wetlands, dune and swale wetlands, as well as 2 large unique embayments: Green Bay (WI, MI) and Saginaw Bay (MI). For a more detailed examination of this topic, including definitions of terms, see Chow-Fraser and Albert (1999).

In Lakes Ontario and Erie, wetlands on the U.S. shoreline tend to be either barrier beaches (L. Ontario) or diked wetlands (L. Erie), while wetlands on the Canadian shore are located primarily in rivermouths and protected embayments. Similarly, Canadian wetlands of L. Huron are largely protected embayments and rivermouths, while there are a greater proportion of dune and swale wetlands in the U.S. waters. The U.S. shoreline of L. Huron is also home to Saginaw Bay (MI). As the only large protected embayment this far south, the vegetation assemblages found here are likely unique to the Great Lakes. Similarly, the wetlands of Green Bay, a large embayment of L. Michigan, contain unique vegetation characteristics existing along a gradient of degradation from the degraded lower bay to the more pristine upper bay. L. Michigan, the only lake entirely within U.S. borders, also contains a relatively large representation of dune and swale, delta and sand-spit wetlands. Finally, the north and south shorelines of L. Superior are also very different. The geomorphology of the south (U.S.) shore of Lake Superior is more diverse and, in many parts less exposed, than the northern Canadian shoreline. As a result, there is a greater variety of wetland types in the U.S., including barrier beaches and dune and swale wetlands, while northern shoreline wetlands on the Canadian shore are largely protected embayments.

Wetland degradation

Recently, governments in both Canada and the United States have become alarmed at the accelerated loss and degradation of wetlands in the Great Lakes basin, particularly in the highly developed lower Great Lakes region. Historically, the primary cause of wetland loss was drainage and infilling to accommodate growing agricultural and urban needs along the shoreline of the lakes. Heavily settled areas of the lower Great Lakes region have lost a large proportion of both coastal (Whillans 1982) and inland (see Detenbeck et al. 1999) wetlands. At present, the remaining wetlands are at risk from factors related to human settlement such as water level regulation, non-point source pollution from urban and agricultural land use, disturbance by exotic species such as common carp (*Cyprinus carpio*) and internal loading of nutrients (e.g. Keddy and Reznicek 1986; Chow-Fraser et al. 1998; Crosbie and Chow-Fraser 1999; Detenbeck et al. 1999; Mayer et al. 1999).

The regulation of water levels in the Great Lakes for shipping purposes, most apparent in L. Ontario, has generally reduced the occurrence of alternating flooded and dry conditions and therefore has resulted in the dominance of woody plants and monocultures of *Typha*, as well as the loss of species that regenerated from seed during low water levels (Keddy and Reznicek 1986). In particular, sustained high water levels have resulted in reduced areal cover of emergent vegetation in some L. Ontario coastal marshes (e.g. Chow-Fraser 1998).

The remaining disturbance factors (i.e. land use, carp activity and internal loading) have important consequences for the light environment. While plants that have the majority of their growth at or above the surface of the water (e.g. emergent plants) tend to be affected by water level changes, submersed plants that live entirely in the water column are affected primarily by reductions in water clarity. Light available for macrophyte growth may be reduced by algal biomass, periphytic growth and non-algal turbidity (Phillips et al. 1978, Brönmark and Weisner 1995; Skubinna et al. 1995). With increasing light stress, macrophytes use stored energy reserves more quickly than they produce them. Eventually the light received and required for photosynthesis is not sufficient to compensate for respiration and plants gradually disappear (Phillips et al. 1978).

As reviewed by Carpenter et al. (1998), non-point source pollution due to urban and agricultural run-off is one of the primary causes of surface water degradation in North America. Both nutrient and sediment levels have been shown to increase significantly in aquatic systems surrounded by developed land areas (Johnson et al. 1997; Crosbie and Chow-Fraser 1999) because of factors such as: erosion from exposed soils in agricultural fields; reduced cover of vegetation, especially along riparian zones; run-off from impervious urban surfaces and construction sites during storm events; agricultural fertilizer use and livestock wastes; as well as logging (Maynard and Wilcox 1997; Carpenter et al. 1998).

In a study of wetlands in the lower Great Lakes basin, Crosbie and Chow-Fraser (1999) found a direct link between land use impacts, water quality impairment and reduced aquatic plant diversity; however, no basin-wide studies have been completed to determine the role of hydrogeomorphic factors in this relationship. In particular, characteristics of coastal wetlands such as exposure to wind and wave action and mixing with lake water (Chow-Fraser 1999; Botts 1999) may moderate land use effects.

The common carp (*Cyprinus carpio*) is an exotic benthivorous fish from Eurasia which was introduced to North American waters in the early 1800s and stocked into the Great Lakes in the 1870s (Mills et al. 1993). The physical destruction of submersed macrophyte beds by the bottom-feeding and spawning activities of carp is well documented (Robel 1962; Crivelli 1983); however, the indirect effects of carp activity on water quality are not as well understood. The presence of mixed communities of benthivorous fish has been shown to reduce water clarity via feeding- or spawning-related sediment resuspension (Meijer et al. 1990; Qin and Threlkeld 1990; Richardson et al. 1990; Breukelaar et al. 1994) and, in some studies, the presence of benthivores was also found to increase nutrient and/or algal levels (Meijer et al. 1990; Breukelaar et al. 1994; Cline et al. 1994). There are, however, no studies that can be directly applied to the situation in the Laurentian Great Lakes where managers of coastal wetlands are implementing large-scale, extremely costly and unproven carp exclusion restoration techniques (e.g. Cootes Paradise in L. Ontario; Metzger Marsh in L. Erie) (Wilcox and

Whillans 1999) with the hopes of improving water clarity and promoting the growth of submersed aquatic vegetation. Due to the scarcity of research on these wetlands and the multitude of possible disturbance factors degrading them, it is unclear what impact carp removal will have on water clarity and submergent plant growth.

Recent attempts in ecosystem restoration through the bi-national Great lakes Remedial Action Plans (see Krantzberg et al. 1997) have provided the opportunity to formally test biomanipulation and restoration theories in individual Great Lakes coastal wetlands. However, given the diversity of wetland hydrogeomorphic types in the Great Lakes basin, applying lessons learned from rehabilitating individual wetlands to all other wetland types may be inappropriate. We need to understand what differentiates wetlands throughout the basin with respect to primary stressors (e.g. land use, carp), the macrophyte community, as well as hydrogeomorphic and climatic effects.

Effects of wetland degradation on zooplankton

Because of their position in aquatic food webs, providing a vital link between primary producers and higher trophic levels, zooplankton are crucial to the overall functioning of aquatic ecosystems. They are affected by both top-down and bottom-up processes; therefore, any variations in nutrient availability, algal growth and planktivore or piscivore abundance, can potentially have important consequences for the zooplankton community.

Many fish species use Great Lakes coastal wetlands for part, if not all, of their life cycle (e.g. Jude and Pappas 1992). Given the high productive capacity of coastal wetlands relative to pelagic environments, connectedness between these two habitats likely provides migrating fish taxa with access to abundant prey items, as well as spawning and nursery habitat (e.g. Jude and Pappas 1992). In particular, zooplankton are an important dietary item to the fish community, especially for larval stages (e.g. Leslie and Moore 1985). Consequently, any changes that restrict access to these wetlands, or otherwise render them unsuitable habitat for the fish or zooplankton communities may have wide-ranging repercussions on the Great Lakes ecosystem.

In addition to this crucial role in energy transfer, zooplankton may also affect the availability of nutrients and primary production. Hansen et al. (1997) illustrated that, in moderately eutrophic systems, the zooplankton community may periodically contribute to the growth of algae by regeneration of nutrients or to the decline in algae via grazing. In shallow, eutrophic European lakes, large-bodied zooplankton have been shown to increase water clarity via grazing on algae (Timms and Moss 1984; Schriver et al. 1995), whereas smaller-bodied animals are less efficient grazers of phytoplankton (Gliwicz 1990). Hence, successful aquatic food web biomanipulation often requires promoting the growth of large populations of these large and efficient zooplankton grazers to initiate clearing of the water column (e.g. Moss et al. 1996).

Despite these pivotal roles, very little research has been carried out on the ecology of these invertebrates in Great Lakes coastal wetlands. Any suggestions regarding the influence of habitat differences, environmental quality or among-lake variability on the zooplankton community of these wetlands, or regarding the relationship between zooplankton and the migratory and resident fish populations are largely speculative. In fact, Krieger (1992) stated:

> "Given the paucity of information on invertebrate ecology in Great Lakes coastal wetlands, research on almost any aspect of their ecology will significantly advance our state of knowledge about these communities."

When I began this research in May 1994, there had been few published studies on zooplankton in Great Lakes wetlands. Krieger and Klarer (1991) had described how the zooplankton taxa in a degraded, sparsely vegetated L. Erie wetland were distinct from those in the lake itself and Krieger (1992) pooled the species lists from several previously unpublished reports to illustrate the considerable variability present among the zooplankton in Great Lakes wetlands. More recently, other authors have looked at the zooplankton in relatively pristine sites in L. Huron (Cardinale et al. 1998; Gathman et al. 1999) and L. Erie (Botts 1999). Within each of these wetlands, factors such as the presence of aquatic vegetation, distance from open water, the flushing action of storm events and chemical gradients have been suggested as possible factors influencing marsh zooplankton ecology. However, these papers were largely descriptive in nature with very little emphasis on water and habitat quality. Consequently, there is insufficient information to evaluate the effects of wetland degradation and restoration on the lower trophic levels, or to develop relevant zooplankton indicators of wetland quality.

The presence of macrophytes in Great Lakes coastal wetlands likely plays a pivotal role in the provision of habitat to both aquatic and terrestrial organisms; however, there are little data to support this assertion. Similarly, there are a scarcity of reports describing how the macrophyte community changes with wetland quality. Several authors have recorded changes in the marsh vegetation over time at individual Great Lakes coastal marshes, especially those in the settled areas of L. Erie and L. Ontario (e.g. Crowder and Bristow 1986; Klarer and Millie 1992; Chow-Fraser et al. 1998; Lundholm and Simser 1999). However, except for the strong structuring effects of fluctuating water levels that affect year-to-year changes in areal cover of emergent vegetation (Keddy and Reznicek 1986; Klarer and Millie 1992; Chow-Fraser et al. 1998), other underlying factors have rarely been investigated, especially at a basin-wide scale (Smith et al. 1991; Minc 1997; Crosbie and Chow-Fraser 1999). The most comprehensive studies (e.g. Minc 1997) are not published in an easily accessible form, although they provide valuable insights on the importance of hydrogeomorphology and latitude in structuring the macrophyte community in the Great Lakes.

Thesis objectives

Quantitative knowledge of the ecological functions provided by wetlands is lacking; in particular, very little research has been carried out on the ecology of invertebrates in wetland ecosystems. The overall objective of this study was to provide much needed information on the ecology of coastal wetlands of the Great Lakes. In particular, the aim was to assess the restoration of Cootes Paradise Marsh (via carp exclusion) by looking at zooplankton and how they are affected by water quality and habitat structure. Sixty additional marshes in the Great Lakes basin were visited to assess the quality of Cootes Paradise relative to these wetlands and to provide wetland managers throughout the basin with a large database with which to compare the restoration and degradation of other threatened marsh habitats.

Chapter 1 summarizes results from a 2-year survey of the zooplankton community in Cootes Paradise Marsh prior to carp exclusion. The primary goal was to determine if zooplankton communities in coastal wetlands were structured by similar factors as zooplankton in lake ecosystems. These baseline data were used to: 1) generate recommendations for the monitoring program that will be used to evaluate the success of the remedial actions in Cootes Paradise; 2) to formulate predictions for the marsh-wide carp exclusion; and, 3) to allow comparison with the post-exclusion zooplankton community.

Chapter 2 describes results from carp enclosure experiments designed to examine the relationship between carp biomass, water quality, zooplankton and submerged macrophytes in Cootes Paradise Marsh. The primary objective of this paper was to provide a basis for improved decisions about wetland restoration and carp management in the Great Lakes by determining the impact of a different carp biomass levels on the water quality of wetlands, and, therefore, what proportion and/or size of carp must be removed to achieve desired improvements in water clarity and submergent plant growth

Chapter 3 evaluates the response of Cootes Paradise Marsh to carp exclusion using data on zooplankton, phytoplankton and water quality collected for 2 years prior to carp exclusion and 2 years post exclusion. The primary goal of this study was to evaluate the relative importance of carp removal as a forcing variable in triggering the switch to the clear-water state from the turbid state for degraded coastal marshes, and to examine the effectiveness of carp exclusion as a restoration strategy. From previous work (Chapter 1) documenting extreme site-to-site variations with respect to water turbidity and the plankton community, we predicted that the response to carp exclusion would be spatially variable.

Chapter 4 compares the macrophyte community composition of 62 wetlands in the Canadian portion of the Great Lakes basin to examine how water and sediment quality affect the taxonomic composition and community structure of the macrophyte community and relate these to land use in their watershed. The goals of this study were to: 1) determine the relative importance of environmental and hydrogeomorphic factors in structuring the aquatic macrophyte community at a basin-wide scale, 2) confirm the published observations of Crosbie and Chow-Fraser (1999) that showed wetland water quality and submergent plant species richness are affected by surrounding land use and, 3) use these data to illustrate how the macrophyte community in Cootes Paradise Marsh responded to carp exclusion.

Chapter 5 describes the development and use of an index based on water quality and observed associations of zooplankton with aquatic vegetation that can be used to assess the quality of wetlands across the Great Lakes basin. We collected information from 60 wetlands, ranging in quality from pristine to highly degraded, that were located along the shoreline or within the basin of the four Canadian Great Lakes. The main goals of this study were to 1) develop a zooplankton index that could be used to assess wetland quality across the Great Lakes basin, 2) assess the strength of this index relative to other measures of zooplankton community structure and, 3) use this index to assess the response of the zooplankton community in Cootes Paradise Marsh to carp exclusion as a restoration technique (see Chapter 3).

Table i-1: Selected physical and developmental characteristics of the Laurentian Great Lakes (modified from Environment Canada and U.S. Environmental Protection Agency 1995).

	Superior	Michigan	Huron	Erie	Ontario
Elevation (m)	183	176	176	173	74
Max. Depth (m)	406	282	229	64	244
Volume (km^3)	12,100	4,920	3,540	484	1,640
Water area (km^2)	82,100	57,800	59,600	25,700	18,960
Land Drainage Area (km^2)	127,700	118,000	134,100	78,000	64,030
Retention Time (years)	191	99	22	2.6	6
Population:					
U.S. (1990)	425,548	10,057,026	1,502, 687	10,017,530	2,704,284
Canada (1991)	181,573	-	1,191,467	1,664,639	5,446,611
Basin land use (1985):					
Agricultural (%)	3	44	27	67	39
Residential (%)	1	9	2	10	7
Forest (%)	91	41	68	21	49
Other (%)	5	6	3	1	5

Figure i-1: Characteristic vegetation zonation of Great Lakes coastal wetlands (from Minc 1997).

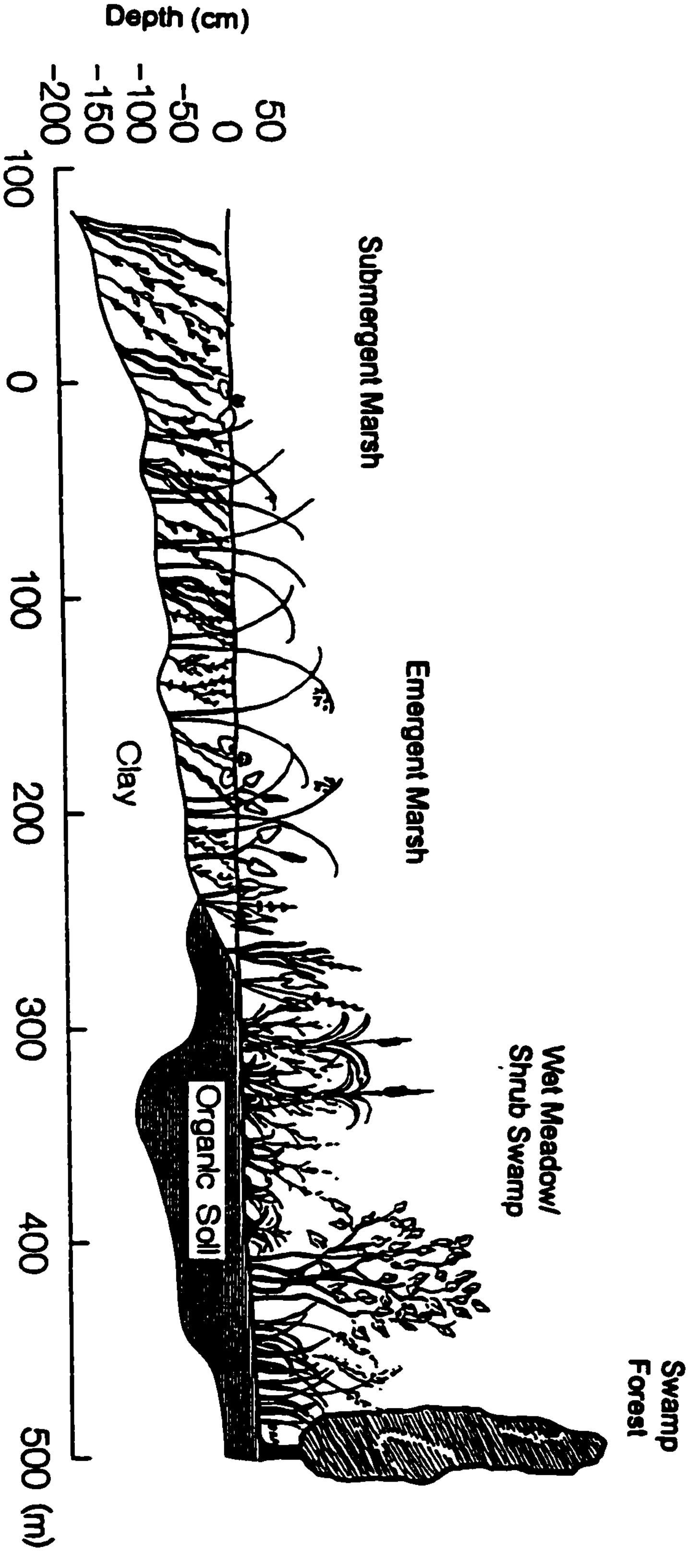

Depth (cm)
50
0
-50
-100
-150
-200
100
0
100
200
300
400
500 (m)
Submergent Marsh
Emergent Marsh
Wet Meadow/
Shrub Swamp
Swamp
Forest
Clay
Organic Soil

Figure i-2: The Laurentian Great Lakes (from Minc 1997).

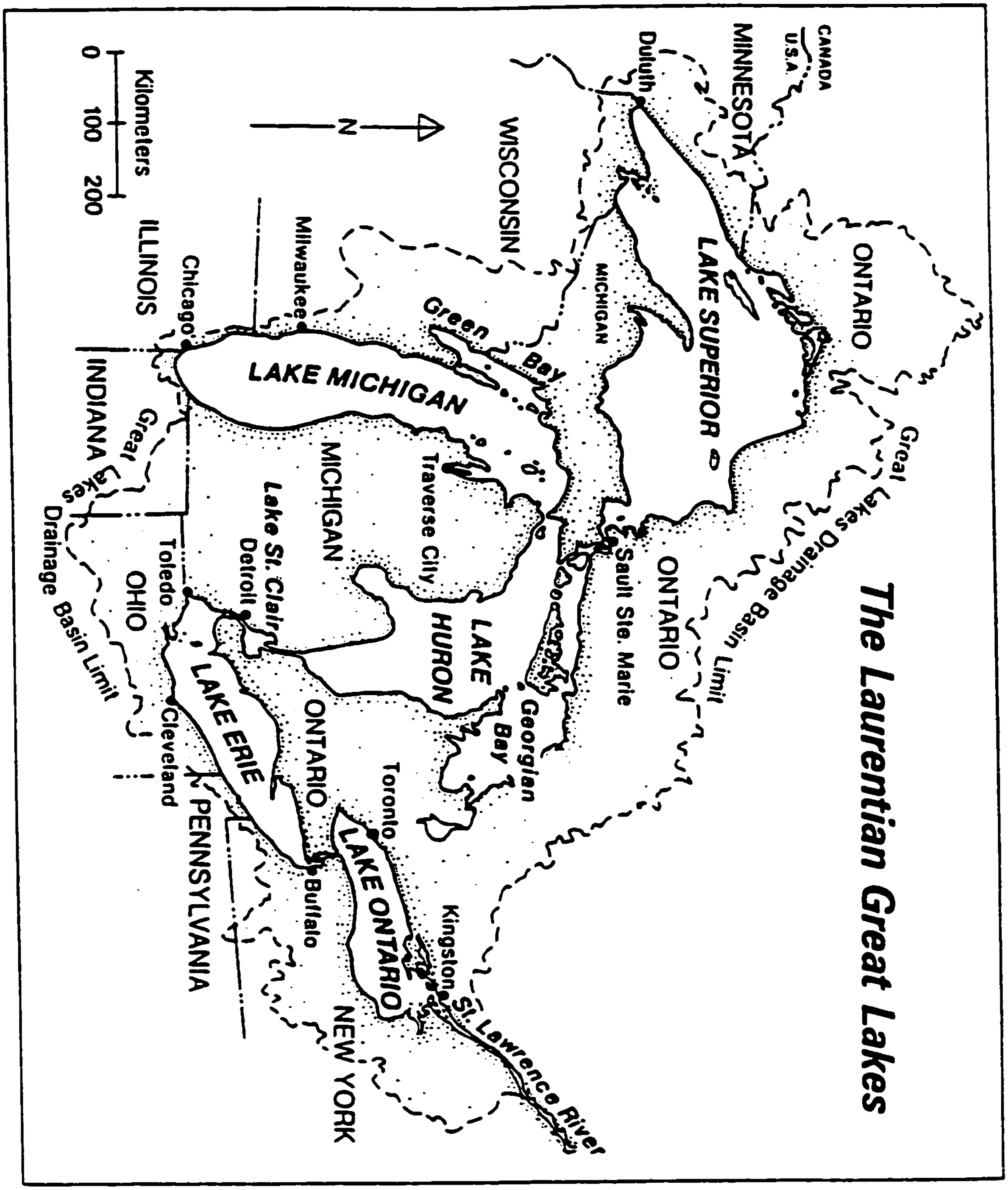
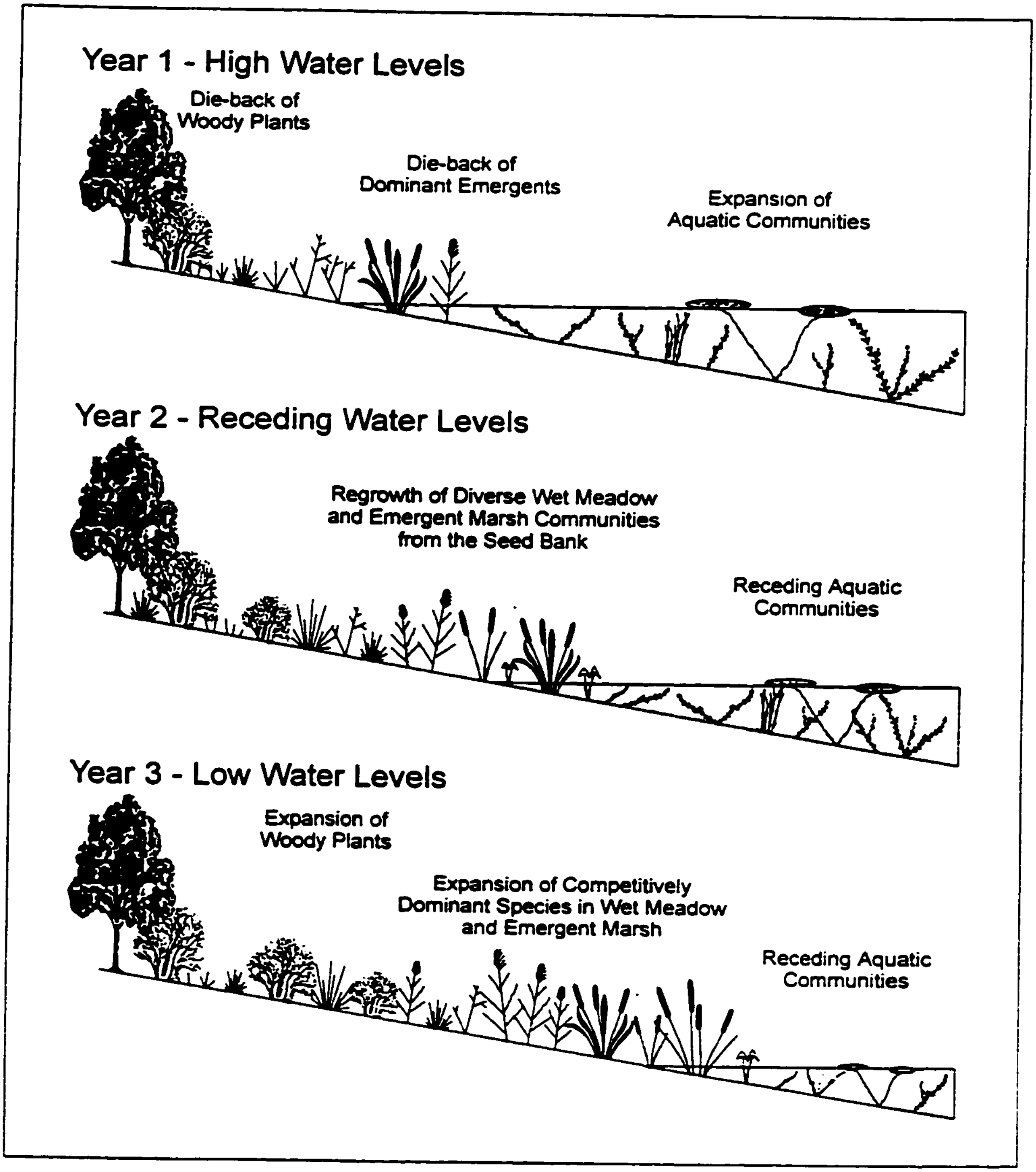

The Laurentian Great Lakes
CANADA
U.S.A.
MINNESOTA
Duluth
ONTARIO
LAKE SUPERIOR
WISCONSIN
MICHIGAN
Green Bay
Milwaukee
Chicago
ILLINOIS
LAKE MICHIGAN
INDIANA
Great Lakes Drainage Basin Limit
Traverse City
MICHIGAN
Sault Ste. Marie
ONTARIO
LAKE HURON
Georgian Bay
Lake St. Clair
Detroit
Toledo
OHIO
Cleveland
LAKE ERIE
ONTARIO
Toronto
LAKE ONTARIO
Buffalo
PENNSYLVANIA
NEW YORK
Kingston
St. Lawrence River
Great Lakes Drainage Basin Limit
N
Kilometers
0
100
200

Figure i-3: Simplified diagram of the effects of water-level fluctuations on coastal wetland plant communities (from Maynard and Wilcox 1997).


Year 1 - High Water Levels
Die-back of Woody Plants
Die-back of Dominant Emergents
Expansion of Aquatic Communities
Year 2 - Receding Water Levels
Regrowth of Diverse Wet Meadow and Emergent Marsh Communities from the Seed Bank
Receding Aquatic Communities
Year 3 - Low Water Levels
Expansion of Woody Plants
Expansion of Competitively Dominant Species in Wet Meadow and Emergent Marsh
Receding Aquatic Communities

CHAPTER 1:

Factors that regulate the zooplankton community structure of a turbid, hypereutrophic Great Lakes wetland.

Lougheed, V.L. and P. Chow-Fraser. 1998. Can. J. Fish. Aquat. Sci. 55: 150-161.

ABSTRACT: We sampled zooplankton from mid-May to early September over 2 years to study the spatial and seasonal distribution of animals in a large urban wetland of L. Ontario. Samples were collected at several habitat types including: open water, vegetated areas, fast–flow areas, and a sewage lagoon. Mean seasonal densities ranged from a low of 17 ind/L (5 µg/L) in fast-flow areas to a high of 1800 ind/L (1100 µg/L) in low–flow, highly vegetated areas. All of our sites were dominated by herbivorous rotifers (e.g. *Brachionus* sp., *Polyarthra* sp., *Keratella* sp.), small herbivorous cladocerans (*Bosmina longirostris*; mean length < 300 µm), cyclopoid nauplii, and medium–sized cladocerans (e.g. *Moina micrura*; mean length 300–600 µm), which were absent from the most eutrophic sites. The high levels of inorganic suspended solids in the marsh appeared to select against large filter–feeders such as *Daphnia* and allowed smaller zooplankton to dominate. Multivariate analyses indicated that the distribution of zooplankton was related to the flow rate, the extent of macrophyte cover and the level of degradation at the site. If the forthcoming carp (*Cyprinus carpio*) exclusion from Cootes Paradise Marsh results in increased macrophyte growth in existing or colonized areas of the marsh, we predict that zooplankton biomass will increase and that the zooplankton community may shift to larger forms.

INTRODUCTION

Wetlands are highly productive and complex systems with links to both the watershed and the open water which provide diverse habitats to a variety of resident and migratory aquatic life such as fish (Jude & Pappas 1992) and waterfowl (Prince et al. 1992). In the Laurentian Great Lakes basin, many of these habitats are being degraded by nutrient and sediment load from the watershed, fluctuating water levels, as well as the activities of the common carp (*Cyprinus carpio*) (Whillans 1996). Variability in abiotic factors, as well as the patchy distribution of aquatic vegetation, contribute to seasonal and spatial variability in water quality characteristics and the amount of available habitat for fish and aquatic invertebrates.

Throughout the Great Lakes basin, a number of restoration projects has been initiated to improve water quality and increase macrophyte growth in degraded wetlands (Cootes Paradise Marsh, Hamilton; Second Marsh, Oshawa; Toronto Harbour, Toronto; Metzger Marsh, Lake Erie). In many of these projects, managers have put much of the blame on the presence of large populations of the common carp which are thought to cause water turbidity and uproot aquatic vegetation through their spawning and feeding activities. This assumption is based on studies that have shown that the removal of other benthivorous fish communities has caused an increase in water clarity (Hanson & Butler 1990; Meijer et al. 1990a, 1990b) and an associated reduction in nutrient levels (Havens 1991, 1993; Breukelaar et al. 1994; Cline et al. 1994) that ultimately led to an improvement in plant growth (Hanson & Butler 1990; Meijer et al. 1990a). Some studies have found increased zooplankton biomass and mean body size (Hanson & Butler 1990;

Havens 1993), while others have found no effect on zooplankton (Meijer et al. 1990a) from these manipulations.

An understanding of the complex abiotic and biotic components that control the dynamics of lower trophic levels in wetlands is necessary to assist in the planning of remedial actions aimed at increasing and/or saving aquatic habitat. Zooplankton are an important part of Great Lakes food webs, providing a vital link between primary producers and the higher trophic levels, as well as contributing substantially to the detritus. Despite their pivotal role, very little research has been carried out on the ecology of these invertebrates, especially those in Great Lakes coastal wetlands (Krieger 1992).

Although little is known regarding the zooplankton communities in wetland ecosystems, comparatively more work has been done on zooplankton dynamics in lake ecosystems. These studies suggest that zooplankton communities are structured by biotic components, such as the effects of macrophyte refugia (Timms & Moss 1984; Hansen & Jeppesen 1992; Schriver et al. 1995), fish predation (Brooks & Dodson 1965; Cristoffersen et al. 1993; Ronneberger et al. 1993) and food availability (Starkweather & Bogdan 1980; McCauley & Kalff 1981; Stemberger 1981; Chow-Fraser & Knoechel 1985; Chow-Fraser 1986; Zurek & Bucka 1994), as well as abiotic components such as turbidity (Zettler & Carter 1986; Hart 1988, 1990; Kirk & Gilbert 1990; Kirk 1991), nutrient status (Bays & Crisman 1983; Hanson & Peters 1983; Pace 1986) and temperature (Galkovskaja 1987; Hart 1988; Gulati et al. 1992). Given that these factors are highly variable through time and space, it is not surprising that a great deal of spatial and temporal variation in zooplankton community structure and abundance has also been reported in Great Lakes wetlands such as Old Woman's Creek Estuary on Lake Erie (Krieger & Klarer 1991, 1992), the Bay of Quinte marshes of eastern Lake Ontario (Cooley et al. 1986) and Saginaw Bay, Lake Huron (Bridgeman et al. 1995).

In this two-year study, we examined the zooplankton community composition and dynamics of Cootes Paradise Marsh, a turbid, hypereutrophic Great Lakes wetland with a focus on the factors that structure this community. We used canonical correlation analysis to determine the key environmental variables that control zooplankton biomass in the marsh. Results from this 2-year survey are used to formulate predictions for the marsh-wide carp exclusion that is currently taking place as part of the Hamilton Harbour Remedial Action Plan (HHRAP). These valuable baseline data allow us to generate recommendations for the monitoring program that will be used to evaluate the success of the remedial actions and ultimately allow comparison with the post-exclusion zooplankton community.

METHODS

Study Site

Cootes Paradise is a 250-ha drowned river-mouth marsh, located at the western end of Lake Ontario (Fig. 1-1). It has been severely degraded due to eutrophication, high water turbidity and water level fluctuations that are out of synchrony with the growth requirements of aquatic vegetation (HHRAP 1992). The marsh is part of the Hamilton Harbour watershed, which was designated an area of concern by the International Joint Commission in 1987 and is the site of a large-scale restoration as part of the HHRAP. Only 15% of the marsh is now covered by aquatic vegetation, mainly cattails (*Typha* spp.) and manna grass (*Glyceria* sp.) (unpubl. data). Eutrophication has resulted from the discharge of primary-treated sewage (1919 to the early 1960s) from the Dundas sewage treatment plant (STP) at the western end of the marsh, and continues to be a problem today due to internal loading, inputs from several combined sewer overflows, and inputs from the two main tributaries, Spencer and Chedoke Creeks (Chow-Fraser et al. 1996). Both creeks and run-off also contribute high sediment load from the watershed. It is suggested that, in Cootes Paradise Marsh, this sediment is kept in suspension by the prevailing winds and the feeding and spawning activities of bottom-feeding fish such as the common carp (HHRAP 1992).

Although water-quality monitoring has been taking place in Cootes Paradise Marsh for the past twenty years, this is the first extensive study on zooplankton community structure since the 1940s, when the marsh was more than half covered by vegetation and had mean summer Secchi depths 2 times higher than those of present day

(41 cm (Kay 1949) vs. 19 cm: this study; site 1). In this study, 6 sampling sites (See Fig. 1-1; numbers 1, 12, 3, 4, 5, 6) were established along the long axis of the marsh, ranging from open water sites near Hamilton Harbour, to the Dundas STP. A seventh long-term site (7) was located in Spencer Creek, which enters the marsh at the southwest end. In addition to these sites, there were five more sites (8, 9, 10, 13, 16) in or near the embayments and remnant marsh areas of Cootes Paradise. Mean water quality characteristics of these sites for 1993 and 1994 are reported in Table 1-1. Using Ward's clustering procedure, Chow-Fraser (unpubl. data) has grouped these sites according to similarities in their water quality characteristics. Sites 1 and 12, the open water sites were most similar to site 13, which is located at the outskirts of Westdale Cut. Site 9 and 10, located near vegetated sites in Mac Landing, were also similar, while the two vegetated sites, 8 and 16, were grouped together. West Pond (5), a former sewage lagoon, was the most unique among the in-marsh sites, being the most eutrophic and turbid (Table 1-1). Among those sites flowing into the marsh, sites exposed to the flowing water entering the marsh via Spencer Creek, such as the delta (3), the Desjardins canal (4) and in the creek itself (7), were most similar. Site 6, located on the outskirts of the marsh at the STP outfall was unique compared to all other sites. Based on these clusters of water quality parameters, we selected 5 sites representative of the range of variation within the marsh (1, 3, 5, 8, & 9) on which to concentrate our zooplankton surveys and analyzed samples collected bi-weekly in 1993 and 1994 (7 or 8 samples per site per year). For the remainder of this paper, we will refer to site 1 as open water, site 3 as the delta, site 5 as West Pond, site 8 as the vegetated site and site 9 as near vegetation (~10m from cattails).

We also include information on other sites (4, 6, 7, 10, 12, 13, & 16) that had been sampled monthly in 1993 (3 or 4 samples per site) to illustrate the variety of zooplankton communities in the marsh.

Sample Methods

Water and zooplankton samples were collected from mid-May to the beginning of September (when the marsh dried up at the western end) in 1993 and 1994. Because of the shallow depth of this system and high level of wind-induced mixing (see Table 1-1 for wind speed; see also Sager 1996), all samples were taken from the middle of the water column. Zooplankton was collected using a 5-L Schindler-Patalas trap with a 63-µm Nitex mesh cup; high suspended sediment levels in the marsh did not make it feasible to use a smaller mesh. Samples were preserved immediately in 4% sugar-formalin. Subsamples of at least 100 organisms, including at least 20 large organisms (>300 µm mean length) were identified and counted under a dissecting microscope at 40X magnification. The whole sample was also surveyed for large and rare organisms. Initial identification was aided by a phase-contrast microscope at 200 to 400X. Measurements of all organisms were made with the aid of the Bioscan Optimas image analysis system. Lengths were not corrected for the effect of preservative (Campbell and Chow-Fraser 1995), but shrinkage in rotifers and cyclopoids, which formed the majority of zooplankton in our samples, were assumed to be negligible.

Water samples were collected using a 1-L Van Dorn bottle. Water quality variables such as total phosphorus (TP) and total nitrogen (TN) were determined using

Hach reagents according to Hach protocols and standard methods (APHA 1992). Suspended solids (TSS) were also determined using standard methods (APHA 1992). Temperature was determined using an H2O® Hydrolab and Scout® monitor; water depth and Secchi depth were measured using a 20 cm diameter Secchi disc. Chlorophyll-*a* (CHL*a*) was extracted using 90% acetone and a 1-h extraction period in the freezer; absorbance readings were taken with a Milton Roy spectrophotometer. Results in this study have been corrected for phaeopigments by acidification (Likens and Wetzel 1991). Additional variables not included in this study due to their correlation with other variables or their lack of in-marsh variability (soluble reactive phosphorus, total ammonia nitrogen, total nitrate nitrogen, pH, dissolved oxygen, turbidity) have also been collected and this information is available from the second author.

Rotifer identification was based on Chengalath et al. (1971) and Stemberger (1979), while crustacean identification was based on Balcer et al. (1984), Pennak (1989) and Thorp & Covich (1991). Identification was to the level of species for all common organisms except *Asplanchna* and *Polyarthra* which were to genus, *Acanthocyclops vernalis* and *Ectocyclops phalerutus*, which were grouped together as cyclopoid copepods in counting, and all copepod nauplii. Total abundance and biomass for each sample were first calculated on an individual basis, then combined for species and functional group total.

We used published length-weight relationships and dry-weight estimates from Dumont et al. (1975) and Malley et al. (1989) to estimate dry-weight for the zooplankton in this study. Bottrel et al. (1976), Geller and Muller (1985) and Malley et al. (1989)

have cautioned against using borrowed relationships because of seasonal and lake-to-lake variations; however, because of the time-consuming nature of dry-weight determination, we used published values and assumed the error due to sampling variability was greater than that due to the length-weight regressions. We ensured that any equations and dry-weight estimates were used for organisms in the same length range. To minimize errors, equations taken from Malley et al. (1989) were from an artificially eutrophied lake (Lake 227). Given the scarcity of information on rotifer biomass, dry weight estimates used from Dumont et al. (1975) were largely averages of biomass values obtained from a variety of locations. In certain cases (not for any common species) where specific dry weight values were not available, estimations were made by comparison with similar species.

Statistical Analyses

All calculations and statistical analyses were performed using SAS.JMP (SAS Institute Inc., 1992), and graphical analysis was performed using Cricket Graph III. Canonical correlation analysis was used to summarize the relationship between environmental and response variables by finding linear combinations of these variables that have the highest possible between-set correlation. For details on canonical correlation analysis see Gittens (1980) and ter Braak (1990, 1995). This multivariate analysis has been used successfully in other studies to determine the environmental variables that control plankton production in lake ecosystems (Munawar and Wilson 1978; Varis et al. 1989; Varis 1991). In this study, canonical correlation was used in conjunction with descriptions of the dynamics and composition of the zooplankton community to identify the relationship between the key variables in each data set. This analysis was performed on two different data sets: i) data from the representative sites (1, 3, 5, 8, 9) sampled bi-weekly in 1993 and ii) a similar data set from 1994.

Concentrations of TN, TP, CHL*a* and TSS, physical variables such as temperature and depth, and variables representing proximity to macrophytes and water flow were entered as independent variables; the biomass of respective functional taxa were entered as the dependent variables. Zooplankton taxa with a low frequency of occurrence were excluded (i.e. macrograzers). Water flow was recorded as either 0 (no observable flow) or 1 (visible flow) to represent the overall hydrologic character of the site over the season and was not based on measured flow rates. We classified sites according to proximity to macrophytes as follows: 1= >20m from plants; 2= <10m from plants. All data were standardized to zero mean and unit variance, and the zooplankton data were normalized using a transformation of log(x+1). The correlation of the zooplankton taxa and environmental variables with the canonical variates of the first two canonical axes were plotted in canonical biplots, where the loadings from axis 2 were plotted against the loadings from axis 1.

RESULTS

Zooplankton community structure

Common species of zooplankton in Cootes Paradise Marsh (frequency of occurrence >50%) included the rotifers *Asplanchna* sp., *Brachionus angularis*, *B. calyciflorus*, *B. caudatus*, *Filinia longiseta* and *Polyarthra* sp., the cladocerans *Bosmina longirostris*, *Moina micrura*, the cyclopoid copepods *Acanthocyclops vernalis* and *Ectocyclops phalerutus*, and copepod nauplii (Table 1-2). The rotifers contributed the largest numbers of species (22) followed by cladocerans (9) and copepods (3). We analyzed the relative distribution of the zooplankton by grouping them according to their size-specific functional role in the ecosystem rather than by taxonomic affiliation. Herbivorous rotifers included all rotifers except *Asplanchna*, which was classified as a predaceous rotifer. Other grazers were grouped either as microcladocerans (< 300 µm mean length), medium cladocerans (300-600 µm mean length), macrograzers (> 600 µm mean length) or nauplii and copepodids. The term microcladocerans was used to represent *Bosmina*; medium cladocerans included species such as *Moina*, *Diaphanosoma* and *Scapholeberis*; while macrograzers consisted of *Daphnia* and *Diaptomus*. Cyclopoid predators included *Acanthocyclops* and *Ectocyclops*.

Mean total biomass and abundance tended to be lowest at the flowing sites associated with Spencer Creek (3, 4, 7) (Table 1-3 & 1-4). Low to moderate biomass and abundance were observed for the more turbid and eutrophic open water site (5), followed by other open water sites (1, 10, 12), as well as the near-vegetation site (9). A vegetated site (8), and a less exposed, open water site (13) had moderate to high abundances and biomass. The highest biomass levels were seen at a vegetated site near a combined sewer overflow outfall (16), while the highest abundances were seen at the STP outfall (6). Differences in sampling frequency should be noted (n; Tables 1-3 & 1-4). It should also be noted that site 16 could not be sampled in 1994 due to experimental manipulations in Westdale Cut. Mean total zooplankton biomass and densities were generally higher in 1994 compared to 1993 (Table 1-3 & 1-4), although there were no significant differences between years (ANOVA, $p>0.05$).

Although peaks in zooplankton biomass and abundance occurred at different times in 1993 versus 1994, there were no striking differences in zooplankton composition between years, except at site 5 (Fig. 1-2 and 1-3). The most unique distribution pattern was associated with this site, a turbid and eutrophic sewage lagoon, where medium cladocerans were virtually absent and the total biomass and abundance of zooplankton was relatively low. There was also relatively low zooplankton levels at site 3, the flowing water site; however, zooplankton composition at this site was not obviously different from the other sites sampled biweekly (Fig. 1-2 and 1-3). The other flowing sites (4, 7, 6), which were sampled at a much lower frequency, had a disproportionate representation of herbivorous rotifers, with site 6, the most eutrophic of the flowing sites, having a species composition intermediate between that of the riverine (7) and sewage lagoon (5) sites (Fig. 1-4). By comparison, greater total biomass and abundance was observed throughout the summer at the open water site (1) and inside (8) or near (9) the vegetation (Fig. 1-2 and 1-3). Proportionally (Fig. 1-4), site 8 had relatively low levels of herbivorous rotifers, as did the other site found inside the vegetation (16), although otherwise the zooplankton communities at these two sites were very different from each other. All other sites in the marsh (1, 9, 10, 12, 13) had similar zooplankton compositions (Fig. 1-2, 1-3 and 1-4). One notable difference was that, although not visible in the graphical presentation, macrograzers occurred almost exclusively at site 1 but at very low densities (1 to 3 individuals./L).

Predictors of zooplankton community structure.

Canonical correlation analysis effectively summarized the patterns of variation in the zooplankton and environmental data; the first 2 axes explained 71% and 83% of the variation in the data set for 1993 and 1994, respectively, and the correlation between taxa and environmental data varied from 67% to 93% (Table 1-5).

The distribution of environmental variables along the first two canonical axes revealed several prominent trends in the data set which were maintained between years (Fig. 1-5a and b), and which can be interpreted based on water quality differences between sites and years. Variables indicating trophic state, such as TP, TN and CHL*a*, were closely correlated; however, their correlation to the axes, as indicated by the length of the vector, was stronger in 1994. In 1994, TSS was also correlated with these variables, while in 1993 the correlation of TSS with the axes was very weak. The weakness of these associations in 1993 was likely due to the high water levels seen in this year (Fig. 1-6) which diluted nutrient and turbidity effects for most of the season (Chow-Fraser, unpubl. data) and resulted in much weaker relationships between these 4 variables (TP, TNN, CHL*a*, TSS). In both years, these trophic state variables did not reach mid-summer maxima and therefore, in the canonical analysis were not correlated with temperature in either year. The generally warmer environment at the shallow, vegetated site (Table 1-1) was reflected in a positive correlation between plants and temperature; however, site 5 was also relatively warm and therefore the vector for temperature tended to fall partway between plants and the variables indicative of degradation. In 1993, plants were negatively correlated with the variables associated with trophic state; however, in 1994, there was no correlation between these variables. As expected the water flow was negatively correlated with temperature and plants.

With few exceptions, in both 1993 and 1994, all zooplankton taxa tended to be positively correlated with each other. In general, all taxa were positively correlated with temperature and plants; however, microcladocerans, medium cladocerans and cyclopoids were consistently most strongly correlated with these variables. This is to be expected given the mid-summer maxima in biomass of these taxa, most notably at the vegetated site (8). The exceptions to this generality were predaceous rotifers which occurred at lower temperatures in the spring of 1993, and were negatively correlated to their prey, herbivorous rotifers and nauplii. The negative correlation of most taxa with nutrients and turbidity is expected since the site that was most consistently eutrophic (5) had relatively low biomass of zooplankton. Similarly, given the overall low biomass at the flowing site (3), all taxa were negatively correlated with flow.

DISCUSSION

Marshes are temporally and spatially dynamic systems that are highly variable with respect to water flow, water depth, distribution of aquatic vegetation and the concentration of nutrients and suspended solids. This study is one of the first to link such variation to taxonomic composition and biomass structure of zooplankton in a Great Lakes coastal wetland.

Macrophytes are known to play an important role in the ecology of zooplankton in the littoral regions of lakes. Studies in a shallow, eutrophic Danish lake showed that an increase in macrophyte cover changed the zooplankton community from rotifers to larger cladocerans (Hansen & Jeppesen 1992). In Cootes Paradise, the reduced proportion of rotifers at the vegetated site (8) suggests that, in the presence of aquatic macrophytes, rotifers were outcompeted by other taxa. Sensitivity to fish predation is known to decrease with increased macrophyte cover since cladocerans use macrophytes as refugia against predation. This allows larger zooplankton to hide during the day and horizontally migrate out of the weeds at night to graze (Timms & Moss 1984). In more eutrophic systems, macrophyte protection from fish predation may allow grazers to increase their population size sufficiently to control phytoplankton growth (Schriver et al. 1995). We suggest that the relatively low chlorophyll-*a* levels in the vegetated site (Table 1-1) relative to most other sites is evidence that grazing zooplankton were preferentially using macrophyte cover, presumably as refugia. Preliminary studies (Chow-Fraser et al. 1998) in a different area of the marsh (site 15: cattail beds north of site 10), indicate that phytoplankton biomass increased, while large herbivore biomass decreased with distance (up to 15m away) from the cattail beds.

We confirm the findings of Krieger and Klarer (1991), who reported that sites near the marsh outflow have zooplankton assemblages that are more similar to that in the receiving waters. Aerial photos tracking turbidity patterns in Cootes Paradise Marsh have indicated that the exchange of water between the marsh and the receiving water, Hamilton Harbour, can be reversed and is dependant on watershed inputs and wind direction (Chow-Fraser, unpubl. data). In this study, the intrusion of harbour water into the marsh on some dates was supported by a reduction in pH, temperature and suspended solids at site 1 that was more consistent with the harbour water. *Daphnia* were found nearly exclusively at the open water site (1) near the marsh outflow, coincident with the presence of moderately high numbers of *D. retrocurva* in Hamilton Harbour (unpubl. data), and we suggest that they were carried via intrusion from the harbour. We speculate that the presence of macrograzers, such as *Daphnia*, in the open waters of Cootes Paradise Marsh may be transient and not representative of self-sustaining populations. The only other location in the marsh where *Daphnia* have been found is at the vegetated site (15) north of site 10, which was sampled for the first time in 1996, and where *Daphnia* were also found at a very low density (1 individuals/L) during the mid-summer peak in biomass. The existence of low densities of several species of *Daphnia* (*D. longispina*, *D. retrocurva*, *D. parvula*) in remote vegetated areas suggests that *Daphnia* may become a more prominent grazer once the marsh is restored to a macrophyte-dominated system.

The consistently low biomass of medium cladocerans and macrograzers in the marsh suggests the presence of factors inhibiting the survival of these larger grazers. Grazing by large filter-feeders is generally thought to be inhibited in highly turbid systems (Hart 1988; Kirk & Gilbert 1990; Kirk 1991), or systems with blue-green alga blooms (Chow-Fraser and Sprules 1986). Unlike other hypereutrophic systems, where blue-green alga blooms occur frequently, Cootes Paradise has no such blooms because of the high TN:TP ratio (Chow-Fraser unpubl. data); however, Cootes is an extremely turbid system, with turbidity levels 10 to 20 times higher than those reported for other studies. In the 1940s, when the water was on average twice as clear as present day, many species of *Daphnia* were found associated with the submergent and emergent vegetated areas of the marsh (Kay 1949). This suggests that reduced macrophyte cover and mechanical interference due to increased turbidity through time may have been responsible for the low numbers of *Daphnia* in Cootes Paradise. That *Moina*, a genus known to be tolerant of turbidity, was the most abundant large herbivore in the marsh is consistent with the literature (*M. brachiata*: Hart 1988) which indicates that high turbidity selects for this medium-sized cladoceran. The relative absence of large herbivores at the most degraded site (5), in combination with the highest turbidity levels, is in support of this; however, overall low zooplankton biomass of all taxa suggests that additional factors, besides turbidity and the absence of vegetation, may also have been important at this site.

Zooplankton distribution and biomass may also be structured by differences in food availability. Zooplankton are known to have specific food and food size preferences (Starkweather & Bogdan 1980; McCauley & Kalff 1981; Stemberger 1981; Chow-Fraser

& Knoechel 1985; Chow-Fraser 1986; Zurek & Bucka 1994). As in other Great Lakes wetlands (Klarer & Millie 1994), the species composition and total biomass of phytoplankton is highly variable seasonally and from site-to-site in Cootes Paradise Marsh (Chow-Fraser, unpubl. data), which is consistent with the results seen for water quality and zooplankton. Although it appears, from chlorophyll-*a* values alone, that site 5 was the most food-rich site, and should therefore have a higher biomass of zooplankton, much of the phytoplankton biomass at this site consisted of large, flagellated phytoplankton (>30 μm), including both Euglenoids and large Cryptomonads (Chow-Fraser, unpubl. data) which were likely inedible to those smaller organisms able to withstand the high levels of turbidity at this site.

In conclusion, it appears that zooplankton community dynamics in Cootes Paradise Marsh are primarily structured by proximity to macrophytes and water turbidity, while zooplankton at sites on the outskirts of the marsh were further influenced by flowing water. Differences in food availability and predation pressure likely also played a role in structuring the zooplankton communities. Although there does not appear to be a direct relationship between body size and marsh fertility, larger bodied zooplankton may be disadvantaged by high water turbidity in the absence of vegetation, while smaller zooplankton taxa may be constrained by the effect of hypereutrophication on the phytoplankton community.

One of the goals of the Hamilton Harbour Remedial Action Plan is to exclude carp from Cootes Paradise Marsh, and therefore increase macrophyte growth and improve water quality. There is, however, little experimental evidence that clearly links the exclusion of large carp from degraded Great Lakes wetlands with water clarity or quality improvements sufficient to allow the establishment of a healthy marsh community, including emergent and submergent macrophytes. Further research on these issues, such as that by Lougheed et al. (1998), will contribute valuable knowledge to wetland managers on those conditions necessary for Great Lakes wetlands to start recovering from years of abuse.

From this pre-manipulation study of the zooplankton in Cootes Paradise, we can predict that increased emergent macrophyte growth in existing or colonized areas of the marsh will increase the total zooplankton biomass and shift the zooplankton community to larger bodied forms, irrespective of any change in predation pressure arising from the biomanipulation. Similarly, based on past conditions in the marsh (Kay 1949), we can predict that the introduction of submergent macrophytes may also allow larger grazers to persist. The monitoring program following carp exclusion should focus on those sites which are most likely to be affected, in particular the vegetated areas (8) and the near-vegetated areas (9) where emergent macrophytes may become established. Large to medium sized zooplankton may also have an increased competitive advantage at the open water sites (1 & 5), where reductions in turbidity and internal loading in the absence of macrophyte growth may occur; however, at these exposed and unvegetated sites the effect of wind in stirring up nutrient-rich bottom sediment may be of further concern. Zooplankton communities in flowing water sites at the marsh inputs will probably not change in response to carp exclusion, but are more likely to be altered by watershed or sewage treatment plant alterations.

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Table 1-1. Mean water quality and physical variables at 12 sampling sites in Cootes Paradise Marsh over the summers of 1993 and 1994, from mid-May to mid-September.

Site	n	Wind (m/s)	Depth (cm)	Temp. (°C)	TP (μg/L)	TN (μg/L)	CHL*a* (μg/L)	TSS (mg/L)	Secchi (cm)	Flow[a]	Plants[a]
1	20	3	109	21	144	3222	39	57	19	N	N
3	19	1	75	19	97	3492	18	60	26	Y	N
4	19	1	77	17	84	3052	12	49	23	Y	N
5	18	3	54	22	315	7558	146	105	13	N	N
6	18	1	163	20	174	11570	34	27	43	Y	N
7	18	1	130	17	49	2509	4	44	44	Y	N
8	16	1	38	23	216	3091	27	79	20	N	Y
9	18	2	46	22	209	3372	52	76	16	N	Y
10	18	3	51	22	149	3377	57	86	16	N	N
12	20	2	72	21	157	2770	51	56	19	N	N
13	18	2	122	21	187	3095	50	69	18	N	N
16	8	0	31	21	592	3287	8	94	20	N	Y

NOTE: Site 16 was only sampled in 1993; [a]: Y, yes (present); N, no (absent).

Table 1-2. Frequency (in percent) of occurrence of each zooplankton species for the whole marsh (total frequency) and for 3 representative sites from mid-May to early September of 1993 and 1994.

	Total Frequency	1993			1994		
		Open Water	West Pond	Veg'n	Open Water	West Pond	Veg'n
ROTIFERA							
Asplanchna sp.	72	71	86	71	75	62	71
Brachionus angularis	58	71	71	71	50	50	57
Brachionus bidentata	12	14	0	14	0	50	0
Brachionus calyciflorus	80	100	100	57	75	75	86
Brachionus caudatus	60	100	43	43	38	75	29
Brachionus diversicornus	25	43	14	29	12	12	0
Brachionus havanaensis	12	14	0	14	0	0	0
Brachionus quadridentatus	9	0	14	29	0	0	14
Brachionus rubens	6	0	0	0	0	0	29
Brachionus urceolaris	45	14	71	43	0	75	57
Filinia longiseta	55	43	57	57	62	38	57
Filinia brachiata	1	0	1	0	0	0	0
Kellicotia sp.	0	0	0	0	25	0	14
Keratella cochlearis	35	29	14	14	75	12	71
Keratella quadrata	41	57	43	43	38	0	57
Lecane luna	6	0	0	57	0	0	0
Monostyla bulla	4	0	0	0	0	12	29
Notholca sp.	1	0	0	0	0	0	0
Platyas patulas	3	0	0	0	0	0	29
Polyarthra sp.	77	71	43	86	88	88	86
Trichocerca cylindrica	20	57	43	14	0	12	0
CLADOCERA							
Bosmina longirostris	90	100	86	100	100	38	100
Diaphanosoma birgei	19	14	14	0	25	50	29
Daphnia retrocurva	8	14	0	0	50	0	0
Kurzia sp.	4	0	0	29	0	12	0
Leydigia sp.	1	0	0	0	0	0	0
Macrothrix sp.	9	14	0	14	0	0	29
Moina micrura	54	71	29	71	62	62	71
Scapholeberis sp.	12	14	0	43	0	0	100
Simocephalus sp.	1	0	0	14	0	0	0
COPEPODA							
nauplii	97	100	100	100	100	100	100
Cyclopoid copepods	90	100	86	86	100	88	100
Diaptomus minutus	9	29	0	29	12	0	0
N (no. samples included)	101	7	7	7	8	8	7

NOTE: Frequency of occurrence = [number of sites where a species occurs / number of sites sampled (N)] * 100.

Table 1-3. Minimum, mean and maximum total zooplankton biomass (μg/L) at 12 sampling sites in Cootes Paradise sampled n times from mid-May to early September of 1993 and 1994.

	1993				1994			
Site	n	Min	Mean	Max	n	Min	Mean	Max
1	7	5	327	979	8	64	611	1765
3	7	3	102	239	8	1	130	517
4	4	24	38	55	-			
5	7	33	207	715	8	21	392	1494
6	3	85	787	2137	-			
7	4	3	5	5	-			
8	7	22	767	1507	7	77	1109	3273
9	7	34	577	1656	8	133	628	1346
10	4	96	588	974	-			
12	4	69	666	1721	-			
13	4	57	719	1228	-			
16	4	64	1064	2242	-			

Table 1-4. Minimum, mean and maximum total zooplankton abundance (individuals./L) at 12 sampling sites in Cootes Paradise sampled n times from mid-May to early September of 1993 and 1994.

	1993				1994			
Site	n	Min	Mean	Max	n	Min	Mean	Max
1	7	14	786	1941	8	85	1331	3278
3	7	33	225	592	8	6	385	2169
4	4	44	122	246	-			
5	7	185	582	1400	8	38	1050	2607
6	3	256	2504	6858	-			
7	4	16	17	18	-			
8	7	76	1226	3525	7	233	1800	3472
9	7	110	1249	2120	8	347	1422	3066
10	4	88	1547	2566	-			
12	4	204	1323	2376	-			
13	4	103	1512	2369	-			
16	4	124	1463	4060	-			

Table 1-5. Table showing the characteristics of the first four canonical correlations.

Canonical correlation	Cumulative proportion of sum of eigenvalues	Canonical r^2
1993		
1	0.51	0.93
2	0.71	0.85
3	0.86	0.81
4	0.96	0.75
1994		
1	0.65	0.86
2	0.83	0.67
3	0.92	0.54
4	0.96	0.39

Figure 1-1. Location of sampling sites in Cootes Paradise Marsh, Lake Ontario; larger dots indicate the representative sites (see text for details); arrows indicate the inflows and outflows of the marsh; shaded areas indicate the presence of emergent vegetation.

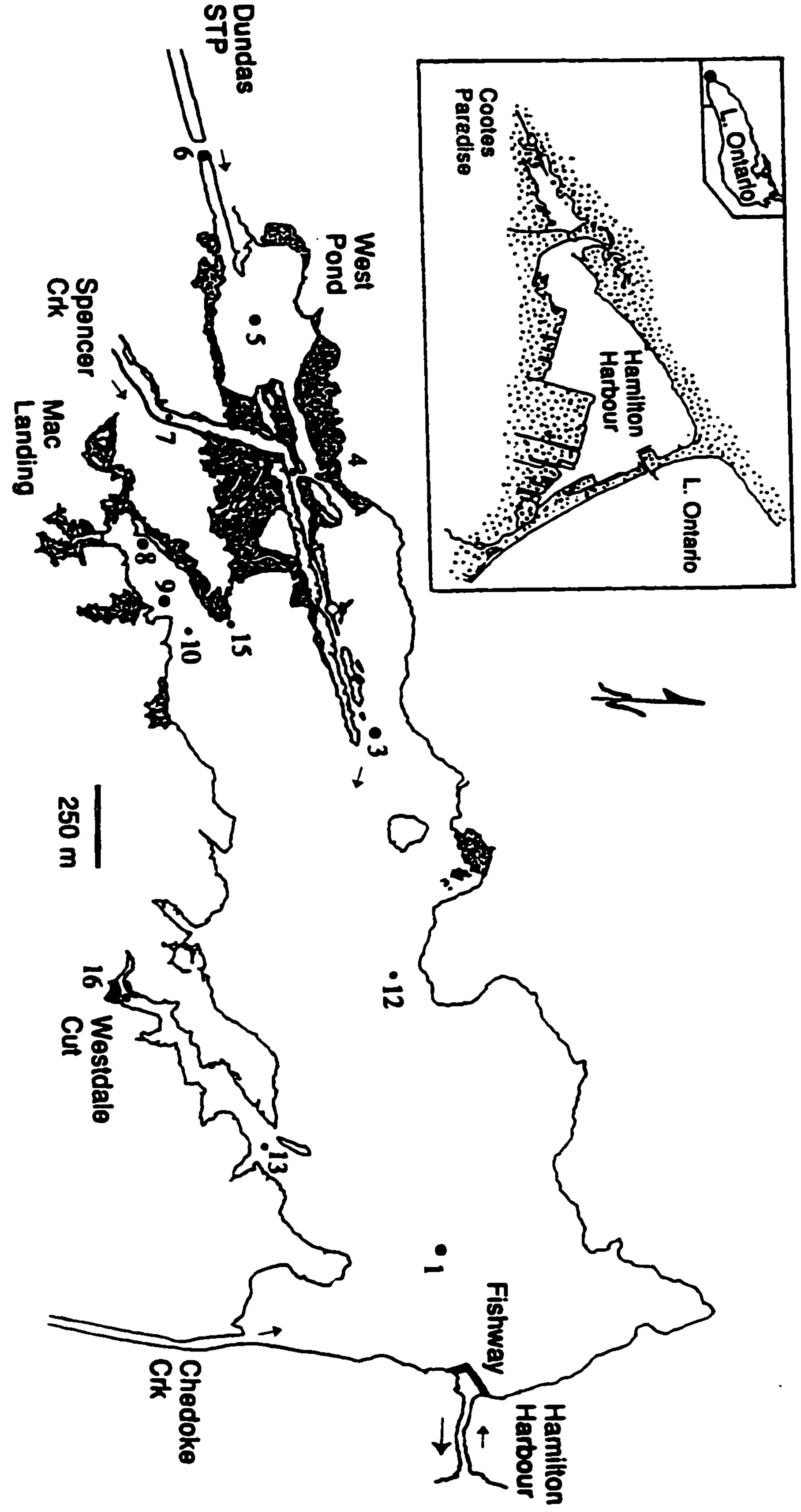

L. Ontario
Cootes Paradise
Hamilton Harbour
L. Ontario
Dundas STP
6
West Pond
5
Spencer Crk
7
Mac Landing
4
8
9
10
15
3
250 m
12
16
Westdale Cut
13
1
Fishway
Chedoke Crk
Hamilton Harbour

Figure 1-2. Changes in the biomass (µg/L) of zooplankton taxa over the summers of 1993 (left column) and 1994 (right column) at 5 representative sites in the marsh (sites 1, 3, 5, 8, and 9).

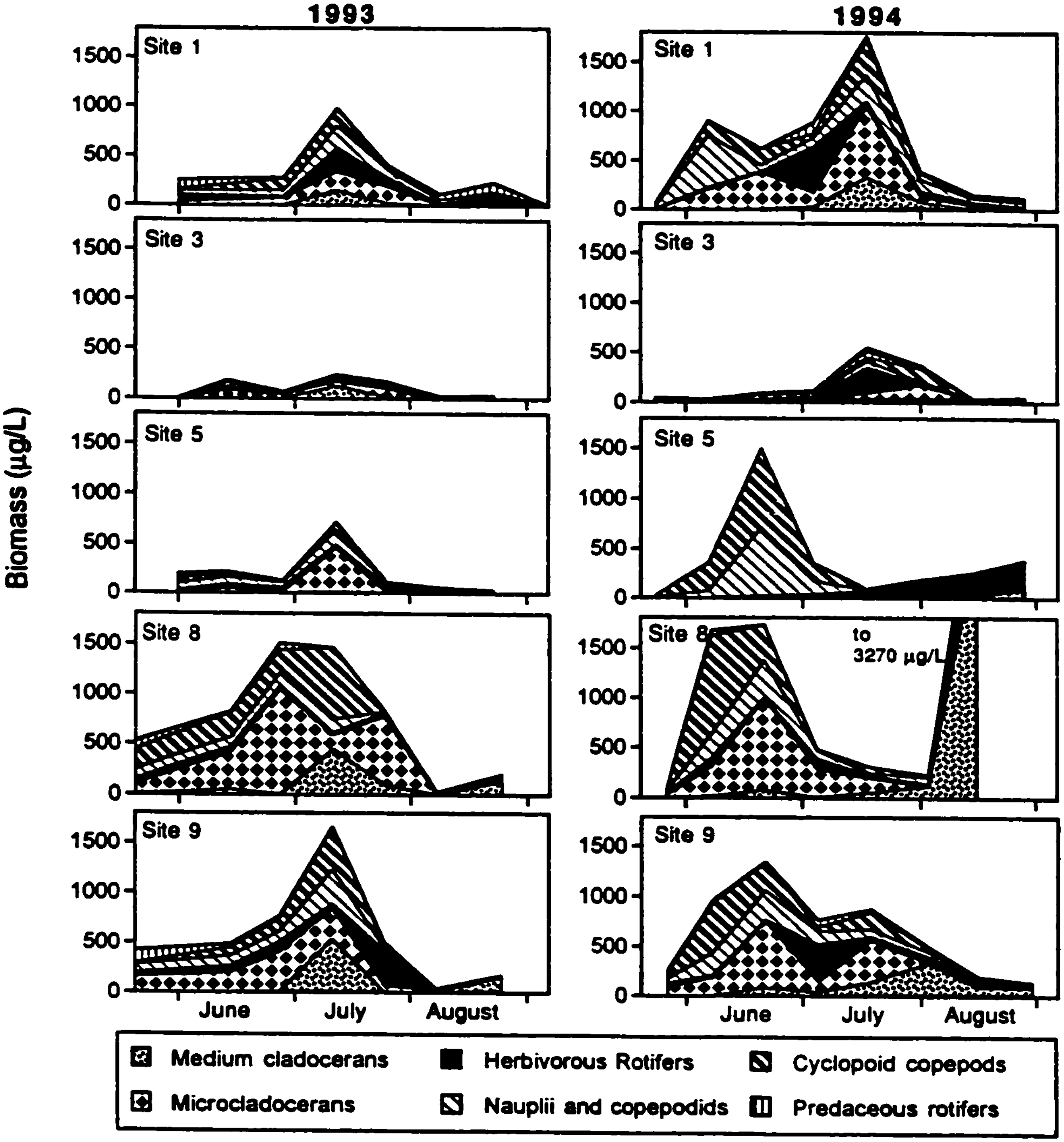

1993
1994
Site 1
Site 3
Site 5
Site 8
Site 9
to
3270 µg/L
1500
1000
500
0
Biomass (µg/L)
June
July
August
Medium cladocerans
Herbivorous Rotifers
Cyclopoid copepods
Microcladocerans
Nauplii and copepodids
Predaceous rotifers

Figure 1-3. Changes in the density (individuals./L) of zooplankton taxa over the summers of 1993 (left column) and 1994 (right column) at 5 representative sites in the marsh (sites 1, 3, 5, 8, and 9).

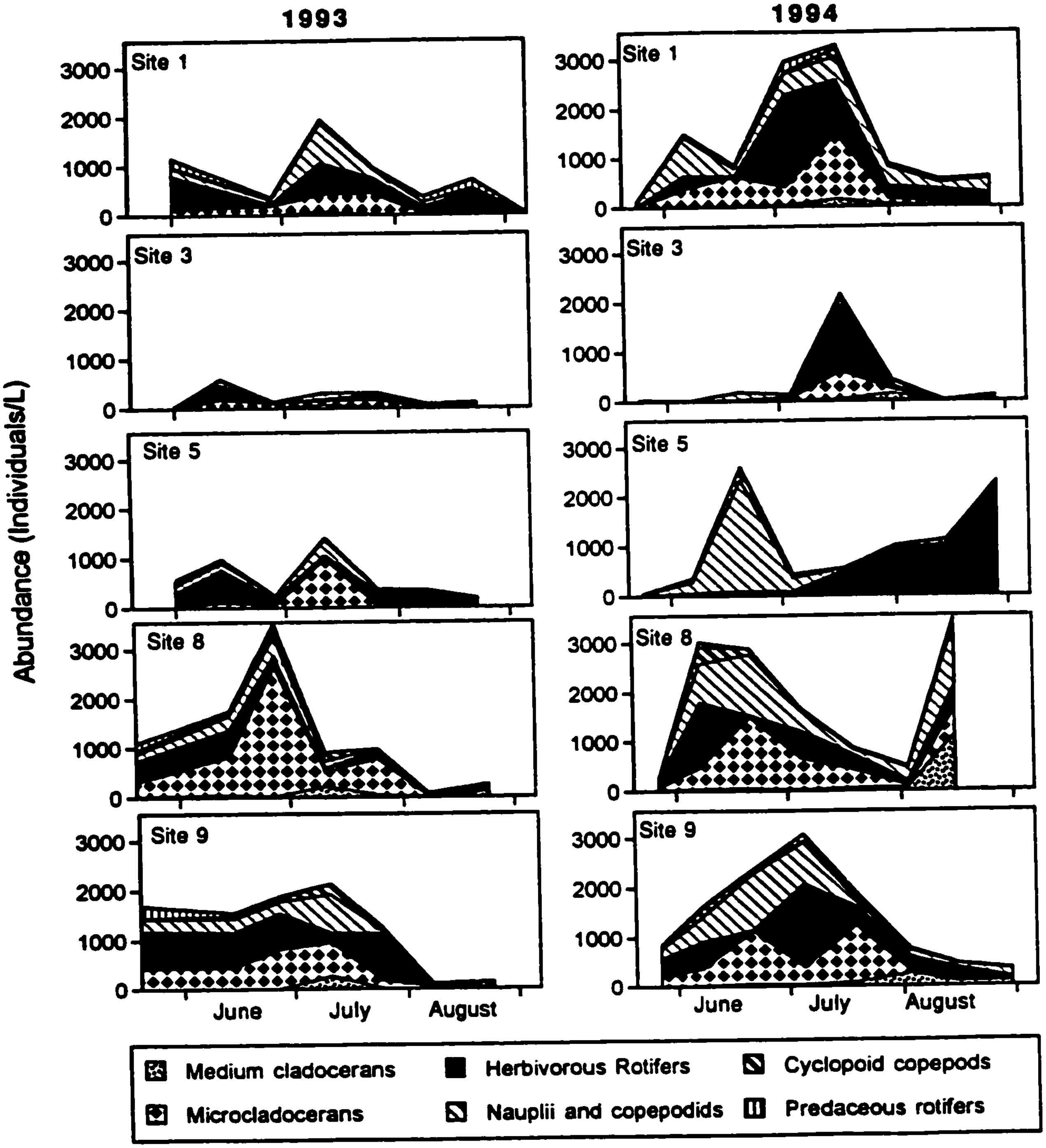

1993
1994
Site 1
Site 3
Site 5
Site 8
Site 9
3000
2000
1000
0
Abundance (Individuals/L)
June
July
August
Medium cladocerans
Herbivorous Rotifers
Cyclopoid copepods
Microcladocerans
Nauplii and copepodids
Predaceous rotifers

Figure 1-4. Mean relative proportion (percent biomass) of zooplankton taxa at all sites sampled monthly in the marsh in 1993.

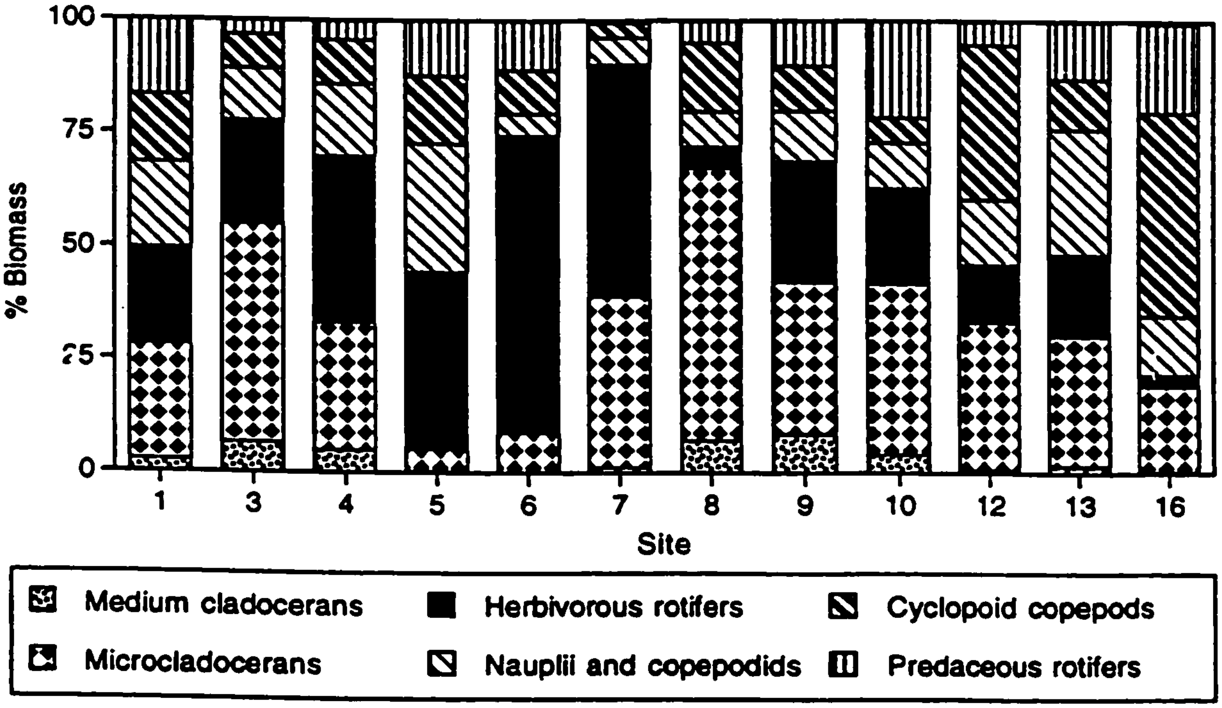

100
75
50
25
0
% Biomass
1
3
4
5
6
7
8
9
10
12
13
16
Site
Medium cladocerans
Herbivorous rotifers
Cyclopoid copepods
Microcladocerans
Nauplii and copepodids
Predaceous rotifers

Figure 1-5. Biplot display (axis 2 versus axis 1) of the canonical loadings of environmental variables (solid line) and zooplankton taxa (broken line) for (a) 1993 (b) 1994. CHL*a*, chlorophyll-*a*; PLANT, proximity to macrophytes; TEMP, temperature; TN, total nitrogen; TP, total phosphorus; TSS, total suspended solids; asp, predaceous rotifers; cycl, cyclopoid copepods; rot, herbivorous rotifers; micro, microcladocerans; med, medium cladocerans; n/c, nauplii and copepodids.

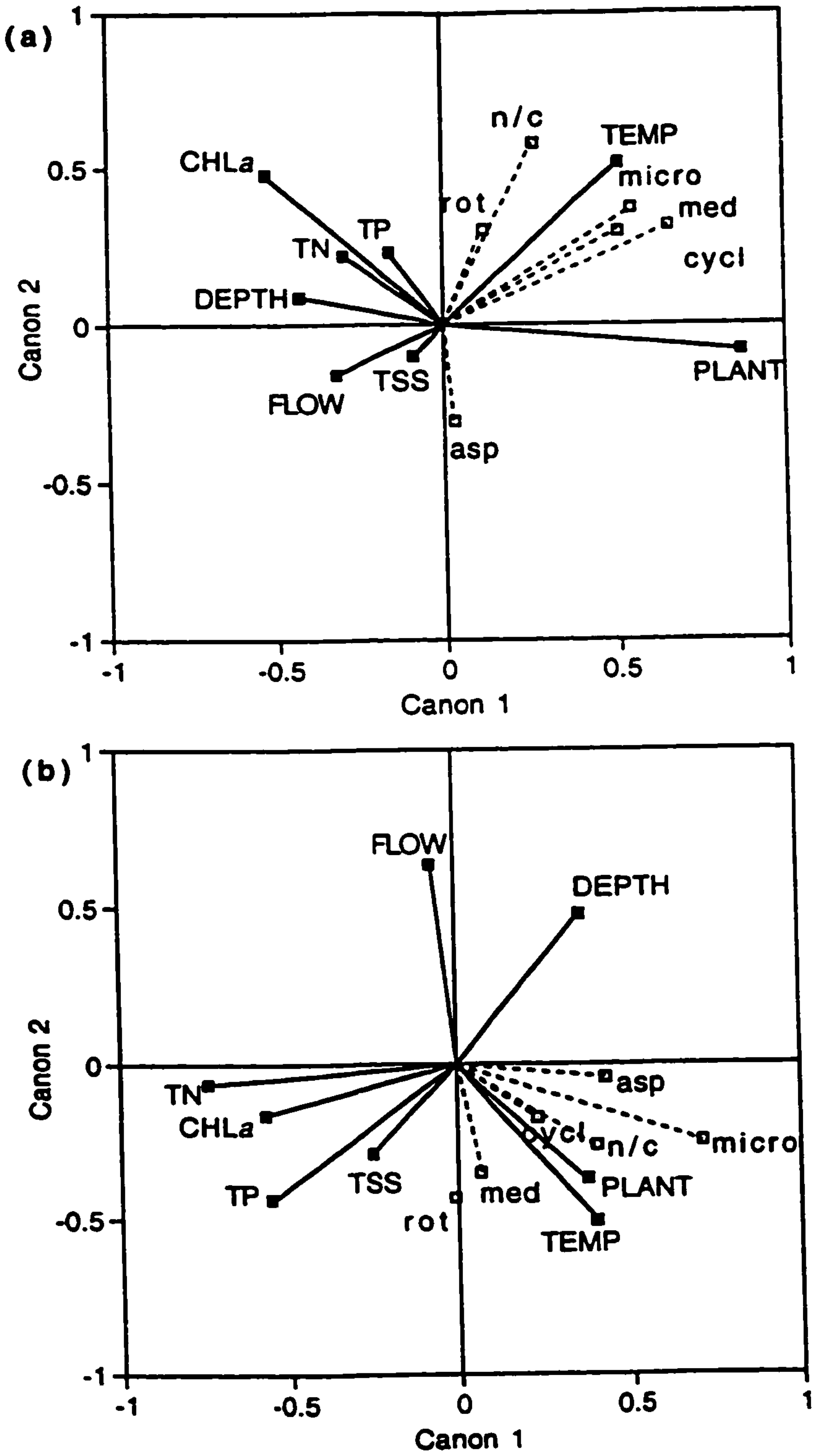
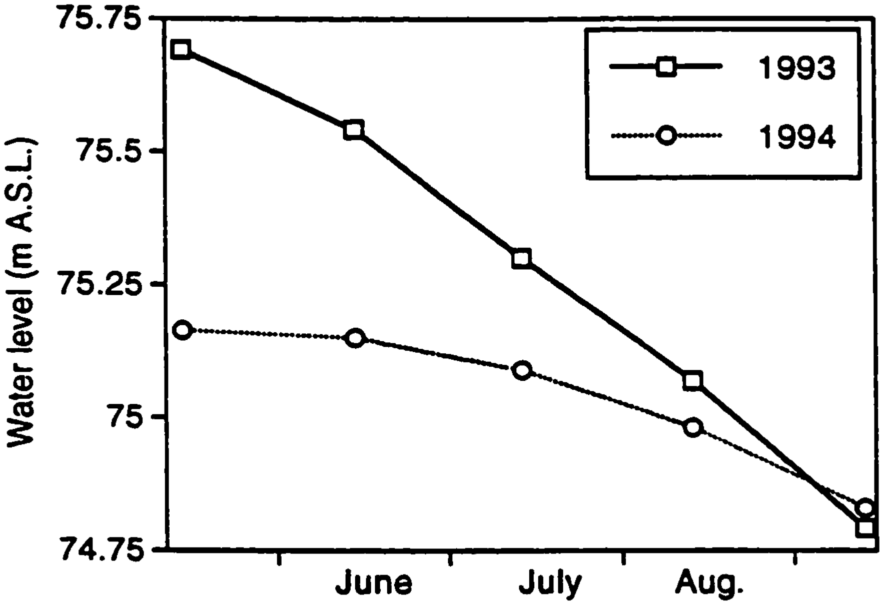

(a)
1
0.5
0
-0.5
-1
Canon 2
-1
-0.5
0
0.5
1
Canon 1
n/c
TEMP
micro
med
cycl
rot
CHLa
TP
TN
DEPTH
FLOW
TSS
asp
PLANT
(b)
1
0.5
0
-0.5
-1
Canon 2
-1
-0.5
0
0.5
1
Canon 1
FLOW
DEPTH
asp
micro
n/c
cycl
PLANT
TEMP
med
rot
TN
CHLa
TP
TSS

Figure 1-6. Change in mean monthly water level from May to September for 1993 (broken line) and 1994 (dashed line).


75.75
75.5
75.25
75
74.75
Water level (m A.S.L.)
June
July
Aug.
1993
1994

CHAPTER 2:

Predictions on the effect of carp exclusion on water quality, zooplankton and submergent macrophytes in a Great Lakes wetland.

Lougheed, V.L., B. Crosbie and P. Chow-Fraser. 1998.
Can. J. Fish. Aquat. Sci. 55: 1189-1197.

ABSTRACT: We conducted a study to examine the relationship between carp exclusion, water quality, zooplankton and submergent macrophytes. Twelve 50m^2 *in situ* experimental enclosures were installed in degraded Cootes Paradise Marsh during the carp spawning period in 1995. Enclosures were stocked with two or three carp of similar size, ranging from 13 cm to 59 cm and in total biomass from 23 to 2100 kg/ha. Turbidity, total phosphorus, and total ammonia concentrations increased predictably with total carp biomass in the enclosures. Although carp had no direct effect on zooplankton community structure, increased turbidity and nutrient load associated with carp activity resulted in reduced total zooplankton biomass. We developed a relationship between species richness and water turbidity for 19 wetlands in the Great Lakes basin which indicated that above an apparent threshold of 20 NTU there were less than 5 species of submergent plants, while a more diverse community existed in less turbid systems. We predict that water turbidity in Cootes Paradise may not be reduced below this threshold value of 20 NTU following carp exclusion. We emphasize the need to consider other factors that may contribute to increases in water turbidity and nutrient concentrations, including wind resuspension and substrate characteristics.

INTRODUCTION

Many authors have described the existence of two alternative stable states within shallow lakes or wetlands: one with clear water, dominated by submergent vegetation, and the other with turbid water, dominated by phytoplankton. Moss (1990) and Scheffer (1990) suggested that restoration of either state requires identifying and removing the stressor(s) that initiated the switch. To restore macrophytes, this could involve reducing nutrient levels to decrease phytoplankton biomass (e.g. Perrow et al. 1994; Mjelde & Faafeng 1997), adding piscivores and/or removing planktivores and benthivores to reduce algae through trophic cascade effects (e.g. Brönmark & Weisner 1992; Hanson and Butler 1994) or removing benthivorous fish to increase water clarity (Meijer 1990). Wetland managers in the Great Lakes basin are now attempting to restore degraded turbid, algal-dominated marshes to clear-water, macrophyte-dominated systems (e.g. HHRAP 1992; Whillans 1996); however, in many of these marshes where the nutrient levels are high, and the fish community is dominated by both planktivores and common carp, the key strategy that must be implemented to initiate such a switch is often difficult to identify.

The mechanical damage of submergent aquatic vegetation by common carp is well documented (Robel 1962; Crivelli 1983). Macrophyte growth may also be hindered by shading from high algal biomass (Brönmark and Weisner 1992) and elevated turbidity (Skubinna et al. 1995), both of which have been shown to increase in the presence of carp and other benthivorous fish (Meijer et al. 1990; Qin and Threlkeld 1990; Richardson et al. 1990; Breukelaar et al. 1994). In some of these studies, benthivores were also found to increase nutrient levels (Meijer et al. 1990; Breukelaar et al. 1994; Cline et al. 1994), although this has not been consistently observed for both phosphorus and nitrogen (Meijer et al. 1990; Qin and Threlkeld 1990; Richardson et al. 1990; Cline et al. 1994). Carp may also indirectly lead to elimination of large-bodied zooplankton such as *Daphnia*, since high turbidity inhibits their ingestion of phytoplankton (e.g. Kirk & Gilbert 1990; Kirk 1991), and loss of plant refugia permits them to be readily consumed by planktivores (e.g. Schriver et al. 1995). However, studies that included analysis of zooplankton community response to carp manipulation have been in plantless outdoor tanks and have been inconclusive, showing either a suppression of (Richardson et al. 1990) or no effect on (Qin & Threlkeld 1990; Cline et al. 1994) large zooplankton.

Although the direct physical destruction of natural communities of submersed vegetation by carp is well documented, the indirect effects, through sediment resuspension, and increased nutrient and algal concentrations are not well understood. Although the manipulation of benthivorous fish communities appears well studied, it has been suggested that different benthivorous species have different levels of benthic activity (Meijer et al. 1990; Breukelaar et al. 1994). To date, no studies exist that document the impact of a range of carp biomass on water quality and the zooplankton community *in situ*, in the absence of macrophytes. Moreover, there is little field evidence that clearly links improvement in water clarity to increased diversity of submersed aquatic vegetation, a condition that must be met if carp exclusion is to be promoted as an general management strategy. The primary objective of this paper is to address these deficiencies in the literature, and to provide a basis for improved decisions about wetland restoration and carp management in the Great Lakes.

Study site

Cootes Paradise Marsh (Fig. 2-1) is located in the Hamilton Harbour watershed at the western end of Lake Ontario. It is a severely degraded, 250-ha drowned river-mouth marsh, with an estimated carp density of 3500 individuals/ha in the near marsh areas during spawning, compared to 400 individuals/ha outside of spawning season (T. Theismeijer, McMaster Univ., pers. comm.). In the early 1900's, 90 percent of the marsh was covered with diverse emergent vegetation interspersed with smaller patches of submergents. Since the 1940's, the marsh has receded to less than 15% cover, consisting mainly of cattails (*Typha* sp.) and manna grass (*Glyceria* sp.). The loss of emergents has been attributed primarily to increased water levels, while submergent loss was likely due to decreased water clarity, resulting from reduced wind protection and increased carp disturbance, as well as increased nutrient load from the developing watershed (Chow-Fraser et al., In press). Cootes Paradise Marsh is being restored as part of the Remedial Action Plan for Hamilton Harbour (HHRAP) in order to create spawning and nursery habitat for warmwater fish species, mainly largemouth bass, smallmouth bass and northern pike, in the Hamilton Harbour ecosystem (HHRAP 1992). To accomplish this, the HHRAP calls for exclusion of large carp (>30 cm) in order to improve water quality and to re-establish submergent aquatic vegetation.

METHODS AND MATERIALS

Experimental design

Twelve 50 m^2 *in situ* enclosures were built in a shallow (40-70 cm), non-vegetated area of the marsh (Fig. 2-1a) where the sediment was composed of fine sand and silt and the mean summer phosphorus content of the sediment was approximately 0.921 mg SRP/g dry weight. Each side of an enclosure was 7.3 m and consisted of three adjoining panels, sunk 10 to 30 cm into the sediment and connected with plastic cable ties. Each panel was constructed with welded-wire fencing attached with plastic cable ties to a frame of 4 cast iron T-shape bars. Silt screen (estimated mesh size: 10 µm) was hand-sewn to each frame forming overlapping flaps where each panel met. The silt screen was chosen over less permeable plastic sheeting as it better resists tearing due to wind and wave action (pers. obs.) and, in a productive system like the study site, quickly becomes impermeable due to build-up of periphyton and sediment. To ensure build-up of detritus, the enclosures were left standing empty for two weeks prior to the start of the experiment.

On May 19, 1995 (day 1), after all fish were removed from the enclosures using a seine net, two or three carp of the same size were randomly placed in each of nine enclosures; three enclosures were randomly selected as controls and received no carp (Table 2-1; Fig. 2-1b). To encourage spawning, we intended to put 2 female and 1 male carp in each of our enclosures but two females perished due to handling stress; the final carp numbers (see sex ratio), mean length and biomass in each enclosure are provided in Table 2-1. The size of the carp was chosen based on those readily caught in Cootes

Paradise and surrounding areas. Although carp were not retrieved from the enclosures after the experiment, their presence was verified throughout the experiment by the presence of sediment clouds, a sign of carp activity.

Enclosure sampling methods

Plankton and water samples were collected from each enclosure and a nearby open water site between 04:00 and 06:00 on a total of four dates from May 19 (day 1) to June 2, 1995 (day 15), the period when carp were spawning in the marsh. The open-marsh site was included to provide a water quality reference that could be used to quantify enclosure effects. Water samples were taken at mid-depth with a peristaltic pump (capacity: 1.4 L/min) which was located in a canoe outside of the enclosures; samples were delivered through plastic tubing (inner diameter 6.4 mm) installed so as to withdraw water from the center of the enclosures and thus avoid edge effects.

Water samples were analyzed for total phosphorus (TP), soluble reactive phosphorus (SRP), nitrate nitrogen (NO_3-N), ammonia nitrogen (NH_3-N), suspended solids (SS) and dissolved oxygen (Winkler Method). Analyses were performed according to standard methods (APHA 1992), using Hach protocols and Hach chemicals as required. Turbidity was measured using a portable Hach turbidimeter (model 2100P). Chlorophyll-*a* was extracted using 90% acetone and a 1-h extraction period. Absorbance measurements were made with a Milton Roy spectrophotometer and results were corrected for phaeopigments by acidification.

Zooplankton were pumped into a 5-L beaker, filtered through 63 µm-mesh Nitex screen, backwashed into 60 mL bottles and preserved in 4% sugar-formalin. Samples collected on days 7, 11 and 15 were enumerated and identified and dry-weights were estimated as described in Lougheed and Chow-Fraser (1998). The earliest sampling date was not analyzed to allow zooplankton one week to respond to the different treatments. Zooplankton were grouped into size-specific functional groups for all analyses (i.e. herbivorous rotifers, microcladocerans (< 300 µm), medium-sized cladocerans (300 - 600 µm), macrocladocerans (600 µm), nauplii and copepodids, cyclopoid copepods, and predaceous rotifers), although medium- and macrocladocerans were not visible in the graphical output due to their low levels.

Wetland sampling

Nineteen wetlands located mainly in the Great Lakes basin were sampled twice each in the ice-free seasons of 1995 or 1996 for various factors including turbidity and submergent macrophyte richness (Table 2-2; Crosbie 1997). These wetlands ranged from pristine to severely degraded and were chosen to ensure a large gradient of disturbance. Ontario Wetland Evaluation reports (Ontario Ministry of Natural Resources), as well as personal observation were used to determine whether carp were present in each marsh. We recorded every species of submergent plant encountered within a 3-m radius of a randomly selected vegetated site. In wetlands with less than two species, the sparse distribution of individual plants (estimated as <5 plants/m^2) necessitated surveying the shoreline for approximately 100 meters. Keys by Fassett

(1940) were used to identify the submergent macrophyte species. Turbidity readings were taken in triplicate from the middle of the water column, approximately 3-m from aquatic vegetation using a portable Hach turbidimeter (model 2100P).

Statistical analysis

All calculations and statistical analyses were performed using SAS.JMP software (SAS Institute Inc. 1982), and graphical analysis was performed using Cricket Graph III. For all enclosure analyses, we excluded data from enclosure 1 (carp biomass = 0.11 kg/encl.) because a patch of sago pondweed (*Potamogeton pectinatus*) developed in this enclosure whereas all other control and experimental enclosures were devoid of plants. In the presence of submergent plants, turbulence created by the water pump dispersed sediment and epiphytes from plant surfaces and contaminated water samples. Simple linear regressions were performed on means of all sampling dates for both enclosure and wetland survey data. For analysis of zooplankton-water-quality relationships, zooplankton biomass and water quality parameters were transformed using a log (x+1) relationship. To describe changes in the zooplankton community through time, an ANOVA was constructed on arcsin-transformed percent biomass data for each functional taxon using enclosures as replicates for the 3 sampling dates. A Tukey-Kramer test was performed to confirm the significance tests of all combinations of dates. For wetlands, turbidity data entered into the Student t-test, the multi-pair comparisons and the regression against submergent plant species were log-transformed to ensure equal variances. Historical data from Cootes Paradise in 1948 and 1973 (Chow-Fraser et al.

1998) were also included in the wetland regression of number of submergent species versus log turbidity.

RESULTS

Water quality characteristics

To determine the overall impact of carp on water quality parameters, we calculated mean values for each enclosure over the 4 sampling dates and plotted these against carp biomass (Figs. 2-2 and 2-3) . There was a highly significant relationship between water turbidity and carp biomass ($p=0.0023$) that explained 76% of the variation (Fig. 2-2a); variation explained by this relationship increased to 83% ($p=0.0047$) when a second-order polynomial was used. Relationships between other water quality parameters and carp biomass were similar but weaker. Both total suspended solids (TSS) and inorganic suspended solids (ISS) varied significantly with carp biomass (Figs. 2-2b and c) with approximately 50% of the variation explained by a linear relationship and 70% explained by a non-linear relationship, in both cases. NH_3-N also increased linearly with carp biomass ($r^2=0.50$; Figs. 2-3a), while NO_3^--N showed no significant relationship (Fig. 2-3a & b). By contrast, TP and SRP (Fig. 2-3c & d) concentrations varied nonlinearly with carp biomass (no significant linear relationship was found; $p>0.05$); TP concentrations peaked at intermediate carp biomass whereas SRP concentrations were lowest at this biomass. Chlorophyll-*a* was not significantly related to carp biomass or nutrient levels during this study. Mean turbidity at the open marsh site was 80 NTU, as compared to 45-60 NTU measured in the enclosures, which corresponds to a 25 to 45% reduction in turbidity within the enclosures. This is consistent with earlier experiments showing that exclusion of carp from similar silt-screened enclosures reduced turbidity by approximately 50% (Chow-Fraser, unpubl. data).

Zooplankton

Seasonal succession was evident in the enclosures over the study period as rotifers such as *Brachionus*, *Keratella*, *Filinia* and *Asplanchna* were replaced by small-bodied cladocerans such as *Bosmina*, cyclopoid nauplii and small numbers of medium-sized cladocerans as the temperature increased from 13 to 22°C over the 15-day period. These differences between sampling dates were significant (ANOVA, $p<0.05$; Table 2-3). There were, however, no obvious differences among enclosures in terms of overall zooplankton community composition (Fig. 2-4).

Mean total zooplankton biomass decreased significantly with both TSS and ISS, with approximately 50% of the variation explained by a linear relationship and 60% explained by a nonlinear relationship (Fig 2-5a & b). Zooplankton biomass also declined significantly with increasing TP and NO_3-N (Fig 2-5c & d). We observed that, regardless of carp biomass, the community was dominated by small-bodied cladocerans, herbivorous rotifers and cyclopoid copepods and their nauplii.

Water clarity, submergent growth and presence of carp

When sorted by presence or absence of carp, the number of submergent species differed significantly between groups of wetlands (n=19, t-test; t=2.65; p=0.0169), with an average of 5 or fewer species in wetlands that supported carp, compared with 10 or more species in wetlands that did not. There were also highly significant differences (n=19; t-test; t=4.58; p=0.0003) between groups with respect to turbidity, with a mean turbidity of 26.1 NTU in marshes with carp, compared with 2.1 NTU in those without.

We found that the number of submergent species decreased significantly with mean seasonal water turbidity in the 19 wetlands and 2 historical Cootes samples, explaining 81% of the variation in the data (Fig. 2-6). Above an apparent threshold of 20 NTU, species richness of aquatic vegetation was reduced to <5 species. In the highly turbid systems, *Potamogeton pectinatus*, a species known to be tolerant of high water turbidity, was the only submerged macrophyte.

According to our enclosure experiments, removing large carp from Cootes Paradise Marsh would at most reduce turbidity, from existing levels of 80 NTU (open marsh site) to a low of 45 NTU (based on enclosures with no carp). This level of turbidity corresponds to <5 species of submergents (Fig. 2-6), far fewer than the 10+ species that existed in Cootes Paradise during a 1948 census when water clarity was only 5 NTU, and no improvement over 1973 conditions (Chow-Fraser et al., 1998).

DISCUSSION

Recent studies of mixed fish assemblages, which compared control and fish treatments (Richardson et al. 1990; Qin and Threlkeld 1990; Breukelaar et al. 1994; Cline et al. 1994) or total lake benthivore biomass before and after biomanipulation (Meijer et al. 1990) suggested that common carp play an important role in increasing turbidity and sometimes nutrient levels. Our data confirm that water turbidity and nutrient levels increased predictably with the biomass of spawning carp. Carp activity clearly resulted in increased sediment resuspension. The increase in phosphate and ammonia levels with carp biomass likely reflected both resuspension of nutrient-laden sediments and a proportionate increase in excretion rates by larger fish. Although benthivorous fish excrete mostly SRP and NH_3-N (Brabrand et al. 1990), bioavailable phosphorus can be easily removed from the water column by adsorption to particles under aerobic conditions, forming phosphate-rich inorganic particles (Holdren & Armstrong 1980). In our study, the resuspension of sediment by the larger spawners may have provided more surfaces for phosphate adsorption, therefore resulting in a reduction in SRP with a concomitant increase in TP.

Although levels of turbidity and nutrients generally increased with carp biomass, surprisingly high levels were still found in enclosures containing small carp (enclosure 2) and no carp (i.e. controls) (Fig. 2-2 & 2-3). Levels of turbidity and nutrients measured in these enclosures far exceeded those values reported by other researchers studying small benthivores (Horpilla & Kairesalo 1990; Qin & Threlkeld 1990; Richardson et al. 1990). Wind speed and fetch increase sediment resuspension (Sager 1996) as well as nutrient release in shallow systems (Hamilton and Mitchell 1997) and may have played an important role in reducing water clarity and increasing nutrient load in the enclosures located on the edges of the site (including C1, C3, enclosure 2) which were exposed to relatively high winds (3 m/s) at this shallow (40-70 cm) and exposed location. In addition, reduced benthivorous fish levels, as was the case in the control enclosures and those enclosures containing smaller carp, may result in an increased benthic invertebrate population that has the potential to increase phosphorus release by bioturbation (Holdren & Armstrong 1980; Phillips et al. 1994).

Phosphorus release from sediment is not only dependent on resuspension and bioturbation but also on the characteristics of the sediment, such as iron, aluminum, organic and TP content (Holdren & Armstrong 1980; Ostrofsky et al. 1989; Phillips et al. 1994) which can vary greatly among systems (Nürnberg 1988). For example, clay particles have a greater capacity for forming complexes with phosphorus; however, even within systems containing clay particles there exists variation in nutrient release. Meijer et al. (1990) and Breukelaar et al. (1994), working in systems with mainly sand and clay substrate, both found significant relationships between suspended sediment and carp and bream biomass; however, while Breukelaar et al. (1994) found an associated increase in phosphorus load, Meijer et al. (1990) did not. This discrepancy may be attributed to differences in sediment characteristics, and deserves further investigation. The inclusion of substrate descriptions in future studies would permit more accurate predictions regarding nutrient regeneration related to benthivorous feeding activities.

Unlike other studies where zooplankton community composition changed with removal of carp (Richardson et al. 1990), there were no obvious between-enclosure differences in zooplankton community structure in this study. In addition to residual effects, the time-period of this study, corresponding to carp spawning season, was an obvious limitation to these results in that the study was restricted to only two weeks in the spring, when zooplankton in the marsh were typically composed of low to moderate numbers of small animals (Lougheed and Chow-Fraser, 1998) which are less sensitive than the larger grazers to changes in water clarity (Kirk and Gilbert 1990; Kirk 1991). Overall, a reduction in total zooplankton biomass was associated with increased levels of suspended solids, as well as TP and NO_3-N, that were presumably due to carp activity. We therefore predict that by excluding spawning carp from Cootes Paradise, and thereby reducing the suspended solid and nutrient levels, total zooplankton biomass should increase, and that if suitable macrophyte habitats became available, previous work (Lougheed and Chow-Fraser, In press) suggests that this increased biomass would consist of larger grazers. A larger population of macrograzers may lead to further increases in clarity due to zooplankton grazing (Hanson & Butler 1994; Schriver et al. 1995); however, it appears that an increased biomass of smaller grazers will have no impact on algae, as indicated by chlorophyll-*a* in this study.

Scheffer (1990) theorized that in shallow lakes of homogeneous depth, submergent plants will disappear suddenly when a threshold turbidity is exceeded, which renders most of the lake unsuitable for plant growth. We found support for this theory in wetlands where above an apparent threshold of 20 NTU there were less than 5 species of submergents, while a more diverse community of macrophytes existed in clearer water. It is noteworthy that marshes where carp were absent had uniformly clear water (< 6 NTU), and a relatively diverse (> 7 species) and dense (estimated as >20 plants/m^2) submergent flora; however, while carp-free systems were always macrophyte dominated, macrophyte-dominated systems were not always carp-free (i.e. Big Creek, Hay Bay, Sawguin, and Turkey Creek). An obvious limitation to these results was the absence of data on carp biomass, which is known to be related to submergent plant cover (Robel 1962; Crivelli 1983). In addition, the presence of established submerged macrophytes could stabilize sediment and maintain water clarity (Hamilton and Mitchell 1996) in the presence of carp. Nonetheless, because these four wetlands were significantly clearer than other wetlands containing carp and were not significantly different from carp-free wetlands (ANOVA, p=0.0000, F=62.6, df= 2 & 16; confirmed with Tukey-Kramer), we suggest that this is additional evidence that water turbidity in Great Lake marshes must affected by factors other than carp, such as wind resuspension of sediment, high algal concentration, and fine substrate composition.

Further remedial actions will likely be necessary to promote the restoration of Cootes Paradise Marsh, as the increase in water clarity which will result from carp removal in the marsh is unlikely to be sufficient to allow the establishment of a diverse community of submergent vegetation. Carp-free enclosures had a mean turbidity of 45 NTU throughout the experimental period which was much higher than the 20 NTU required for submergent growth. We must acknowledge, however, that there are limitations to this prediction. Whole systems and enclosed systems behave differently, especially as it pertains to flow, turbulence and the settling of particles (Bloesch et al. 1988; Horpilla and Kairesalo 1990). In addition, the plantless enclosures may have inhibited carp activity during spawning season as carp tend to spawn near plants (Balon 1995), notably in Cootes Paradise where they congregated near the cattails at levels eight times higher than outside of spawning season (T. Theismeijer, McMaster University, pers. comm.). The 25 to 45 percent reduction in turbidity in the enclosures compared to the open marsh may, in part, reflect these limitations.

This study provides promising management applications towards predicting the extent of improvement in water quality from carp reduction schemes, as well as indicating the required improvement in water clarity for diverse submergent plant growth. At first glance these results may appear discouraging for Cootes Paradise Marsh; however, acknowledging that there is more than one stressor maintaining the marsh in its turbid state is an important step towards restoration. Although the ability to extrapolate across systems is useful, we must emphasize the need to accurately identify the stressor(s) which are degrading each specific system. We suggest that the relative impact of reductions in carp biomass on turbidity will be identical for most wetlands in the Great Lakes; however, the ambient conditions in each marsh will determine the ultimate result of any manipulation. Although carp activity is likely one of the primary agents degrading many of the Great Lakes wetlands, managers must consider all factors that may contribute to increases in water turbidity and nutrient concentrations, including wind resuspension, benthic bioturbation, algal concentrations, internal nutrient loading and substrate type, to ensure that the desired response from carp reduction or exclusion will be obtained in marsh restoration programs.

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Table 2-1. Biomass (kg/enclosure and kg/ha), sex ratio and mean fork length of carp added to each enclosure on May 19, 1995 (day 1).

Enclosure	Sex Ratio (F:M)	Type	Mean fork length (cm)	Total Biomass (kg/enclosure)	Total Biomass (kg/ha)
C1	-	Control	0	0	0
C2	-	Control	0	0	0
C3	-	Control	0	0	0
1	2:1	Immature	9.7	0.11	22.8
2	2:1	Immature	13.3	0.22	45.6
3	2:1	Mature	33.3	2.88	596
4	2:1	Mature	41.8	3.94	816
5	1:1	Mature	43.2	3.48	721
6	2:1	Mature	47.2	6.40	1326
7	2:1	Mature	52.3	8.18	1695
8	2:1	Mature	55.3	9.97	2066
9	1:1	Mature	59.3	10.10	2093

Table 2-2. Location and summary of mean turbidity, depth and number of common submergent plants for the 19 wetlands.

Wetland	Latitude	Longitude	Carp present (Y/N)	Depth (cm)	Mean turbidity (NTU)	No. of Submergent Plants
15 Mile Crk	43° 10' 00"	79° 19' 00"	Y	35	81	2
Big Crk	42° 57' 20"	80° 26' 50"	Y	105	4	9
Christie L.	44° 47' 00"	76° 28' 00"	N	40	2	9
Cootes Paradise	43° 16' 00"	79° 55' 00"	Y	20	83	1
Harris L.	45° 42' 00"	80° 82' 00"	N	78	2	10
Hay Bay	44° 10' 30"	76° 55' 30"	Y	86	3	15
Holiday	42° 02' 05"	83° 03' 00"	Y	30	276	0
Humber R.	43° 38' 00"	79° 29' 00"	Y	25	68	1
Joe's L.	45° 08' 00"	76° 41' 00"	N	80	1	10
Jordan Harbour	43° 11' 00"	79° 23' 00"	Y	46	56	2
Martindale Pond	43° 10' 07"	79° 16' 00"	Y	128	44	1
Presqu'ile Marsh	44° 00' 00"	77° 43' 00"	N	75	1	11
Sawguin Marsh	44° 06' 00"	77° 23' 00"	Y	80	4	9
Shebeshekong R.	45° 24' 30"	80° 19' 00"	N	80	6	8
Stump L.	44° 56' 48"	76° 38' 12"	N	53	2	12
Tay R. Marsh	44° 52' 45"	76° 10' 30"	N	50	1	14
Tobies Bay	44° 51' 00"	79° 47' 00"	N	123	3	7
Turkey Crk	42° 14' 08"	83° 05' 07"	Y	28	11	11
Waterford Pond	42° 56' 10"	80° 18' 45"	Y	44	23	4

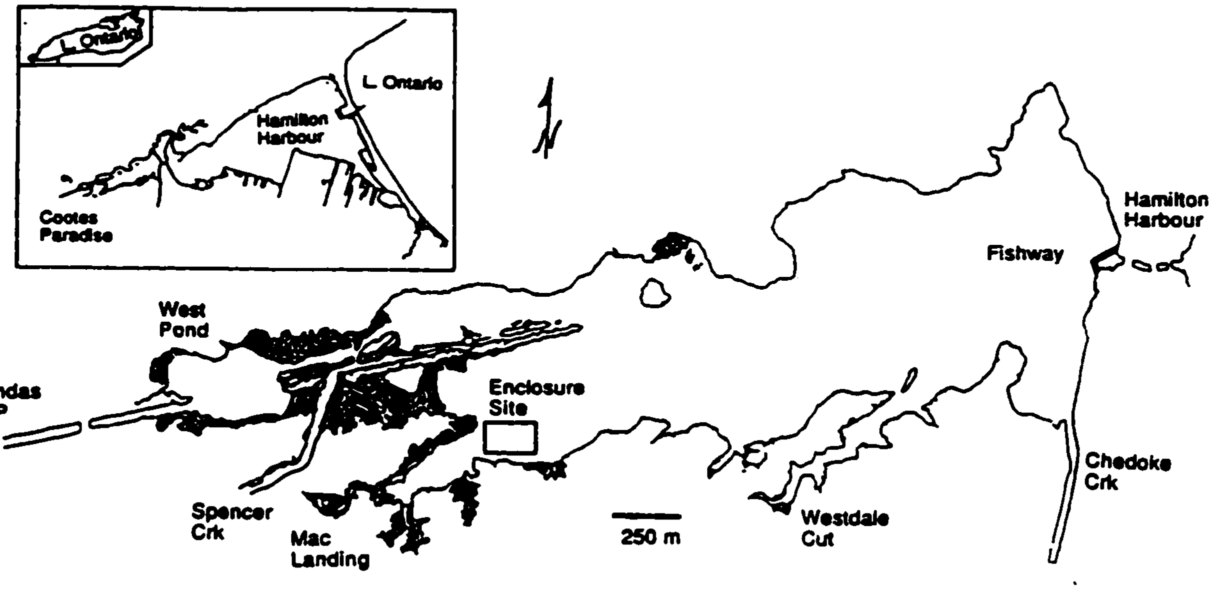
Table 2-3. Characteristics of the ANOVA of arcsin-transformed percent biomass data for each functional taxon compared for three sampling dates (days 7, 11 and 15).

Taxa	r^2	F Ratio	p-value	Significant Differences
Herbivorous rotifers	0.94	232.13	0.0000	Day 7 > 11 > 15
Microcladocerans	0.70	35.18	0.0000	Day 15 > 11 > 7
Medium-sized cladocerans	0.37	8.78	0.0010	Day 15 > 11 & 7
Macrocladocerans	0.13	2.23	0.1249	-
Nauplii and copepodids	0.43	11.35	0.0002	Day 15 > 11 & 7
Cyclopoid copepods	0.08	1.29	0.2897	-
Predaceous rotifers	0.63	25.29	0.0000	Day 11 > 7 & 15

NOTE: The degrees of freedom for the regression and the residual were 2 and 30, respectively. The significant differences between dates were confirmed with a Tukey-Kramer test.

Figure 2-1. Map of Cootes Paradise Marsh showing A) remnant aquatic vegetation (shaded areas) and the enclosure site and B) the location of the enclosures relative to each other.

a)


L. Ontario
L. Ontario
Hamilton Harbour
Cootes Paradise
Hamilton Harbour
Fishway
West Pond
Dundas STP
Enclosure Site
Chedoke Crk
Spencer Crk
Mac Landing
250 m
Westdale Cut

b)

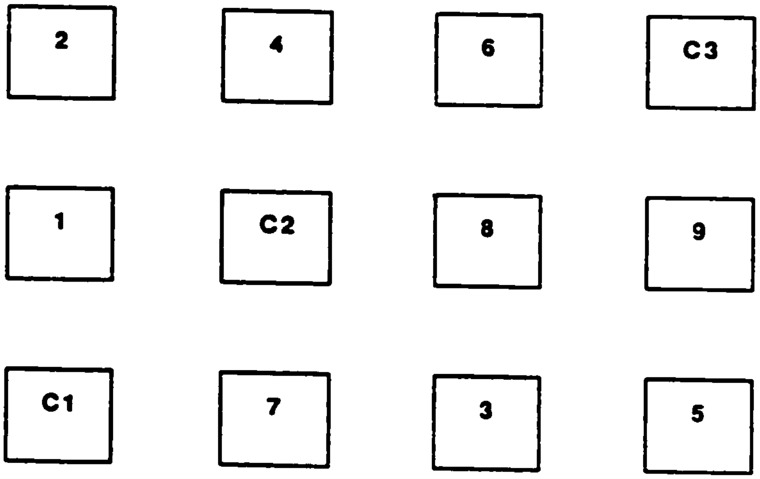

2
4
6
C3
1
C2
8
9
C1
7
3
5

Figure 2-2. Relationship between mean carp biomass and a) turbidity, b) total suspended solids (TSS) and, c) inorganic suspended solids (ISS) in enclosures over two weeks during carp spawning season.

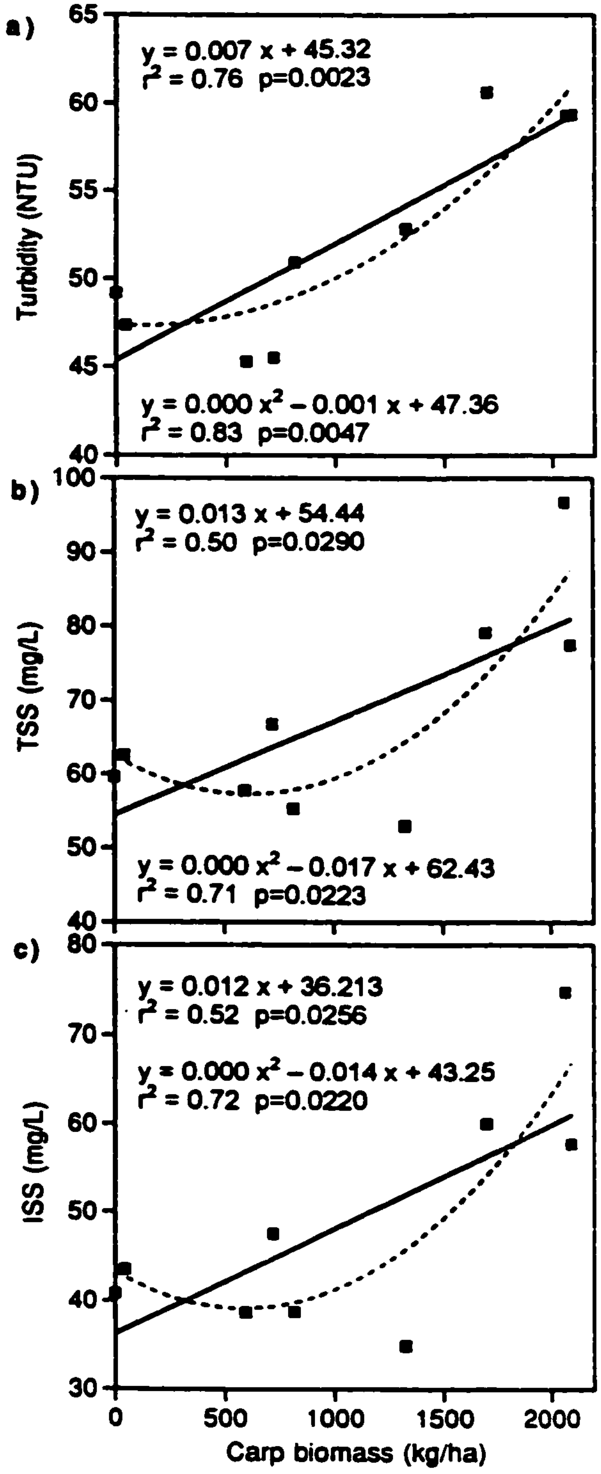

a)
y = 0.007 x + 45.32
r² = 0.76 p=0.0023
y = 0.000 x² – 0.001 x + 47.36
r² = 0.83 p=0.0047
Turbidity (NTU)
65
60
55
50
45
40
b)
y = 0.013 x + 54.44
r² = 0.50 p=0.0290
y = 0.000 x² – 0.017 x + 62.43
r² = 0.71 p=0.0223
TSS (mg/L)
100
90
80
70
60
50
40
c)
y = 0.012 x + 36.213
r² = 0.52 p=0.0256
y = 0.000 x² – 0.014 x + 43.25
r² = 0.72 p=0.0220
ISS (mg/L)
80
70
60
50
40
30
0
500
1000
1500
2000
Carp biomass (kg/ha)

Figure 2-3. Relationship between carp biomass and a) NH_3-N, b) NO_3-N, c) TP and d) SRP.

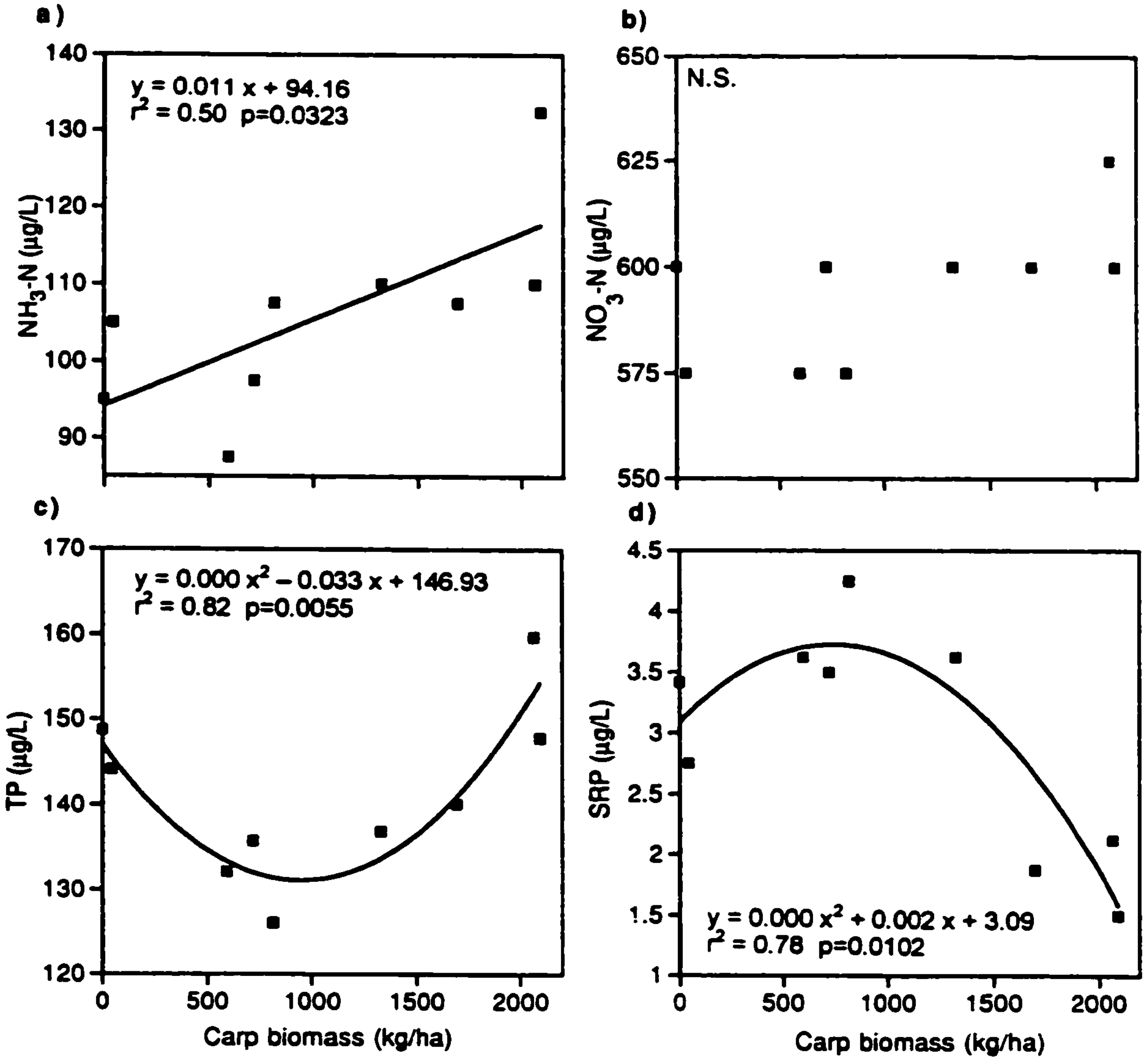

a)
140
130
120
110
100
90
NH$_3$-N (µg/L)
y = 0.011 x + 94.16
r^2 = 0.50 p=0.0323
b)
650
625
600
575
550
NO$_3$-N (µg/L)
N.S.
c)
170
160
150
140
130
120
TP (µg/L)
y = 0.000 x^2 – 0.033 x + 146.93
r^2 = 0.82 p=0.0055
0
500
1000
1500
2000
Carp biomass (kg/ha)
d)
4.5
4
3.5
3
2.5
2
1.5
1
SRP (µg/L)
y = 0.000 x^2 + 0.002 x + 3.09
r^2 = 0.78 p=0.0102
0
500
1000
1500
2000
Carp biomass (kg/ha)

Figure 2-4. Mean percent biomass of zooplankton functional groups in all enclosures (except enclosure 1; see text for details).

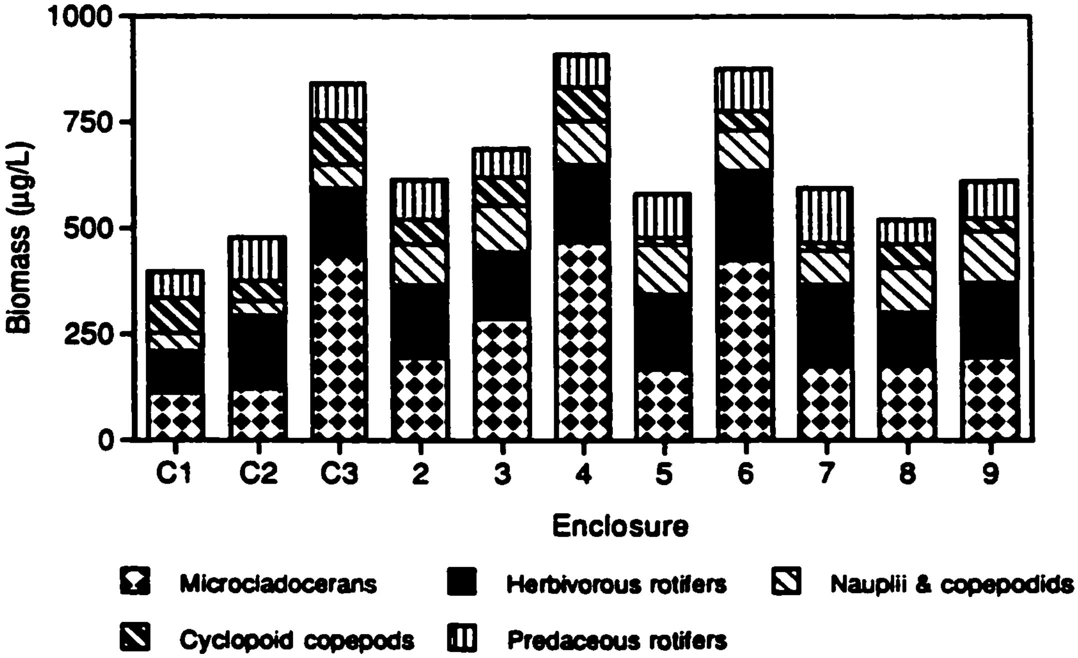

1000
750
500
250
0
Biomass (µg/L)
C1
C2
C3
2
3
4
5
6
7
8
9
Enclosure
Microcladocerans
Herbivorous rotifers
Nauplii & copepodids
Cyclopoid copepods
Predaceous rotifers

Figure 2-5. Relationship between total zooplankton biomass (ZB) and a) TSS, b) ISS, c) TP and d) NO_3-N.

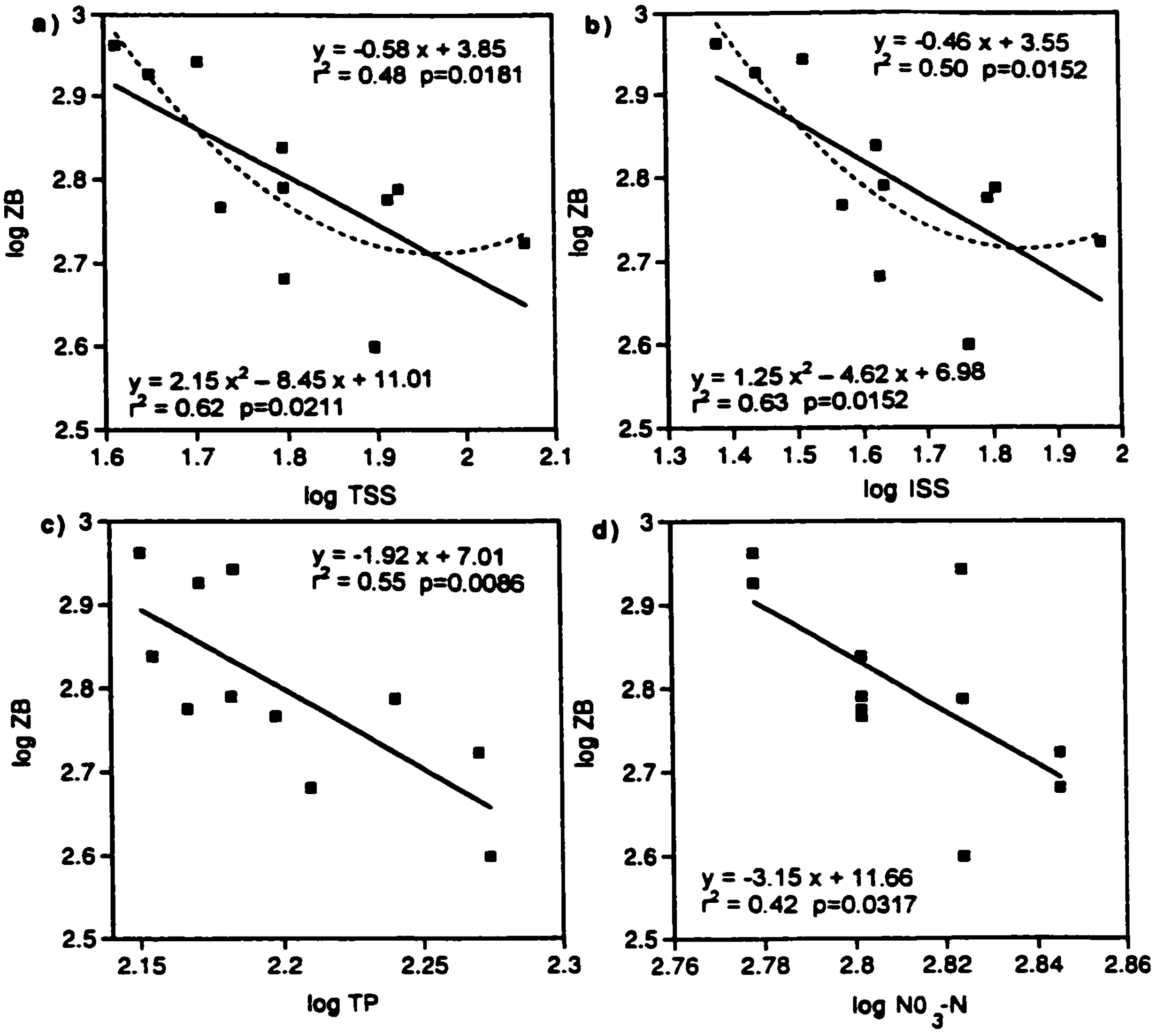
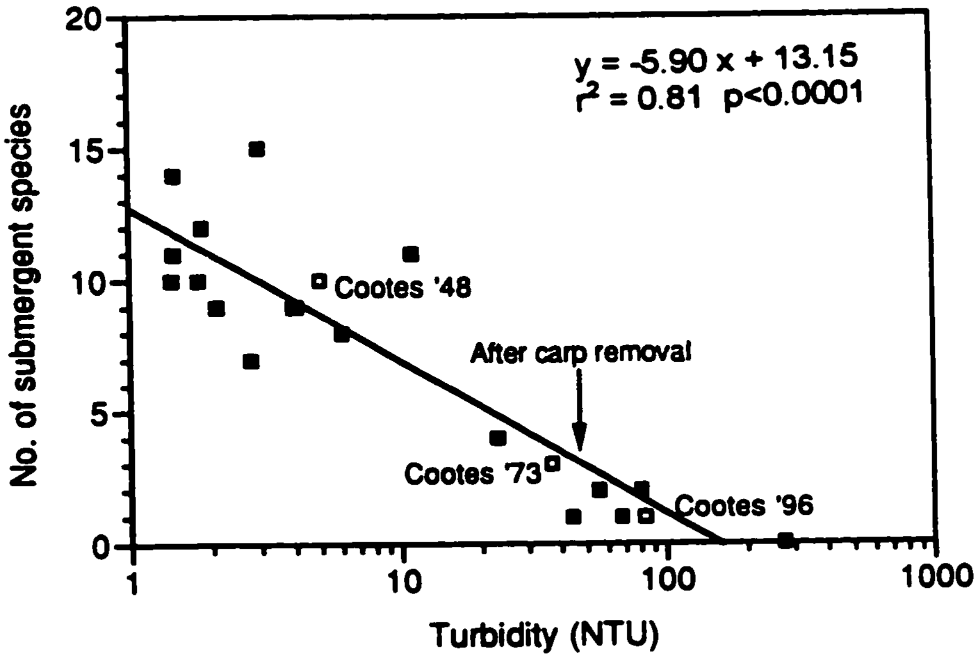

a)
y = -0.58 x + 3.85
r^2 = 0.48 p=0.0181
y = 2.15 x^2 – 8.45 x + 11.01
r^2 = 0.62 p=0.0211
log ZB
3
2.9
2.8
2.7
2.6
2.5
1.6
1.7
1.8
1.9
2
2.1
log TSS
b)
y = -0.46 x + 3.55
r^2 = 0.50 p=0.0152
y = 1.25 x^2 – 4.62 x + 6.98
r^2 = 0.63 p=0.0152
log ZB
1.3
1.4
1.5
1.6
1.7
1.8
1.9
2
log ISS
c)
y = -1.92 x + 7.01
r^2 = 0.55 p=0.0086
log ZB
2.15
2.2
2.25
2.3
log TP
d)
y = -3.15 x + 11.66
r^2 = 0.42 p=0.0317
log ZB
2.76
2.78
2.8
2.82
2.84
2.86
log NO_3-N

Figure 2-6. Relationship between the number of submergent plant species versus log turbidity (log scale) for 18 marshes in the Great Lakes basin (solid squares) and Cootes Paradise from 1948, 1973 and 1996 (open squares). Also indicated is the predicted water clarity following carp removal (45 NTU) in Cootes Paradise Marsh.


y = -5.90 x + 13.15
r² = 0.81 p<0.0001
Cootes '48
After carp removal
Cootes '73
Cootes '96
No. of submergent species
0
5
10
15
20
1
10
100
1000
Turbidity (NTU)

CHAPTER 3:

Spatial variability in the response of lower trophic levels after biomanipulation in a freshwater marsh.

Lougheed, V.L. and P. Chow-Fraser

ABSTRACT: A turbid, eutrophic coastal marsh of Lake Ontario was sampled 2 seasons prior to (1993, 1994) and following (1997, 1998) carp exclusion to study changes in water quality, submersed macrophyte growth, and shifts in community structure of phytoplankton and zooplankton. Samples were collected from May to September in three habitats: open water, vegetated (cattail beds) and sewage lagoon. In the first year after carp exclusion, mean seasonal water turbidity decreased at all sites by 49-75%; this was accompanied by growth of submergent plants in shallow, sheltered areas including in the vicinity of the cattails at the vegetated site. This drop in turbidity was not significant in the second year after exclusion at the open water and lagoon sites, with turbidity levels declining by only 26-43% of 1993-1994 values; only the vegetated site showed a sustained decrease in turbidity and persistent growth of submergent plants. At the vegetated site, increased clarity was concurrent with a significant reduction in edible algal biomass and an increased representation of large zooplankton grazers and substrate-associated cladocerans. At the open water site, a spring clear-water phase was only evident during the first year of exclusion and this coincided with the unusual appearance of a large population of *Daphnia*. The lagoon site remained turbid throughout the study. Results of this study indicate that: 1) response of lower trophic levels to biomanipulation was variable from site-to-site and contributed to the co-existence of two alternative states in the marsh; 2) both benthivore removal (to reduce bioturbation) and planktivore reductions (to produce top down effects) were required to produce clear water and allow submersed macrophyte growth; and, 3) a positive feedback system between zooplankton and submergent macrophytes helped maintain water clarity in vegetated areas.

INTRODUCTION

Use of biomanipulation to force a switch from turbid, phytoplankton-dominated lakes to clear-water, macrophyte-dominated systems is a well documented restoration strategy for shallow freshwater lakes (see Moss et al. 1996; Scheffer 1998). Despite the large number of cases documenting the switch between these two alternative states, it has often been difficult to distinguish between two possible mechanisms that lead to the initial increase in light penetration: 1) reduction in sediment resuspension by removal of benthivorous fish such as common carp (*Cyprinus carpio*) or bream (*Abramis brama*) (e.g. Meijer et al. 1990), or 2) trophic cascade-induced clarity through removal of planktivores with subsequent increase in top-down control of phytoplankton by zooplankton (e.g. Ozimek et al. 1990; van Donk et al. 1990; Hanson and Butler 1994). In either case, successful biomanipulations have been followed rapidly by increased water transparency, and the development of submersed aquatic vegetation throughout the lake.

The stability of the clear-water state has also been difficult to predict (Scheffer 1998) and may be due to differences among lakes with respect to interactions at the lower trophic levels. For example, establishment of aquatic vegetation may help maintain water clarity in some lakes by stabilizing the sediment and reducing sediment resuspension by wind (Hamilton and Mitchell 1997). It may also suppress algal growth through competition for nitrogen (Ozimek et al. 1990; van Donk et al. 1990) and some macrophyte taxa contain chemicals which can have an allelopathic effect on algae (e.g. Wium-Anderson et al. 1982). Increase in macrophyte cover can also provide refugia for large-bodied zooplankton grazers such as *Daphnia*, and this has been used to explain the shift in zooplankton community from rotifers and small-bodied cladocerans to larger-bodied forms following biomanipulation (Hansen and Jeppesen 1992; Hanson and Butler 1994) with enhanced top-down control of algae (Timms and Moss 1984; Schriver et al. 1995). Clearly, the outcome of biomanipulation, both in terms of degree of success and stability of the altered state, can be affected by any number of these factors, and it is becoming increasingly important to understand the different roles played by these forcing variables so that effective management strategies can be devised.

Although the theory of alternative stable states has been applied widely to shallow eutrophic lakes in Europe (80% of reported biomanipulations in Drenner and Hambright 1999), it has not received as much attention in North America, and has seldom been applied to coastal wetlands of the Laurentian Great Lakes, even though these wetlands are similar to shallow lakes in a number of ways. First, like shallow lakes, they are highly influenced by anthropogenic stressors such as urban and agricultural runoff (Crosbie and Chow-Fraser 1999). Secondly, loss of submergent vegetation in these wetlands have been blamed on increased nutrient and sediment loads from developing watersheds, as well as sediment resuspension from benthivorous fish such as the common carp, *Cyprinus carpio* (Whillans 1996; Chow-Fraser 1998, 1999). However, there are also key differences between shallow lakes and wetlands, notably with respect to hydrology and seasonal fish migrations. For example, unlike most shallow lakes, coastal wetlands are subject to large-lake processes, including long-term and seasonal fluctuations in water level (Maynard and Wilcox 1996). In Cootes Paradise Marsh (Lake Ontario), where mean depth is 0.7 m, water levels have fluctuated by more than a meter over an 8-to-10-year cycle, and by more than 0.5 m seasonally (about 15% of the marsh routinely dries up by the end of the summer) (Chow-Fraser et al. 1998; Chow-Fraser 1999). Secondly, coastal wetlands have highly variable and relatively short residence times (< 1 week to 41 d in Cootes Paradise Marsh; Chow-Fraser, unpub. data) compared with residence times of months to years for shallow lakes. Finally, the connectedness between large lakes and coastal wetlands allows seasonal migrations by the fish community. Some fish species use wetlands for only part of their life (e.g. spawning, feeding, or nursery area) and are present only seasonally, while others are permanent residents (Jude and Pappas 1992). Hence, the fish community in coastal wetlands tends to vary substantially from year to year.

Because of such seasonal variations, as well as site-to-site differences with respect water turbidity (Chow-Fraser 1998) and the zooplankton community (Lougheed and Chow-Fraser 1998), coastal wetlands might be expected to exhibit highly variable temporal and spatial responses to biomanipulation. Although spatially variable responses to fish removal have been observed within large, shallow European lakes (e.g. Meijer and Hosper 1997), studies have yet to provide comparative statistical analyses of changes in water quality, phytoplankton and zooplankton among several sites and explain how these site-to-site differences are maintained within a single system. Such a comparison is necessary for predicting the effectiveness of biomanipulation in triggering the switch to a clear-water state when temporally and spatially variable ecosystems are being restored. In this paper, we describe contemporaneous changes in lower trophic levels at three characteristically different sites in Cootes Paradise Marsh, a degraded urban coastal marsh of Lake Ontario, from which carp have been actively excluded since 1997 (Wilcox and Whillans 1999). The overall goal of this paper is to evaluate the impact of benthivore removal on water quality, plankton communities and submersed aquatic vegetation, paying particular attention to site-to-site variations in the response. Our results should indicate the relative importance of benthivore removal as a forcing variable in triggering the switch to the clear-water state from the turbid state for degraded coastal marshes, and the effectiveness of carp exclusion as a restoration strategy in a spatially variable marsh.

STUDY SITE

Compared with the large number of biomanipulation studies on shallow lakes, there have only been a few studies on Great Lakes coastal wetlands, which have mainly been confined to small-scale enclosure experiments (Havens 1991; Lougheed et al. 1998). Fortunately, recent attempts in ecosystem restoration through the Binational Great Lakes Remedial Action Plans (see Krantzberg et al. 1997) have provided a rare opportunity to formally test biomanipulation theory in these wetlands. The restoration of Cootes Paradise Marsh is one of the most ambitious restoration projects in the Great Lakes basin, designed to restore aquatic vegetation through a carp exclusion scheme (Hamilton Harbour Remedial Action Plan Stage 2 1992; Wilcox and Whillans 1999).

Cootes Paradise is a 250-ha drowned river-mouth marsh located at the westernmost point of Lake Ontario (43° N, 79° W) (Figure 3-1). At the turn of the century, a diverse community of emergent and submergent vegetation covered 90 percent of the marsh; however, by the 1970's only 15% of the marsh retained cover, primarily cattails (*Typha* sp.) and manna grass (*Glyceria* sp.). The loss of emergents has been attributed primarily to increased water levels, while submergent loss has been blamed on decreased water clarity resulting from sediment resuspension from wind and carp activity, as well as excessive inputs of nutrients from sewage and runoff (Chow-Fraser 1998).

Prior to biomanipulation, carp formed the majority of the fish biomass in Cootes Paradise Marsh. The seasonal migration of fish such as carp in and out of the marsh in the spring and fall facilitated the exclusion of these migrating species via the construction of a fishway at the outlet of Cootes Paradise (see Figure 3-1) during the winter. The fishway used 5-cm wide grating to physically exclude large fish from the marsh (see Wilcox and Whillans 1999). Fish not capable of passing through the grating were manually processed such that all fish other than carp were released into the marsh, whereas carp were released outside Cootes Paradise. This effectively prevented large carp (>30 cm) from entering the marsh after February 1997. Carp densities in the marsh declined from approximately 700 kg/ha before exclusion (1996) to 50 kg/ha (1997), while young-of-the year carp were not reduced in abundance in the marsh, likely due to carp spawning in areas outside the marsh. Furthermore, in 1997, larval fish production peaked later than usual in the region due to unseasonably cool spring conditions, (T. Theijsmeijer, Royal Botanical Gardens, pers. comm).

Table 3-1 shows that, over the course of the study period, mean yearly water levels in L. Ontario varied from relatively high (1993) to moderate (1997, 1998) to low (1994, 1995, 1999); however, even in low water years macrophytes were not observed to increase in abundance in the marsh. It was not until carp were excluded from the marsh that dense patches (>2500 stems/ha) of submergent vegetation, primarily *Potamogeton pectinatus*, grew in shallow and sheltered areas of the marsh, most notably in the vicinity of established cattail beds; however, the exposed sections of the marsh remained essentially devoid of vegetation (Lundholm and Simser 1999).

METHODS

Sampling and counting methods

Water, phytoplankton and zooplankton were collected bi-weekly from mid-May to late August for two years pre-exclusion (1993 and 1994) and two years post-exclusion (1997 and 1998). Three sites, all approximately 1 km apart, were studied (Figure 3-1). There was a relatively deep open water site near the marsh outflow (mean depth ranges from 97-127 cm); a shallow lagoon site that historically received loadings from the Dundas Sewage Treatment Plant (depth 43-69 cm); and a vegetated site within the cattails beds of a marsh inlet (depth 23-49 cm). Following exclusion, there were also dense patches of submersed macrophytes in the vicinity of the vegetated site; however, the sampling location remained within the cattail beds. Depth, selected water quality characteristics and submersed macrophyte densities from each site are summarized in

Table 3-2. All sites were sampled 8 times per year with the exception of the vegetated site in 1993 (n=7) and 1994 (n=7) and the lagoon site in 1998 (n=6) because access was restricted due to factors beyond our control.

All samples for water, zooplankton and phytoplankton analyses were collected from the middle of the water column at each site. Water and zooplankton were analyzed as summarized in Lougheed and Chow-Fraser (1998). For statistical and graphical analyses, zooplankton were divided into the following categories: microcladocerans (<300 µm), medium cladocerans (300-600 µm), macrocladocerans (*Daphnia*; >600 µm), herbivorous rotifers, nauplii and copepodids, cyclopoid copepods, predaceous rotifers and substrate-associated cladocerans (incl. *Simocephalus* and Chydorid cladocerans). Phytoplankton samples were collected using a Van Dorn bottle and preserved with Lugol's Iodine. Subsamples of 5-mL were settled for 24-hours in algal settling chambers, with very concentrated samples diluted by 10 to 20 times with distilled water. Algal cells and colonies were identified using up to 400X magnification and measured along one full transect of each settled slide under a phase microscope at 200X magnification. The entire slide was also surveyed for large cells and colonies. Algal bio-volumes were calculated by approximation to geometric shapes. Taxa were divided into algal groups (blue-greens, greens, euglenoids, chrysophytes, diatoms, cryptophytes and dinoflagellates) and either edible (<30 µm) or inedible (>30 µm) size classes after Chow-Fraser and Knoechel (1985).

Statistical analyses

Statistical analyses were performed using SAS.Jmp software (SAS Institute Inc., Cary, N.C., version 3.1.5). Changes in the frequency of occurrence of zooplankton taxa were determined using a chi-square test ($p<0.05$). The number of sampling trips where a species was present at a given site in a given year was compared to the expected occurrence, assuming that each species was equally likely to occur at any site at anytime (i.e. sum of all occurrences divided by the total number of samples (92)).

Comparisons of mean water quality variables, phytoplankton biomass and zooplankton biomass between years and clusters were analyzed with an analysis of variance followed by Tukey-Kramer multiple comparisons at the 95% significance level. These data were $\log_{10}$-transformed to normalize the distribution. Where relevant, yearly data were divided into early summer and late summer sampling trips. The division point was selected as July 9 for all years, to ensure 4 sample dates before and after this date for all those sites visited 8 times per year. Cluster analysis was performed on $\log_{10}$-transformed means (phytoplankton and zooplankton) of each given site in a given year using Ward's minimum variance method. Data were divided into taxonomic and functional categories as described above.

RESULTS

Water quality

Table 3-2 summarizes selected mean water quality variables for each of the sites. All sites were generally eutrophic and turbid (TP = 121-435 μg/L; TNN = 300-5095 μg/L; Turbidity = 10.7-91 NTU). The lagoon site usually experienced higher turbidity, nutrient and algal levels relative to the other sites. At the vegetated site, water turbidity for both years after exclusion was significantly reduced by 55 to 75% relative to pre-exclusion years (Figure 3-2). Post-exclusion turbidity at the open water and lagoon sites was more variable. In 1997, turbidity at these 2 sites was reduced by greater than 49% relative to pre-exclusion years. This decrease was significant at the open water site. In 1998 these changes were not significant with 26% (open water) and 43% (lagoon) reductions. Figure 3-2 also illustrates how the reductions in water turbidity compared to the 45% maximum reduction predicted by Lougheed et al. (1998). The vegetated site surpassed this predicted increase in clarity for both years following exclusion.

Similarly, total and edible phytoplankton biomass were significantly reduced at the vegetated site for both years following carp exclusion (Figure 3-3). There were no consistent changes in mean seasonal phytoplankton biomass observed at the other 2 sites following exclusion. There was, however, a significant increase in total, edible and inedible phytoplankton at the open water site in 1998. Finally, there were no significant differences between pre- and post-exclusion years for either TP or TNN concentrations; although TP was higher at all sites in 1998 (Table 3-2), with the open water site having significantly higher levels in 1998 relative to all other years (ANOVA, Tukey-Kramer, $p<0.05$).

Phytoplankton

Marsh-wide, there was not an obvious change in the number of phytoplankton taxa following exclusion. The number of phytoplankton taxa before exclusion (79-88) overlapped that seen after the exclusion (73-84), and the marsh-wide species list was identical to that summarized in Chow-Fraser et al. (1998) for 1993 and 1994, with the exception of a few rare green species (i.e. *Lagerheimia*, *Penium*, *Planctonema*, *Pseudotetraedron*, *Ulothrix*) which were absent in the post-exclusion samples. The phytoplankton community throughout the marsh was generally dominated by cryptophytes, diatoms, euglenoids and green algae (Figure 3-4)

Comparison of phytoplankton composition at each site revealed no statistically significant differences in mean taxonomic composition between 1993 and 1994. After exclusion, however, there were some notable changes. In 1998, there was a significant (ANOVA; Tukey-Kramer; $p<0.005$) decline in euglenoids at the open water site, as well as significantly higher (ANOVA; Tukey-Kramer; $p<0.005$) contribution of blue-green algae to the late summer community. There was also an increase in cryptophyte biomass at both the open water (ANOVA; Tukey-Kramer; $p<0.005$) and lagoon sites ($p>0.05$) in early summer 1998.

Cluster analysis of the phytoplankton community functional groups revealed 4 main clusters (Figure 3-5). The first cluster (A) grouped together the open water site from 1993 to 1997, as well as the vegetated site in 1994 where there was moderate biomass of the common groups of edible phytoplankton (i.e. greens, cryptophytes) and high biomass of euglenoids and edible diatoms. The second cluster (B) separated the open water site in 1998 from the open water site in all other years. In 1998, this site was characterized by low biomass of euglenoids, moderate to high biomass of edible greens and cryptophytes and high biomass of inedible blue-greens and diatoms. The third cluster (C) consisted of the lagoon site in all years as well as the vegetated site in 1993 where there was relatively high biomass of most groups of edible phytoplankton and moderate to high levels of inedible blue-greens, greens and diatoms. The final cluster (D) consisted of post-exclusion vegetated sites which had lower biomass of nearly all edible algal groups, as well as reduced inedible blue-green and diatom levels.

Zooplankton

The total number of zooplankton species in the marsh following carp exclusion increased from 27 species (1993-1994) to 40 species (1997-1998) (Table 3-3). Individually, only the vegetated site showed a sustained increase in species richness, from less than 26 to more than 32 species. This increase included both an increase in rotifers (9 new species) and cladocerans (6 new species) (Table 3-4). No zooplankton species disappeared completely from the marsh. A complete list of zooplankton species found pre-exclusion can be found in Lougheed and Chow-Fraser (1998).

The fewest changes in zooplankton species composition occurred at the open water site, while the largest number of changes occurred at the vegetated site (Table 3-4).

Both the lagoon and vegetated sites lost 2 rotifer taxa following carp exclusion, while they acquired many new rotifer species. All the new rotifers encountered in the marsh post-exclusion (Table 3-4; 9 species) were found at the vegetated site, and 2 species that were uncommon before exclusion (*M. bulla*, *P. patulus*) occurred more frequently than expected (Chi-square, $p<0.05$). The lagoon site showed the greatest increase in the number of cladoceran taxa, including both taxa that were new to the marsh (*Ceriodaphnia*, *Chydorus*, *Daphnia*, *Pleuroxus*) and taxa previously observed at the other sites (*Leydigia*, *Scapholeberis*, *Simocephalus*). The only cladocerans that appeared more frequently than expected following exclusion (Chi-square, $p<0.05$), were the large cladoceran grazers: *Daphnia* at the open water site, and *Simocephalus* at the vegetated site.

Comparison of zooplankton composition revealed no striking differences in zooplankton composition between pre-exclusion years, except at the lagoon site (Figure 3-6) where micrograzers dominated in 1993 and cyclopoids dominated in 1994. Post-exclusion, the appearance of macrograzers at the open water site and substrate-associated cladocerans at the vegetated site were the most notable changes in seasonal dynamics in the marsh. At the open water site, macrograzer biomass in early summer 1997 was significantly higher than in early summer of pre-exclusion years (ANOVA, Tukey-Kramer, $p<0.05$), when *Daphnia* never occurred above a level of 3 individuals/L. These *Daphnia* reached a level of 530 individuals/L (4000 µg/L) in June 1997 before the population crashed abruptly at the start of July (Figure 3-7). This trend was not repeated in 1998. Similarly, at the vegetated site, the biomass of *Daphnia* was significantly greater in early summer 1997 than it was in early summer of pre-exclusion years (ANOVA, Tukey-Kramer, $p<0.05$); although this represented a much lower biomass than that seen at the open water site (Figure 3-7). The only apparent sustained change in the zooplankton community following carp exclusion was the increased biomass of substrate-associated cladocerans at the vegetated site in both post-exclusion years relative to both pre-exclusion years (ANOVA, Tukey-Kramer, $p<0.05$). Cyclopoid biomass was numerically higher in 1998 at the open water site, although only significantly higher when compared to 1993 and 1997 data (ANOVA, Tukey-Kramer, $p<0.05$). Finally, there was a significant reduction in herbivorous rotifer biomass at the lagoon site in 1998 relative to previous years (ANOVA, Tukey-Kramer, $p<0.05$).

Cluster analysis of the site-year data resulted in 5 main groups based on similarity of biomass in the zooplankton functional groups (Figure 3-8). The pre-exclusion open water and vegetated sites, as well as the open water site in 1998 formed one group (A) characterized by relatively high biomass of microcladocerans and herbivorous rotifers, as well as moderate levels of medium-sized cladoceran grazers. The second cluster (B) grouped together the lagoon in 1993, 1994 and 1997, characterized by low biomass of most functional groups, but relatively high levels of herbivorous rotifers. The third cluster (C) included only the open water site in 1997, which, as seen in Figure 3-6, displayed a relatively unique zooplankton assemblage, consisting of a high proportion of herbivorous rotifers and macrocladocerans (*Daphnia*), and relatively low biomass of other groups. The fourth cluster (D) uniquely identified the vegetated site in 1997, which had a relatively high biomass of substrate-associated zooplankton and medium-sized cladocerans, moderate levels of macrocladocerans, as well as a low biomass of herbivorous rotifers. The final cluster (E) grouped together the lagoon and vegetated site in 1998. These sites had greater biomass of substrate-associated cladocerans and cyclopoid copepods and reduced biomass of herbivorous rotifers.

DISCUSSION

Using a series of enclosure experiments Lougheed et al. (1998) predicted that the exclusion of large carp from shallow, non-vegetated areas of Cootes Paradise would at most increase water clarity by 45% of ambient levels; however, the initial results in 1997 showed an improvement of 49 to 75%. We attribute this greater than expected increase in water clarity to the unchecked zooplankton grazing made possible by the delayed arrival of young-of-the-year (YOY) fish (T. Theijsmeijer, Royal Botanical Gardens, pers. comm.) due to unseasonably cool spring conditions. This unexpected, temporary removal of zooplanktivory initiated a zooplankton-mediated spring clear-water phase which increased water clarity sufficiently to promote the establishment of submergent plants in shallow, sheltered areas and thus prolonged the clear-water period.

An important finding in this study was that the three sites within the marsh followed different trajectories following biomanipulation due to different mechanisms acting at the lower trophic levels. Water clarity and macrophyte growth improved most in those areas of the marsh that were least degraded (i.e. areas with emergent vegetation), whereas the other sites remained turbid and devoid of vegetation or only exhibited temporary changes in water clarity. This confirms Chow-Fraser's (1998) conclusion that without further remedial measures, factors such as wind and wave action, high sediment loading and high algal biomass will likely continue to keep the rest of marsh in a relatively turbid state.

The occurrence of a spring clear-water phase due to cladoceran grazing, typified by reduced algal biomass, a reduced proportion of small particles and increased *Daphnia* biomass, has been noted in nutrient-rich lakes (Lampert et al. 1986; Ozimek et al. 1990; Hanson and Butler 1994). The open water site was near the outlet to Hamilton Harbour and was approximately 0.5 km from any shoreline or vegetated habitat. In May 1997, *Daphnia galeata mendotae*, a species previously unrecorded in Cootes Paradise, entered the marsh from the relatively cool and clear harbour (Chow-Fraser, unpubl. data), rapidly peaked in population size at the open water site, and then crashed abruptly. This crash was coincident with the appearance of YOY fish and was followed immediately by the rise in phytoplankton biomass (Figure 3-7). During the *Daphnia* bloom, the water cleared and the bottom (>1 m; Table 3-1) was illuminated for approximately a week in early summer 1997. By using the published length-filtering rate equation of Chow-Fraser and Knoechel (1985), we estimate that at this peak, *Daphnia* were filtering the water column almost 5 times a day (community grazing rate of 4.84 L filtered/L/day). By comparison, in the second year following exclusion (1998) when YOY fish actually appeared earlier than expected (T. Theijsmeijer, Royal Botanical Gardens, pers. comm.) due to an unusually warm spring, we did not see any proliferation of *Daphnia*, nor any evidence of a clear-water phase. Apparently, without a sustained decrease in planktivory (natural or induced), this spring clear-water phase is not likely to be repeated at the open water site.

Although it appeared that the open water site returned to pre-exclusion conditions in 1998, several changes occurred at the lower trophic levels which illustrate that the communities at this site remained in a state of transition following carp exclusion. Consistent with other studies in which cyclopoids tended to dominate when faced with increased fish predation (Schriver et al. 1995), cyclopoid copepods contributed substantially to the zooplankton biomass at the open water site in the second year following biomanipulation (1998), when YOY fish actually appeared earlier than expected. Cyclopoid predominance may occur in spite of the presence of sufficient edible algae for cladoceran grazers (Schriver et al. 1995), because they are better than cladocerans at escaping predators. Changes in predation pressure may also have played a role in structuring the phytoplankton community. Following periods of intense zooplankton grazing, some studies have shown an increase in cryptophyte biomass (e.g. Hanson and Butler 1994; Schriver et al. 1995), such as that observed in early summer 1998 at the open water and lagoon sites. Chow-Fraser et al. (1998) noted that increased eutrophication in Cootes Paradise through the 1970's resulted in an increased proportion of phytoplankton capable of heterotrophic uptake and tolerant of low light environments (euglenoids and cryptophytes). Although euglenoids appear to have been reduced following exclusion at the open water site, cryptophytes still contribute substantially to the population, indicating that increases in clarity were insufficient to reduce the competitive advantage of these taxa.

Like the open water site, there was significantly higher biomass of *Daphnia* in early summer 1997 at the vegetated site, although the spring peak in herbivorous zooplankton biomass was composed primarily of *Bosmina* (Figure 3-7). This resulted in a substantially lower community grazing rate relative to the open water site; however, zooplankton were still capable of filtering the water column nearly three times per day (2.78 L filtered/L/day) in June 1997. In fact, greater than 55% of the variation in edible phytoplankton biomass at these two sites in 1997 can be explained by estimations of zooplankton grazing rates ($\log_{10}$-linear regression; $p<0.04$). Although some authors have suggested that reduced bioturbation of nutrient-laden sediment, rather than zooplankton grazing, may be more important in controlling algal biomass in shallow, hypereutrophic systems (Horpilla and Kairesalo 1990; Havens 1991), reduced algal biomass at these two sites in the absence of nutrient reductions argues strongly against this hypothesis.

The vegetated site experienced a longer-term increase in clarity following biomanipulation, due in part to the development of dense patches of submersed macrophytes in the vicinity of cattail beds; this resurgence in vegetation also occurred in other shallow and sheltered regions of the marsh during 1997 (Lundholm and Simser 1999). Macrophytes may contribute to the maintenance of clarity by stabilizing sediment (Hamilton and Mitchell 1997), competing with phytoplankton for nitrogen (Ozimek et al. 1990; van Donk et al. 1990), preventing algal growth through allelopathy (Wium-Anderson et al. 1982) and providing zooplankton refugia against predation (Timms and Moss 1984). For example, a mid-summer peak in the biomass of substrate-associated cladocerans coincided with a reduction in edible biomass levels at this site in 1997 (Figure 3-7), and a similar trend was observed in 1998 (not shown). Because of their relative isolation and reduced outflow from these inlets except during storm events, the submersed macrophyte beds had only a localized effect on water clarity and the distribution of the zooplankton community (Scheffer 1998). This effect will probably be maintained in future years since submergent macrophytes (especially turbidity-tolerant canopy-forming taxa such as *P. pectinatus*) were able to persist despite the lack of a clear-water phase in the spring of 1998.

The post-exclusion increase in large-bodied zooplankton such as *Daphnia* and *Simocephalus* at the vegetated site had been predicted by Lougheed and Chow-Fraser (1998). This rise in abundance coincided with a significant reduction in the biomass of edible algae, especially edible green algae, and may be partially attributed to an increase in submersed macrophytes in the vicinity of the cattail beds which may have provided better habitat for zooplankton grazers. Isolated emergent macrophyte beds (*Typha* sp.) in the shallow inlets and bays of Cootes Paradise have historically provided refugia for larger zooplankton grazers (Kay 1949; Lougheed and Chow-Fraser 1998; Chow-Fraser et al. 1998) which had contributed to moderate decreases in edible phytoplankton biomass relative to adjacent open water areas (Chow-Fraser et al. 1998); however, zooplankton were unable to noticeably control algal standing crop in vegetated areas until submergent plants became established after the reduction in carp activity and the zooplankton-mediated spring clear-water phase. This agrees with the suggestions of other studies which showed that large herbivorous cladocerans increased water clarity when they were provided with macrophyte refugia from predation (Timms and Moss 1984; Schriver et al. 1995).

The increased diversity of habitats in submerged vegetation has been associated with an increased diversity of zooplankton species (Pennak 1966; Paterson 1993; Gaiser and Lang 1998), especially plant-associated taxa such as *Simocephalus* and some chydorids, (Pennak 1966; Timms and Moss 1984; Gaiser and Lang 1998) or taxa associated with detritus and sediment (e.g. *Pleuroxus*)(Fryer 1968). Our results definitely support these findings. Of the three study sites, only the vegetated site showed a sustained increase in species richness, from less than 26 to more than 32 species, including 9 new rotifer species and 5 new cladoceran species. Of these 14 new taxa, at least 8 are known to frequent vegetated environments, including the rotifers *Euchlanis*, *Lepadella*, *Monostyla quadridentata*, *Mytilina* and *Trichocerca elongata* (Pennak 1966) and the cladocerans *Pleuroxus*, *Ceriodaphnia* and *Chydorus* (Pennak 1966, Quade 1969, Beklioglu and Moss 1996).

We suggest that, following carp exclusion, the open water and vegetated sites represented 2 alternative states existing in one system. The trophic state of these two sites was relatively similar, with no significant differences between mean TP or TNN levels observed for the open (TP = 171.5 µg/L; TNN = 555.3 µg/L) and vegetated sites (TP = 222.7 µg/L; TNN = 504.5 µg/L). However, using data from 1998 for illustrative purposes, the open water site was turbid (44 NTU) and algal dominated (13.3 mg/L phytoplankton; ~50 stems/ha submersed macrophytes), while the vegetated site represented the clear (11 NTU), macrophyte-dominated (2500 stems/ha; 1.4 mg/L phytoplankton) state. While we observed these differences for 2 years following carp exclusion, the stability of the macrophyte-dominated state in isolated regions of Cootes Paradise is uncertain, especially given that Jeppeson et al. (1990) have shown that above a phosphorus level of 150 µg/L, the macrophyte-dominated state cannot be maintained over the long term.

Relatively hydrologically separate from these 2 sites was the lagoon, which also appeared not to have been affected by the biomanipulation. As pointed out by Moss et al. (1996) and Jeppeson et al. (1990), three conditions necessary for stabilization of a clear-water macrophyte dominated system are: 1) low nitrate concentration, 2) low phosphorus levels and 3) presence of large grazers. In systems dominated by aquatic vegetation, phytoplankton is often nitrogen limited as plants remove nitrogen from the water column and provide the alternating aerobic and anaerobic conditions required for denitrification (Scheffer 1998). The concentration of nitrate nitrogen is extremely high at this site (Table 3-1) owing to aeration of ammonia in the effluent discharged from the Dundas Sewage Treatment Plant (Chow-Fraser et al. 1998). The rich source of nitrate in the sewage effluent essentially ensures that algae are never nitrogen limited in the lagoon and consequently aquatic plants never gain a competitive advantage. This is not as much of a concern in other areas of the marsh because nitrate concentration decreases by an order of magnitude (Chow-Fraser et al. 1998) as water flows east towards Hamilton Harbour and is diluted by inflows from Spencer's Creek and Borer's Creek (see Figure 3-1).

Total phosphorus levels at the lagoon site varied between 139 and 593 µg/L over the course of this study, while the other two sites had phosphorus levels between 48-473 µg/L (open water) and 39-482 µg/L (vegetated site). Jeppeson et al. (1990) stated that the long-term stability of biomanipulation efforts is unlikely when phosphorus levels exceed 150 µg/L. With increased eutrophication there is higher predation pressure on zooplankton by an abundant planktivorous fish population and water clarity is insufficient to allow submergent plant colonization. This may have important consequences for the long-term success of the biomanipulation of Cootes Paradise Marsh as a whole; however, this is especially true of the lagoon site, where total phosphorus levels always exceeded 139 µg/L.

Besides the effect of planktivory in controlling the zooplankton population, the absence of large grazers may also be attributed to the high turbidity at this site, as elevated turbidity can mechanically interfere with cladoceran feeding (Kirk and Gilbert 1990); however, the moderate increase in the biomass of most size classes of cladocerans following carp exclusion suggests that the zooplankton community in the lagoon may have partially responded to the reduced turbidity. The appearance of eight new species of cladoceran grazers after the exclusion was coincident with a reduction in turbidity from >70 NTU to <51 NTU. Four cladoceran taxa (*Ceriodaphnia*, *Chydorus*, *Daphnia*, *Pleuroxus*) were new to the marsh, while three other taxa (*Leydigia*, *Scapholeberis*, *Simocephalus*) were present at other sites, pre-exclusion. We suggest that the establishment of larger zooplankton at this site may be limited by water turbidity rather than food for two reasons: 1) the reduction in turbidity was not accompanied by a change in algal biomass and 2) edible phytoplankton contributed on average greater than 75% of the total algal biomass at this site in each year studied (Figure 3). It is difficult to separate the direct effects of reduced turbidity from those that are indirect (i.e. macrophyte growth) without the use of experimental enclosures; however, marsh-wide increases in the number of medium and large cladoceran species (even at unvegetated sites), following exclusion suggests that the reduced turbidity may have conferred a competitive ability to those species adapted to a less turbid environment.

The discussion to this point has focused largely on changes in lower trophic levels and turbidity, because these elements responded most strongly to the carp exclusion; however, it is worth noting that TP levels also appear to have been affected. Reduction of benthivorous fish biomass has been associated with a reduction in TP levels (e.g. Horpilla and Kairesalo 1990; Havens 1991; Breukelaar et al. 1994); however, enclosure experiments by Lougheed et al. (1998) suggested that removing carp from Cootes Paradise Marsh may in fact indirectly lead to higher phosphorus release through bioturbation from a larger benthic invertebrate population (Holdren and Armstrong 1980; Phillips et al. 1994). This is supported by the increase in phosphorus levels at the open water site in 1998. This situation needs to be monitored further in light of 1) elevated biomass of blue-greens at this site in 1998, 2) new species of N-fixing blue-green filaments appearing at all sites in 1998 (unpubl. data), and 3) the increased role of phytoplankton in explaining water clarity in the marsh (unpubl. data). The improved light environment in shallow regions of the marsh following exclusion, together with the nutrient-rich sediment appear to be promoting the growth of benthic algal blooms (primarily *Spirogyra* sp.) (V. Lougheed, pers. obs.) which have not been reported in the marsh since the 1940's (Chow-Fraser et al. 1998). This is consistent with other Great Lakes studies in which filamentous green benthic algae have been shown to increase following improvements in the light environment (e.g. Lowe and Pillsbury 1995). These changes may have important implications for the flow of energy through the benthic food web in Cootes Paradise Marsh and should be further investigated.

Conclusions and management implications

These results detail the mechanisms acting at lower trophic levels that promoted the maintenance of two alternative states: a turbid, algal-dominated state and a clear-water, macrophyte-dominated state (e.g. Moss et al. 1996; Scheffer 1998), within a single ecosystem that is structurally highly variable. Many trophic interactions, both human-induced and natural, played a role in these changes. The exclusion of benthivorous carp to reduce sediment resuspension (Meijer 1990; Lougheed et al. 1998), in conjunction with the natural delay in the arrival of planktivorous YOY fish (T. Theijsmeijer, Royal Botanical Gardens, pers. comm.) combined to promote the presence of large grazers in the first year of biomanipulation. This initiated a spring clear-water phase (e.g. Lampert et al. 1986; Hanson and Butler 1994) which promoted macrophyte growth in shallow, sheltered areas of the marsh. The establishment of submersed macrophytes at the vegetated site subsequently promoted water clarity due, in part, to provision of better habitat for large zooplankton grazers (Timms and Moss 1984). Conversely, a combination of wind-induced and algal turbidity, as well as nitrogen enrichment (at the lagoon site), act to restrict the growth of submergent macrophytes and large zooplankton grazers and thus maintain both the deeper, open water site and shallow, hypereutrophic lagoon site in a turbid state.

Zooplankton have played a large role in the changes seen in Cootes Paradise Marsh: including the initiation of a spring clear-water phase in 1997 and the maintenance of water clarity at the vegetated site post-exclusion. Although a direct trajectory from turbid to clear water was only recorded at the vegetated site, it is too early to tell if the response has been delayed at the other sites. Nevertheless, we speculate that without further manipulation – in the form of macrophyte plantings, water level manipulation, fetch control, reduced loadings of sediment and nutrients – only isolated, vegetated parts of the marsh will provide suitable wetland habitat for a diverse zooplankton community.

Cootes Paradise Marsh will need to be continually monitored over the next decade to determine the ultimate effect of the carp exclusion and other restorative efforts. At this early stage, the long-term stability of the biomanipulation remains uncertain. Unfortunately, the results of this experiment will probably be confounded by another uncontrollable environmental variable – water level. The Laurentian Great Lakes are now (1999) experiencing the lowest water levels seen since the 1960s, approximately half a meter lower than levels recorded in 1997 and 1998. Ground surveys and aerial photos are showing that emergent vegetation is expanding quickly into newly available habitat in Cootes Paradise Marsh (unpubl. data); whether this will displace submergent macrophytes or promote their expansion into other areas of the marsh remains to be seen. If this low water period is sustained, the expansion of cattail beds may prove beneficial in providing fetch breaks and thereby reducing wind-induced turbidity, although this will occur at the expense of the recovery of the submergent plant community. The confounding effect of fluctuating water level will need to be factored out of our overall evaluation of the impact of carp exclusion before we can ultimately recommend this as a restoration strategy for other degraded Great Lakes wetlands.

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Table 3-1. Mean yearly water level (m above sea level) for Lake Ontario (referred to International Great Lakes Datum 1985). Data are from Canadian Hydrographic Services, Department of Fisheries and Oceans. Burlington, Ontario, Canada.

Year	Water level (meters A.S.L.)
1993	75.04
1994	74.76
1995	74.74
1996	74.87
1997	74.96
1998	74.92
1999	74.57

Table 3-2. Means of bi-weekly sampling trips from mid-May to late August each year before (1993 and 1994) and after (1997 and 1998) carp exclusion for selected water quality variables and submergent plant densities (from Lundholm and Simser 1999) at each site.

	1993	1994	1997	1998
OPEN WATER				
Depth(cm)	126.7	97.5	114.4	95.2
Turbidity (NTU)	73.7	59.5	25.7	44.0
TP(µg/L)	156.5	126.3	121.4	281.9
TNN (µg/L)	671.1	512.5	387.5	650
Submergent plants (stems/ha)*	0	0	50	50
LAGOON				
Depth(cm)	69.4	42.8	53.4	51.7
Turbidity (NTU)	70.9	91.0	36.4	51.1
TP(µg/L)	287.9	363.8	271.7	435.8
TNN (µg/L)	3485.7	4116.7	5095	3950
Submergent plants (stems/ha)*	0	0	0	0
VEGETATED				
Depth(cm)	48.9	22.6	32.9	26.9
Turbidity (NTU)	23.8	42.7	10.7	10.8
TP(µg/L)	197.9	197.4	230.7	264.8
TNN (µg/L)	483.3	328.6	300	906.3
Submergent plants (stems/ha)*	0	0	2500	2500

*NOTE: Submergent plant densities were determined by Lundholm and Simser (1999) along transects near our sampling sites. There is no published information on submergent plant densities after 1997; however, we have no reason to believe they decreased from 1997 levels.

Table 3-3. Comparison of the total number of zooplankton species before (1993-1994) and after (1997-1998) carp exclusion for the whole marsh and for individual sites.

	Before	exclusion	After	exclusion
	1993	1994	1997	1998
All sites	27	27	40	40
Open water	25	25	25	23
Lagoon	25	26	28	23
Vegetated	26	25	32	34

Table 3-4. List of rotifer and cladoceran taxa that were extirpated (occurred in both years pre-exclusion; not found post-exclusion) or were new (not found pre-exclusion) at the 3 study sites following carp exclusion.

	Open water	Lagoon	Vegetated
Extirpated		*Brachionus caudatus*	*Brachionus quadridentatus*
		Trichocerca sp.	*Keratella quadrata*
New		*Euchlanis* sp.	*Euchlanis* sp.
		Monostyla quadridentata	*Lepadella* sp.
		Platyias patulas	*Monostyla quadridentata*
		Platyias quadricornis	*Monostyla cornuta*
		Trichocerca elongata	*Mytilina* sp.
			Notholca sp.
			Platyias quadricornis
			Ploesoma sp.
			Trichocerca elongata
	Camptocercus macrurus	*Ceriodaphnia reticulata*	*Ceriodaphnia reticulata*
	Ceriodaphnia reticulata	*Chydorus sphaericus*	*Chydorus sphaericus*
	Chydorus sphaericus	*Daphnia galeata mendotae*	*Daphnia galeata mendotae*
	Daphnia galeata mendotae	*Leydigia leydigii*	*Pleuroxus denticulatus*
	Leydigia leydigii	*Pleuroxus denticulatus*	*Pleuroxus procurvatus*
	Pleuroxus denticulatus	*Pleuroxus procurvatus*	
	Simocephalus exspinosus	*Scapholeberis mucronata*	
		Simocephalus exspinosus	

Figure 3-1. Location of sampling sites (LAGOON, VEGETATED and OPEN) in Cootes Paradise Marsh. Shaded areas indicate the presence of emergent vegetation throughout the study period.

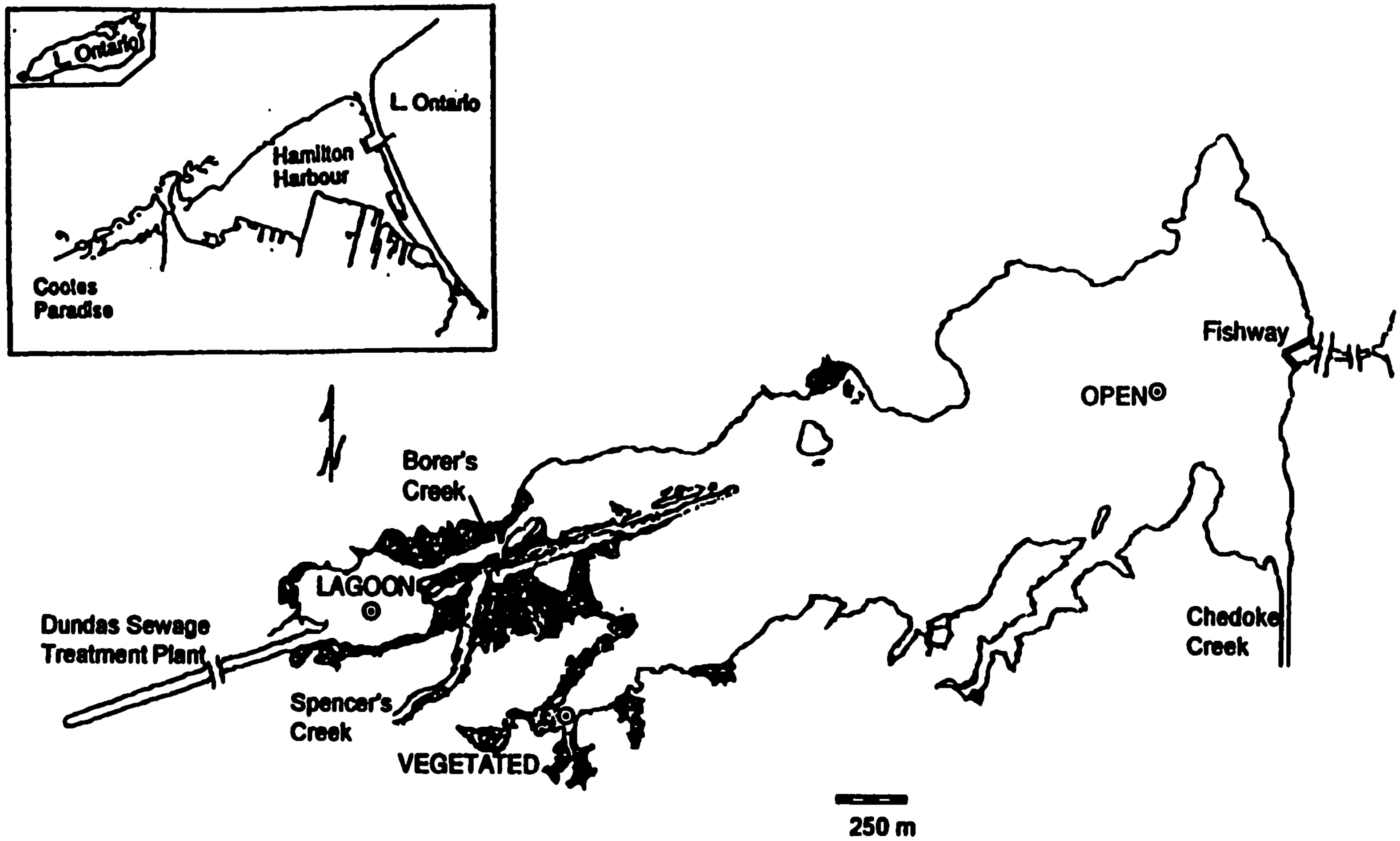

L. Ontario
L. Ontario
Hamilton Harbour
Cootes Paradise
N
Borer's Creek
LAGOON
Dundas Sewage Treatment Plant
Spencer's Creek
VEGETATED
OPEN
Fishway
Chedoke Creek
250 m

Figure 3-2. Comparison of mean turbidity levels prior to (1993 & 1994) and following (1997 & 1998) carp exclusion at three sites in Cootes Paradise Marsh. Dashed lines represent the range of turbidity expected following carp exclusion as predicted by enclosure experiments (Lougheed and Chow-Fraser, 1998). Asterisks indicate significant differences between years (ANOVA, Tukey-Kramer, $p<0.05$).

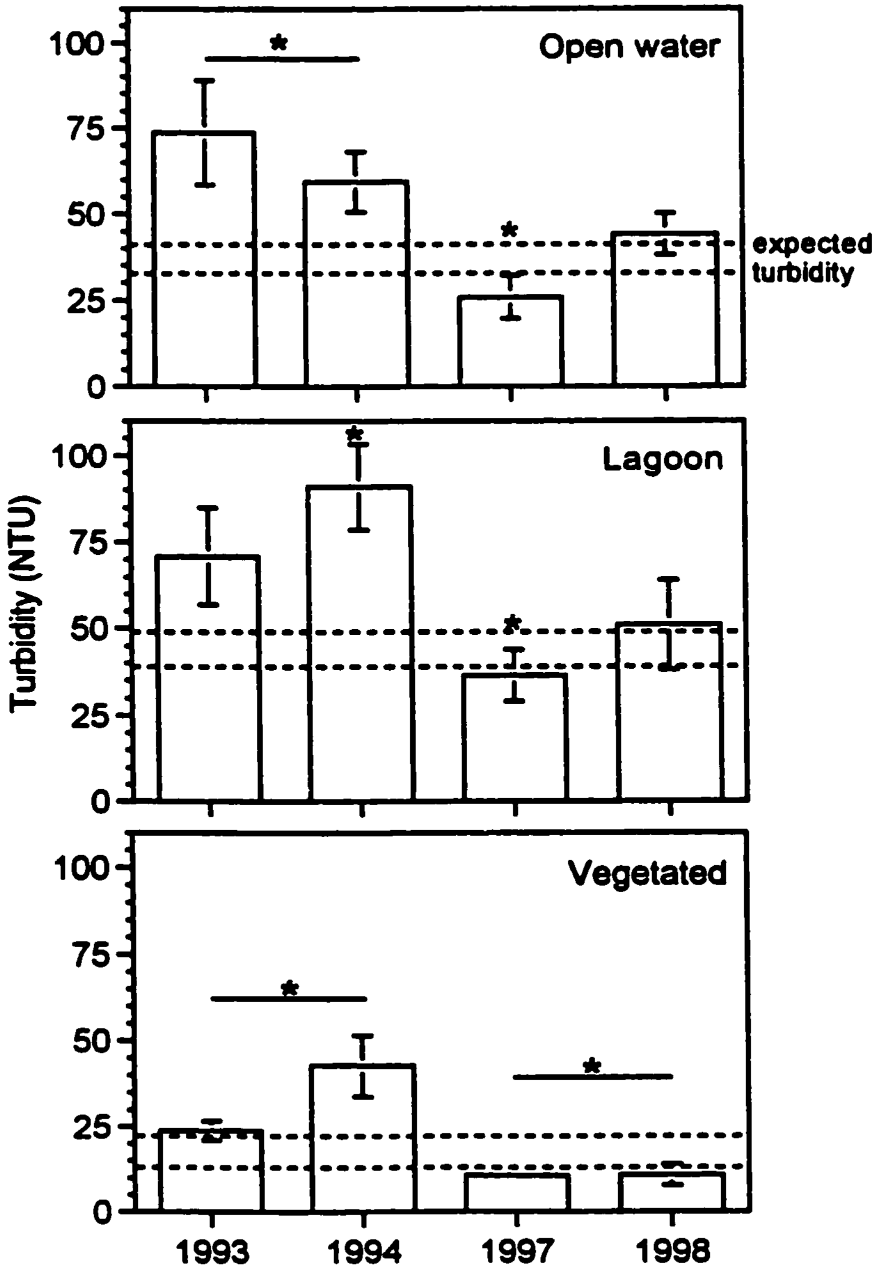

Open water
Lagoon
Vegetated
expected turbidity
Turbidity (NTU)
0
25
50
75
100
*
1993
1994
1997
1998

Figure 3-3. Comparison of total, edible and inedible phytoplankton biomass prior to (1993 & 1994) and following (1997 & 1998) carp exclusion at three sites in Cootes Paradise Marsh. Symbols indicate significant differences between years (ANOVA, Tukey-Kramer, $p<0.05$) for total (*), edible (e) or inedible (i) phytoplankton.

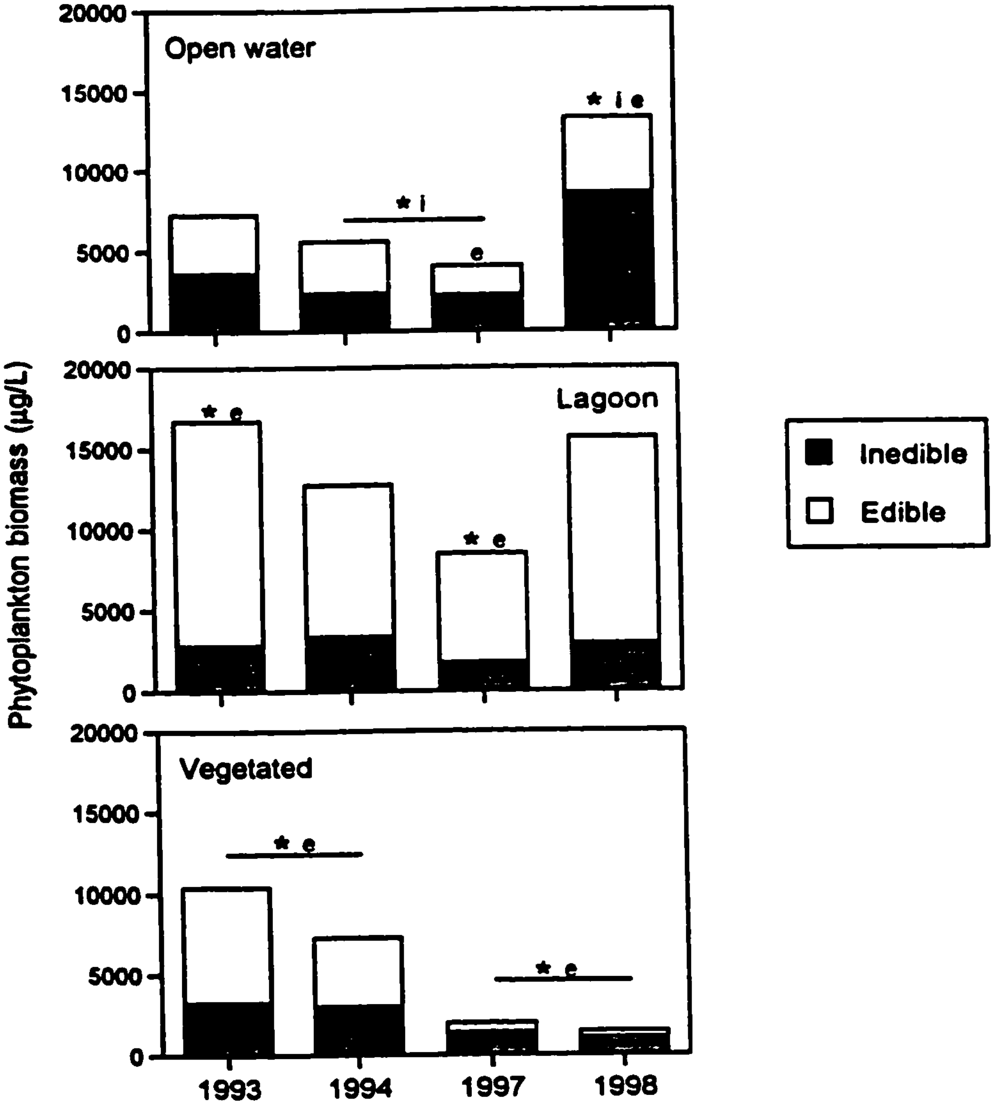

Phytoplankton biomass (µg/L)
Open water
Lagoon
Vegetated
20000
15000
10000
5000
0
1993
1994
1997
1998
* i e
* i
e
* e
* e
* e
* e
Inedible
Edible

Figure 3-4. Mean relative proportion (percent biomass) of phytoplankton taxa before carp exclusion (1993 & 1994) and after carp exclusion (1997 & 1998) at three representative sites in the marsh.

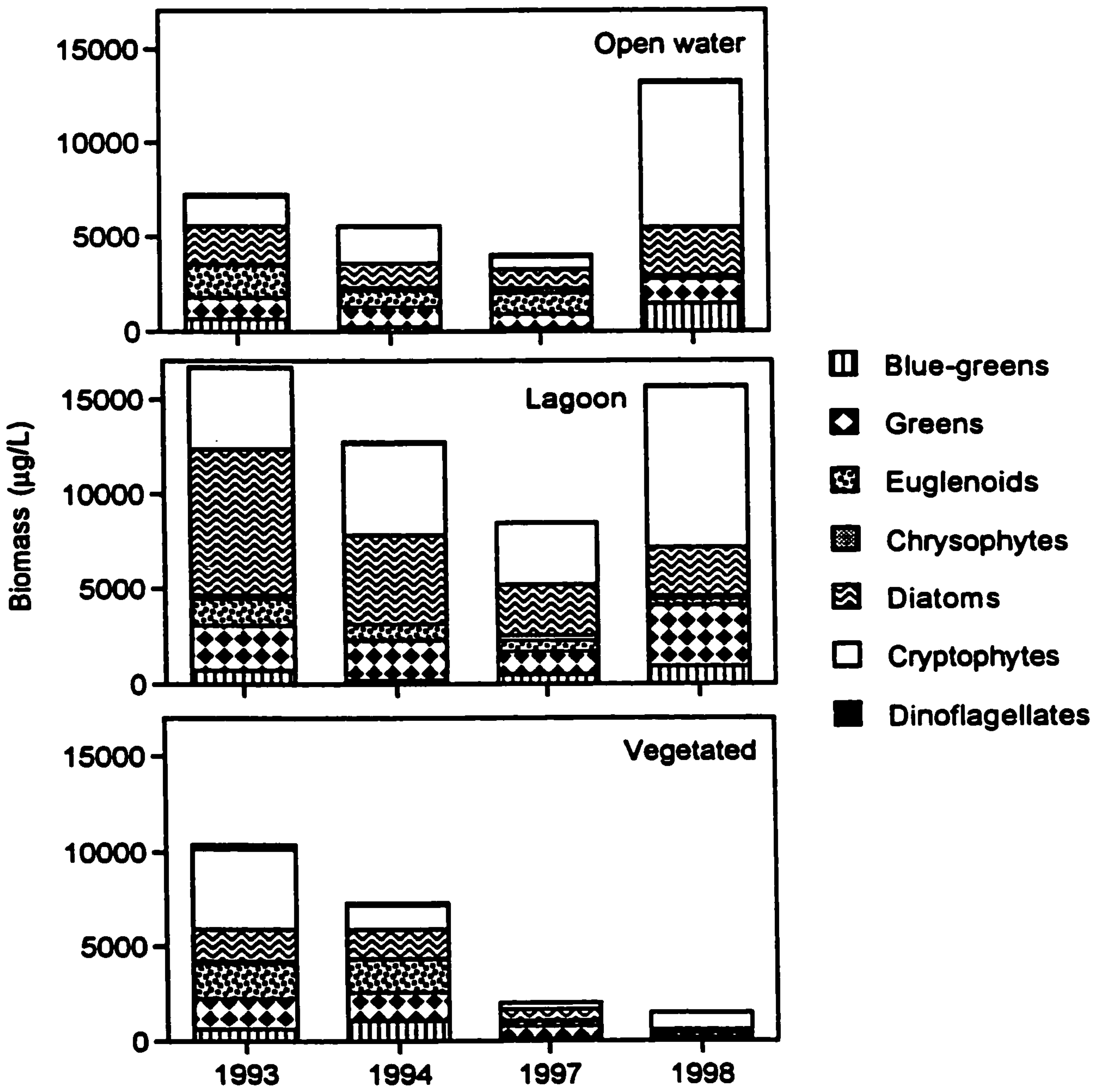

Open water
Lagoon
Vegetated
15000
10000
5000
0
Biomass (µg/L)
1993
1994
1997
1998
Blue-greens
Greens
Euglenoids
Chrysophytes
Diatoms
Cryptophytes
Dinoflagellates

Figure 3-5. Cluster analysis (Ward's method) of sites as grouped by mean yearly phytoplankton functional group biomass (four main clusters are labeled A, B, C and D).

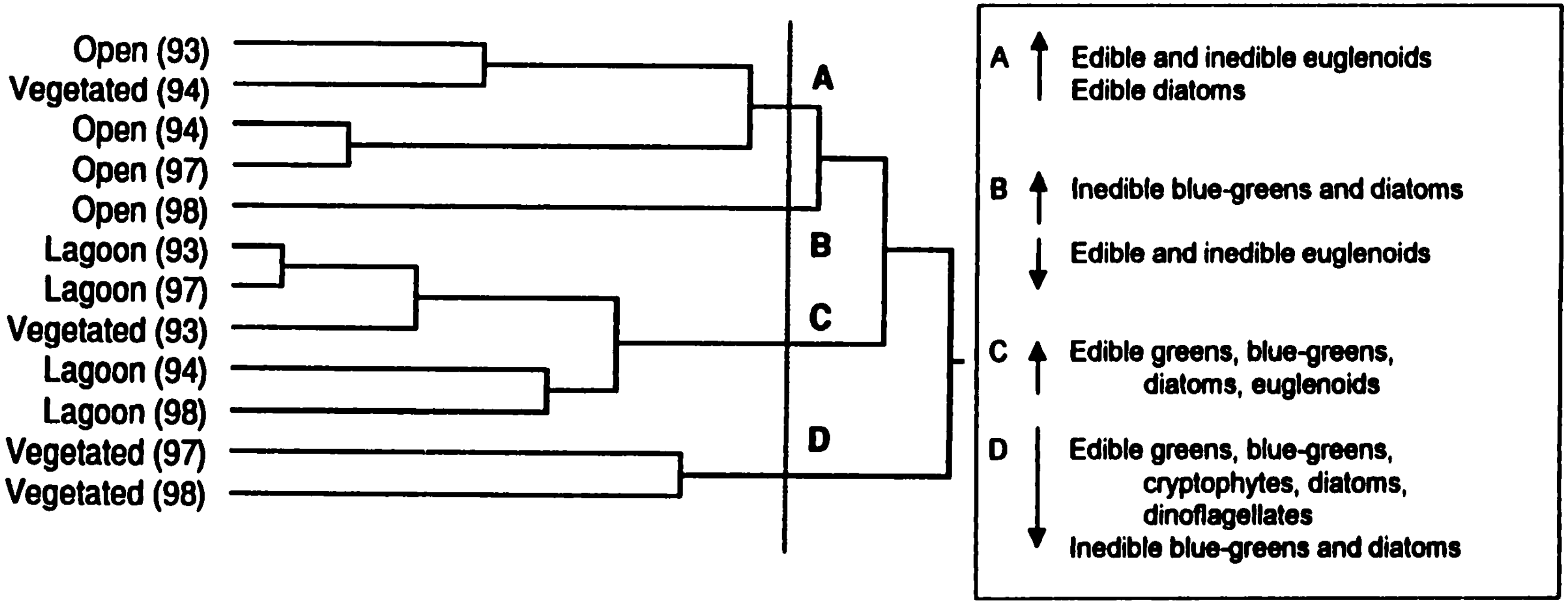

Open (93)
Vegetated (94)
Open (94)
Open (97)
Open (98)
Lagoon (93)
Lagoon (97)
Vegetated (93)
Lagoon (94)
Lagoon (98)
Vegetated (97)
Vegetated (98)
A
B
C
D
A ↑ Edible and inedible euglenoids
Edible diatoms
B ↑ Inedible blue-greens and diatoms
↓ Edible and inedible euglenoids
C ↑ Edible greens, blue-greens, diatoms, euglenoids
D ↑ Edible greens, blue-greens, cryptophytes, diatoms, dinoflagellates
↓ Inedible blue-greens and diatoms

Figure 3-6. Mean relative proportion (percent biomass) of zooplankton taxa before carp exclusion (1993 & 1994) and after carp exclusion (1997 & 1998) at three representative sites in the marsh.

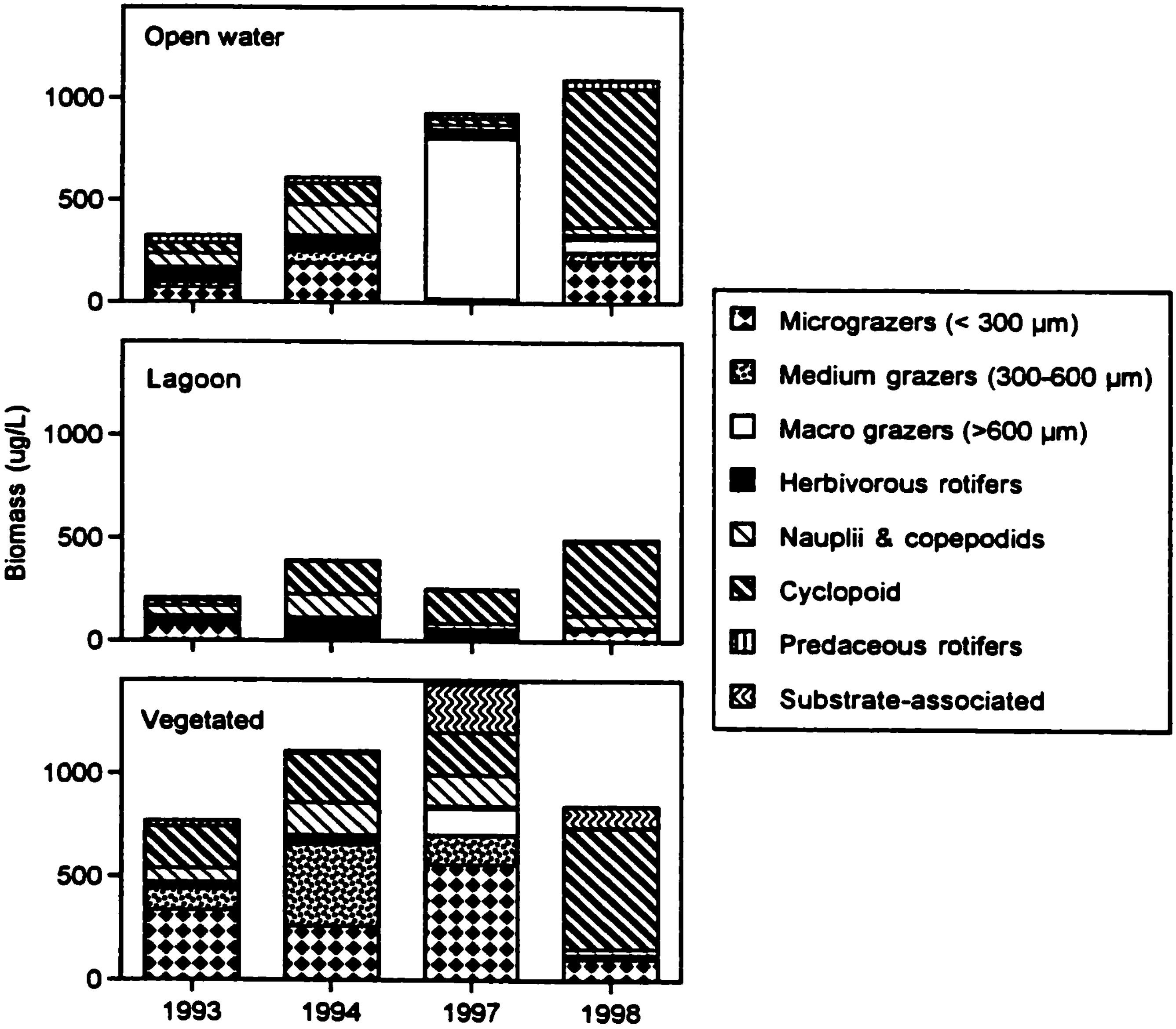

Open water
Lagoon
Vegetated
Biomass (ug/L)
0
500
1000
1993
1994
1997
1998
Micrograzers (< 300 μm)
Medium grazers (300-600 μm)
Macro grazers (>600 μm)
Herbivorous rotifers
Nauplii & copepodids
Cyclopoid
Predaceous rotifers
Substrate-associated

Figure 3-7. Changes in zooplankton and phytoplankton biomass over the summer of 1997 at the open water and vegetated sites.

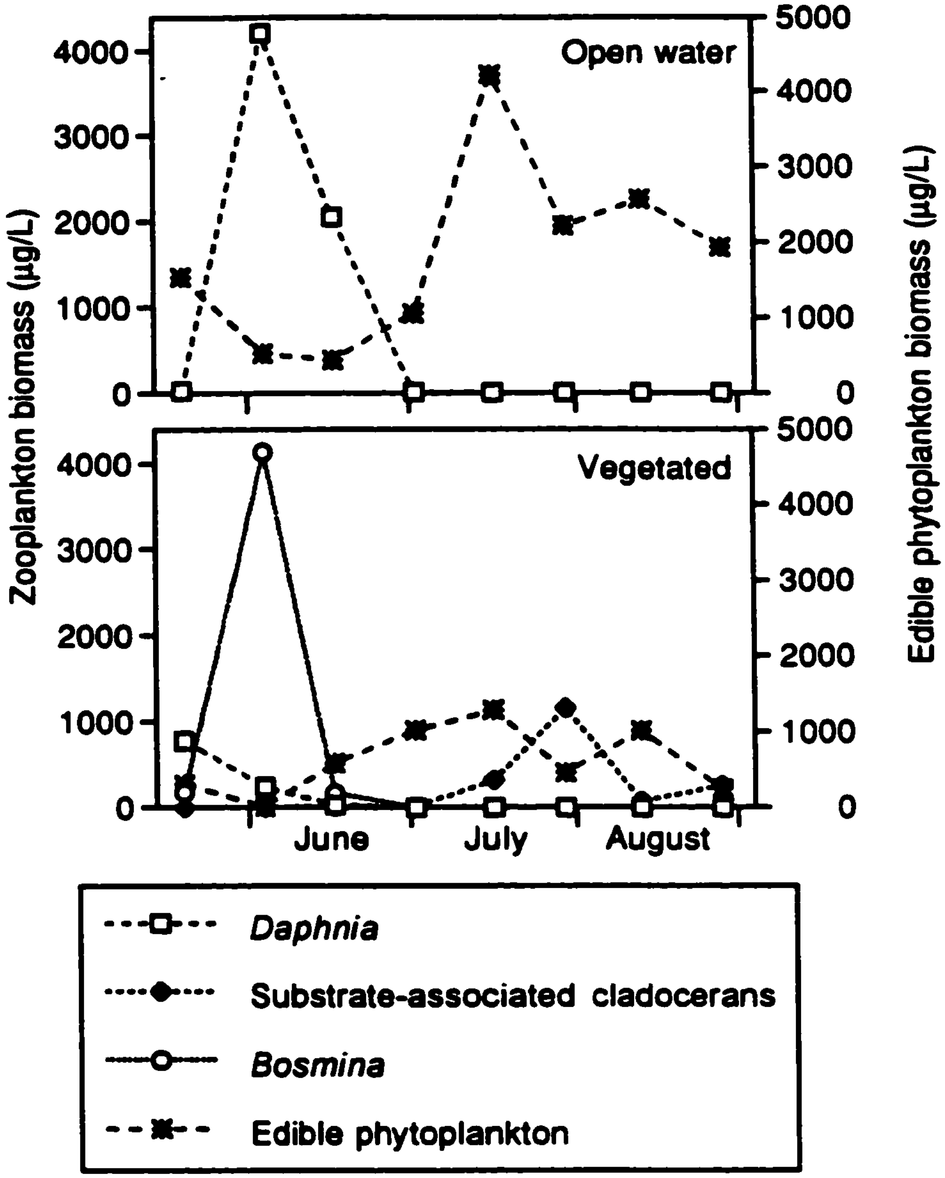
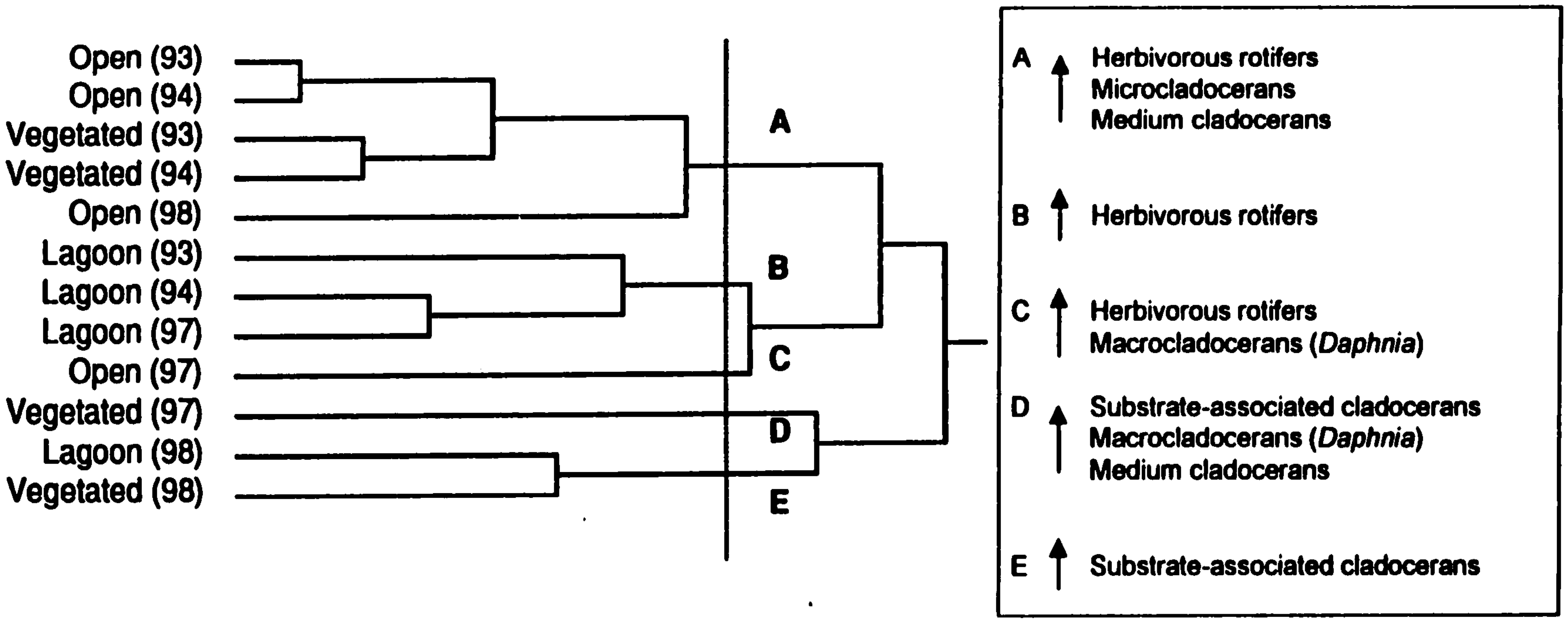

Open water
Vegetated
Zooplankton biomass (μg/L)
Edible phytoplankton biomass (μg/L)
0
1000
2000
3000
4000
5000
June
July
August
Daphnia
Substrate-associated cladocerans
Bosmina
Edible phytoplankton

Figure 3-8. Cluster analysis (Ward's method) of sites as grouped by mean yearly zooplankton functional group biomass (five main clusters are labeled A, B, C, D and E).


Open (93)
Open (94)
Vegetated (93)
Vegetated (94)
Open (98)
Lagoon (93)
Lagoon (94)
Lagoon (97)
Open (97)
Vegetated (97)
Lagoon (98)
Vegetated (98)
A
B
C
D
E
A ↑ Herbivorous rotifers
Microcladocerans
Medium cladocerans
B ↑ Herbivorous rotifers
C ↑ Herbivorous rotifers
Macrocladocerans (*Daphnia*)
D ↑ Substrate-associated cladocerans
Macrocladocerans (*Daphnia*)
Medium cladocerans
E ↑ Substrate-associated cladocerans

CHAPTER 4:

Role of natural environmental variability and anthropogenic stressors in structuring the macrophyte community in 62 marshes across the Great Lakes basin.

Vanessa L. Lougheed, Barb Crosbie and Patricia Chow-Fraser.

ABSTRACT: We collected water quality and aquatic macrophyte information from 62 wetlands in the Great Lakes basin and found that the species richness and community structure of aquatic macrophytes was a function of geographic location, water quality degradation and exposure. For inland wetlands, the primary source of water quality degradation was inputs of nutrients and sediment associated with land use. While in coastal wetlands water quality was also influenced by exposure to and mixing with water in the lake proper. In particular, wetlands in the less developed and more exposed upper Great Lakes had unique physical and ecological characteristics when compared to more developed and less exposed wetlands of the lower Great Lakes and inland locations.

Degraded wetlands were characterized by a fringe of emergent vegetation, with only a few sparsely distributed submergent plant species, while high quality wetlands contained a mix of emergent and floating-leaf taxa with a diverse and dense submergent plant community. Certain macrophyte taxa were identified as intolerant of degraded conditions (e.g. *Pontederia cordata, Najas flaxilis*), while others were tolerant of a wider range of conditions (e.g. *Typha, Potamogeton pectinatus*) and occurred in both high and low quality wetlands.

We used this large data set to assess the changes in water quality and macrophyte community structure in Cootes Paradise Marsh. Although the carp exclusion promoted a definite improvement in the species richness of the macrophyte community, the quality of the marsh remained moderate to low relative to other Great Lakes marshes. We suggest

that wetlands disturbed by both land use and carp may be more degraded than those stressed by carp activity alone.

INTRODUCTION:

Long-term changes in the macrophyte communities of individual Great Lakes coastal marshes, especially those located in settled areas of Lakes Erie and Ontario, have been well documented over the past two decades (e.g. Crowder and Bristow 1986; Klarer and Millie 1992; Chow-Fraser et al. 1998; Lundholm and Simser 1999); however, the underlying factors causing these changes have rarely been investigated. These preliminary studies have indicated that year-to-year changes in areal cover of emergent vegetation are probably controlled by fluctuating water levels (Keddy and Reznicek 1986; Chow-Fraser et al. 1998), whereas growth and diversity of submergent vegetation are more likely controlled by water clarity (Chow-Fraser et al. 1998; Lougheed et al. 1998).

The combined effects of hydrology, local bedrock geology, and wetland morphology, referred to jointly as hydrogeomorphic factors, tend to be the primary regional determinants of plant community structure in wetlands and littoral systems (e.g. Minc 1997; Thiébaut and Muller 1998; Keough et al. 1999). Where the Great Lakes basin is concerned, hydrogeomorphic variation and climatic differences associated with a total shoreline length of 12,017 km contribute to a great diversity of physical environments (Smith et al. 1991; Keough et al. 1999). These regional differences have important consequences for human settlement and land use patterns with the most productive agricultural land and largest urban centers occurring south of the 46th parallel (Environment Canada and U.S. Environmental Protection Agency 1995). Consequently, although wetlands throughout the entire Great Lakes basin are at risk from non-point source pollution (Crosbie and Chow-Fraser 1999), water level regulation (Keddy and Reznicek 1986), disturbance by nuisance exotic species such as common carp (*Cyprinus carpio*) (Lougheed et al. 1998) and internal loading of phosphorus (Chow-Fraser 1998; Mayer et al. 1999), these disturbance factors tend to predominate in the lower lakes. In particular, agricultural and urban land use in wetland catchments of the lower lakes has been shown to affect nutrient enrichment, water clarity and sediment quality (Crosbie and Chow-Fraser 1999) and will therefore likely have profound effects on submersed macrophyte growth (e.g. Phillips et al. 1978; Barko and Smart 1983; Magee et al. 1999) and distribution (Lougheed et al. 1998; Crosbie and Chow-Fraser 1999).

The challenge facing managers is determining the degree to which each of these hydrogeomorphic, climatic and disturbance factors individually or in combination alter wetland plant communities. In this paper, we compare the macrophyte community composition of 62 wetlands in the Canadian part of the Great Lakes basin to examine how water and sediment quality variables affect the taxonomic composition and community structure of the macrophyte community and relate these to land use in their watershed. In addition to the 22 marshes sampled by Crosbie and Chow-Fraser (1999) located primarily along the shoreline of the lower lakes, our data set also includes 40 other coastal and inland wetlands, ranging from degraded to pristine conditions, covering all four Canadian Great Lakes. We will present data on water and sediment quality, land use in wetland watersheds, presence of carp, and taxonomic composition of submersed, emergent and floating-leaf aquatic vegetation. A multivariate descriptor of wetland quality, constructed from Principal Components Analysis, will be regressed against the relative proportions of agricultural, urban and forested land in each watershed, and against the species richness of submerged macrophytes to confirm published observations of Crosbie and Chow-Fraser (1999) who found a direct link between land use impacts, water quality impairment and wetland plant diversity. We will use canonical correspondence analysis (CCA) to examine the relationship between macrophyte distribution and different environmental factors. In particular, the relative roles of hydrogeomorphic factors and changes in development pressure with latitude in determining the composition of the macrophyte community will be discussed. We will use the CCA to illustrate how the macrophyte community in a degraded coastal wetland of L. Ontario (Cootes Paradise Marsh) responded to carp exclusion as a restoration strategy. And finally, we will describe the effect of carp on water clarity in other wetlands in the Great Lakes basin. This study will contribute much needed information to help wetland managers determine the relative importance of these various factors in structuring the aquatic macrophyte community at a basin-wide scale.

METHODS:

Sixty-two marshes in the Great Lakes basin were visited between 1995 and 1999 and sampled for water quality and macrophyte community information. Wetlands were distributed from the St. Lawrence River just east of Cornwall, down to the Windsor/Detroit area and Lake St. Clair, and up to Lake Superior and the Ontario/Minnesota border (Figure 4-1). Fourteen wetlands were on the coast of the upper Great Lakes (Lake Huron and Lake Superior), 32 were coastal wetlands of the lower Great Lakes region (Lake Ontario, Lake Erie, Lake St. Clair, St. Lawrence River), while 16 were inland marshes in watersheds of the Great Lakes/St. Lawrence basin. All wetlands were visited once in mid-summer (18th June to July 30th); in addition, 15 were sampled again in late summer and 5 were sampled monthly from June to September. Where applicable, water quality data were pooled by wetland to produce seasonal averages because there were no significant differences between sampling trips with respect to water-quality data (Crosbie and Chow-Fraser 1999).

The protocol for sampling and analysis of water samples has been documented elsewhere (Lougheed and Chow-Fraser 2000, Chapter 3). For each wetland, we analyzed samples for total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen (TN) (sum of total kjeldahl nitrogen (TKN) and total nitrate nitrogen (TNN)), total ammonium nitrogen (TAN), total suspended solids (TSS) and total inorganic suspended solids (TISS). Planktonic chlorophyll-*a* (CHL-*a*) was extracted using 90% acetone, with results corrected for phaeopigments by acidification. Temperature, pH, dissolved oxygen and conductivity were determined using an H2O® Hydrolab and

Scout® monitor. Turbidity readings were taken in triplicate using a portable Hach turbidimeter (model 2100P).

Sediment samples were collected at an open water site 3-m from the edge of macrophyte beds using either an Eckman grab sampler or 5-cm Plexiglas tube equipped with a plunger. Samples were dried at 100°C, homogenized and combusted at 550°C to determine the proportion of inorganic matter in the sample ($INORG_{SED}$). Total phosphorus in the sediment (TP_{SED}) was extracted in 1M HCl according to Andersen (1976) and the resulting sample was measured according to the protocol for TP (above). The maximum and predominant sediment grain size observed in each sediment sample (approx 20 to 70 g dry sediment) was classified according to the Wentworth Scale (Wotton 1990); wetlands visited by Crosbie and Chow-Fraser (1999) were not analyzed for sediment size.

We counted every species of submergent, emergent and floating-leaf vegetation encountered within a 3-m radius of a selected vegetated site. Wetlands where the submergent plant distribution was sparse (<5 plants/m^2) were noted and we conducted an expanded survey along approximately 100-m of shoreline. Keys by Fassett (1940) and Newmaster et al. (1997) were used to identify the macrophyte specimens to species where possible. Because many wetlands were visited only once, and because certain species are difficult to identify accurately without flowering parts, many taxa were identified to genus only. Most submergent taxa were identified to genus, except for several common species which were keyed to species (see Table 4-5). All emergent taxa encountered were identified at least to genus, and the dominant taxa were noted.

The objective of this plant survey was not meant to be exhaustive, but rather to obtain floristic information on common taxa in a structurally diverse plant community that would include emergent, submergent and floating-leaf components. Consequently, we did not sample along parallel transects of a systematic grid, an approach employed in studies designed to produce comprehensive species lists (e.g. Minc 1997; Magee et al. 1999). Our approach therefore likely excluded rare species and many grasses, rushes and sedges that would have been more common in wet meadow environments (e.g. Minc 1997).

Land use and wetland type.

Where applicable, we used 1:50,000 National Topographic Series maps to delineate wetland watersheds and land use was determined by overlaying Ontario Agricultural Land Use Series (current to mid-1980s). Triplicate planimetry measurements were used to quantify the size of the watershed and each of the three land uses (agricultural, urban and forested). For the three largest watersheds (>1500 km^2), land use estimates were collected from Detenbeck et al. (1999; Goulais and Spanish River) and the Grand River Conservation Authority (www.grandriver.on.ca). Wetlands were classified into land use categories as follows: (1) wetlands were assigned to the dominant land use category if the majority (> 50%) of their watershed was of that land use, and if < 30% of the remaining catchment area were of another land use; (2) wetlands were assigned to a combined land use category (e.g. agriculture/forested) if no land use type accounted for > 50% of the total catchment area, and the difference between any two types was less than 20%; (3) wetlands that occurred as fringes along the Great Lakes shoreline which did not have any obvious inflows were not classified to any land use category.

The predominant wetland type (riverine, lacustrine, palustrine) was determined with reference to Ontario Wetland Evaluation Reports (Ontario Ministry of Natural Resources), 1:50,000 National Topographic Series maps, as well as personal observation. None of the wetlands visited were entirely palustrine, but rather consisted of palustrine areas associated with riverine systems, therefore these wetlands were classified as riverine/palustrine.

Presence of carp

The presence of carp at each wetland was visually verified during our sampling trips and (or) was determined from a variety of published (Hurley 1986; Stephenson 1990; Minns et al. 1994; Leslie and Timmins 1993, 1997; Chow-Fraser and Albert 1998) and unpublished sources (T. Theismeijer, Royal Botanical Gardens, pers. comm; Ontario Wetland Evaluation Reports; Great Lakes 2000 Cleanup Fund). These data are largely qualitative, as they represent only the presence or absence of carp; however, if a report identified carp as rare (<10%) we classified the wetland as carp-less. Wetlands for which we found no reliable data were not classified and, therefore, we have carp data for only 46 wetlands.

Carp have been physically excluded from the Cootes Paradise Marsh (L. Ontario) since the winter of 1997 by the Cootes Paradise Fishway (Wilcox and Whillans 1999;

see Lougheed and Chow-Fraser 2000, Chapter 3). Prior to carp exclusion, carp biomass was on average 800 kg/ha in the marsh, and was reduced by 90% by the operation of the fishway (T. Theismeijer, Royal Botanical Gardens, pers.comm). We will compare macrophyte information collected prior to carp exclusion (1996) with data collected following exclusion (1997) to illustrate how the macrophyte community changed and how the assemblage compares to other wetlands in the basin.

Statistical analyses

All statistical analyses were performed using SAS.Jmp software (SAS Institute Inc., Cary, N.C.), except for canonical correspondence analysis, which was performed using CANOCO (version 4.0; ter Braak and Smilauer 1998). Principal components analysis was used to create linear combinations of the environmental data to describe the underlying environmental gradients in the data. Environmental data were $\log_{10}$-transformed to approximate normal distributions and standardized to zero mean and unit variance. Canonical correspondence analysis (CCA) was used to determine the best environmental factors to predict aquatic macrophyte distribution and has been used in similar studies relating macrophytes to their environment (e.g. ter Braak 1986; Srivastava et al. 1995; Toivonen and Huttunen 1995; Bini et al. 1999; Magee et al. 1999). CCA maximizes the separation of species optima along synthetic axes which represent linear combinations of environmental variables. This is a useful technique when species data have been collected over a large enough habitat range to show a unimodal relationship with environmental variables (Jongman et al. 1995). CCA was appropriate in this study because the gradient lengths obtained from detrended correspondence analysis (CANOCO 4.0) indicated that the species data were moderately unimodal (unpubl. data; ter Braak and Smilauer 1998).

Variables that were entered into the CCA included the occurrence of macrophyte taxa encountered in >10% of wetlands as well as accompanying environmental variables (i.e. TP, TN, TSS, CHL*a*, pH, COND, TP_{SED}, $INORG_{SED}$ and LATITUDE (measured as decimal degrees)). These environmental variables were $\log_{10}$-transformed to approximate normal distributions and standardized to zero mean and unit variance. We excluded turbidity, SRP, TISS, TAN, TKN and TNN from the CCA because they either showed a high degree of multi-collinearity with chosen variables, or contributed little to explaining the variation in the data set. All the included variables had variance inflation factors less than 20, indicating that they contributed uniquely to the analysis (ter Braak and Smilauer 1998). The statistical significance of the relationship between the species data and the whole set of environmental variables was determined using Monte Carlo permutations (199 random permutations) (ter Braak and Smilauer 1998).

RESULTS:

Water and sediment quality

Wetlands in this study correspond to a wide range of environmental conditions (Table 4-1). Principal components analysis (PCA) was initially used to determine which environmental variables explained the greatest amount of variation in the data set (Table 4-2). The first 3 axes explained 72% of the variation in the data set (Table 4-2), with nearly 50% of it being explained by PC axis 1. This axis was highly and positively correlated with variables associated with nutrient status (TN, TP, TNN) and particulate content (TSS, TISS, Turbidity, CHL-*a*) of the water. Conductivity, an indication of the ionic strength of the water, was also highly correlated with this axis. Data in Table 4-1 are sorted according to PC axis 1, therefore, wetlands near the top of the table (No. 1) are clearer and more oligotrophic, while wetlands nearer to the bottom (No. 62) are more turbid and eutrophic. The second axis explained 16% of the variance and was positively correlated with the inorganic content of the sediment and negatively correlated with the phosphorus in the sediment. Wetlands with high PC axis 2 scores also had relatively high pH. Axis 3, which explained only 10% of the variation in the data, was positively correlated with SRP and temperature.

Since PC axis 1 is associated with a nutrient/turbidity gradient, wetlands to the extreme right in Figure 4-2 are turbid, hypereutrophic marshes, whereas those to the extreme left are clear, oligotrophic marshes. The majority of turbid, nutrient-rich wetlands in our data set are coastal wetlands of the lower Great Lakes (crosses), while clear, nutrient-poor wetlands correspond to inland wetlands (squares) and coastal wetlands of the upper Great Lakes (circles). The second PC axis, which separates wetlands with high organic content, high sediment fertility, and low pH, from those with high inorganic content, low sediment fertility, and high pH, is a good discriminator for inland wetlands and upper coastal wetlands which appear to be more variable with respect to sediment characteristics and pH. Coastal wetlands in the upper lakes (Huron and Superior) tend to have a higher pH and a greater proportion of inorganic sediment ($p<0.05$; ANOVA; Tukey-Kramer), while inland wetlands tend to have more organic sediment and higher sediment TP ($p<0.05$; ANOVA; Tukey-Kramer).

Land use

Given development patterns in the Great Lakes basin over the past century, it was not surprising that the proportion of agricultural ($r^2 = 0.50$; $p<0.0001$) and urban ($r^2 = 0.08$; $p<0.05$) land decreased significantly with latitude, while the proportion of forested land increased ($r^2 = 0.72$; $p<0.001$). To determine the effect of land use on water and sediment quality, we regressed PC 1 scores against the proportion of the three different land use categories (11 wetlands were excluded from this analysis because we could not obtain land use estimates for them). PC 1 scores were positively related to percent agricultural land ($r^2=0.39$; Figure 4-3a) and negatively correlated with percent forested land ($r^2=0.40$; Figure 4-3b). Although we found no significant relationship between PC 1 scores and the proportion of urban land use, likely due to the small number of wetlands with >10% urban land in their watershed (n=6), we found a significant regression when both percentage agricultural and urban land were combined ($r^2=0.48$; Figure 4-3c).

The wetlands were further divided into three groups according to their location in the Great Lakes basin: inland wetlands (INLAND), coastal wetlands of the lower Great Lakes (LOWER), and coastal wetlands of the upper Great Lakes (UPPER). For INLAND wetlands, land use explained a large amount of variation in PC axis 1 (indicative of water quality) and PC axis 2 scores (indicative of sediment quality). By contrast, land use was not as good a predictor for LOWER coastal wetlands, and was not a significant predictor for UPPER coastal wetlands at all (Table 4-3).

Sediment grain size and organic content of the sediment also can be affected by land use, as well as by geological factors and exposure. Because the PCA showed that sediment characteristics tended to vary by location, wetlands were again divided into the three groups according to their location. In INLAND wetlands, agricultural watersheds had significantly lower percent organic sediment relative to other land use types, and forested wetlands had significantly larger maximum sediment grain size (Table 4-4). There were no significant trends observed in the more exposed LOWER and UPPER coastal wetlands, where all wetlands contained significantly more inorganic soils relative to INLAND wetlands, especially in the upper lakes (ANOVA; Tukey-Kramer; $p<0.05$).

Submergent plant species richness

The number of submergent plant species in the wetlands varied inversely with both PC axes 1 and 2 scores, although there was a great deal of scatter about the best-fit line ($r^2=0.32$ and 0.15, respectively; Figure 4-4). When data were sorted according to location, however, the percent variance explained by PC axis 1 increased for INLAND (squares; $r^2=0.58$; $p<0.001$) and LOWER (crosses; $r^2=0.54$; $p<0.001$) wetlands but was not significant for UPPER lakes (circles; $p>0.05$). PC axis 2 explained 51% of the variance in species richness for INLAND wetlands, but was not significant for either LOWER or UPPER wetlands. Figure 4-4 also shows that there were generally fewer submergent taxa in UPPER (circle) wetlands compared with LOWER (crosses) and INLAND (squares) wetlands with similar PC 1 or PC 2 axis scores.

Macrophyte community structure

All three types of aquatic plants (i.e. submergent, emergent and floating-leaf) were well represented in this study (Table 4-5). Taxa that were identified in greater than 10% of the wetlands visited were given two-letter codes which identify them in the CCA bi-plot. Submergent taxa which occurred in > 50% of the wetlands included: *Ceratophyllum*, *Elodea*, *Myriophyllum*, *Potamogeton pectinatus*, *P. richardsonii* and *Vallisneria*; *Typha*, *Scirpus* and *Lythrum salicaria* were the most prevalent emergents, while *Nymphaea* and *Nuphar* also occurred in at least half of the wetlands. As explained in the methods section, the list of emergent species is only representative of the dominant forms encountered in these wetlands.

We performed a canonical correspondence analysis (CCA) to determine the association between environmental variables and the distribution of macrophytes. Figure 4-5 explains 62% of the variation in macrophyte distribution along the first two synthetic environmental gradients. The most important predictors of macrophyte distribution, as indicated by their correlation with CCA axis 1, were TSS ($r=0.79$), TP ($r=0.73$), CHLa (r=0.70), TN (r=0.65) and COND (r=0.61). The second CCA axis was correlated with variables indicative of sediment quality (TP_{SED}: r=-0.54; $INORG_{SED}$: r=0.34) and pH (r=0.41), although the strength of these correlations was weaker than that for axis 1 scores. Not surprisingly, these variables are also the primary descriptors of the PCA axes and the variables describing most of the variation in the submerged macrophyte species richness data. LATITUDE was moderately correlated with both axes 1 (r=-0.38) and 2 (r=0.38), and therefore confirms that higher latitude sites had clearer water, but less nutrient- and organic-rich sediment.

Location of plant taxa to the right of the origin suggest that these plants tolerate turbid, nutrient-rich conditions in the water column (Figure 4-5). These included the emergent taxa *Typha*, *Sagittaria*, and *Lythrum*, submergent taxa, *Potamogeton pectinatus* and *P. crispus*, and the floating taxa, *Nuphar variegatum* and *Nymphaea odorata*. Those taxa that were least tolerant of turbidity and eutrophication included the emergent taxa *Pontederia cordata* and *Sparganium* sp., majority of the submergent taxa (e.g. *Potamogeton richardsonii, Najas flexilis, Utricularia* sp.) and the floating-leaf species *Potamogeton natans*. Submergent taxa that were moderately tolerant of turbid water included *Elodea canadensis* and *Ceratophyllum demersum*. Taxa more influenced by CCA axis 2 and common in more inorganic, infertile soils at higher latitudes included *Scirpus* sp. and *P. richardsonii*. Several taxa were excluded from the CCA because of their rare occurrence, and some of these taxa displayed obvious trends in their distribution. Most notably, *Potamogeton gramineus*, *Eleocharis smallii*, *Isoetes* sp. and

Zizania palustris were found north of 44° latitude in wetlands with relatively low water turbidity and nutrient concentrations.

Figure 4-6 displays the location of the sites scores for the CCA analysis. In general, CCA axis 1 separates the more degraded wetlands in highly agricultural (squares) and urban watersheds (crosses) from the clearer, more oligotrophic wetlands located in moderately to largely forested watersheds (diamonds). CCA axis 2 separates higher latitude forested sites (diamonds in the upper left quadrant) from all other sites. Three main macrophyte community types are apparent. In the upper left quadrant of the CCA bi-plot are higher latitude sites in forested watersheds where the emergent vegetation is often dominated by *Scirpus sp.*, *Eleocharis smallii*, *Potamogeton gramineus* and *P. richardsonii*. The mean number of submergent taxa found in these wetlands was 6.5, and one-quarter of the wetlands in this quadrant had a low stem density of submergents (<5 /m^2). By contrast, *Typha* was the dominant emergent in the lower latitude sites, which are plotted in the lower half of the bi-plot. Wetlands located in the lower left quadrant correspond to relatively high-quality wetlands in forested watersheds with relatively high species richness of submergent taxa (mean = 10.3 species) where the submergents formed dense mats (all wetlands >5 stems/m^2). Wetlands located in the right-hand side of the bi-plot, however, correspond to degraded wetlands with highly developed watersheds. These contain relatively few submergent taxa (mean = 3.6 taxa), with 45% of the wetlands containing a low stem density of submergents (<5 /m^2) and only a fringe of *Typha*.

Figure 4-6 also illustrates how the site score for Cootes Paradise before exclusion (1996) compares to that after exclusion (1997). The distance between site scores in the bi-plot is a direct measure of the similarity between them (Ter Braak and Verdoschot 1995). The macrophyte community changed from an extremely sparse community with low submergent richness (1 species; *P. pectinatus*) to somewhat moderate conditions with 6 submergent plant species existing in dense communities in shallow, sheltered regions of the marsh. This included taxa located centrally or to the right of the origin (0,0) in the CCA bi-plot (*P. pectinatus*, *P. crispus*, *Elodea*, *Ceratophyllum*, *Myriophyllum*, *Vallisneria*). The marsh maintained a fringe community of cattails, as well as scattered populations of *Lythrum*, *Nymphaea* and *Lemna* throughout the study period.

The majority (19 out of 25) of the wetlands with carp were located in the lower lakes, while only 4 (out of 23) lower lake wetlands were carp-less (Table 4-1). The level of total suspended solids was significantly greater in wetlands containing carp (41.35 mg/L) compared with wetlands without carp or where carp were rare (9.42 mg/L) (Figure 4-7a) and carp-less wetlands tended to be found in less developed watersheds (Figure 4-7b). With the exception of sites in the upper lakes, which tended to have reduced species richness and density relative to lower and inland sites of similar quality, wetlands without carp contained relatively dense beds of greater than 9 species of submergents. Conversely, wetlands containing carp had more variable submergent plant densities and the number of submergent plant species ranged from 0 to 15. In these wetlands with carp, the level of total suspended solids was significantly greater in the sparsely vegetated wetlands (77.35 mg/L) than in those that were densely vegetated (14.94 mg/L) (Figure 4-

7c). Furthermore, wetlands with carp where the sediment was composed primarily of clay or silt tended to be more turbid (52.36 mg/L) than wetlands with larger sandy sediment (16.62 mg/L) (Figure 4-7d).

DISCUSSION:

The species richness and community structure of aquatic macrophytes in wetlands of the Great Lakes basin appeared to be a function of various factors: 1) geographic location of the wetland (i.e. whether they are associated with the upper or lower Great Lakes, or located inland) 2) degree of water quality degradation and 3) degree of exposure to wind and wave action from the lake in question. For inland wetlands, the primary source of water quality degradation was excess inputs of nutrients and sediment associated with agricultural development in the watershed. For coastal wetlands, however, water quality was also influenced by carp activity, especially in the lower lakes, and by exposure to and mixing with water in the lake proper. In particular, wetlands in the less developed and more exposed upper Great Lakes had unique physical and ecological characteristics when compared to more developed and less exposed wetlands of the lower Great Lakes and inland locations.

The proportion of agricultural and urban land in wetland watersheds was a highly significant predictor of water quality (PC axis 1 scores), explaining almost half of the variation in the dependent variables (Figure 4-3). These results are consistent with previous studies where water quality was related to land use in the watershed (e.g.

Johnson et al 1997; Crosbie and Chow-Fraser 1999). There was, however, a great deal of variability observed due to climatic and geological differences associated with different latitudes (upper vs. lower lakes) and exposure (inland vs. coastal). Water quality in inland wetlands was substantially degraded by urban and agricultural land use. Inland wetlands that received a disproportionate amount of urban and agricultural run-off tended to have a greater proportion of fine, inorganic silts and clays in their sediment compared with those in mainly forested watersheds that have a deep layer of organic muck and larger gravels in their substrate (Minc 1997). The presence of high silt and clay content in the sediment is undesirable since plants grow better in organic than in inorganic substrates (Day et al. 1988), and small inorganic particles in the sediment can become easily resuspended and stay in suspension (Hamilton and Mitchell 1997), thus keeping the water column turbid and light-limited for macrophytes. Conversely, forested land appeared to attenuate the delivery of sediment from the watershed to inland wetlands; even a modest amount of forested land (i.e. forested and agricultural/forested watersheds) can apparently sustain a greater level of organic muck in these wetlands.

It is noteworthy that land use effects were greatest on water and sediment quality in inland systems which do not have direct hydrological links with the Great Lakes. The flow of water between the marsh and the lake in question can be reversed depending on watershed inputs, wind direction, and water level in the Great Lake (Chow-Fraser 1999; Botts 1999), and hence mixing with lakewater may ameliorate the effects of non-point source pollution in coastal wetlands that are open to the lake proper. Wind and wave action in exposed coastal marshes may also lead to export of organic matter from the coastal wetland to the lake (Day et al. 1988) and to reduced water clarity through sediment resuspension (Hamilton and Mitchell 1997).

The geomorphological characteristics of the Canadian shorelines of the Great Lakes have resulted in a large number of riverine-type wetlands and a smaller proportion of protected lacustrine embayments in Lakes Erie and Ontario, while the wetlands on the Canadian shores of the upper lakes are primarily lacustrine embayments (Chow-Fraser and Albert 1999). Our data set reflects these trends, with 70% of our upper lake wetlands and only 33% of the lower lake wetlands classified as lacustrine (Table 4-1). Where unique geological factors have produced largely exposed shorelines along the upper lakes (Smith et al. 1991), intrusion by lake water and exposure to wave action may play an even larger role in affecting wetland water quality than in the more protected wetlands of the lower lakes.

Many studies have shown that nutrient enrichment can cause substantial changes in the species richness, density and species composition of aquatic vegetation in lakes (e.g. Lachavanne et al. 1991; Srivistava et al. 1995; Toivonen and Huttunen 1995; Bini et al. 1999; Magee et al. 1999). The inverse relationship we have established between species richness of submergent taxa and PC axis 1 scores (Figure 4-4a) confirm that submergent macrophyte biodiversity in Great Lakes wetlands is susceptible to deterioration in water quality (increased water turbidity and nutrient concentrations). Our findings are also consistent with other studies that found reduced species richness of both aquatic and terrestrial organisms with increasing development in wetland and stream watersheds (Findlay and Houlahan 1997; Harding et al. 1998). However, differences due to climate and geology confounded the relationship for wetlands of the upper Great Lakes since there was a general reduction in the number of aquatic macrophyte taxa in these wetlands that was not related to water quality.

Macrophyte growth is limited by both water and sediment quality (e.g. Day et al. 1988; Barko et al. 1991). Light availability is a primary factor determining photosynthetic potential and can be reduced by non-algal and algal turbidity, including periphytic growth (Phillips et al. 1978). As such, details on the nutrient status, sediment quality and particulate content of the water are required to make conclusions regarding the causative effects of macrophyte community changes. Although taxonomic surveys of macrophyte communities in individual Great Lakes coastal wetlands have been published by several authors (e.g. Crowder and Bristow 1986; Klarer and Millie 1992; Chow-Fraser et al. 1998; Lundholm and Simser 1999), there have been no published studies which account for all of these variables and their roles in causing species replacement in the macrophyte community on a basin-wide scale. The most comprehensive study that we have found was an unpublished report by Minc (1997), who analyzed macrophyte data from 110 coastal wetlands in the U.S. waters of the Great Lakes and listed the primary determinants of macrophyte distribution as latitude, soil pH, water temperature and turbidity; however, several important factors were excluded from this study, including trophic state and sediment fertility. In Canadian waters, Smith et al. (1991) published a study which described the differences in the physical attributes of 160 coastal wetlands in the 3 southern-most Canadian Great Lakes. Their study provided evidence that geology, exposure and disturbance vary statistically among the three lakes, but provided no information on water quality and taxonomic composition of submerged macrophytes that could be affected by changes in sediment and nutrient load.

The synergistic effects of many factors including eutrophication, algal and non-algal turbidity (Phillips et al. 1978) and sediment characteristics (Barko and Smart 1983; Carignan and Kalff 1980; Day et al. 1988) can all affect submersed macrophyte growth. Because of their sensitivity to this large suite of physical and chemical variables, many macrophyte taxa have been used as indicators of trophic state in other systems (e.g. Seddon 1972; Grasmuck et al. 1995; Thiébaut and Muller 1998). In this study, there appears to be certain taxa that are intolerant of degraded conditions (e.g. *Pontederia cordata*, *Potamogeton richardsonii*, *Najas flexilis*, *Utricularia* sp.; Figure 4-5), but none that occur exclusively in degraded sites. Although some taxa appear more tolerant of water and sediment quality degradation (e.g. *Typha*, *Sagittaria*, *P. pectinatus*, *Nuphar*, *Nymphaea*), even these taxa can be found in high-quality wetlands that are not turbid and eutrophic. Similarly, exotic species such as purple loosestrife (*Lythrum salicaria*) and curly-leaf pondweed (*Potamogeton crispus*) were more tolerant of degraded conditions but also present in more pristine systems. What appears to be a better indicator of wetland quality is the type of community present, rather than the presence of certain indicator species. For example, presence of a fringe emergent community with only a few sparsely distributed submergent taxa is highly indicative of a degraded wetland, whereas a mix of emergent and floating-leaf taxa with a diverse and dense submergent community is highly indicative of a high quality wetland.

The tolerance of aquatic macrophytes to reduced light availability is tightly linked to their structural characteristics. While emergent and floating-leaf macrophytes are not generally affected by light availability (Seddon 1972; Day et al. 1988; Toivonen and Huttunen 1995; Bini et al. 1999), submergents tend to be more greatly influenced by reduced water clarity. Submerged macrophytes which are canopy-formers such as *Potamogeton pectinatus*, *Myriophyllum* sp. and *Ceratophyllum* are able to survive longer in situations of light limitation, as opposed to species such as *Chara* and other *Potamogeton* spp., whose leaves grow below the surface (Chambers and Kalff 1987; Srivastava et al. 1995; Minc 1997). Although our data generally confirm these trends, we did find that some taxa that tended to grow below the surface were generally tolerant of moderate degradation, including *Elodea* and *Vallisneria*, while some canopy-formers or floating submergents, such as *Utricularia* and *Ranunculus*, were excluded from degraded sites.

Species richness and plant density tend to be low in oligotrophic systems. As nutrient concentrations increase in these impoverished systems, both the stem density and diversity of macrophytes increase, until such time as light becomes limiting and plant abundance starts to level off (Lachavanne 1985; Toivonen and Huttunen 1995). The most oligotrophic sites in this study tended to be associated with the upper lakes (Table 4-1), where species richness and density were substantially lower than in the lower lakes; however, inland wetlands of similar trophic state showed greater species richness and plant density. In the Great Lakes basin, the relationship between water quality and the macrophyte community is definitely confounded by the strong latitudinal gradient that exists from the southern- to northern-most points (Smith et al. 1991). The macrophyte communities in the upper and lower lakes differed substantially in their dominant species. In lower latitudes, emergent marshes tended to be dominated by *Typha* sp., while in the upper lakes the dominant emergent tended to be *Scirpus* sp. or *Eleocharis smallii*. There were fewer submergent taxa overall in the upper lakes, with the most frequently observed being relatively sparse beds of *P. gramineus*, *P. richardsonii* and *Isoetes* sp. Conversely, there was a more diverse, dense and variable submergent plant community in the high quality wetlands of the lower lakes, and fewer submergent species present in more degraded sparsely vegetated wetlands.

The importance of latitude in structuring the macrophyte community in the Great Lakes basin is due to several factors, including climate and geology (Smith et al. 1991; Minc 1997). A strong latitudinal gradient exists between the upper and lower lakes which affects the length of the growing season and the annual input of solar radiation. Furthermore, the soft sedimentary rock underlying the lower lakes provides expansive areas of shallow water and fine-textured substrates favorable to marsh development, while the older, igneous and metamorphic bedrock in Lake Superior and Georgian Bay (Lake Huron) results in a deeper and more exposed shoreline with large-textured inorganic substrates. Plants grow best in organically-rich and fertile substrates (e.g. Barko and Smart 1983) which are generally lacking in the upper lakes. Consequently, we saw sparse vegetative communities consisting of species better adapted to the shorter growing season and lower substrate fertility of the northern lakes, such as *Scirpus*, *Eleocharis*, *Equisetum*, *P. gramineus* and *Isoetes* (Day et al. 1988; Minc 1997). These taxa were largely absent from the lower lakes, and replaced by taxa more indicative of a southern community, such as *Ceratophyllum* (Minc 1997).

Lougheed et al. (1998) predicted that, following carp exclusion from Cootes Paradise Marsh, the submergent plant community would contain fewer than 5 species, far less than the 10+ species that existed in the marsh during a 1948 census when clarity was much higher (5 NTU). In this study, this estimation was exceeded when the submergent plants encountered in the first year following exclusion totaled 6 (up from 1 species prior to exclusion). Although the carp exclusion promoted a definite improvement in the diversity of the macrophyte community, the quality of this coastal marsh remains moderate to low relative to other Great Lakes marshes. In particular, the highest quality wetlands in the lower left quadrant of the CCA bi-plot (Figure 4-6) contained, on average, 10.3 species of submergent plants.

Carp biomass was reduced by 90% following carp exclusion from Cootes Paradise Marsh; however, carp could still not be classified as rare and the marsh remained relatively turbid (TSS = 54.4 mg/L). The predominantly agricultural watershed and the rapidly expanding residential population in the Cootes Paradise watershed are likely contributing a substantial amount of pollutants to the marsh and maintaining the marsh in a moderately degraded state. In addition, Cootes Paradise has a large fetch (>2 km) which may lead to the resuspension of the fine silty sediment in the marsh (Hamilton and Mitchell 1997).

Common carp occurred in many of the wetlands we sampled in the lower Great Lakes, and tended to be more rare inland and in the upper lakes. Some authors have suggested that common carp may cause problems in already degraded wetlands, while having little effect on healthy marshes (Maynard and Wilcox 1997). Healthy beds of submersed macrophytes may stabilize the bottom sediment (Hamilton and Mitchell 1997) in the presence of bottom-feeding fish, and only when stressed beyond a threshold of light availability, do plants decline in abundance (e.g. Scheffer 1990). Although our study was not designed to study this effect, we confirm the results of Lougheed et al. (1998) who showed that wetlands containing carp were not always degraded and often contained dense and diverse beds of submersed macrophytes. Furthermore, carp may contribute more to reducing water clarity in wetlands containing a larger proportion of fine sediments, which we associated with increased agricultural and urban land-use in the watershed. For example, Hurley (1986) and Minns et al. (1994) showed that carp were common in wetlands in the Bay of Quinte in eastern L. Ontario. Our Bay of Quinte study wetlands (Wellers Bay, Blessington Bay, West Lake, Hay Bay, Sawguin Creek, Napanee River) each had a prevalence of sand in their sediment and greater than 6 species of submersed macrophytes found in dense beds. Conversely, marshes at the western end of L. Ontario (e.g. Pickering Harbour, Second Marsh, Humber River, Bronte Creek, Cootes Paradise) were also carp dominated (Stephenson 1990, Theismeijer, pers. comm., Great Lakes 2000 Cleanup Fund), but were characterized by silty sediments, turbid water and a sparse community of submersed vegetation. An obvious limitation to these results was the absence of data on carp biomass, which is related to water turbidity (Lougheed et al. 1998). Furthermore, the concomitant increase in watershed development and the prevalence of carp in the lower lakes makes it difficult to separate the effects of these two disturbance factors. These data do, however, indicate that wetlands stressed by both the presence of carp and development in the watershed tend to be turbid and sparsely vegetated.

In conclusion, as has been observed in several other studies (Smith et al. 1991; Minc 1997), physical factors largely related to geology and latitude such as exposure, sediment composition, and length of growing season may be important determinants of macrophyte community composition in coastal wetlands of the Great Lakes. In lower coastal and inland wetlands, plants are distributed according to a nutrient and clarity gradient, which was inextricably linked to land use in the watershed, and in some cases carp activity. In coastal lacustrine wetlands, especially in the upper lakes, land use plays less of a role in affecting water and sediment quality than mixing with the lake proper. We echo the management challenge issued to all levels of government at the most recent State of the Lake Conference (1997) to promote land use that is both efficient and protective of high value near-shore habitat in the Great Lakes.

This basin-wide variation in the distribution of macrophyte communities with wetland degradation likely has important consequences for fish and invertebrate habitat. Macrophyte habitat heterogeneity is relatively easy to quantify and could easily be incorporated into assessment protocols as an indicator of wetland quality (Wissinger 1999); however, the role that different macrophyte taxa play in providing habitat for the variety of organisms that use wetlands must first be determined. More research, such as that by Lougheed and Chow-Fraser (2000, Chapter 5), should be directed at determining the associations between water quality, macrophyte community structure and other aquatic organisms such as zooplankton in wetlands in the Great Lakes basin.

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Table 4-1. Characteristics of the 60 wetlands sorted by PC axis 1, including location, physico-chemical variables, the number of submergent species found, the wetland type (riverine, lacustrine or riverine/palustrine), and the percent forest cover in the watershed.

	WETLAND	LAKE	LAT	LONG	CHL-a (µg/L)	TSS (mg/L)	TP (µg/L)	TN (µg/L)	CARP	# subs	Type	% Forest
1	Cloud Bay	Superior	48°05'00"	89°26'00"	1.1	4.8	16.2	930	N	4	lac	100
2	Echo Bay	Huron	46°29'00"	84°04'00"	1.7	5.3	43.0	920		5	lac	100
3	Oliphant Bay	Huron	44°44'00"	81°16'00"	2.3	4.6	22.3	1150		6	lac	
4	Harris Lake	Inland	45°42'00"	80°82'00"	2.0	3.8	81.4	1105	N	9	lac	75
5	Baie du Doré	Huron	44°20'00"	81°33'00"	0.3	4.6	20.8	1200		4	lac	40
6	Hurkett Cove	Superior	48°50'00"	88°30'00"	0.3	5.4	26.8	1710	N	4	lac	100
7	Sturgeon Bay (LS)	Superior	48°12'00"	89°19'00"	1.4	4.8	20.8	1010	N	6	lac	100
8	Joe Lake	Inland	45°08'00"	76°41'00"	7.1	5.4	23.4	1211	N	10	riv	86
9	Presqu'ile Prov. Park	Ontario	44°00'00"	77°43'00"	2.4	4.8	54.4	1006	N	12	lac	33
10	Christie Lake	Inland	44°47'00"	76°28'00"	4.8	9.4	31.0	1428	N	10	riv/pal	95
11	Stump Lake	Inland	44°56'48"	76°38'12"	6.4	4.7	42.2	1277	N	12	lac	80
12	Shebeshekong River	Inland	45°24'30"	80°19'00"	6.1	9.5	69.3	1535	N	10	riv	70
13	Wellers Bay	Ontario	44°01'00"	77°36'00"	1.4	4.6	21.8	1680	Y	15	lac	
14	Long Point Prov. Park	Erie	42°35'00"	80°23'00"	1.4	5.2	19.8	1680	N	10	lac	
15	Tay River	Inland	44°52'45"	76°10'30"	4.3	8.4	50.1	1386	N	14	riv/pal	33
16	Goulais River Oxbow	Superior	46°43'00"	84°25'00"	4.0	5.9	30.4	1650	N	5	riv/pal	90
17	Spanish River	Huron	46°12'00"	82°21'00"	9.9	7.3	29.4	1320		5	riv	90
18	Turkey Point	Erie	42°40'00"	80°22'00"	5.1	6.4	26.3	1500	N	13	lac	38
19	Sturgeon Bay (GB)	Huron	44°44'00"	79°44'00"	0.0	3.4	30.4	2040	Y	8	lac	63
20	Madoma Crk	St. Lawr	44°16'00"	76°23'00"	1.7	4.6	45.5	1580		10	riv	58
21	Rondeau Prov. Pk	Erie	42°17'00"	81°51' 00"	0.6	7.7	25.3	1950		7	lac	
22	Isaac Lake	Inland	44°47'00"	81°14'00"	4.0	6.6	32.4	1690		6	lac	76
23	Blessington Bay	Ontario	44°10'00"	77°20'00"	7.1	5.3	62.6	1450	Y	8	lac	
24	Big Creek (Long Point)	Erie	42°34'00"	81°15'00"	2.3	5.3	52.5	1460	Y	4	riv/pal	16
25	West Lake	Ontario	43°56'00"	77°17'00"	6.8	6.2	35.9	1350	Y	6	lac	
26	Near Tobies Bay	Inland	44°51'00"	79°47'00"	22.3	7.4	139.1	1759	N	9	riv/pal	77
27	Chippewa Park	Superior	48°19'00"	89°12'00"	5.7	12.2	44.5	1800	N	0	lac	98
28	Hay Bay	Ontario	44°10'30"	76°55'30"	5.1	3.7	62.1	1411	Y	15	lac	21
29	Indian River	Inland	44°14'00"	78°09'00"	4.3	6.4	54.0	1640		8	riv	76
30	Wye Marsh	Inland	44°42'00"	79°51'00"	1.1	4.4	65.6	1900		8	riv	41
31	Collingwood Harbour	Huron	44°30'00"	80°13'00"	5.7	17.8	66.6	1010	Y	2	lac	34
32	Upper Canada BS	St. Lawr	44°59'00"	75°00'00"	2.6	16.4	33.9	1600		3	lac	
33	Sawguin Creek	Ontario	44°06'00"	77°23'00"	14.9	6.4	76.5	1749	Y	10	lac	28
34	Matchedash Bay	Huron	44°44'00"	79°40'00"	0.0	9.1	39.2	1970	Y	8	riv	46
35	Lake St. Clair	St. Clair	44°35'00	82°46'00"	10.4	13.2	38.5	2513	N	10	lac	
36	Waterford Pond	Inland	42°56'10"	80°18'45"	11.4	11.6	41.5	2375	Y	6	lac	21
37	Mission Island	Superior	48°22'00"	89°12'00"	47.6	16.8	87.3	2300	N	3	lac	
38	Napanee River	Ontario	44°14'00"	76°59'00"	19.0	7.9	124.1	2100	Y	6	lac	65
39	Mud Lake	Inland	42°57'00"	80°53'00"	8.5	12.7	101.4	2900		5	lac	
40	Wiltse Lake	Inland	44°36'00"	75°57'00"	19.2	23.8	64.6	2750		5	lac	42
41	Pine Bay	Superior	48°03'00"	89°31'00"	4.5	23.6	76.2	2820	N	3	riv	99
42	Pte. Mouillée Crk	St. Lawr	45°10'00"	74°22'00"	10.5	13.7	57.6	2350		5	riv	42
43	Turkey Creek	Erie	42°14'08"	83°05'07"	29.0	20.8	66.1	3052	Y	11	riv	6
44	Selkirk Prov. Park	Erie	42°49'00"	79°57'00"	5.7	18.4	184.5	2090		5	riv	18
45	Big Creek (Teeterville)	Inland	42°57'20"	80°26'50"	10.1	7.4	54.4	5705	Y	10	riv/pal	2
46	Little Cataraqui Crk	St. Lawr	44°13'00"	76°33'00"	15.3	6.9	114.5	3200		2	riv	17
47	Pickering Harbour	Ontario	43°49'00"	79°05'00"	35.8	40.2	138.7	2200	Y	1	lac	21
48	Johnstown Crk	St. Lawr	44°44'00"	75°28'00"	42.9	25.8	126.1	3250		10	riv	43
49	Willowbank Marsh	St. Lawr	44°19'00"	76°13'00"	51.1	17.7	206.7	3100		5	riv	11
50	Tremblay Beach Pond	Inland	42°18'00"	82°39'00"	9.3	31.1	129.1	3500	N	2	riv/pal	
51	Sutton Pond	Inland	42°50'00"	80°18'00"	18.5	41.8	80.0	4594	Y	1	riv	23
52	Second Marsh	Ontario	43°52'00"	79°51'00"	66.8	23.8	407.0	3166	Y	3	lac	8
53	Humber River	Ontario	43°38'00"	79°29'00"	52.0	57.3	214.4	1566	Y	1	riv	23
54	Martindale Pond	Ontario	43°10'07"	79°16'00"	53.4	39.1	180.5	3275	Y	2	riv	1
55	Jordan Harbour	Ontario	43°11'00"	79°23'00"	51.5	37.4	286.8	3215	Y	1	riv	15
56	Grand River - Dunville	Erie	42°54'00"	79°36'00"	64.8	60.2	160.8	3550	Y	2	riv	19
57	Bronte Crk	Ontario	43°23'00"	79°42'00"	7.4	116.6	126.6	4250	Y	1	riv	22
58	Cootes Paradise - after	Ontario	43°16'00"	79°55'00"	92.1	54.5 –	269.5	4110	Y	5	riv	34
59	15 Mile Creek	Ontario	43°10'00"	79°19'00"	23.9	124.3	344.8	2413	Y	2	riv	18
60	Grindstone Crk	Ontario	43°17'00"	79°53'00"	18.2	97.2	167.9	5760	Y	0	riv	32
61	Cootes Paradise -before	Ontario	43°16'00"	79°55'00"	87.8	63.9 –	241.7	4443	Y	1	riv	34
62	Holiday Cons. Area	Erie	42°02'05"	83°03'00"	239.1	209.2	670.3	9161	Y	1	riv	0

Table 4-2. Correlation co-efficients between principal components scores and environmental variables.

	Variance explained (%)	Environmental variable	r
PCA 1	45.7	TSS	0.92
		Turbidity	0.89
		TN	0.88
		TP	0.87
		TISS	0.87
		CHL-*a*	0.83
		COND	0.76
		TNN	0.71
PCA 2	15.8	TP_{sed}	-0.85
		$Inorg_{sed}$	0.78
		pH	0.68
PCA 3	10.4	TEMP	0.68
		SRP	0.52

Table 4-3. Characteristics of the regression relating land use in each region (Inland, Lower coastal and Upper coastal) to principal components axes 1 and 2.

		PC axis 1		PC axis 2	
	region	r^2	p-value	r^2	p-value
%AGRIC	INLAND	0.67	0.0003	0.34	0.0284
	LOWER	0.16	0.0489	-	-
	UPPER	-	-	-	-
%AGR+URB	INLAND	0.61	0.0009	0.29	0.0457
	LOWER	0.22	0.0181	-	-
	UPPER	-	-	-	-
%FOREST	INLAND	0.60	0.0012	0.23	0.08
	LOWER	0.16	0.0511	-	-
	UPPER	-	-	-	-

Table 4-4. Comparisons of means (and standard errors) of the percent organic composition of the sediment and the maximum sediment size (µm) observed in wetlands characterized by different land use types in inland, lower coastal and upper coastal systems. Asterisks (*) indicate significantly differences among INLAND sites.

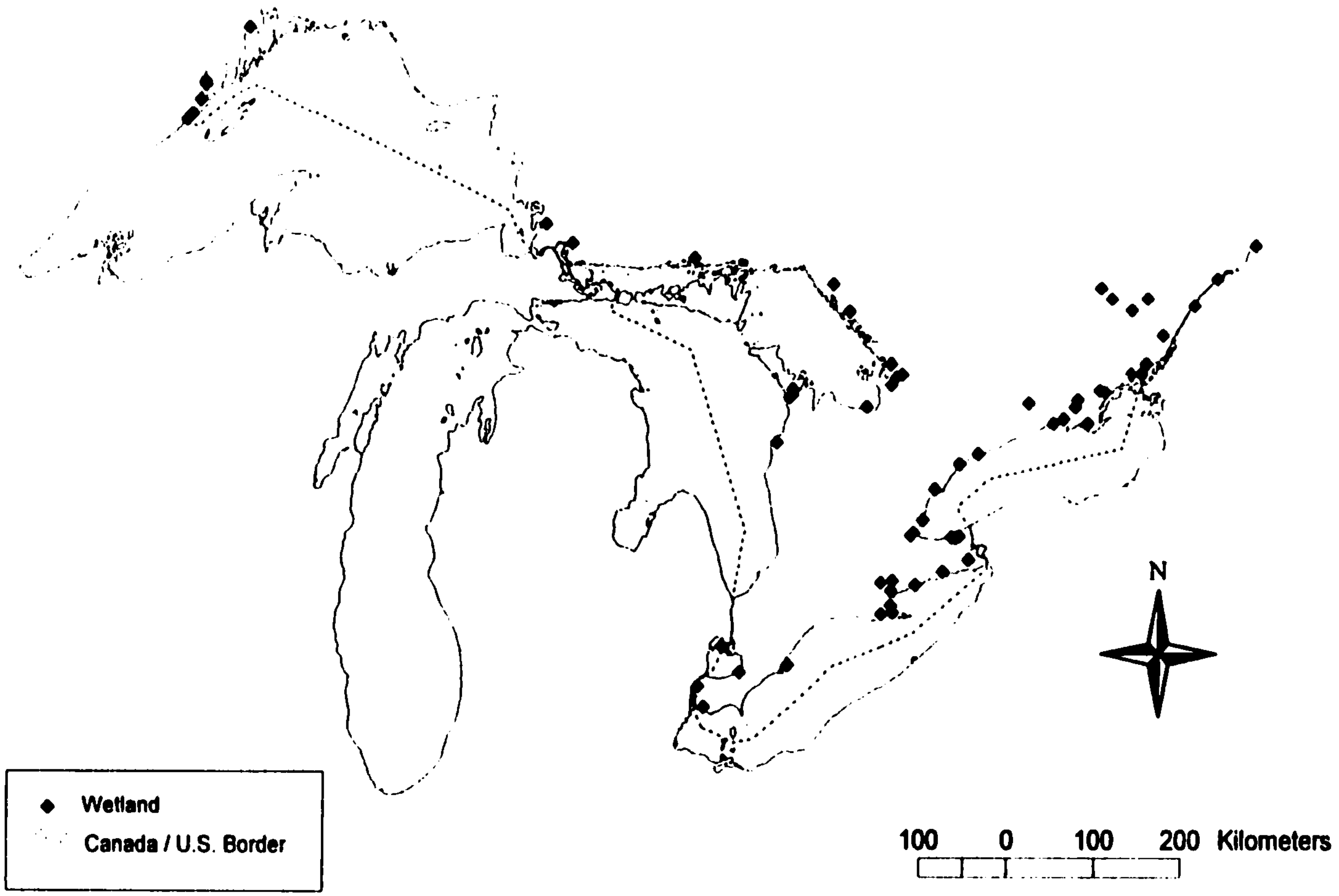
		n	% Organic	Max Sed Size
INLAND	Agricultural	4	16.5 (4.3)*	0.156 (0.094)
	Forest	8	49.8 (6.8)	16 (0)*
	Agric/Forest	2	76.1 (1.7)	0.0039 (0)
LOWER	Agricultural	17	17.2 (4.3)	0.094 (1.98)
	Forest	2	23.9 (14.8)	8.03 (7.97)
	Agric/Forest	2	21.8 (0.6)	0.25 (0)
	Urban	4	29.1 (11.4)	0.125 (0)
UPPER	Agricultural	1	6.62 (0)	0.0625 (0)
	Forest	8	3.0 (0.8)	9 (2.91)
	Agric/Forest	2	8.73 (7.58)	8.03 (7.97)

Table 4-5. Plant taxa identified in the wetlands are grouped according to their structural nature. All taxa not assigned a code were excluded from CCA analysis since they occurred in <10% of wetlands.

SUBMERGENT		EMERGENT	
Ceratophyllum demersum	CE	*Eleocharis smallii*	
Chara sp.	CH	*Equisetum* sp.	
Elodea canadensis	EL	*Lythrum salicaria*	LY
Isoetes sp.		*Phragmites* sp.	
Myriophyllum sp.	MY	*Pontederia cordata*	PO
Najas flexilis	NA	*Sagittaria latifolia*	SA
Nitella sp.		*Scirpus* sp.	SC
Potamogeton sp.*	PS	*Sparganium* sp.	
Potamogeton crispus	PC	*Typha* sp.	TY
Potamogeton gramineus		*Zizania palustris*	
Potamogeton pectinatus	PP		
Potamogeton richarsonii	PR	FLOATING-LEAF	
Ranunculus sp.	RA	*Brasenia schrebieri*	
Utricularia sp.	UT	*Lemna* sp.	
Vallisneria americana	VA	*Nuphar variegatum*	NU
		Nymphaea odorata	NY
		Polygonum amphibium	
		Potamogeton natans	PN
		Spirodela sp.	

**Potamogeton* sp. represents all other *Potamogeton* species not listed here.

Figure 4-1. Map of Great Lakes region showing the location of 62 wetlands sampled between 1995 and 1999, including the location of Cootes Paradise Marsh (L. Ontario).



◆ Wetland
Canada / U.S. Border
100 0 100 200 Kilometers
N

Figure 4-2. Plot of PC axis 1 scores versus PC axis 2 scores.

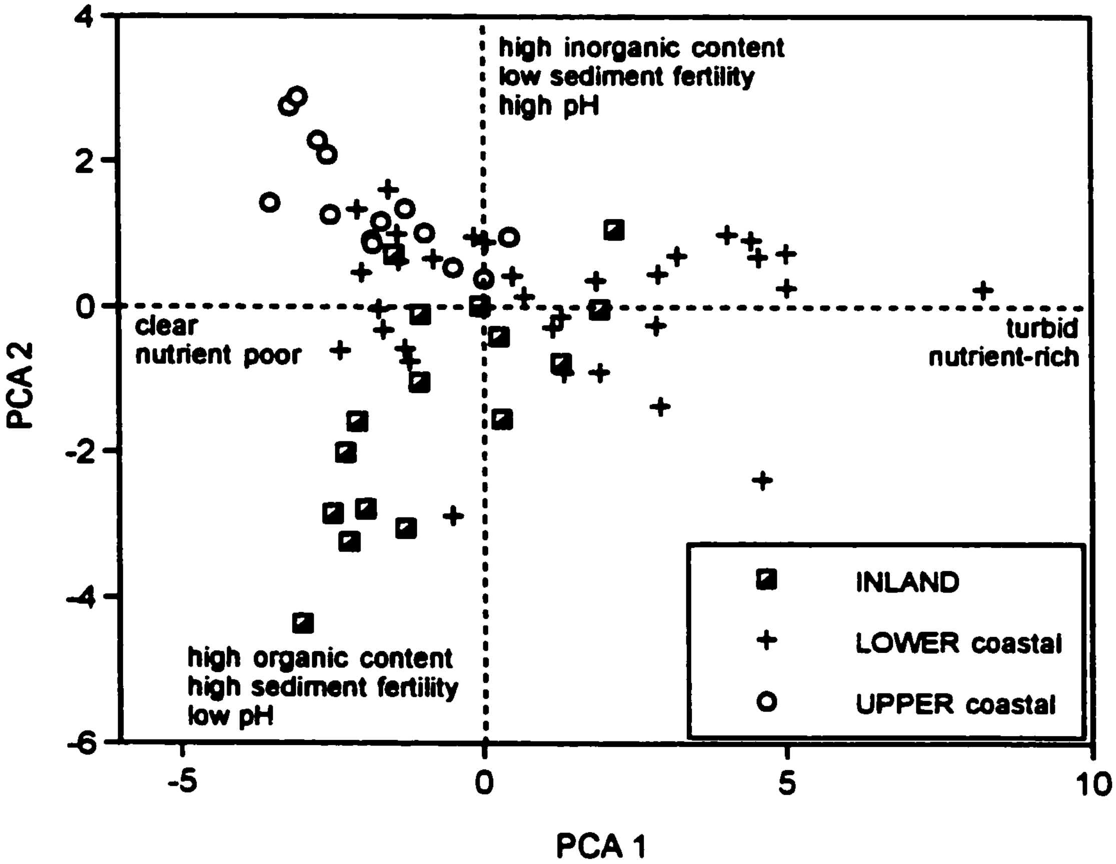
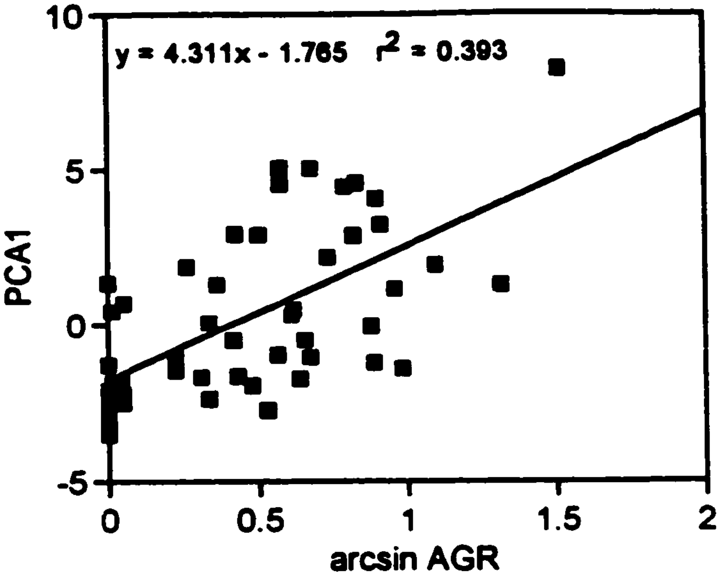
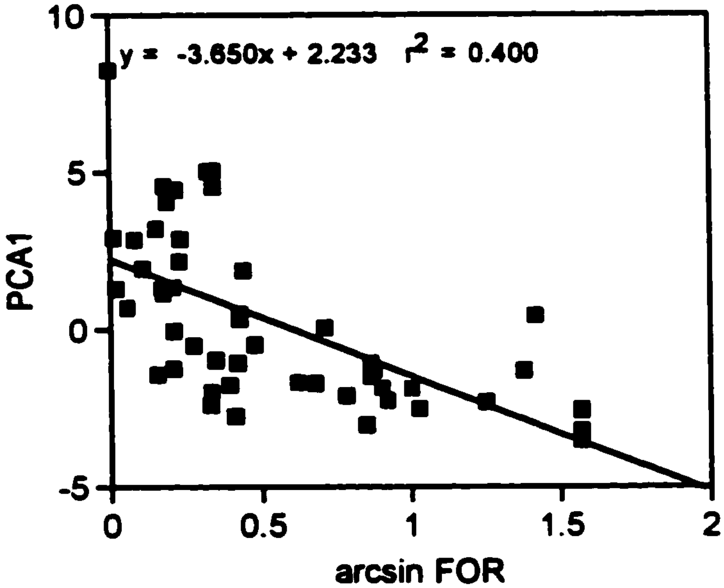

high inorganic content
low sediment fertility
high pH
clear
nutrient poor
turbid
nutrient-rich
high organic content
high sediment fertility
low pH
INLAND
LOWER coastal
UPPER coastal
PCA 2
PCA 1
4
2
0
-2
-4
-6
-5
0
5
10

Figure 4-3. PC axis 1 scores against a) arcsine-transformed percent agricultural land (AGR), b) arcsine-transformed percent forested land (FOR) and c) arcsine-transformed percent agricultural and urban land (AGR+URB).


y = 4.311x - 1.765 r^2 = 0.393
PCA1
arcsin AGR
10
5
0
-5
0
0.5
1
1.5
2


y = -3.650x + 2.233 r^2 = 0.400
PCA1
arcsin FOR
10
5
0
-5
0
0.5
1
1.5
2

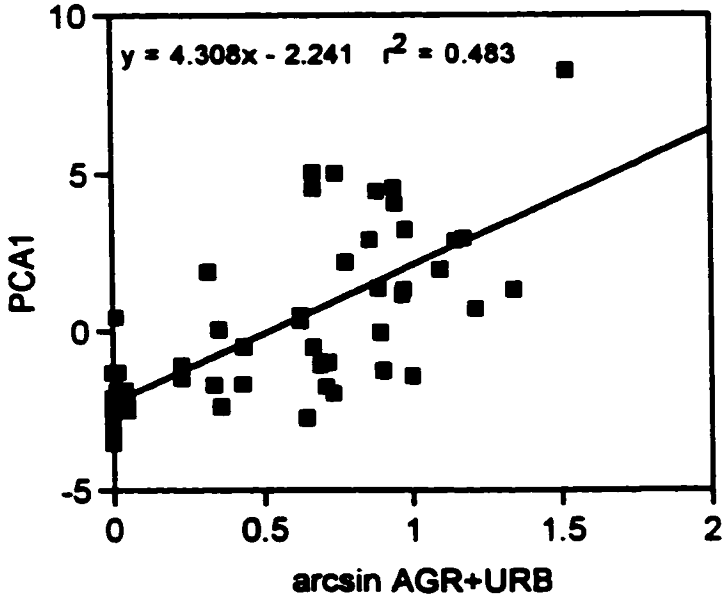
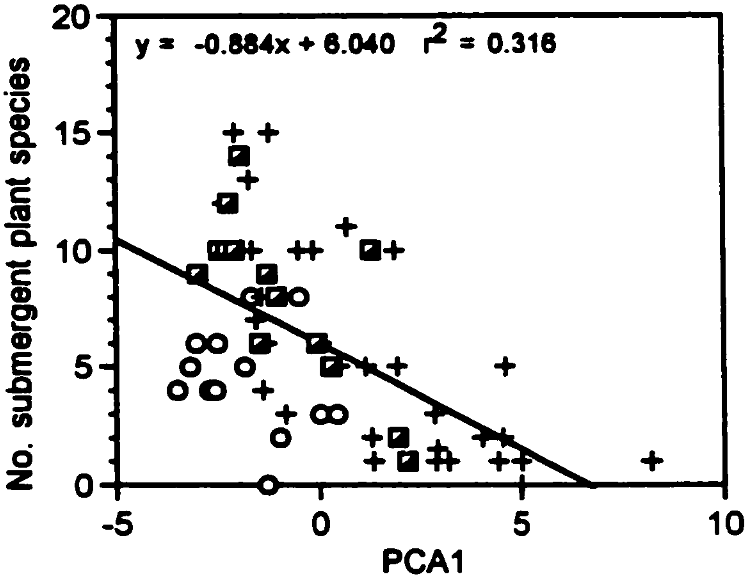

y = 4.308x - 2.241 r^2 = 0.483
PCA1
arcsin AGR+URB
10
5
0
-5
0
0.5
1
1.5
2

Figure 4-4. Number of submersed plant taxa plotted against a) PC axis 1 and b) PC axis 2 scores.


y = -0.884x + 6.040 r^2 = 0.316
No. submergent plant species
0
5
10
15
20
-5
0
5
10
PCA1

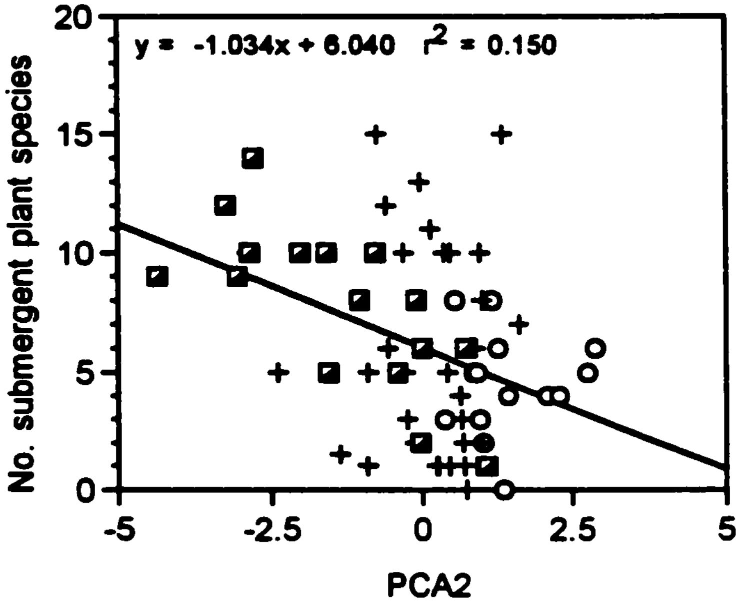

y = -1.034x + 6.040 r^2 = 0.150
No. submergent plant species
0
5
10
15
20
-5
-2.5
0
2.5
5
PCA2

Figure 4-5. Bi-plot of the CCA (axis 1 versis axis 2), showing the location of macrophyte species points.

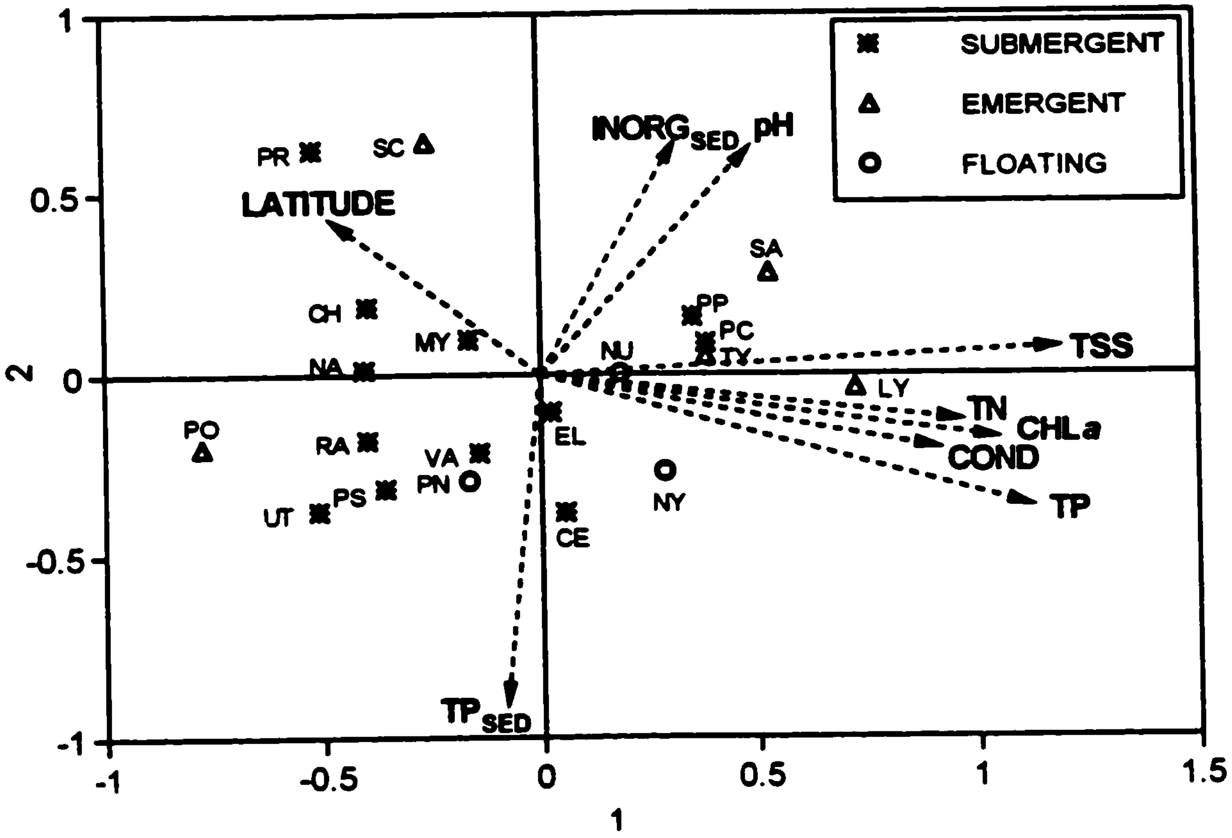

SUBMERGENT
EMERGENT
FLOATING
INORG$_{SED}$
pH
LATITUDE
TSS
TN
CHL*a*
COND
TP
TP$_{SED}$
PR
SC
CH
MY
NA
PO
RA
VA
PN
PS
UT
NU
SA
PP
PC
TY
LY
EL
NY
CE
1
0.5
0
-0.5
-1
-1
-0.5
0
0.5
1
1.5
2
1

Figure 4-6. Bi-plot of the CCA (axis 1 versis axis 2), showing the location of site scores and the location of Cootes Paradise site scores before (96) and after (97) carp exclusion.

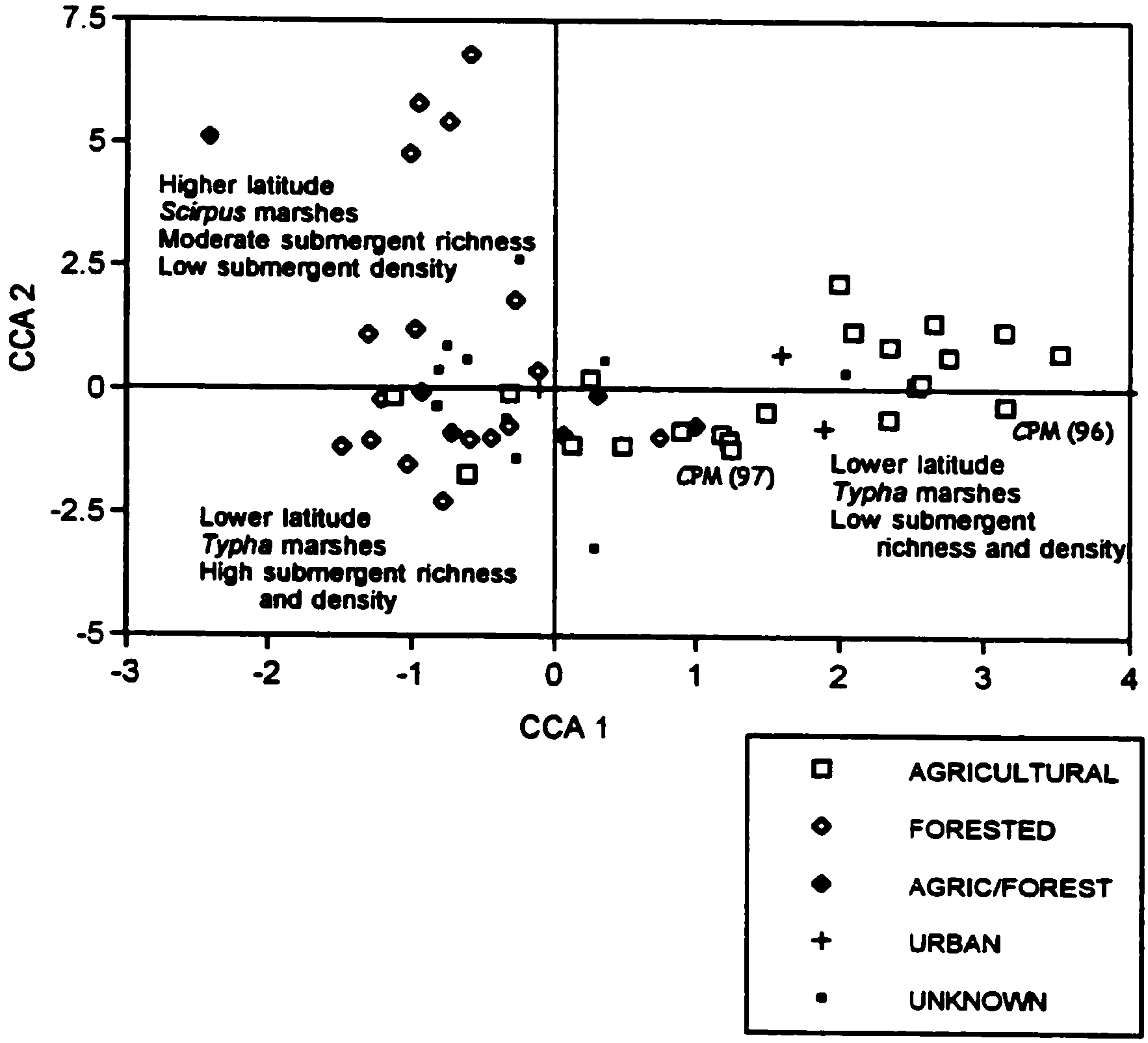
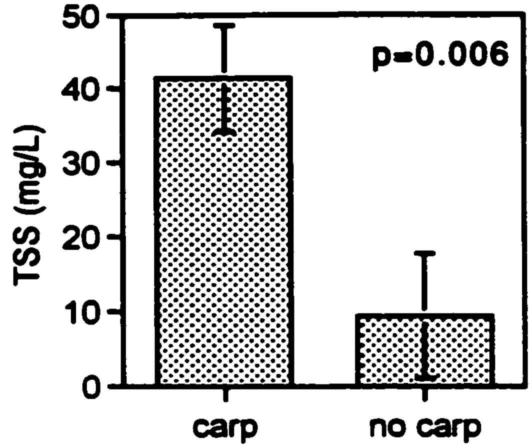
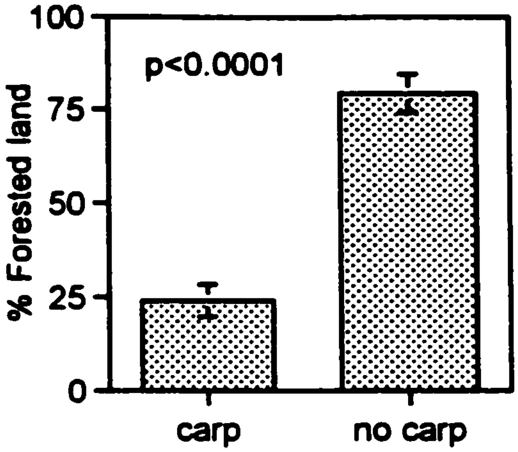

7.5
5
2.5
0
-2.5
-5
-3
-2
-1
0
1
2
3
4
CCA 2
CCA 1
Higher latitude
Scirpus marshes
Moderate submergent richness
Low submergent density
Lower latitude
Typha marshes
High submergent richness
and density
Lower latitude
Typha marshes
Low submergent
richness and density
CPM (97)
CPM (96)
AGRICULTURAL
FORESTED
AGRIC/FOREST
URBAN
UNKNOWN

Figure 4-7. Comparison of a) TSS and b) % forested land in wetlands with and without carp. For wetlands with carp, comparison of c) TSS in wetlands with sparse or dense submergent beds and d) TSS in wetlands dominated by sandy or silty sediment.

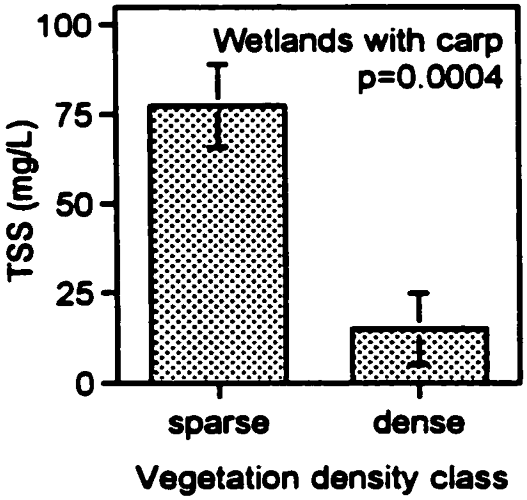
7 a


50
40
30
20
10
0
TSS (mg/L)
p=0.006
carp
no carp

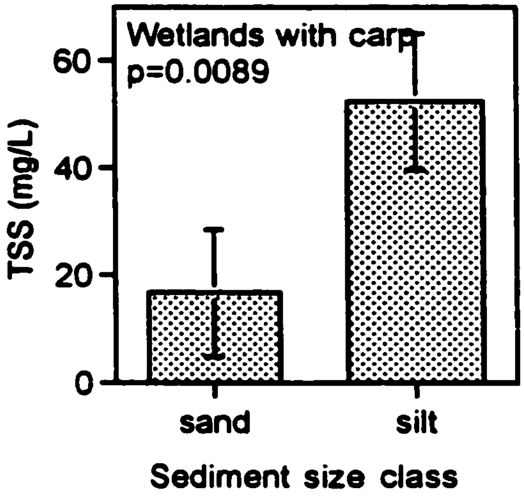
7 b


100
75
50
25
0
% Forested land
p<0.0001
carp
no carp

7 c


100
75
50
25
0
TSS (mg/L)
Wetlands with carp
p=0.0004
sparse
dense
Vegetation density class

7 d


60
40
20
0
TSS (mg/L)
Wetlands with carp
p=0.0089
sand
silt
Sediment size class

CHAPTER 5:

Development and use of a zooplankton index to monitor wetland quality in Canadian marshes of the Great Lakes basin.

Lougheed, V.L. and P. Chow-Fraser.

ABSTRACT: We used information on water-quality and zooplankton associations with aquatic vegetation (emergent, submergent and floating-leaf) from 60 coastal and inland marshes in the Canadian Great Lakes basin to develop an index that could be used to assess wetland quality across the Great Lakes region. Wetlands ranged from pristine systems, with good representation of emergent, submergent and floating-leaf aquatic taxa, to highly degraded systems, with only a fringe of emergent vegetation and some floating-leaf plants. Partial canonical correspondence analysis (pCCA) showed that plant-associated taxa such as chydorid cladocerans were common in high-quality wetlands while more open-water, pollution-tolerant taxa (e.g. *Brachionus*, *Moina*) dominated degraded wetlands. We used the results of the pCCA to determine the environmental conditions preferred by rotifer and cladoceran taxa and then used these data to develop the wetland zooplankton index (WZI). The index was tested by assessing the response of a degraded Great Lakes coastal wetland, Cootes Paradise Marsh, to carp exclusion as a marsh restoration technique.

The WZI was found to be robust, and more useful than indices of diversity (H', species richness) and measures of community structure (mean size, total abundance) for indicating wetland quality. It was sufficiently sensitive to detect site-specific improvements in Cootes Paradise Marsh during the initial two years of marsh restoration (carp exclusion). Since wetlands used in this study covered a wide environmental and geographic range, the index should be broadly applicable across the Great Lakes basin; however, it must be used with caution in U.S. waters; in wetlands dominated by taxa identified as rare indicator species; and, in comparisons of upper and lower Great Lakes.

INTRODUCTION

Recently, governments in both Canada and the United States have become alarmed at the accelerated loss and degradation of wetlands in developed areas of the Great Lakes basin. Whillans (1982) estimated that heavily settled areas of the lower Great Lakes have lost 75% of their wetland area, with some areas experiencing 100% loss. Those wetlands remaining have often become degraded as a result of the dominance of exotic benthivorous common carp (*Cyprinus carpio*) and increased water turbidity and nutrient concentrations due to changes in land use patterns over the past several decades (Whillans 1996; Chow-Fraser 1998, 1999). To track these long-term changes in ecosystem quality and quantity, managers require simple, robust indicators that can be applied across the basin by many environmental agencies. Not surprisingly, one of the goals of the 1998 State of the Lakes Ecosystem Conference (SOLEC; a biennial conference hosted by both governments to examine issues concerning the Laurentian Great Lakes) has been to develop appropriate indicators of ecosystem health for coastal wetlands of the Great Lakes (Bertram and Stadler-Salt 1999).

A great impediment to the development of these indicators is the lack of a sufficiently large database that would permit the emergence of a community index based on biota as well as water quality variables. We propose to use zooplankton, and their association with macrophytes and relevant water quality variables, to indicate the quality of coastal marshes in the Great Lakes basin. Although zooplankton are known to respond quickly to environmental conditions (Schindler 1987), only a few attempts have been made to use the zooplankton community to indicate quality of aquatic ecosystems (e.g. Gannon and Stemberger 1978; Sládecek 1983; Stemberger and Lazorchak 1994; Gaiser and Lang 1998). Our rationale for choosing zooplankton are three-fold. First, there are well-documented plant-associated zooplankton taxa whose presence in a system are highly dependent on the presence of submersed macrophytes (e.g. Quade 1969; Paterson 1993). Hence, the taxonomic composition of the zooplankton community should reflect the presence and distribution of submergent plants in the wetland. Secondly, zooplankton taxa often have different preferences for trophic state (e.g. Berzins and Bertilsson 1989; Berzins and Pejler 1989) and water clarity (e.g. Lougheed and Chow-Fraser 1998), and therefore, species replacement will also occur with water quality degradation. Finally, since the species richness of submersed macrophytes declines as marshes become eutrophic and degraded (Crosbie and Chow-Fraser 1999; Lougheed et al., 2000, Chapter 4), we hypothesize that the zooplankton community should reflect changes in the plant community as we proceed along the trophic/degradation gradient.

In general, biotic indices integrate the sensitivity of several taxonomic groups to environmental conditions (e.g. acidity, degree of degradation, etc.) into a single index value. These indices are particularly useful in situations where data must be statistically analyzed and conveyed to non-biologists. A common criticism is that these indices may oversimplify effects on the community in question, especially when organisms are grouped into higher taxonomic groups, where responses of individual members may vary greatly (e.g. Sládecek 1983; Gaiser and Lang 1998). However, we feel that these integrative indices are superior to measures that result in loss of species-specific information (e.g. diversity) or those that rely only on a select number of taxa (e.g. indicator species; index of biotic integrity).

One benefit of a sound biotic index is that it could be used as a tool to evaluate restoration techniques across ecosystems, especially if the indicator is sufficiently sensitive that changes over the short-term (i.e. several years) can be tracked. The recent removal/exclusion of carp from several Great Lakes coastal wetlands (Cootes Paradise Marsh in Lake Ontario; Metzgers Marsh in Lake Erie) (Lougheed et al. 1998; Wilcox and Whillans 1999) could be evaluated in this fashion, to determine if this expensive and labor-intensive approach should be recommended as an effective restoration technique.

In this paper, we develop an index based on water quality and observed associations of zooplankton with aquatic vegetation that can be used to assess the quality of wetlands across the Great Lakes basin. We collected information from 60 wetlands, ranging in quality from pristine to highly degraded, that were located along the shoreline or within the basin of the four Canadian Great Lakes. We first use partial canonical correspondence analysis (pCCA) to examine the statistical relationship between the distribution of zooplankton taxa, a suite of water quality variables, and the macrophyte community structure of the wetland (i.e. submergent, emergent or floating-leaf aquatic vegetation). We then use results of the pCCA to develop a wetland zooplankton index (WZI) for rotifers and cladocerans, and compare this biotic index with commonly used indicators of community quality such as the Shannon-Wiener species diversity index.

In addition, we use this index to assess the response of Cootes Paradise Marsh to carp exclusion as a restoration technique. Cootes Paradise Marsh is a degraded 250-ha drowned river-mouth marsh located at the western end of Lake Ontario (43° N, 79° W) (see Figure 5-1). Carp have been physically excluded from the marsh since the winter of 1997 by the Cootes Paradise Fishway (Wilcox and Whillans 1999; see Lougheed and Chow-Fraser 2000, Chapter 4). We plan to use data collected in the summer of 1993 and 1994 (prior to exclusion), and those collected in the summer of 1997 and 1998 (following exclusion) to calculate corresponding WZI values and evaluate the ability of this index to track site-specific changes in the marsh following carp exclusion.

METHODS

Water and zooplankton samples were collected from 60 marshes in the Great Lakes basin from 1995 to 1999. Wetlands ranged from St. Lawrence River sites just east of Cornwall, down to the Windsor/Detroit area and Lake St. Clair, up to Lake Superior and the Ontario/Minnesota border (Figure 5-1). Forty-four of these were coastal marshes (lying within 2-km of Great Lakes shoreline or connecting channels but not separated hydrologically from the lakes due to dams or waterfalls) of the upper (L. Michigan and L. Superior) and lower (L. Ontario, L. Erie) lakes, while the remaining sixteen were inland wetlands located within the Great Lakes/St. Lawrence River basin. All wetlands were visited at least once in mid-summer (mid-June to end of July), while a subset were also visited in early summer (May to mid-June) and/or late summer (August). Zooplankton samples collected in mid-summer constituted two-thirds of all samples included in this study. To ensure consistent measurements of both water quality and zooplankton communities, both of which have been shown to be affected by storm events (Krieger and Klarer 1991; Chow-Fraser 1999), wetlands were visited no sooner than 48 hours following a rain event; however, several inland wetlands were unavoidably sampled during a rain storm which had already lasted several days. Fortunately, these wetlands were among those sampled on more than one occasion and provided an informative comparison of the effect of storm flow on the zooplankton communities in different wetland types.

We were interested in characterizing the plankton communities within four different habitat site types in each wetland: open water 10-m from the outermost edge of aquatic plants (OPEN 10-m), open water 3-m from aquatic plants (OPEN 3-m), within submergent plant beds (>5 stems/m^2) (SUB) and within or immediately adjacent to emergent aquatic vegetation (EM). When submergent or emergent beds were absent or inaccessible, plankton below floating aquatics were sampled (FLTG). The species richness of submergent plants in each wetland was determined as described in Lougheed et al. (1998).

All water samples were collected from the middle of the water column at the OPEN 3-m site. Because of the large site-to-site, year-to-year and seasonal variation in water levels, which are characteristic of Great Lakes coastal marshes (Maynard and Wilcox 1997; Chow-Fraser 1999), water depths in this study ranged from 5 cm to 260 cm, depending on wetland site, time of year, and the sampling year in question. Water samples were analyzed according to standard methods (APHA 1992) for total phosphorus (TP), total nitrogen (TN) (sum of total kjeldahl nitrogen (TKN) and total nitrate nitrogen

(TNN)) and total suspended solids (TSS). Following digestion by potassium persulfate, TP was analyzed according to Murphy and Riley (1962) and measured on a Milton Roy spectrophotometer. Nitrogen analyses (TKN and TNN) were performed using Hach protocols and Hach reagents (Hach Company 1989) and measured on a Hach DR2000 spectrophotometer. Planktonic chlorophyll-*a* (CHL-*a*) was extracted using 90% acetone and a 1-h extraction period. Absorbance measurements were made with a Milton Roy spectrophotometer and results were corrected for phaeopigments by acidification. Temperature, pH, dissolved oxygen and conductivity were determined using a H2O® Hydrolab multiprobe and Scout® monitor.

All zooplankton samples were collected from the middle of the water column at each of the habitat site types named above (where available). Zooplankton at open water sites were collected using a 5-L Schindler-Patalas trap, while zooplankton in vegetation were collected using a 1-L beaker inverted 3 times into adjacent areas of vegetation for a total sample volume of 3-L. All samples were filtered through 64-µm-mesh Nitex screen, backwashed into 60-mL bottles and preserved in 4% sugar-formalin. Samples were thoroughly mixed and sub-sampled to obtain at least 100 animals. Abundances and lengths of all animals present in the subsamples were recorded, but biomass could not be determined because of the absence of published length-weight relationships for many of the taxa encountered. Copepods were identified to sub-order only (i.e. cyclopoids, calanoids, harpacticoids), and therefore we report on their abundances but exclude them from all subsequent, more species-specific analyses. The published sources used to identify the cladocerans and rotifers to species are described elsewhere (Lougheed and Chow-Fraser 1998).

All statistical analyses were performed using SAS.Jmp software (version 3.1.5, SAS Institute Inc., Cary, N.C.), with the exception of canonical correspondence analysis, which was performed using CANOCO 4.0 (ter Braak and Smilauer 1998) and Shannon-Wiener diversity index which was calculated using MVSP (version 3.1, Kovach Computing Services, Ithaca, N.Y.).

Multivariate statistical analyses

Canonical correspondence analysis (CCA) is a useful technique when species data have been collected over a suitably large habitat range to display a unimodal relationship to the measured environmental variables (Jongman et al. 1995), and has been used by many authors to relate the distribution of zooplankton taxa to their environment (e.g. Hessen et al. 1995; Romo et al. 1996; Attayde and Bozelli 1998). CCA maximizes the separation of species optima along synthetic axes representing the primary environmental gradients in the data set. To confirm that CCA was an appropriate model for this data set, we first entered the species data into a detrended correspondence analysis (CANOCO 4.0; not shown), which revealed sufficiently large gradient lengths (> 4 SD) to indicate that zooplankton distributions in this study showed a clear unimodal response along the environmental gradient (ter Braak and Smilauer 1998). Then, because samples were collected over a four month period, we performed a partial CCA (pCCA) instead of a regular CCA, which eliminated background variation due to the co-variable time (i.e. Julian day) (Jongman et al. 1995; ter Braak and Verdonschot 1995).

Environmental parameters entered into the pCCA analysis included continuous variables such as: TP, TN, TSS, CHL-*a*, TEMP, DO, pH, COND and LATITUDE (measured as decimal degrees), along with more qualitative variables that described habitat type: SUB, EM, FLTG (within submergent, emergent and floating-leaf macrophyte beds, respectively), OPEN 3-m and OPEN 10-m (open water 3m and 10m away from macrophyte beds, respectively). All continuous environmental variables were $\log_{10}$-transformed to approximate normal distributions and standardized to zero mean and unit variance.

Although our analyses included rare zooplankton taxa, we confirmed in a preliminary analysis that the general conclusions were unaffected when rare taxa were removed prior to the pCCA being run. Zooplankton abundances were $\log_{10}$-transformed ($\log(x + 1)$) to normalize the data and reduce the sample variance. Statistical significance of the pCCA was determined using Monte Carlo permutations (199 random permutations) (ter Braak and Smilauer 1998).

Development of the wetland zooplankton index

The wetland zooplankton index (WZI) was developed based on trends observed in the pCCA, which will be discussed in detail in the Results. We assigned 'optimum' (U) and 'tolerance' (T) values (ter Braak and Verdonschot 1995) to each grouping that emerged from the pCCA as a suitable taxonomic unit (referred to henceforth as 'taxon').

For this purpose, we ran a pCCA (not shown in this paper) using the collapsed taxonomic groupings shown in Table 5-4 instead of individual species; it is important to note that the environmental and species trends displayed by this pCCA were virtually identical to those of the species-specific pCCA (Figure 5-2). Each taxonomic group was assigned a weight that indicated its optimum along the pCCA axis 1 where 1=most tolerant of degraded conditions and 5=most intolerant of degraded conditions. The weighted standard deviations of the taxon scores on the pCCA axis 1 were then used to indicate tolerance, that is, whether the taxon had a narrow (3), intermediate (2), or broad (1) niche breadth. Accordingly, those taxa given higher tolerance weights occurred across very narrow ranges and were therefore assumed to be better indicators of specific environmental conditions than taxa that were more ubiquitous. By comparison, very rare taxa (those that occurred in <10% of the wetlands) were assigned a low tolerance score because their sparse distribution could not be used reliably to reflect specific environmental conditions.

The index was calculated using tolerance-weighted weighted averages in the following equation (Zelinka and Marvan 1961; Lenat 1993; Kelly and Whitton 1995):

$$\mathrm{WZI} = \frac{\sum_{i=1}^{n} Y_i\, T_i\, U_i}{\sum_{i=1}^{n} Y_i\, T_i}$$

where Y_i = abundance or presence of species i, T_i = tolerance (1-3) and U_i = optimum (1-5). The index can therefore range from 1 (indicative of low quality) to 5 (indicative of high quality wetland). In this paper, most WZI analyses were performed using zooplankton abundances; however, when presence/absence data were used, the index was labeled $WZI_{P\text{-}A}$.

Assessment of marsh restoration on wetland quality

In the on-going long-term study of Cootes Paradise Marsh (see Chow-Fraser 1999; Lougheed and Chow-Fraser 2000), 3 sites in the marsh were sampled bi-weekly over the summer (May-August inclusive) for 2 years prior to carp exclusion (1993 and 1994) and 2 years following (1997 and 1999). Two sites were classified as OPEN 10-m sites: a relatively deep open water site near the marsh outflow (mean depth ranged from 97-127 cm) and a shallow lagoon site that historically received loadings from the Dundas Sewage Treatment Plant (depth 43-69 cm). The third site was within the cattail beds of a marsh inlet (depth 23-49 cm), and therefore was classified as an emergent site (EM). In total, ninety samples of zooplankton were enumerated and identified over the four years, but none of these were used in the development of the WZI. We use these data to evaluate the usefulness of the WZI in tracking site-specific changes in marsh quality following marsh exclusion and to determine the effect of sampling frequency on WZI values.

Seasonal and year-to-year variability in the zooplankton community

To assess the effect of season on the calculation of the zooplankton index, we used data from wetlands sampled on more that one occasion over the summer of 1996.

This included 13 wetlands that had been sampled twice (July/July and August/September) and 5 wetlands sampled monthly (May to August) (see Crosbie and Chow-Fraser 1999, excluding wetlands 1, 3, 15 and 18). To assess the effect of year-to-year variation, we used data for 2 wetlands that had been sampled at least once in mid-summer in 3 different years (Cootes Paradise Marsh and Big Creek Marsh; see Lougheed et al. 2000, Chapter 4 for descriptions).

RESULTS

Environmental variation

Wetlands in this study represented a wide range of conditions from oligotrophic to extremely hypereutrophic (Table 5-1). Initially, principal components analysis (PCA) was used to determine which environmental parameters explained the greatest amount of variation in the data set. Nearly 50% of the variation in the continuous environmental variables was explained by principal components axis 1. PC axis 1 was significantly ($p<0.0001$) and positively correlated with variables that are indicative of the nutrient status (TP: $r = 0.82$; TN: $r = 0.79$), particulate content (TSS: $r = 0.87$; CHL-*a*: $r = 0.85$) and ionic strength (COND: $r = 0.77$) of the water and negatively correlated with LATITUDE ($r = -0.73$). Therefore, PC axis 1 generally contrasted degraded wetlands in highly developed southern latitudes of the lower Great Lakes, with high-quality wetlands of central and northern Ontario.

Zooplankton composition

A total of 55 cladoceran species and 76 rotifer species were identified in these wetland samples. Only half of all species (38 rotifers; 25 cladocerans) occurred commonly (defined as occurring in >10 % of wetlands; bolded values in Table 5-2). Very few occurred in >50% of the wetlands sampled, and these included the rotifers *Asplanchna* sp., *Keratella cochlearis*, *Platyias patulus* and *Polyarthra* sp. Common cladocerans included four chydorids (*Acroperus harpae*, *Camptocercus macrurus*, *Chydorus sphaericus*, *Pleuroxus denticulatus*), *Scapholeberis mucronata*, *Simocephalus exspinosus*, *Sida crystallina* and *Bosmina longirostris*.

Relative to the open water sites, the vegetated sites tended to have greater species richness, abundances, Shannon-Wiener diversity (H') and larger mean size of zooplankton (Table 5-3). In particular, there was disproportionate representation of larger taxa in vegetated sites including Chydoridae, Daphnidae (but not *Daphnia*), Sididae and Macrothricidae. By comparison, rotifers and *Bosmina* formed a greater proportion of organisms encountered at open water sites. Both mature and immature forms of copepods tended to occur with greater abundances with the vegetation.

Partial Canonical Correspondence Analysis (pCCA)

Bi-plots of the first two pCCA axes are found in Figure 5-2a and b; for clarity, data corresponding to rotifers and cladocerans are shown in separate bi-plots. These figures explain 44% of the variation in zooplankton distribution along the first two synthetic environmental axes. The significance of each of the environmental variables in explaining the distribution of zooplankton species was assessed using the forward selection procedure of CANOCO. All variables were significant at the $p<0.05$ level, except for TN; hence the latter was excluded from the final analysis. The most important predictors of zooplankton distribution, as indicated by their correlation with pCCA axis 1 were TSS (0.834), CHL-*a* (0.748), TP (0.730), COND (0.613) and the presence of submergent vegetation (SUB) (-0.496). Because all water-quality data were collected at the OPEN 3-m site, this axis does not reflect differences in water quality between open water and vegetated sites in any individual wetland; instead, it indicates heavily vegetated wetlands have clearer water and a statistically unique zooplankton community, whereas wetlands with sparse macrophyte distribution tend to be more turbid, and are associated with taxa that are more typically found in limnetic ecosystems. By comparison, the 2nd axis of the pCCA, which distinguished urbanized wetlands, occurring primarily in southern Ontario, from more pristine northerly wetlands, was highly correlated with LATITUDE (0.600) and COND (-0.662).

To reduce clutter, we have plotted only the common (occurring in >10% of wetlands) rotifer and cladoceran taxa on the bi-plots, using the first three letters of the genus and species as labels (Figure 5-2a and b, respectively). Species of the same rotifer genera tended to show similar environmental preferences along pCCA axis 1 (e.g. *Monostyla* in Figure 5-2a) as did similar species of cladocerans (e.g. *Alona* in Figure 5-2b). Wetlands that had clear water with substantial submersed aquatic vegetation tended to be associated with specific rotifer genera. For example, all 8 species of *Monostyla* encountered in this study tended to occur within submersed macrophyte beds. Similarly, 9 of 11 species of *Lecane*, 6 of 7 species of *Euchlanis*, all 5 species of *Lepadella*, 3 of 4 species of *Trichocerca* and less speciose taxa such as *Platyias patulus* and *Mytilina* sp. were commonly found associated with submergent vegetation. Species of cladocerans that were well represented in heavily vegetated wetlands included 21 of 24 species of chydorids encountered in this study, 7 of 9 species of macrothricids, *Simocephalus* sp., *Polyphemus pediculus*, *Sida crystallina*, *Diaphanosoma brachyurum*, *Scapholeberis mucronata* and *Ceriodaphnia reticulata*.

By comparison, there were only a few taxa tolerant of highly degraded, sparsely vegetated wetlands and these included 10 of 10 species of *Brachionus*, *Filinia*, *Asplanchna*, *Polyarthra* and 6 of 7 species of *Keratella* ; cladoceran species that were found consistently in degraded wetlands included 2 of 2 species of *Moina*, 3 of 4 species of *Daphnia* and the bosminids, *Bosmina longirostris* and *Eubosmina coregoni*. Taxa which appeared to be found more exclusively in the lower latitudes were *Pleuroxus denticulatus*, *Pleuroxus procurvatus*, *Kurzia latissima* and *Scapholeberis mucronata*, whereas *Ophyroxus gracilis* occurred commonly in the northern reaches of the study area.

Development of Wetland Zooplankton Index (WZI)

As mentioned previously, we wanted to first reduce the total number of taxa in our data set before calculating the WZI. Taxonomic groupings were formed by grouping species of the same genera according to their location on the first axis of the pCCA biplot (Table 5-4). Grouping taxa together has a practical benefit because some taxa (e.g.

chydorids) are difficult to key to species, and therefore using the index would require more training and time if species-specific identification was required. There were however, some taxa which could not be grouped together due to apparently different habitat requirements. For example, most of the chydorids were placed into one group because they were similarly intolerant of degraded conditions and occurred far to the left of the origin (0,0) on pCCA axis 1 (Figure 5-2b). However, several chydorids could not be included in this large group (e.g. *Kurzia*, *Pleuroxus denticulatus*, and *P. procurvatus*; Table 4) because they were more tolerant of degraded conditions and accordingly their positions in the bi-plot occurred more centrally or further to the right-hand side of pCCA axis 1.

Optimum (U; center of distribution) and tolerance (T; range of distribution) values were determined for each taxon based on a pCCA using these collapsed taxonomic groupings (Table 4). The location of a taxon on pCCA axis 1 represented its center of distribution along this primary synthetic axis formed by several key environmental variables. Details of the assignment of U and T are outlined in the Methods. Table 5-4 shows that, in general, taxa tolerant of degraded conditions (U=1-2) had broader tolerance (T =1-2), while those less tolerant (U=4-5) had narrower tolerances (T=3).

We calculated WZI values for zooplankton communities in each of the habitat types in the 60 wetlands and regressed them against pCCA axis 1 scores to confirm their overall relationship with the primary synthetic axis, which contrasted turbid, eutrophic, sparsely vegetated systems with clear-water, oligotrophic, densely vegetated wetlands (Figure 5-3). When we used zooplankton abundances to calculate the WZI, axis 1 scores explained 74% of the variation in index values; by comparison, when we used presence/absence information to generate index (WZI_{P-A}) values, the axis 1 scores explained 73% of the variance ($p<0.0001$). Regression of the WZI against each of the $\log_{10}$-transformed water-quality variables resulted in highly significant ($p<0.0001$) r^2-values: 0.146 (COND), 0.211 (CHLa), 0.211 (TP) and 0.223 (TSS), although there was a great deal of variability about these regression lines. Aquatic vegetation also appeared to have been an important determinant of WZI values since those associated with sites containing submergent and/or emergent vegetation were significantly higher than those associated with open water (Table 5-3). In fact, the WZI increased significantly with the species richness of submerged macrophytes observed in each of these wetlands (Figure 5-4; $r^2 = 0.32$, $p<0.0001$).

We wanted to see how the WZI compared against more standard measures of zooplankton community structure (e.g. Shannon-Wiener diversity index (H'), species richness, total zooplankton abundance, mean size) for predicting the degree of degradation of wetland ecosystems. Since the WZI relied on information generated by the pCCA, we decided to use Principal Components Analysis (PCA) axis 1 as the independent variable. Figure 5-5 shows that the WZI correlated most highly with PCA axis 1 ($r^2 = 0.31$, $p<0.05$), compared with $\log_{10}$ zooplankton abundance ($r^2 = 0.11$, $p<0.05$), mean size of plankton ($r^2 = 0.02$, $p<0.05$), Shannon-Wiener diversity index, H' ($p>0.05$), and species richness ($p>0.05$). The WZI also consistently explained more variation in regressions with variables such as TP, COND, CHLa, and TSS, compared with other measures.

We also used this principal components axis to compare the WZI calculated based on abundances versus the index values calculated from presence/absence data (WZI_{P-A})(Figure 5-5). The slopes of the lines were statistically similar (ANCOVA; $p>0.05$), but comparison of the intercepts indicated that the WZI_{P-A} values were approximately 0.5 units greater than the corresponding WZI at any given PC axis 1 value (intercept = 3.65 and 3.08, respectively; $p<0.05$; ANCOVA).

Case study: Cootes Paradise

Lougheed and Chow-Fraser (2000, Chapter 3) showed that water clarity increased and submersed macrophytes became established in shallow, sheltered, vegetated areas of Cootes Paradise Marsh (1997 and 1998) after most of the large common carp were excluded in the spring of 1997. These changes at the vegetated site were concomitant with a significant reduction in edible algal biomass and increased representation of large zooplankton grazers and substrate-associated cladocerans. By contrast, open areas in the marsh remained turbid and devoid of vegetation and only exhibited temporary changes in water clarity; there were also fewer changes in the zooplankton community at the open-water sites.

We calculated WZI values for three different sites in the marsh (i.e. vegetated, lagoon and open-water, see Methods) for each of two years prior to carp exclusion (1993 and 1994) and two years following carp exclusion (1997 and 1998). Figure 5-6 compares the WZI values calculated for each site-year combination in Cootes Paradise to similar site types in other L. Ontario coastal wetlands. There were no significant differences seen between years at the open water sites, and the mean WZI values for open water and lagoon sites did not generally exceed the mean for all other OPEN-10 m sites in L. Ontario (Table 5-5). By comparison, the mean for the vegetated site increased significantly (ANOVA, Tukey-Kramer, $p<0.05$) following exclusion from a value below the mean to one slightly above the mean for all other corresponding L. Ontario sites. Despite this significant increase, however, the average summer index value was still considerably lower than the maximum index value measured in higher quality L. Ontario wetlands.

Seasonal and year-to-year variation

The long-term monitoring program of Cootes Paradise Marsh provided a large data set that was used to determine the degree to which WZI values varied throughout the summer. Figure 5-7 reveals that at all sites, WZI values varied over a range of approximately 1.0 and within 10 to 40% (co-efficient of variation) of the mean value in any given summer. Seasonal variation did not appear to follow any obvious trends, except at the vegetated site. Prior to carp exclusion (1993 & 1994), when submersed vegetation was virtually absent from the marsh, the WZI remained fairly steady throughout the year. Following carp exclusion (1997 & 1998), submergent plants became established in the vicinity of the emergent site but since they must re-establish each spring they were generally absent until mid-summer. Consequently, WZI values tended to be low in early summer, increased as submergent plants became abundant, and reached a plateau in mid-June. Our experience in Cootes Paradise Marsh suggests that early summer zooplankton samples may not accurately reflect the overall summer zooplankton community, especially in wetlands with a prominent submersed aquatic plant component.

We examined seasonal variation in WZI values for a number of wetlands of varying quality that had been sampled monthly or bimonthly in a single year (1996) or over a period of 3 years. Tables 5-6 confirms that WZI values tended to be consistent, generally falling within a range of 1.0 over a season and from year to year. In fact, over a season (excluding early summer data) WZI values at any given wetlands varied within a range of 0.01 to 1.93, with the 50th percentile being 0.68. It is interesting that all wetlands whose WZI values varied by more than 0.93 over the season had a large riverine component. The largest differences were observed at one of the wetlands (Joe) sampled during the storm event, which was classified as 'Low-Moderate' quality in August (during the storm) but 'High' quality in June. In the other wetlands sampled during the storm event, zooplankton in the more lacustrine wetlands (Stump) and protected palustrine areas (Tay) were less affected. These comparisons suggest that between-year and between-trip WZI values can be expected to vary by at most 1.0, if sampling in early summer and following storm events are avoided. In particular, sampling in predominantly riverine wetlands may require sampling in both storm- and base-flow conditions to capture the overall variability of the site.

DISCUSSION

We have developed an index based on water quality and distribution of zooplankton, which can be used to evaluate wetland quality across the Great Lakes basin. In doing this, we offer managers an important assessment tool to track restoration and degradation of wetland habitat, one of the primary challenges given to the scientific community during the 1996 State of the Lakes Ecosystem Conference (Bertram and Stadler-Salt 1999). Because the database we used to develop this index includes wetlands from all four Canadian Great Lakes, including a diverse range of wetland quality (Table 5-1; Lougheed et al., 2000, Chapter 3), wetland types (i.e. lacustrine, riverine, palustrine) and geomorphological settings (e.g. open shoreline, river delta, barrier beach etc.) (Maynard and Wilcox 1997; Chow-Fraser and Albert 1999), we are confident that it will have wide applicability. Compared to other indices, such as the Index of Biotic Integrity (IBI) which has been applied to Great Lakes littoral fish (Minns et al. 1994) and wetland macroinvertebrate (Burton et al. 1999) communities, the WZI is relatively easy to use, can be determined using presence/ absence data, and its calculation includes a comprehensive list of taxa, as opposed to the often subjectively selected and defined metrics of the IBI.

As in previous studies (e.g. Crosbie and Chow-Fraser 1999), we found that water quality and the distribution of submersed aquatic vegetation in wetlands were governed by a number of factors. Principal components analysis showed that nearly 50% of the variation in the water quality data could be explained by the first axis which contrasted turbid, nutrient-rich wetlands in the lower latitudes with clearer wetlands in less developed upper Great Lakes. We also found a significant negative relationship between species richness of submergent plant taxa and water quality (Lougheed et al., 2000), which is consistent with Crosbie and Chow-Fraser's (1999) observation that there is a direct link between land-use development, water quality impairment and wetland plant diversity in a subset of wetlands in this study (n=22).

Wetlands in our database fall on a continuum: at one extreme are turbid, eutrophic and algal-rich systems with few, if any, submersed macrophytes; at the other extreme are high-quality wetlands that are relatively clear, oligotrophic with abundant and diverse submergent macrophyte beds (Table 5-1). This gradient in wetland quality was accompanied by a predictable change in the taxonomic composition of the zooplankton community, as indicated by the pCCA which showed that plant-associated taxa dominated high-quality wetlands while more pollution-tolerant taxa dominated degraded wetlands. Others have reported on the association between increased diversity of habitats in submergent plants and increased diversity of zooplankton taxa (Paterson 1993), especially increased representation of plant-associated taxa such as *Simocephalus*, *Sida*, macrothricids and many chydorids (Pennak 1966; Gaiser & Lang 1998), detritus- and sediment-associated taxa (e.g. *Pleuroxus*) (Fryer 1968), and rotifers commonly identified in littoral areas (e.g. *Euchlanis*, *Monostyla* and *Lepadella*) (Slådecek 1983). Conversely, the cladocerans *Moina*, *Bosmina* and *Diaphanosoma birgei* (Gaiser and Lang 1998; Lougheed and Chow-Fraser 1998) and the rotifers *Brachionus* and *Filinia* (Gannon and Stemberger 1978; Slådecek 1983) have been shown to occur in greater abundance in more eutrophic, unvegetated wetlands.

Although only a few studies on zooplankton in Great Lakes wetlands have been published (Krieger 1992), results from these studies are consistent with our findings. For example, Krieger and Klarer (1991) also found the cladocerans *Diaphanosoma birgei*, *Moina micrura* and Bosminids in a degraded L. Erie wetland, while other authors found plant-associated cladocerans such as chydorids, *Simocephalus* and *Sida*, and *Ceriodaphnia* occurring in relatively pristine L. Huron (Cardinale et al. 1998; Gathman et al. 1999) and L. Erie wetlands (Botts 1999). Nogrady (1989) found many of the same species of rotifers reported here in two other Great Lakes wetlands, although he did not indicate the trophic status of the systems.

There were some differences in the zooplankton communities observed in coastal versus inland wetlands. For example, there were twelve rare rotifers and six rare cladocerans that were found only in inland sites. Conversely,only three taxa (*Diaphanosoma birgei*, *Moina micrura*, *Brachionus caudatus*) that could be classified as common were absent from inland wetlands (Table 5-3). We felt it was necessary to include inland wetlands in this study to ensure we had some relatively pristine sites to broaden our gradient since almost all coastal wetlands in southern Ontario have been disturbed to a certain degree. That six of the ten most pristine wetlands in this study were located inland should not be interpreted as being indicative of all inland wetlands, because we purposely chose these wetlands for their undisturbed condition.

The 1987 revision to the Great Lakes Water Quality Agreement (GLWQA) acknowledges the importance of biological systems in the monitoring and assessment of the Great Lakes ecosystem, and endorses an ecosystem approach. Biotic indices are useful as they illustrate that changes in environmental quality are accompanied by ecological changes. The WZI is a more useful indicator of wetland degradation than indices of diversity (H', species richness) and measures of community structure (mean size, total abundance) likely because the latter ignore taxon-specific information. Furthermore, some simpler indices which are based on ratios of taxonomic groups are also inferior. For example, the ratio of calanoids to cyclopoids and cladocerans, which has been used by Gannon and Stemberger (1978) to indicate lake quality cannot be applied to these wetlands because > 75% of them, including many of the more oligotrophic systems, do not have calanoids. Indices based on only a few genera (e.g. ratio of *Brachionus* to *Trichocerca*; Sládecek 1983) are also inappropriate as they cannot describe conditions at sites where both these taxa are absent, which in this case represents nearly half of all sites sampled.

The strong relationship between WZI values and wetland degradation is due to several factors. The most obvious reason is that zooplankton community composition is dependent on the presence of submersed macrophytes (e.g. Quade 1969; Paterson 1993), trophic state (e.g. Berzins and Bertilsson 1989; Berzins and Pejler 1989) and water clarity (e.g. Lougheed and Chow-Fraser 1998), three factors that played a primary role in the construction of the index. There was, however, an additional factor not directly accounted for in the index. Lougheed et al. (2000) found that species richness of submersed macrophyte species increased with wetland quality. In this study, the WZI tended to increase with species richness of submergent plants presumably because they provided a more diverse habitat for zooplankton. Hence, heterogeneity associated with different vegetation types likely plays an important role in the relationships described here and is therefore the subject of on-going investigations (Lougheed, unpubl. data).

The index that we have developed is robust, relatively easy to use and should be widely applicable because we have purposely sampled wetlands that cover a wide range of environmental quality. It gives zero weight to absent species of rotifers and cladocerans to ensure that wetlands will not be misclassified simply because they are located outside the geographic home range of a particular taxon, because of seasonal variability in species occurrences or because of differences in sampling effort. We have also tried to reduce the expertise and time required to key organisms involved in this index by grouping all rotifers into genera, most of the chydorids and macrothricids into a single taxon, and by excluding copepods, which despite their abundance in wetlands, are difficult to identify to species because adult stages (critical for identification) are not always present in samples.

There are several limitations to the index that must be recognized. First, although the WZI is broadly applicable to Canadian wetlands, it has not yet been applied to U.S. wetlands, including those on the shoreline of L. Michigan and the U.S. shoreline of the other four Great Lakes. It will also have limited applicability to diked wetlands in L. Erie and L. St. Clair whose water levels are regulated and which are isolated from lake waters and the surrounding landscape (Maynard and Wilcox 1997). Secondly, this index should be cautiously applied to wetlands which are dominated by taxa identified as rare indicator species (Table 5-4) as well as those which had been grouped with other species into a single taxon because of their rare occurrence (Table 5-3). Grouping species into genera may ease identification, but it may also obscure important differences in habitat preferences of useful indicator species (e.g. Sládecek 1983; Gaiser and Lang 1998). Future studies should focus on collecting sufficient information on these "rare" taxa so that corresponding optimum and tolerance values can be updated, and criteria for inclusion of taxa into larger groups could be confirmed. Finally, index values based on abundances (WZI) should not be compared to index values based on presence/absence data (WZI_{P-A}), even though either method is valid on its own.

This index was based on a synthetic axis (pCCA 1) that related marsh quality to its trophic state and concentration of suspended particulates in the water; it largely ignored the geographic location of the wetland (i.e. latitude) and degree of development in the watershed, which loaded significantly on the second axis of the pCCA. This can be a problem when wetlands across lakes are compared because both the abundance and species richness of rotifers and cladocerans vary inversely with latitude ($r^2=0.05$; $p<0.0001$). For example, of the 131 zooplankton taxa identified in this study, 66 did not occur in either Lakes Huron or Superior wetlands (Table 5-3), and these included a large proportion of species with an optimum value of 4 or 5 (i.e. requiring high quality conditions). Consequently, the maximum WZI value in the upper lakes tended to be lower than those of the lower lakes (Table 5-5). Other authors have also shown that the wetland environments in the upper and lower lakes are unique, due largely to differences in climate, geology and exposure (Smith et al. 1991), and that this has important consequences for the macrophyte community (Minc 1997; Lougheed et al. 2000). Hence, we advise against the indiscriminant comparison of index values across lakes since wetlands with the same WZI value from upper versus lower Great Lakes are not directly comparable.

Similarly, it is important to restrict comparisons to similar sampling site types. Open water sites (OPEN-10 m and OPEN-3m), which are the only type that could be accessible by larger boats, are usually associated with lower WZI values compared with vegetated sites, which tend to be accessible only by canoe or in waders. Another important observation is that samples collected from these open water sites under-represent the range of taxa encountered at the two other site types. In fact, sampling OPEN-10m sites did not contribute any new information to the species list obtained by sampling all other site types, whereas unique species were identified from both emergent, submergent and OPEN 3-m habitats. We therefore recommend that, for the purposes of among marsh comparisons, WZI values be based on samples collected in the less accessible vegetated sites.

In general, index values were reproducible seasonally and year-to-year, with the exception of data collected in early summer and following storm events. The flushing of resident water out of riverine marshes due to storm run-off may eliminate or severely reduce the abundance of many zooplankton taxa in these marshes (Krieger and Klarer 1991). Although we generally avoided storm events by 48 hours, an impoverished zooplankton community may persist for weeks or months following a severe run-off event, and only a few species may recover their pre-storm abundance (Krieger and Klarer 1991). Therefore, sampling in riverine systems should be done in as sheltered a location as possible to ensure a comprehensive species list.

Seasonal variation in WZI values is not surprising since the index reflects changes in zooplankton distribution that are due to many factors. Zooplankton dependent on submergent plants for habitat may not appear until this vegetation becomes established in mid-summer. In addition, there may be differential seasonal responses of species to planktivory, temperature changes, and species competition that may not be directly related to wetland quality per se. By comparison, year-to-year variation may be due to the same set of factors, compounded by delay in spring-melt or annual migration of planktivores into wetlands (e.g. Lougheed and Chow-Fraser 2000). A seasonal or year-to-year range of approximately 1.0 can be expected between the lowest and highest calculated WZI value for any given wetland; therefore, to accurately assess restoration techniques, we advise that a bi-weekly sampling regime be established. If it is not possible or necessary to conduct a comprehensive monthly sampling program, we recommend sampling between mid- and late summer to obtain as representative a species list as possible.

This study illustrates the ability of the WZI to rapidly track site-specific improvements in Cootes Paradise Marsh following implementation of carp exclusion in the spring of 1997. Lougheed and Chow-Fraser (2000) used a statistical approach to evaluate changes in water quality and the response of the zooplankton and phytoplankton communities, and found that only the vegetated site exhibited a prolonged positive response to remedial actions. We arrived at the same conclusion using the WZI, without having to use additional information or specialized equipment other than a plankton sampler and microscope; in addition, we were able to compare the WZI of Cootes

Paradise to those of other wetlands in L. Ontario to illustrate that even with the carp exclusion, marsh quality in most areas of Cootes Paradise was only moderate compared to high-quality coastal marshes existing elsewhere in L. Ontario.

The WZI should not be used as a sole indicator of wetland quality, but as a complement to water quality information and surveys of other trophic levels where possible. The index could be improved by incorporating information on rare taxa and by making it truly bi-national through a sampling program that includes U.S. wetlands, especially those in L. Michigan. Furthermore, more effort should be directed at comparing the utility of the WZI against other indices based on fish (IBI; Minns et al. 1994), benthos (IBI; Burton et al. 1999) and macrophytes to determine the most cost-effective and accurate combination of methods for routine assessment of wetland quality.

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Table 5-1. Range of environmental variables observed at 60 wetlands in the Great Lakes basin.

Variable	Mean	Range of values
Total phosphorus (µg/L)	122	15 - 959
Total nitrogen (µg/L)	2793	572 - 13000
Total suspended solids (mg/L)	27.0	0.1 - 283
Chlorophyll-a (µg/L)	32.1	0 - 396
Temperature (°C)	22.7	11.5 – 30
Dissolved oxygen (mg/L)	8.44	1.55 – 20
pH	7.6	6.0 – 9.4
Conductivity (µS/cm)	414	39 - 1387

Table 5-2a. List of cladocerans observed at 60 wetlands in the Great Lakes basin. Taxa are identified as being found only in lower coastal (L), upper coastal (U) or inland (I) wetlands. Also the number of wetlands in which a taxa was found is indicated (bolded values indicate taxa that occur in greater than 10% of wetlands visited).

CHYDORIDAE		
Acroperus harpae		**32**
Alonella excisa	I,L	**11**
Alona barbulata	L	1
Alona costata		**15**
Alona guttata		**16**
Alona quadrangularis		**12**
Alona rustica	I,L	**15**
Biapertura affinis	L	1
Camptocercus macrurus		**35**
Chydorus sphaericus		**52**
Chydorus faviformis	I,L	4
Disparalona rostrata		4
Dunhevedia crassa	I,L	3
Eurycercus sp.	I,L	**22**
Graptoleberis testudinaria	I,L	**10**
Kurzia latissima	I,L	**7**
Leydigia leydigi	L	4
Monospilus dispar		1
Pleuroxus aduncus	I	1
Pleuroxus denticulatus		**33**
Pleuroxus laevis		6
Pleuroxus procurvatus		**19**
Pleuroxus striatus	I,L	**9**
Rhynchotalona falcata	L	1
MACROTHRICIDAE		
Acantholeberis curvirostris	I	1
Bunops serricaudata	I,L	4
Echinisca rosea		6
Ilyocryptus sordidus		1
Ilyocryptus spinifer	I	5
Lathonura rectirostris	L	1
Macrothrix sp.	L	3
Ophryoxus gracilis		**8**
Streblocerus serricaudatus	I,L	2

DAPHNIIDAE		
Ceriodaphnia pulchella	I,L	5
Ceriodaphnia quadrangula	I,L	**10**
Ceriodaphnia reticulata		**20**
Daphnia galeata mendotae	I,L	3
Daphnia longiremis	L	1
Daphnia parvula		**9**
Daphnia retrocruva		6
Megafenestra aurita	L	3
Scapholeberis mucronata		**40**
Simocephalus exspinosus		**36**
Simocephalus vetulus	I	3
SIDIDAE		
Diaphanosoma birgei	L	**9**
Diaphanosoma brachyurum		**28**
Latona parviremis	I	3
Latonopsis occidentalis		4
Sida crystallina		**34**
POLYPHEMIDAE		
Polyphemus pediculus		**19**
MOINIDAE		
Moina micrura	U,L	**13**
Moina macropa	L	1
BOSMINIDAE		
Bosmina longirostris		**57**
Eubosmina coregoni	L	2
HOLOPEPIDAE		
Holopedium gibberum	I	1

Table 5-2b. List of rotifers found in 60 wetlands in the Great Lakes basin. See Table 5-2a for legend.

ROTIFERS			*Lecane leontina*	I,L	4
Anuropsis sp.	L	1	*Lecane ludwigi*	L	1
Ascomorpha sp.	L	1	*Lecane luna*		16
Asplanchna spp.		34	*Lecane mira*	I,L	4
Asplanchna brightwelli	I	1	*Lecane stokesi*	I	2
Brachionus angularis		18	*Lecane tenuiseta*		5
Brachionus bidentata	I,L	9	*Lecane tudicola*	I,U	4
Brachionus calyciflorus		21	*Lecane ungulata*		4
Brachionus caudatus	L	7	*Lepadella acuminata*	I	1
Brachionus diversicornus	I,L	7	*Lepadella cristata*	I	2
Brachionus havanaensis	I,L	7	*Lepadella ovalis*	I,L	5
Brachionus quadridentatus		11	*Lepadella patella*		4
Brachionus rubens	L	1	*Lepadella rhomboides*	I,L	2
Brachionus urceolaris		15	*Lophocaris* sp.	L	1
Brachionus variabilis	L	1	*Monostyla bulla*		25
Cephalodella sp.	I,L	4	*Monostyla copeis*	L	1
Collotheca sp.		19	*Monostyla cornuta*		20
Conochilidae	I,L	10	*Monostyla crenata*	I	3
Euchlanis alata	I,U	3	*Monostyla laevis*	L	1
Euchlanis calpidia		14	*Monostyla lunaris*		14
Euchlanis dilatata	L,U	3	*Monostyla quadridenta*	I,L	16
Euchlanis menata	L,U	4	*Monostyla stenroosi*		1
Euchlanis parva		8	*Mytilina* sp.		25
Euchlanis pellucida		16	*Notholca* spp.		4
Euchlanis triquetra	I,L	8	*Platyias patulus*		30
Filinia spp.		21	*Platyias quadricornus*	I,L	5
Gastropus sp.	I,L	2	*Ploesoma hudsoni*	L,U	4
Hexarthra sp.	L	5	*Ploesoma lenticulare*		5
Kellicotia sp.		7	*Ploesoma truncatum*	L	1
Keratella cochlearis		48	*Polyarthra* sp.		56
Keratella cochlearis tecta		14	*Pompholyx* sp.	I,L	3
Keratella hispida	I	1	*Scaridium* sp.	L	1
Keratella quadrata		12	*Testudinella* spp.		21
Keratella serrulata		10	*Trichocerca elongata*		21
Keratella taurocephalus	I	2	*Trichocerca lata*	L,U	4
Keratella valga tropica	L	3	*Trichocerca longiseta*	I,L	11
Lecane crepida	L	1	*Trichocerca multicrinis*		7
Lecane flexilis	L	1	*Trichotria* sp.	I,L	7
Lecane inermis	I	1			

Table 5-3. Comparison of means (standard errors) of zooplankton community structure at 5 habitat types.

	OPEN 10-m	OPEN 3-m	EM	SUB	FLTG	Stats ($p<0.05$)
N	55	91	80	55	10	
Species richness	7.73 (0.38)	8.59 (0.34)	11.53 (0.48)	12.93 (0.64)	12 (1.35)	S, E > 10, 3
H'	1.08 (0.05)	1.14 (0.05)	1.44 (0.06)	1.61 (0.07)	1.35 (0.18)	S, E > 10,3
Abundance (#/L)						
Rotifers	492 (106)	286 (57)	222 (41)	300 (58)	221 (121)	N.S.
Cladocerans	138 (27)	177 (48)	678 (273)	255 (45)	328 (160)	S, E > 10, 3
Copepods & copepodids	54 (18)	45 (10)	154 (30)	266 (48)	220 (81)	S, E > 10, 3
Nauplii	121 (25)	165 (44)	211 (42)	265 (60)	460 (253)	S > 10,3
Mean size (µm)						
Cladocerans	238 (17)	274 (13)	325 (14)	341 (17)	305 (48)	S, E >10; S > 3
Herbivorous rotifers	154 (8)	183 (40)	198 (21)	187 (7)	219 (24)	N.S.
% Abundance (excl. copepods)						
Rotifers	63 (5)	60 (3)	45 (4)	46 (4)	39 (9)	E < 10, 3
Chydoridae	2 (1)	5 (1)	13 (2)	24 (3)	27 (9)	F, E, S > 3, 10
Daphnidae	4 (1)	6 (2)	13 (2)	13 (2)	13 (5)	E > 3, 10; S > 10
Sididae	1 (0)	2 (1)	3 (1)	3 (1)	5 (2)	F > 10
Macrothricidae	0	0	1 (1)	1 (1)	1 (1)	N.S.
Bosmididae	26 (4)	23 (3)	19 (3)	11 (3)	10 (6)	S < 10
Others cladocerans	4 (1)	5 (2)	7 (2)	2 (1)	3 (1)	N.S.
WZI	2.45 (0.09)	2.79 (0.08)	3.32 (0.07)	3.37 (0.31)	3.41 (0.31)	S, E > 3, 10; F > 10

NOTE: Statistical comparisons (Stats) are the results of an analysis of variance followed by Tukey-Kramer multiple comparisons ($p<0.05$).

Table 5-4. Optimum (U) and tolerance (T) of zooplankton taxa Taxa that occurred in less than 10% of wetlands were automatically given a tolerance value of 1 (*).

	U	T		U	T
ROTIFERS			**CHYDORIDAE**	5	3
Anuropsis sp.	4	1*	Except:		
Ascomorpha sp.	1	1*	*Alona* sp.	4	2
Asplanchna sp.	2	1	*Chydorus sphaericus*	4	2
Brachionus sp.	1	1	*Kurzia latissima*	3	3
Cephalodella sp.	4	1*	*Leydigia leydigii*	1	1*
Collotheca sp.	5	3	*Monospilus dispar*	2	1*
Conochiloides	3	1	*Pleuroxus denticulatus*	3	2
Euchlanis sp.	4	2	*Pleuroxus procurvatus*	3	2
Filinia sp.	1	1			
Gastropus sp.	2	1*	**MACROTHRICIDAE**	5	3
Hexarthra sp.	1	1*	Except:		
Kellicotia sp.	4	2	*Illiocryptus sordidus*	1	1*
Keratella sp.	3	1	*Macrothrix* sp.	1	1
Lecane sp.	5	2			
Lepadella sp.	4	2	**DAPHNIDAE**		
Lophocaris sp.	3	1*	*Ceriodaphnia* sp.	4	2
Monostyla sp.	5	3	*Daphnia* sp.	2	2
Mytilina sp.	4	3	*Megafenestra* sp.	2	1*
Notholca sp.	3	1*	*Scapholeberis* sp.	4	2
Platyias sp.	4	2	*Simocephalus* sp.	5	3
Ploesoma sp.	3	1			
Polyarthra sp.	3	1	**SIDIDAE**		
Pompholyx sp.	5	1*	*Diaphanosoma birgei*	1	2
Scaridium sp.	5	1*	*D. brachyurum*	5	2
Testudinella sp.	4	2	*Latona parviremis*	5	1*
Trichocerca sp.	4	2	*Latonopsis occidentalis*	5	1*
Trichotria sp.	5	2	*Sida crystallina*	5	3
			Polyphemus sp.	5	3
			Moina sp.	1	2
			Holopedium gibberum	5	1*
			BOSMINIDAE	2	1

Table 5-5. Mean and range of WZI values observed at different habitat types in different sampling regions. Lower coastal wetlands included wetlands in the St. Lawrence River, Lake Ontario, Lake Erie and Lake St. Clair. Upper coastal wetlands were located in Lake Huron and Lake Superior.

Habitat type	N	Region	Mean	Range
Open 10-m	[illegible]	Inland	2.90	2.06 - 4.10
	33	Lower coastal	2.20	1.12 – 3.22
	7	Upper coastal	2.88	2.22 – 3.78
Open 3-m	27	Inland	3.06	2.11 – 4.91
	50	Lower coastal	2.63	1.00 – 4.81
	14	Upper coastal	2.80	2.02 – 3.27
Emergent	19	Inland	3.73	2.27 – 4.83
	48	Lower coastal	3.17	1.44 – 4.78
	13	Upper coastal	3.30	2.46 – 4.32
Submergent	24	Inland	3.73	2.82 – 4.83
	23	Lower coastal	3.85	2.95 – 4.83
	8	Upper coastal	3.47	2.48 – 4.12
Floating-leaved	5	Inland	3.94	3.33 – 4.31
	5	Lower coastal	2.90	1.22 – 4.13

Table 5-6. Comparison of tallied WZI values assigned to OPEN 3-m and SUB sites in wetlands sampled on more than 1 occasion in 1996, and to one wetland sampled in mid-summer over a period of 3 years. Early summer values are excluded.

		WZI category			
	N	Low (1-2)	Low-Mod. (2-3)	Mod.-High (3-4)	High (4-5)
<u>OPEN 3-m</u>					
Big Creek 96	3		II	I	
Big Creek 97	2		II		
Big Creek 98	1		I		
Christie	2			II	
Harris	2		II		
Hay	2			I	I
Holiday	3	II	I		
Humber	2	II			
Joe	2		I		I
Jordan	3	I	II		
Martindale	2		II		
Near Tobies	2			II	
Presqu'ile	2		I	I	
Shebeshekong	2		I	I	
Stump	2		II		
Sawguin	2		I	I	
Turkey	3			III	
Waterford	2		I	I	
<u>SUB</u>					
Big Creek 96	3			II	I
Big Creek 97	2		I	I	
Big Creek 98	1		I		
Hay	2			II	
Joe	2		I		I
Shebeshekong	2			I	I
Sawguin	2			II	
Tay	2			I	I
Turkey	2			I	I
Waterford	2		I	I	

Figure 5-1. Map of Great Lakes region showing the location of 60 wetlands sampled between 1995 and 1999, including the location of Cootes Paradise Marsh (L. Ontario).

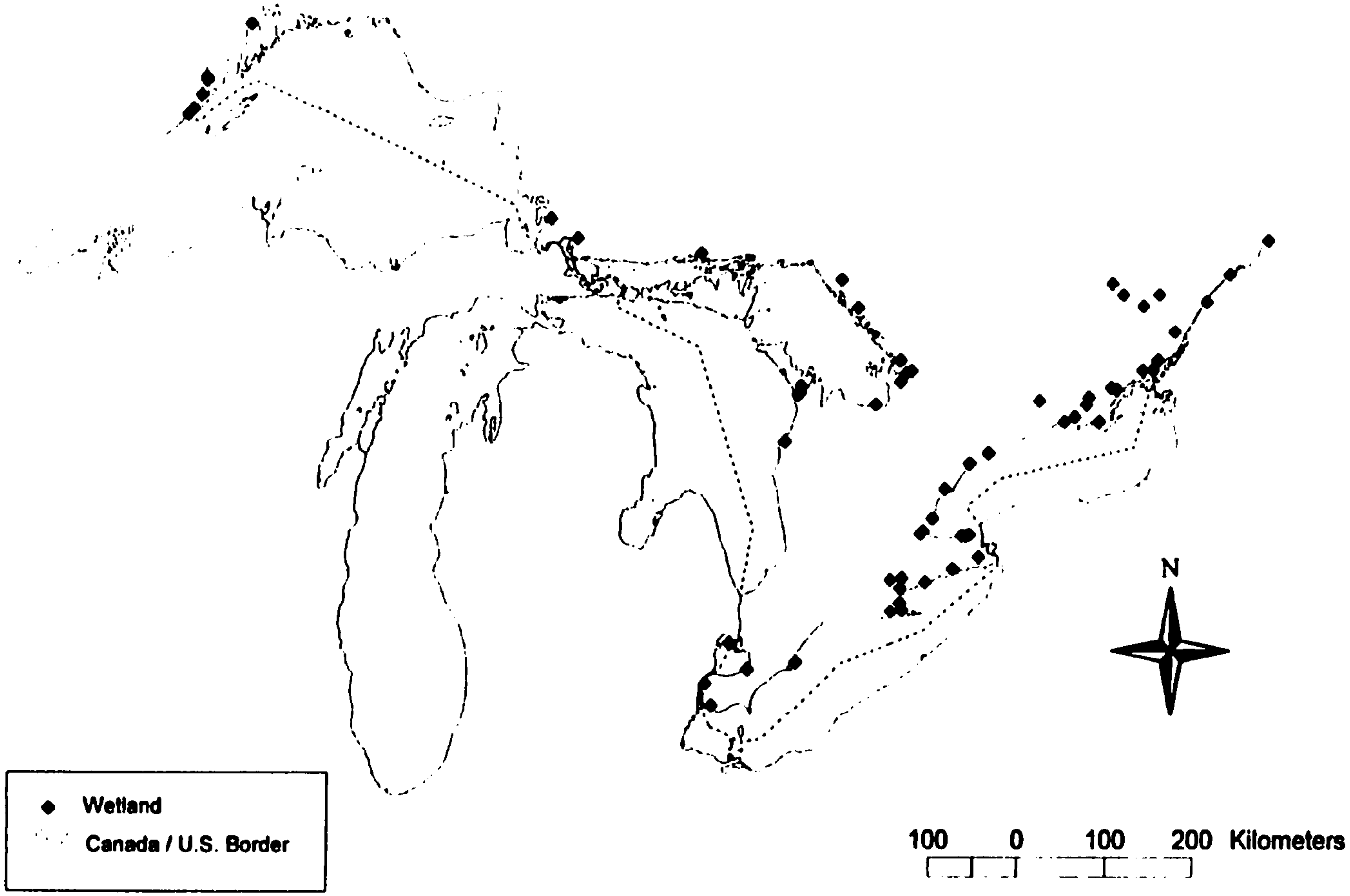
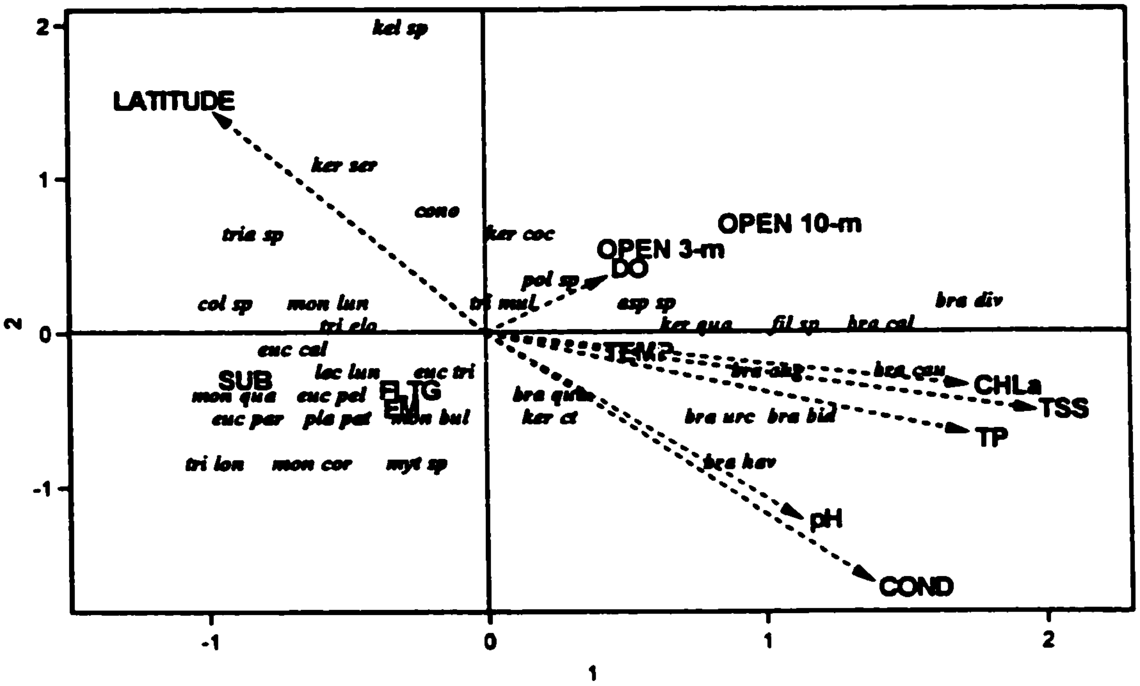

◆ Wetland
Canada / U.S. Border
100
0
100
200 Kilometers
N

Figure 5-2. Bi-plot of the pCCA (axis 1 vs. axis 2) separated into a) rotifer and b) cladoceran data.


2
1
0
-1
2
-1
0
1
2
1
kel sp
LATITUDE
ker ser
cono
tria sp
ker coc
OPEN 10-m
OPEN 3-m
DO
pol sp
col sp
mon lun
tri mul
asp sp
bra div
tri elo
ker qua
fil sp
bra cal
euc cal
TEMP
lec lun
euc tri
bra cau
SUB
bra chg
CHLa
mon qua
euc pel
FLTG
bra qua
TSS
EM
euc par
pla pat
mon bul
ker ct
bra urc
bra bid
TP
tri lon
mon cor
myt sp
bra hav
pH
COND

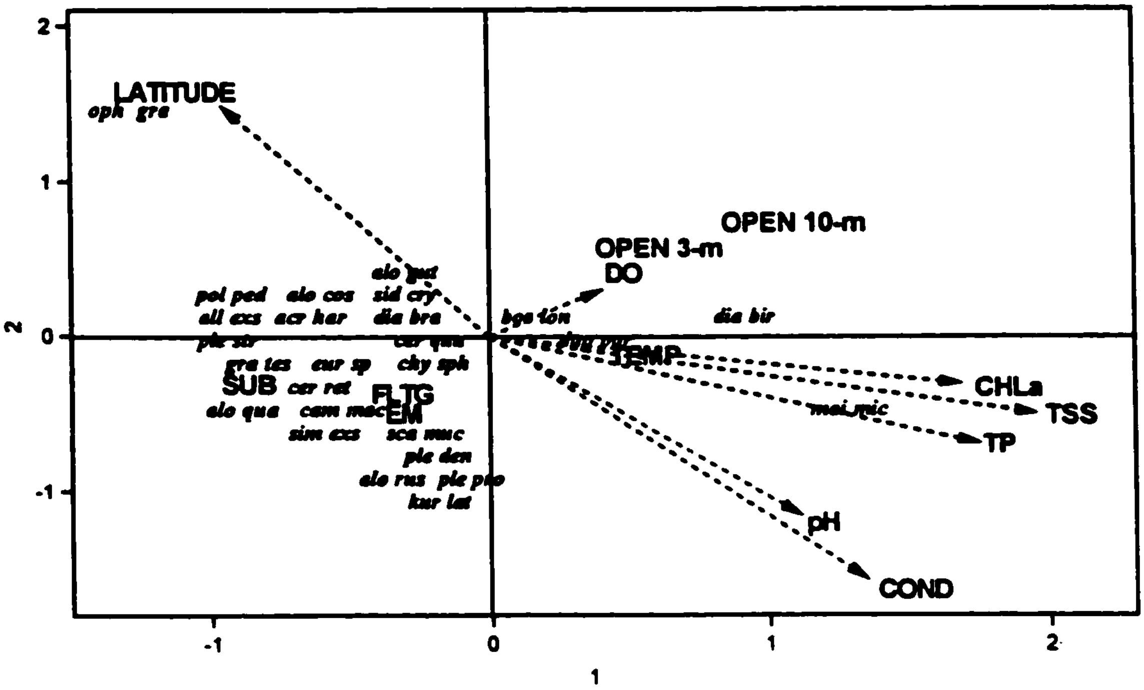

2
1
0
-1
2
-1
0
1
2
1
LATITUDE
oph gra
OPEN 10-m
OPEN 3-m
alo gut
DO
pol ped
alo cos
sid cry
all exs
acr har
dia bra
bga lon
dia bir
ple str
cer qua
TEMP
gra tes
eur sp
chy sph
SUB
cer rat
FLTG
CHLa
alo qua
cam mac
EM
moi mic
TSS
sim exs
sca muc
TP
ple den
alo rus
ple pro
kur lat
pH
COND

Figure 5-3. Relationship between WZI values and pCCA axis 1 for 60 wetlands (all habitat types) in the Great Lakes basin.

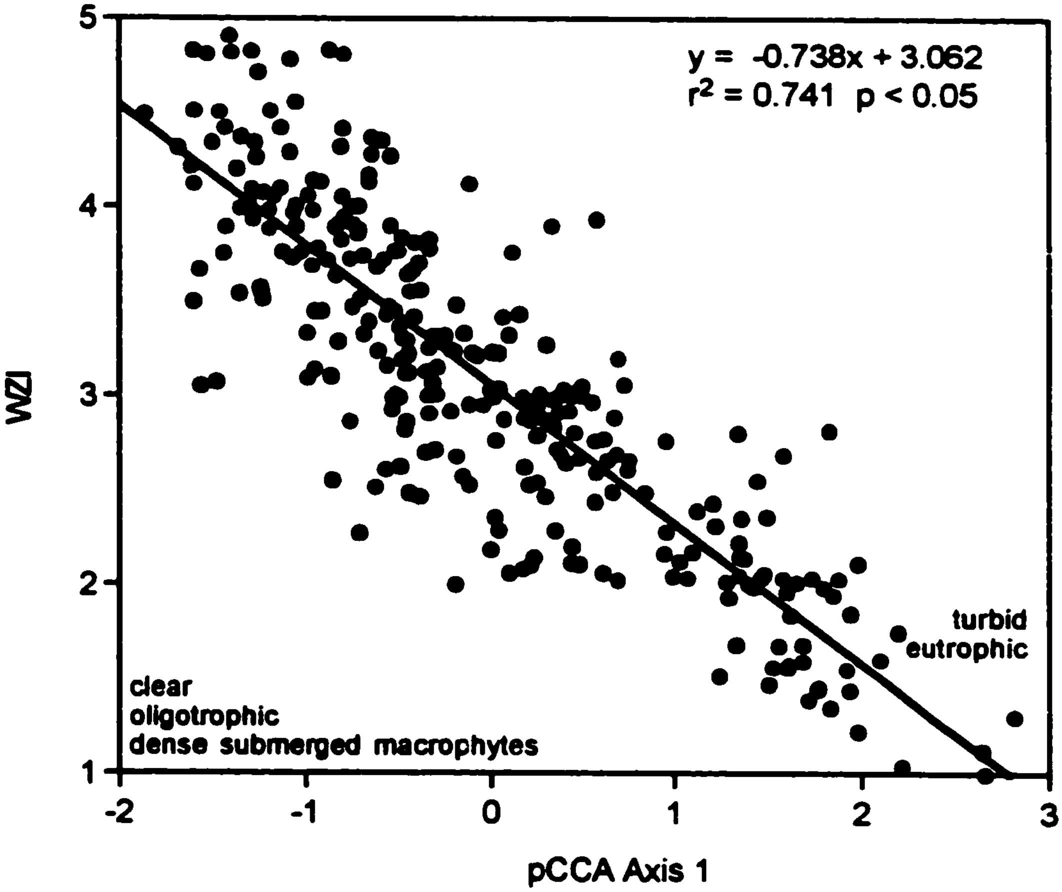

y = -0.738x + 3.062
r^2 = 0.741 p < 0.05
turbid
eutrophic
clear
oligotrophic
dense submerged macrophytes
WZI
5
4
3
2
1
-2
-1
0
1
2
3
pCCA Axis 1

Figure 5-4. Relationship between WZI values and submergent plant species richness for 60 wetlands in the Great Lakes basin.

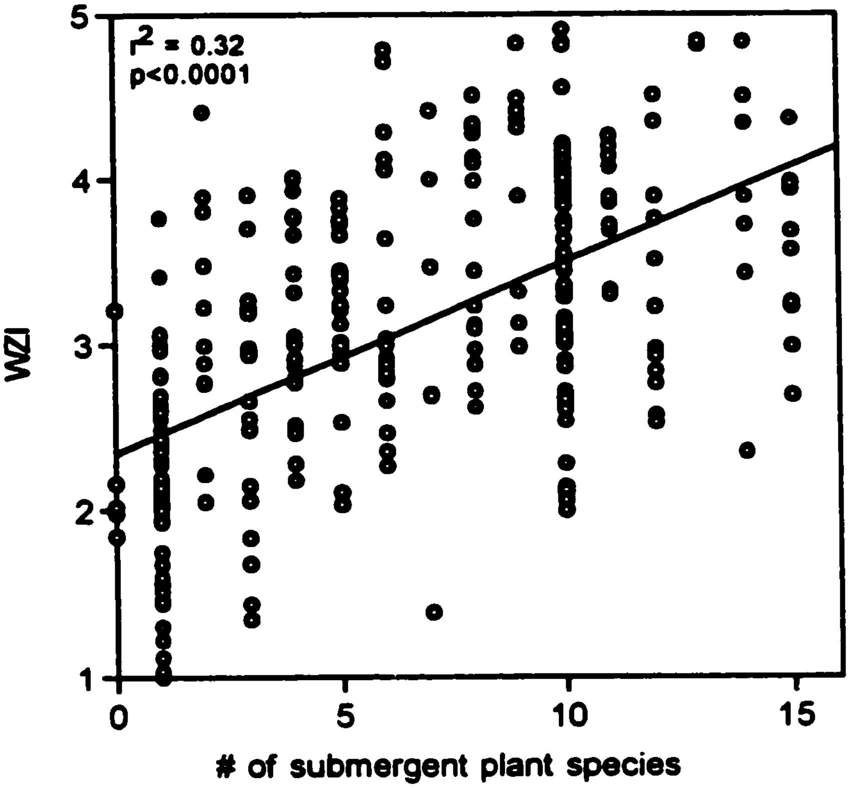

$r^2 = 0.32$
$p<0.0001$
WZI
1
2
3
4
5
0
5
10
15
# of submergent plant species

Figure 5-5. Role of PC axis 1 in explaining variation in several measures of zooplankton community structure: WZI, WZI_{P-A}, H', log total zooplankton abundance, mean size (μm) and species richness of rotifers and cladocerans.

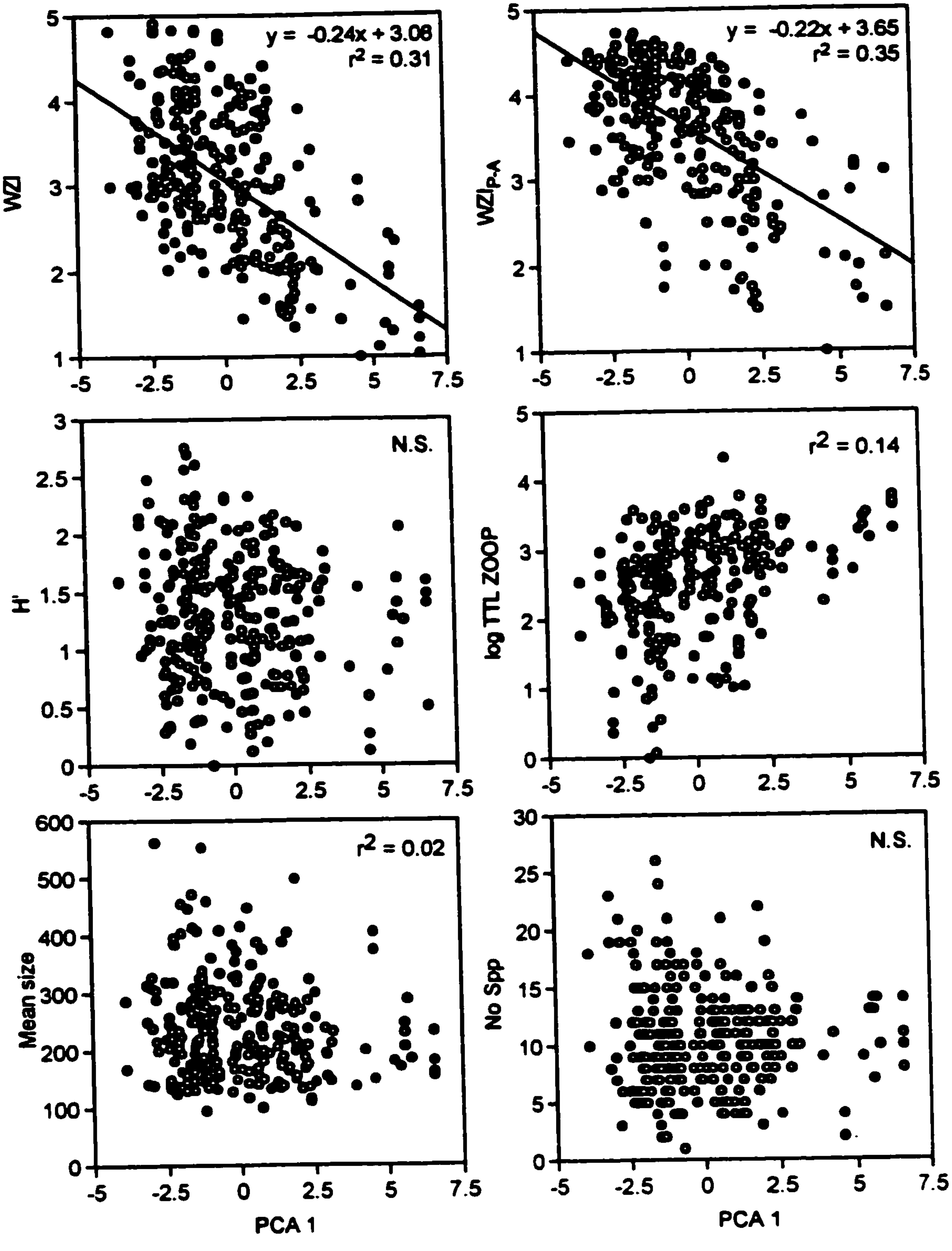

y = -0.24x + 3.08
r2 = 0.31
WZI
5
4
3
2
1
-5
-2.5
0
2.5
5
7.5
y = -0.22x + 3.65
r2 = 0.35
WZIP-A
N.S.
H'
3
2.5
2
1.5
1
0.5
0
r2 = 0.14
log TTL ZOOP
r2 = 0.02
Mean size
600
500
400
300
200
100
0
N.S.
No Spp
30
25
20
15
10
5
0
PCA 1
PCA 1

Figure 5-6. Comparison of WZI values before (1993 and 1994) and after (1997 and 1998) carp exclusion from 3 sites: a) open water, b) lagoon, c) vegetated in Cootes Paradise Marsh. The minimum, mean and maximum WZI values observed at similar habitat types: a) & b) OPEN 10-m and c) EM in L. Ontario is indicated by dashed lines.

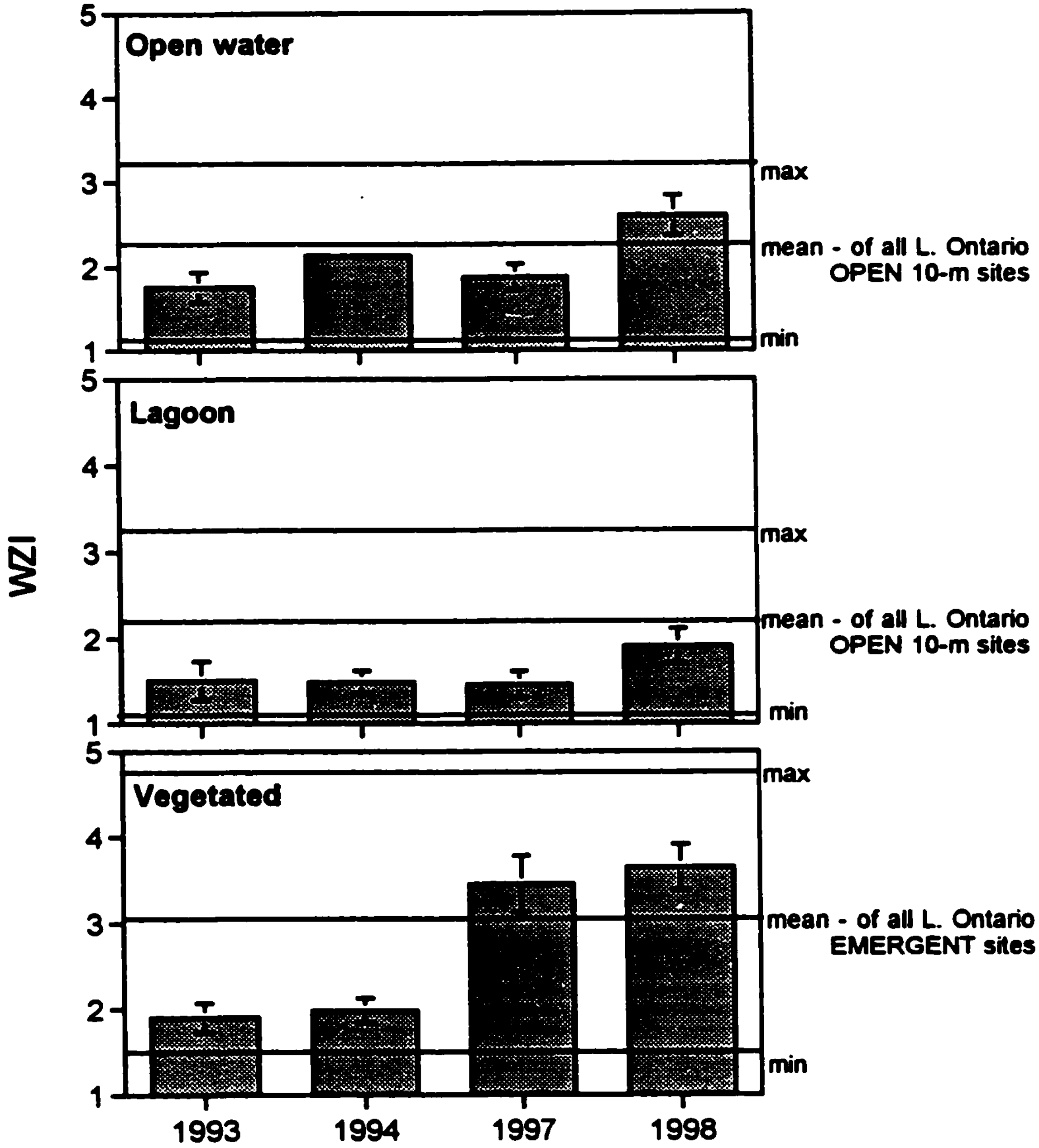
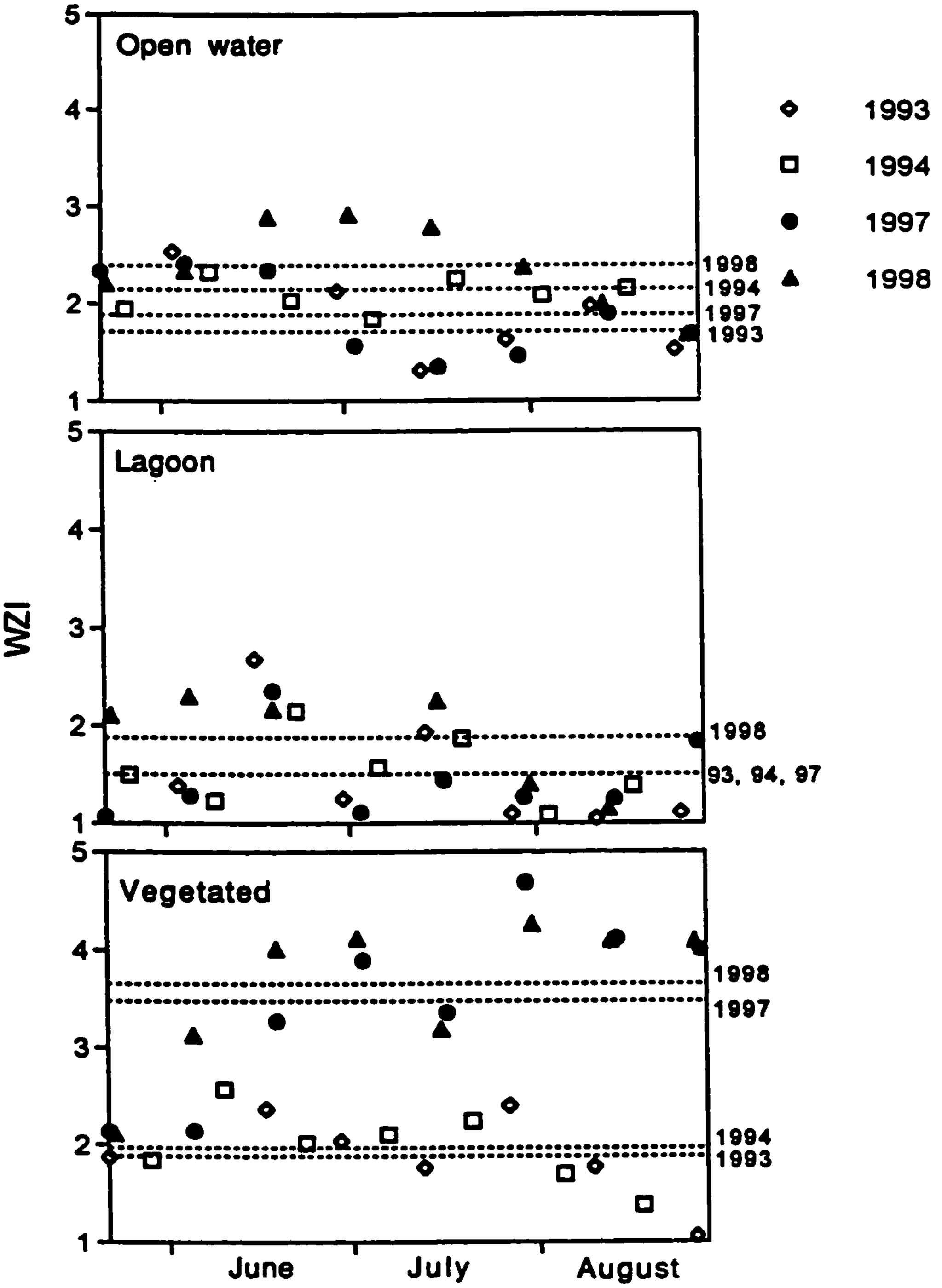

Open water
Lagoon
Vegetated
WZI
5
4
3
2
1
max
mean - of all L. Ontario OPEN 10-m sites
mean - of all L. Ontario EMERGENT sites
min
1993
1994
1997
1998

Figure 5-7. Change in WZI values through time before (1993 and 1994) and after (1997 and 1998) carp exclusion from 3 sites (open water, lagoon, vegetated) in Cootes Paradise Marsh. The yearly mean for each site is indicated by dashed lines.


Open water
Lagoon
Vegetated
WZI
5
4
3
2
1
1998
1994
1997
1993
93, 94, 97
June
July
August
◇ 1993
□ 1994
● 1997
▲ 1998

GENERAL CONCLUSIONS

Summary

The overall objective of this study was to provide much needed information on the ecology of coastal wetlands of the Great Lakes. In particular, the aim was to assess the restoration of Cootes Paradise Marsh by focusing on zooplankton and how they are affected by water quality and habitat structure.

In Chapter 1 we showed that, prior to carp exclusion, zooplankton community dynamics in Cootes Paradise Marsh were structured primarily by proximity to macrophytes and water turbidity. We predicted that if emergent or submergent macrophytes increased in abundance following carp exclusion, the total zooplankton biomass would increase and the zooplankton community would shift to larger bodied forms. We also predicted that these changes would be most evident in shallow and sheltered regions near remnant marsh areas.

In Chapter 2 it was shown through experimental methods that the increase in water clarity which would result from carp removal in the marsh was unlikely to be sufficient to allow the establishment of a diverse community of submergent vegetation and that further remedial actions would likely be necessary to promote the restoration of Cootes Paradise Marsh. We also provided evidence that water turbidity in Great Lakes coastal wetlands must be affected by factors other than carp activity, including land use contributions, wind-driven resuspension of sediment, high algal concentration and substrate composition.

Several predictions introduced in Chapters 1 and 2 were verified in Chapter 3. First, as predicted in Chapter 1 (Lougheed & Chow-Fraser 1998), the response of the lower trophic levels to carp exclusion varied from site-to-site. At the vegetated site, there was a significant reduction in edible algal biomass and an increased representation of large zooplankton grazers and substrate-associated cladocerans. At the more open water sites, changes in the biotic community were not statistically significant, except for a temporary increase in macrograzer abundance in early summer 1997. Second, Lougheed et al. (1998; Chapter 2) predicted that water clarity would increase by no more than 45% following carp exclusion. The initial results in 1997 showed a greater than expected improvement of 49 to 75%; however, we attributed this to unchecked zooplankton grazing made possible by the delayed arrival of young-of-the-year fish due to an unseasonably cool spring. In 1998, observed reductions in water turbidity were closer to this predicted value. This illustrated that both benthivore removal (to reduce bioturbation) and planktivore reductions (to produce top down effects) were required to produce clear water and allow submersed macrophyte growth. In addition to verifying the predictions of previous chapters, these results indicated that a clear positive feedback system between zooplankton and submergent macrophytes helped to maintain water clarity in vegetated areas.

Chapter 4 and 5 outlined the expansion of our study to include approximately 60 additional marshes in the Great Lakes basin in order to assess the quality of Cootes Paradise Marsh relative to other high quality wetlands in the region.

In Chapter 4 we showed that the species richness and community structure of aquatic macrophytes in wetlands of the Great Lakes basin appeared to be a function of geographic location, water quality degradation and exposure. Using this large data set, we showed that, although the carp exclusion from Cootes Paradise promoted a greater than expected improvement in the species richness of the macrophyte community, the quality of the marsh remained moderate to low relative to other Great Lakes marshes.

In Chapter 5 we developed an index (WZI) based on water quality and distribution of zooplankton, which can be used to evaluate wetland quality across the Great Lakes basin. Using this index, we were able to confirm the results of Chapter 3, in which we used a statistical approach to evaluate changes in water quality and the response of the zooplankton and phytoplankton communities, and found that only the vegetated site exhibited a positive response to carp exclusion. In addition, we were able to compare the WZI of Cootes Paradise to those of other wetlands in L. Ontario to illustrate that even with the carp exclusion, marsh quality in most areas of Cootes Paradise was only moderate compared to high-quality coastal marshes existing elsewhere in L. Ontario.

Management implications

Chow-Fraser (1999) showed that much of the interannual variability in water clarity in Cootes Paradise Marsh could be attributed to water level changes. When water levels were low, suspended matter was diluted in a smaller volume of water and wind effects were stronger. Seasonally, primary sources of suspended sediment varied depending on the time and location of sampling. For example, the tributaries contributed more sediment following rainstorms; wind-driven resuspension was more prevalent at more exposed sites; algal blooms proliferated in the hypereutrophic lagoon site; intrusion from the harbour occurred when the marsh was filling in spring; and, carp affected water clarity in the shallow, protected weedy areas during their spawning season in May and June (Chow-Fraser 1999). Consequently, determining the primary cause of water quality degradation in Cootes Paradise March is complicated.

Crosbie (1997) suggested that land use may have a minimal impact on water quality in Cootes Paradise, as inputs of sediments and phosphorus from the tributaries represented less than one-quarter of the current annual loadings to the marsh (HHRAP 1992; Prescott and Tsanis 1997). This agrees with the findings of Lougheed et al. (2000; Chapter 4) who showed that, in coastal wetlands of the lower Great Lakes, agricultural and urban land use explained 22% of the variation in a multi-variate descriptor of wetland water quality, which was highly correlated with nutrient and sediment levels. Although watershed inputs increased substantially during storm events, the overall importance of these loadings to reduced water quality remained second in importance relative to internal loading.

Reflux from the sediment likely contributes to more than 50% of the sediment and nutrient load in Cootes Paradise Marsh (Prescott and Tsanis 1997; N. Kelton, McMaster University, unpubl. data). For example, Chow-Fraser (1999) estimated that 62% of the variation in water clarity in the marsh during carp spawning season was due to sediment resuspension, with 41% explained by wind resuspension and 21% due to the presence of carp. In areas near emergent vegetation, enclosure experiments by Lougheed et al. (1998; Chapter 2) predicted that the removal of carp from Cootes Paradise would decrease water turbidity by a maximum of 45%. This is not independent of land use effects, however, as Lougheed et al. (2000; Chapter 4) showed that wetlands in developed watersheds were more likely to have fine silt or clay sediments which may be more readily resuspended. Silt is the dominant grain size throughout Cootes Paradise Marsh, (Chow-Fraser, unpubl. data), and once resuspended by wind and carp, these fine sediments may stay in resuspension for an extended period of time.

The resuspension of fine nutrient-rich sediment may also lead to increased total phosphorus measured in the water column; however, internal loading of phosphorus is also dependent on factors such as the characteristics of the sediment, bioturbation by benthos and the occurrence of anoxic conditions. The lagoon site, in particular, has a great potential for internal loading due to nutrient-rich sediment (N. Kelton, unpubl. data) and the anoxic conditions that occur following the crash of dense algal blooms. Although the influence of algae on the distribution of suspended matter in the marsh was generally low, representing less than 15% of the total suspended matter in the water column (Chow-Fraser 1999), at the hypereutrophic lagoon site and the open water site described by Lougheed and Chow-Fraser. (2000a, b; Chapters 3 and 5), chlorophyll-*a* explained 76% and 41%, respectively, of the variation in total suspended solids (Chow-Fraser 1999).

Detailed comparisons of water quality, macrophyte (Lougheed et al. 2000; Chapter 4) and zooplankton communities in Cootes Paradise (Lougheed and Chow-Fraser 2000a, b; Chapter 3 and 5) showed that there were statistically significant changes observed in water quality and the biotic community at shallow and protected areas following carp exclusion; however, open and exposed sites remained basically unchanged relative to pre-exclusion conditions. Lougheed and Chow-Fraser (2000a; Chapter 3) concluded that the changes observed in Cootes Paradise Marsh were not necessarily due to carp exclusion alone, but rather a consequence of many trophic interactions, both human-induced and natural. In particular, both benthivore removal (to reduce bioturbation) and planktivore reductions (to produce top down effects) were required to produce clear water and allow submersed macrophyte growth.

Wetland managers must consider all factors that may contribute to increases in water turbidity and nutrient concentrations to ensure that the desired response will be obtained in marsh restoration programs. In Cootes Paradise Marsh, carp activity was a primary factor reducing water clarity; however, wind-related resuspension remains an important agent of water quality degradation. It appears that clear water conditions are possible in much of the marsh, given that a zooplankton-mediated spring clear water phase occurred in 1997 despite this wind effect (Lougheed and Chow-Fraser 2000a, Chapter 3). Unfortunately, several trends reported in the literature suggest that, without further remedial actions the long term stability of this biomanipulation is improbable.

Jeppeson et al. (1990) suggested that long-term stability of alternative states is closely linked to the ability of the system to create a self-perpetuating increase in the ratio of piscivores to planktivores. The results of Chapter 3 suggest that only with a reduction in the planktivorous fish population will a clear water state be seen again in the marsh. The success of populations of piscivorous fish, such as northern pike (*Esox lucius*), must be actively encouraged in Cootes Paradise. Due largely to habitat restoration projects in nearby Grindstone Creek, the numbers of northern pike passing through the fishway has increased with each year following exclusion, as has the population of pike spawning in Grinstone Creek (Theismeijer, Royal Botanical Gardens, pers. comm.); however, the importance of this trend in promoting a clear-water environment has been overlooked.

The success of biomanipulation is also related to the establishment of a permanent and wide distribution of submersed aquatic macrophytes (Jeppeson et al. 1990). Submergent plants colonize to a maximum depth, largely dependent on the clarity of the water (Chambers and Kalff 1985). Once established, submergent plants may contribute to further increasing water clarity by stabilizing sediment (Hamilton and Mitchell 1997) and providing refugia for large zooplankton grazers (Lougheed and Chow-Fraser 1998, 2000a & b; Chapter 1, 3 and 5). Consequently, the sheer size and depth of Cootes Paradise may have limited the success of remedial measures to date. Carp tend to spawn near macrophyte beds (Balon 1995; Chow-Fraser 1999) and, consequently, their removal had the greatest positive impact in shallow, protected areas surrounded by cattail beds

(Lougheed and Chow-Fraser 2000a & b; Chapter 3 & 5); however, the increase in water clarity was not sufficient to allow submersed plants to grow in deeper areas of the marsh. Furthermore, submergent plants have only a localized effect on water clarity if they are located in isolated areas of reduced outflow (Scheffer 1998); therefore, expansion of submersed macrophytes is unlikely without further increases in water clarity.

Finally, the long term stability of a biomanipulation is dependent on the nutrient levels of the system. Between phosphorus levels of approximately 50 and 150 µg/L, two alternative states are possible in shallow aquatic environments: a turbid and phytoplankton-dominated state or a clear-water and macrophyte-dominated state (e.g. Jeppeson et al. 1990; Moss et al. 1996). A perturbation, often via food web biomanipulation, is generally required to initiate a switch between these 2 states. Conversely, long term stability of biomanipulation efforts is unlikely when phosphorus levels exceed 150 µg/L. This is due to many factors including increased predation pressure on zooplankton and growth of abundant phytoplankton populations (Jeppeson et al. 1990). Although an initial improvement may be observed in these nutrient-rich systems, the macrophyte-dominated state will not be maintained. It is evident from Chapter 3 (Lougheed and Chow-Fraser 2000a) that mean seasonal TP levels in Cootes Paradise do not generally fall within this range for successful biomanipulation, and consequently, it would seem that a sustained clear-water state is improbable. Most notably, the hypereutrophic lagoon area is the least likely to become macrophyte-dominated.

In conclusion, the carp barrier alone did not result in any significant improvements in water clarity in the marsh. It is uncertain whether any sustained improvements in water clarity at the vegetated site would have been seen in the absence of the peak in zooplankton grazing and the self-perpetuating effect of subsequent submersed macrophyte establishment. In the eyes of all stakeholders, eventually the marsh must thrive without the barrier in place, and only by reducing the impact of all stressors, besides carp, will this be possible. In particular, the rehabilitation of piscivore populations and spawning grounds in the region must be continued. This should promote the control of planktivirous fish populations and eventually promote a zooplankton community capable of consistently improving water clarity in Cootes Paradise Marsh. Furthermore, phosphorus levels in the marsh must be reduced so that a stable macrophyte-dominated state is possible. Given that internal loading likely contributes the largest proportion to the total phosphorus load in the marsh, reducing current external loads as low as possible through land use management and infrastructure improvements such as combined sewer overflows, and waiting while internal loading reaches an equilibrium in the system may be the only viable option. This has been estimated in some European systems to take as long as 30 years (e.g. Jeppessen et al. 2000), but this time frame needs to be determined to plan for the long term restoration and operation of the fishway in Cootes Paradise Marsh.

Research implications

Besides these important management implications, this study provided information on the environmental factors that structure zooplankton and macrophyte communities in Great Lakes wetlands. There are two main areas that we identified during this study that require further investigation: macrophyte-zooplankton interactions and food web interactions within wetland ecosystems.

The role of specific macrophyte taxa in providing structural habitat or a food source (i.e. detritus, periphyton) for invertebrate filter feeders and grazers is unknown. This study has shown that wetlands with dense and diverse submergent plant beds have a distinct and more speciose zooplankton community than degraded wetlands with only a fringe of emergent macrophytes; however, studies detailing the specific mechanisms causing these changes are lacking.

Examples of research questions include:

- do different plant species or plant structural types (e.g. broad- versus fine-leaf submergents) support different zooplankton communities;
- do mixed communities of submergents contain a more diverse zooplankton than monocultures;
- does submergent plant density (independent of water quality) affect the zooplankton community;
- does the sediment support different zooplankton communities than the macrophytes and how is this affected by sediment characteristics;
- and, how does the plant community affects food web interactions?

Complex food web interactions involving several trophic levels in Great Lakes coastal wetlands are poorly understood. Wetlands are important habitat for zooplankton (Krieger and Klarer 1991; this thesis), macroinvertebrates (e.g. Cardinale et al. 1998; Gathman et al. 1999), fish (e.g. Leslie and Timmins 1991, 1992, 1995; Jude and Pappas 1992; Brazner and Beals 1997) and waterfowl (Prince et al. 1992); however, there are no studies examining trophic links between these levels (Krieger 1992).

Besides several studies describing zooplankton grazing rates in the water column of Great Lakes wetlands (Havens 1991; Bridgeman et al. 1995; Lougheed et al. 2000, Chapter 3), the role of zooplankton as primary consumers in the transfer of energy from producers to higher trophic levels in coastal wetlands is relatively unknown. In particular, the relative importance of phytoplankton, benthic algae, periphyton and macrophyte detritus in the diets of different invertebrates taxa should be tested. Several authors have suggested the use of stable isotopes for this purpose (Hann 1999; Wissinger 1999).

Furthermore, the role that these trophic interactions have in transferring energy from highly productive wetlands to the lake via fish migration is also unknown. Many fish species use Great Lakes coastal wetlands for part, if not all, of their life cycle (Jude and Pappas 1992) and migration of fish from these highly productive wetlands to the open water is likely a valuable source of energy to the Great Lakes proper. Studies on species-specific habitat and dietary preferences through all stages of fish development are required to understand the importance of wetlands and the wetland invertebrate community in providing valuable and productive habitat to both resident and migratory fish species.

At the State of the Lakes Ecosystem Conference in 1996, which focused on the nearshore environments of the Great Lakes, it was recognized that to target protection activities effectively, we must better understand nearshore ecosystems, including coastal wetlands. In particular, there is a need for science directed at identifying the species and habitats occurring in nearshore environments, as well as identifying individual species requirements. The conference participants concluded that indicators should be developed that would: objectively reveal the state of ecosystem; be easily understood to policy makers and the public; be relevant to multiple users and therefore prevent dilution of monitoring efforts; and also be cost-effective by summarizing high quality data within limited resources.

The research outlined in this thesis makes substantial strides towards achieving these goals – both in understanding the ecology of the zooplankton community in Great Lakes coastal wetlands, as well as applying this understanding to the development of indicators. The community composition, mean individual size and biomass of zooplankton populations have been listed as indicators of nearshore and open water environmental quality; however, zooplankton were not listed as coastal wetland indicators (Bertram and Stadler-Salt 1999). I recommend that the wetland zooplankton index developed in Chapter 5 be added to the list of indicators of coastal wetland quality identified by SOLEC (Bertram and Stadler-Salt 1999), as it was developed from the most comprehensive data set published to date on Great Lakes coastal wetlands.

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