SPATIAL AND TEMPORAL DYNAMICS OF GREAT LAKES MARSHES

SPATIAL AND TEMPORAL DYNAMICS OF LAURENTIAN GREAT LAKES COASTAL MARSHES

BY

SARAH THOMASEN, B.Sc.

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AUTHOR: Sarah Thomasen, B.Sc. (McMaster University)

SUPERVISOR: Professor Patricia Chow-Fraser

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GENERAL ABSTRACT

Despite their ecological and economical values, degradation of coastal marshes in the Laurentian Great Lakes is widespread. In order to restore degraded marshes and protect high-quality ones we need to understand the interactions between abiotic and biotic factors and how these change over space and time. The over-arching goal of this thesis is to gain greater understanding about the temporal and spatial dynamics that shape coastal marshes.

Chapter 1 evaluates the response of the biotic and abiotic components to restoration efforts at Cootes Paradise, a degraded coastal marsh of Lake Ontario. We used three approaches: 1) we analysed changes in water quality parameters and the community composition of zooplankton, macrophytes and fish 2) we used ecological indices based on water quality, zooplankton, macrophyte and fish communities to track changes in quality and 3) we evaluated changes in the wetland quality in comparison with two other coastal wetlands of the Laurentian Great Lakes for which long-term data exist. Our results show that there has been variable improvement in wetland quality at Cootes Paradise, but compared to the two other wetlands, it is still the most degraded in all aspects studied. We detected an overall trend towards moderately better water quality conditions in Cootes Paradise over the past decade but this is not directly reflected in the zooplankton, macrophyte and fish communities. We believe that high nutrient levels and high turbidity are preventing the progression to a clear-water macrophyte dominated system.

Chapter 2 examines the influence of environmental variation on the zooplankton assemblage at nearshore Long Point Bay, Lake Erie. We visited 102 sites along the nearshore and sampled for zooplankton and a suite of environmental variables. Afterwards, we evaluated the impacts of exposure using wind and fetch data to calculate a Relative Exposure Index (REI). Ordination techniques revealed a large variation in physical disturbance, water clarity, nutrient concentrations, water chemistry and aquatic vegetation that explained the distribution pattern of zooplankton at the 102 sites. Gradients of REI are strongly positively correlated with environmental variables, such as pH, dissolved oxygen, and temperature and highly negatively correlated with conductivity and dissolved organic carbon. The results of this study highlight the impacts of exposure on the zooplankton community and the effects of connectivity to larger water bodies.

PREFACE

The following M. Sc. thesis consists of two chapters which form separate manuscripts for publication in peer-reviewed journals. Chapter 1 has been submitted to *Ecological Indicators* and is currently in press. Chapter 2 is being prepared for submission to *Freshwater Biology*.

Besides my supervisor, Dr. Patricia Chow-Fraser, Chapter 2 is co-authored by Dr. Janice Gilbert, Wetland Consultant Biologist. As first author, I analyzed all zooplankton samples, performed all statistical analyses and wrote all of the manuscripts. Chapter 1 is a compilation of 16-years of field and laboratory-work conducted by past members of the Chow-Fraser lab; however I helped with the final two-years of data collection and analysis. Dr. Gilbert collected all *in-situ* measurements used in Chapter 2. The following are the proper citations for these papers, including co-authorship:

Thomasen, S. and P. Chow-Fraser. (in press) Detecting changes in ecosystem quality following long-term restoration efforts in Cootes Paradise Marsh. *Ecological Indicators*

Thomasen, S., J. Gilbert, and P. Chow-Fraser. Importance of physical disturbance and hydrologic connectivity in creating microhabitats and diversity in zooplankton assemblages at nearshore Long Point Bay, Lake Erie

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ABBREVIATIONS

AOC	Area of Concern
CANCOR	Canonical correlation
CHL	Chlorophyll a
COND	Conductivity
CP	Cootes Paradise
DO	Dissolved oxygen
DOC	Dissolved organic carbon
FL	Number of floating species, variable in canonical correlation
HH	Hamilton Harbour
HHRAP	Hamilton Harbour Remedial Action Plan
ISS	Inorganic suspended solids
LP	Long Point
MB	Matchedash Bay
NMS	Non-metric multidimensional scaling
PCA	Principal components analysis
REI	Relative exposure index
SET_{ENV}	Canonical correlation environmental dataset
SET_{SP}	Canonical correlation species dataset
SRP	Soluble reactive phosphorous
TEMP	Temperature
TN	Total nitrogen
TP	Total phosphorous
TSS	Total suspended solids
UNESCO	United Nations Educational, Scientific and Cultural Organization
WFI	Wetland Fish Index
WMI	Wetland Macrophyte Index
WQI	Water Quality Index
WZI	Wetland Zooplankton Index

GENERAL INTRODUCTION

Coastal marshes

A wetland is an area where soil is saturated with water long enough to promote aquatic processes (NWWG, 1998). Wetlands hydrologically connected to large bodies of water, such as the Laurentian Great Lakes, are described as coastal. The most common type of coastal wetland and the focus of this thesis is the coastal marsh. Coastal marshes occur at the transition from permanent terrestrial upland environments to permanent water bodies (Maynard and Wilcox, 1997). They can be permanently, semi-permanently or seasonally flooded and are typically dominated by soft-stemmed emergent aquatic plants in shallower waters and submerged and floating-leaf plants in deeper waters (Mitsch and Gosselink, 1993).

Coastal marshes provide numerous ecological functions, many of which are not realized until the marsh is destroyed. Aquatic vegetation of coastal marshes dampens fluid energy common in the Great Lakes, allowing for suspended sediments to settle, increasing water clarity (Meeker, 1996). Many nutrients and contaminants adhere to sediment particles (Newcombe and Macdonald, 1991) and settling removes the adhered contaminants from the water column. Vegetation also prevents erosion of the shoreline and provides flood mitigation (Herdendorf, 1992). Aquatic plants and periphyton directly uptake nutrients from the water for growth, reducing concentrations in the water column (Wetzel, 1992). The composition and abundance of aquatic vegetation is directly linked with the functional capacity of marshes to promote high water-quality, through reduced nutrient loading and improved water clarity.

Coastal marshes also provide tremendous value, irrespective of benefits to humans. They host high diversity of aquatic, terrestrial, and wetland-specific flora and fauna. Numerous fish (Jude and Pappas, 1992; Wei et al., 2004) and birds (Prince et al., 1992) utilize these habitats for all or part of their life cycles. The Great Lakes ecosystem supports 46 endemic species, 180 native fish species and 279 globally rare plants, animals and natural communities (GLIN, 2010). Spatial and temporal variability create a diverse range of niches for exploitation. Coastal marshes are dynamic systems, shaped by both land-use practices (Chow-Fraser, 2006; Trebitz et al., 2007) as well as large-lake processes such as waves, seiches and water-level fluctuations (Maynard and Wilcox, 1997). Environmental characteristics such as exposure, sediment and water chemistry fluctuate widely.

Laurentian Great Lakes

The Laurentian Great Lakes are comprised of five lakes, Superior, Huron, Michigan, Erie, and Ontario, spanning eight American states and one Canadian province. They are the largest fresh-surface-water system in the world, containing approximately 18% of the world's water supply, and 95% of North America's (Botts and Krushelnicki, 1993). Because of their large size, physical characteristics such as climate, geology and topography vary across the basin. The upper lakes have a colder climate and are dominated by the Canadian Shield; Precambrian rocks overlain by a thin layer of acidic soil. Moving southward, the

Precambrian rocks are replaced by sedimentary rock, a warmer climate and rich fertile soil, which make the lower lakes basin ideal for agriculture. The human population has capitalized on this resource, replacing the original deciduous forests with agriculture and urban development.

Forty-million Canadians and Americans reside within the Great Lakes basin, concentrated in the lower lakes region (Rang, 2009). The Great Lakes are heavily impacted by human use, including point and non-point source pollution from urban and agricultural land use (Carpenter et al., 1998), land-use conversion (Wolter et al., 2006), demand for withdrawal and diversion, shipping, as well as shoreline development (Maynard and Wilcox, 1997). Over 70% of Ontarians rely on the Great Lakes for drinking water (Rang, 2009) and the lakes support commercial and sport fisheries (Rothlisberger et al., 2010) and recreation, not to mention the diverse biota that call the Great Lakes home (Maynard and Wilcox, 1997).

As a result of the high population density and heavy use of this system, the Great Lakes are highly susceptible to negative inputs. Since the opening of the St. Lawrence Seaway in 1959, transoceanic ships exchanging ballast water in the Great Lakes system have introduced approximately 70% of non-native species (Holeck et al., 2004). Also for shipping purposes, water outflows are actively managed at the St. Lawrence Seaway and the St. Mary's River in Lake Superior (Lenters, 2001). The current Lake Ontario regulation plan does not allow for natural fluctuations which are key to sustaining abundance and diversity of coastal marshes (Hudon et al., 2006). The regulation plan for the Lake Superior outflow is currently under review over concerns of low water levels and climate change (IJC, 2010). Due to converted land use there is increased nutrient input through both point and non-point source pollution (Carpenter et al., 1998) and the areas of highest density (i.e. the lower lakes) have the poorest water-quality (Chow-Fraser, 2006; Trebitz et al., 2007).

Since European settlement of the Great Lakes basin in the mid-19th century, over 60% of wetland cover has been lost in southern Ontario due to infilling, conversion to other land use and general destruction of wetlands (Snell, 1987). More recently, coastal wetlands have become especially threatened with new development concentrated in areas within ten kilometres of the Great Lakes shoreline, with the majority occurring within one-kilometre (Wolter et al., 2006). It is estimated that 75% of Great Lakes coastal wetlands have been lost since European settlement (Jude and Pappas, 1992). Of the remaining wetlands, many are degraded primarily due to land-use alterations in their watershed (Crosbie and Chow-Fraser, 1999; Trebitz et al., 2007).

Ecosystem quality

As a result of these conflicting pressures throughout the Great Lakes numerous organizations are dedicated to research and improvement of current conditions such as International Joint Commission (IJC), Great Lakes Coastal Wetland Consortium (GLCWC), and the State of the Lakes Ecosystem Conference (SOLEC). Research is focused on understanding the variety of components of these complex systems and developing useful tools for managers and policy-makers to utilize. Research has lead to the identification and classification of high-functioning often undisturbed systems, as well as heavily impacted systems with impaired functioning. The concept of quality has been developed to describe ecosystems replacing the anthropomorphically derived term "health".

Coastal marshes can be classified along a gradient of quality. High quality coastal marshes are high-functioning with a diverse array of species and are typically un-impacted by humans. Most are found in the northern Great Lakes, such as Georgian Bay of Lake Huron, since these areas have relatively low human development and land-use alteration (Cvetkovic, 2008). Communities are characterized by clear low-nutrient waters allowing for high diversity of submergent vegetation and periphyton. The diverse vegetation supports a wide variety of wetland specialists and generalists throughout all levels of the food chain.

At the opposite end of the quality gradient, are highly degraded sites with impaired functionality. The most degraded sites are in the lower lakes, especially in areas that are heavily impacted by urban development, agriculture and industry (Chow-Fraser, 2006). Nutrient and sediment enrichment cause a loss of submergent plants due to increased turbidity (Lougheed et al., 1998). Organisms which require submergent vegetation for various stages of their life history, such as feeding and reproduction, are replaced by species tolerant to turbid-phytoplankton dominated states (Jeppesen et al., 2000; Jude and Pappas, 1992; Lougheed and Chow-Fraser, 1998; Seilheimer and Chow-Fraser, 2006). These sites are characterized by fringing emergent vegetation, turbid water and dominance by generalist and non-native species.

The identification of disturbance gradients and distinctive features of high and low quality marshes has led to the development of useful monitoring tools. Indicators of quality are useful because they provide quick assessments and communicate complex information in a simplified form. Species and system specific indicators (Chow-Fraser, 2006; Croft and Chow-Fraser, 2007; Frieswyk et al., 2007; Green et al. 1989; Lougheed and Chow-Fraser 2002; Seilheimer and Chow-Fraser, 2006) have been developed as tools for policy makers and managers. They can be used to monitor the status of specific components of an ecosystem and infer overall quality.

Thesis objectives

Coastal marshes have immense intrinsic and anthropocentric value; however, increasing human pressure is threatening their existence. In order to effectively protect high-quality marshes and restore degraded ones we must understand the multitude of factors that comprise and regulate these systems. Although we have a basic understanding of many parts of these ecosystems, there is still a large amount of temporal and spatial variation that obscures our current understanding of the entire ecosystem. This project is my contribution to improve our understanding of the factors that control temporal and spatial variability in coastal marshes.

The first chapter of my thesis addresses temporal variation of Cootes Paradise, a degraded coastal marsh of Lake Ontario. I evaluate the progress of long-term restoration efforts by examining trends in abiotic and biotic factors. During these analyses, I identified a spatially explicit response to restoration efforts. In response to this observation, I identified a current gap in the literature in understanding how different trophic levels respond to external processes over time.

The second chapter investigates this gap by focusing on the influence of environmental variation in structuring the zooplankton assemblage from a spatial perspective. The study took place at a relatively high-quality marsh complex and surrounding nearshore area of Lake Erie, called Long Point Bay. Although this area has been recognized as internationally significant (UNESCO biosphere reserve), the nearshore zooplankton community has never been analysed before.

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CHAPTER 1:

Detecting changes in ecosystem quality following long-term restoration efforts in Cootes Paradise Marsh

Abstract

Cootes Paradise Marsh is a large urban wetland of western Lake Ontario that has undergone major restoration as part of the Hamilton Harbour Remedial Action Plan. A key component of the restoration plan is exclusion of common carp (*Cyprinus carpio*) via construction of the Cootes Paradise Fishway that became operational in 1997. Here, we evaluate the response of the marsh community to carp exclusion using three approaches. First of all we analyse changes in water quality parameters and the community composition of zooplankton, macrophytes and fish. Secondly, we use ecological indices based on water quality, zooplankton, macrophyte and fish communities to track changes in quality. Lastly, we evaluate changes in the wetland quality of Cootes Paradise over the past decade in comparison with two other coastal wetlands of the Laurentian Great Lakes for which long-term data exist (Matchedash Bay of Lake Huron and Long Point Marsh of Lake Erie). Our results show that there has been variable improvement in wetland quality at Cootes Paradise, but compared to the two other wetlands, it is still the most degraded in all aspects studied. The overall trend towards moderately better water quality conditions in Cootes Paradise over the past decade is not directly reflected in the zooplankton, macrophyte and fish communities. We believe that high nutrient levels and high turbidity are preventing the progression to a clear-water macrophyte dominated system. This is one of few long-term studies that tracks the progress of restoration in a degraded

marsh. It underscores the difficulty in trying to restore a 'novel ecosystem' to its original biotic and abiotic characteristics.

Introduction

Cootes Paradise Marsh (CP) is a large (250-ha) drowned river-mouth marsh, located in Hamilton Harbour at the extreme western end of Lake Ontario (Lougheed et al., 1998). At the turn of the twentieth century, over 90% of this wetland was covered with diverse vegetation, however the marsh had receded to less than 15% cover by the 1990s (Chow-Fraser et al., 1998). Coinciding with the vegetation decline, the fishery shifted from an important warmwater fishery of northern pike and largemouth bass to one dominated by planktivorous and benthivorous species such as bullheads and invasive common carp and alewife (Chow-Fraser, 1998). Despite this degradation, Cootes Paradise still provides a valuable stopover for migratory waterfowl and wetland birds (Smith and Chow-Fraser, 2010) and remains a major fish nursery for Lake Ontario (Holmes, 1988).

The degradation of CP can be attributed to a number of human activities. Agricultural and urban development of the previously forested watershed coupled with discharge of sewage effluent into the marsh for over nine decades (Chow-Fraser et al., 1998) has resulted in hypereutrophic conditions (Kelton et al., 2004). In addition, common carp (*Cyprinus carpio*), an exotic species introduced into Lake Ontario at the end of the 20th century, became established in CP, accounting for more than 90% of the fish biomass by the 1990s (Lougheed et al., 2004). Both the spawning (Lougheed et al., 1998) and feeding behaviours (Chow-Fraser, 1999) of the common carp accounted for up to 35-40% of the overall water turbidity in CP (Lougheed et al., 2004). These factors together contribute to some of the most turbid water conditions in a Great Lakes coastal wetland (Chow-Fraser, 2006), and prevent sufficient light penetration to support the growth of submersed aquatic vegetation, which is a critical component of the fish (Chow-Fraser, 1998; Randall et al., 1996) and waterfowl habitat (Prince et al., 1992). High turbidity has many other detrimental effects throughout all trophic levels, such as reducing light penetration to a level that is insufficient for periphyton growth (Newcombe and MacDonald, 1991), clogging filter-feeding structures of invertebrates (Kirk, 1991), and affecting the behaviour and survival of visually hunting predators and mating fish (Miner and Stein, 1993).

In 1985, the International Joint Commission designated Hamilton Harbour (HH) as one of 43 Areas of Concern (AOC); the harbour ecosystem had all fourteen " beneficial use impairments," one of which was "loss of fish and wildlife habitat" (Hamilton Harbour Remedial Action Plan Stage 2, 1992). The largest remaining spawning and nursery habitat in the HH ecosystem is CP, and therefore a large component of the HHRAP is to restore the fish and wildlife habitat in the marsh. Thus, the HHRAP included a carp exclusion program via installation of the Cootes Paradise Fishway at the CP inlet into HH, which takes advantage of the natural migration of fish into and out of the marsh during the spring and fall (Lougheed and Chow-Fraser, 2001). The Fishway physically excludes large fish (e.g. mature breeding-age carp) from moving between the marsh and the harbour and captures them for sorting, at which point the carp are returned to HH (Wilcox and Whillans, 1999). CP is in a steady turbid-phytoplankton dominated state and it was predicted that the exclusion of common carp from the marsh would cause a shift to its former clear-macrophyte dominated state, as has been observed in many systems (Ibelings et al., 2007; Madgwick, 1999; Moss et al., 1996).

Although other restoration strategies have been implemented in addition to carp exclusion (e.g. nutrient reduction, marsh planting program), operation of the Fishway was the only one that was expected to initiate a switch to a clear-macrophyte dominated state. For this reason, we have chosen the initial date of Fishway operation as the starting point to evaluate the effectiveness of remedial actions on the overall quality of the ecosystem. In this study, ecosystem quality refers to biodiversity (species richness, diversity of functional groups in the ecosystem), presence of non-native species, and presence and abundance of known pollutant-tolerant and generalist species.

Our primary goal is to determine how ecosystem quality has responded to biomanipulation. We will use three approaches to evaluate this response. First, we will track how water quality parameters, zooplankton, macrophyte and fish species have changed from before Fishway operation to at least a decade afterwards. Secondly, we will use these measurements to calculate ecological indices developed specifically for use in Great Lakes wetlands which will provide a long-term trend to gauge the overall progress in marsh restoration. The four indices we will use are the Water Quality Index (WQI; Chow-Fraser, 2006), the modified Wetland Zooplankton Index (WZI; Lougheed and Chow-Fraser, 2002;

Yantsis, 2009), the Wetland Macrophyte Index (WMI; Croft and Chow-Fraser, 2007), and the Wetland Fish Index (WFI; Seilheimer and Chow-Fraser, 2006, 2007). Lastly, to interpret the response of CP to restoration efforts in context of other coastal wetlands in the Great Lakes basin, we will compare changes with those in two other wetlands: Matchedash Bay (MB) and Long Point Marsh (LP) (location shown in Figure 1-1, see Materials and methods for site descriptions).

Materials and methods

Study sites

The three wetlands in this study occur along the coast of the Great Lakes (Figure 1-1) and were all sampled between May and August from 1993 to 2009. CP is a windswept turbid system that is dominated by open water with a fringe of emergent and floating vegetation occurring along the shore and in two embayments. We sampled along the length of the wetland, including open-water sites located near the eastern outflow (close to the Fishway (CP1)), sites close to vegetation in the two embayments (Mac Landing (CP10) and Westdale Cut (CP16)), in a lagoon (West Pond (CP5)) near the outfall of the sewage treatment facility, and within the outflow of the main tributary, Spencer's Creek (CP4) (see Figure 1-1 inset). Many of the long-term sampling stations established in Chow-Fraser et al. (1998) have been retained in this study.

The second wetland, Matchedash Bay (MB) is one of several bays in southern Georgian Bay, Lake Huron, in an area known as Severn Sound. Similar to CP, MB provides critical habitat for a diverse range of birds and wildlife (Sherman, 2002; Wilson and Cheskey, 2001) despite a moderately degraded state. Severn Sound was identified by the International Joint Commission as an AOC because of problems with nutrient enrichment (Sherman 2002). A RAP was developed and implemented in 1989 to reduce nutrient inputs, and environmental conditions have improved sufficiently such that in 2003, Severn Sound was delisted as an AOC. MB is large and variable, and we have sampled at various sites within the wetland between 1998 and 2008. To ensure validity of the long-term comparison, we only use data that were collected at the same place and time during the year.

LP is one of the most extensive wild areas remaining in southwestern Ontario and offers a diverse range of habitats, particularly for migratory and resident species of waterfowl (Wilcox et al., 2003), wetland birds (Smith and Chow-Fraser, 2010) and fish (Mahon and Balon, 1977). Unlike the other two marshes, Long Point (LP) is a clear-water system with diverse assemblages of emergent, submergent and floating plants, and has many habitat types that vary in depth and degree of wind exposure (Thomasen and Chow-Fraser, unpub. data). For the comparison of long-term changes, there were only suitable historic data collected near the Provincial Park between 1998 and 2008.

Data collection

Details of all protocols used for water sampling and processing can be found in many of the previous publications (e.g. Chow-Fraser, 2006; Lougheed et al., 1998). It is important to note that the data included in this study span 16 years, and had not been collected intentionally for this long-term evaluation. Therefore, not all variables are available on each sampling occasion. Nevertheless, all data were collected and processed with standardized protocols and methods, and were scrutinized with respect to temporal and spatial consistency. We also ensured that water quality data (see Table 1-1) collected during fair-weather conditions were used because storm events can greatly alter nutrient and sediment concentrations. Zooplankton samples were collected following the protocol outlined in Lougheed and Chow-Fraser (2002). Samples were collected from June to August and a minimum of three zooplankton samples were used to calculate an average WZI score based on the recommendations by Yantsis (2009). To analyze the relative distribution of zooplankton according to their taxonomic and functional roles, we grouped zooplankton according to their size and feeding guild as suggested by Lougheed and Chow-Fraser (1998) in their analysis of the zooplankton community in CP. Herbivorous rotifers included all rotifers except for *Asplanchna,* which were classified as a predaceous rotifer. Cladocerans were grouped according to size: micro-cladoceran (< 300 μm), medium cladoceran (300-600 μm) and macro-cladoceran (>600 μm). Adult copepods were grouped together according to order (cyclopoids, calanoids, or harpacticoids) and nauplii and copepods were classified as immature copepods.

The aquatic plant community was surveyed between late June and August according to the methods of Croft and Chow-Fraser (2007). In this protocol, 10-15 quadrats in representative areas of each wetland were surveyed for the presence of submergent, floating, and emergent plant taxa. Since we were only interested in fish habitat, wet meadow species were excluded.

Both electrofishing and paired fyke nets (set overnight) were used to collect fish data for the WFI calculation. Chow-Fraser et al. (2006) revealed biases in fish abundances and sizes associated with these two methods. A subsequent study showed that such differences did not lead to differences in WFI scores (Kostuk, 2006). Boat electrofishing (see protocol in Lougheed et al., 2004) was conducted in May of 1996, 1997, and 1998, whereas paired fyke nets (see protocol in Seilheimer and Chow-Fraser, 2006) were used from May to early August in 2001 to 2009. We compared May 1996 to May 2008 using the Mann-Whitney Test (see Section 2.4) to control for seasonal effects. We also used Scott and Crossman (1998) to classify the fish based on species and life stages into the following functional feeding guilds: planktivorous (consuming primarily zooplankton), piscivorous, omnivorous (consuming both algae and zooplankton), herbivorous (consuming algae and plant material), carnivorous (consuming insects and other invertebrates) or benthivorous (consuming primarily benthic invertebrates and other sediment-associated organisms).

Description of ecological indices

The four indices we have chosen were developed specifically for coastal marshes in the Great Lakes. They are based on the premise that anthropogenic activities cause degradation in water quality and thus lead to dominance of plants, zooplankton and fish that reflect the degraded state. Operationally, the indices can be interpreted as being indicative of high-quality ecosystems when the values are high and of degraded ecosystems when values are low. Each biotic index reflects conditions of one trophic level in the ecosystem. Taken together, the abiotic index as well as biotic indices, contribute information regarding the overall condition experienced by the marsh community within the water column.

Chow-Fraser (2006) developed the abiotic index called the Water Quality Index (WQI), which ranks the degree of water quality impairment based on 12 environmental parameters (i.e. major nutrients, suspended solids, chlorophyll concentrations, and physical characteristics - see Table 1-1 for a complete list) collected from 110 wetlands throughout the Great Lakes. Chow-Fraser (2006) used Principal Components Analysis to create an index yielding a score ranging from -3 to +3 which indicates the effect of human-induced land-use alterations on wetland quality. WQI scores were significantly related to land-use alteration and sensitive to human-induced degradation of water quality in coastal wetlands. Chow-Fraser (2006) considered all sites associated with scores below zero to be degraded by human activities.

The three biotic indices (WZI, WMI and WFI) may be thought of as surrogates of the WQI. Lougheed and Chow-Fraser (2002) found that certain zooplankton taxa tended to be associated with clear water, macrophyte-dominated sites while others were associated with turbid, algal-dominated sites, and used this information to develop the WZI for 70 wetlands in the Great Lakes basin, excluding the pristine wetlands of eastern Georgian Bay. Yantsis (2009) modified the WZI to integrate the high-quality sites of Georgian Bay and made it more robust. The WMI was developed by Croft and Chow-Fraser (2007) who related the presence of aquatic plant species to water quality conditions in 127 wetlands from all five Great Lakes. Similar to the WMI, the basis of the WFI, developed by Seilheimer and Chow-Fraser (2006), is that the degree of water quality impairment is reflected in the taxonomic composition of the fish community. The WFI was initially developed from 40 wetlands located primarily in Lakes Ontario, Erie and Michigan and was later updated when Seilheimer and Chow-Fraser (2007) included 60 additional wetlands from Lakes Superior and Huron (including pristine sites of eastern Georgian Bay) so that the WFI could be applied to all five Great Lakes.

Canonical Correspondence Analysis was used in all three biotic indices to quantify the relationship between species occurrence and environmental variables in the form of species-specific values denoted as U and T values. First, U values (whole numbers ranging from 1 to 5) were assigned based on the species' position on the synthetic degradation axis, where 1 was assigned to those that were most tolerant to degradation, and 5 to those that were least tolerant. Secondly, T values (whole numbers ranging from 1 to 3) were assigned according to the weighted standard deviation of the species scores along the axis of degradation, where 1 was assigned to species with a wide niche breadth, and 3 to those with narrow niche breadth. An index score is then calculated with respective U and T values in the following equation (1):

$$\text{Index Score} = \frac{\sum_{i=0}^{n} Y_i\, U_i T_i}{\sum_{i=0}^{n} Y_i T_i} \qquad (1)$$

where Y_i is the presence or abundance ($\log_{10}(x+1)$) of species i. The index scores can range from 1 to 5, with higher values indicating better wetland quality. The U and T values for the species in this study are listed in Table 1-2, 1-3 and 1-4. We refer readers to the original published papers for more details on the index development and application.

Statistical analysis

We first used a simple linear regression to detect significant changes over time for each ecological index. We also employed the Mann-Whitney Test, also called the Wilcoxon-Mann-Whitney Test, which is a non-parametric method equivalent to the t-test (Zar, 2010), to compare mean scores before and after the biomanipulation. To test our hypothesis that the indicator scores based on Cootes Paradise data will be significantly lower than those for Long Point Marsh and Matchedash Bay, we used the Kruskal-Wallis single factor analysis of variance by ranks, which is the non-parametric equivalent of an analysis of variance. To determine significant group-to-group differences, we employed the post-hoc non-parametric Tukey-type multiple comparison test, called the Nemenyi Test. All of the non-parametric tests we used are based on ranking the values, as opposed to the absolute values and were employed based on Zar (2010). We set the significance level to $\alpha = 0.05$ for all tests.

Results

Water quality and biotic communities

All water quality parameters except for TN, temperature and pH have followed a decreasing trend from 1993 to 2008 (Table 1-1). TN is the only nutrient that has not decreased over the study period, although we were unable to measure TN in 2008 (Table 1-1). Turbidity, conductivity and TNN have significantly decreased (Table 1-1). Mean turbidity following exclusion (33.7± 4.3 NTU, 1998-2008) decreased by almost half of its original value during the pre-exclusion years (60.7± 4.3 NTU, 1993-1996).

The zooplankton community in 1996, the year prior to carp exclusion, was dominated by small-bodied organisms. Herbivorous rotifers, micro-cladocerans and immature copepods represented 92% of the relative abundance (Figure 1-2). *Bosmina longirostris*, *Polyarthra* sp., and *Brachionus* sp. were the most common (Table 1-2). The zooplankton community in 2008 shifted to larger-bodied organisms and was more diverse and heterogeneous (Figure 1-2). Medium cladocerans were the most common functional group (28%, Figure 1-2), largely comprised of *Ceriodaphnia* sp. and *Diaphanosoma birgei* (Table 1-2). Overall the distribution of functional groups became more balanced, with the appearance of larger zooplankton such as macro-cladocerans and calanoid and harpacticoid copepods (Figure 1-2). Although the absolute density of the cladoceran zooplankton in 2008 was not nearly as high as in 1996 (~1600L^{-1} vs. ~160L^{-1}), species richness had increased from 20 to 23 (Table 1-2).

The number of macrophyte species in CP has fluctuated over the years, with the highest richness occurring in 1993 (20 species, Figure 1-3) and the lowest in 2008 (10 species, Figure 1-3). Relative to native species, there has been a relatively constant presence of non-native species (*Myriophyllum spicatum, Potamogetan crispus, Lythrum salicaria, Typha angustifolia, and T. x glauca* - Table 1-3, Figure 1-3). With the exception of 2006, the proportion of submergent species has increased since the Fishway became operational, and this appears to have been at the expense of the emergent vegetation (Figure 1-4A). The proportion of floating species has remained relatively constant post carp exclusion (Figure 1-4A).

The fish community has clearly changed since 1996, when benthivores dominated (47% common carp); the community following carp exclusion had < 40% benthivores (< 10% common carp) (Figure 1-5A). In recent years, brown bullhead and bluntnose minnows have added to the diversity of the benthivore niche (Table 1-4). The proportion of other types of fish has also increased. For instance, the percentage of carnivores increased two to four-fold (17-22% to 40-90%) following exclusion (Figure 1-5A). Piscivores, which had been noticeably absent prior to carp exclusion reappeared beginning in 1998, however they still do not represent a large proportion of the community (Figure 1-5A). Due to sampling bias related to the different gear types used, no conclusions can be made regarding the absolute abundance of catch (e.g. 4110 white perch in 2002,Table 1-4).

Ecological indices

We calculated the annual mean WQI score from all CP sampling stations (Figure 1-1 inset) to examine how water quality conditions have changed in the marsh from 1993 to 2008 and found that mean WQI scores have increased significantly over the 15 years (Figure 1-6A, r^2=0.72, p=0.02). We also divided the data into two periods, before and after operation of the Fishway in 1997, and found that the mean WQI score was significantly higher for the period following exclusion compared with the period before (Mann-Whitney, $p < 0.05$). Unlike the WQI, the WZI was not able to detect a significant improvement in CP through the 14 years (Figure 1-6B, r^2=0.04, p=0.70), and we did not find a significant difference between mean WZI scores before (1996) and after (2008) the Fishway operation (Mann Whitney, $p > 0.05$). In addition, the WMI was unable to detect a significant trend in scores between 1993 and 2009 (Figure 1-6C, $r^2 = 0.05$, $p = 0.58$); when we calculated mean WMI scores by grouping data before and after carp exclusion, we found no significant differences (Mann-Whitney, $p > 0.05$). Though not statistically significant, there has been a slight trend towards an increase in WFI scores from 1996 to 2008 (Figure 1-6D, r^2=0.25, p=0.32). Nevertheless, when we compared scores for the period prior to carp exclusion (1996) with those obtained after carp exclusion (2008), we found the scores post-exclusion have significantly improved (Mann-Whitney, $p < 0.05$).

We also recognized some site-to-site variability in the marsh. We were able to calculate WQI and WZI for various sites within CP. In 1993, all of the sites were below a WQI score of -2, except for the embayment known as Westdale Cut (CP16), which was slightly higher at -1.5 (Figure 1-7). By 2008, water quality conditions at the open water site (CP1), the sewage lagoon (CP5), and at another embayment known as Mac Landing (CP10) had all improved to scores between -1.2 and -1.8, while water in Spencer's Creek outflow (CP4) had improved to -0.9, similar to that in Westdale Cut (CP16) (Figure 1-7). It is noteworthy that both CP4 and CP16 had greater amount of residual vegetation compared with the other three sites. In addition, we calculated individual WZI scores for sites in CP in 1996 and 2008, and found that the sites with vegetation had higher scores (Mann-Whitney, $p < 0.05$).

Coastal marsh comparison

The comparison across wetlands is necessarily restricted to data collected following the Fishway implementation because no data had been collected prior to 1998 in Long Point (LP) or Matchedash Bay (MB). All of the index scores for CP were consistently lower than those for LP and MB (Figure 1-8). Of all three wetlands, MB has improved the most over 10 years, as indicated by the steepest slope relating WQI and WMI to time (Figure 1-8A, 1-8C). When all three marshes were compared, we found significant differences among the three sites (Kruskal-Wallis, $p < 0.05$). WQI and WMI scores associated with LP were significantly higher than those for CP; however, scores associated with MB were not significantly different from those of either wetland (Nemenyi Test). WQI scores at MB were found to be intermediate between LP and CP (Figure 1-8A), and corresponding WMI scores were more similar to those of the degraded CP in 1998 but more similar to higher quality LP in 2009 (Figure 1-8C).

Compared with CP, both MB and LP have lower water turbidity and a higher proportion of submergent species (Figure 1-4). Similarly, WZI scores corresponding to LP and MB were both higher than those corresponding to CP, even though they were statistically similar to each other (Kruskal-Wallis, $p < 0.05$; Nemenyi Test). Consistent with expectation, WFI scores for MB were also significantly higher than those for CP (Mann-Whitney, $p < 0.05$; Figure 1-8D). Unfortunately, there were no fish data available for LP to conduct a comparison with CP. When we examined changes in the structure of the fish community, we found a higher proportion of carnivores and piscivores in MB compared with CP; by contrast, CP had a greater number of feeding guilds (Figure 1-5), including a species of herbivorous fish (gizzard shad), which consumes algae. It is important to note that despite the biomanipulation, benthivores still comprise a larger proportion of the total catch in CP compared with MB (Figure 1-5).

Discussion

Evaluation of CP quality

Our primary goal was to determine how ecosystem quality has responded to the biomanipulation in CP. We used three approaches to evaluate the response of CP to the Fishway implementation: 1) analyzing changes in water quality parameters, zooplankton, macrophyte and fish 2) using indices to quantify and assimilate information that have been proven to be indicative of ecosystem quality and 3) comparing long-term changes in CP to that of two other coastal wetlands in the Great Lakes basin. The goal of carp exclusion was to trigger the switch from the current turbid, phytoplankton-dominated state to its former clear-water, macrophyte-dominated state. Thus we will also evaluate the progress of this restoration goal, in addition to an overall assessment of the quality of CP.

Most water quality variables (Turbidity, TSS, ISS, Chl-*a,* TP, SRP, TAN, TNN,) in CP have decreased over the period of study, indicating an overall improvement in wetland quality (Table 1-1). These observations are confirmed by an increasing trend in WQI scores, which incorporated all 12 variables into a single score (Figure 1-6A). It is noteworthy that the overall WQI score is still below zero, which indicates that human-induced degradation is still occurring in the marsh. Nutrient levels in CP are still sufficiently high that conventional classification systems (e.g. Carlson's (1977) Trophic State Index) would identify it as hypereutrophic.

The zooplankton community has shifted to larger-bodied organisms (Figure 1-2), which other studies have found is indicative of more oligotrophic conditions (Gannon and Stemberger, 1978; Jeppesen et al., 2000). Lougheed and Chow-Fraser (2002) observed that in general, good-quality wetlands tended to be dominated by large-bodied zooplankton that feed on epiphytic algae, whereas degraded wetlands tended to be dominated by small-bodied zooplankton that feed primarily on phytoplankton. Consistent with these observations, we found that representation by medium-sized cladocerans increased from 1% of total abundance in 1996 (prior to carp exclusion) to 28% in 2008 (Figure 1-2). This group consisted of *Ceriodaphnia* sp. and species of chydoridae that are known to be associated with aquatic plants (Fairchild, 1981; Paterson, 1993) and also have higher U and T values (see Table 1-2 for a list of species U and T values). Despite the obvious increased representation of species with high U and T values, WZI scores did not reflect any improvement in quality after the carp exclusion (Figure 1-6B, Mann-Whitney $p > 0.05$). This may be attributed to the relatively large drop in species with low scores (e.g. *Brachionus* sp.) as compared to the smaller increase in species with high scores (e.g. *Ceriodaphnia* sp.).

Total species richness of macrophytes did not increase substantially following carp exclusion, and the proportion of non-native species has not diminished; in some years (i.e. 2008) it has greatly increased (Figure 1-3). Studies on the dynamics of the species present in the marsh (*Typha latifolia, Phragmites australis* – Wei and Chow-Fraser, 2006; *Typha spp., P. australis* - Wilcox et al.,

2003) suggest that low water levels that we are currently experiencing may inadvertently benefit these non-native species at the expense of native species. This has been reported for some U.S. restoration sites, where a high potential for dominance by non-native species has halted the succession to more desirable native species (Zedler, 2000). We have also seen an increase in the proportion of submergent species in the marsh (Figure 1-4A), although the plant community in the two other Great Lakes marshes used for comparison still have a higher representation (Figure 1-4B and 1-4C). The WMI was not able to reflect the improved water quality in CP (Figure 1-6C) since most of the species found in CP were pollution tolerant species that had low U and T values

As expected, the operation of the CP Fishway resulted in a dramatic reduction in the common carp population (Table 1-4). Not surprisingly, the feeding guilds present in the marsh following the carp exclusion have become more diverse (Figure 1-5, Table 1-4). As mentioned previously, we have to exercise caution when comparing fish abundance and community structure information since two different sampling gears were used and there are known biases associated with each method (Chow-Fraser et al., 2006). Electrofishing was used to collect the pre-exclusion data, which in theory will target the larger piscivores, whereas the fyke nets used following the biomanipulation should target smaller fish, such as planktivores and carnivores. Therefore, the increased representation of piscivore through time cannot be attributed to a sampling bias related to different gear. However, the increased diversity of fish in more recent surveys may be attributed to the use of fyke nets since Chow-Fraser et al. (2006) showed a tendency for fyke nets to catch fish with more diverse feeding niches in degraded wetlands. Nevertheless, Kostuk (2006) showed that such differences did not lead to differences in WFI scores; therefore the higher scores in 2008 compared to 1996 are not an artefact of sampling gear (Mann-Whitney 1996-2008, $p < 0.05$). Despite the increasing trend, there were insufficient data to show a significant increase in WFI scores through time (Figure 1-6D, $r^2=0.25$, $p=0.32$).

In summary, both individual water quality parameters and the WQI scores show that the marsh has improved in quality following carp exclusion; however, the current status of CP is still degraded when compared with other wetlands (Chow-Fraser 2006, Figure 1-8). Although the zooplankton and fish communities have become more diverse, many species are still pollutant-tolerant generalists (e.g. *Moina* sp., brown bullhead). Species richness and the proportion of submergent species have increased, but non-native species remain prominent, and many of the native species are pollutant-tolerant generalists (e.g. *Lemna minor*, *Ceretaphyllum dermersum*). Overall, the improvement in water quality has not been accompanied by significant increases in the biotic indicators and CP remains in a turbid, algal-dominated state after more than 10 years of carp exclusion. We have observed, however, that portions of the marsh that had residual plant communities have progressed further than the open-water sites.

Suggestions why CP is in a stable turbid state

Degraded communities, such as CP, do not always respond predictably to management efforts (Angeler et al., 2003; Zedler, 2000). Many European shallow lakes became turbid-phytoplankton dominated systems due to external nutrient loading, and did not switch back to clear-macrophyte dominated systems with corresponding nutrient reduction (Ibeling et al., 2007; Madgwick, 1999; Moss et al., 1996). We know that CP is capable of switching to a clearer state. In 1997, abnormally low spring temperatures caused a delay of fish migration into the marsh (including planktivores), which released the zooplankton population from predation, resulting in zooplankton-mediated improvement in water clarity and an expansion of submergent vegetation in previously unvegetated shallows (Lougheed et al., 2004). However, this state was short-lived and CP switched back to its former turbid state. Many other researchers have encountered this apparent stability of the turbid-phytoplankton state and there are many explanations for the mechanisms such as herestesis (Ibelings et al., 2007), and the development of feedback between abiotic and biotic factors (Suding et al., 2004). Chow-Fraser (1998) developed a conceptual model explaining the factors that play a role in the degraded and former high-quality state of CP. It is clear that there are a number of positive and negative feedback mechanisms that are keeping CP in its current degraded state.

Chow-Fraser (1998) predicted that a reduced carp population would cause lower turbidity, but a number of other factors such as wind and wave action, high sediment loading from the watershed, and high algal biomass would continue to cause high turbidity in the marsh. Lougheed et al. (1998) predicted that exclusion of 90% of the carp would reduce water turbidity in Cootes Paradise by up to 45%, and this has largely been confirmed in the present study. Prior to biomanipulation (1993-1996), turbidity had been approximately 60 NTU, but after the Fishway became operational (1998-2008), turbidity was reduced by 44% to 33.7 NTU (Table 1-1). Chow-Fraser (1999) suggested that background levels (25.4 NTU) could be attributed to wind re-suspension and algal growth. Lougheed et al. (1998) also predicted that wetlands with turbidity higher than 20 NTU would likely have fewer than five species of submergent taxa, whereas wetlands below this turbidity threshold would have a more diverse aquatic plant community. According to data from the last 10 years of monitoring, CP will probably continue to have turbidity levels well above this threshold, and there is low probability that a large number of submergent species will become re-established in the near future.

In addition to high turbidity there are a number of other factors that are not facilitating the switch to a clear-water macrophyte dominated system. For example, nutrients are still very high. Summer mean TP must fall below 0.1 mg/L (Hosper and Meijer, 1993; Jeppesen et al., 2000) and TN must be below 2mg/L (Gonzalez et al., 2005) before macrophytes can regain high areal cover. In CP, the lowest summer mean TP occurred in 2008 and was 0.14 mg/L in 2008 (Table

1-1). Although we did not measure TN in 2008, the lowest historic value measured in 1993 (~ 4mg/L, Table 1-1) was twice as high as the desired level.

Expansion of the current macrophyte population is essential to the improvement in quality of CP, as macrophytes are key to stable clear-water states (Hosper and Meijer, 1993; Ibeling et al., 2007). The positive effects of the macrophyte community can be observed in CP. We observed a differential response in both WQI (Figure 1-7) and WZI scores in vegetated sites, similar to that observed in other systems (Angeler 2003; Moss et al., 1996; Ibeling et al. 2007). Even if CP switches to a stable clear-water system with further management actions, it would not likely return to its original undisturbed state. CP is an excellent example of a 'novel ecosystem' (Hobbs et al., 2006) that has been so transformed by human actions that it is essentially a new system, with different species assemblages, often dominated by invasive species, and should therefore be treated as such (Lindenmayer et al., 2008).

Conclusion

We have analyzed the response of the abiotic and biotic components of Cootes Paradise to restoration efforts. Although water quality is improving, it has not improved sufficiently to allow for a shift in the biotic communities towards species representative of higher quality condition. In general the communities are becoming more diverse, yet they are dominated by pollutant-tolerant species, which is reflected in the index values. This study reveals the complexity of restoration projects in highly degraded systems such as Cootes Paradise, and provides insight into the functionality of these indices as a useful management tool. The recovery of a system as complex, large and degraded as Cootes Paradise cannot be expected to be simple or inexpensive. Cootes Paradise offers a good opportunity to educate the public about unintended harmful actions caused by humans on natural systems, and serves as an important reminder that a degraded ecosystem can be difficult, if not impossible, to restore and may require management actions that are different than those appropriate for its original state.

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Table 1-1: Water quality parameters for Cootes Paradise from 1993 to 2008, used in the calculation of the Water Quality Index scores. Bolded p-values indicate a significant relationship between parameters and time. n/a = not available

Parameters	1993	1994	1996	1998	2000	2002	2008	R^2	p	Overall Trend
Turbidity (NTU)	63.4	63.0	55.7	33.0	37.8	28.0	35.9	0.6	**0.04**	↓
TSS (mg/L)	42.9	63.9	53.1	54.5	32.9	31.2	43.2	0.24	0.26	↓
ISS (mg/L)	27.2	43.5	39.1	31.1	15.5	17.6	24.0	0.34	0.17	↓
Chl *a* (ug/L)	18.4	87.8	24.6	92.1	71.4	22.1	29.0	0.05	0.65	↓
TP (ug/L)	158.7	241.7	200.0	269.5	159.3	189.0	141.9	0.19	0.33	↓
SRP (ug/L)	13.0	32.8	29.7	41.3	6.1	26.3	15.3	0.07	0.57	↓
TN (ug/L)	3599	4443	4402	4110	9992	5096	n/a	0.29	0.27	↑
TNN (ug/L)	1410	1104	485	1064	452	548	87	0.7	**0.02**	↓
TAN (ug/L)	182	237	440	268	745	559	146	0.01	0.85	↓
Conductivity (us/cm)	757	815	683	771	668	518	572	0.64	**0.03**	↓
Temperature (°C)	25.4	22.6	25.8	22.8	24.3	23.6	24.9	0.002	0.92	↑
pH	8.30	7.98	7.08	8.17	8.61	8.07	8.04	0.02	0.76	↑
WQI Score	-2.33	-2.20	-1.72	-2.09	-1.82	-1.56	-1.39	0.72	**0.02**	↑

Table 1-2: Mean zooplankton density (# individuals/L) at Cootes Paradise from 1994 to 2008, used in the calculation of the Wetland Zooplankton Index scores. Dash (-) indicates no individuals found. (U, T) values used to calculate the WZI are listed after each species' name. Note: Species without (U,T) values are not included in the WZI.

	1994	1996	1997	1998	2008
Copepoda					
Calanoid	0.6	2.9	-	0.2	1.0
Cyclopoid	44.2	55.4	34.3	161.0	83.8
Harpacticoid	-	-	-	-	0.3
Copepodid	31.2	61.7	92.4	238.4	10.3
Nauplii	359.6	515.2	199.0	362.5	79.3
Cladocera					
Alona sp. (4,2)	-	-	2.0	-	1.0
Bosmina sp. (3,2)	414.4	578.9	15.8	66.6	45.2
Bunops serricaudata (5,3)	-	-	-	-	0.2
Ceriodaphnia sp. (4,2)	2.2	4.2	6.6	27.9	20.3
Chydorus sp. (4,2)	12.3	6.4	40.6	67.7	25.3
Daphnia sp. (2,2)	1.3	2.2	-	0.6	20.0
Diaphanosoma birgei (1,2)	0.7	0.5	0.1	1.0	6.6
Diaphanosoma brachyurum (3,1)	-	-	-	-	0.2
Eubosmina sp. (3,2)	-	-	-	-	1.0
Hexarthra sp. (1,1)	-	-	1.3	-	-
Kurzia sp. (3,3)	-	0.2	4.2	-	-
Leydigia sp. (1,1)	0.2	3.4	0.1	-	-
Moina sp.(1,1)	51.5	15.0	0.1	28.7	2.1
Ophryoxus gracilis (5,3)	-	-	-	-	0.2
Pleoroxus sp. (4,2)	1.1	0.6	14.9	9.0	3.4
Polyphemus pediculus (5,3)	-	-	-	-	0.2
Scapholeberis sp. (4,2)	13.5	32.5	0.3	-	8.9
Sida crystallina (5,3)	-	-	-	-	3.8
Simocephalus sp. (5,3)	0.4	-	9.4	39.3	0.8
Rotifera					
Ascomorpha sp. (1,1)	45.1	180.4	-	-	-
Asplanchna sp. (2,1)	41.0	59.3	8.9	21.7	6.4
Brachionus sp. (2,1)	100.6	186.6	516.5	404.4	10.7

Conochilus sp.	-	-	1.1	-	-
Conochiloides sp.(4,2)	2.5	37.8	-	118.5	-
Euchlanis sp.(3,1)	0.3	-	5.1	12.2	0.2
Filinia sp. (1,1)	7.1	23.5	3.9	4.5	0.5
Keratella sp. (5,2)	13.0	45.8	1.9	13.4	0.5
Lecane sp. (5,2)	1.4	25.2	-	-	-
Lepadella sp. (4,2)	-	-	1.5	-	-
Monostyla sp. (5,2)	-	-	52.4	48.9	-
Mytilina sp. (5,3)	-	-	16.7	6.1	-
Notholca sp. (3,1)	-	-	1.6	-	0.4
Platyias sp. (4,2)	0.3	0.2	5.4	213.9	1.4
Ploesoma sp. (4,2)	-	-	1.4	-	-
Polyarthra sp. (3,1)	294.8	373.9	119.5	115.7	-
Pompholyx sp. (1,1)	8.7	34.6	-	-	-
Testudinella sp.(4,2)	0.5	-	-	-	-
Trichocerca sp. (4,2)	-	-	2.4	6.1	-

Table 1-3: Macrophyte species at Cootes Paradise from 1998 to 2008, used in the calculation of the Wetland Macrophyte Index scores. Presence indicated by "X". Asterisks indicate non-native species. (U,T) values used to calculate the WMI are listed after each species. Note: Species without (U,T) values are not included in the WMI.

	1993	1994	1996	1998	2002	2003	2006	2008	2009
Floating									
Lemna minor (1,1)	X				X	X	X		X
Nuphar advena (1,3)	X								
Nuphar variegate (2,1)	X	X		X					X
Nymphaea odorata (2,1)	X	X	X	X	X	X	X	X	X
Potamogetan natans (2,1)		X		X					
Submergent									
Ceretaphyllum demersum (1,1)	X		X	X	X	X		X	X
Chara sp.(3,2)					X		X		
Elodea canadensis (2,1)	X		X	X	X			X	X
*Myriophyllum spicatum** (1,1)			X		X	X		X	X
Najas flexilis (3,2)					X	X			
*Potamogetan crispus** (1,1)				X		X	X	X	X
Potamogeton foliosus (2,1)							X		
Potamogetan pusillus (2,1)									X
Potamogeton sp.(1,2)					X	X			
Stuckenia pectinata (1,1)	X	X	X	X	X	X		X	
Vallisneria americana (3,1)	X					X			
Emergent									
*Lythrum salicaria** (1,1)		X	X	X	X			X	
Phragmites sp.	X	X	X	X				X	
Polygonum amphibium (1,1)	X					X	X	X	X
Pontederia cordata (3,2)	X								
Sagitaria latifolia (2,1)	X				X		X		X
Schoenoplectus sp. (4,1)		X	X	X					
Schoenoplectus validus (4,1)	X				X		X		
Sparganium androcladum (4,3)									X
Sparganium eurycarpum (3,2)	X				X		X		
*Typha angustifolia** (1,1)	X	X	X						

Typha latifolia (3,2)	X	X	X	X	X	X	X	X
*Typha x glauca** (1,2)	X	X	X		X		X	X

Table 1-4: Absolute abundance of fish species at Cootes Paradise from 1993 to 2008, used in the calculation of the Wetland Fish Index scores. Dash (-) indicates no individuals found. Data from 1996 to 1998 correspond to boat electrofishing transects (#/100 m^2); data from 2001 to 2008 correspond to three sets of paired fyke nets. (U,T) values used to calculate the WFI follow each common name.

		1996	**1997**	**1998**	**2001**	**2002**	**2008**
Benthivore							
Bluntnose minnow (4,2)	*Pimephales notatus*	-	-	2	8	2	24
Brown bullhead (2,1)	*Ameiurus nebulosus*	43	7	50	2	254	17
Channel catfish (1,2)	*Ictalurus punctatus*	-	-	-	27	-	-
Common carp (1,1)	*Cyprinus carpio*	90	5	24	1	35	4
White sucker (3,2)	*Catostomus commersonii*	-	1	-	-	-	-
Carnivore							
Black crappie (3,2)	*Pomoxis nigromaculatus*	-	-	-	-	-	1
Bluegill sunfish (3,1)	*Lepomis macrochirus*	2	-	2	59	25	-
Brook silverside (4,2)	*Labidesthes sicculus*	1	-	-	-	-	-
Logperch (4,2)	*Percina caprodes*	-	-	6	1	-	-
Pumpkinseed (3,2)	*Lepomis gibbosus*	32	-	94	56	33	34
Smallmouth bass (4,2)	*Micropterus dolomieu*	-	-	-	-	1	-
Spotfin shiner (1,1)	*Cyprinella spiloptera*	-	-	-	6	-	-
Sunfish (3,2)	*Lepomis sp.*	-	-	-	106	-	2
White bass (1,1)	*Morone chrysops*	-	-	-	34	-	-
White perch (1,2)	*Morone americana*	7	3	2	-	4110	15

Herbivore							
Gizzard shad (1,2)	*Dorosoma cepedianum*	4	-	-	14	91	-
Omnivore							
Fathead minnow (2,1)	*Pimephales promelas*	-	-	2	5	-	12
Golden shiner (3,2)	*Notemigonus crysoleucas*	-	-	-	-	1	-
Mimic shiner (5,3)	*Notropis volucellus*	-	-	-	-	-	3
Spottail shiner (1,1)	*Notropis hudsonius*	13	2	2	8	14	-
Piscivore							
Largemouth bass (3,2)	*Micropterus salmoides*	-	-	4	-	1	-
Northern pike (4,2)	*Esox lucius*	-	-	-	-	-	2
White crappie (1,1)	*Poxomis annularis*	-	-	-	-	2	-
Yellow perch (3,2)	*Perca flavescens*	-	-	54	12	7	5
Planktivore							
Emerald shiner (3,2)	*Notropis atherinoides*	-	-	2	1	-	-
Alewife (1,2)	*Alosa pseudoharengus*	-	-	-	-	1	-

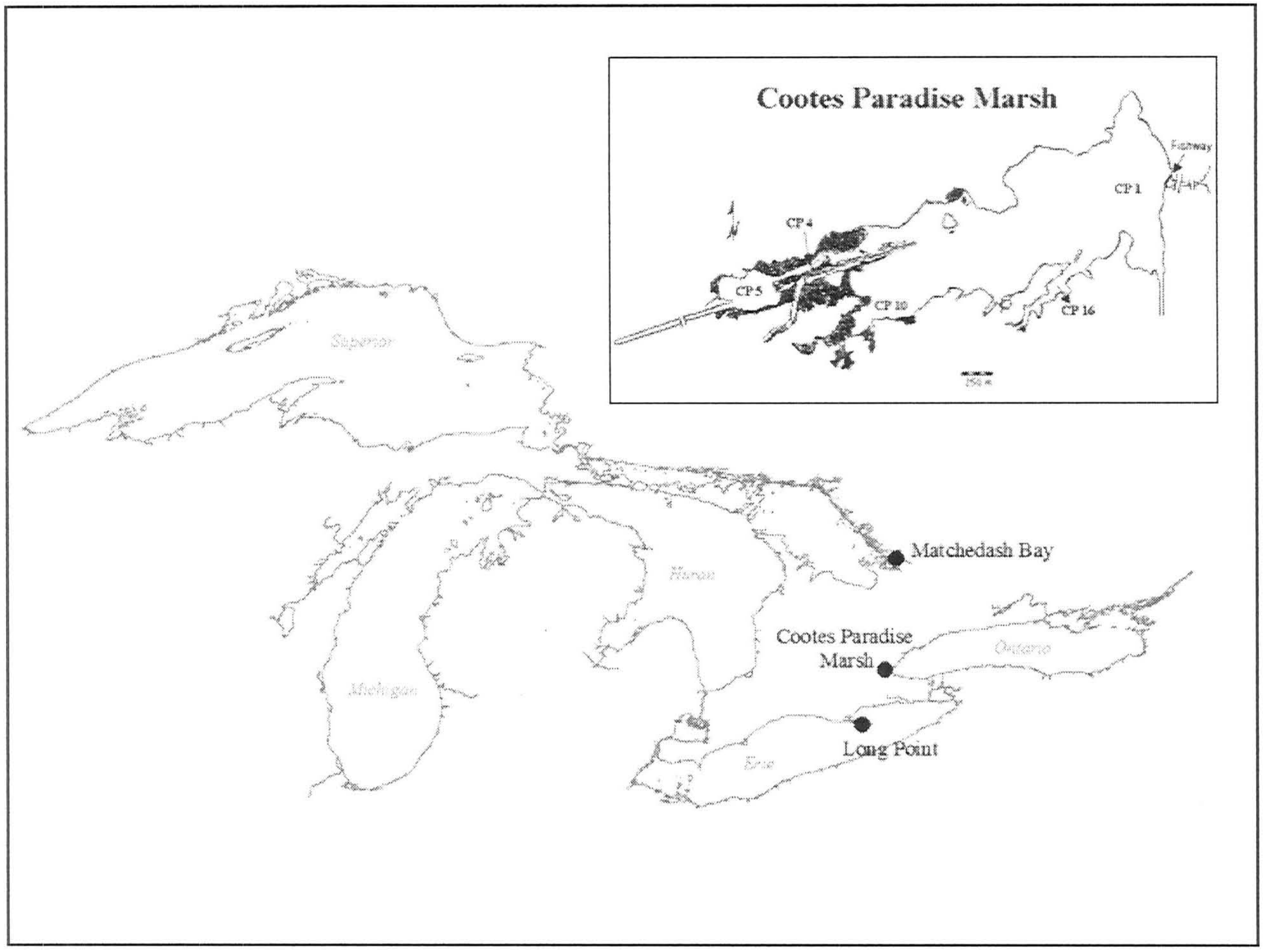

Figure 1-1: Location of study wetlands, Cootes Paradise, Matchedash Bay and Long Point. Inset shows locations of sampling sites in Cootes Paradise (Sites 1, 4, 5, 10 and 16).

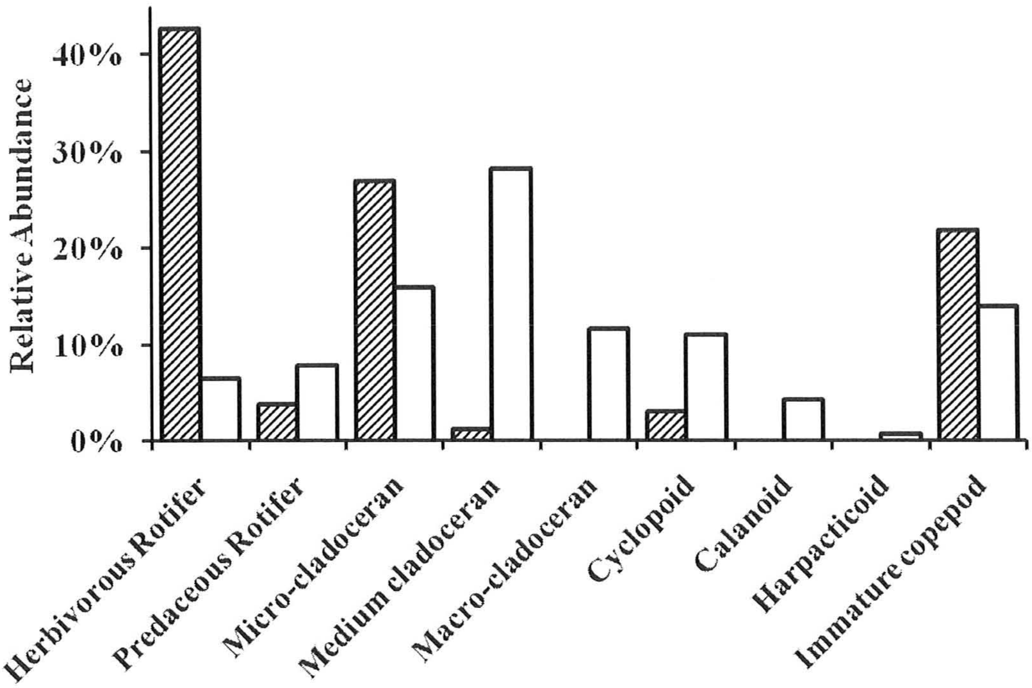

Figure 1-2: Relative abundance of functional feeding categories for the Cootes Paradise zooplankton community in 1996 (hatched bars) and 2008 (open bars).

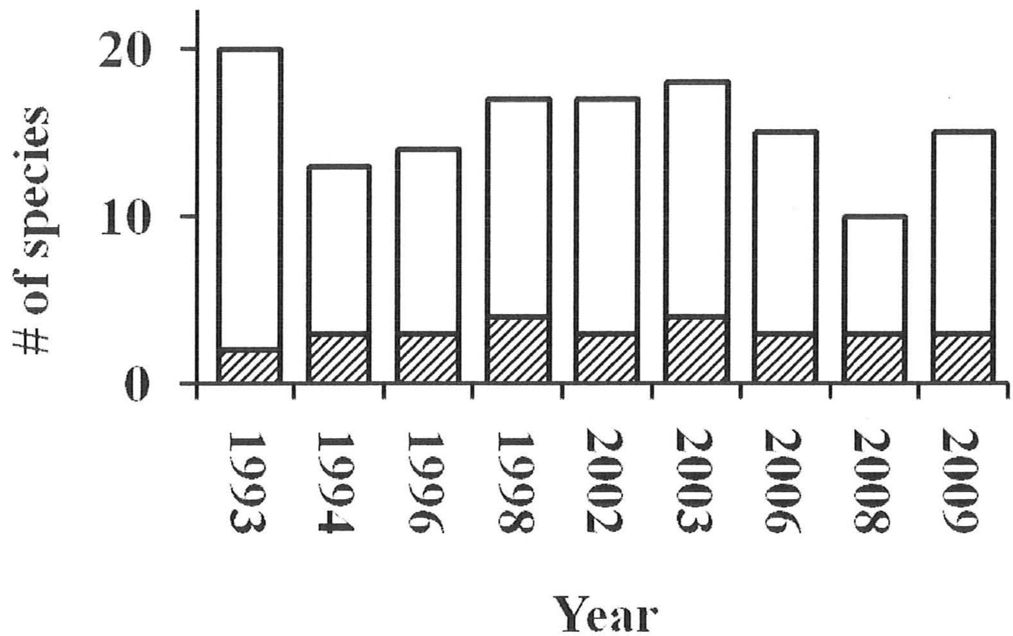

Figure 1-3: Number of native (open bars) and non-native macrophyte species (hatched bars) at Cootes Paradise.

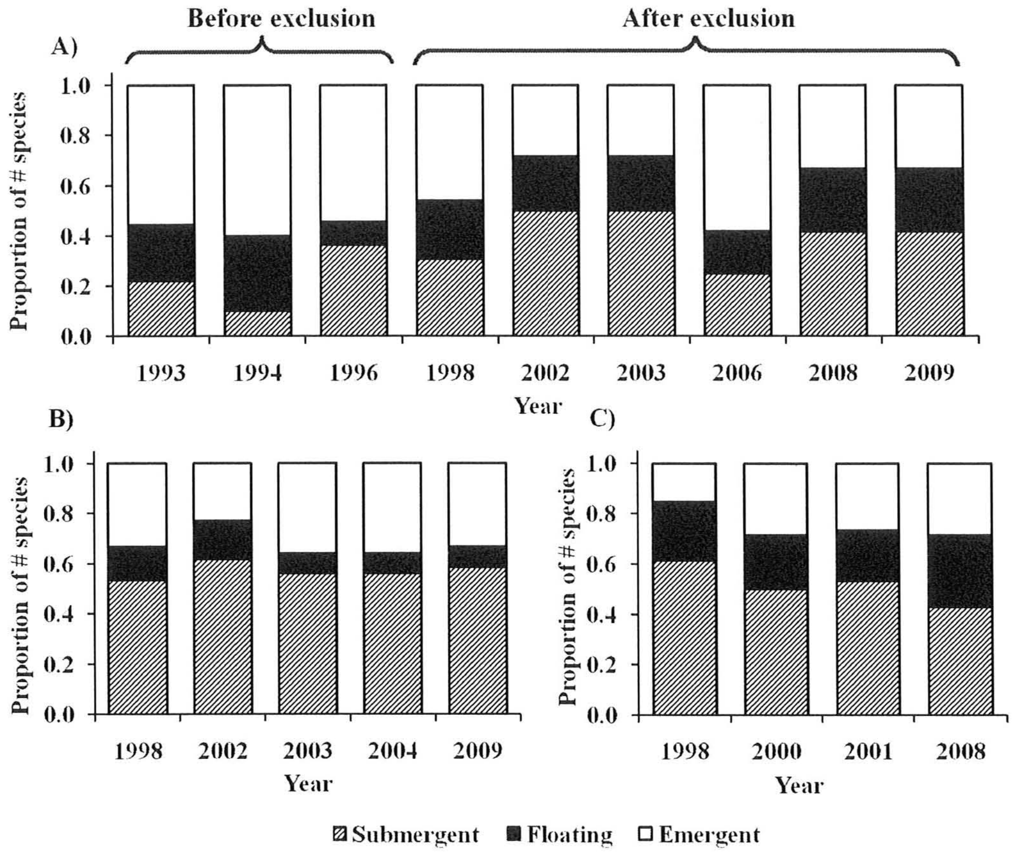

Figure 1-4: Proportion of macrophyte species' types in A) Cootes Paradise B) Matchedash Bay C) Long Point.

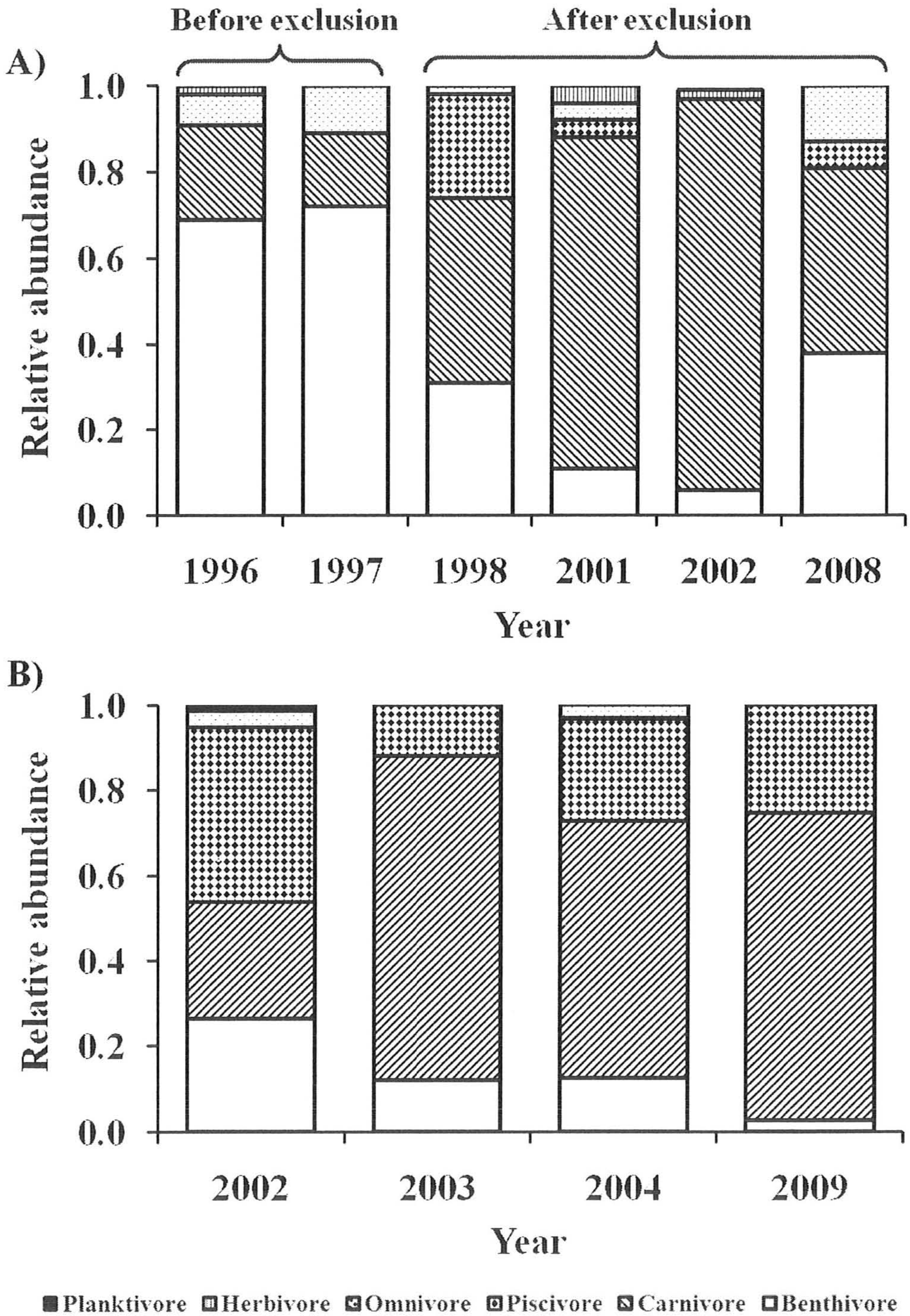

Figure 1-5: Relative abundance of fish by functional feeding niche for each year sampled at A) Cootes Paradise B) Matchedash Bay.

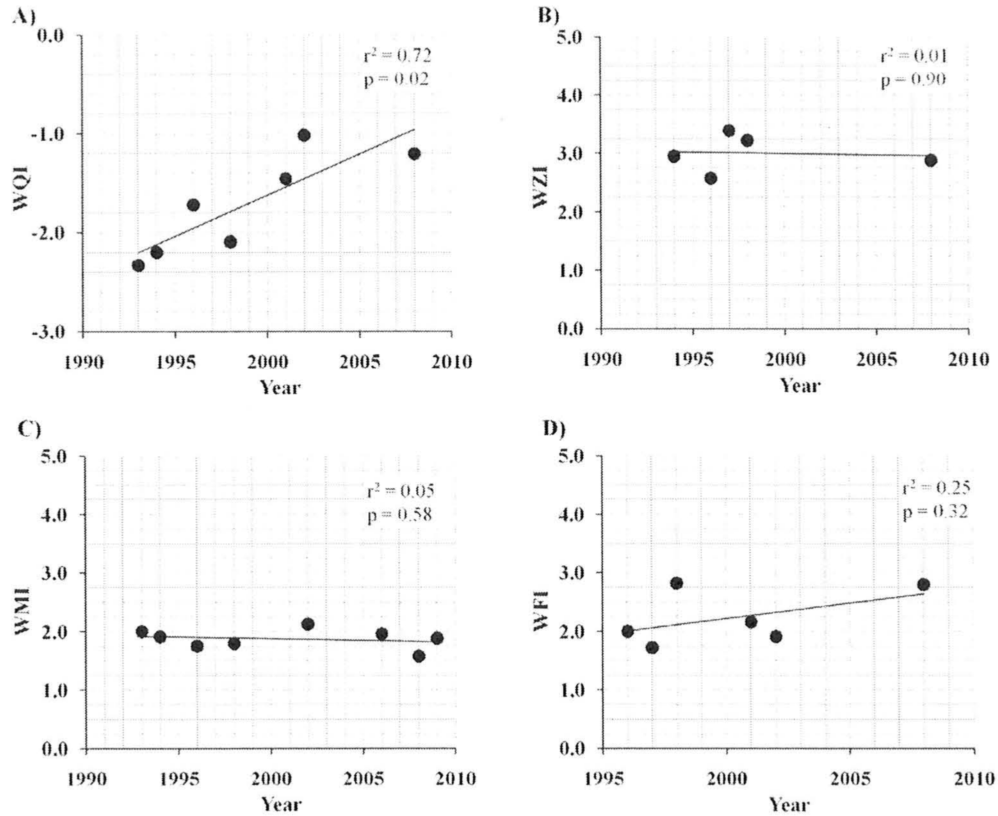

Figure 1-6: Index scores for Cootes Paradise over the study period A) Water Quality Index B) Wetland Zooplankton Index C) Wetland Macrophyte Index D) Wetland Fish Index.

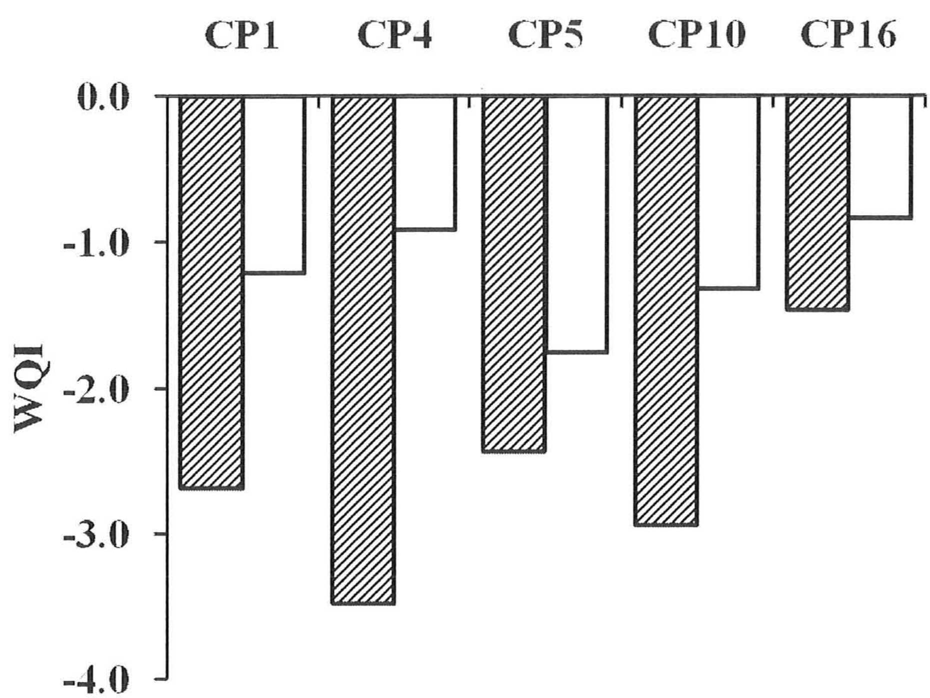

Figure 1-7: WQI scores calculated for water samples collected at five sites in Cootes Paradise (as shown in Figure 1-1 inset) during 1993 (hatched bars) and 2008 (open bars).

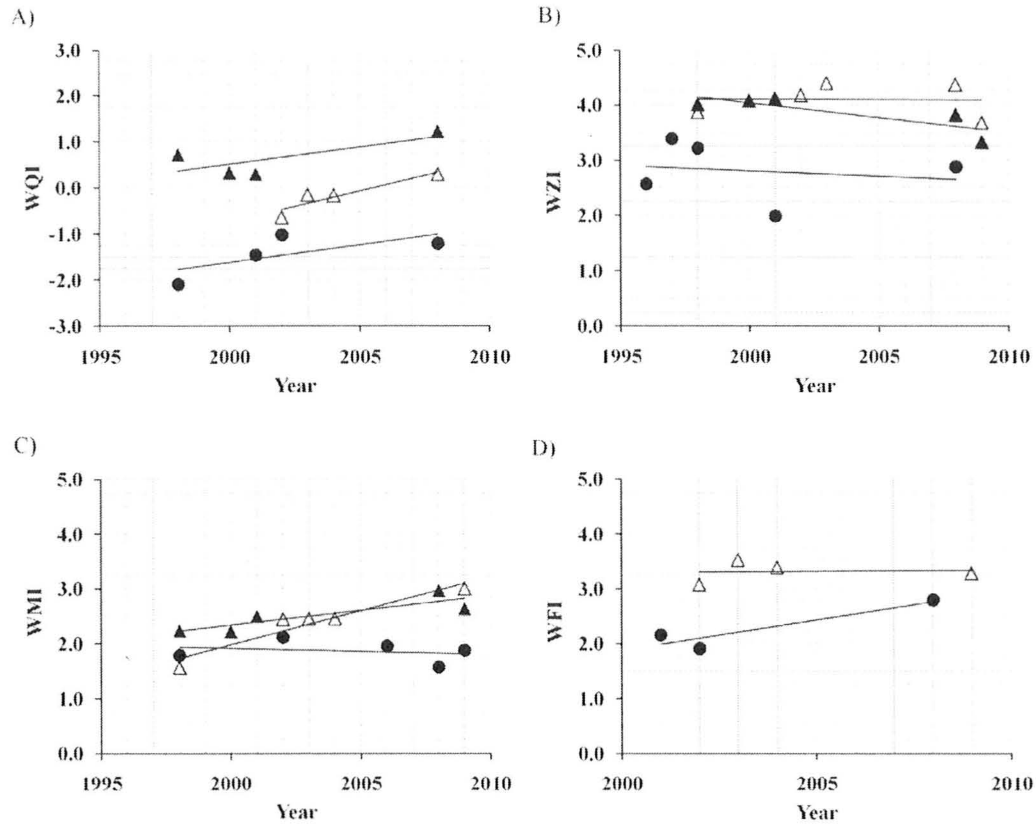

Figure 1-8: Index scores for Cootes Paradise (closed circle), Matchedash Bay (open triangle) and Long Point (closed triangle) over the study period A) Water Quality Index B) Wetland Zooplankton Index C) Wetland Macrophyte Index D) Wetland Fish Index.

CHAPTER 2:

Importance of physical disturbance and hydrologic connectivity in creating microhabitats and diversity in zooplankton assemblages at nearshore Long Point Bay, Lake Erie

Abstract

Long Point Bay is located within the UNESCO Long Point Biosphere Reserve (26,250 ha) and encompasses the largest wetland complex in the Great Lakes system. During an 11-day period in August 2008, we visited 102 sites along the nearshore (~60 km) and sampled for zooplankton, macrophytes, temperature, specific conductance, pH, dissolved oxygen, dissolved organic carbon, water clarity, total nitrogen, and depth. We evaluated the impacts of exposure using wind and fetch data to calculate a Relative Exposure Index (REI). Ordination techniques revealed a large variation in physical disturbance, water clarity, nutrient concentrations, water chemistry and aquatic vegetation that explained the distribution pattern of zooplankton at the 102 sites. Gradients of REI are strongly positively correlated with environmental variables, such as pH, dissolved oxygen, and temperature and highly negatively correlated with conductivity and dissolved organic carbon. Visual inspection of the ordination site scores revealed the 102 sites clustering into six main groups based on spatial location and degree of connectivity to Long Point Bay. Sheltered sites have much higher abundance of zooplankton whereas sites that have high REI scores are characterized by relatively low zooplankton abundance, with a high prevalence of *Polyarthra* sp. The results of this study highlight the impacts of exposure on the zooplankton community and the effects of connectivity to larger water bodies.

Introduction

Zooplankton live in a three-dimensional environment where they must forage for food, reproduce and escape predation, often within a very localized setting. In shallow areas along the lakeshore, these settings can be windswept, open water or quiescent with dense floating, emergent and submergent vegetation. Such habitats can be highly variable with respect to physical and chemical characteristics, and zooplankton that are distributed in these littoral habitats are largely governed by their tolerances and preferences for environmental variables such as dissolved oxygen (Stenson, 1983), temperature (Edmondson, 1965; Stenson, 1983), dissolved organic carbon (Strecker et al., 2008), and wind and wave action (Cardinale et al., 1998). Their distribution can also be influenced by the presence of aquatic vegetation. Research has shown that zooplankton biomass and diversity tend to be higher in vegetated environments (Pennak, 1966; Schriver et al., 1995), where cladocerans and copepods escape predation from fish (Duggan, 2001; Timms and Moss, 1984), sessile rotifers and cladocerans find substrate (Edmondson, 1944; Fairchild, 1981), and where many zooplankton (e.g. chydoridae) feed on epiphytic algae that grow on macrophytes (Fryer, 1968; Duggan, 2001).

Within the Laurentian Great Lakes basin, studies that examine factors governing the distribution of zooplankton have been conducted at two spatial scales. At the large regional scale, synoptic surveys have been conducted over hundreds of sites across the Great Lakes, and these have confirmed trends in zooplankton distributions that are associated with gradients in turbidity and nutrients, often related to human disturbance (e.g. Lougheed and Chow-Fraser, 2002; Patalas, 1972; Watson and Wilson, 1978). At the local scale, focused studies conducted at a single wetland have demonstrated that site-to-site variation in zooplankton abundances can be related to differences in the plant community and distance from point-source pollution (Krieger and Klarer, 1991; Lougheed and Chow-Fraser, 1998; Thomasen and Chow-Fraser, in press). No study has demonstrated the importance of physical turbulence (wind and wave action) in structuring the cladoceran and rotifer community, presumably because of the overriding influence of other factors. One reason for this may be related to the scale used in the previous studies. In this paper, we show how a strategic sampling program conducted at an appropriate scale can be used to evaluate the influence of physical disturbance and hydrologic connectivity on zooplankton distributions. We hypothesize that in the absence of human-induced disturbance, variation in physico-chemical characteristics induced by wind and wave exposure can be as important a structuring variable as nutrient and macrophyte density.

We conducted our study at Long Point Bay, a large embayment located in north central Lake Erie. The Long Point area (26,250 ha) has been designated as an UNESCO Biosphere Reserve due to its many habitat types (e.g. marsh, undisturbed sand dunes, grassy ridges) supporting high biodiversity of flora and fauna. Its sports fishery is considered the best in Lake Erie, although there have been declines and restrictions on some populations such as smallmouth bass

(Nelson and Wilcox, 1996). Recreational use of the marsh is primarily fishing, but also includes waterfowl hunting, nature-viewing, and water-based activities such as canoeing and swimming (Kreutzwiser, 1981). The bay and surrounding marsh provide important resources for migratory waterfowl (Leach, 1981; Nelson and Wilcox, 1996; Prince et al., 1992) because of the good water quality (Leach, 1981) and abundant aquatic vegetation (Herdendorf, 1992; Knapton and Petrie, 1999). The biotic community of this ecosystem has been examined extensively, including studies on fish, marsh birds and waterfowl (see www.longpointbiosphere.com for a list of projects), but data on the zooplankton community are rare and do not exist for the nearshore area. To better manage the fish and bird communities that fuel the economy of the local area, the Ontario Ministry of Natural Resources began a large-scale comprehensive survey of the entire food web in Long Point Bay, funded in part by the Canada-Ontario Agreement respecting the Great Lakes Basin Ecosystem.

Methods

The 102 sites sampled in this study are part of the Long Point Bay Asssessment, conducted by the Ontario Ministry of Natural Resources between 2007 and 2009. The sites are located throughout Long Point Bay extending from the southern shore (Bouck's Creek) to the northern shore (Turkey Point Marsh), and include 27 interior coastal wetland sites within Crown Marsh (Figure 2-1). Fifteen of the Crown Marsh sites have been hydrologically isolated from the bay, having been excavated and enclosed by berms several years ago. The other twelve sites are still hydrologically connected to Long Point Bay via boat channels that are maintained by dredging. All sites were sampled for water characteristics, zooplankton, and macrophyte species richness and composition between August 11- 21, 2008.

Sampling design

We used a Garmin Global Positioning System (GPS) hand-held unit (Garmin GPSmap76; accuracy of 10 m) to georeference all sites. Water temperature (TEMP), dissolved oxygen (DO), specific conductance (COND), and pH were measured with a hand-held YSI™ 600 QS multi-parameter monitoring unit (YSI, Yellow Springs, Ohio). We collected water samples (1-L capacity) in polyethylene bottles at 20-cm depth for analysis of total ammonia/ammonium nitrogen (TAN), biological oxygen demand (BOD-5) and total nitrite-nitrate nitrogen (TNN). Subsamples were poured into100-ml polypropylene bottles and preserved with 50% sulphuric acid for later analysis of total Kjeldahl nitrogen

(TKN). Total nitrogen (TN) was determined as the sum of TKN and TNN. All samples were immediately placed in coolers with ice and then transported on the same day to a walk-in cooler (4ºC). Within one week of collection, samples were transported on ice to E3 Laboratories Inc. (Niagara-on-the-Lake, ON) and analyzed. Since the DO and TEMP data were collected at different times over the 11-day sampling period, we screened the data to ensure that different measurements at each site were not confounded by differences in air temperature and the hour at which they had been sampled.

We assessed the aquatic macrophyte community within a 15-m^2 grid extending from the shoreline out and enclosing the water and zooplankton sampling station. All macrophytes within this grid were identified and ranked for abundance according to a coarse scale: dense (70-100% coverage); common (20-60% coverage) and sparse (1-15% coverage). Voucher samples were collected when samples could not be identified in the field. In plots with both emergent and submergent taxa, percent coverage was estimated separately above and below the water surface. Scientific nomenclature followed Crow and Hellquist (2000) and Gleason and Cronquist (1991).

We sampled for zooplankton at the same time and place of water sample collection. All samples were collected from mid-depth with a 5-L Schindler-Patalas trap, filtered through 63-µm Nitex mesh, backwashed into 60-mL bottles and immediately preserved in 4% sugar formalin. Organisms were identified, enumerated and measured with a dissection microscope at 40x-magnification. A light microscope at 200-400x magnification aided initial identification. When samples were dense, subsamples were taken and at least 100 individuals of dominant species were counted. The entire sample was scanned for rare and large organisms. Copepods were categorised as adult, copepodite or nauplii. Adult copepods were identified to order (cyclopoid, harpacticoid, calanoid). Cladocera and Rotifera were identified to genus or species. Rotifer identification was based on Stemberger (1979) and crustacean identification was based on Pennak (1989).

Quantifying wind and wave action

We refer to the effects of wind and wave action as exposure and have modified the Relative Exposure Index (REI), developed by Keddy (1982) in order to quantify these effects at each site. The REI is calculated using the following equation:

$$\mathrm{REI} = \sum_{i=1}^{12} (\mathrm{V}_i \times \mathrm{P}_i \times \mathrm{F}_i) \qquad (1)$$

where i is the ith compass heading (1 to 12), V is the average monthly wind speed (ms^{-1}), P is the percent frequency with which wind occurred from the ith direction, and F is effective fetch (m). Wind speed and direction were obtained from the Environment Canada weather station located in the town of Long Point. Keddy (1982) found that although the magnitude of the index changed according to the months from which wind data were used, the relative difference did not. Thus, we calculated the index based on the growing season (May – September) since this is the period of time that we are most interested in. We calculated fetch using high-resolution (30-cm) imagery from the Southwestern Ontario Orthophotography Project (SWOOP) collected during the leaf-off season of 2006 using ArcView 9.2.

Statistical methods

Before carrying out parametric techniques to explore relationships in the dataset, we used SAS JMP software (Version7.0.1, SAS Institute Inc., Cary, North Carolina, USA) to transform the data using either a least-squares method or log-transformation. For our first ordination technique, we conducted a Principal Components Analysis (PCA; JMP 7.0.1 software). A correlation matrix condensed least-squares transformed environmental variables (Table 2-1) into synthetic axes that best explained variation in the dataset (McCune and Grace, 2002). Only axes with an eigenvalue greater than one were retained for further analysis. We interpreted principal component (PC) axes by using Spearman correlation (JMP 7.0.1 software) to examine the strength of the relationships between the environmental variables and each retained PC axis.

Secondly, we used non-metric multidimensional scaling (NMS; PC-ORD, version 4.25, MjM software, Gleneden Beach, Oregon, USA) to analyze the patterns in the macrophyte community. NMS ranks the distances between sites to create synthetic axes based on the macrophyte community (McCune and Grace, 2002). We assessed the dimensionality of the solution by first performing a 6-dimensional analysis with Sørensen's distance measure and then examining the change in stress (a measure of the lack of fit) as a function of dimension. A 3-

dimensional solution was identified as being best so we ran multiple NMS analyses restrained to three dimensions with random starting configurations. The final stress values (range from 18.2 – 18.6) slightly varied among the analyses, and we chose the solution with the lowest stress. The final stress was still relatively high, indicating that the NMS was not able to extract any major gradients. We used Spearman correlations (JMP 7.0.1 software) between the respective axes and individual macrophyte species coverage to infer the strength of the relationships between plant coverage and the synthetic axes.

Canonical correlation (CANCOR; PASW Statistics 18, IBM software, Chicago, Illonois, USA) is the final ordination technique we applied to our dataset. This method maximizes the linear relationship between environmental data and zooplankton abundances by finding linear combinations of these variables that have the highest possible between-set correlations (Tabachnick and Fidell, 2007). In order to interpret the canonical variates, we examined the cross loadings of the environmental variables and the zooplankton species. Redundancy analysis (PASW 18) explained the amount of variance that the canonical variates of the environmental variables extracted from the zooplankton species, and vice versa. In discussing results of the CANCOR, we will refer to the dataset for species as SET_{SP} and that for environmental variables as SET_{ENV}.

In order to assess trends in zooplankton distribution we classified cladoceran and rotifer taxa based on their habitat preference and functional feeding group. Habitat preferences were grouped according to those that favoured

1) vegetation, 2) open- water, 3) no strong preference for either, and 4) benthos, based on the following studies: Duggan (2001), Duggan et al. (2001), Fairchild (1981), Fryer (1974), Paterson (1993), Pejler (1962), Pejler and Berzins (1994) and Pennak (1966). Feeding groups were either raptorial, planktonic, scraper or mechanical and based on the findings of Fairchild (1981), Fryer (1968, 1974), Obertegger et al. (2011), Paterson (1993), and Smith (2001). Macrothricidae were the only zooplankton in this study classified as benthic and mechanical feeders, however due to their low occurrence they were excluded from further analyses. Differences among microhabitat groupings were determined with one-way ANOVA and a post-hoc Tukey-Kramer test using JMP 7.0.1 software. We also used the procedure outlined in Lougheed and Chow-Fraser (1998) to estimate dry-weights (biomass) by applying appropriate length-weight regression equations obtained from the literature.

Results

Environmental variables

All of the physico-chemical variables we measured showed large variation among the 102 sites (Table 2-1). Currently, Long Point is predominantly an alkaline system, with only a few interior sites that are circumneutral (see Figure 2-2A). Oxygen levels ranged from anoxic to supersaturated, but most sites were well-oxygenated (mean for 102 sites was 8.6 mg/L; Figure 2-2B). Despite the order-of-magnitude variation in both TN and CHL values, Long Point is primarily oligotrophic with mean values of 0.78 mgL^{-1} and 2.9 μgL^{-1}, respectively (Table 2-1). Conductivity ranges widely from 240 – 567 μscm^{-1}, with sites further inland having highest values (Figure 2-2C). All sites were less than 2-m deep (Table 2-1) and the degree of exposure varied from completely protected to relatively exposed (REI of 0 – 2.4 x 10^7; Figure 2-2D).

A PCA of physico-chemical variables (listed in Table 2-1) yielded three axes with eigenvalues greater than one, together explaining 76.3% of the variation in the dataset (Table 2-2). PC1 explained 45.7% of the variation in the dataset, and showed strong positive correlations with REI, pH, DO and TEMP, and strong negative correlations with COND, TN, and DOC (Table 2-2). PC2 explained an additional 19.8% of the variation and was highly positively correlated with TSS, CHL, pH, DEPTH, and REI, and was negatively correlated with DOC and COND. PC3 explained an additional 10.8% of variation and was strongly positively correlated with DEPTH and negatively correlated with COND. PC1 represents a gradient from highly exposed, alkaline, well-oxygenated, warm water to high COND and high concentrations of TN and DOC. PC2 represents a gradient from deep sites with low water clarity to shallower sites with higher water clarity.

Of the 102 sites, only five did not have any vegetation; in the remaining 97 sites, we identified 39 taxa of aquatic macrophytes (see Figure 2-1; Table 2-3). Submergent taxa were the dominant growth form, occurring in 91% of all 102 sites. *Chara* spp. (stonewort) was the most common submergent taxa, and was detected at 74% of our sites, providing >20% cover in 51 sites. Other common submergent taxa present in our surveys included *Elodea canadensis*, (common waterweed), *Nitella* spp., *Potamogetan pectinatus* (sago pondweed), *Utricularis vulgaris* (common bladderwort), *Vallisneria americana* (wild celery) and the non-native species *Myriophyllum spicatum* (Eurasian water milfoil). They were detected at 23-34% of the sites and primarily provided sparse (1-15%) coverage. *Zizania aquatica* (southern wild rice) was the dominant emergent species, providing more than 20% coverage at 12 sites and sparse coverage at an additional 20 sites. *Schoenplectus acutus* (hardstem bulrush) and *Sagittaria rigida* (stiff arrowhead) were less common (17% and 10% occurrence, Table 2-3), providing only sparse coverage. The most common floating taxa were *Nymphaea odorata* (fragrant white water lily) and *Potamogeton natans* (floating pondweed) which occurred in 25% and 27% of sites, respectively (Table 2-3). Both species provided sparse coverage, except for 12 sites where white water lily covered at least 20% of the sample quadrat.

Data from the 97 quadrats containing vegetation were entered into an NMS. High scores on Axis 1 were correlated with high coverage of *U. vulgaris* and *Sparganium eurycarpum*, (large-fruited burreed) while low scores on Axis 1 were correlated with high coverage of *P. natans* and *Typha angustifolia* (narrow-leaved cattail) (Table 2-4). High scores on Axis 2 correlated with dense coverage of floating species (*N. odorata* and *Nuphar variegatum*) and *Myriophyllum verticallatum* (bracted water milfoil), whereas low scores were correlated with *V. americana*, *S. acutus*, and *M. spicatum* (Table 2-4). Axis 2 represents a transition from native to non-native milfoil species. The third axis separated plant species that were nutrient tolerant (e.g. *Hydrocharis morsus-ranae, Ceratophyllum demersum*) from those that were intolerant (e.g. *V. americana, Najas flexilis*).

Zooplankton

In total we identified 89 zooplankton taxa: 55 rotifers, 29 cladocerans and 3 copepods. Table 2-5 summarizes characteristics of the zooplankton detected in our surveys. The most common zooplankton were nauplii (mean density $64L^{-1}$) and *Lecane* sp. (mean density $3L^{-1}$), which were found at every site (Table 2-5). The cladoceran *Bosmina longirostris* was also very common, occurring at all but 15 sites with a mean density of $20L^{-1}$. Other common rotifers included *Polyarthra sp.*, *Euchlanis* sp. and *Filinia brachiata*, which were detected at 75-82% of all sites (Table 2-5). *Filina brachiata* had the highest mean and absolute density of any rotifer or cladoceran in this study (mean $77L^{-1}$, absolute $1495L^{-1}$). Common cladocerans included *Ceriodaphnia* sp., *Diaphanosoma brachyurum*, and members of the chydoridae family (*Acroperus harpae* and *Chydorus* sp.). Cyclopoid copepods (78% occurrence) were more common than either calanoid (42%) or harpacticoid (32%) copepods (Table 2-5).

We used a Canonical Correlation Analysis (CANCOR) to determine the best linear combinations of the ten physico-chemical variables (listed in Table 2-1) and three macrophyte variables (total macrophyte richness, number of submergent species and number of floating species) that describes variation in zooplankton abundances across the 102 sites (listed in Table 2-5). The CANCOR yielded five axes that were significantly different from zero. The correlations among the first five variates ranged from 0.85 to 0.98, with 71-95% of overlapping variance between the variates (Table 2-6). The first five canonical variates extracted 58% of the variance from the environmental variables and 28% from the species. Along the first five variates, 24% variance in the species dataset (SET_{SP}) is predicted by the variance in the environmental dataset (SET_{ENV}). The SET_{ENV} extracted two to three times more variance than the SET_{SP} along the first two variates, indicating that it explains the SET_{SP} best. The first two variates explained the largest proportion of redundancy for both the environmental variables (0.503, 0.160 Table 2-6) and the species (0.331, 0.161, Table 2-6). Despite the large value of the third canonical correlation (0.905), the third canonical variates extracted only a small amount of variance (4% environmental and species, Table 2-6). The remaining axes explained very little of the remaining variation in the datasets.

To interpret the canonical variates, we examined the canonical loadings of the environmental variables and the species abundances (Figure 2-3A). We only display loadings greater than 0.25 in order to reduce the background noise. The macrophyte-community variables were associated with much lower loadings than the physico-chemical variables. The loadings contributing to water clarity (TSS and CHL) and number of floating species (FL) were closely correlated with each other and were only weakly correlated with the other environmental variables. Physical variables (REI, pH, TEMP and DO) were strongly positively correlated with each other and negatively correlated with water chemistry (TN, DOC and COND). Axis 1 represents a gradient from exposed well-oxygenated alkaline water to high floating species richness and high concentrations of TN and DOC. Axis 2 represents a gradient from high COND to lower water clarity (high TSS). Warmer water (REI) is correlated with high scores on axis 1 and low scores on axis 2 while high CHL is correlated with low scores on both axes 1 and 2.

Overall, most zooplankton loadings were found in the third quadrant of the biplot and were thus correlated with CHL (Figure 2-3A). The rotifers *Asplachna* sp. (AP), *Lecane* sp. (LE), *Euchlanis* sp. (EC), cladocerans *Bosmina longirostris* (BOLO) and *Chydorus* sp. (CH), and copepods (calanoid - CA, cyclopoid - CY, copepodid - CP, nauplii - NA) had higher abundances in locations characterized by higher productivity (high TSS and CHL) and more floating vegetation species. The rotifers *Monostyla* sp. (MO), *Platyias* sp. (PL) and *Collotheca* sp. (CO), and the cladoceran *Ceriodaphnia* sp. (CE) were found in abundance at sites with high concentrations of DOC and TN, many floating species, and low exposure (REI). *Polyarthra* sp. (PY) is the only species most abundant in the warm exposed alkaline sites. The rotifers *Ploesoma* sp. (PO) and *Trichotria* sp. (TT), and chydoridae *Alonella* sp.(AO) were correlated with higher concentrations of COND and higher water clarity (low TSS).

Characteristics of microhabitat groupings

We also produced biplots of site scores for all three types of ordination (CANCOR: Figure 2-3B, PCA: Figure 2-4A, NMS: Figure 2-4B) which revealed that sites with similar scores are located in the same geographic areas (see Figure 2-1 for microhabitat locations). An exception to this grouping is the interior sites of Crown Marsh. The fifteen hydrologically isolated sites (PDN) have features unique from the twelve nearby hydrologically connected sites (PD), as indicated by the distinctive clustering in the ordination biplots (Figure 2-3B, 2-4A). Using the gradients explained by the ordination techniques (Table 2-2, 2-4, Figure 2-3A) and the location of the site scores in the ordination diagrams (Figure 2-3A, 2-4) we were able to discern the characteristics of the microhabitat groupings.

The interior sites in Crown Marsh (PDN and PD) tended to be very sheltered from wind and wave exposure, with more stagnant water that was circumneutral pH and higher in COND and DOC. These conditions promoted growth of dense vegetation that tended to shade out sunlight, keeping the water cooler and creating fewer opportunities for re-oxygenation. This explains why DO levels were also lower in these ponds, with some of the PDN sites approaching anoxic levels. Sites in microhabitats to the west (WS) and north (TP) were more exposed and open to the influence of Long Point Bay. With less vegetation cover, they tended to be warmer and better oxygenated; the greater mixing with bay water meant that these sites had lower COND and DOC, and higher pH. Turkey Point (TP) was one of the most exposed sites, and water there was associated with the lowest nutrients (DOC and TN).

Even though the NMS indicated no obvious gradients across sites with respect to the aquatic plant community, visual inspection of the site scores revealed some consistent trends across microhabitat groupings (Figure 2-4B). Sites in Turkey Point (TP) were the only ones that had high coverage of *T. angustifolia* and *P. natans*, whereas those in Crown Marsh (PD, PDN), Bouck's Creek (CC), and along the western shore (WS) were associated with high coverage of *S. eurycarpum*, *U. vulgaris* and *H. morsus-ranae*. Floating lilies *N. odorata* and *N. variegatum*, which are commonly found in sheltered environments, had high coverage in inland sites of Bouck's Creek (CC) and the disconnected ponds of Crown Marsh (PDN). By contrast, sites in the "SS" grouping along the southern shoreline did not have a unique plant community.

Zooplankton biomass found in the hydrologially disconnected sites of Crown Marsh (PDN) was up to several orders of magnitude higher than those found in other sites (Table 2-7) and was comprised mostly of species for which preference of either vegetation or open-water has not been detected (see Methods for description of classification). Typical species included *Bosmina longirostris* and *Ceriodaphnia* sp., which also comprised a large component of the cladoceran community in the rest of Long Point. Biomass of planktonic feeders was also highest at PDN (Table 2-7), and was largely driven by high occurrence of the rotifer, *Filinia brachiata.* Scraper biomass was lowest at sites along the southern shore (SS) and in Bouck's Creek (CC) and highest at the Crown Marsh sites hydrologically connected to Long Point Bay (PD) (Table 2-7).

The outliers of the ordination biplots identify sites with extreme values of the environmental variables and zooplankton communities. The sites circled on the PCA biplot (Figure 2-4A) labelled as PiP have the highest CHL of any sites sampled (mean CHL = $24\mu gL^{-1}$). The other set of sites circled and labelled as BC are located at the outfall of Big Creek, one of the major tributaries emptying into Long Point Bay. They have the highest COND (mean COND = 565 μscm^{-1}) and TN (mean TN = 3.1 mgL^{-1}) of any sites sampled. BC are also outliers on the NMS biplot (Figure 2-4B) due to the presence of *S. eurycarpum,* relatively lower species richness, and lack of submergent vegetation. On the CANCOR biplot, PDN are clearly distinct from the other sites (Figure 2-3B), due to the extremely high abundance of zooplankton. ZZP (circled on Figure 2-3B) was distinguished from the PD grouping due to the comparatively higher abundance of *Ploesoma* sp. and *Alonella* sp. (Figure 2-3B). The sites near Port Rowan on the western shore (labelled PR) have high TSS (mean 28 mgL^{-1}) and a high prevalence of *Asplanchna* sp. and *Macrochaetus* sp.

Discussion

We hypothesized that variation in physico-chemical characteristics induced by wind and wave exposure can be as important a structuring variable for the zooplankton community as are nutrient and macrophyte density. The canonical loadings of the macrophyte variables in the CANCOR were much lower than all of the physico-chemical variables except for depth (Figure 2-3A), indicating that the environmental variables were better than aquatic vegetation for describing variation in the data set. We interpret the high correlation between exposure (REI) and many of the environmental variables as evidence that site-to-site variation in water chemistry is largely driven by wind and wave action. In addition, the ordination diagrams (Figure 2-3B and 2-4) revealed that sites within the six microhabitat groups were located in similar geographic locations around the bay, and were likely similarly affected by wind and wave action

In general, the highly exposed sites (large REI) were well-oxygenated, had lower COND, DOC, and higher pH. By contrast, sheltered sites within Crown Marsh (small REI) that had limited mixing with bay water had poorly-oxygenated water, higher COND, DOC and circumneutral pH. Additionally, water temperature seemed to be related to exposure due to of the persistence of dense vegetation in the sheltered sites that provided more shade and cooler temperatures. The 15 sites in Crown Marsh that had no connectivity to Inner Bay (PDN in Figure 2-1) were associated with the most extreme conditions relative to the other sites and were the most unique. Although not as distinctive as the variation in physical and chemical characteristics, the plant communities in the six microhabitats also showed some spatial trends with respect to the distribution of the 39 macrophyte taxa. Sites in Turkey Point (TP) typically had high coverage of *T. angustifolia* and *P. natans*, and sheltered sites in interior Crown Marsh (PD, PDN) and Bouck's Creek (CC) had higher coverage of floating lilies, *N. odorata* and *N. variegatum*.

In this system highly exposed sites have characteristics similar to the surrounding bay water whereas less exposed sites are more heavily influenced by the land. Brant and Herdendorf (1972) made similar observations when studying the intrusion of Lake Erie water into drowned river mouths, noticing that highly conductive river water was diluted by the lake water. Wind action also tended to keep the water well oxygenated, consistent with the findings of Brodersen (1995). Exposure causes a more turbulent environment that prevents the development of dense vegetation. By contrast, the plant community can become very dense in sheltered sites and the shade results in much cooler conditions such as that in the sites of Crown Marsh. We suspect that higher concentrations of CHL and TN at these sites are related to the lack of dilution from bay water but further investigations are required to verify this. Stations along the Big Creek outfall had higher COND (mean of 565 μs/cm) and higher concentrations of TN (mean of 3.1 mgL^{-1}), likely due to watershed influence since Big Creek drains primarily agricultural land with many roads.

The CANCOR indicated several species that were highly correlated with exposure. *Polyarthra* sp. was the only taxon whose abundance was positively correlated with REI (Figure 2-3A), with higher abundances at exposed sites such as those in Turkey Point and the western shore (Figure 2-5A). Smith (2001) observed that this rotifer is mostly found in deep open-water areas, although Pennak (1966) observed no strong preference for open-water when compared with vegetation. Duggan et al. (2001) can explain this disparity in the literature by their findings that when *Polyarthra* are found among macrophyte beds, they seem to tolerate plant species with small narrow leaves that allow them to swim among the foliage and maintain their planktonic habits. Species that were highly negatively correlated with REI included *Ceriodaphnia* sp. and the rotifers *Monostyla* sp. and *Platyias* sp. (Figure 2-3A). These species are more commonly associated with macrophytes in the littoral zone (Pennak, 1966; Fairchild, 1981), and this is consistent with our finding that they were most abundant in the sheltered sites of Crown Marsh with high vegetation coverage (Figure 2-5B, 2-5C and 2-5D). It is interesting to note that the most exposed site of Bouck's Creek (Figure 2-2D) was dominated by *Polyarthra* and as the sites moved further inland there was an increase in *Ceriodaphnia* sp, *Monostyla* sp. and *Platyias* sp. (Figure 2-5).

The zooplankton community in the nearshore of Long Point Bay appears to be driven chiefly by physical conditions at the site level. In addition to exposure, hydrological connectivity to the bay is an important feature impacting the zooplankton community. The most striking feature is the high biomass of zooplankton at the sites that were no longer connected to Inner Long Point Bay (i.e. PDN - Table 2-7). There are a number of explanations for this observation, such as the higher food availability (highest CHL at these sites) that may be supporting a higher zooplankton biomass. Another explanation could be the absence of predatory fish, since fish predation has profound impacts on the distribution of zooplankton (Dodson, 1974; Luecke and Litt, 1987; Lynch, 1979). These sites are likely uninhabitable by fish because of the low oxygen concentrations and the hydrologic isolation. They also have high DOC and plant cover which suggests that if predators are present, zooplankton have many opportunities to evade capture (Strecker et al., 2008; Timms and Moss, 1984). Further investigation is required to determine the exact reason for the extremely high zooplankton biomass.

The observation that exposure and connectivity have a large influence on the zooplankton community is an important consideration when predicting the effects of changing water levels and climate change on this system. In the first consideration, water level fluctuations will affect hydrologic connectivity to the bay. We can predict that if areas become hydrologically disconnected, they will have lower oxygen levels and higher concentrations of DOC, TN, CHL and COND, as well as higher zooplankton biomass. If water levels rise so that connectivity is regained, then such differences may be eradicated. The second consideration is the impact of predicted increase in severity and frequency of storm events due to climate change (Bates et al., 2008), which has the potential to magnify the impacts of exposure as well.

Abundance of zooplankton has been directly linked to the foraging success of larval fish (Bremigan and Stein, 1994) and the bay provides important spawning and nursery habitat for both local and lake-wide populations (MacGregor and Witzel, 1987 as cited in Nelson and Wilcox, 1996). The highest zooplankton biomass in nearshore Long Point was found in the ponds of Crown Marsh (PDN, Table 2-7). However, these sites also have oxygen levels that approach anoxic conditions and they are hydrologically disconnected from the bay. Therefore, sites in Crown Marsh that have adequate oxygen, hydrologic connectivity, and high zooplankton biomass are predicted to offer the best nursery habitat for larval fish (i.e. PD, Figure 2-1). By determining which factors influence the zooplankton community and how resolution of scale alters trends we will be able to predict the prime nursery habitat for larval fish. This information will help managers understand the influence of environmental variation on lower trophic levels, and thus make informed management decisions when considering spawning and nursery habitat protection and management.

The lower trophic levels of nearshore Long Point Bay have never been examined before and this study provides a starting point for future research. The data collected for this study cover a brief window of time (11 days in late August) and establish a basic description of the zooplankton community, physico-chemical environment, and aquatic vegetation. The scale of this study allowed us to examine the effects of physical disturbance and understand how it shapes the water chemistry and zooplankton assemblage in the system. Further investigations into temporal trends of the zooplankton community are necessary to fully understand the dynamics of the system. It will also be beneficial to incorporate studies on the habitat and other food web components of nearshore Long Point, such as fish distribution. In summary, Long Point is one of the largest remaining wild areas in southern Ontario and there is an urgent need to conduct research at the appropriate scale to ensure its protection and conservation for future generations.

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Table 2-1: Description of the environmental variables at 102 sites located along the shoreline of Long Point Bay sampled during August 2008.

Environmental Variable	Abbreviation	Mean ± SE	Range
Temperature (°c)	TEMP	22.72 ± 0.24	17.42 - 26.92
Conductivity (µs/cm)	COND	318.38 ± 7.03	240 - 567
pH	pH	8.22 ± 0.06	7.09 - 9.65
Dissolved Oxygen (mg/L)	DO	8.61 ± 0.34	0.22 - 16.20
Dissolved Organic Carbon (mg/L)	DOC	7.17 ± 0.30	2.9 -15.5
Total Suspended Solids (mg/L)	TSS	7.65 ± 1.23	0-101
Total Nitrogen (µg/L)	TN	783.17 ± 49.81	300 - 3190
Chlorophyll a (µg/L)	CHL	2.93 ± 0.40	0.77 - 24.09
Depth (m)	DEPTH	0.72 ± 0.02	0.3 - 1.9
Relative Exposure Index	REI	$5.9 \times 10^6 \pm 6.5 \times 10^5$	$0 - 2.4 \times 10^7$

Table 2-2: Spearman correlations with the first three principal components (PC) axes ($n = 102$) with $p < 0.05$

Axis	Variance explained (%)	Variable	ρ	p-value
PC1	45.7	REI	0.85	<0.001
		pH	0.84	<0.001
		COND	-0.76	<0.001
		TN	-0.74	<0.001
		DOC	-0.68	<0.001
		DO	0.67	<0.001
		TEMP	0.67	<0.001
PC2	19.8	TSS	0.82	<0.001
		CHL	0.73	<0.001
		DOC	-0.62	<0.001
		pH	0.45	<0.001
		DEPTH	0.37	<0.001
		REI	0.36	<0.001
		COND	-0.34	<0.001
PC3	10.8	DEPTH	0.88	<0.001
		COND	-0.19	0.040

Table 2-3: Macrophyte species detected at 102 sites located along the shoreline of Long Point Bay sampled during August 2008. Asterisk indicates non-native species.

Codes	Scientific Name	Common Name	% occurrence
Floating			
HYMO	*Hydrocharis morsus-ranae**	Frogbit	9
NELU	*Nelumbo lutea*	Yellow water lotus	2
NUVA	*Nuphar variegatum*	Yellow pond lily	9
NYOD	*Nymphaea odorata*	Fragrant white water lily	25
PONA	*Potamogetan natans*	Floating pondweed	27
Emergent			
ELSM	*Eleocharis smallii*	Marsh spikerush	2
JUSP	*Juncus sp.*	Rush	1
PHRG	*Phragmites australis* subsp. *americanus*	Common reed	1
POCO	*Pontederia cordata*	Pickerelweed	1
SCAC	*Schoenplectus acutus*	Hardstem bulrush	17
SCCY	*Schoenplectu cyperinus*	Woolgrass	2
SCPU	*Schoenplectu pungens*	Common three-square	5
SCTA	*Schoenplectu tabernaemontani*	Soft-stem bulrush	2
SGLA	*Sagittaria latifolia*	Broad-leaved arrrowhead	2
SGRI	*Sagittaria rigida*	Stiff arrowhead	10
SPEU	*Sparganium eurycarpum*	Large-fruited burreed	6
TYAN	*Typha angustifolia**	Narrow-leaved cattail	7
TYLA	*Typha latifolia*	Common cattail	1
ZIAQ	*Zizania aquatica*	Southern wild rice	31
Submergent			
CAVE	*Callitriche verna*	Common water-starwort	8
CEDE	*Certaphyllum demersum*	Coontail	10
CHSP	*Chara spp.*	Stonewort	74
ELCA	*Elodea canadensis*	Common waterweed	24
MEBE	*Megalodonta beckii*	Water marigold	5
MYEX	*Myriophyllym exalbescens*	Northern water milfoil	3
MYSC	*Myriophyllum spicatum**	Eurasian water milfoil	23
MYSP	*Myriophyllum sp.*	Milfoil	5
MYVE	*Myriophyllum verticillatum*	Bracted water milfoil	14
NAFL	*Najas flexilis*	Slender naiad	6
NISP	*Nitella spp.*	Nitella	34
POAM	*Potamogetan amplifolius*	Bigleaf pondweed	3
POEP	*Potamogetan epihydrous*	Leafy pondweed	1
POGR	*Potamogetan gramineus*	Variable pondweed	3
POPE	*Potamogetan pectinatus*	Sago pondweed	24
POZO	*Potamogetan zosteriformis*	Flat-stemmed pondweed	2
UTPU	*Utricularia pusilla*	Tiny bladderwort	1
UTVU	*Utricularia vulgaris*	Common bladderwort	23
VAAM	*Vallisneria americana*	Wild celery	33

Table 2-4: Spearman correlations of % coverage of aquatic plant taxa with the three axes of the non-metric multidimensional scaling (n = 97) with p < 0.05. See Table 2-3 for explanation of plant codes.

Axis	Variable	ρ	p-value
1	UTVU	0.38	<0.001
	SPEU	0.37	<0.001
	PONA	-0.34	0.001
	TYAN	-0.30	0.003
	VAAM	-0.28	0.005
	HYMO	0.28	0.006
	NAFL	0.27	0.008
	ELCA	0.25	0.010
	CEDE	0.21	0.040
	SCCY	0.21	0.040
	SGLA	0.21	0.040
	SCPU	-0.20	0.040
2			
	VAAM	-0.62	<0.001
	SCAC	-0.56	<0.001
	NYOD	0.50	<0.001
	MYSC	-0.47	<0.001
	MYVE	0.40	<0.001
	NUVA	0.34	0.001
	UTVU	0.32	0.001
	ZIAQ	-0.30	0.003
	SGRI	0.30	0.003
	NISP	0.27	0.008
	CEDE	0.25	0.020
	SCPU	0.24	0.020
	CHSP	-0.24	0.020
	CAVE	-0.24	0.020
3	CHSP	0.64	<0.001
	NYOD	-0.59	<0.001
	ELCA	-0.49	<0.001
	CEDE	-0.48	<0.001
	MYVE	-0.41	<0.001
	HYMO	-0.35	<0.001
	POPE	-0.31	0.002
	ZIAQ	0.28	0.005
	NAFL	0.26	0.009
	NUVA	-0.25	0.014
	PONA	-0.24	0.017
	SCCY	0.24	0.019
	SGLA	0.24	0.019
	POZO	-0.23	0.022

Table 2-5: Common zooplankton species detected at 102 sites located along the shoreline of Long Point Bay sampled during August 2008. Species that occurred at less than 5% of sites are not listed.

Code	Species	Habitat Preference	Feeding Classification	% occurrence	Mean Density (#/L)
Cladoceran					
ACHA	*Acroperus harpae*	Vegetation	Scraper	59	5.9
AL	*Alona* sp.	Vegetation	Scraper	27	2.6
AO	*Alonella* sp.	Vegetation	Scraper	5	0.9
BOLO	*Bosmina longirostris*	Vegetation/Open-water	Planktonic	85	19.6
BUSE	*Bunops serricaudata*	Benthic	Mechanical	13	10.9
CE	*Ceriodaphnia* sp.	Vegetation/Open-water	Planktonic	78	10.9
CH	*Chydorus* sp.	Vegetation	Scraper	51	4.5
CM	*Camptocercus* sp.	Vegetation	Scraper	6	0.5
DIBI	*Diaphanosoma birgei*	Vegetation/Open-water	Planktonic	4	2.6
DIBR	*Diaphanosoma brachyurum*	Open	Planktonic	47	2.2
EHRO	*Echinisca rosea*	Benthic	Mechanical	10	4.3
ER	*Eurycercus* sp	Vegetation	Scraper	7	0.5
EU	*Eubosmina* sp.	Vegetation/Open-water	Planktonic	6	0.7
GR	*Graptoleberis* sp.	Vegetation	Scraper	6	0.7
OPGR	*Ophryoxus gracilis*	Vegetation	Scraper	5	0.5
PE	*Pleuroxus* sp.	Vegetation	Scraper	19	8.3
SA	*Scapholeberis* sp.	Vegetation/Open-water	Planktonic	6	5.7
SICR	*Sida crystallina*	Vegetation	Planktonic	7	1.5
SM	*Simocephalus* sp.	Vegetation	Planktonic	13	8.7

Rotifer					
AP	*Asplachna* sp.	Vegetation/Open-water	Raptorial	19	1.4
AS	*Ascomorpha* sp.	Vegetation	Raptorial	32	1.9
CO	*Collotheca* sp.	Vegetation	Raptorial	22	7.9
EC	*Euchlanis* sp.	Vegetation	Planktonic	75	8.3
FIBR	*Filinia brachiata*	Open-water	Planktonic	75	77.3
KELO	*Kellicotia longispina*	Open-water	Planktonic	12	0.2
KR	*Keratella* sp.	Vegetation/Open-water	Planktonic	69	13.9
LE	*Lecane* sp.	Vegetation	Planktonic	100	2.6
MA	*Macrochaetus* sp.	Vegetation/Open-water	Planktonic	26	1.6
MO	*Monostyla*	Vegetation	Planktonic	65	2.2
MY	*Mylitina* sp.	Vegetation	Planktonic	11	1.2
NO	*Notommata* sp.	Vegetation	Raptorial	8	0.5
PLPA	*Platyias patulus*	Vegetation	Planktonic	30	5.5
PO	*Ploesoma* sp.	Vegetation/Open-water	Raptorial	12	1.0
PY	*Polyarthra* sp.	Vegetation/Open-water	Raptorial	82	16.2
SC	*Scaridium* sp.	Vegetation	Raptorial	5	1.4
TR	*Trichoceca* sp.	Vegetation	Raptorial	58	1.1
TT	*Trichotria* sp.	Vegetation	Planktonic	17	0.5
Copepod					
CA	Calanoid	-	-	42	6.3
CP	Copepodid	-	-	83	12.9
CY	Cyclopoid	-	-	78	20.9
HA	Harpacticoid	-	-	32	3.4
NA	Nauplius	-	-	100	63.8

Table 2-6: Description of canonical variates 1-5 from the canonical correlation between environmental variables (13) and zooplankton species (45 taxa).

Environmental Variables Dataset (SET_{ENV})					
Root	Canonical Correlation (R)	R^2	Variance Extracted	Redundancy (Env. by Sp.)	Proportion of Total Redundancy
1	0.976	0.953	0.285	0.271	0.503
2	0.950	0.903	0.096	0.087	0.160
3	0.905	0.819	0.044	0.036	0.067
4	0.879	0.773	0.046	0.036	0.066
5	0.845	0.714	0.104	0.074	0.137

Species Dataset (SET_{SP})					
Root	Canonical Correlation (R)	R^2	Variance Extracted	Redundancy (Sp. by Env.)	Proportion of Total Redundancy
1	0.976	0.953	0.097	0.092	0.331
2	0.950	0.903	0.050	0.045	0.161
3	0.905	0.819	0.043	0.035	0.126
4	0.879	0.773	0.053	0.041	0.147
5	0.845	0.714	0.035	0.025	0.089

Table 2-7: Mean zooplankton biomass (µg/L) associated with six microhabitats occurring along the shoreline of Long Point Bay. Analyses were performed for different groups of zooplankton based on their habitat preferences or feeding modes. Group A refers to all taxa that are associated with aquatic plants; Group B refers to those found within plants or open-water; Group C refers to those found only in open-water; Group D refers to raptorial feeders; Group E refers to planktonic feeders and Group F refers to scrapers. Different letters indicate sites are significantly different from each other.

Category	TP	WS	PDN	PD	SS	CC
All zooplankton	7.0$_{BC}$	38.3$_{BC}$	217.2$_{A}$	48.0$_{B}$	8.5$_{BC}$	6.9$_{C}$
Group A	1.2$_{BC}$	4.0$_{AB}$	23.3$_{A}$	12.2$_{A}$	0.8$_{C}$	0.5$_{C}$
Group B	3.4$_{B}$	10.2$_{B}$	77.3$_{A}$	6.9$_{B}$	4.5$_{B}$	1.6$_{C}$
Group C	1.2	8.0	22.7	6.9	1.6	3.9
Group D	0.9	2.3	2.3	0.5	sult0.5	0.5
Group E	3.6$_{B}$	16.1$_{B}$	101.7$_{A}$	18.7$_{B}$	5.0$_{B}$	5.3$_{B}$
Group F	1.2$_{ABC}$	3.8$_{AB}$	20.2$_{ABC}$	7.3$_{A}$	0.6$_{BC}$	0.2$_{C}$

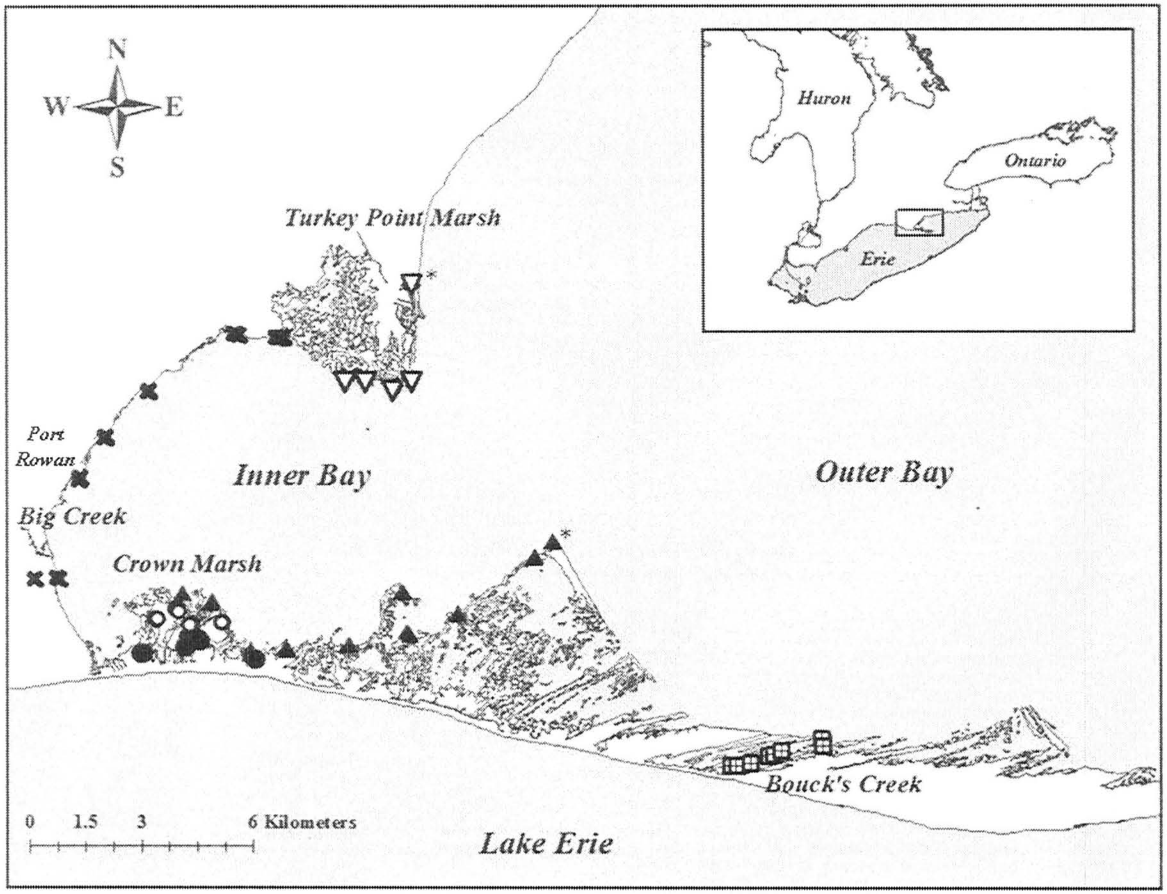


Figure 2-1: Location of study sites sampled in August 2008 at Long Point Bay, Lake Erie. Symbols correspond to microhabitat groupings TP (Δ), WS (✕), PDN (●), PD (○), SS (▲) and CC (⊞). Asterisk indicates sites without any vegetation.

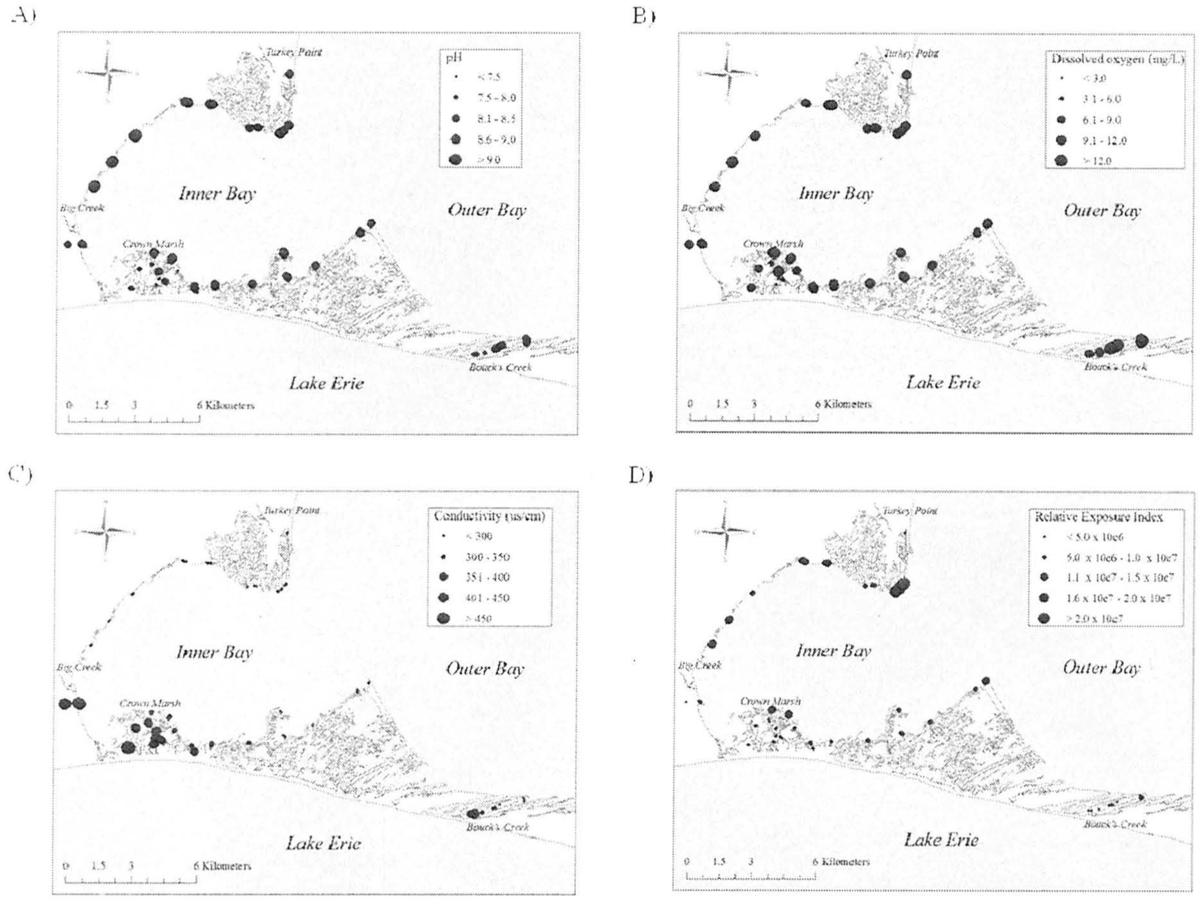


Figure 2-2: Map showing A) pH, B) Dissolved oxygen, C) Conductivity, and D) Relative Exposure Index scores recorded during this study along the nearshore of Long Point Bay.

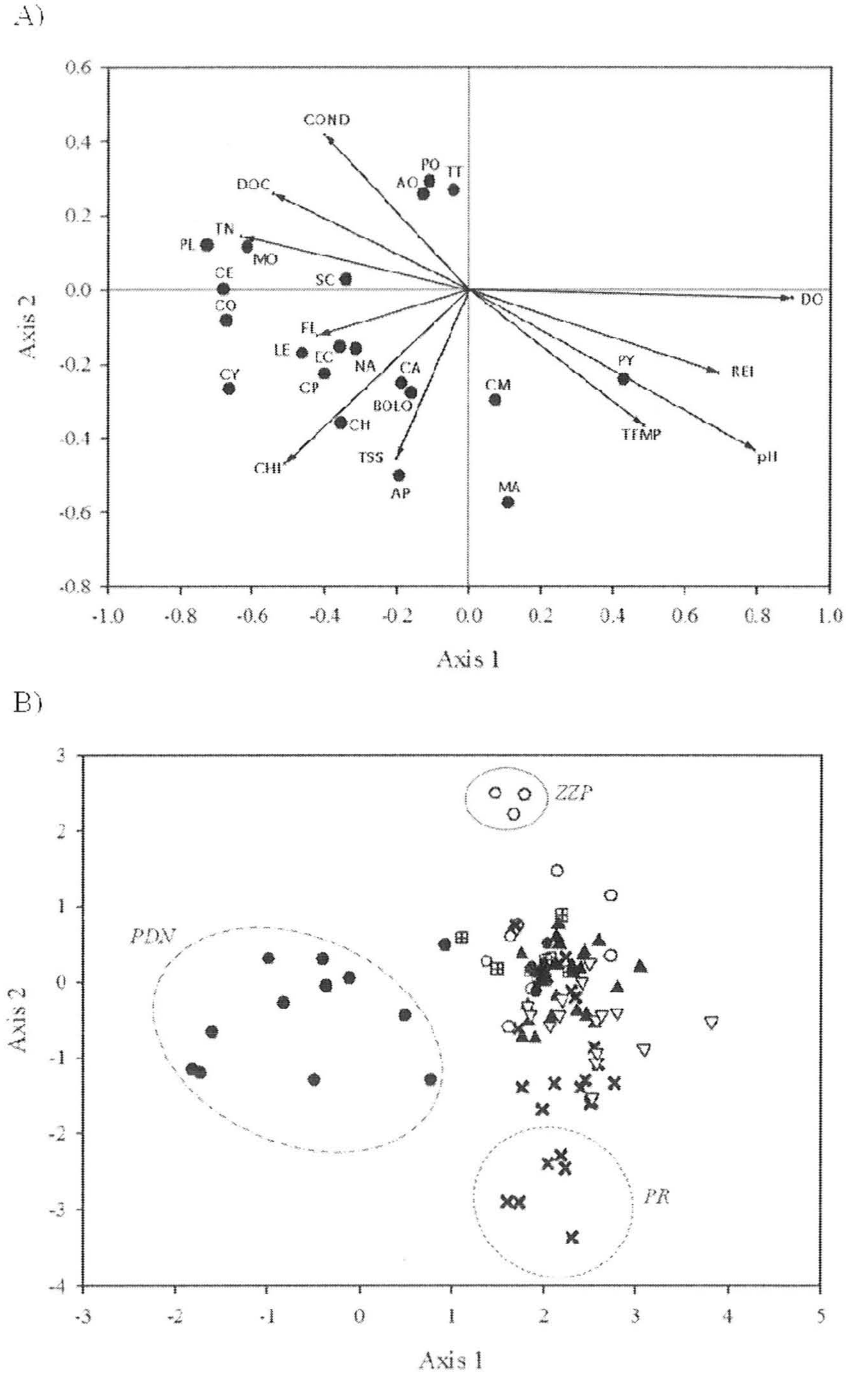
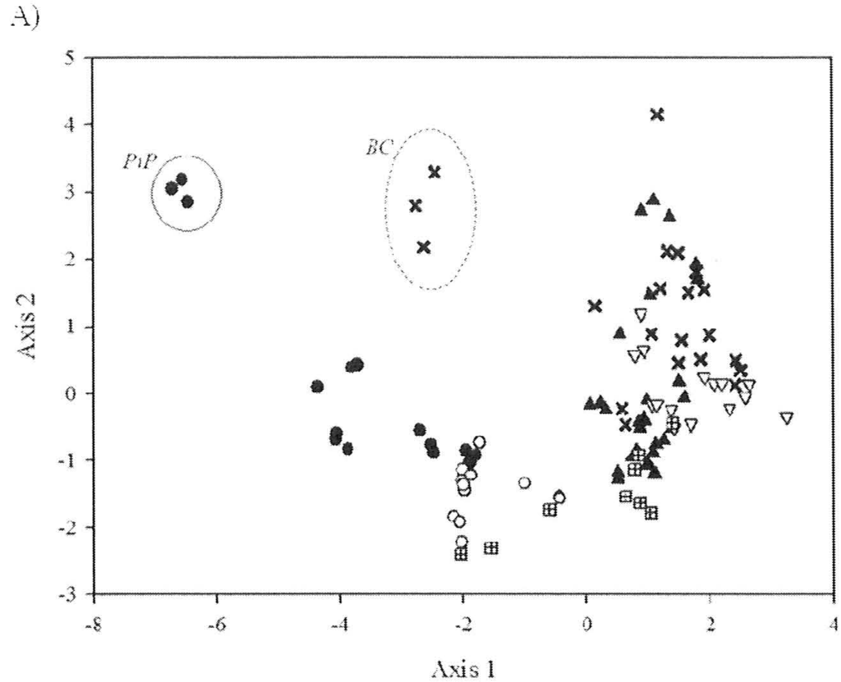


Figure 2-3: Results from the CANCOR showing A) Canonical loadings > 0.25 and B) Site scores corresponding to the first two axes. Symbols correspond to sites shown in Figure 1. PDN (●) SS (▲) PD (○) WS (✕) CC (⊞) TP (Δ). See text for explanation of ellipses and abbreviations.



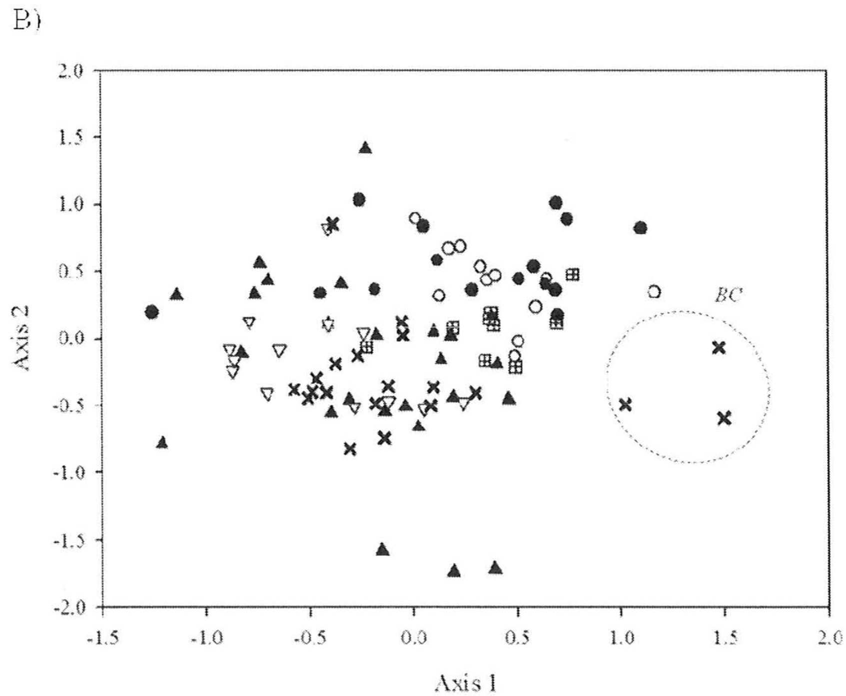


Figure 2-4: Biplots of the sites scores from the A) PCA and B) NMS analyses. The symbols correspond to sites shown in Figure 2-1. PDN (●) SS (▲) PD (○) WS (X) CC (⊞) TP (Δ). See text for explanation of ellipses and abbreviations.

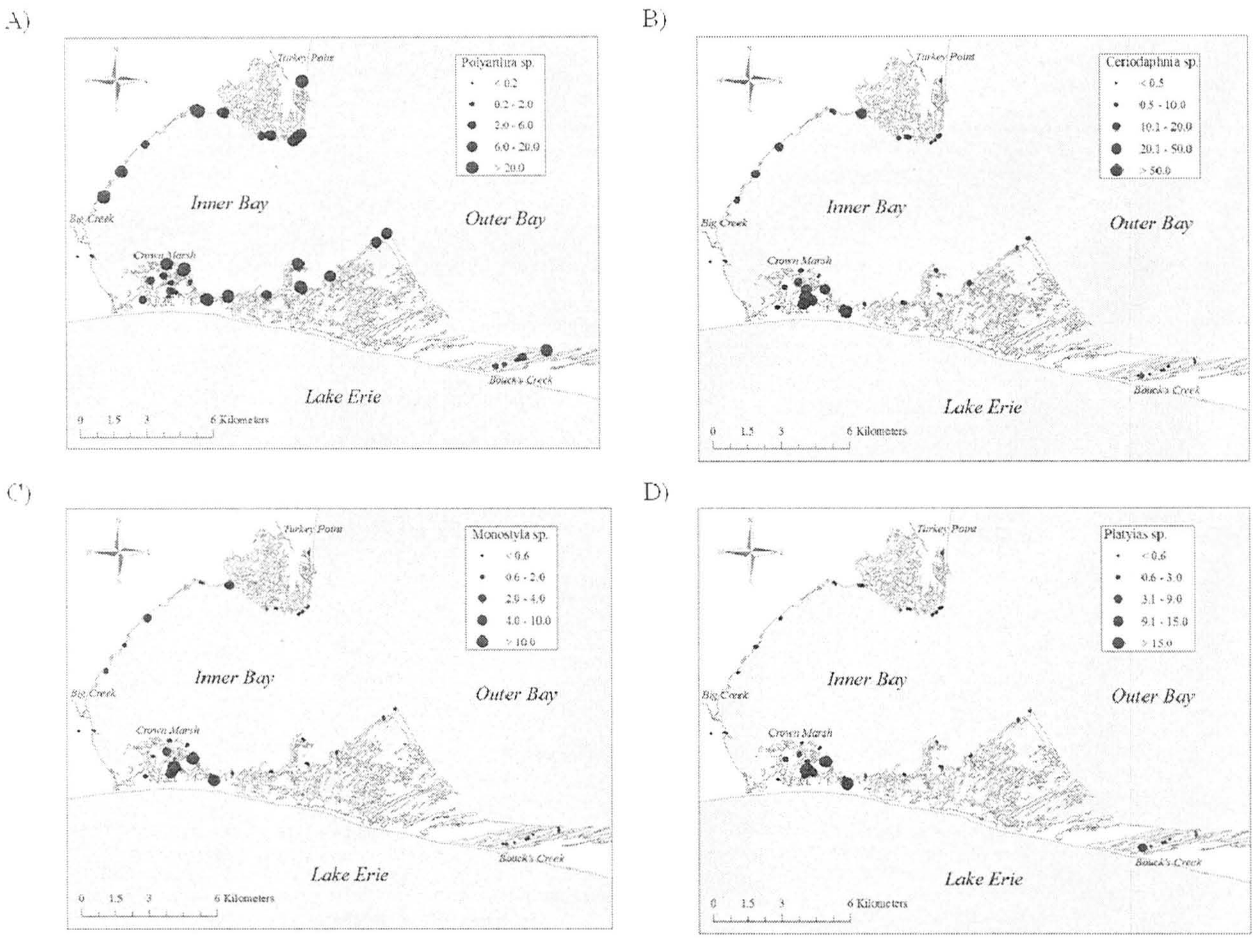


Figure 2-5: Abundance (#/L) of A) *Polyarthra* sp., B) *Ceriodaphnia* sp., C) *Monostyla* sp., and D) *Platyias* sp. at sampling stations in Long Point Bay.

GENERAL CONCLUSION

This thesis reveals the large amount of variation that temporal and spatial fluctuations introduce in a coastal marsh. In the first chapter I determined that over the past 16 years, water-quality has improved at Cootes Paradise; however it is still considered degraded in comparison with other coastal marshes (Figure 1-8; Chow-Fraser, 2006). Even though the communities are changing, no overall improvement in quality was detected (Figure 1-2, Figure 1-4, Figure 1-5, Figure 1-7), although I did detect site-to-site variation in improvement of water quality and zooplankton. Specifically, WQI and WZI scores were higher at sites with vegetation when compared with data obtained at sites in open-water that did not have vegetation. This variable response in the lower trophic levels is similar to the findings of Lougheed and Chow-Fraser (2001), who examined the response of Cootes Paradise Marsh immediately after two years of carp exclusion. In the second chapter I investigated the spatial variation that can occur in a system by studying the environmental variation and zooplankton community at nearshore Long Point Bay. Results indicated that wind and wave action are an important structuring factor in zooplankton assemblages (Figure 2-3B).

The water-quality, zooplankton, macrophyte and fish communities at Cootes Paradise are still degraded, despite over a decade of carp exclusion. A number of factors other than common carp are responsible for the current state of Cootes Paradise (Chow-Fraser, 1998; Chow-Fraser, 2005; Lougheed and Chow-Fraser, 2001). In the past, the effects of wind and wave action have been implicated as a factor that requires mitigation in order for progress in restoration to proceed. The results from the second chapter of this thesis reveal the large influence of wind and wave action acting on zooplankton assemblages. As a result, in addition to carp exclusion, I believe that desired improvements in Cootes Paradise Marsh will not be possible until the negative effects of wind and wave can be mitigated.

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