

Carp Exclusion, Food-web Interactions, and the Restoration of Cootes Paradise Marsh

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ABSTRACT. Carp were excluded from Cootes Paradise Marsh (Lake Ontario) in 1997 in order to improve water clarity and promote submerged plant growth. On average, turbidity at open water and vegetated areas was reduced by 40 and 60 percent, respectively, following carp exclusion. However, responses by plants and other trophic levels have been both spatially and temporally variable due in part to annual variation in environmental conditions and fish-zooplankton interactions. In 1997, an unusually cool spring delayed the migration of spawning fish, including a usually abundant planktivore population, into the marsh. This had three main effects: 1) large *Daphnia* were released from predation in early summer and reached unprecedented numbers (530 *Daphnia*/L) in open water areas, 2) despite the lack of vegetated marsh habitat, larval fish production was high due to reduced predation and abundant zooplankton prey, and 3) zooplankton grazing initiated a spring clear-water phase which, together with carp exclusion, promoted submerged plant growth in shallow areas previously devoid of vegetation. These newly vegetated areas showed the greatest improvements in clarity and macrophyte growth in the first 2 years following exclusion. Currently, however, the future of the biomanipulation remains uncertain, due in part to natural climatic confounding factors, and further remedial actions will be required before this wetland represents a stable, clear-water, macrophyte dominated state.

INDEX WORDS: Carp exclusion, coastal wetlands, restoration, food web.

INTRODUCTION

Since the time of European settlement, heavily settled areas of the lower Laurentian Great Lakes basin have lost a large proportion of both coastal (Whillans 1982) and inland (Detenbeck *et al.* 1999) wetlands. Historically, the primary cause of wetland loss was drainage and infilling to accommodate growing agricultural and urban needs along the shoreline of the lakes. At present, the remaining wetlands are at risk from factors related to human settlement (Chow-Fraser *et al.* 1998, Crosbie and Chow-Fraser 1999, Lougheed *et al.* 2001) such as water level stabilization, non-point source pollution from urban and agricultural land use, disturbance

by exotic benthivorous carp (*Cyprinus carpio*), as well as internal loading of nutrients.

Many Great Lakes coastal wetlands, which were formerly clear-water, plant-dominated systems, have become turbid and phytoplankton-dominated (e.g., Chow-Fraser *et al.* 1998) and strategies are currently being considered for their rehabilitation. In Cootes Paradise Marsh (Lake Ontario, Canada), biomanipulation via carp removal was selected as a likely trigger to force the switch between these two alternate states. In enclosure experiments, carp were identified as contributing to approximately 45% of the water turbidity in the marsh during their spawning season (Lougheed *et al.* 1998); however, several other factors have been shown to contribute substantially to water quality degradation in this marsh including: wind driven resuspension of sediment, internal loading of nutrients and inputs of

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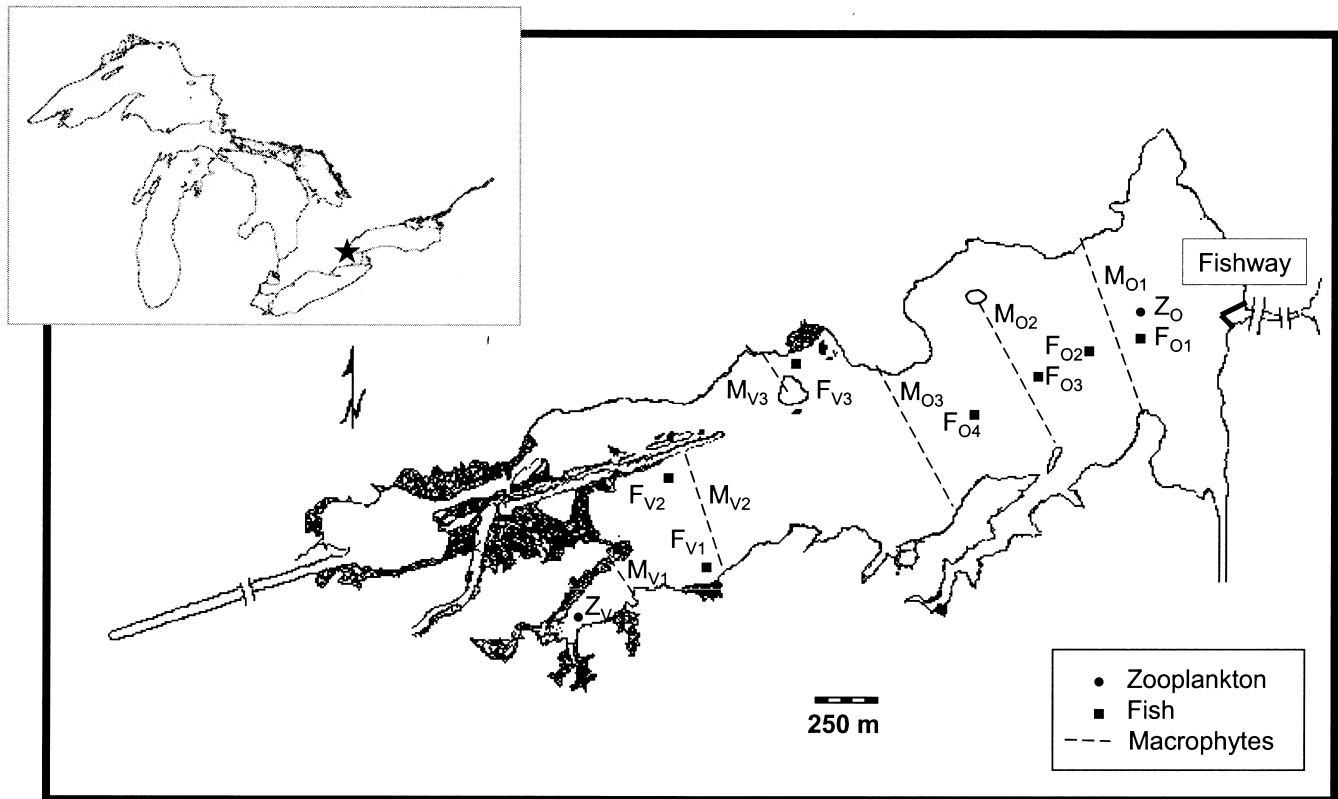


FIG. 1. Map of Cootes Paradise showing location in Laurentian Great Lakes basin (inset) and vegetated (vx) and open water (ox) sampling locations for water and zooplankton (Z), fish (F) and submersed macrophytes (M). Transects for fish and macrophytes are numbered from 1 to 3 (or 4).

pollutants from the watershed (Chow-Fraser 1999). While the biomanipulation was expected to have an immediate impact on the marsh system, reductions in nutrient and sediment inputs were part of longer-term management actions.

Biomanipulation is a well-documented restoration strategy, especially for shallow European freshwater lakes and there exist many examples of both successful and unsuccessful biomanipulations (Moss *et al.* 1996, Scheffer 1998). Besides benthivorous fish removal, other possible triggers initiating the switch to a clear water state may include removal of planktivorous fish and/or stocking of piscivores to achieve clearer water through trophic cascade effects. Accurately identifying the primary stressors and reducing their impact over a sustained period of time is key to a successful, stable restoration (Moss *et al.* 1996).

In this paper, we bring together three datasets describing: 1) water quality and plankton (Loughheed and Chow-Fraser 2001); 2) submersed macrophytes (Smith *et al.* 2001); and, 3) the fish community of

Cootes Paradise Marsh. Although these data were not collected simultaneously, nor necessarily as part of the same research program, each dataset shares a common goal: to study the response of abiotic and biotic components of the open water and vegetated areas of Cootes Paradise Marsh to carp exclusion as a restoration strategy. Together, these data represent a unique dataset that is invaluable to entirely view and understand the changes that occurred. We will discuss each dataset separately, using all available data collected between 1993 and 2000, followed by a comparison of 3 years where data exist for all three projects: 1996 (pre-exclusion), 1997, and 1998 (post-exclusion).

STUDY SITE

Cootes Paradise is a 250-ha drowned river-mouth marsh located at the westernmost point of Hamilton Harbour, Lake Ontario (43° N, 79° W) (Fig. 1). Because of its size and location, it is an important migratory stop for waterfowl, as well as a major fish

nursery for Lake Ontario. At the turn of the century, 90% of the marsh was covered by a diverse community of emergent and submergent vegetation; however, by the 1970s cover had declined to 15% and was dominated by cattails (*Typha* spp.) and exotic European manna grass (*Glyceria maxima*). The loss of emergent cover has been attributed primarily to stabilization of water levels in Lake Ontario and physical destruction by carp, while submergent loss has been blamed on decreased water clarity resulting from sediment resuspension from wind and carp activity, as well as excessive inputs of nutrients from sewage and runoff (Chow-Fraser 1998). Prior to biomanipulation, an estimated 70,000 carp existed within Cootes Paradise Marsh, with an average marsh-wide biomass of 800 kg/ha. This was equivalent to 90% of the total fish community biomass. The average size of carp was 52 cm (2.5 kg), with some individuals as large as 100 cm (25 kg).

The restoration of Cootes Paradise Marsh was designed to restore aquatic vegetation, and thereby improve habitat values, by reducing carp biomass to 50 kg/ha through a carp exclusion strategy (Hamilton Harbour Remedial Action Plan 1992, Wilcox and Whillans 1999). The seasonal migration of fish (including carp) in the spring and fall facilitated the exclusion of these migrating species via the construction of a carp barrier (or fishway) at the outlet of Cootes Paradise (see Fig. 1). The fishway became operational during the winter of 1997 and used 5.4- to 6.2-cm wide grating to physically exclude large fish, targeting carp, from the marsh. Fish not capable of passing through the grating were manually processed in fish traps such that all fish other than carp were allowed access into and out of the marsh, whereas carp were returned to waters outside Cootes Paradise. This effectively prevented large carp (> 40 cm) from entering the marsh after February 1997.

METHODS

Water Quality and Plankton

Detailed water chemistry monitoring at a series of sites in the marsh has been completed bi-weekly from May through August since 1993 (see Chow-Fraser 1999), with the exception of 1995. Here we present data on TP (total phosphorus), NO₃-N (nitrate nitrogen), turbidity (NTU), and water temperature, collected and processed as described in Lougheed and Chow-Fraser (2001). In concert with water quality monitoring, phytoplankton and zooplankton were collected bi-weekly in 1993–94 and

1997–98, as well as monthly in 1996. Counting, identification and estimates of grazing rate were completed as described in Lougheed and Chow-Fraser (1998, 2001). For this paper we present information on water quality and plankton collected from one open-water site located near the marsh outflow and one vegetated site located near cattail beds in a sheltered inlet of the marsh (Fig. 1).

Submersed Macrophytes

Similarly, we present submersed macrophyte data collected in open water and vegetated bays. Submergent plant stem density (stems/ha) was surveyed along 0.5 to 3-m wide transects in June of 1996 through 2000. Precise methods and species lists are presented in Lundholm and Simser (1999) and Smith *et al.* (2001). In this paper we present data from six transects: three bisecting open water areas and three in vegetated, sheltered bays (Fig. 1). Although there are no detailed transect data for submergent plants prior to 1996, anecdotally we can confirm that submergent plants were extremely rare and generally absent from the marsh, since their demise in the middle of the last century (Chow-Fraser *et al.* 1998).

Fish

We present fish community data collected monthly along seven 50- X 2-m electrofishing transects in open water and vegetated areas (Fig. 1) from April through October (1995–96), April through September (1997), and May through August (1998). For statistical comparison of changes in the fish community, only data from May through August were used to ensure year-to-year comparability. These seven transects were a subset of a larger monitoring program coordinated by the Royal Botanical Gardens (Burlington, ON) and were selected based on their correspondence to the zooplankton and aquatic plant data. Electrofishing was completed with a Smith Root 5GPP punt electrofisher, with settings varying from 400–600 volts and 4–6 amps, depending on conditions. It is important to note that these methods caught no fish smaller than 20 mm, and therefore descriptions of young-of-the-year abundance exclude smaller fish, including larvae. Fish community composition was usually expressed as catch per unit effort (CPUE) for each ~100 m² transect area. Estimates of biomass were also calculated based on individual fish weights measured in the field and extrapolated to an

estimate of area covered by the electrofishing transect (~100 m²).

Statistical Analysis

Non-parametric analyses of variance by means of a Mantel test were used to determine if changes had occurred in the community composition of phytoplankton, zooplankton and fish between pre- versus post-exclusion years. This test allows the comparison of two matrices collected from the same sample units and therefore does not require independent samples (Sokal and Rohlf 1995, McCune and Grace 2002) which were not possible in this spatially and temporally dependent data set. Mantel tests were performed on Sorenson's index of similarity, and significance was tested using 1,000 Monte Carlo randomizations (PC-ORD, version 4.10).

RESULTS

Water Quality and Temperature

The primary physical difference between the open water and vegetated areas was that the open areas were generally deeper (Fig. 2) and exposed, while the vegetated areas were shallower and in close proximity to cattail beds. Often these were in bays sheltered from wind and wave action. Nutrient chemistry was similar in both areas throughout the study period (Lougheed and Chow-Fraser 2001). Nutrient levels at the open water site (TP = 121–282 µg/L; NO₃-N = 388–670 µg/L) and vegetated site (TP = 197–265 µg/L; NO₃-N = 300–906 µg/L) were generally eutrophic.

Comparison of carp-less enclosures and an unenclosed marsh site indicated that turbidity would be reduced by 45% following exclusion (Lougheed *et al.* 1998). The dashed lines on the turbidity graphs of Figure 2 represent a 45% reduction relative to the turbidity observed in pre-exclusion years. At the vegetated site, water turbidity for the 2 years (1997–98) immediately following exclusion was clearer than predicted by exclusion experiments. We could not sample the vegetated site in 1999 because of low water levels; however, in 2000, water turbidity increased slightly to be more in line with expected levels. At the open water site in 1997, turbidity was lower than predicted; however, in the subsequent three years (1998–2000) turbidity varied at near to above predicted levels.

Generally, waters in the marsh have warmed up to about 19°C by mid-May; however, in the first successful year of carp exclusion (1997), tempera-

ture was still about 11°C at this time (Fig. 3). This delayed warming is noteworthy, because the cues that trigger spawning in fish and migration to their spawning areas are largely temperature dependent. We suggest that this had important consequences for the marsh community, as shall be outlined shortly.

Aquatic Plant Community

The open water areas of the marsh remained largely plantless throughout the study period. However, at the vegetated transects, increased clarity in 1997 coincided with increased growth of submergent plants which peaked in 1998 at an average of 32,000 stems/ha; thereafter, the distribution became patchy throughout the bays (co-efficient of variation = 150%). The submersed plant community observed along the transects was most speciose in 1998 and was dominated by *P. pectinatus* (62% stem density), followed by *P. foliosus* (17%), *P. crispus* (13%), and several other less common species (< 5%): *Myriophyllum spicatum*, *Zannichellia palustris*, *Elodea canadensis* and *Ceratophyllum demersum* (Fig. 4); however, species dominance did change as the summer progressed (Smith *et al.* 2001). In particular, large patches of the exotic *Myriophyllum spicatum* were observed in more open water areas in 1998. Extremely low water levels in 1999 (~50 cm lower than normal; Lougheed and Chow-Fraser 2001) encouraged emergent plant expansion at the expense of submergent habitat (Smith *et al.* 2001). Ground surveys document a modest increase from 13.7% emergent cover in 1993 to 18.8% cover in 1999. Hence, submergent plant decline in 1999–2000 partially reflects a replacement by emergents, rather than a complete loss of newly vegetated habitat.

Plankton Community

Non-parametric analysis of variance, by means of a Mantel test, indicated that the zooplankton species composition at the vegetated site changed following carp exclusion (Table 1, $p < 0.05$). More specifically, this test showed that species composition in post-exclusion years was more similar among years (97–98) than compared to all pre-exclusion years (93, 94, 96). With regards to functional groups, there was no apparent significant difference.

Table 2 shows mean abundance of zooplankton functional groups. The most notable changes were

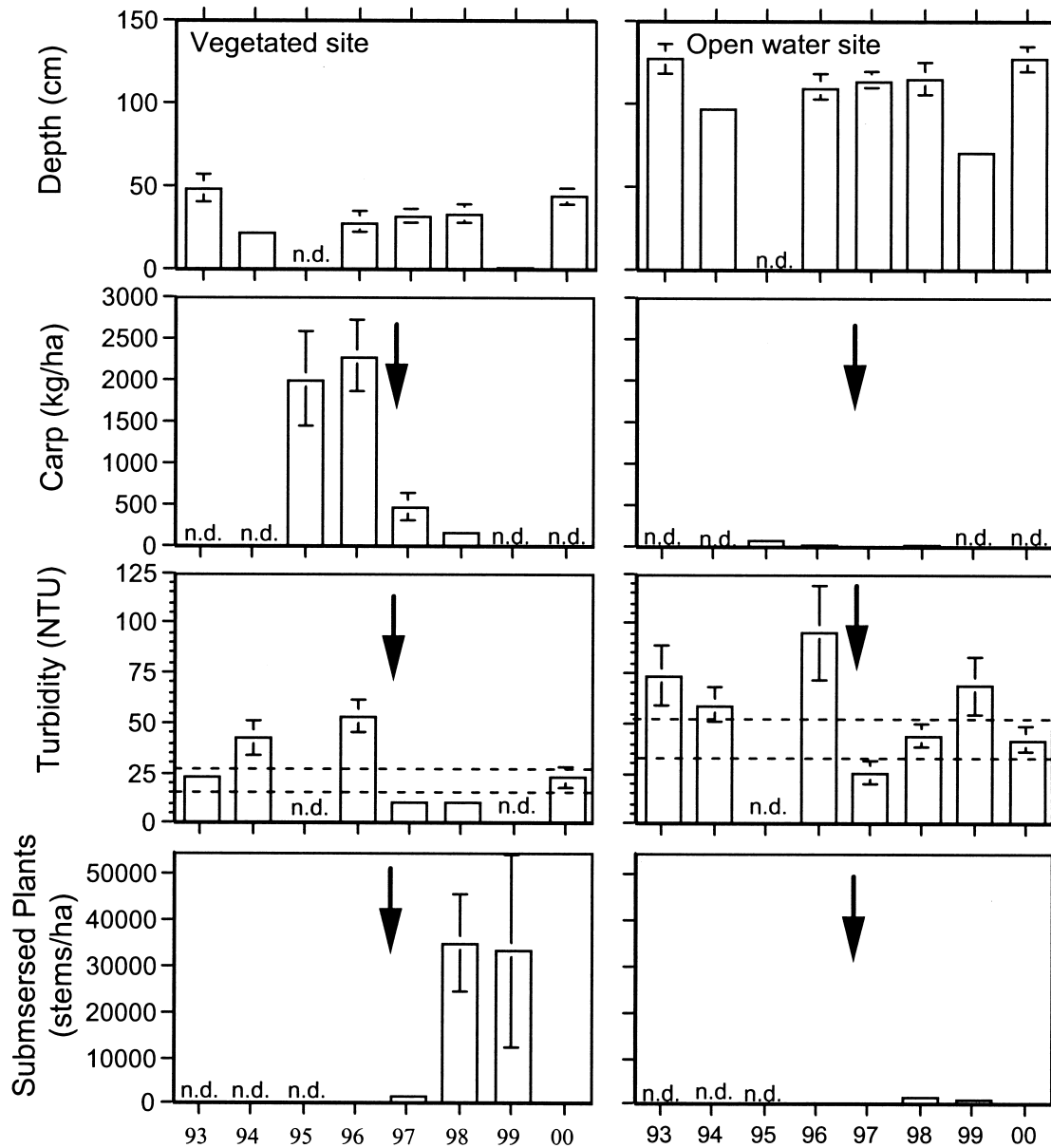


FIG. 2. Comparison of yearly means and standard errors of depth (cm), carp biomass (kg/ha), turbidity (NTU) and submersed stem density (ha^{-1}) from 1993–2000 at open water and vegetated locations in Cootes Paradise Marsh. Years where no data were collected are indicated by “n.d.” The arrows indicate the start of the operation of the fish-way. In graphs of turbidity, dashed lines represent the range of turbidity expected following carp exclusion (Lougheed et al. 1998).

those where taxa increased from near-zero levels prior to exclusion. At the open water site, the abundance of magrograzers ($> 600 \mu m$ mean length) increased to a mean of 50 individuals/L from a pre-exclusion mean of two individuals/L. In particular, *Daphnia galeata mendotae* reached a maximum of > 400 individuals/L in early June 1997. By

comparison, there was a notable increase in substrate-associated cladoceran (e.g., chydorids, *Simocephalus*) abundance at the vegetated site for both years following exclusion. Prior to exclusion, numbers did not exceed six individuals/L on any given date, whereas post-exclusion they averaged 31 individuals/L. In particular, this change was due to a

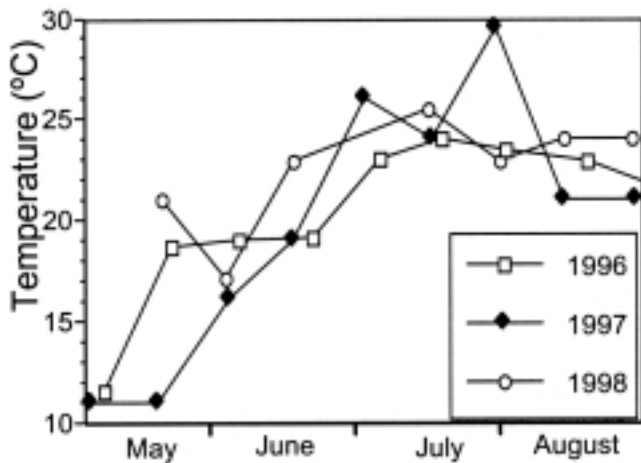


FIG. 3. Water temperature in open water area of Cootes Paradise Marsh in 1996, 1997, and 1998.

mid to late summer increase in the abundance (> 100 individuals/L) of the substrate-associated cladoceran, *Simocephalus exspinosus*.

In 1997, these increases corresponded to a mean yearly grazing rate of > 800 mL/day/L and a maximum of 2,777 and 4,839 mL/day/L at the vegetated and open sites, respectively (Fig. 5). Because these values are calculated as milliliters filtered per liter, these values indicate the water column was being cleared from 2.8 to 4.8 times per day at maximum zooplankton abundance.

The phytoplankton community also changed following exclusion at both the vegetated and open water sites (Mantel ANOVA, $p < 0.05$ and $p < 0.10$, respectively). Changes at the group level are presented in Loughheed and Chow-Fraser (2001). Over-

all, the mean seasonal biomass of edible algae (< 30 μm) declined by at least half at both sites following exclusion, although it subsequently increased to above recorded levels at the open water site in 1998 (Fig. 5).

Fish Community

Throughout the study, the vegetated transects were numerically dominated (> 10% CPUE) by pumpkinseed sunfish, common carp and brown bullhead, while the open water was dominated by gizzard shad, alewife, and lesser proportions of Clupeidae and Centrarchidae (Tables 3 and 4). Carp were never abundant or common at the open water transects. Following carp exclusion, carp biomass at the vegetated areas decreased by 75–80% in 1997 to a total reduction of 95% in 1998 (Fig. 2), which was equivalent to the biomanipulation target of 50 kg/ha. Total fish biomass tracked the changes in carp biomass observed at the vegetated transects and also declined substantially in both years following exclusion from more than 2,600 kg/ha, averaged over May through August, to less than 600 kg/ha. On average, the vegetated area housed more than an order of magnitude more young-of-the-year (YOY) and older (1+) fish than the open water areas (see Fig. 6).

At the vegetated transects, fish species composition changed following carp exclusion (Mantel test, $p < 0.05$), while there was no apparent significant change in the open water areas. Families which appeared to change in abundance between pre (1995–96) and post (1997–98) exclusion years are as follows. At the vegetated transects, there was an in-

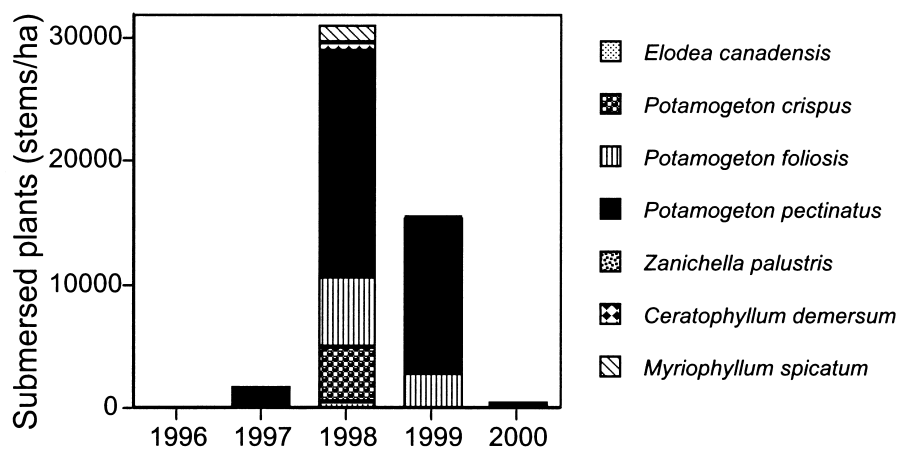


FIG. 4. Average submergent plant species composition in vegetated bays in Cootes Paradise from 1996 to 2000.

TABLE 1. Results of non-parametric analysis of variance, by means of a Mantel test, to compare monthly means of communities of zooplankton, fish, and phytoplankton both within and between pre- and post-exclusion years. Significance level determined by 1,000 Monte Carlo randomizations. All comparisons consisted of Sorenson's index of similarity for 16-20 month-year combinations.

Variable	Vegetated	Open Water
Zooplankton Species	$r = 0.24^{**}$	
Fish Species	$r = 0.19^{**}$	
Phytoplankton		
Functional Groups	$r = 0.33^{**}$	$r = 0.09^*$

** $p < 0.05$; * $p < 0.10$

crease in CPUE of Percidae, non-carp Cyprinidae, and Ictaluridae, whereas there was a decline in the numbers of Cyprinidae (carp and goldfish) and Percichthyidae. Trends in mean CPUE are hard to discern in the open water areas, due to low overall numbers at the family level; however, despite no significant change in overall composition, seven species were either new or increased in percent CPUE, while four declined or disappeared (Table 3).

TABLE 2. Mean abundances (individuals per liter) of zooplankton functional groups for pre- (1993, 94, 96) and post-exclusion (1997, 98) years.

Functional Groups	Vegetated		Open Water	
	Pre-	Post-	Pre-	Post-
Herbivorous rotifers	314	186	532	859
Predaceous rotifers	8	7	7	7
Microcladocerans (< 300 μm)	523	286	274	213
Medium cladocerans (300-600 μm)	143	109	18	18
Macrocladocerans (> 600 μm)	<1	10	2	50
Substrate associated cladocerans	<1	31	<1	<1
Cyclopoid copepods	70	124	41	79
Nauplius/Copepodites	286	580	307	441

Community Dynamics

At the open water site, the timing of peak abundance of 1+ planktivorous fish was delayed in 1997 (July), relative to either 1996 or 1998 (June of both years) (Fig. 6). Coincident with this reduced plank-

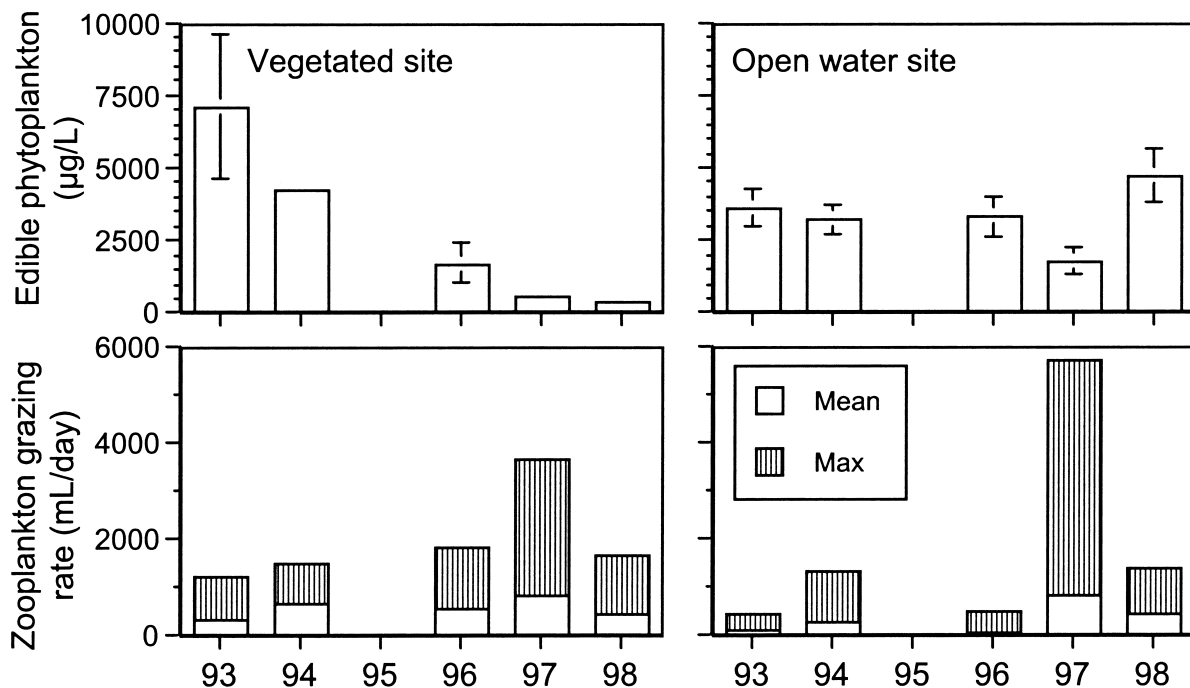


FIG. 5. Comparison of mean seasonal edible algae (top) and mean/maximum zooplankton grazing rate (bottom) for vegetated (left) and open water (right) sites in Cootes Paradise Marsh.

TABLE 3. Mean percent catch of fish at the vegetated and open sites before (1995 and 1996) and after (1997 and 1998) carp exclusion. A = abundant (> 50% total catch), C = common (20–50%), O = occasional (10–19%), U = uncommon (1–9%), R = rare (0–1%).

Scientific Name	Common Name	Vegetated		Open Water	
		Pre-	Post-	Pre-	Post-
CLUPEIDAE					
<i>Alosa pseudoharengus</i>	Alewife	—	—	O	O
<i>Dorosoma cepedianum</i>	Gizzard Shad	U	U	C	C
CYPRINIDAE					
<i>Notropis hudsonius</i>	Spottail shiner	U	U	O	U
<i>N. atherinoides</i>	Emerald shiner	R	R	R	O
<i>Pimephales notatus</i>	Bluntnose minnow	U	U	—	R
<i>P. promelas</i>	Fathead minnow	R	U	—	U
<i>Cyprinus carpio</i>	Common carp	C	C	O	U
<i>Carassius auratus</i>	Goldfish	U	—	—	—
CATOSTOMIDAE					
<i>Catostomus commersoni</i>	White sucker	R	R	U	U
ICTALURIDAE					
<i>Ictalurus nebulosus</i>	Brown bullhead	O	O	U	U
<i>Ictalurus punctatus</i>	Channel catfish	—	—	R	—
<i>Noturus gyrinus</i>	Tadpole madtom	—	R	—	—
ESOCIDAE					
<i>Esox lucius</i>	Northern pike	—	—	U	—
SALMONIDAE					
<i>Oncorhynchus mykiss</i>	Rainbow trout	—	—	U	U
PERCICHTHYIDAE					
<i>Morone americana</i>	White perch	U	U	U	U
CENTRARCHIDAE					
<i>Micropterus salmoides</i>	Largemouth bass	U	R	—	—
<i>Lepomis cyanellus</i>	Green sunfish	R	R	—	—
<i>L. gibbosus</i>	Pumpkinseed	C	C	U	O
<i>L. macrochirus</i>	Bluegill	U	U	—	U
<i>Pomoxis nigromaculatis</i>	Black crappie	R	R	—	—
PERCIDAE					
<i>Perca flavescens</i>	Yellow perch	R	U	—	R
<i>Percina caprodes</i>	Logperch	R	R	—	U
PERCOPSIDAE					
<i>Percopsis omiscomaycus</i>	Trout perch	—	—	R	—
SCIAENIDAE					
<i>Aplodinotus grunniens</i>	Freshwater drum	—	—	U	R
ATHERINIDAE					
<i>Labidesthes sicculus</i>	Brook silverside	R	R	U	U

tivory, herbivorous cladocerans reached unusually high numbers in early summer 1997 (640 individuals/L), and this was accompanied by near-zero levels of edible algae (Fig. 6) and turbidity. When the abundance of planktivores peaked in July 1997, the zooplankton community crashed and remained low for the rest of the summer. In 1998, we did not see a similar proliferation of *Daphnia*, nor did we witness a clearing of the water column, and both the water quality and the dynamics of the fish community closely mirrored those seen in 1996.

The shallow, vegetated areas of the marsh housed relatively large numbers (10–30 CPUE) of adult planktivores in the spring of 1996 and 1998; however, in 1997 their numbers were much reduced (< 2 CPUE) (Fig. 6). The reduced planktivory during the spring of 1997 coincided with the development of a large zooplankton population and a much reduced algal biomass. Subsequently, YOY increased up to 620 CPUE, which was likely a response to lower than expected predation, on the one hand, and the abundant zooplankton food source,

TABLE 4. Mean catch per unit effort of fish families for pre- (1995–96) and post-exclusion (1997–98) years.

Family	Vegetated		Open Water	
	Pre-	Post-	Pre-	Post-
Clupeidae	3	2	2	2
Cyprinidae (non-carp)	1	4	1	2
Cyprinidae (carp)	25	14	< 1	< 1
Catostomidae	< 1	< 1	< 1	0
Ictaluridae	13	65	< 1	< 1
Esocidae	0	0	< 1	0
Salmonidae	0	0	0	< 1
Percichthyidae	5	1	< 1	< 1
Centrarchidae	39	44	< 1	1
Percidae	1	7	0	< 1
Percopsidae	0	0	< 1	0
Scianidae	0	0	< 1	< 1
Atherinidae	< 1	< 1	0	< 1

on the other. As with the open water site, the herbivorous zooplankton population crashed in mid-June 1997; however, following the establishment of submersed macrophytes in these areas in mid-summer 1997, the abundance of plant-associated zooplankton taxa rose slightly (> 100 individuals/L). In the second year following carp exclusion, algal biomass remained low, while zooplankton biomass returned to near pre-exclusion levels.

There has been a steady decline in the mean seasonal biomass of phytoplankton as submersed plants have become established at the vegetated site (Fig. 7). This may be due, in part, to competition between plants and algae for nutrients but is also likely due to a positive effect of macrophytes on the zooplankton community. In 1997, we compared the zooplankton communities at two vegetated locations in the marsh, which were approximately 200 m apart. In an area where submergent plants existed in very sparse patches (< 5 stems/m²) and water turbidity was relatively high (26.2 NTU), the mean size of the cladoceran zooplankton community differed very little between the open water and vegetated sites (Student's t-test, $p > 0.05$) and consisted largely of small, inefficient grazers (226 μm mean length). In a more sheltered location, where submergents were relatively dense (> 20 stems/m²) and water was clearer (10.1 NTU), mean body size of zooplankton was significantly greater in the vegetated areas than in nearby open water (Student's t-test, $p < 0.05$). The cladocerans in the cattail beds consisted of large-bodied species (524 μm mean length), such as *Simocephalus exspinosus*, which

were rarely seen prior to exclusion, while zooplankton in open water nearby consisted of smaller species (248 μm mean length). As submergent density increased, much as it did between 1997 and 1998, the grazing of algae by zooplankton may also have increased due to the presence of larger-bodied, more efficient grazers.

DISCUSSION

On average, turbidity at open water and vegetated areas was reduced by 40 and 60 percent, respectively, following carp exclusion; however, responses by plants and other trophic levels have been both spatially and temporally variable. In 1997, improvements in water clarity were initially greater than expected due to a spring clear water phase caused by zooplankton grazing. Here we suggest that an unusual climatic event, which delayed the return of fish into the marsh in the spring and thus reduced planktivory, was the ultimate cause of this clear-water state. Although carp exclusion contributed to a substantial improvement in water clarity, the initial submergent plant growth evidenced in 1997 was likely initiated by this zooplankton-mediated improvement in water clarity that occurred during a critical period in plant growth.

The occurrence of a spring clear-water phase caused by zooplankton grazing is not unusual in productive systems when colder spring temperatures correspond with reduced fish predation and high food availability (Lampert *et al.* 1986; Luecke *et al.* 1990). This phenomena has been key in the restoration, temporary or otherwise, of shallow lakes following fish removal (Hanson and Butler 1994, Meijer and Hosper 1997). In Cootes Paradise Marsh, this spring clear-water phase occurred in the spring of 1997, the same year that the carp barrier began operating successfully. Unfortunately, the timing and effect of this confounding factor has made it difficult to accurately assess the role of the carp exclusion in contributing to environmental improvements.

Spawning by fish was substantially delayed in the atypically cool spring of 1997 and this resulted in an unusual chain of events in Cootes Paradise Marsh. In response to reduced fish predation and an abundant algal food source, zooplankton production reached large numbers. Lougheed and Chow-Fraser (2001) estimate that, at peak production, these zooplankton were capable of filtering the water column from 2.78 (vegetated site) to 4.84 times per day (open site). Consequently, we saw a decline in edi-

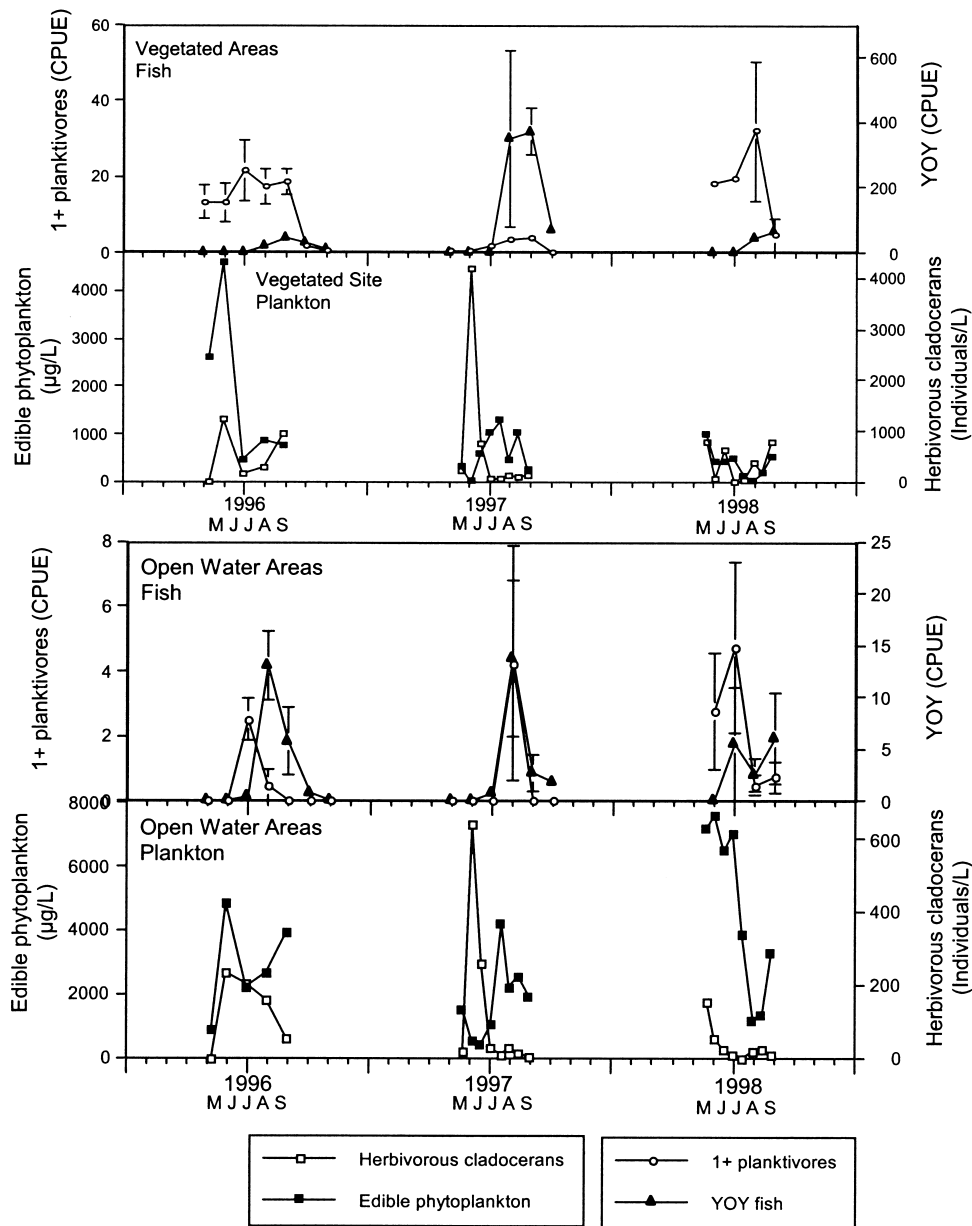


FIG. 6. Seasonal dynamics of planktivorous 1+ and young-of-the-year fish, edible phytoplankton and herbivorous zooplankton in vegetated bays (top) and open water areas (bottom) of Cootes Paradise Marsh from 1996 to 1998.

ble algae biomass in early summer 1997 at both sites (Lougheed and Chow-Fraser 2001). When larval fish were produced, these reached unprecedented numbers at the vegetated site, where there was a refuge from predation and an abundant zooplankton food source. The zooplankton community subsequently declined sharply in abundance due to this increased predation. At the open water site, YOY fish were likely kept near “normal” levels by

the now abundant planktivorous adult fish population and the absence of protection afforded by aquatic vegetation. These planktivorous fish likely contributed to the control of zooplankton throughout the marsh for the remainder of the sampling season.

Concurrent with the increased clarity in the spring of 1997, submergent plants became established in the shallow and sheltered areas of the marsh and this

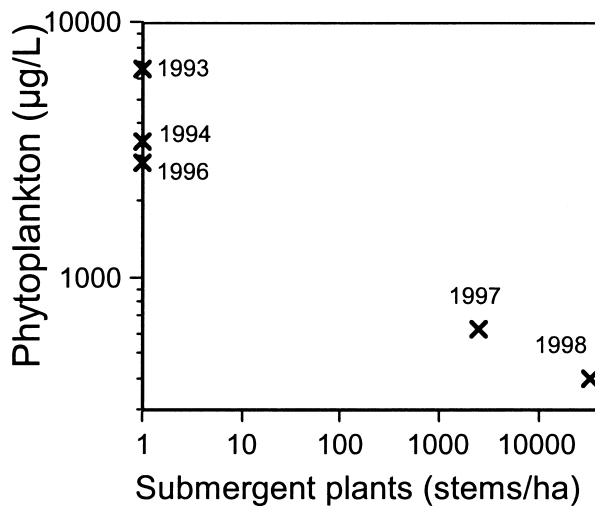


FIG. 7. Relationship between mean seasonal phytoplankton biomass ($\mu\text{g/L}$) and submergent plant density (ha^{-1}) in vegetated bay of Cootes Paradise Marsh.

likely prolonged a clear water state in these areas through 1998; however, the open water areas of the marsh remained virtually plant-less and somewhat turbid following exclusion. Establishment of aquatic vegetation may help maintain water clarity in some systems by stabilizing sediment and reducing sediment resuspension by wind (Hamilton and Mitchell 1997). Macrophytes may also suppress algal growth through competition for nitrogen (Ozimek *et al.* 1990, van Donk *et al.* 1990) and some may have an allelopathic effect on algae (e.g., Wium-Anderson *et al.* 1982). Increase in macrophyte cover can also provide refuge for large-bodied zooplankton grazers such as *Daphnia*, which may contribute to enhanced top-down control of algae (Timms and Moss 1984, Schriver *et al.* 1995). Zooplankton at the vegetated site were able to withstand the higher levels of fish predation than those in the open water areas. For example, in 1997, herbivorous cladoceran abundance at the open water site was constrained to near zero levels (< 32 individuals/L) from June on; however, at the vegetated site, where YOY were observed at levels 15X greater than at the open water site, zooplankton were able to maintain levels between 70 and 130 individuals/L. Although the precise mechanisms maintaining clarity in the vegetated areas of Cootes Paradise is uncertain, zooplankton grazing almost certainly plays a role, given the presence of larger grazers in these areas.

The submergent plant community in the marsh that appeared in the summer of 1997 was dominated by several species of *Potamogeton*, as well as some

other taxa which tend to be tolerant of degraded water and sediment quality (Lougheed *et al.* 2001). This new growth represented a substantial improvement in habitat for aquatic organisms. Lougheed and Chow-Fraser (2001) showed that the vegetated site experienced a sustained increase in zooplankton species richness, from less than 26 to more than 32 species following the establishment of submergent plants, while the open water site showed no consistent changes in zooplankton species richness. There were no new species of fish observed in the marsh following exclusion; however, there were some initial shifts in composition and abundance that would seem to suggest that further growth of vegetation would have a large impact on the fish community. In particular, the percent catch of black crappie ($r = 0.26$), bluegill ($r = 0.24$), bluntnose minnow ($r = 0.36$), fathead minnow ($r = 0.38$), pumpkinseed ($r = 0.32$), and yellow perch ($r = 0.59$) were all positively correlated with submergent stem density (Spearman's Rho, $p < 0.05$). No fish species was negatively correlated with stem density.

Unfortunately, following a peak in submergent plant density and species richness in 1998, the submergent plant community began to disappear marsh-wide. This decline in submergent plants bodes poorly for the marsh community as a whole. Low winter water levels in 1998–99 and 1999–2000 have had a negative effect, with much of the marsh sediment being exposed and frozen, eliminating existing submergent plants. Aerial photos indicate that, in 1999, emergent plants expanded into habitat formerly occupied by submergents; between 1993 and 1999, emergent cover increased by 18 ha or 5.1%. Undoubtedly, some of this emergent growth was due to reduced mechanical damage by carp as indicated by the lack of emergent expansion in shallow, unprotected areas outside Cootes Paradise Marsh; however, water level related emergent expansion also played a primary role (Smith *et al.* 2001). In 1999, the Great Lakes experienced the lowest water levels seen since the 1960s. Macrophyte species intolerant of drying (i.e., submergents) were replaced by emergents germinating from seeds on exposed mudflats. This has created another confounding factor, related to natural climatic variation, impeding the assessment of the carp exclusion strategy.

Management Implications

Chow-Fraser (1999) showed that much of the interannual variability in water clarity in Cootes Par-

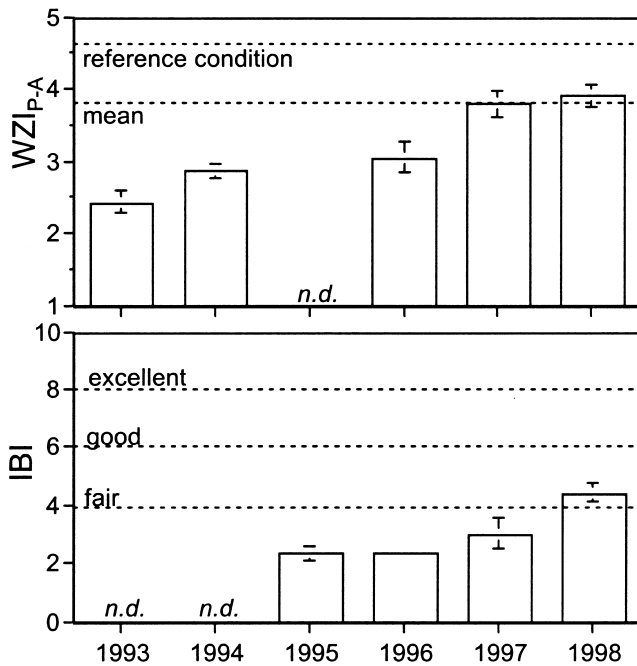


FIG. 8. Comparison of Wetland Zooplankton Index (top) and Fish Index of Biotic Integrity (bottom) values calculated for the vegetated areas of Cootes Paradise Marsh.

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

It appears that clear water conditions are possible in Cootes Paradise Marsh, given that a zooplankton-mediated spring clear water phase occurred in 1997, and despite other degrading factors (Lougheed and Chow-Fraser 2001). Using a zooplankton index of wetland quality, Lougheed and Chow-Fraser (2002) showed that the zooplankton community in Cootes Paradise was representative of a wetland of moderate quality, indicating that

further remedial actions are required before this wetland is as valuable a habitat as other, more pristine coastal marshes of Lake Ontario. Similarly, an Index of Biotic Integrity developed for fishes of the littoral zone of the Great Lakes (Minns *et al.* 1994) and applied to the Cootes Paradise data (Fig. 8) indicates that the fish community at the vegetated site could be considered “fair” in quality. Unfortunately, current trends indicate submergent plant cover is declining and, although water turbidity has not declined to pre-exclusion levels, it is still prohibitive to submergent plant growth (Lougheed *et al.* 1998). Several trends reported in the literature suggest that the long term stability of this biomanipulation is improbable without further remedial actions.

Jeppeson *et al.* (1990) suggested that long-term stability of alternative states is closely linked to the ability of the system to create a self-perpetuating increase in the ratio of piscivores to planktivores. Result of our study suggest that a reduction in the planktivorous fish population, especially in spring and early summer, will be a prerequisite to a clear water state in the marsh. It remains to be seen whether stocking piscivores is the solution needed to control planktivorous fish populations in Hamilton Harbour and Cootes Paradise. In particular, any attempts to restructure the fish community would also require habitat improvements. For example, the most significant area of floodplain habitat in Cootes Paradise, West Pond, is severely degraded by high phosphorus (272–436 $\mu\text{g/L}$ TP) and nitrate (3,486–5,095 $\mu\text{g/L}$ $\text{NO}_3\text{-N}$) levels. Similarly, formerly expansive spawning reefs in Hamilton Harbour have been dredged for shipping purposes.

The success of biomanipulation is also related to the establishment of a permanent and wide distribution of submersed aquatic macrophytes (Jeppeson *et al.* 1990). The sheer size and spatial variability in depth of Cootes Paradise may have limited the success of remedial measures to date. Submergent plants colonize to a maximum depth, largely dependent on the clarity of the water (Chambers and Kalff 1985). Although the sediment surface at the open water site was illuminated for a brief time in 1997, this was insufficient to promote extensive plant growth in these deeper areas. Carp tend to spawn near macrophyte beds (Balon 1995, Chow-Fraser 1999) and, consequently, their removal had the greatest positive impact on shallow, protected areas surrounded by cattail beds (Lougheed and Chow-Fraser 2001) through both reduced sediment resuspension and reduced mechanical damage. A general overall decline in submersed macrophyte

cover in recent years, as well as replacement by emergent plants, has confounded the evaluation of biomanipulative efforts; however, despite moderate improvements, it cannot be denied that Cootes Paradise remains a turbid, algal-dominated system.

Finally, the long-term stability of a biomanipulation is dependent on the nutrient levels of the system. Between phosphorus levels of approximately 50 and 150 µg/L, two alternative states are possible in shallow aquatic environments: a turbid and phytoplankton-dominated state or a clear-water and macrophyte-dominated state (e.g., Jeppeson *et al.* 1990, Moss *et al.* 1996). Conversely, long-term stability of the clear water state is unlikely when phosphorus levels exceed ~150 µg/L. This is due to many factors including increased predation pressure on zooplankton and growth of abundant phytoplankton populations (Jeppeson *et al.* 1990). Although an initial improvement may be observed in these nutrient-rich systems, the macrophyte-dominated state will not be maintained. It is evident that mean seasonal TP levels in Cootes Paradise (121–282 µg/L) do not generally fall within this range for successful biomanipulation, and consequently, it would seem that a sustained clear-water state is improbable. Both urban runoff and internal loading currently contribute substantially to phosphorus loading to the marsh (e.g., Prescott and Tسانيس 1997, Kelton 2001). Management options must be selected and implemented to address these issues.

In the eyes of all stakeholders, eventually the marsh must thrive without the fishway in place, and only by reducing the impact of all stressors, besides carp, will this be possible. In particular, the rehabilitation of piscivore populations and spawning grounds in the region must be continued. This should promote the control of planktivorous fish populations and promote a zooplankton community capable of consistently improving water clarity in Cootes Paradise Marsh. Furthermore, phosphorus levels in the marsh must be reduced so that a stable macrophyte-dominated state is possible. Given the roles of both external and internal loading in contributing to the large total phosphorus load in the marsh, reducing current external loads as low as possible through land use management and infrastructure improvements and waiting while internal loading reaches an equilibrium in the system will be necessary to ensure a successful restoration. The time frame over which nutrient levels will remain an impediment to restoration need to be determined to plan for the long term rehabilitation and operation of the fishway in Cootes Paradise Marsh.

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