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Long-term response of the biotic community to fluctuating water levels and changes in water quality in Cootes Paradise Marsh, a degraded coastal wetland of Lake Ontario

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Abstract

During the early 1900s, more than 90% of the surface area of Cootes Paradise Marsh was covered with emergent vegetation; currently, less than 15% of the surface is covered with aquatic vegetation and the remainder is wind-swept, turbid, open water. The loss of emergent cover is significantly correlated with mean annual water levels that increased more than 1.5 m over the past 60 years. Species diversity and the percent cover of the submerged macrophtye community also declined dramatically after the 1940s, coincident with decreased water clarity and increased nutrients from pollution by sewage and stormwater effluent. Phosphorus levels in the marsh dropped ten-fold after the sewage plant was upgraded to a tertiary-treatment facility in 1978; however, there was no measurable improvement in water clarity, in spite of a decrease in chlorophyll concentrations. Long-term changes in the composition of the planktonic, benthic and fish communities accompanied changes in water clarity, nutrient status and macrophyte cover. Phytoplankton changed from a community dominated by diverse taxa of green algae and diatoms during the 1940s, to a less diverse community dominated by a few taxa of green and blue-green algae in the 1970s, then to a much more diverse community recently, including many taxa of green algae, diatoms and chrysophytes; however, because water turbidity continues to be high, and algae tolerant of low light levels are now very abundant. *Daphnia*, which were prominent during the 1940s (especially in the vegetated sites) were replaced in the 1970s by smaller zooplankton such as the cladoceran, *Bosmina*, and several rotifer species including *Brachionus, Asplanchna* and *Keratella*. In the recent survey conducted in 1993 and 1994, small-bodied forms still dominate the turbid open-water areas, while medium-sized cladocerans such as *Moina* were common near macrophyte beds. Generally, total herbivorous zooplankton biomass tended to be highest next to *Typha* beds and declined with increasing distance from the plants. Conversely, biomass of edible algae at these sites increased with distance from the macrophytes. Species diversity of aquatic insects declined dramatically over the past 40 years, from 57 genera (23 families and 6 orders) in 1948, to 9 genera (6 families and 3 orders) in 1978, to only 5 genera (3 families and 2 orders) in 1995. The diverse benthic community present 5 decades ago has now been replaced by a community consisting primarily of chironomid larvae, oligochaetes and other worms associated with low-oxygen environments. These successional changes illustrate the impact of natural (fluctuating water levels) and anthropogenic (deterioration in water quality) stressors on the character of the biotic communities, and reveal the complex interactions among the various trophic levels and the abiotic environment as degradation and remediation proceeded.

Introduction

Coastal marshes of the Laurentian Great Lakes are highly productive and complex systems with links to both the watershed and the open water, and provide diverse habitats to a variety of resident and migratory fish (Jude and Pappas, 1992) and waterfowl (Prince et al., 1992). In the Lake Ontario basin, many of these habitats are being degraded by nutrient and sediment load from the watershed, high water levels, and disruptive activities of the common carp (*Cyprinus carpio*)

(Whillans, 1996). Since close to 60% of the baseline marsh areas in the Canadian shoreline of Lake Ontario have already been claimed by infilling, dredging, and industrial and urban development (Whillans, 1982), projects have been initiated throughout the basin to stem wetland losses, and to restore ecological functions of degraded marshes where possible (Maynard and Wilcox, 1996).

Wetland managers require a good scientific database to guide rehabilitation and fortunately, there are a number of published studies that pertain to coastal wetlands. For instance, studies have been published that estimate the relative importance of physical and biological factors on nutrient retention (Minns et al., 1986; Mitsch and Reeder, 1991). A few describe the dynamic interactions within plankton (Krieger and Klarer, 1991; Klarer and Millie, 1994) and benthos (Krieger, 1992), or try to account for long-term changes in the macrophyte (Crowder and Bristow, 1986) or fish communities (Hurley, 1986; Whillans, 1996). These studies indicate that there are a number of natural and anthropogenic stressors responsible for the degradation of emergent and submergent marshes, and it is a challenge for wetland managers to correctly identify their relative impacts to expedite rehabilitation.

One problem with past studies is that they rarely extend beyond years or decades. This is inappropriate considering that water levels in the Great Lakes fluctuate over cycles that last from 7 to 10 years (Lyon et al., 1984; Kelley et al., 1985; Whillans, 1996). These fluctuations are known to keep coastal wetlands alternating between emergent marshes during years of low water levels, and submergent marshes during years of high levels (Keddy and Reznicek, 1986). Species replacement under such conditions are natural and should not be interpreted as anthropogenic damage. Denny (1994) has suggested that long-term biodiversity surveys and monitoring programs spanning decades should be conducted to distinguish between these ‘natural’ changes attributable to the type of catastrophic ecosystem succession produced by fluctuating water levels, and those brought on by anthropogenic stresses (e.g., eutrophication, sedimentation, introduction of exotic species).

This paper will contribute to our understanding of the relative impacts of natural versus anthropogenic stressors on a coastal marsh of Lake Ontario. We will chronicle the long-term response of the biotic community to environmental degradation produced by both natural (fluctuating water levels) and anthropogenic (deterioration in water quality resulting from cultural eutrophication) sources over a 60-y period. We will integrate information from historic aerial photos, written accounts, and published and unpublished field surveys to document the decline in aquatic plant community in relation to water levels and water quality during the six decades. We will show how the ecological interactions among the various trophic levels (macrophytes, benthos, plankton and fish) have changed in response to eutrophication and a subsequent nutrient-abatement program. This will be one of the first comprehensive, long-term studies of how different trophic levels, especially those in the lower food-web of coastal wetlands, have responded to major ecosystem stressors (Krieger et al., 1992). It will provide a basis for distinguishing between natural versus anthropogenic impacts, and ultimately guide remedial efforts for this and other degraded coastal wetlands.

Methods and materials

Description of study site

Located at the extreme west end of Hamilton Harbour, Cootes Paradise Marsh is an urban marsh, bordered by the town of Dundas to the west, the town of Flamborough (Village of Waterdown) to the northeast, and the city of Hamilton to the south (Figure 1). It is the largest marsh (250 ha) in the western end of the Canadian shoreline of Lake Ontario (Whillans, 1982) and is also an important staging area for waterfowl. It is also known within the region for providing excellent scientific and educational opportunities, and for providing important nursery and spawning habitat for sportfish (Remedial Action Plan for Hamilton Harbour, Stage 1 Report, 1992; Chow-Fraser and Lukasik, 1995).

There are three main tributaries that empty into the marsh, the largest of which is the Spencer’s Creek system (Station 7 in Figure 1), which drains 79% of the total watershed of Cootes Paradise Marsh (290.9 km^2). The other two tributaries are much smaller: Borer’s Creek (Station 18) and Chedoke Creek (Station 11), which drain 6.9 and 9.4% of the watershed respectively (T. Horvat, Hamilton Region Conservation Authority, pers. comm.). The Desjardins Canal, which was dredged in 1837 to connect the town of Dundas to Lake Ontario, is no longer navigable, but its banks have been colonized by willows and make it a prominent feature which dissects the marsh longitudinally at the western end.

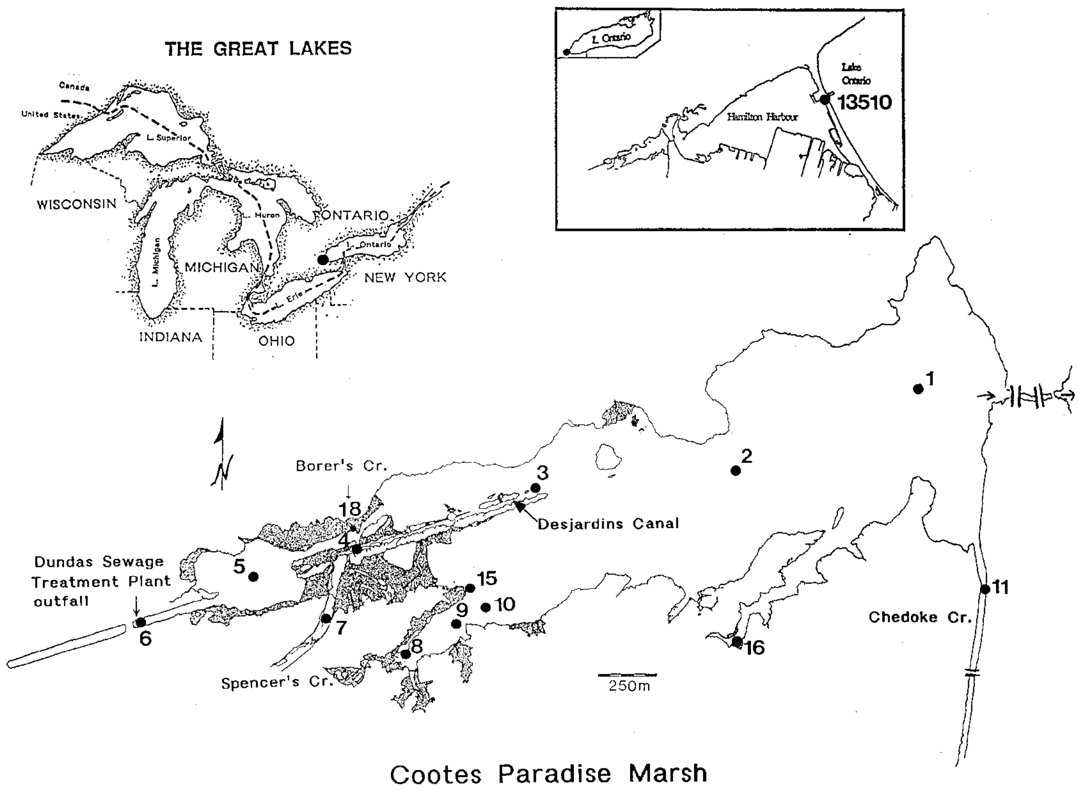

Figure 1. Map of Cootes Paradise Marsh showing the various sampling stations in this study.

From 1919 to 1962, a sewage treatment plant (STP) had discharged primary-treated sewage into the western end of the Desjardins Canal (Figure 1; McLarty and Thachuk, 1986). As nearby Dundas and Waterdown became developed, more sewage was discharged into the marsh, and it became necessary to upgrade the plant to a secondary treatment facility in 1962. Phosphorus loading from the sewage plant in the early 1970s was estimated at 45 kg d^{-1} (Semkin et al., 1976) and caused advanced cultural eutrophication in the marsh. In 1978, the plant was upgraded to a tertiary-treatment facility, and sand filters were added to further reduce the loading of phosphorus into the marsh in 1987. Data provided by the Hamilton-Wentworth Region indicate that P-loads from the sewage plant have steadily decreased to levels well below 4 kg d^{-1} in recent years.

Water levels

Approximately weekly water-level data were collected between May and September in 1992 from a benchmark located near the southwestern end of the marsh (Station 10 in Figure 1). Continuous water levels had been recorded since 1970 at station 13150 which is located at the Burlington ship canal connecting Hamilton Harbour to Lake Ontario (see Figure 1 inset of Hamilton Harbour). These data were obtained from the Marine Environmental Data Services Branch of the Department of Fisheries and Oceans, Ottawa (1971–1988) and from the Tides, Currents and Water Levels at the Canada Centre for Inland Waters, Burlington (1989–1996) and were referenced to the 1985 International Great Lakes Datum (IGLD). A predictive relationship was developed between water levels measured at the benchmark in 1992 and those measured contemporaneously at the Burlington station (Equation 1), and this was subsequently used to derive a 26-y record of monthly water levels for Cootes Paradise Marsh.

$$\mathrm{WL\ (C)} = 1.038\ (\pm 0.029) * \mathrm{WL\ (B)} - 2.802 \qquad (1)$$

$$n = 38 \quad r^2 = 0.88 \quad P < 0.0001$$

where WL(C) and WL(B) are the water levels (m) for Cootes and Burlington, respectively.

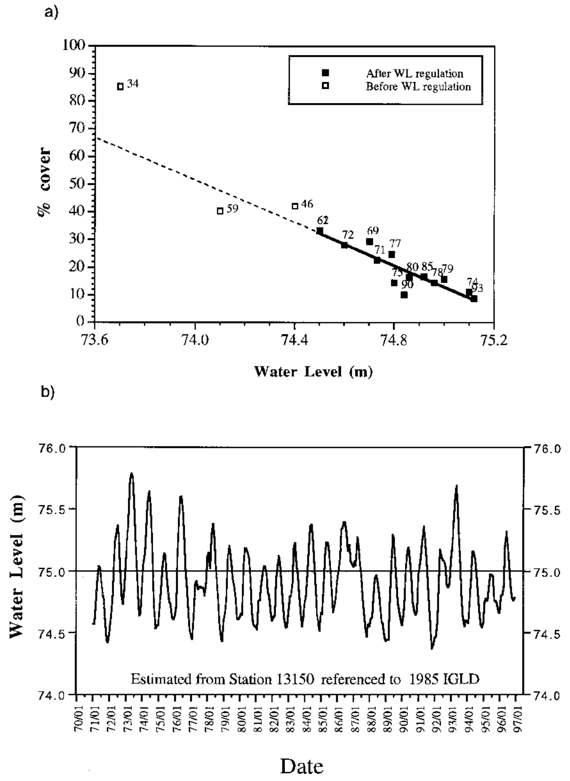

Figure 2. a) Percent areal cover of emergent vegetation versus mean summer water level in Cootes Paradise Marsh. Open and solid squares correspond to years before and after operation of the St. Lawrence Seaway in 1959, respectively. The linear regression equation corresponding to the best-fit line through data points after 1960 is: % cover = 38.829 Mean Water Level +2924.97 $r^2 = 0.812$ $P < 0.0001$. b) Changes in mean monthly water levels (m above sea level) for Cootes Paradise Marsh from 1971 to 1996 inclusive (see Methods for explanation of how we calculated water levels for the marsh). The reference line indicates 75.0 m above sea level.

We used data derived from Equation 1 to calculate mean summer (May to August inclusive) water levels to use with areal percent cover data in Figure 2a. For years prior to 1970, we used data reported in Lavender (1987), which had been collected by the Department of Fisheries and Oceans at a Toronto, Ontario station.

Distribution and taxonomic composition of aquatic vegetation

We obtained twenty estimates of areal cover of emergent vegetation between 1934 and 1993 for Cootes Paradise Marsh (Table 1). These estimates were obtained in several ways. Lavender (1987) obtained historical aerial photographs that varied in scale from 1:1400 to 1:50 000), and determined % aerial cover from digitized photos. Field data were collected by staff of the Royal Botanical Gardens (L.E. Wragg, A. Tamsalu, J. Lord and L. Simser) between 1946 and 1993. These data were digitized by J. Minor from the McMaster Eco-Research Program for Hamilton Harbour using ARCINFO. This produced vegetation maps that were later used to estimate percent cover by the authors. Chow-Fraser used a planimeter to estimate the 1990 value from a color aerial photograph (1:5000). In spite of differences in techniques, estimates from aerial photographs are comparable to those obtained from digitizing vegetation maps since estimates produced by both methods for 1974 were similar (11.0 and 8.0%, respectively). Summary lists of aquatic plants found in Cootes Paradise Marsh between 1946 and 1993 were prepared from Lamoureux (1957), Simser (1982) and Benckhuysen and Pomfret (unpub. data, Royal Botanical Gardens)

Table 1. Summary of areal cover of emergent vegetation in Cootes Paradise Marsh. See Methods for explanation of data sources

Year	% areal cover	Data source
1934	85.4	Lavender (1987)
1946	42.1	L.E. Wragg (unpub. data)
1950	25.1	Lavender (1987)
1953	12.6	A. Tamsalu (1953)
1954	20.2	Lavender (1987)
1959	40.3	Lavender (1987)
1961	33.2	Lavender (1987)
1962	33.3	Lavender (1987)
1969	29.4	Lavender (1987)
1971	22.7	Lord (unpub. data)
1972	28.0	Lavender (1987)
1974	11.0	Lavender (1987)
1975	14.5	Lord (unpub. data)
1977	24.8	Simser (unpub. data)
1978	14.5	Simser (unpub. data)
1979	15.8	Simser (unpub. data)
1980	16.4	Lavender (1987)
1985	16.6	Lavender (1987)
1990	10.0	Chow-Fraser (unpub. data)
1993	13.7	Simser (unpub. data)

Water quality

Three major limnological studies were conducted between 1948 and 1994 by Kay (1949), Bacchus (1974) and Lougheed and Chow-Fraser (1998). Data corresponding to three comparable stations in each of these studies have been used for this retrospective. One station was located at the eastern open-water area (near Station 1, Figure 1), and another at Dundas Sewage Treatment Plant (STP) outfall at the far western end of the Desjardins Canal (Station 6, Figure 1). The third was in a vegetated area but because of differences in plant distribution, the location of this has changed between the study periods. As discussed later, the location of the vegetated station was much further west in the most recent survey compared with that in the 1948 study.

We also used a long-term monitoring database to determine changes in water quality along a west-to-east gradient from 1973 to 1996. Data had been collected by Bacchus (1974) in 1973, L. Simser (unpub. data, Royal Botanical Gardens) from 1975 to 1992, and P. Chow-Fraser (unpub. data, McMaster University) from 1993 to 1996, at 6 sampling sites (Stations 1 to 6, Figure 1). Four standard nutrient variables (see Chapman, 1992) will be reported in this study, including total phosphorus (Total P), soluble reactive phosphorus (Soluble reactive P), total ammonia nitrogen (Total NH_4-N) and total nitrate nitrogen (Total NO_3-N). In addition, PAR (the photosynthetically active radiation) was measured with a LiCor photometer and spherical submersible sensor at 10-cm intervals throughout the water column at all sites to calculate total light extinction coefficients. This coefficient is the negative slope of the regression of the natural log of light intensity against depth (m), and can be interpreted as the rate of light attenuation; therefore, the more turbid the water, the faster light attenuates, and the higher the coefficient.

Biotic communities

A species list of phytoplankton was compiled using data collected in 1948–9 (Sims, 1949), 1973–4 (Bacchus, 1974) and 1993–1996 (Chow-Fraser, unpub. data). Samples were collected from at least 3 stations in each of these studies during the summer months. Sims collected samples from two open-water and one vegetated site; Bacchus collected from at least three open-water sites while Chow-Fraser collected from three open-water sites and three vegetated sites. Unfortunately, no direct comparison of algal biomass can be made because the authors did not include size measurements in the earlier studies. During 1993, 1994 and 1996, Chow-Fraser collected monthly samples at several stations in the open water, Station 1, 3, 5 and 9 to determine the relationship between phytoplankton biomass and phosphorus concentration. In 1996, we examined the relationship between algae and macrophytes by conducting a more intensive sampling program in the southern marsh inlets. We collected daytime (July 31, 1996) and nighttime (August 1, 1996) samples at Stations 8, 9 and 16, and at increasing distances from Station 15 along a 32-m transect. These are referred to as 15a, 15b and 15c, and are 6, 12 and 32 m, respectively away from the macrophyte bed at Station 15. We followed the method used by Chow-Fraser and Knoechel (1985) to identify and enumerate algae.

Mean densities of zooplankton (#/L) were assembled from studies by Kay (1949), Simser (1982) and Lougheed and Chow-Fraser (1998). These were calculated separately for open-water and vegetated sites, and represent means of samples collected between May and September. The vegetated site in Lougheed and Chow-Fraser's study corresponds to Station 8 in Figure 1. We used average dimensions measured during the most recent study and applied length-weight regressions (see Lougheed and Chow-Fraser, 1998) to estimate zooplankton biomass for comparison among the three time periods. We conducted a program to monitor the spatial distribution of zooplankton in the marsh inlets on July 31 and August 1, 1996 to parallel the phytoplankton samples collected at Stations 8, 9, 16, 15, 15a, 15b and 15c.

Aquatic insects found in Cootes Paradise between 1948 and 1995 were assembled from Judd (1955), Simser (1982) and Fitzgerald (1996). The earlier survey included data from both vegetated and open-water areas, although the more recent surveys concentrated on open-water areas. The composition of benthic invertebrates has been used extensively in the literature to indicate environmental quality in streams and lakes, and in particular to test for adverse impacts of pollutants discharged into watercourses (e.g., Borchardt and Statzner, 1990; Maltby et al., 1995). However, it is difficult to compare benthic communities among studies unless the same methodology is used, and since we could not ascertain that the same sampling methods had been used in the three studies, we only report changes with respect to the relative increase in pollution-tolerant organisms or the disappearance of pollution-intolerant ones to indicate deterioration in the environment (Pitt and Bozeman, 1982; Striegl, 1985; Pitt et al, 1995).

Presence/absence data of dominant fish species in Cootes Paradise from 1948 to 1981 have been collected and published extensively elsewhere (Kay,

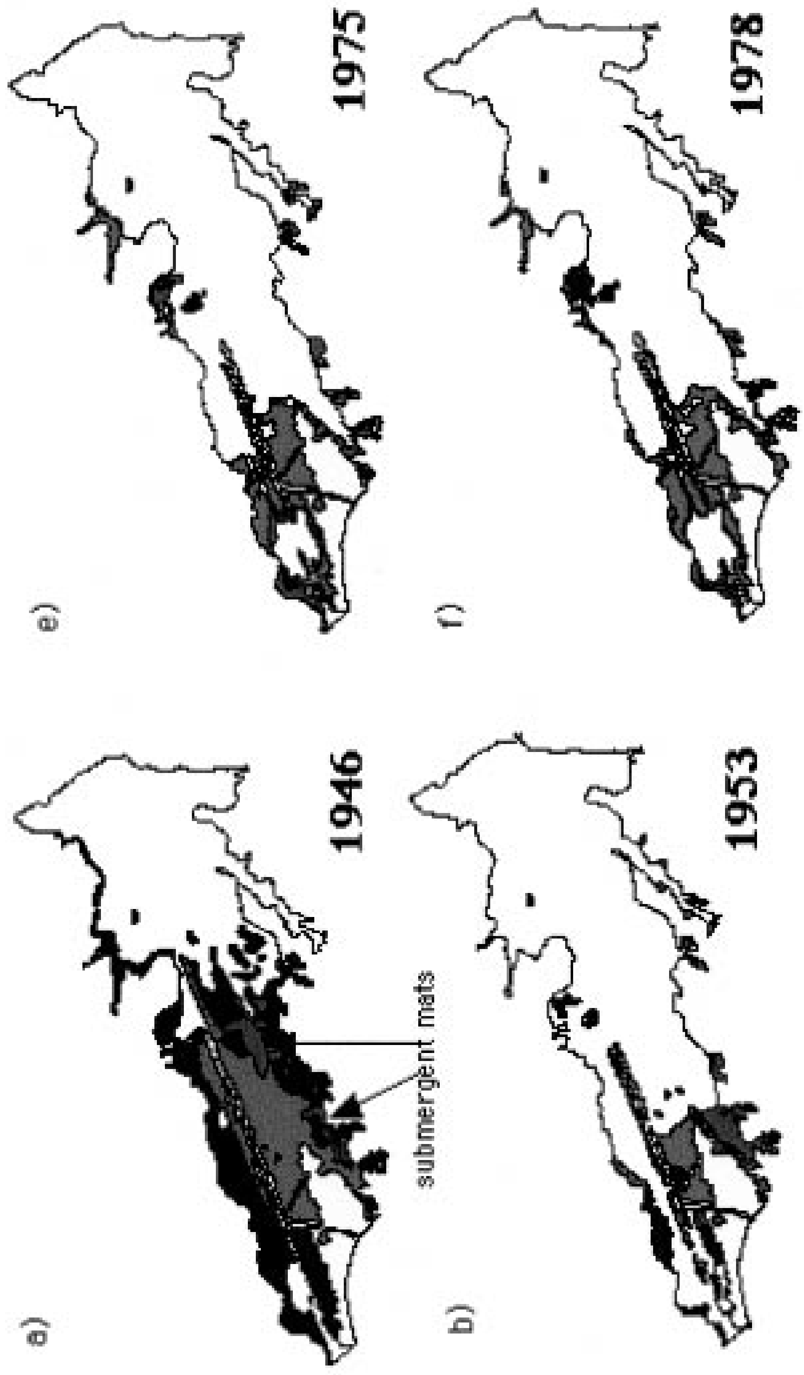

Figure 3.

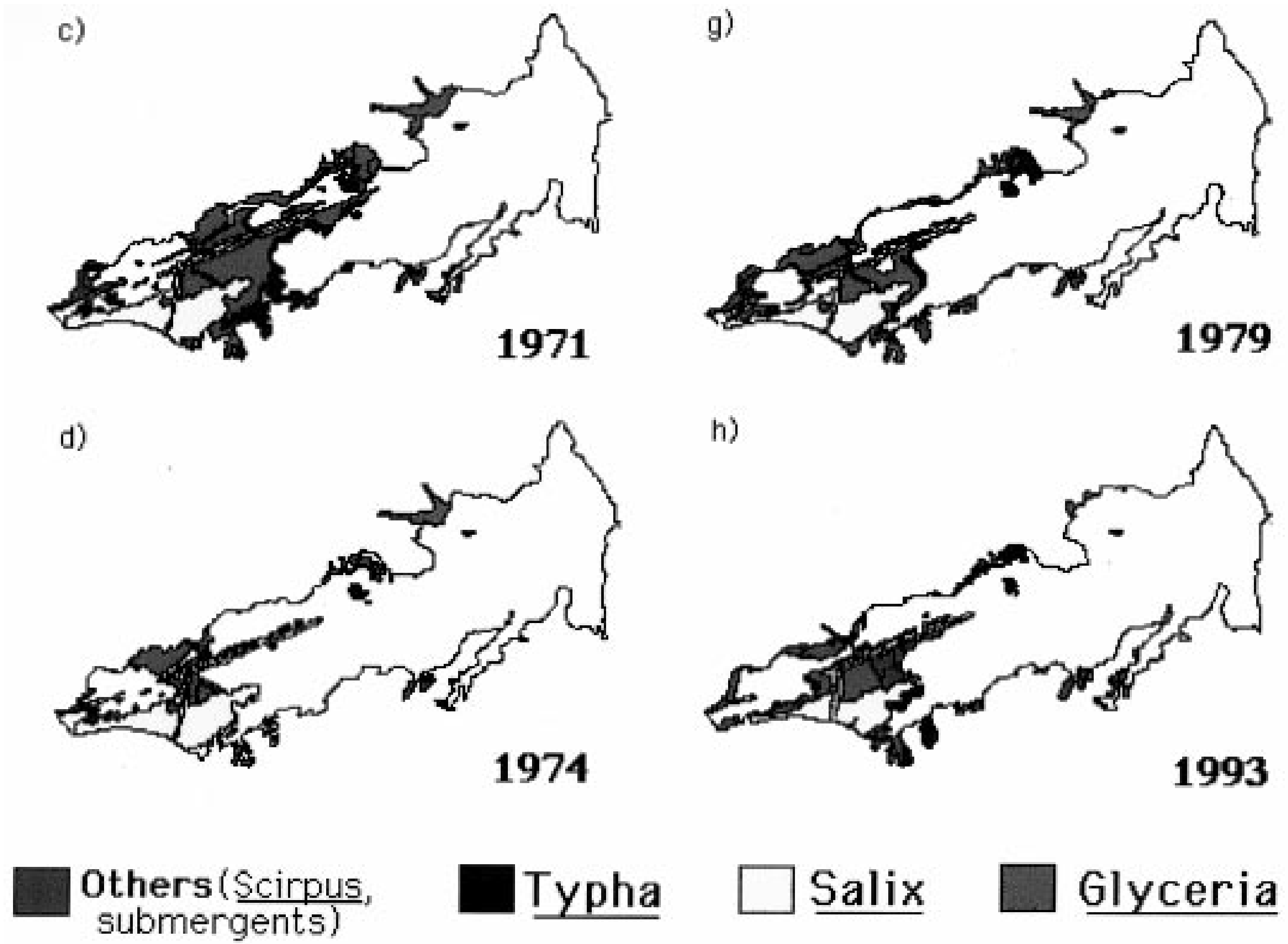

Figure 3. Vegetation maps of Cootes Paradise Marsh from 1946 to 1993. See Table 1 for data sources. These maps have been digitized into ARCINFO by the McMaster Eco-Research Program for Hamilton Harbour at McMaster University.

1949; Whillans, 1982; Holmes and Whillans, 1984; Holmes, 1988). However, no published sources of fish data for Cootes Paradise are available for the more recent period, and therefore, we will not include a table for comparison but will instead refer to several unpublished surveys conducted between 1993 and 1996 by the Department of Fisheries and Oceans and the Royal Botanical Gardens. We will also use results from Randall et al. (1993) to give an overall indication of the recent trophic structure of the fish community in nearby Hamilton Harbour since many of the fish migrate from the harbor into Cootes and visa versa.

Results

Percent areal cover

According to Whillans (1982), 76% of the areal cover of emergent vegetation which had originally been present in Cootes Paradise and nearby Hamilton Harbour during the early 1800s, had disappeared by the late 1970s. From vegetation maps and aerial photographs of Cootes Paradise itself, it is clear that the decline actually began shortly after 1934 (Table 1), when the mean summer water level was at about 73.7 m (Lavender, 1987). Twelve years later, when seasonal water levels were extremely high, emergent vegetation covered only 42% of the marsh (Kay, 1949). Water levels continued to be high over the next decade, and when levels exceeded 75.0 m during the early 1950s, areal cover plunged below 25%. During this period, the common carp (*Cyprinus carpio*), an exotic species which had been introduced to the marsh in 1908, became abundant and was also implicated in the decline (Kay, 1949; Wragg, 1949; Whillans, 1996). Royal Botanical Gardens, which owns and manages the marsh, carried out a carp removal program between 1952 and 1956 and netted a total of 93 000 carp (Simser, 1982). Although a survey conducted in 1959 showed that the cover of emergent vegetation had increased to 40%, it is difficult to attribute this recovery entirely to the removal of carp since attending water levels had also dropped to 74.0 m.

With construction of the St. Lawrence Seaway in 1959, water levels in Lake Ontario became regulated and the occurrence of low water levels was eliminated in subsequent years (Maynard and Wilcox, 1996). Mean summer water levels obtained for the 1960s ranged from 74.5 to 74.7, and corresponding areal cover (29 to 33% fell close to the best-fit line relating percent cover to mean water level (Figure 2a). Record high water levels were recorded during the summer of 1973 (Figure 2b) and in the following year, the areal cover dropped to 11% (Table 1; Figure 2a). In 1977, summer water levels receded again (Figure 2b) and this was accompanied by a substantial recovery of emergent vegetation (24.8%) (Table 1). From the highly significant inverse relationship between water levels and areal cover for years since 1960 (best-fit line in Figure 2a), it is clear that the primary determinant of emergent cover was mean summer water level. It is worth noting that the 1934 data point sits well above the line of best fit for data corresponding to years after 1960, and this may be evidence that carp disturbance and sewage discharge in later years has had a measurable impact on the growth of emergents in Cootes Paradise Marsh.

Change in aquatic plant distribution and species composition

Until the mid-1900s, 90% of Cootes Paradise was a densely covered cattail (*Typha latifolia*) marsh, rich in associated species that included wild rice (*Zizania aquatica*), along with substantial growth of submergent plants such as waterweed (*Elodea canadensis*), bladderwort (*Utricularia* sp.) and coontail (*Ceratophyllum demersum*) (Lord, 1993). By the 1940s, the emergent marsh began receding westward until the whole eastern end was open water. This pattern of retreat reflected the depth gradient that ranged from 30 cm in the southwestern end to 150 cm in the eastern end (Kay, 1949). Field surveys conducted between 1946 and 1948 indicate that the aquatic vegetation was well represented by emergent, submergent and floating taxa (Table 2), even though the distribution of submergent species was limited to only two small areas (Figure 3a).

Two subsequent surveys, conducted between 1968–72 and again in 1993, revealed a dramatic decline in the species richness of submergent plants over the 4 decades; the 16 species present during the 1946 survey had been reduced to 7 in the 1968–72 survey and only 5 in the 1993 study, comprising much less than 1% of the surface area of the marsh (Table 2; Figure 3h). A number of emergent taxa had also diminished in abundance or completely disappeared in 1971 making way for the expansion of manna grass (*Glyceria maxima*; Figure 3c) which may have been introduced only decades earlier (Lord, 1993). By

Table 2. List of aquatic plants found in Cootes Paradise Marsh between 1946 and 1993. Data source: B. Lamoureux (1950), Simser (1982), and Pomfret and Benckhuysen (unpub. data, Royal Botanical Gardens). 1 = not common or dominant; 2 = common but not abundant; 3 = abundant and dominant; X = present but relative abundance not recorded. The macroscopic alga, Chara, was also present during the 1946–8 survey

Type	Genus & Species	Common name	1946–8	1968–72	1993
Emergent	*Decodon verticillatus*	Swamp Loosestrife	2	1	1
	Echinochloa frumentacea	Japanese Millet	3		
	Fagopyrum esculentum	Buckwheat	X		
	Fagopyrum tataricum	Duckwheat	X		
	Glyceria maxima	Manna Grass	3	3	3
	Iris versicolor	Wild Iris (Blue Flag)	X	X	X
	Iris pseudacorus	Fleur de Lis (Yellow Flag)	X	X	X
	Peltandra virginica	Arrow Arum	2	1	1
	Phragmites australis	Common Reed (introduced)		2	2
	Polygonum coccineum	Marsh Smartweed	2	1	1
	Pontederia cordata	Pickerel Weed	2	1	1
	Sagittaria latifolia	Arrowhead (Duck Potato)	2	1	1
	Sagittaria cuneata	Arrowhead (Wapato)	2		
	Scirpus acutus	Hardstem Bulrush	2	X	
	Scirpus americanus	Three-square Rush	2		
	Scirpus fluviatilis	River Bulrush	2	X	
	Scirpus validus	Softstem Bulrush			X
	Sparganium eurycarpum	Giant Burreed	2	2	1
	Typha angustifolia	Narrow-leaved Cattail			1
	Typha × *glauca*	Hybrid Cattail			3
	Typha latifolia	Broad-leaved Cattail	3	3	1
	Zizania aquatica	Wild Rice	X		
Submergent	*Ceratophyllum demersum*	Coontail	3	2	1
	Elodea canadensis	Waterweed	2	1	X
	Megalodonta beckii	Water Marigold	1		
	Myriophyllum verticillatum	Green Water Milfoil	3		
	Najas flexilis	Bushy Pondweed	1		
	Polygonum amphibium	Water Smartweed	2	1	1
	Potamogeton berchtoldii	Small Pondweed	1		
	Potamogeton crispus	Pondweed	2	2	
	Potamogeton foliosus	Leafy Pondweed	1		
	Potamogeton nodosus	Knotty Pondweed	2	1	
	Potamogeton pectinatus	Sago Pondweed	2	3	2
	Potamogeton perfoliatus	Pondweed	1		
	Potamogeton zosteriformis	Pondweed	2		
	Utricularia vulgaris	Bladderwort	3		
	Vallisneria americana	Wild celery (eel grass)	2	1	X
Floating	*Lemna minor*	Lesser Duckweed	3	3	2
	Lemna trisulca	Star Duckweed	1		
	Nuphar advena	Spatterdock	3		X
	Nuphar variegatum	Yellow Water Lily	3	2	1
	Nymphaea odorata	Fragrant Water Lily	3		X
	Nymphaea tuberosa	White Water Lily	3	3	1
	Spirodela polyrhiza	Greater Duckweed	1	1	

Table 3. Summary of changes in water quality characteristics of Cootes Paradise Marsh from 1948 to 1994. Data represent seasonal means (May to September) and were obtained from Kay (1949), Bacchus (1974) and Lougheed and Chow-Fraser (1997). See Figure 1 and 4 for location of sampling stations. Asterisks indicate that the value was estimated from empirically-derived relationship between turbidity and 1/Secchi depth at respective stations during the 1993–4 study. 'STP' refers to the Dundas Sewage Treatment Plant

Station	Parameter	1948	1973	1993	1994
Open water	Secchi depth (cm)	40	23	17	22
	Dissolved oxygen (mg L^{-1}) – surface	8.8	10.5	10.0	9.4
	– bottom	7.6	–	–	–
	pH	8.6	–	8.5	8.1
	Turbidity (FTU)	*31	37	69	54
	Chlorophyll-*a* (μg L^{-1})	–	189	23	54
	Total Phosphorus (mg L^{-1})	–	2.22	0.16	0.13
	Total Nitrate Nitrogen (mg L^{-1})	0.88	0.70	0.67	0.58
	Total Ammonia Nitrogen (mg L^{-1})	1.00	0.45	0.12	0.14
	Total Nitrogen (mg L^{-1})	–	–	3.24	3.22
	Total Dissolved Phosphorus (mg L^{-1})	–	0.96	0.03	0.02
	Suspended Solids (mg L^{-1})	–	–	43.4	72.3
Vegetated	Secchi depth (cm)	76	–	23.4	16.8
	Dissolved oxygen (mg L^{-1}) – surface	3.6	–	6.3	7.3
	– bottom	2.3	–	–	–
	pH	8.0	–	8.0	7.9
	Turbidity (FTU)	*5	–	24.8	50.3
	Chlorophyll-*a* (μg L^{-1})	–	–	6	45
	Total Phosphorus (mg L^{-1})	–	–	0.23	0.21
	Total Nitrate Nitrogen (mg L^{-1})	1.20	–	0.50	0.35
	Total Ammonia Nitrogen (mg L^{-1})	0.60	–	0.17	0.16
	Total Nitrogen (mg L^{-1})	–	–	3.59	2.60
	Total Dissolved Phosphorus (mg L^{-1})	–	–	0.08	0.06
	Suspended Solids (mg L^{-1})	–	–	60.5	100.0
STP outfall	Secchi depth (cm)	–	42	37	49
	Dissolved oxygen (mg L^{-1}) – surface	–	7.4	10.9	11.1
	– bottom	–	–	–	–
	pH	7.7	–	8.0	7.8
	Turbidity (FTU)	–	16.8	16.5	15.4
	Chlorophyll-*a* (μg L^{-1})	–	206	17	51
	Total Phosphorus (mg L^{-1})	–	15.4	.20	.15
	Total Nitrate Nitrogen (mg L^{-1})	1.00	2.16	7.77	10.26
	Total Ammonia Nitrogen (mg L^{-1})	10.00	8.27	0.26	0.27
	Total Nitrogen (mg L^{-1})	–	–	11.49	12.64
	Total Dissolved Phosphorus (mg L^{-1})	–	10.69	0.06	0.07
	Suspended Solids (mg L^{-1})	–	–	19.2	35.1

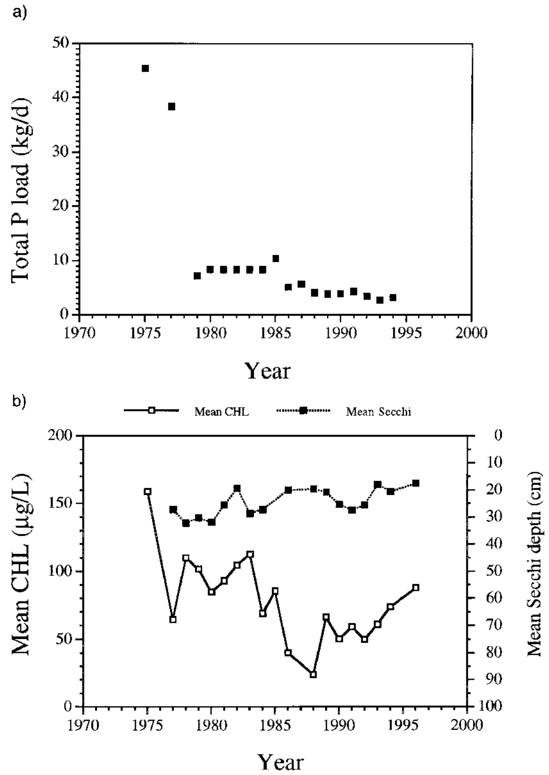

Figure 4. a) Changes in the total phosphorus load from the Dundas Sewage Treatment Plant from 1975 to 1994. b) Changes in mean chlorophyll a (CHL) concentration and mean Secchi depth transparencies corresponding to data collected from Stations 1 to 5 inclusive from 1975 to 1996.

1993, the emergent marsh had retreated to the western rim of Cootes Paradise, both manna grass and cattails comprising 43 and 27%, respectively of the area covered by aquatic plants (Figure 3h). The introduced species, common reed (*Phragmites australis*) and purple loosestrife (*Lythrum salicaria*) were also prominent members of the emergent plant community during the 1993 survey. By comparison, there were few changes in the species composition of floating aquatic vegetation, even though their relative abundance had declined over the four decades; remarkably, five of the original seven species surveyed in 1946 were still present in 1993 (Table 2).

History of water quality changes

Table 3 summarizes changes in water quality from 1948 to 1994. Water clarity at the open-water station (Station 1 in Figure 1) had been relatively poor even in 1948, with Secchi depth transparency of 40 cm and corresponding water turbidity of 31 FTU. A 1949 aerial photograph of Cootes Paradise Marsh shows that much of the land surrounding the marsh had been cleared for agriculture and probably contributed a great deal of sediment and nutrients to the wetland (Ehrenfeld, 1983; Roth et al., 1996; Crosbie and Chow-Fraser, manuscript). Both Kay (1949) and Sims (1949) reported that the open-water of the marsh was windswept and very turbid. As a result of increased algal growth, this situation worsened in 1973 and light penetration became even shallower (Secchi depth and water turbidity of 17 and 37, respectively). In the most recent survey, water clarity has not improved despite the substantial reduction in concentrations of total phosphorus (2.2 versus 0.15 in 1973 and 1993) and chlorophyll (189 versus 23 μg L^{-1} in 1973 and 1993) following upgrade of the sewage plant to a tertiary-treatment facility.

By contrast, water had been very clear at the vegetated station during 1948 (inside submergent mat in Figure 3a), with Secchi depth transparency of 76 cm (that probably reached the sediment), and corresponding water turbidity of only 5 FTU (Table 3). However, by 1993, water turbidity at comparable sites had increased five-to-ten-fold, and corresponding Secchi depth were only marginally better than that measured at the open-water site.

The wind in the open-water tended to keep the water column mixed and well-oxygenated down to the bottom; however, Kay (1949) reported that the vegetated station became anoxic during nighttime in mid-summer, particularly near the sediment, where plant and animal material decomposed (Table 3). In the more recent surveys, oxygen concentrations have consistently been found close to saturation except for the vegetated site where levels have dropped to 5 to 6 mg L^{-1} during the day, and below 2 mg L^{-1} during the night (Chow-Fraser, unpub. data). There have also been dramatic changes in the concentrations of primary nutrients in the water column that reflected improvement in the quality of the sewage effluent after the treatment plant became upgraded in 1978 (Table 3). In the 1948 survey, the best evidence of the sewage effluent was the extremely high levels of total ammonia (10 mg L^{-1}) at a station near the STP outfall (Station 6).; this level would greatly exceed permissible levels according to today's standards. Unfortunately, there were no measurements of phosphorus and we do not know if the marsh had been able to assimilate the incoming phosphorus loads during the 1940s. By 1973, however, the marsh had clearly become hypereutrophic, with total phosphorus (TP)

Table 4. Summary of the concentration of inorganic suspended solids (mg L^{-1}) and the proportion that it represents in the total suspended solids

Year	Inorganic Suspended Solids	% Inorganic
1988	33.3	44
1991	34.2	40
1993	32.6	66
1994	71.6	81
1995	65.0	73
1996	55.1	76

concentrations of 15.4 and 2.2 mg L^{-1} at STP outfall and open-water sites (Station 1), respectively. These levels were attended by some of the highest chlorophyll (CHL) concentrations ever documented (as high as 3900 μg L^{-1} and a seasonal mean of 700 μg L^{-1} at Station 5; Harris and Bacchus, 1974). Total ammonia levels remained at unacceptable levels at the STP outfall, although concentrations at the open-water site were much lower.

The significant decrease in phosphorus loads from the sewage treatment plant since 1978 (Figure 4a) has not been accompanied by improvements in water clarity. On the contrary, there has been a significant decrease in mean Secchi depth transparency in the marsh (Figure 4b; Kendall's tau statistic, $P < 0.02$) despite a corresponding decrease in CHL concentrations (Figure 4b; Kendall's tau statistic, $P = 0.009$). A possible cause for this discrepancy may be that erosion from the watershed has increased over the past decade, and this is supported by the disproportionate increase in inorganic suspended solids (i.e., not combustible at 550 °C) in the water column since 1988 (Table 4). In recent years, approximately 80–90% of the suspended solids in the tributaries of Cootes Paradise Marsh has been inorganic, rather than organic (including algae and bacteria) (Chow-Fraser et al., 1996). The erosional material is very fine silt and clay of the Niagara Escarpment, and is easily kept in suspension by the prevailing winds and by bioturbation (activities by bottom feeders such as common carp) (Sager, 1996; Lougheed et al., 1998).

Water quality data collected at six stations, located at fairly regular distances downstream of the Sewage Treatment Plant (Stations 1 to 6; Figure 1) are used to evaluate the effectiveness of the sewage upgrades on nutrient concentrations in the marsh. Prior to tertiary treatment, there was a very steep west-to-east gradient of all four nutrients from the sewage plant outfall to the marsh outflow (Figure 5a-d). Mean concentrations of Total P and Soluble reactive P entering the marsh at the sewage outfall (Station 6) were almost five-fold higher than those measured at Station 1 (Figure 5a and b, respectively), while Total NH4-N levels were more than ten times higher, and Total NO_3-N five times higher (Figure 5c and d, respectively). These steep gradients indicate that the Sewage Treatment Plant was a gross polluter of the marsh environment.

In the eight years following upgrade to a tertiary facility, the sharp west-to-east gradient in phosphorus concentrations disappeared (Figure 5a and b), but the slight differential between Stations 6 and 1 with respect to Total NH_4-N concentrations was still evident (Figure 5c). During this period, the treatment plant aerated the sewage effluent to reduce the loading of Total NH_4-N to the marsh , but in so doing, they increased the loading of Total NO3-N. Consequently, nitrate concentrations since 1978 have doubled at Station 6, and have been consistently ten times higher than those measured at Station 1 (Figure 5d). Nevertheless, the nitrate pollution seems to have a disproportionate effect on West Pond (Station 5) since levels measured at the three stations downstream of Station 4 have not changed greatly over the study period. The addition of sand filters to further reduce phosphorus concentrations in the sewage effluent in 1988 has had a measurable but small improvement on the phosphorus concentration at Station 6 but no significant impact on the nutrient status in the rest of the marsh (Figure 5a and b).

History of changes in the biotic communities

Phytoplankton

There were corresponding changes in the algal community of Cootes Paradise Marsh over the past 4 decades that mirrored changes in water quality and loss of aquatic plant cover (Table 5). Sims (1949) sampled from an open-water station in the northeast corner of the marsh, a station in the Princess Inlet (upstream of Station 11 in Figure 1), and a vegetated station close to where Kay (1949) found submergent plants on the south shore of the marsh (Figure 3a). During this time, the western half of Cootes Paradise had been covered with emergent vegetation. Princess Inlet was thought to be polluted by runoff from a domestic disposal lot, and effluent from a storm sewer that discharged

Table 5. List of phytoplankton found in Cootes Paradise from 1948 to 1994. Data were obtained from Sims (1949), Bacchus (1974), and from this study. Data reported here are representative of open-water sites (including West Pond) sampled regularly over the ice-free season. 'XX' indicates that the genus was very abundant

Algal Group	Genus	1948–9	1973–4	1993–4
Cyanophyceae	*Anabaena*		XX	X
	Aphanizomenon	XX	XX	
	Aphanocapsa	X	XX	X
	Chroococcus		X	X
	Coelosphaerium	X		
	Dactylococcus		X	
	Gleotrichia		XX	
	Lyngbya		X	
	Merismopedia		XX	X
	Microcystis	X		
	Nostoc		XX	
	Oscillatoria	X	XX	X
	Pelonema			X
	Rhabdoderma			X
Chlorophyceae	*Actinastrum*	XX	X	X
	Ankistrodesmus	X	X	X
	Arthrodesmus	X		X
	Asterococcus	X	X	
	Carteria		X	XX
	Chlamydomonas	X	X	XX
	Chlorella		X	XX
	Chlorococcus		X	XX
	Chlorogonium		X	X
	Closteriopsis	X	X	X
	Closterium	XX	X	X
	Coccomonas			XX
	Coelastrum	XX	X	X
	Cosmarium	X	X	X
	Crucigenia	X		X
	Dictyosphaerium	XX		X
	Didymogenes			X
	Echinosphaerella	X		
	Elakatothrix			X
	Euastrum			X
	Eudorina	X		
	Franchia		X	
	Gloeococcus			X
	Golenkinia	X		
	Gonium	X		XX
	Kirchneriella		X	X
	Lagerheimia	X		X
	Micractinium	XX	X	
	Oocystis	X	X	X
	Pachycladon	X		
	Pandorina	X		
	Pediastrum	XX	X	X

Table 5. (continued)

Algal Group	Genus	1948–9	1973–4	1993–4
	Penium			X
	Planctonema			X
	Planktosphaeria	X		XX
	Pseudotetraedron			X
	Quadrigula			X
	Scenedesmus	XX	XX	XX
	Schizochlamys	X		
	Selenastrum	XX	X	X
	Sorastrum	X		
	Spermatozoopsis			X
	Sphaerocystis	X		X
	Sphaerozosma	X		
	Spondylosium	XX		
	Staurastrum	XX		X
	Tetraedron	X	X	X
	Tetradesmus		X	
	Tetrastrum	X		X
	Trochiscia		X	
	Ulothrix			X
Euglenophyceae	*Astasia*			X
	Euglena		XX	XX
	Lepocinclis		X	XX
	Phacus		X	XX
	Trachelomonas		X	X
Chrysophyceae	*Chlorobotrys*	X		
	Chromulina			XX
	Cyclonexis	X		
	Dinobryon			X
	Mallomonas			X
	Ochromonas			XX
	Synura	X	X	X
	Uroglena			X
Bacillariophyceae	*Achnanthes*		X	
	Amphora			XX
	Anomoeoneis		X	
	Asterionella	XX	X	X
	Cyclotella		X	X
	Fragilaria	X		X
	Gomphonema	X		
	Gyrosigma	X	X	XX
	Melosira	X	XX	XX
	Meridion	X		
	Navicula	XX	X	XX
	Neidium			X
	Nitzschia		X	XX
	Rhizosolenia	X		
	Rhopalodia	X		
	Stauroneis	X		
	Stephanodiscus	XX		

Table 5. (continued)

Algal Group	Genus	1948–9	1973–4	1993–4
	Surirella			
	Synedra	X	X	XX
	Tabellaria	X		
Cryptophyceae	*Cryptomonas*		X	XX
	Rhodomonas			X
Dinophyceae	*Amphidinium*			X
	Gymnodinium			X
	Peridinium	X		X
	Glenodinium	X		X

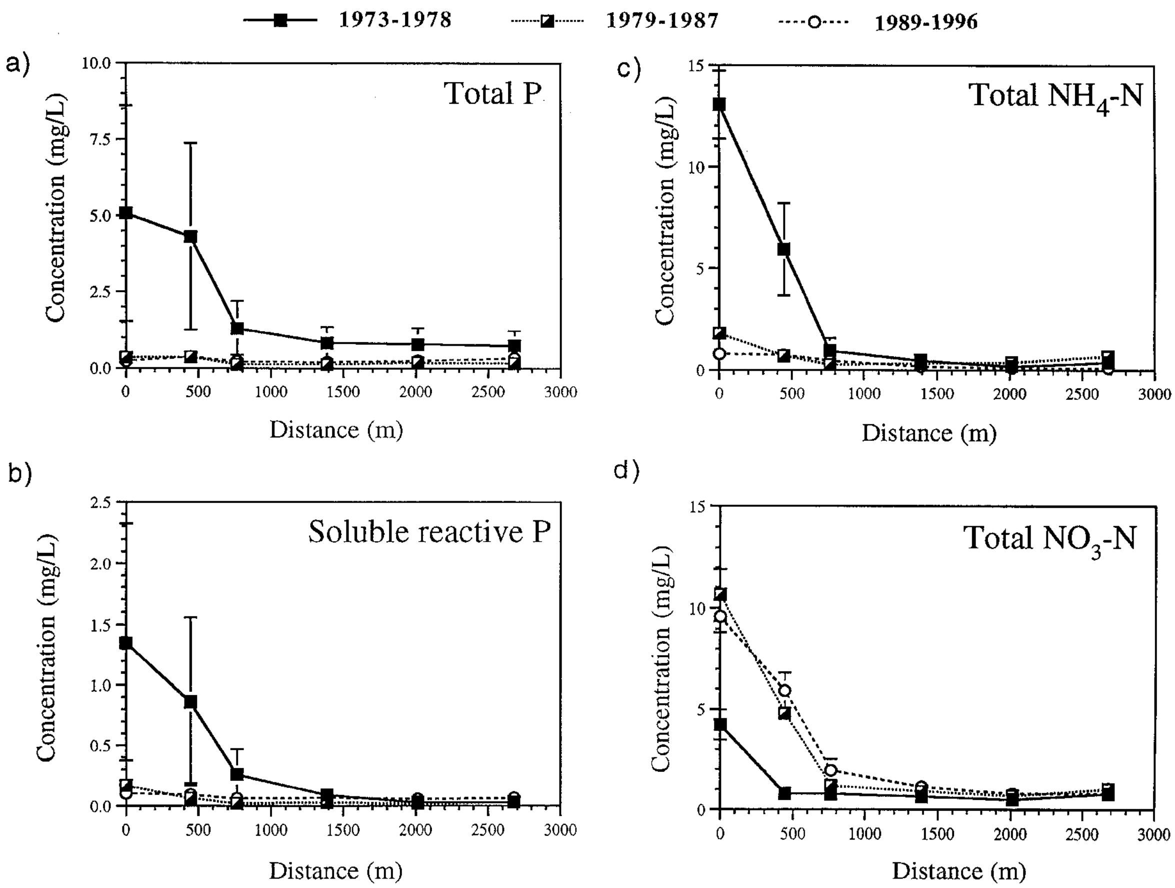

Figure 5. Changes in mean concentration of a) total phosphorus, b) soluble reactive phosphorus, c) total ammonia-nitrogen, and d) total nitrate nitrogen with increasing distance from the Dundas Sewage treatment Plant outfall (sites correspond to Stations 6 to 1, respectively). Seasonal means were calculated for each station in all available years from 1973 to 1996. Data were then sorted according to the timing of sewage plant upgrades. Since the sewage plant was upgraded to a tertiary facility in the fall of 1978, the period prior to upgrade included data collected from May 1973 to Sept. 1978. Because sand filters were installed in July, 1988 (Painter et al. 1991), data from 1988 were excluded. Data between 1979 and 1987 were grouped to evaluate improvements resulting from upgrades to a tertiary facility, whereas data from 1989 to 1996 were grouped to evaluate the effectiveness of the sand filters.

untreated sewage and industrial wastes from parts of West Hamilton. Pollution did not appear to greatly affect the floristic make-up at the three stations. There were abundant green algae (Chlorophyceae) such as *Scenedesmus*, *Closterium*, and *Actinastrum* at all three sites. Diatoms (Bacillariophyceae) such as *Stephanodiscus*, *Asterionella* and *Navicula* appeared in great numbers throughout the marsh, and there were several taxa of yellow-green algae (Chrysophyceae) (Table 5). The periodicity of all taxa occurred approximately at the same time at the three stations. The main exception appeared to be that the blue-green (Cyanophyceae) filament, *Aphanizomenon*, had been abundant at the open-water station and at Princess Inlet throughout the summer months, but only made a brief appearance at the vegetated site. At Princess Inlet, there were also fewer diatoms, and many more colonial green algae such as *Pandorina*, *Eudorina* and *Dictyosphaerium*.

Although pollution did not apparently affect the type of algae found in the marsh, it did, however, appear to affect the quantity of algae collected at the various stations. Sims (1949) noted large differences in average cell densities, which were 5 times higher at Princess inlet compared with the open-water station and 125 times higher than that at the vegetated site. He attributed the higher algal counts at the Princess Inlet to nutrient enrichment from the storm sewer, and runoff from a nearby domestic landfill. The lower algal densities at the vegetated site were attributed to poor light penetration because of presence of submergent mats, and lower nutrient availability.

Twenty years later, emergent vegetation which had receded to the western rim, accounted for only 11% of the surface area. When Bacchus (1974) conducted his sampling, the submergent mat that had been present in the 1948 survey had disappeared, and the phosphorus loading to the marsh had been greatly increased. Filamentous blue-green algae capable of fixing nitrogen such as *Aphanizomenon*, *Anabaena* and *Oscillatoria*, became prominent, although the dominant algae were still members of Green algae, especially species of *Scenedesmus*. At certain times of the year, Bacchus reported that the algae consisted almost entirely of *Scenedesmus*. In addition, the marsh had lost representatives of Chyrsophyceae that had been present in the 1948 survey (Table 5). Instead, species of Euglenophyceae and Cryptophyceae, which are tolerant of low light conditions and capable of heterotrophic growth, were well represented in the marsh.

By 1993, effects of the phosphorus-abatement program (through conversion of the Dundas sewage plant to a tertiary-treatment facility) had become evident in both the water quality and the phytoplankton in the open-water areas of the marsh (Tables 3 and 5, respectively). Blue-green algae were no longer prominent in the algal community, while the species diversity of green algae had markedly increased, surpassing the richness seen in the 1948 survey (Table 6). There was also a return of Chrysophyceae to the marsh, reflecting a return to less eutrophic conditions (Table 3). However, because of high water turbidity, light penetration was still very poor, and this may explain why cryptomonads and euglenophytes were still very abundant compared to the 1973-4 study (Tables 5 and 6). The most significant improvement in terms of the algal community is that phytoplankton standing stock in the open water are now phosphorus limited since both CHL-*a* concentrations and phytoplankton biomass are significantly regressed against total phosphorus concentrations (Figure 6a).

A study was conducted in 1996 to confirm the quantitative differences between vegetated and open-water areas noted in the 1948 survey (Sims, 1949). We collected samples at various distances from cattail beds in the southern marsh inlets (Stations 8, 16, 15, 15a-c, see Methods; Figure 1). Although the algal composition were similar at all these sites, the total phytoplankton biomass increased significantly with linear distance from macrophyte bed. When we included only edible algae (< 10 μm are considered edible to all of the small and large zooplankters in the marsh; Chow-Fraser and Knoechel, 1985; Chow-Fraser, 1986), we found a highly significant curvilinear relationship that explained 89% of the variation (Figure 6b). We also noted that the species richness of the total phytoplankton community increased with distance from the macrophyte bed (Figure 6c), and this is consistent with the less diverse algal assemblage

Table 7. Summary of mean seasonal light extinction coefficients for vegetated and open-water sites during 1994 and 1996. 'n/a' indicates that the station had not been sampled. See Figure 1 for location of the various stations

	Mean Extinction Coefficient					
	Open-water Stations			Vegetated		
Year	1	2	10	8	9	16
1994	6.22	7.79	7.13	8.28	6.79	n/a
1996	8.25	n/a	8.63	7.99	6.61	6.78

Table 6. Summary of number of phytoplankton taxa found in Cootes Paradise Marsh from 1949 to 1994

Study	Cyanophyceae (Bluegreen)	Chloro-phyceae (Green)	Eugleno-phyceae	Chyrsophyceae (Yellow-green)	Bacillario-phyceae (Diatoms)	Crypto-phyceae	Dinophyceae (Dino-flagellates)	Total Community
1949	5	32	0	3	13	0	2	55
1973	10	22	4	1	9	1	0	48
1993–4	7	37	5	6	10	2	4	70

Study Period	Number of Families	Number of Genera
1947	23	57
1976–7	6	9
1995	1	2

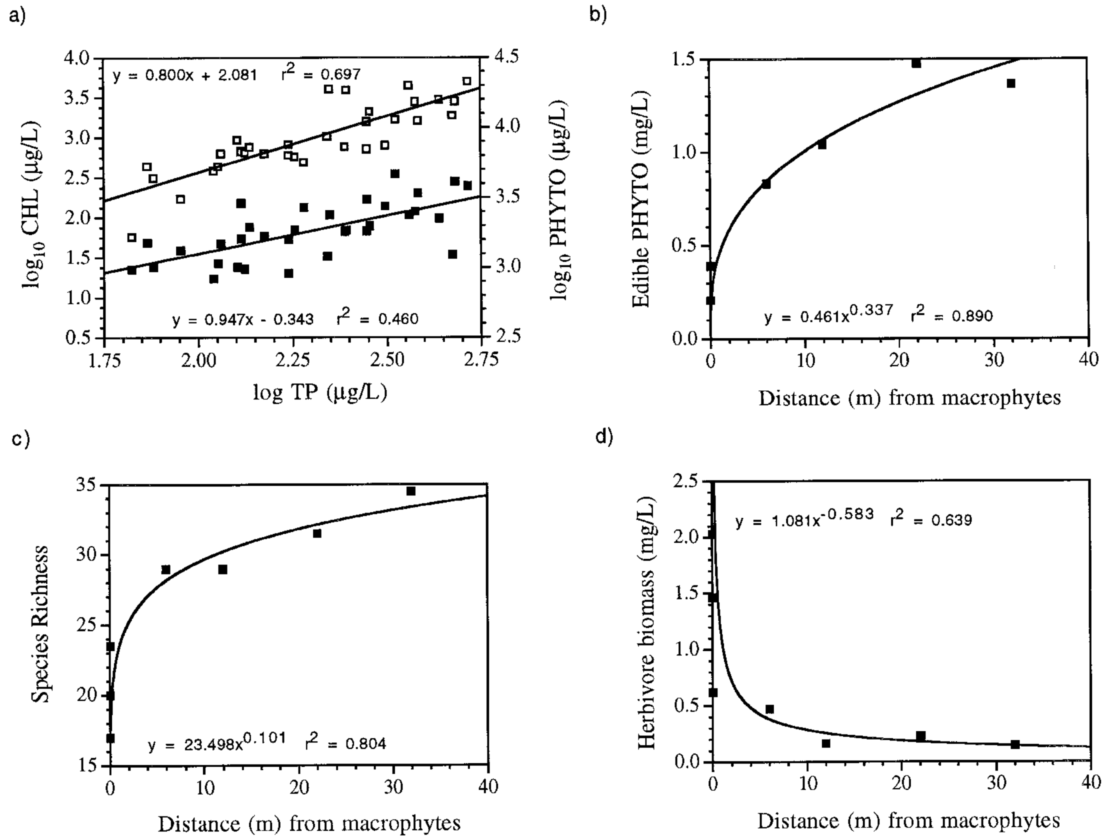

Figure 6. a) $\log_{10}$ chlorophyll *a* concentration (CHL; solid squares) and $\log_{10}$ phytoplankton biomass concentration (PHYTO; open squares) versus log total phosphorus (TP) concentration. Data correspond to samples collected monthly from Stations 1, 5 and 9 in the marsh during the 1993 and 1994 seasons (May to Sept). Lines represent the results of least-squares linear regressions through respective data sets; regression equations for CHL vs. TP and PHYTO vs. TP appear at top and bottom of the panel, respectively. b) Changes in edible (< 10 μm longest linear dimension) phytoplankton biomass (PHYTO) with distance from macrophyte beds. Data are averages for daytime (July 31, 1996) and nighttime (Aug. 1, 1996) samples collected at the following stations: Station 8, 16, and 15 (0 m); Station 15a (6 m); Station 15b (12 m); Station 9 (22 m); and Station 15c (32 m). c) Changes in mean number of species of all phytoplankton found in samples collected at various distances from macrophyte beds. Samples correspond to those in Figure 6b. d) Changes in total biomass of herbivorous zooplankton with distance from macrophyte beds. Location of stations and sample date correspond to those in Figure 6b.

recorded at the vegetated site compared with the two open-water sites in Sims' (1949) study.

Sims postulated that phytoplankton near macrophyte beds had been light-limited. We tested this hypothesis by comparing light extinction data between open-water and vegetated stations for the 1994 and 1996 sampling seasons. Since mean seasonal coefficients corresponding to vegetated sites were very similar to those measured at open-water sites (Table 7), light limitation is not likely the reason for lower algal concentrations near the macrophyte beds.

Zooplankton

The most pronounced change in the zooplankton has been the virtual disappearance of the large cladoceran, *Daphnia*, from Cootes Paradise Marsh. This herbivore is a very efficient filter-feeder that was very common in both the open water and vegetated areas in 1949 (Table 8). On July 23, 1949, Kay (1949) counted more than 300 individuals/L in the vegetated area, while there were much lower densities at two open-water stations (12 and 32 individuals/L). By 1979, Simser (1982) found only 1 animal/L, and this situation did not improve in the 1993-4 survey for either the open-water or vegetated site (Lougheed and Chow-Fraser, 1998). In its place, the smaller cladoceran, *Bosmina*, had become more prominent, and together with *Moina* (a slightly larger cladoceran) accounted for almost all of the herbivorous biomass at the vegetated site.

Although species richness and overall species diversity of the zooplankton has increased over the study period (Table 8), the number of functional groups has actually decreased because the disappearance of *Daphnia* has not been replaced by another large herbivore. When we increased our sampling effort to include sites close to vegetation (Station 15 in Figure 1), we found marginally more *Daphnia* (densities increased from $<$ 1.0 to close to 7 individuals/L at night) (Table 9) but these densities did not approach those enumerated in the vegetated areas in the 1949 survey.

Lougheed and Chow-Fraser (1998) found clear differences in zooplankton biomass and community structure between vegetated and open-water sites (Table 8). Zooplankton densities and the proportion of larger animals were higher in the vegetated areas. Results from our 1996 survey confirmed these trends and indicated a strong inverse relationship between the biomass of herbivorous zooplankton and distance from macrophytes (Figure 6d), which mirrored the significant increase of edible phytoplankton biomass with distance from cattail beds (Figure 6b).

Aquatic insects

In 1948, Judd (1955) surveyed Cootes Paradise Marsh and found 57 genera of larval insects belonging to 23 families and 6 orders (trichopterans, dipterans, ephemeropterans, odonates, lepidopterans and hymenopterans). In 1976, the Ontario Ministry of Environment conducted a benthic survey and found only 9 genera, belonging to 6 families and 3 orders (ephemeropterans, dipterans and hemipterans) (Simser, 1982). Insect diversity continued to decline through the next two decades, and in 1995, Fitzgerald (1996) found only 5 genera, belonging to three families and two orders (dipterans and odonates). The dipterans consisted primarily of chironomids (bloodworms) that are very tolerant of low-oxygen concentrations.

Fish

The historical checklist of fish found in Cootes Paradise Marsh dates back to the 1800s, when the marsh supported an important warmwater fishery (Holmes, 1988; Whillans, 1996). The lists included largemouth and smallmouth bass ((*Micropterus salmoides* (Lacepede) and *M. dolomieui* (Lacepde), respectively), northern pike (*Esox lucius* Linnaeus), muskellunge (*Esox masquinongy* Mitchill), rock bass (*Ambloplites rupestris* (Rafinesque)), brown bullhead (*Ictalurus nebulosus* (Lesueur)), white sucker (*Castostomus commersoni* (Lacepede)) and many cyprinid species, but did not include the common carp (*Cyprinus carpio* (Linnaeus)), which did not make its appearance until 1908 (Holmes, 1988). From 1948 to 1978, the sportfish community declined while the carp population grew. During the 1970s, the population of alewife (*Alosa pseudoharengus* (Wilson)) and perch were seasonally very abundant. Alewife usually migrated from Lake Ontario into embayments and marshes during June and July and fed voraciously on plankton. Their high densities were made possible because of the demise of piscivores such as pike and bass. Gizzard shad, which feed on both filamentous algae and zooplankton were very abundant during this period. Pacific salmon ((e.g. *Oncorhynchus gorbuscha* (Walbaum), *O. kisutch* (Walbaum)) and other migrants also frequented the marsh during the fall to spawn in Spencer's Creek.

The most abundant fish caught in the marsh in recent fish surveys (1993 to 1995) have been cyprinids

Table 8. Density (individuals/L) of zooplankton found in Cootes Paradise Marsh between 1949 and 1994. Data were obtained from Kay (1949; Table 17), Simser (1982; Table 1) and Lougheed and Chow-Fraser (1997). Data for 1949 and 1993–4 are presented for open-water and vegetated sites, separately, whereas data for 1979 had been combined for three stations similar to those sampled by Kay

	1949		1979	1993–4	
Genus	Open	Vegetated	Combined	Open	Vegetated
Copepoda					
Cyclopoid	41	32	45.9	34	34
Calanoid	0.3	0	0	0.7	0.1
Nauplii	107	55	176	237	317
Cladocera					
Bosmina	154	52.4	338	256	431
Daphnia	12	35	1.0	0.9	0
Diaphanosoma	–	–	–	0.2	1.7
Moina	–	–	–	18.5	112
Scapholeberis	–	–	–	0.1	13.5
Rotifera					
Asplanchna	–	–	17	61	25.5
Brachionus	54	2.9	194	178	89
Conochiloides	–	–	330	–	–
Filinia	–	–	1.6	11.2	27.5
Keratella	–	–	128	71	61
Noteus	5.8	6	–	–	–
Notholca	5.7	–	–	–	–
Polyarthra	102	21.5	27.3	150	135
Total (L)	506	209	1259	1058	1321
Total (μg L^{-1})	140	160	164	469	980

Table 9. Summary of densities (L^{-1}) and biomass (μg L^{-1}) of *Daphnia* sp. found at various locations in Cootes Paradise Marsh during daytime July 31 and nighttime August 1, 1996. Numbers in bracket beside station identifier indicates the distance (m) from macrophyte beds. All samples were collected near the mid-point of the water column

	Density		Biomass	
Station	Daytime	Nighttime	Daytime	Nighttime
15c (32 m)	2.0	0.8	1.64	0.64
15b (10 m)	2.6	7.4	2.28	9.79
15a (6 m)	0.2	5.0	0.02	4.33
15 (0 m)	0	1.0	0	3.42

(common carp and hybrids), centrarchids (pumpkinseeds), and clupeids (gizzard shad (*Dorosoma cepedianum* (Lesueur) and alewife)). Brown bullhead (*Ictalurus nebulosus* (Lesueur)), channel catfish (*Ictalurus punctatus* (Rafinesque)), white perch (*Morone americana* (Gmelin)) and yellow perch (*Perca flavescens* (Mitchill)) are also common, while the piscivores such as pike and bass have been exceedingly rare. In nearby Hamilton Harbour, Randall et al. (1993) reported that carp contributed by far the most biomass, while alewife were the most abundant. Other fish that were dominant included brown bullhead and gizzard shad.

Discussion

Keddy and Reznicek (1986) have shown how water-level fluctuations keep the aquatic plant community in coastal marshes very diverse, by killing dominant emergent species during high-water periods and creating gaps which permit other species to colonize during low water years. During the 1940s, *Typha latifolia* (broad-leaved cattail) and the introduced grass, *Glyceria maxima* (manna grass) were co-dominant in Cootes Paradise Marsh (Figure 3a), the latter possibly having been introduced into the marsh only decades earlier (Lord, 1993). By 1971, after a decade of relatively low water levels, *Glyceria* had expanded considerably (Figure 3c), taking over areas originally colonized by *T. latifolia* in 1946 (Figure 3a). Record high water levels during 1973 (Figure 2b), however, killed off most of the emergent vegetation (Figure 3d; Table 1), and left only small mixed stands of T. latifolia, *Scirpus* sp. and *Glyceria*.

There are now three species of *Typha* in Cootes Paradise Marsh, although during the 1940s only the native species, *T. latifolia* (the common or broad-leaved cattail) was present (Table 2). The other two species present are *T. angustifolia* (the narrow-leaved cattail) and the putative hybrid, *T. xglauca*. By means of a DNA-marker system known as ‘Random Amplified Polymorphic DNA’, M. Marcinko-Kuehn (pers. comm., McMaster University) identified majority of the mature stands now present in the marsh as *T. xglauca*. Apparently, *T. xglauca* has increased at the expense of *T. latifolia*. This type of species succession in cattails has been noted elsewhere and can be explained by relative differences in their tolerances for deep water. McDonald (1955) noted that *T. latifolia* is least tolerant of deep water, while *T. angustifolia* is most tolerant. Harris and Marshall (1963) found that *T. latifolia* did not survive when they were exposed for 2–3 y in water deeper than 45 cm in a northern marshland. On the other hand, the Typha hybrid survived and encroached on openings created by death of the other species. This same situation may have occurred in Cootes Paradise Marsh since almost all of the marsh inlet (Stations 8 to 10) had been mudflat during the 1940s when *Typha latifolia* covered the entire area (Figure 3a; Kay, 1949; Sims, 1949), whereas water depths in recent years have exceeded 50 cm at Station 9 and *Typha* (mostly *T. xglauca*) are constrained to the periphery of the inlet (Figure 3h).

Thus, in Cootes Paradise, raised water levels in the early 1950s initially destroyed *T. latifolia* and released new habitat for *Glyceria*. Following operation of the St. Lawrence Seaway in 1959, the marsh no longer experienced extremes in low water levels, conditions that would have favored the common cattail. The hybrid species, *T. xglauca*, was able to tolerate the deeper water and managed to stay in the marsh through aggressive vegetative growth, but because it is an F1 hybrid (M. Marcinko-Kuehn, pers. comm.), it cannot reclaim large areas through sexual reproduction without the two parental species, which are finding it exceedingly difficult to become established in the current scheme.

The importance of emergent vegetation in attenuating sediment loads in wetlands is well known (Weisner, 1987; Dieter, 1990; Engel and Nicholas, 1994). Once the emergent marsh in Cootes Paradise receded to the west half due to rising water levels (Figure 4a), open-water in the eastern half became windswept and turbid, because the strong prevailing winds readily re-suspended the incoming fine silt and clay of the Niagara Escarpment. Since submergent plants require clear water (Chambers and Kalff, 1985, 1987; Hough et al., 1989, Crowder and Painter, 1991; Skubinna et al., 1995), they began to disappear with increased water turbidities (Table 3). In addition, the common carp, which had become abundant by mid-century, are known to destroy submersed aquatic vegetation directly by damaging macrophyte beds when they feed on the benthos (Threinen and Helm, 1954; Crivelli, 1983), and indirectly by diminishing light availability by re-suspending the sediment (Breukelaar et al., 1994; Lougheed et al., 1998), increasing nutrient loading to the water column (Lamarra, 1975; Cline et al., 1994) and raising the phytoplankton biomass (Bruekelaar et al., 1994).

There are other feed-back interactions between the plant community and the carp that reinforce the degraded environmental state and thus make it difficult for piscivorous fish to re-invade. Kay (1949) noted that the piscivores such as northern pike and bass were kept out of the vegetated station by the low oxygen levels encountered there, especially at night (Table 3). These observations are supported by Bronmark and Weisner (1992) who found that fish species differed in their susceptibility to anoxia; piscivores, especially large esocids (Casselman and Harvey, 1975), were much more sensitive to low oxygen levels than were cyprinids. In eutrophic environments, where dissolved oxygen levels showed wide diurnal fluctuations such as those in Cootes Paradise, Haines (1973) has also found a reduction in the growth of smallmouth bass.

Compared to the 1948 conditions, water quality in Cootes Paradise Marsh had deteriorated considerably by the mid-1970s (Table 3). The higher turbidities fostered the growth of organisms capable of heterotrophic uptake and tolerant of low light environments (Euglenophyceae and Cryptophyceae). The extremely phosphorus-rich water promoted the growth of opportunistic species (green colonial forms) that grew quickly and made it difficult for others to colonize. With low N:P ratios, species capable of nitrogen fixation (blue-green filaments), had a competitive advantage and became abundant (Table 5). Currently, however, the marsh is once more phosphorus limited (Figure 6a), and since the N:P ratios generally exceed 30, there is no evidence of blue-green algal blooms.

In vegetated areas within the marsh inlets, however, algae appear to be controlled by zooplankton grazing. This is supported by the reciprocal observations that edible phytoplankton biomass increased with distance from macrophytes (Figure 6b) while herbivorous zooplankton biomass decreased (Figure 6d). Our results agree well with published studies in which clearing of the water column near aquatic vegetation in shallow lakes were attributed to zooplankton grazing (Timms and Moss, 1984; Hanson and Butler, 1990; Schriver et al., 1995). Other studies have also found that the level of plant-related zooplankton increase with macrophyte abundance (Irvine et al., 1989; Patterson, 1993; Beklioglu and Moss, 1996a, 1996b). Hansen et al. (1997) studied the relative control of algae by bottom-up (nutrients) and top-down (zooplankton grazing) forces in a non-stratified meso-oligotrophic lake and they concluded that at certain times of the year, both forces can be important in structuring the phytoplankton.

Decline in the macrophyte community of Cootes Paradise was probably an important factor in the disappearance of large herbivorous zooplankton (Table 8). In many shallow lakes, large herbivorous zooplankton such as *Daphnia* are vulnerable to fish predation. In shallow lakes and ponds where vertical migration is not possible, large cladocerans are forced to migrate horizontally into weed beds (Timms and Moss, 1984; Lauridsen and Buenk, 1996; Lauridsen and Lodge, 1996). Since planktivorous fish (e.g., alewife, gizzard shad, young-of-the-year carp), have been very abundant in Cootes Paradise for the past two decades, *Daphnia* probably has not been able to establish themselves without aquatic plants there to provide refugia.

The concomitant disappearance of the pollution sensitive insect larvae such as trichopterans and plecopterans with increased representation of pollution-tolerant insects such as chironomids and oligochaetes that burrow in the relatively homogeneous soft sediment are undoubtedly linked to the disappearance of macrophytes. Several studies have shown the importance of macrophytes as substrate for macroinvertebrates (Rasmussen, 1988; Cyr and Downing, 1988; Hanson, 1990). These authors found that littoral zoobenthic biomass increased strongly with macrophyte abundance and the fraction of the macroinvertebrate community found within the sediment decreased sharply with presence of aquatic vegetation. Butler et al. (1992) also found that when macrophytes were present in a lake, the benthos was more likely to include a diverse assemblage of mayflies, beetles and midges. In addition, plants can provide suitable hiding places for both predator and prey, as well as a ready food source for herbivores that feed on periphyton growing on the stems and leaves.

We have shown that high water levels in the 1940s and 1950s was the original cause for loss of emergent vegetation in Cootes Paradise Marsh. In the absence of other anthropogenic stressors such as the deterioration of water quality, encroachment by development, and introduction of exotic species, the emergent marsh might have been able to recover in subsequent decades. However, high water levels will continue to be a natural stressor, and the altered food-web that has resulted from the degradation will keep the marsh in a turbid, open-water state unless interventions are made. By knowing the interactions among various components of today's ecosystem and thereby deriving a model of how the marsh functions in its degraded state, we hope to develop successful restoration and management options for this and other coastal marshes.

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