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A conceptual ecological model to aid restoration of Cootes Paradise Marsh, a degraded coastal wetland of Lake Ontario, Canada

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Abstract

An ecological model is derived from recent studies, based on 60 years of empirical observations and experimental data, that conceptualizes how Cootes Paradise Marsh was transformed from a lush emergent marsh with considerable ecological diversity in all trophic levels, to one that is currently turbid, devoid of vegetation, and dominated by a few exotic plant and fish species. This conceptual model contains 17 key components that interact and contribute to the overall unhealthy state of the marsh. The most influential component is high water level which caused the initial loss of emergent vegetation in the 1940s and 1950s. In the absence of plants to attenuate sediment and assimilate nutrients, the marsh became turbid and windswept, and this led to the disappearance of submergent vegetation over the next two decades. Currently, high water turbidity is being maintained by wind re-suspension, high sediment loading from the watershed during the summer, high algal biomass resulting from excessive nutrient loads from sewage effluent and surface runoff, and the feeding and spawning activities of a very large population of common carp (*Cyprinus carpio*). Due to vegetation loss, the substrate has become mostly loose sediment that is no longer suitable for the diverse assemblage of aquatic insect larvae that lived on the plants and detrital material in the 1940s. Benthic grazers have been kept in low abundances due to predation by benthivorous carp; consequently, epiphytic algae have proliferated and further contribute to light limitation of macrophytes. High nutrient loadings contribute to high diurnal fluxes in dissolved oxygen levels that tend to select against less tolerant organisms such as insect larvae (other than chironomids) and piscivores (northern pike and largemouth bass). Without piscivores in the marsh, the planktivores have become dominant and have virtually eliminated all of the large herbivorous zooplankton (e.g., *Daphnia*), except for a few pockets in the marsh inlets close to residual macrophyte beds. Because of the dominance of small-bodied inefficient grazers (rotifers and small cladocerans), algal biomass is high, and the community has a large proportion of heterotrophic forms that tolerate low light environments. This ecological model suggests that the current turbid un-vegetated state of Cootes Paradise may be very stable. It will persist as long as water levels remain unfavorable for natural re-colonization by the emergent flora, and/or water turbidities remain sufficiently high to suppress the growth of submergent vegetation. Using this conceptual model, I developed a model of how Cootes Paradise Marsh may have functioned as a healthy marsh prior to the 1940s, and use these models as a basis to explore a number of restoration and management options and discuss their implications on the aquatic foodweb.

Introduction

Scientists and managers have recognized for more than a decade that coastal wetlands of the Laurentian Great Lakes are disappearing at an alarming rate (McCullough, 1981; Whillans, 1982; Krieger et al., 1992). Heavily settled environments have lost up to 75% of their baseline wetland areas that appeared on 18th century maps (Whillans, 1982). The Canadian shorelines of Lakes Ontario and Erie continue to be threatened by urban encroachment, sedimentation from watershed, invasion by exotic species and water-level control and regulation (Maynard and Wilcox, 1996). Snell (1987) estimated that wetlands in S. Ontario are being lost at a rate of 0.2% annually. Such loss of natural capital is unacceptable considering the great economic and ecological benefits they offer in terms of services and biodiversity (Denny, 1994). Consequently, governments in both Canada and the United States have acknowledged the urgent need to develop and implement strategies to restore degraded wetlands of the Great Lakes basin.

Smith et al. (1991) enumerated 65 coastal wetlands on Lake Ontario, totaling almost 12 000 ha. Most of these marshes are formed behind barrier beaches, in rivers and drowned river mouths, in protected bays, while some smaller percent are exposed to the lake proper. Each type experiences a variety of stressors, both natural and anthropogenic, and not all stressors will exert the same impact on all types (Maynard and Wilcox, 1996). Despite these differences in marsh types and stressors, however, degraded marshes share many common features which include high levels of turbidity, nutrients and phytoplankton biomass, and the reduction or disappearance of aquatic macrophytes. These features are also characteristic of shallow eutrophic lakes in North America (Lake Okeechobee, Philips et al., 1993), in the Norfolk broads (Moss, 1990), in Denmark (Sondergaard et al., 1990) and in New Zealand (Mitchell, 1989). Therefore, restoration strategies developed for coastal wetlands of the Laurentian Great Lakes may be widely applicable to many shallow aquatic ecosystems throughout the world.

Modeling is one of several tools that ecologists can apply to wetland restoration. Although the most popular model in the literature is a mass-balance model which can yield quantitative predictions of outcomes for proposed rehabilitation schemes, investigators have only recently begun to use these quantitative models to aid restoration of freshwater wetlands (Howard-Williams, 1985; Minns, 1986; Breen, 1990; Mitsch and Reeder, 1991; Mitsch et al., 1995; Reinelt and Horner, 1995; Prescott and Tsanis, 1997). Other types of quantitative models have also been developed to evaluate long-term changes in wetland habitats (e.g., Bray, 1996). By comparison, the use of non-quantitative or conceptual models have not yet been explored in this growing discipline, even though they may be more appropriate for guiding restoration since they can be used to simplify very complex interrelationships, and make explicit the ecological links that drive the degraded ecosystem. Conceptual models are therefore invaluable for understanding the pathway of degradation and for generating and evaluating restoration strategies.

In this paper, I develop an approach to guide restoration of a degraded coastal wetland of Lake Ontario through construction of two conceptual models: a model of the marsh in its present degraded state, and another in its former healthy state. To construct the conceptual model, I first identify the key components of the degraded ecosystem (both biotic and abiotic) and investigate the interrelationships among various components. Next, I use hypothesis diagrams to show how the various components interact and contribute to the current degraded state of the marsh. I repeat these steps to construct a corresponding healthy model of the marsh that existed in the past. Finally, I use both models to evaluate the appropriateness of some management/restoration options that have been proposed and/or implemented to rehabilitate the wetland.

Methods

Study site

Cootes Paradise Marsh, the largest coastal wetland in western Lake Ontario, is considered very important habitat for both waterfowl and warmwater fish in Lake Ontario (Chow-Fraser and Lukasik, 1995; Whillans, 1996). It is also the site of a large marsh restoration developed as part of a larger plan to restore the ecological integrity of Hamilton Harbour (located to the east of Cootes Paradise; see Figure 1) (Remedial Action Plan for Hamilton Harbour, 1992). The marsh is relatively large (250 ha) and has been subject to large seasonal and inter-annual fluctuations of water levels and water quality over the past 60 years that have brought about accompanying changes to the biotic communities (discussed in detail elsewhere in this issue; Chow-Fraser et al., 1998).

Key components and hypotheses diagrams

I used several recent studies to derive the key components of the conceptual model. These included a description of the degradation history of Cootes Paradise Marsh over six decades from 1934 to 1996 (Chow-Fraser et al., 1998), a study of the factors that contributed to seasonal variability of water turbidity in Cootes Paradise Marsh during 1993 and 1994 (Chow-Fraser, 1998 in review) and a mass-balance model of the degraded wetland (Prescott and Tsanis, 1997). From these studies, I identified seventeen key components that contribute towards maintenance of the marsh in a degraded state. I then formulated hypotheses to link the various components in the conceptual model. In a similar fashion, I developed a model of how a healthy marsh may have functioned prior to the 1940s.

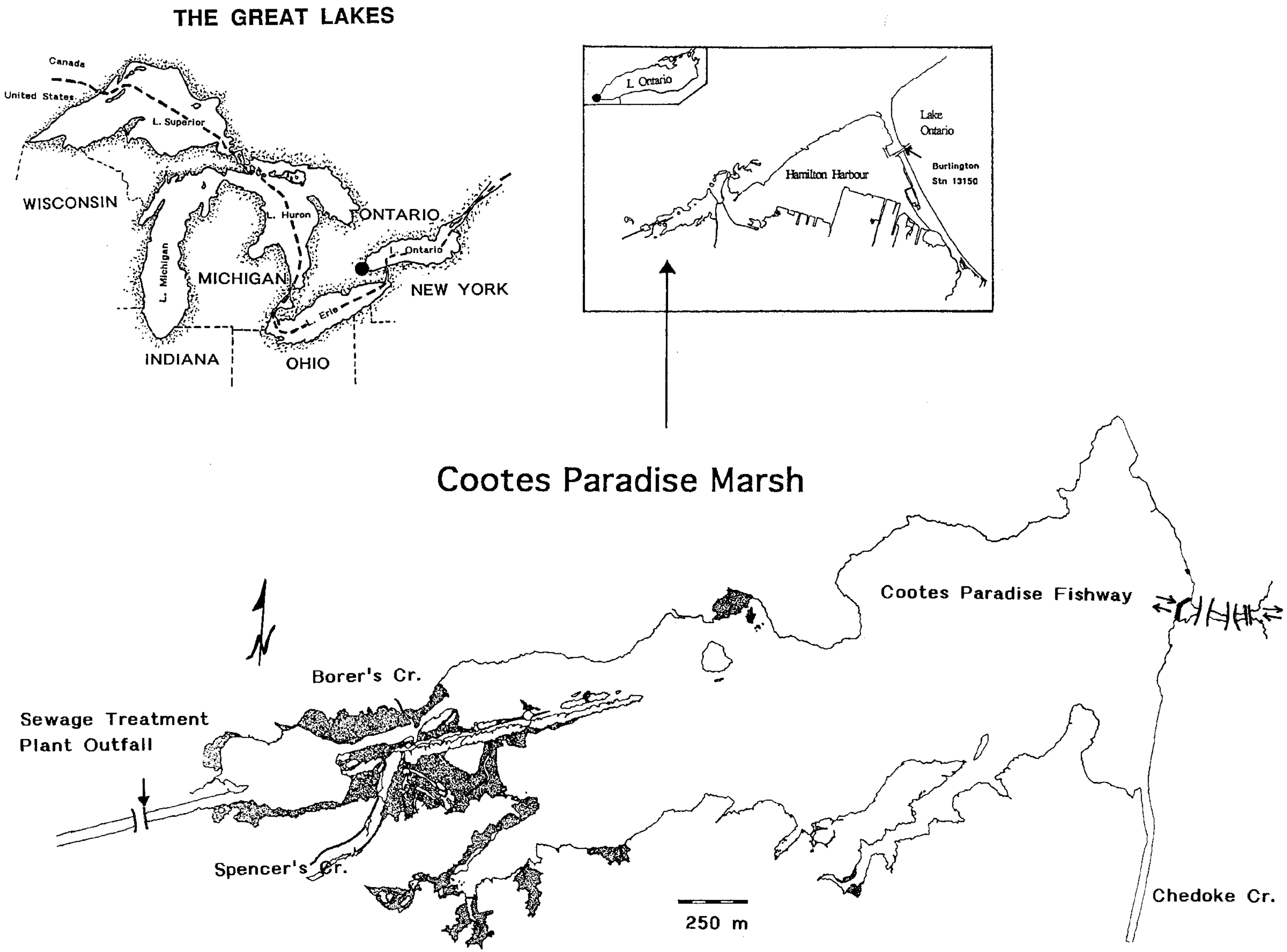

Figure 1. Map of Cootes Paradise Marsh with an inset showing the location of the marsh relative to Hamilton Harbour and Lake Ontario, Ontario, Canada.

In these models, lines joining the key components may be solid (if supporting evidence is direct) or broken (if evidence is only anecdotal or indirect). The thickness of the lines also reflects a qualitative difference in the importance of the interaction between components.

Results

Conceptual model of the degraded marsh

The first conceptual model was developed to provide an understanding of the ecological functions that keep the marsh in a turbid, un-vegetated state (Figure 2). I developed it by synthesizing current knowledge of ecological interactions among several trophic levels in Cootes Paradise and by interpreting trends in experimental and field observations. Each of the lines that join two of the seventeen components is numbered and is an hypothesis based on documented evidence from studies of Cootes Paradise or other similar ecosystems. In chronological order below, I will present these hypotheses and their supporting evidence.

(1) High water level led to loss of areal cover and diversity of emergent vegetation:
The best evidence that high water levels damaged emergent vegetation is the strong inverse relationship between water level and areal cover over the past 60 years. Emergent cover declined from 85% of the surface area in 1934 to $< 10\%$ in 1974 (Chow-Fraser et al., 1998). This hypothesis is consistent with explanations provided by Keddy and Reznicek (1986) of how water levels control the growth of different types of aquatic vegetation in Great Lakes coastal wetlands.

(2) Loss of emergents eliminated certain functional groups of benthic macro-invertebrates:
Loss of aquatic plants in Cootes Paradise was accompanied by a dramatic change in the benthic community, with virtual disappearance of many families and orders of aquatic insects (Chow-Fraser et al., 1998). Taxonomic diversity decreased from 57 genera (23 families and 6 orders) in 1948, to 9 genera (6 families and 3 orders) in 1976, to 5 genera (3 families and 2 orders) in 1995. Lost are the insect larvae such as trichopterans and plecopterans, which require well-oxygenated waters and more coarse-grain and heterogeneous substrate. These have been replaced by pollution-tolerant insects such as chironomids and oligochaetes that burrow in the relatively homogeneous soft sediment. These observations are consistent with published studies that document the relationship between macrophytes and the distribution of macroinvertebrates (Rasmussen, 1988; Cyr and Downing, 1988; Hanson, 1990; Butler et al., 1992).

(3) Loss of emergents has led to wind-induced resuspension:
The importance of emergent vegetation in attenuating sediment loads in wetlands is well known (Weisner, 1987; Dieter, 1990; Engel and Nicholas, 1994). Chow-Fraser et al. (1998) described how the emergent marsh in Cootes Paradise receded to the west half due to rising water levels in the 1950s and exposed the eastern half to wind action which is one of the chief factors responsible for keeping the marsh in a turbid state (Chow-Fraser, in review).

(4) Abundance of spawning carp increased water turbidity:
Spawning behavior of the common carp includes a great deal of splashing in shallow weedy areas, usually much less than a meter in depth; most of it occurs in late spring and early summer when temperatures warm from 17 to 24 °C (Panek, 1987). In field enclosure experiments conducted in Cootes Paradise, Lougheed et al. (1998) showed that water turbidity increased proportionately with carp size and biomass during the spawning period. Water turbidities associated with mature carp increased up to 15 FTU above background levels, depending on the size (and therefore biomass) of the carp. These are consistent with observations that water turbidities were significantly higher in areas where carp were spawning compared with areas where they were absent in a 1992 field survey (Chow-Fraser, 1998).

(5) Abundant carp spawning increased nutrient loading:
Lougheed et al. (1998) conducted experiments with carp that were allowed to spawn in enclosures placed in Cootes Paradise Marsh. They showed that total phosphorus (TP) concentrations increased from 130 to 160 $\mu\text{g L}^{-1}$ with increasing biomass of carp from 10 to 2000 kg ha^{-1}.

(6) Wind re-suspension of the sediment led to high water turbidity:
Strong prevailing winds in Cootes Paradise Marsh can readily re-suspend the fine silt and clay that enter the

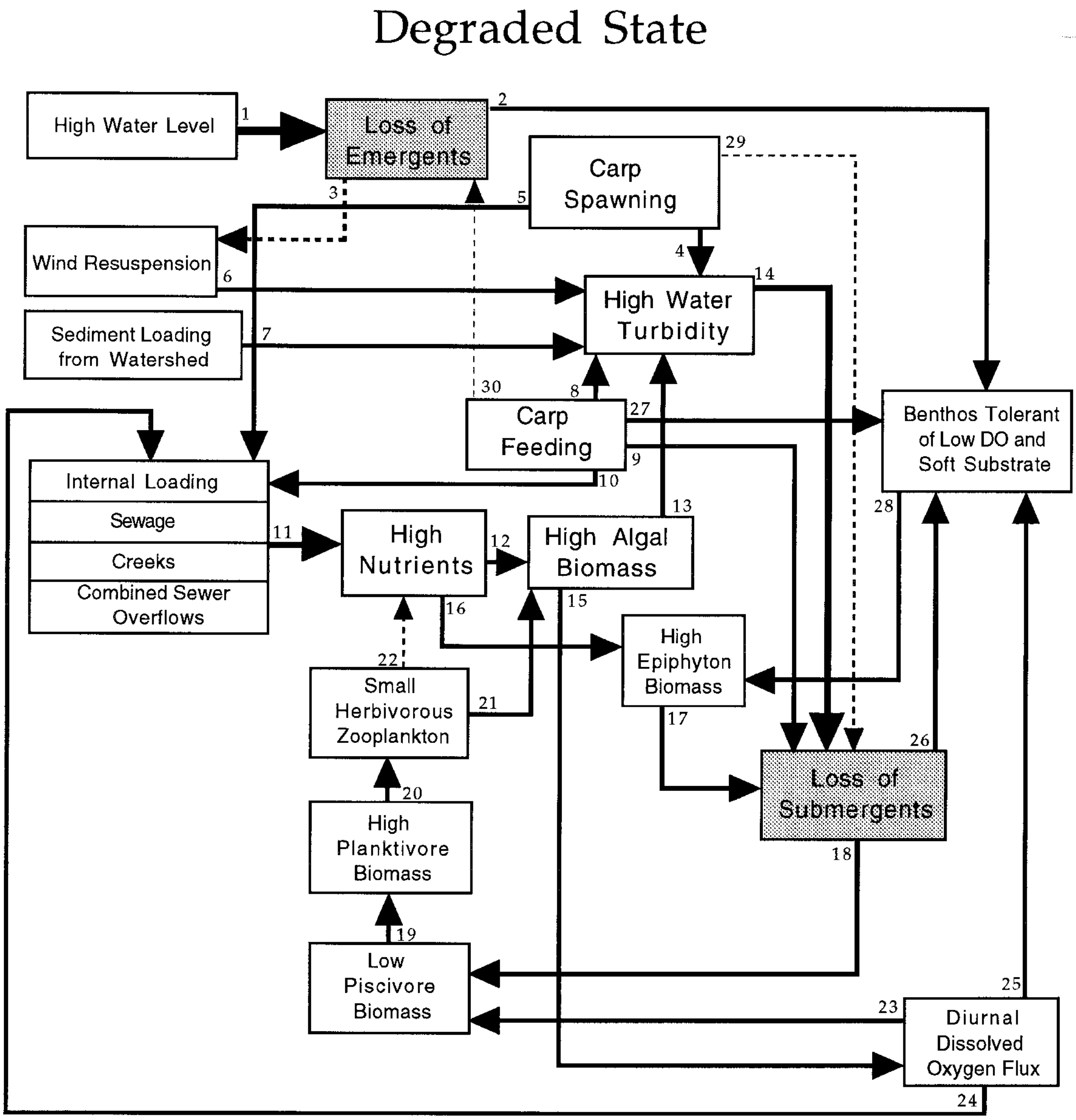

Figure 2. Conceptual model of Cootes Paradise Marsh as a degraded ecosystem, with 17 key components and arrows to indicate interactions between components based on observations and published relationships for Cootes Paradise Marsh.

marsh through the main tributaries. Water turbidities increased significantly with wind speed, independent of carp effects during the 1993 and 1994 surveys (Chow-Fraser, in review).

(7) Sediment loading from the watershed has led to high water turbidity:
The main tributaries, particularly Spencer Creek (see Figure 1), bring in high sediment loads during the spring (via snowmelt) and summer (via rainstorms). Chow-Fraser (in review) showed that from 1985 to 1995, most of the suspended solids that entered Cootes Paradise from this creek occurred in winter and that peak loading occurred during snowmelt in March. During the growing season, the highest sediment load occurred in May, coincident with relatively high wind speeds that would have kept the fine sediment in suspension. This hypothesis is supported by high spring turbidities measured at the eastern open-water areas, and periodic pulse turbidities associated with precipi-

tation events during the summer near tributary mouths.

(8) Carp increased water turbidity through their feeding activities:
Carp feed on benthic organisms living in and on the sediment near macrophytes. Breukelaar et al. (1994) found that the amount of suspended solids in shallow ponds stocked with mature carp (40–50 cm) increased with fish density. Chow-Fraser (in review) also documented a similar increase in water turbidity with increasing number of carp and benthivorous fish stocked in enclosures in Cootes Paradise Marsh.

(9) Carp destroyed submergent vegetation through their feeding activities:
The common carp, which had become abundant in Cootes Paradise Marsh by mid-century (Whillans, 1996), 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 through sediment re-suspension (see Hypothesis 8 above).

(10) Carp increased nutrient loading through their feeding activities:
Lamarra (1975) documented that biomass of mature carp ranging in density from 160 to 1250 kg ha^{-1} increased total phosphorus concentrations from 30 to 45 μg L^{-1} after spending 60 days in shallow enclosures during July and August. Cline et al. (1994) also showed that when carp were placed in tubs without sediment, nitrogen levels increased relative to those in control tubs.

(11) High internal and external loading increased nutrient concentrations in the marsh:
Cootes Paradise Marsh has become hyper-eutrophic from many decades of external loading of phosphorus and nitrogen; sources included effluent discharged from storm sewers and a sewage treatment facility located at the west end of the marsh (Chow-Fraser et al., 1998). The marsh currently receives a large amount of phosphorus and nitrogen from surface runoff through Spencer's Creek (Prescott and Tsanis, 1997). The calculated daily total external P-load varied from 31 to 98 kg total P between 1989 and 1995, with a mean of 56 kg d^{-1} (Chow-Fraser, unpublished data). There is also an estimated internal phosphorus load of 50–70and/or nutrient regeneration from zooplankton, benthos and fish (Prescott and Tsanis, 1997). For the same period, the calculated daily total nitrate-nitrogen load varied from 95 to 460 kg with a mean of 217 kg d^{-1} (Chow-Fraser, unpublished data). Corresponding total ammonia-nitrogen load varied from 2.4 to 39.3 kg with a mean of 11.8 kg d^{-1}.

(12) High nutrient concentrations resulted in high algal biomass in the water column:
Chow-Fraser et al. (1998) uncovered a highly significant $\log_{10}$-linear relationship between TP and chlorophyll-*a* (CHL) and one between TP and phytoplankton biomass in Cootes Paradise Marsh. These regression equations indicate that algal biomass in Cootes Paradise is currently controlled by phosphorus concentrations, as are algae in most freshwater ecosystems (Chow-Fraser et al., 1994).

(13) High algal biomass in the water column contributed to high water turbidity:
Water turbidity in Cootes Paradise is a function of inorganic sediment, algae and non-algal detritus. Chow-Fraser (in review) examined the relative contributions of each of these components to site-to-site variation in water turbidity. Inorganic sediment was the best predictor, explaining almost 80% of the variation in water turbidity in 1994, whereas CHL explained only 15%. However, CHL was found to be important for explaining seasonal variation in water turbidity in West Pond (the sewage lagoon), whereas for all other sites, it was a good predictor of turbidity only after the effects of precipitation events and wind speed are accounted for.

(14) High water turbidity led to loss of submergent vegetation:
Submergent plants are highly dependent on clear water because their entire life cycle takes place within the water column (Chambers and Kalff, 1985, 1987; Hough et al., 1989; Crowder and Painter, 1991; Skubinna et al., 1995; Sager, 1996). Lougheed et al. (1998) showed that the species richness of submergent vegetation decreased predictably with increasing water turbidity in 22 wetlands of the Great Lakes basin. Chow-Fraser et al. (1998) observed that water turbidity increased more than 5-fold over the 40 years of monitoring in Cootes Paradise Marsh, and this magnitude of increase can readily explain the disappearance of submergent taxa. The dominant species noted in a 1993 survey was *Potamogeton pectinatus*, a species that appears to be tolerant of high disturbance and which has also been dominant in other turbid marshes surveyed in the Great Lakes basin (Crosbie and Chow-

Fraser, unpublished data).

(15) High algal concentrations led to high diurnal flux of dissolved oxygen content in the water column:
The dissolved oxygen (DO) concentration in Cootes Paradise tends to undergo extreme diurnal fluctuations near macrophyte beds in the residual marsh inlets. In June 1993, levels fluctuated from 1.9 mg L^{-1} at night to 12.2 mg L^{-1} in mid-afternoon (Chow-Fraser, unpublished data). Kay (1949) observed similarly low DO levels at a vegetated station in the marsh during the night, especially near the sediment surface. Such diurnal fluxes are presumably the reflection of high photosynthesis during the day and high respiration (decomposition) during the night.

(16) High nutrient concentrations contributed to high epiphyton biomass:
Although epiphyton biomass in Cootes Paradise Marsh has not yet been quantified, I have visually inspected the substrate in a section of the marsh and noted the abundance of epiphytic growth on submerged stems and leaves of the aquatic vegetation. Brönmark and Weisner (1992) have noted a similar increase in epiphyton biomass in a shallow lake when it became eutrophic.

(17) High epiphyton biomass diminished light availability for submergent plants:
Brönmark and Weisner (1992) noted that when eutrophication led to increased epiphyton biomass, the algae reduced light availability for submerged macrophytes. I hypothesize that a similar situation exists in Cootes Paradise Marsh, where I have seen submerged vegetation coated with so much epiphytic growth that they appeared brown until epiphytes were washed off their surfaces.

(18) Loss of submergent plants resulted in loss of spawning and nursery habitat for piscivorous fish (pike and bass):
Both northern pike and largemouth bass require submergent plants to spawn, and the loss of these plants is a direct cause of their decline in the marsh (Holmes, 1988; Chow-Fraser et al., 1998). Similar relationship between extent of submergent macrophyte cover and the abundance of piscivores in other Great Lakes wetlands have been reported by Randall et al. (1996).

(19) Planktivore community became abundant because of reduced predation pressure:
When piscivore abundance declined with loss of habitat, the planktivorous fish (cyprinids and clupeids) community in Cootes Paradise Marsh increased (Chow-Fraser et al., 1998). This trophic cascade phenomenon has been well documented in many freshwater ecosystems (e.g., Carpenter et al., 1985; Benndorf et al., 1988). Hurley and Christie (1977) also described a similar change in the fish assemblage in the Bay of Quinte when the submergent marsh became degraded. Combination of a strong year-class and climate anomaly resulted in a dramatic return of piscivorous walleye and the decline of the white perch population in 1978, and this has subsequently led to reversal of the dominance by small-sized planktivorous fish (alewife and white perch) during the 1980s (Hurley, 1986).

(20) High planktivore abundance led to zooplankton community dominated by small herbivores:
Chow-Fraser et al. (1998) showed that large herbivorous zooplankton (i.e., *Daphnia*) were common in the 1948 survey but had become extremely rare in Cootes Paradise Marsh for at least the past two decades (Lougheed and Chow-Fraser, 1998). Their disappearance coincided with the eradication of submergent plants and the increased abundance of planktivorous fish in the marsh. In a 1996 survey, *Daphnia* were found in persistent numbers only near macrophyte beds, where presumably these large grazers were able to find refugia from predation (i.e., Timms and Moss, 1984; Lauridsen and Buenk, 1996; Lauridsen and Lodge, 1996). This shift in size of zooplankton is entirely consistent with the conventional wisdom that planktivores selectively remove the largest prey in lakes and ponds (Brooks and Dodson, 1965), and is similar to the hypothesis proposed by others (Hanson and Butler, 1990; Sondergaard et al., 1990; Brönmark and Weisner, 1992) for shallow lakes and ponds. A study of lakes in Florida reported a similar shift from large-bodied grazers (cladocerans and calanoid copepods) to small-bodied forms (small cladocerans and rotifers) as lakes increased in fertility (Bays and Crisman, 1983).

(21) Small-bodied herbivores, which are inefficient grazers, promoted abundant algal growth:
Several studies have compared the relative efficiencies of large- versus small-bodied grazers and have concluded that large grazers are competitively superior when food quality is good (Ferguson et al., 1982; Kerfoot and DeMott, 1985; Gliwicz, 1990). In Cootes Paradise Marsh, food quality is generally high qual-

ity, with good representation of edible algae since N:P ratios are sufficiently high that nuisance blue-green algae do not tend to proliferate (Chow-Fraser et al., 1998). Therefore, the small-bodied grazers that dominate the zooplankton at present are inefficient at removing algae from the water column.

(22) Herbivorous zooplankton released nutrients that contributed to high nutrient concentrations in the water column:
Hansen et al. (1997) demonstrated experimentally that regeneration of nitrogen and phosphorus by zooplankton were periodically important for algal growth in a shallow mesotrophic lake. Nitrogen regeneration rates varied from 24–29% while those for phosphorus varied from 25–58% of daily internal nutrient input. Small grazers which dominate the marsh at present (see Hypothesis 21 above) are also more efficient at recycling phosphorus compared with larger-bodied grazers (Taylor, 1984).

(23) High diurnal fluxes in dissolved oxygen content selected against piscivores such as pike and bass:
Kay (1949) noted that the piscivores (northern pike and bass) were kept out of the vegetated station in Cootes Paradise Marsh by the low oxygen levels encountered there, especially at night (Chow-Fraser et al., 1998; Table 3). These observations are supported by Brönmark and Weisner (1992) who found that fish species differed in their susceptibility to anoxia with piscivores, especially large esocids (Casselman and Harvey, 1975), being much more sensitive to low oxygen levels than are cyprinids. In eutrophic environments, where dissolved oxygen levels showed wide diurnal fluctuations such as those in Cootes Paradise, the growth of smallmouth bass (*Micropterus salmoides* (Lacepede)) was also significantly reduced (Haines, 1973).

(24) Low redox potential near sediment-water interface led to phosphorus re-mineralization from the sediment (internal loading):
Since phosphorus tends to bind to sediments in wetlands, it can be regenerated at the sediment-water interface under low redox conditions (Golterman, 1995). Phosphorus can also be released from the sediment layer when the gradient between the porewater and overlying water concentrations is high. This type of nutrient regeneration has hampered the recovery of eutrophic lakes after external inputs have decreased (Phillips et al., 1994). Although *in situ* measurements have not been taken, there is evidence that sediments of Cootes Paradise Marsh are generating large quantities of phosphorus into overlying waters (Prescott and Tsanis, 1997; Chow-Fraser, unpublished data).

(25) High dissolved oxygen flux favored benthic organisms tolerant of low oxygen environments:
During the 1940s, the aquatic insects present in Cootes Paradise included many taxa that were pollution intolerant and that required high levels of dissolved oxygen (Chow-Fraser et al., 1998). With deterioration in water quality and the subsequent drop in dissolved oxygen content near macrophyte beds, the taxa that currently dominate are those that tolerate anaerobic environments.

(26) Loss of submergents favored colonization by benthos that burrow in soft substrate:
At present, the substrate in much of Cootes Paradise Marsh is fine silt and clay (Chow-Fraser, in review) that is suitable for benthos that burrow, rather than those that forage by shredding and collecting detritus (plant material). There are very low numbers of benthic grazers such as snails in the marsh; Fitzgerald (1996) reported that Cootes only has 10% of those found on the north shore of Hamilton Harbour. A more detailed discussion of changes in the benthos resulting from loss of aquatic vegetation has been presented in Hypothesis 2 (above).

(27) Carp and other benthivorous fish further diminished the populations of benthic grazers (snails):
Brönmark and Weisner (1992) hypothesized that predation by carp and other benthivorous fish is the main reason that densities of grazing benthic invertebrates have decreased in shallow eutrophic lakes, and this may be another reason why snails have been scarce in Cootes Paradise Marsh in recent surveys.

(28) A reduction in the benthic grazers promoted the growth of epiphytic algae:
Brönmark and Weisner (1992) hypothesized that without the presence of benthic grazers, epiphytic algae were permitted to grow unchecked in shallow eutrophic lakes. I use this same hypothesis to explain the preponderance of epiphytic algae in Cootes Paradise Marsh.

(29) When carp spawned, they destroyed submergent vegetation:
Most authors do not distinguish between spawning and

feeding impacts of carp on submergent plants but they do note that common carp generally destroyed aquatic vegetation when they came in contact with them (McCrimmon, 1968; Crivelli, 1983). McCrimmon (1968) cited several examples of wetland areas across Canada where investigators observed that submergent plants were more susceptible to carp damage than were emergent plants. Unfortunately, the destructive effects of carp on submergent plants in Cootes Paradise have not been observed in recent times because of their scarcity in the marsh.

(30) When carp fed on benthos, they eroded the beds of emergent vegetation:
I conducted experiments during 1994 in Cootes Paradise Marsh that provide indirect evidence that carp may damage emergent vegetation when they feed. Seedlings of cattails (*Typha latifolia*, *T. angustifolia* and *T. Xglauca*) and bulrush (*Scirpus validus*), were planted into triplicate $8' \times 8'$-square exclosures that protected them from disturbance by carp and other animals. The same six species of plants were also planted in triplicate control plots that were left unprotected. When I monitored their growth in 1995, I found that survival rates of both genera were significantly higher in the exclosures relative to control plots (2.1 times higher for *Typha* and 1.25 higher for *Scirpus*). These results suggest that carp, among other animals, may have a negative impact on the survival of seedlings of emergent plants.

Conceptual model of the healthy marsh

Based on the first conceptual model, I developed a second model that describes how the marsh may have functioned in a healthy state, prior to accumulation of the stresses that have kept Cootes Paradise in a turbid, un-vegetated state over the past 40 years. In contrast to the ‘degraded’ model, this ‘healthy’ model only has 13 instead of 17 components and 15 instead of 30 interactions (Figure 3). In many instances, the supporting lines of evidence are simply reversals of those presented for the previous model. To avoid redundancy, I will simply reference the appropriate hypothesis in the ‘degraded’ model.

(1) Low water levels permitted emergent vegetation to invade up to 85% of the surface area of the marsh:
See Hypothesis 1 in degraded model.

(2) Abundant vegetation provided suitable habitat for diverse benthic assemblage that included immature stages of many insects:
See Hypothesis 2 in degraded model.

(3) Abundant emergent vegetation trapped sediment and kept water turbidities low near macrophytes:
Aquatic vegetation are capable of trapping incoming sediment and thus a vegetated coastal marsh acts as a filter for the Great Lakes (Maynard and Wilcox, 1996). Plants can also attenuate waves, and lessen wind re-suspension that are known to keep water turbidities high in Cootes Paradise Marsh (Chow-Fraser, in review).

(4) Nutrients from sewage and the creeks were filtered out by the emergent plants and this kept nutrient concentrations low:
The ability of wetlands to assimilate excess nutrients is well recognized by environmental engineers who have successfully converted many natural and artificial wetlands into treatment facilities of domestic and industrial sewage, and roadway runoff (e.g., Howard-Williams, 1985; Hammer, 1989; Olson, 1992). The emergent marsh in Cootes Paradise was probably very efficient at removing nutrients prior to the 1950s.

(5) Low water turbidities promoted the growth of a diverse submergent community:
See Hypothesis 14 in degraded model.

(6) Diverse submergent community promoted the growth of a species-rich benthic community:
See Hypothesis 26 in degraded model.

(7) The benthos included benthic grazers (snails) that kept down the growth of epiphytic algae:
See Hypothesis 28 in degraded model.

(8) Low epiphyton biomass did not inhibit light availability for submergent plants:
See Hypothesis 17 in degraded model.

(9) Healthy stands of submergent vegetation provided good spawning and nursery habitat for piscivores (pike and bass):
See Hypothesis 18 in degraded model.

(10) Abundant piscivores kept planktivore populations low:
See Hypothesis 19 in degraded model.

Healthy State

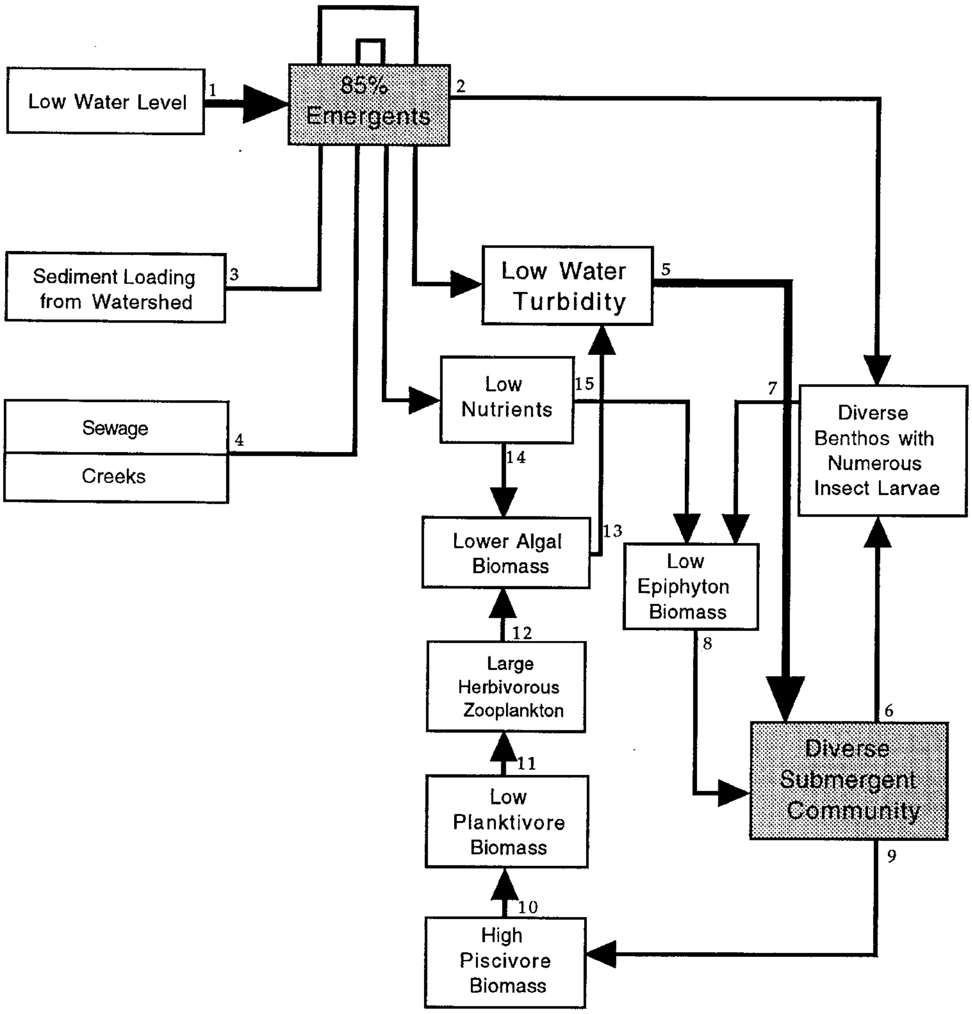

Figure 3. Conceptual model of Cootes Paradise Marsh as a healthy ecosystem, with 13 key components and arrows to indicate interactions between components based on a long-term study of the marsh (Chow-Fraser et al., 1998) and published interactions in shallow lakes and other wetland systems.

(11) Low biomass of planktivores promoted the establishment of large-bodied zooplankton (i.e., *Daphnia*): See Hypothesis 20 in degraded model.

(12) Large herbivorous zooplankton are efficient at keeping water clear of algae:
See Hypothesis 21 in degraded model.

(13) Low algal biomass contributed to relatively clear water:
See Hypothesis 13 in degraded model.

(14) Low nutrient availability supported a diminished community of phytoplankton:
See Hypothesis 12 in degraded model.

(15) Low nutrient availability supported a reduced community of epiphyton:
See Hypothesis 16 in degraded model.

Discussion

The most influential component in the 'degraded' model is high water level which caused the initial loss of emergent vegetation in the 1940s and 1950s. In the absence of plants to attenuate sediment and assimilate nutrients, the marsh became turbid and windswept, and this led to the disappearance of submergent vegetation over the next two decades. Currently, high water turbidity is being maintained by wind re-suspension, high sediment loading from the watershed during the summer, high algal biomass resulting from excessive nutrient loads from sewage effluent and surface runoff, and the feeding and spawning activities of a very large population of common carp. Loss of vegetation led to the disappearance of piscivores, and this resulted in cascading effects on subsequent trophic levels with endpoints that reinforced the un-vegetated state. This model illustrates how positive feedback interactions will keep the marsh turbid and devoid of aquatic vegetation as long as water levels remain unfavorable for emergent flora, and/or water turbidities remain sufficiently high to suppress the growth of submergent vegetation. Another consideration for restoration is that currently the marsh is dominated by *T. Xglauca* rather than *T. latifolia*, which was the only species present in Cootes during the 1940s and 1950s (Chow-Fraser et al., 1998). This is apparently because the hybrid can tolerate deeper waters than can *T. latifolia* (McDonald, 1955; Harris and Marshall, 1963). Given that *T. Xglauca* is an F1 hybrid, restoration efforts should ensure that both parental species (*T. latifolia* and *T. angustifolia*) are present in Cootes Paradise.

Restoration and management options

Emergent plants

The emergent community should recover through hydrologic manipulations but since water-level regulation of the entire marsh is not a viable management option because of logistical considerations (Remedial Action Plan for Hamilton Harbour Stage 2 Report, 1992), a planting program of tolerant emergent taxa must be implemented. This would essentially reverse the damaging effects of high water depths (Hypothesis 1; Figure 2). A mix of all three cattail species may be warranted to ensure that *T. Xglauca* can be established. Experiments should also be conducted to determine what other native species of emergent plants may tolerate the higher water depths.

Submergent plants

To restore the submergent community, water turbidities may be reduced in a number of ways including: 1) carp exclusion (which would be beneficial both in terms of reducing turbidity and nutrient load; Hypotheses 4 and 8) 2) reduction of sediment and nutrient loads from point and non-point sources (Hypotheses 7 and 11), and/or 3) manipulation of the fish community so that planktivores and benthivores would be drastically reduced (Hypothesis 20 and 28, respectively). To assess the relative merits of each of these options, it's important to understand the great temporal and spatial variation in water turbidity and the factors that lead to this high variability in Cootes Paradise Marsh (Chow-Fraser, in review). Depending on the location and the time of year, wind re-suspension and rainstorms can account for majority of the variation in areas of the marsh affected by tributary inputs. Re-suspension due to direct activities of the common carp are restricted to relatively shallow areas, particularly those near the inlets and macrophyte beds. Contributions by algae were on the whole less important than either wind or carp activities, except in West Pond where algal biomass is excessively high (Chow-Fraser et al., 1998; Chow-Fraser, 1998).

From a management perspective, removal of carp, and reduction of nutrients from point sources are more manageable than controlling wind activities or sediment inputs from the watershed during storm events. This is despite the fact that the latter two have an overwhelming influence on marsh turbidity. In my opinion, the Royal Botanical Gardens (owner and manager of the marsh) has opted to tackle the carp problem, not necessarily because it is the greatest stressor, but because carp are involved in many more interactions between key components that keep the marsh in a turbid, plant-free state (Hypotheses 4, 5, 8, 9, 10, 27, 29, and 30; Figure 2). Beginning the spring of 1997, the Royal Botanical Gardens began operation of the Cootes Paradise Fishway to exclude mature carp (> 30 cm long) from the marsh (see Figure 1 for location). Successful operation of this fishway will mean that mature carp will be eliminated from the marsh while small carp and all other fish will be permitted access. Exclusion of carp from the foodweb should lead to lower water turbidity through the hypothesized interactions 4 and 8 in the degraded model (Figure 2). It would also be beneficial by eliminating physical damages that may accrue to submergent and emergent vegetation (Hypotheses 9, 29 and 30). Another possible benefit is that benthic grazers may become abundant again (Hypothesis 27 and 28) and thus reduce the high epiphyton biomass that would have hampered the growth of submergent plants (Hypothesis 17).

High nutrient loads can lead to excessive algal growth and may subsequently contribute to high water turbidity. That is why one of the restoration strategies focuses on reduction of phosphorus from point sources (e.g., effluent from the Sewage Treatment Plant located at the west end of the marsh, and overflow from storm sewers along Chedoke Creek; Remedial Action Plan for Hamilton Harbour, Stage 2 Report 1992). To evaluate the cost-effectiveness of this management option, one must consider that during a very dry summer, the Dundas Sewage Treatment Plant contributes at most a third of the overall external phosphorus load to the marsh over the growing season (June to August), and that during a wet year, it may contribute as little as 10%. However, the internal load varies between 50 to 70% of the total annual load (Prescott and Tsanis, 1997, Chow-Fraser, unpublished data) and this corresponds to a substantially higher percentage of the summer load since most of the phosphorus is released at temperatures greater than 15 °C (Chow-Fraser, unpublished data). Given the great expense in phosphorus removal from sewage and storm sewer effluent, the relatively low influence of the algae on water turbidity (Chow-Fraser, 1998), the relatively large input of nutrients from non-point sources through the tributaries and surface run-off (up to 90% of all external sources annually), and the fact that internal loading may keep the marsh in a eutrophic state for decades, there may be limited value in spending large sums of money to further decrease external phosphorus loading from the sewage treatment facility and storm sewers.

The Degraded model pointed out that algal-mediated turbidity may also be controlled by zooplankton grazing. It is clear that algal biomass in Cootes Paradise is not controlled by grazing when fish are dominated by planktivores and zooplankton are dominated by small-bodied forms (Figure 2). However, as indicated in the conceptual model of the Healthy marsh (Figure 3), the presence of abundant piscivores may reverse these trends and lead to lower algal biomass and clearer water (Brönmark and Weisner, 1992). Since Daphnia are fairly indiscriminate feeders (Chow-Fraser and Knoechel, 1985; DeMott, 1990), they are also more likely to filter out the inorganic suspended solids that contribute a great deal to water turbidity in the marsh. This may be accomplished through introduction of pike or bass, although successful bio-manipulation may necessitate periodic restocking until a self-sustaining fishery is established. Depending on how rapidly submergent plants will re-colonize when the water initially clears, and the accuracy of Whillan's (1996) assertion that the propagule bank is impoverished, this management option may also require a concurrent planting program of submergent vegetation.

There are several promising management options that can be implemented to help restore the water quality and ecological diversity of Cootes Paradise Marsh. Carp exclusion will undoubtedly lead to lower water turbidity in the marsh (Hypotheses 4 and 8; Figure 2) but the other factors, wind and wave action (Hypotheses 6, Figure 2), high sediment loading (Hypothesis 7, Figure 2) and high algal biomass (Hypothesis 13, Figure 2) will still conspire to keep the marsh in a relatively turbid state. However, a concurrent planting program and water-level control in deeper areas of the marsh will help increase the areal cover of emergent plants and thereby reduce wind-induced re-suspension and lessen eutrophication (Hypotheses 3 and 4, Figure 3). Stocking of predators to alter the size structure of the food-web should also lead to positive feedback that would allow the ecosystem to spiral back to a healthier state (Hypotheses 10 to 12, Figure 3).

The conceptual models I have presented here are useful for several reasons. First, they synthesized a set of complex interrelationships and made explicit the ecological links that drove the ecosystem from a ‘healthy’ to a ‘degraded’ state over a 50-y period and should be instructive in helping us reverse the course. Secondly, by formulating hypotheses to link the various key components and finding supporting evidence for these, I have discovered deficiencies in the literature. For example, there is no direct evidence that carp feeding damages emergent vegetation, nor is there evidence that carp spawning affects submergent vegetation. Support for these hypotheses tend to be anecdotal and confounded by other factors. As Minns et al. (1996) pointed out, if marsh restoration is to develop as a science, it must be based on scientific evidence and principles. I therefore suggest that definitive studies be conducted in different wetlands to elucidate the factors that affect the impact of carp activities on aquatic vegetation before carp exclusion as a strategy is promoted for other restoration projects. Lastly, I have been able to use these models to evaluate the appropriateness of several management options and to explore their implications on the ecosystem if/when they are implemented, and I hope that managers of other restoration projects will consider using this modeling approach in their programs.

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References

Bays, J.S. and Crisman, T.L. 1983. Zooplankton and trophic state relationships in Florida lakes. Can. J. Fish. aquat. Sci. 40: 1813–1819.

Benndorf, J., Schultz, H., Benndorf, A, Unger, R., Penz, E., Kneschke, H., Kossatz, K., Dumke, R., Hornig, U., Kruspe, R. and Reichel, S. 1988. Food-web manipulation by enhancement of piscivorous fish stocks: Long-term effects in the hypertrophic Bautzen Reservoir. Limnologica 19: 97–110.

Bray, K.E. 1996. Habitat models as tools for evaluating historic change in St. Marys River. Can. J. Fish. aquat. Sci. 53: 88–98.

Breen, P.F. 1990. A mass balance method for assessing the potential of artificial wetlands for wastewater treatment. Wat. Res. 24: 689–697.

Breukelaar, A.W., Lammens, E.H.R.R., Breteler, J.G. and Tatrai, I. 1994. Effects of benthivorous bream (*Abramis brama*) and carp (*Cyprinus carpio*) on sediment resuspension and concentrations of nutrients and chlorophyll *a*. Fresh. Biol. 32: 113–121.

Brönmark, C. and Weisner, S.E.B. 1992. Indirect effects of fish community structure on submerged vegetation in shallow, eutrophic lakes: an alternative mechanism. Hydrobiologia 243/244: 293–301.

Brooks, J.L. and Dodson, S.T. 1965. Predation, body size and composition of the plankton. Science 150: 29–35.

Butler, R.S., Moyer, E.J., Hukon, M.W. and Williams, V.P. 1992. Littoral zone invertebrate communities are affected by a habitat restoration project on Lake Tohopekaliga, Florida. J. Fresh. Ecol. 7: 317–328.

Carpenter, S.R., Kitchell, J.F. and Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. BioScience 35: 634–639.

Casselman, J.M. and Harvey, H.H. 1975. Selective fish mortality resulting from low winter oxygen. Verh. int. Ver. Limnol. 19: 2418–2429.

Chambers, P. and Kalff, J. 1985. Depth distribution and biomass of submerged aquatic macrophyte communities in relation to Secchi-depth. Can. J. Fish. aquat. Sci. 45: 1010–1017.

Chambers, P. and Kalff, J. 1987. Light and nutrients in the control of aquatic plant community structure. J. Ecol. 75: 611–619.

Chow-Fraser, P. (in review). Factors contributing to seasonal, interannual and spatial variability of water turbidity in a degraded coastal wetland of L. Ontario. J. Great Lakes Res.

Chow-Fraser, P. and Knoechel, R. 1985. Factors regulating in situ filtering rates of Cladocera. Can. J. Fish. aquat. Sci. 42: 567–576.

Chow-Fraser, P., Trew, D.O., Findlay, D. and Stainton, M. 1994. A test of hypotheses to explain the sigmoidal relationship between total phosphorus and chlorophyll a concentrations in Canadian lakes. Can. J. Fish. aquat. Sci. 51: 2052–2065.

Chow-Fraser, P. and Lukasik, L. 1995. Community participation in the restoration of a Great Lakes coastal wetland. Restoration and Management Notes 13: 183–189.

Chow-Fraser, P., Lougheed, V., LeThiec, V., Crosbie, B., Simser, L. and Lord, J. 1998. 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. Wetland Ecology and Management 6: 19–42.

Cline, J.M., East, T.L. and Threlkeld, S.T. 1994. Fish interactions with the sediment-water interface. Hydrobiologia 275/276: 301–311.

Crivelli, A.J. 1983. The destruction of aquatic vegetation by carp. Hydrobiologia 106: 37–41.

Crowder, A. and Painter, D.S. 1991. Submerged macrophytes in Lake Ontario: current knowledge, importance, threats to stability and needed studies. Can. J. Fish. aquat. Sci. 48: 1539–1545.

Cyr, H. and Downing, J.A. 1988. The abundance of phytophilous invertebrates on different species of submerged macrophytes. Freshwat. Biol. 20: 365–374.

DeMott, W.R. 1990. Retention efficiency, perceptual bias, and active choice as mechanisms of food selection by suspension-feeding zooplankton. *In*: Hughes, R.N. (ed.), Behavioural mechanisms of food selection. pp. 569–594. Springer-Verlag.

Denny, P. 1994. Biodiversity and wetlands. Wetlands Ecology and Management 3: 55–61.

Dieter, C.D. 1990. The importance of emergent vegetation in reducing sediment resuspension in wetlands. J. Freshwat. Ecol. 5: 467–473.

Engel, S. and Nicholas, S.A. 1994. Aquatic macrophyte growth in a turbid windswept lake. J. Freshwat. Ecol. 9: 97–109.

Ferguson, A.J.D., Thompson, J.M. and Reynolds, C.S. 1982. Structure and dynamics of zooplankton communities maintained in closed systems, with special reference to the algal food supply. J. Plankton Res. 4: 523–543.

Fitzgerald, E. 1996. Diet of pumpkinseed sunfish (*Lepomis gibbosus*) and brown bullhead (*Amerius nebulosus*) in the littoral zone of Hamilton Harbour. M. Sc. Thesis, McMaster University, Hamilton, Ontario.

Gliwicz, Z.M. 1990. Food thresholds and body size in cladocerans. Nature 343: 638–640.

Golterman, H.L. 1995. The labyrinth of nutrient cycles and buffers in wetlands: results based on research in the Camargue (southern France). Hydrobiologia 315: 39–58.

Haines, T.A. 1973. Effects of nutrient enrichment and a rough fish population (Carp) on a game fish population (Smallmouth Bass). Trans. Am. Fish. Soc. 2: 346–354.

Hammer, D.A. (ed.). 1989. Constructed Wetlands for Wastewater Treatment: Municipal, Industrial and Agricultural. Lewis Publishers, Inc., Chelsea MI.

Hansen, A-M., Andersen, F.O., and Jensen, H.S. 1997. Seasonal pattern in nutrient limitation and grazing control of the phytoplankton community in a non-stratified lake. Freshwat. Biol. 37: 523–534.

Hanson, J.M. 1990. Macroinvertebrate sizes-distributions of two contrasting freshwater macrophyte communities. Freshwat. Biol. 24: 481–491.

Hanson, M.A. and Butler, M.G. 1990. Early responses of plankton and turbidity to biomanipulation in a shallow prairie lake. Hydrobiologia 200/201: 317–327.

Harris, S.W. and Marshall, W.H. 1963. Ecology of water-level manipulations on a northern marsh. Ecology 44: 331–343.

Holmes, J.A. 1988. Potential for fisheries rehabilitation in the Hamilton Harbour-Cootes Paradise Ecosystem of L. Ontario. J. Great Lakes Res. 14: 131–141.

Hough, R.A., Fornwall, M.D., Negele, B.J., Thompson, R.L. and Putt, D.A. 1989. Plant community dynamics in a chain of lakes: principal factors in the decline of rooted macrophytes with eutrophication. Hydrobiologia 173: 199–217.

Howard-Williams, C. 1985. Cycling and retention of nitrogen and phosphorus in wetlands: a theoretical and applied perspective. Freshwat. Biol. 15: 391–431.

Hurley, D.A. 1986. Fish populations of the Bay of Quinte, Lake Ontario, before and after phosphorus control. Can. Spec. Publ. Fish. aquat. Sci. 86: 201–214.

Hurley, D.A. and Christie, W.J. 1977. Depreciation of the warmwater fish community in the Bay of Quinte, Lake Ontario. J. Fish. Res. Bd Can. 34: 1849–1860.

Kay, R.M. 1949. Limnological studies of the Dundas Marsh Region. M.A. Thesis, McMaster University, Hamilton, Ontario.

Keddy, P. and Reznicek, A.A.. 1986. Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. J. Great Lakes Res. 12: 25–36.

Kerfoot, C. and DeMott, W.R. 1985. Interactions among cladocerans: food limitation and exploitative competition. Archiv. Hydrobiol. 21: 431–451.

Krieger, K., Klarer, D.M., Heath, R.T. and Herdendorf, C.E. 1992. Coastal wetlands of the Laurentian Great Lakes: current knowledge and research needs. J. Great Lakes Res. 18: 525–528.

Lamarra, V.A. 1975. Digestive activities of carp as a major contributor to the nutrient loading of lakes. Verh. int. Ver. Limnol. 19: 2461–2468.

Lauridsen, T.L. and Buenk, I. 1996. Diel changes in the distribution of zooplankton in the littoral zone of two shallow eutrophic lakes. Arch. Hydrobiol. 137: 161–176.

Lauridsen, T.L. and Lodge, D.M. 1996. Avoidance of Daphnia magna by fish and macrophytes: chemical cues and predator-mediated use of macrophyte habitat. Limnol. Oceangr. 41: 794–798.

Lougheed, V.L. and Chow-Fraser, P. 1998. Factors that regulate the zooplankton community structure of a turbid, hypereutrophic Great Lakes wetland. Can. J. Fish. aquat. Sci. (In press).

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

Maynard, L. and Wilcox, D. 1996. Coastal Wetlands of the Great Lakes: Background paper for State of the Lakes Conference (SOLEC). Environment Canada and U.S. Environmental Protection Agency. EPA 905-D-96-001c. 74 pp. + addendum.

McCrimmon, H.R. 1968. Carp in Canada. Fish. Res. Bd of Can. Bull. 165.

McCullough, G. 1981. Wetland losses in Lake St. Clair and Lake Ontario. *In*: A. Champagne (ed.), Proceedings of the Ontario Wetlands Conference. pp. 81–89. Federation of Ontario Naturalists, Toronto, Ont.

McDonald, M.E. 1955. Cause and effects of a die-off of emergent vegetation. J. Wildl. Mgmt 19: 24–35.

Minns, C.K. 1986. A simple whole-lake phosphorus model and a trial application to the Bay of Quinte. Can. Spec. Publ. Fish. aquat. Sci. 86: 84–90.

Minns, C.K., Kelso, J.R. and Randall, R.G. 1996. Detecting the response of fish to habitat alterations in freshwater ecosystems. Can. J. Fish. aquat. Sci. 53: 403–414.

Mitchell, S.F. 1989. Primary production in a shallow eutrophic lake dominated alternately by phytoplankton and by submerged macrophytes. Aquat. Bot. 33: 101–110.

Mitsch, W.J. and Reeder, B.C. 1991. Modelling nutrient retention of a freshwater coastal wetland: estimating the roles of primary productivity, sedimentation, resuspension and hydrology. Ecol. Model. 54: 151–187.

Mitsch, W.J., Cronk, J.K., Wu, Xinyuan and Nairn, R.W. 1995. Phosphorus retention in constructed freshwater riparian marshes. Ecol. Appl. 5: 830–845.

Moss, B. 1990. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. Hydrobiologia 200/201: 367–377.

Olson, R.K. 1992. Evaluating the role of created and natural wetlands in controlling nonpoint source pollution. Ecol. Engineer. 1: xi–xv.

Panek, F.M. 1987. Biology and Ecology of Carp. *In*: Cooper, E.L. (ed.), Carp in North America. Am. Fish. Soc.: 1–15.

Philips, E.J., Zimba, P.V., Hopson, M. and Crisman, T.L. 1993. Dynamics of the plankton community in submerged plant dominated regions of L. Okeechobee, Florida U.S.A. Verh. int. Ver. Theor. Angew. Limnol. 25: 423–426.

Phillips, G., Jackson, R., Bennett, C. and Chilvers, A. 1994. The importance of sediment phosphorus release in the restoration of very shallow lakes (The Norfolk Borads, England) and implications for biomanipulation. Hydrobiologia 275/276: 445–456.

Prescott, K. 1996. The application of mass balance and hydrodynamic/pollutant transport models for wetland restoration. M.S. Eng. Thesis, Dept. of Civil Engineering, McMaster University, Hamilton, ON 129 pp.

Randall, R.G., Minns, C.K. and Cairns, V.W. 1996. The relationship between an index of fish production and submerged macrophytes and other habitat features at three littoral areas in the Great Lakes. Can. J. Fish. aquat. Sci. 53: 35–44.

Rasmussen, J.B. 1988. Littoral zoobenthic biomass in lakes, and its relationship to physical, chemical and trophic factors. Can. J. Fish. aquat. Sci. 45: 1436–1447.

Reinelt, L.E. and Horner, R.R. 1995. Pollutant removal from stormwater runoff by palustrine wetlands based on comprehensive budgets. Ecol. Engineer. 4: 77–97.

Remedial Action Plan for Hamilton Harbour. 1992. Goals, Options and Recommendations. Vol. 2 Main Report, RAP Stage 2, Canada-Ontario Publication.

Sager, E. 1996. Factors influencing the light environment in Cootes Paradise, Hamilton Harbour, and other coastal marshes of L. Ontario. Wat. Qual. Res. J. Can. 31: 553–575.

Skubinna, J.P., Coon, T.G. and Batterson, T.R. 1995. Increased abundance and depth of submersed macrophytes in response to decreased turbidity in Saginaw Bay, Lake Huron. J. Great Lakes Res. 21: 476–488.

Smith, P.G.R., Glooschenko, V. and Hagen, D.A. 1991. Coastal wetlands of the three Canadian Great Lakes: inventory, current conservation initiatives and patterns of variation. Can. J. Fish. aquat. Sci. 48: 1581–1594.

Snell, E.A. 1987. Wetland distribution and conversion in southern Ontario. Canada land use monitoring program. Working Paper No. 48. Inland Waters and Lands Directorate, Environment Canada.

Sondergaard, M., Jeppeson, E., Mortensen, E., Dall, E., Kristensen, P. and Sortkjaer, D. 1990. Phytoplankton biomass reduction after planktivorous fish reduction in a shallow, eutrophic lake; a combined effect of reduced internal P-loading and increased zooplankton grazing. Hydrobiologia 200/201: 229–240.

Taylor, W.D. 1984. Phosphorus flux through epilimnetic zooplankton from Lake Ontario: relationship with body size and significance to phytoplankton. Can. J. Fish. aquat. Sci. 41: 1702–1712.

Threinen, C.W. and Helm, W.T. 1954. Experiments and observations designed to show carp destruction of aquatic vegetation. J. Wildl. Mgmt 18: 247–250.

Timms, R.M. and Moss, B. 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. Limnol. Oceangr. 29: 472–486.

Weisner, S.E.B. 1987. The relation between wave exposure and distribution of emergent vegetation in a eutrophic lake. Freshwat. Biol. 18: 537–544.

Whillans, T. 1982. Changes in marsh area along the Canadian shore of Lake Ontario. J. Great Lakes Res. 8: 570–577.

Whillans, T. 1996. Historic and comparative perspectives on rehabilitation of marshes as habitat for fish in the lower Great Lakes basin. Can. J. Fish. aquat. Sci. 53: 56–66.