# Predictions on the effect of common carp (*Cyprinus carpio*) exclusion on water quality, zooplankton, and submergent macrophytes in a Great Lakes wetland

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

**Résumé** : Nous avons étudié la relation entre l’exclusion des carpes (*Cyprinus carpio*), la qualité de l’eau, le zooplancton et les macrophytes submergés. Douze enclos expérimentaux in situ de 50 m$^2$ ont été aménagés dans le marais Cootes Paradise, un marais dégradé, durant la période de fraye des carpes en 1995. Nous avons placé dans les enclos deux ou trois carpes de tailles similaires allant de 13 à 59 cm, pour une biomasse totale de 23 à 2 100 kg/ha. La turbidité et les concentrations de phosphore total et d’ammoniac total se sont accrues comme prévu avec l’accroissement de la biomasse totale de carpes dans les enclos. Bien que les carpes n’aient eu aucun effet direct sur la structure de la communauté zooplanctonique, l’accroissement de la turbidité et de la charge de nutriants lié à l’activité des carpes a eu pour effet de réduire la biomasse totale de zooplancton. Nous avons établi une relation entre la diversité des espèces et la turbidité de l’eau pour 19 milieux humides du bassin des Grands Lacs, relation qui a montré qu’au-dessus d’un seuil apparent de 20 NTU, il y avait moins de cinq espèces de plantes submergées, alors qu’une communauté plus diverse était présente dans des milieux moins turbides. Nous prévoyons que la turbidité de l’eau au marais Cootes Paradise pourrait ne pas être réduite sous ce seuil de 20 NTU après exclusion des carpes. Nous mettons l’accent sur la nécessité de considérer d’autres facteurs pouvant contribuer aux accroissements de la turbidité de l’eau et des concentrations de nutriants, comme la remise en suspension des sédiments sous l’action du vent et les caractéristiques du substrat.
[Traduit par la Rédaction]

## Introduction

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

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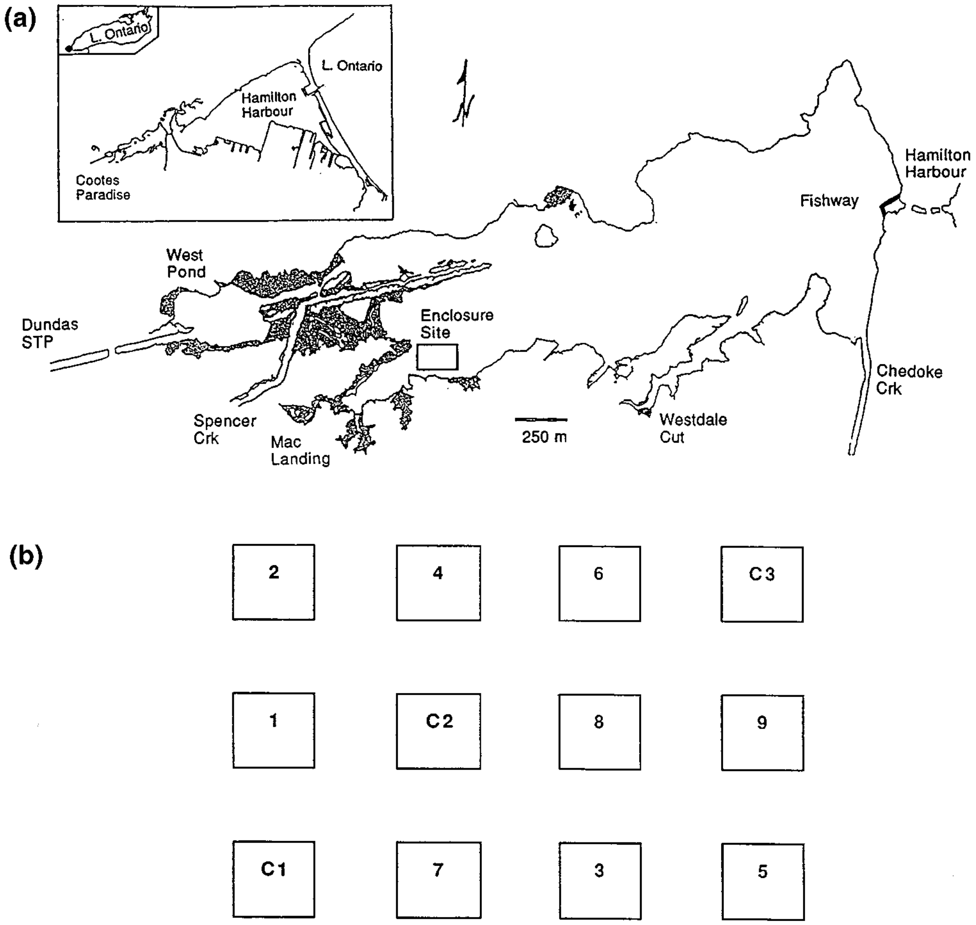
**Fig. 1.** Map of Cootes Paradise Marsh showing (*a*) remnant aquatic vegetation (shaded areas) and the enclosure site and (*b*) the location of the enclosures relative to each other.



*carpio*), the key strategy that must be implemented to initiate such a switch is often difficult to identify.

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

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

## Study site

Cootes Paradise Marsh (Fig. 1) is located in the Hamilton Harbour watershed at the western end of Lake Ontario. It is a severely degraded, 250-ha drowned river-mouth marsh, with

**Table 1.** Sex ratio, mean fork length, and biomass of carp added to each enclosure on May 19, 1995 (day 1).

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

an estimated carp density of 3500 individuals/ha in the near marsh areas during spawning, compared with 400 individuals/ha outside of spawning season (T. Theismeijer, McMaster University, Hamilton, Ont., personal communication). In the early 1900s, 90% of the marsh was covered with diverse emergent vegetation interspersed with smaller patches of submergents. Since the 1940s, the marsh has receded to less than 15% cover, consisting mainly of cattails (*Typha* sp.) and manna grass (*Glyceria* sp.). The loss of emergents has been attributed primarily to increased water levels, while submergent loss was likely due to decreased water clarity, resulting from reduced wind protection and increased carp disturbance, as well as increased nutrient load from the developing watershed (Chow-Fraser et al. 1998). Cootes Paradise Marsh is being restored as part of the HHRAP to create spawning and nursery habitat for warmwater fish species, mainly largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), and northern pike (*Esox lucius*), in the Hamilton Harbour ecosystem (HHRAP 1992). To accomplish this, the HHRAP calls for exclusion of large carp (>30 cm) to improve water quality and to reestablish submergent aquatic vegetation.

## Methods and materials

### Experimental design

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

On May 19, 1995 (day 1), after all fish were removed from the enclosures using a seine net, two or three carp of the same size were randomly placed in each of nine enclosures; three enclosures were randomly selected as controls and received no carp (Table 1; Fig. 1*b*). To encourage spawning, we intended to put two female and one male carp in each of our enclosures but two females perished due to handling stress; the final carp numbers (see sex ratio), mean length, and biomass in each enclosure are provided in Table 1. The size of the carp was chosen based on those readily caught in Cootes Paradise Marsh and surrounding areas. Although carp were not retrieved from the enclosures after the experiment, their presence was verified throughout the experiment by the presence of sediment clouds, a sign of carp activity.

### Enclosure sampling methods

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

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

Zooplankton were pumped into a 5-L beaker, filtered through 63-μm-mesh Nitex screen, backwashed into 60-mL bottles, and preserved in 4% sugar–formalin. Samples collected on days 7, 11, and 15 were enumerated and identified and dry weights were estimated as described in Lougheed and Chow-Fraser (1998). The earliest sampling date was not analyzed to allow zooplankton 1 week to respond to the different treatments. Zooplankton were grouped into

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

| Wetland | Latitude | Longitude | Carp present (Y/N) | Depth (cm) | Mean turbidity (NTU) | No. of submergent plants |
|---|---|---|---|---|---|---|
| 15 Mile Creek | 43°10′00″ | 43°10′00″ | Y | 35 | 81 | 2 |
| Big Creek | 42°57′20″ | 80°26′50″ | Y | 105 | 4 | 9 |
| Christie Lake | 44°47′00″ | 76°28′00″ | N | 40 | 21 | 10 |
| Cootes Paradise Marsh | 43°16′00″ | 79°55′00″ | Y | 20 | 83 | 1 |
| Harris Lake | 45°42′00″ | 80°82′00″ | N | 78 | 2 | 10 |
| Hay Bay | 44°10′30″ | 76°55′30″ | Y | 30 | 3 | 15 |
| Holiday | 42°02′05″ | 83°03′00″ | Y | 30 | 276 | 0 |
| Humber River | 43°38′00″ | 79°29′00″ | Y | 25 | 68 | 1 |
| Joe’s Lake | 45°08′00″ | 76°41′00″ | N | 80 | 1 | 10 |
| Jordan Harbour | 43°11′00″ | 79°23′00″ | Y | 46 | 56 | 2 |
| Martindale Pond | 43°10′07″ | 79°16′00″ | Y | 128 | 44 | 1 |
| Presqu’ile Marsh | 44°00′00″ | 77°43′00″ | N | 75 | 1 | 11 |
| Sawguin Marsh | 44°06′00″ | 77°23′00″ | Y | 80 | 4 | 9 |
| Shebeshekong River | 45°24′30″ | 80°19′00″ | N | 80 | 6 | 8 |
| Stump Lake | 44°56′48″ | 76°38′12″ | N | 53 | 2 | 12 |
| Tay River Marsh | 44°52′45″ | 76°10′30″ | N | 50 | 1 | 14 |
| Tobies Bay | 44°51′00″ | 79°47′00″ | N | 123 | 3 | 7 |
| Turkey Creek | 42°14′08″ | 83°05′07″ | Y | 28 | 11 | 11 |
| Waterford Pond | 42°56′10″ | 80°18′45″ | Y | 44 | 23 | 4 |

size-specific functional groups for all analyses (i.e., herbivorous rotifers, microcladocerans (<300 μm), medium-sized cladocerans (300–600 μm), macrocladocerans (600 μm), nauplii and copepodids, cyclopoid copepods, and predaceous rotifers), although medium- and macrocladocerans were not visible in the graphical output due to their low levels.

### Wetland sampling

Nineteen wetlands located mainly in the Great Lakes basin were sampled twice each in the ice-free seasons of 1995 or 1996 for various factors including turbidity and submergent macrophyte richness (Table 2; Crosbie 1997). These wetlands ranged from pristine to severely degraded and were chosen to ensure a large gradient of disturbance. Ontario Wetland Evaluation reports (Ontario Ministry of Natural Resources) as well as personal observations were used to determine whether carp were present in each marsh. We recorded every species of submergent plant encountered within a 3-m radius of a randomly selected vegetated site. In wetlands with less than two species, the sparse distribution of individual plants (estimated as <5 plants/m$^2$) necessitated surveying the shoreline for about 100 m. Keys by Fassett (1940) were used to identify the submergent macrophytes species. Turbidity readings were taken in triplicate from the middle of the water column, about 3 m from aquatic vegetation, using a portable Hach turbidimeter (model 2100P).

### Statistical analysis

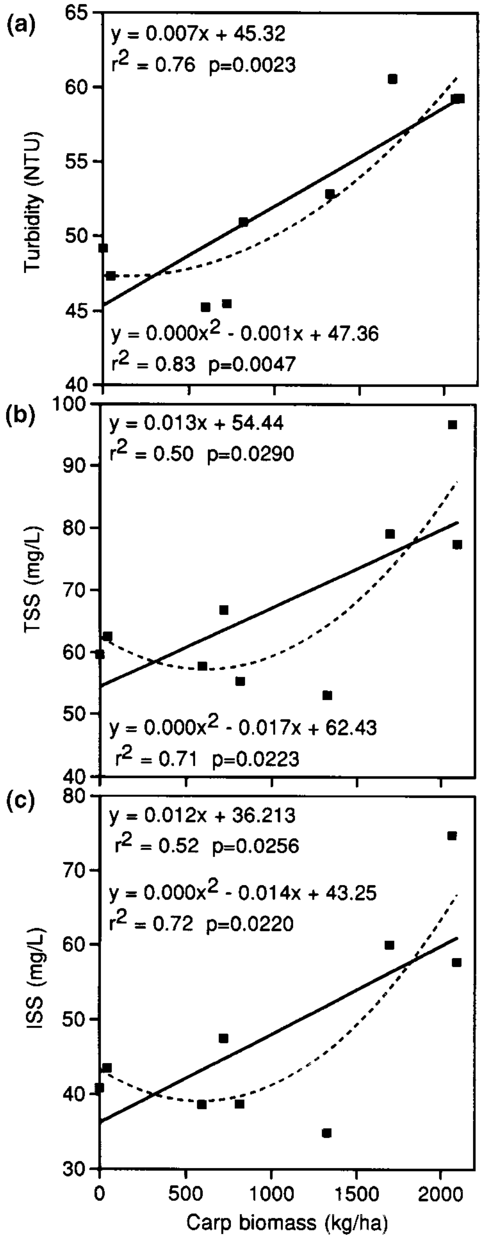
All calculations and statistical analyses were performed using SAS.JMP software (SAS Institute Inc. 1982), and graphical analysis was performed using Cricket Graph III. For all enclosure analyses, we excluded data from enclosure 1 (carp biomass = 0.11 kg/enclosure) because a patch of sago pondweed (*Potamogeton pectinatus*) developed in this enclosure whereas all other control and experimental enclosures were devoid of plants. In the presence of submergent plants, turbulence created by the water pump dispersed sediment and epiphytes from plant surfaces and contaminated water samples. Simple linear regressions were performed on means of all sampling dates for both enclosure and wetland survey data. For analysis of zooplankton – water quality relationships, zooplankton biomass and water quality parameters were transformed using a log($x$ + 1) relationship. To describe changes in the zooplankton community through time, an ANOVA was constructed on arcsin-transformed percent biomass data for each functional taxon using enclosures as replicates for the three sampling dates. A Tukey–Kramer test was performed to confirm the significance tests of all combinations of dates. For wetlands, turbidity data entered into the Student *t*-test, the multipair comparisons, and the regression against submergent plant species were log-transformed to ensure equal variances. Historical data from Cootes Paradise Marsh in 1948 and 1973 (Chow-Fraser et al. 1998) were also included in the wetland regression of number of submergent species versus log turbidity.

## Results

### Water quality characteristics

To determine the overall impact of carp on water quality parameters, we calculated mean values for each enclosure over the four sampling dates and plotted these against carp biomass (Figs. 2 and 3). There was a highly significant relationship between water turbidity and carp biomass ($p$ = 0.0023) that explained 76% of the variation (Fig. 2*a*); variation explained by this relationship increased to 83% ($p$ = 0.0047) when a second-order polynomial was used. Relationships between other water quality parameters and carp biomass were similar but weaker. Both total suspended solids (TSS) and inorganic suspended solids (ISS) varied significantly with carp biomass (Figs. 2*b* and 2*c*), with about 50% of the variation explained by a linear relationship and 70% explained by a nonlinear relationship, in both cases. $NH_3$-N also increased linearly with carp biomass ($r^2$ = 0.50; Fig. 3*a*) whereas $NO_3$-N showed no significant relationship (Figs. 3*a*

**Fig. 2.** Relationship between carp biomass and mean (*a*) turbidity, (*b*) TSS, and (*c*) ISS in enclosures over 2 weeks during the carp spawning season.



and 3*b*). By contrast, TP and SRP (Figs. 3*c* and 3*d*) concentrations varied nonlinearly with carp biomass (no significant linear relationship was found, $p > 0.05$); TP concentrations peaked at intermediate carp biomass whereas SRP concentrations were lowest at this biomass. Chlorophyll *a* was not significantly related to carp biomass or nutrient levels during this study. Mean turbidity at the open marsh site was 80 NTU, as compared with 45–60 NTU measured in the enclosures, which corresponds to a 25–45% reduction in turbidity within the enclosures. This is consistent with earlier experiments showing that exclusion of carp from similar silt-screened enclosures reduced turbidity by about 50% (P. Chow-Fraser, unpublished data).

### Zooplankton

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

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

### Water clarity, submergent growth, and presence of carp

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

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

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

## Discussion

Recent studies of mixed fish assemblages, which compared control and fish treatments (Richardson et al. 1990; Qin and Threlkeld 1990; Breukelaar et al. 1994; Cline et al. 1994) or total lake benthivore biomass before and after biomanipulation (Meijer et al. 1990), suggested that carp play an important role in increasing turbidity and sometimes nutrient levels. Our data confirm that water turbidity and nutrient levels increased predictably with the biomass of spawning carp. Carp activity clearly resulted in increased sediment

**Fig. 3.** Relationship between carp biomass and (*a*) $NH_3$-N, (*b*) $NO_3$-N, (*c*) TP, and (*d*) SRP.

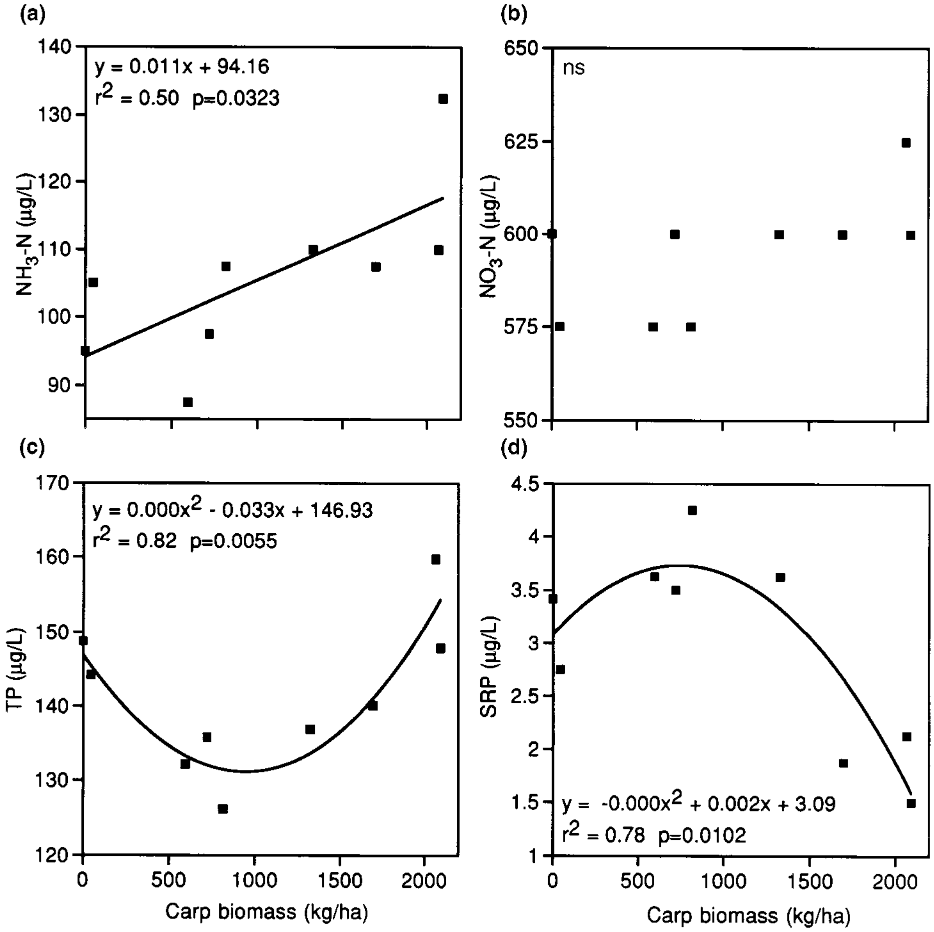


**Table 3.** Characteristics of the ANOVA of arcsin-transformed percent biomass data for each functional taxon compared for three sampling dates (days 7, 11, and 15).

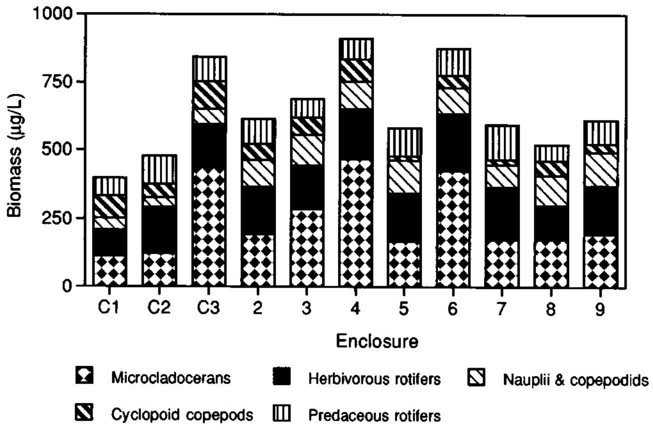
| Taxon | $r^2$ | *F*-ratio | *p*-value | Significant differences |
|---|---|---|---|---|
| Herbivorous rotifers | 0.94 | 232.13 | 0.0000 | Day 7 > 11 > 15 |
| Microcladocerans | 0.07 | 35.18 | 0.0000 | Day 15 > 11 > 7 |
| Medium-sized cladocerans | 0.37 | 8.78 | 0.0010 | Day 15 > 11 and 7 |
| Macrocladocerans | 0.13 | 2.23 | 0.1249 | — |
| Nauplii and copepodids | 0.43 | 11.35 | 0.0002 | Day 15 > 11 and 7 |
| Cyclopoid copepods | 0.08 | 1.29 | 0.2897 | — |
| Predaceous rotifers | 0.63 | 25.29 | 0.0000 | Day 11 > 7 and 15 |

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

resuspension. The increase in phosphate and ammonia levels with carp biomass likely reflected both resuspension of nutrient-laden sediments and a proportionate increase in excretion rates by larger fish. Although benthivorous fish excrete mostly SRP and $NH_3$-N (Brabrand et al. 1990), bioavailable phosphorus can be easily removed from the water column by adsorption to particles under aerobic conditions, forming phosphate-rich inorganic particles (Holdren and Armstrong 1980). In our study, the resuspension of sediment by the larger spawners may have provided more surfaces for phosphate adsorption, therefore resulting in a reduction in SRP with a concomitant increase in TP.

Although levels of turbidity and nutrients generally increased with carp biomass, surprisingly high levels were

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



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

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

Unlike other studies where zooplankton community composition changed with removal of carp (Richardson et al. 1990), there were no obvious between-enclosure differences in zooplankton community structure in this study. In addition to residual effects, the time period of this study, corresponding to carp spawning season, was an obvious limitation to these results in that the study was restricted to only 2 weeks in the spring, when zooplankton in the marsh were typically composed of low to moderate numbers of small animals (Lougheed and Chow-Fraser 1998) which are less sensitive than the larger grazers to changes in water clarity (Kirk and Gilbert 1990; Kirk 1991). Overall, a reduction in total zooplankton biomass was associated with increased levels of suspended solids, as well as TP and $NO_3$-N, that were presumably due to carp activity. We therefore predict that by excluding spawning carp from Cootes Paradise Marsh, and thereby reducing the suspended solid and nutrient levels, total zooplankton biomass should increase, and that if suitable macrophyte habitats became available, previous work (Lougheed and Chow-Fraser 1998) suggested that this increased biomass would consist of larger grazers. A larger population of macrograzers may lead to further increases in clarity due to zooplankton grazing (Hanson and Butler 1994; Schriver et al. 1995); however, it appears that an increased biomass of smaller grazers will have no impact on algae, as indicated by chlorophyll *a* in this study.

Scheffer (1990) theorized that in shallow lakes of homogeneous depth, submergent plants will disappear suddenly when a threshold turbidity is exceeded, which renders most of the lake unsuitable for plant growth. We found support for this theory in wetlands where above an apparent threshold of 20 NTU, there were less than five species of submergents whereas a more diverse community of macrophytes existed in clearer water. It is noteworthy that marshes where carp were absent had uniformly clear water ($<6$ NTU) and a relatively diverse (more than seven species) and dense (estimated as $>20$ plants/m$^2$) submergent flora; however, whereas carp-free systems were always macrophyte dominated, macrophyte-dominated systems were not always carp free (i.e., Big Creek, Hay Bay, Sawguin, and Turkey Creek). An obvious limitation to these results was the absence of data on carp biomass, which is known to be related to submergent plant cover (Robel 1962; Crivelli 1983). In addition, the presence of established submerged macrophytes could stabilize sediment and maintain water clarity (Hamilton and Mitchell 1997) in the presence of carp. Nonetheless, because these four wetlands were significantly clearer than other wetlands containing carp and were not significantly different from carp-free wetlands (ANOVA, $p = 0.0000$, $F = 62.6$, df = 2 and 16; confirmed with Tukey–Kramer), we suggest that this is additional evidence that water turbidity in Great Lakes marshes must be affected by factors other than carp, such as wind resuspension of sediment, high algal concentration, and fine substrate composition.

Further remedial actions will likely be necessary to promote the restoration of Cootes Paradise Marsh, as the increase in water clarity that will result from carp removal in the marsh is unlikely to be sufficient to allow the establishment of a diverse community of submergent vegetation. Carp-free enclosures had a mean turbidity of 45 NTU throughout the experimental period which was much higher than the 20 NTU required for submergent growth. We must acknowledge, however, that there are limitations to this prediction. Whole systems and enclosed systems behave differently, especially as it pertains to flow, turbulence, and the settling of particles (Bloesch et al. 1988; Horpilla and

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

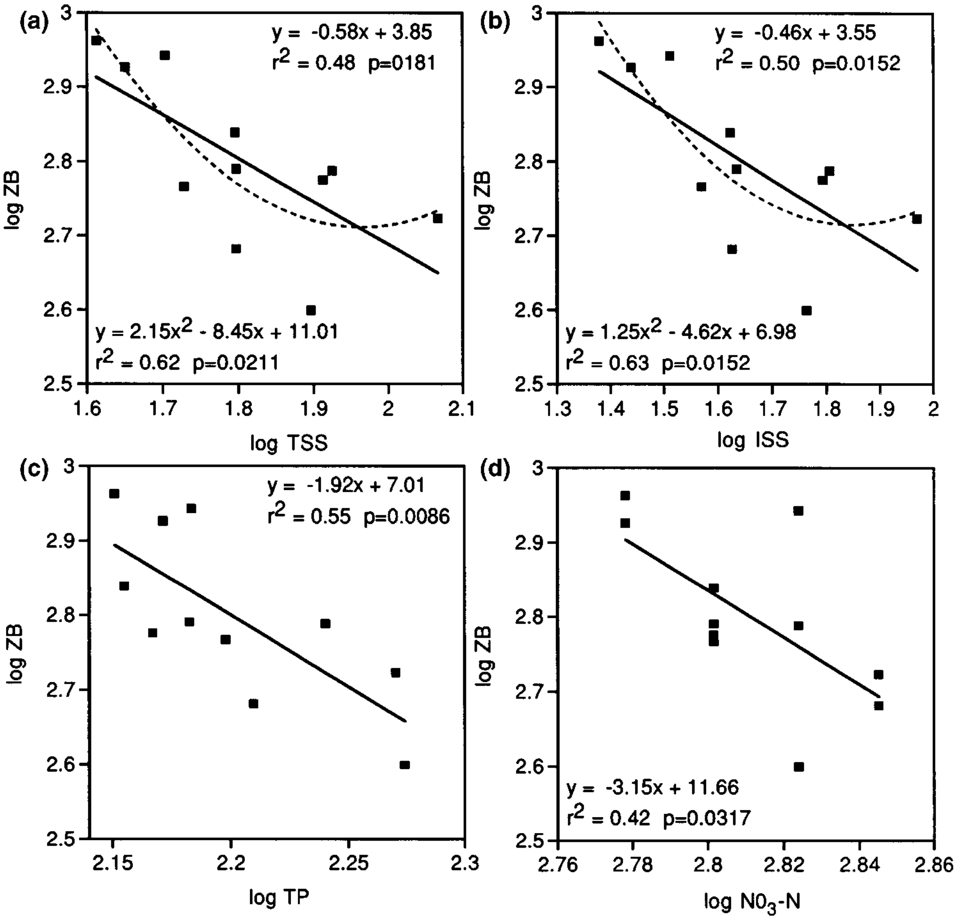
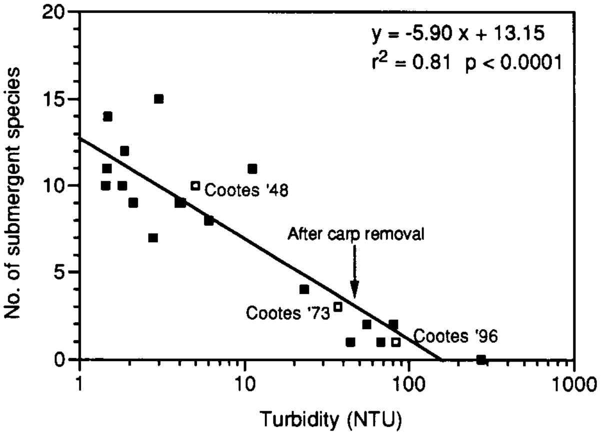


**Fig. 6.** Relationship between the number of submergent plant species versus turbidity (log scale) for 18 marshes in the Great Lakes basin (solid squares) and Cootes Paradise Marsh from 1948, 1973, and 1996 (open squares). Also indicated is the predicted water clarity following carp removal (45 NTU)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



Kairesalo 1990). In addition, the plantless enclosures may have inhibited carp activity during the spawning season, as carp tend to spawn near plants (Balon 1995), notably in Cootes Paradise Marsh where they congregated near the cattails at levels eight times higher than outside of the spawning season (T. Theismeijer, McMaster University, Hamilton, Ont., personal communication). The 25–45% reduction in turbidity in the enclosures compared with the open marsh may, in part, reflect these limitations.

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

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