Spatial variability in the response of lower trophic levels after carp exclusion from a freshwater marsh

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Abstract

Large common carp (*Cyprinus carpio* >30 cm) were excluded from a turbid, eutrophic coastal marsh of Lake Ontario with the construction of a fishway at the outlet. The marsh was sampled intensively for 2 seasons prior to (1993, 1994) and following (1997, 1998) carp exclusion to study changes in water quality and shifts in community structure of phytoplankton and zooplankton. Samples were collected from May to September in three habitats: open water, vegetated (cattail beds) and sewage lagoon. In the first year after carp exclusion, mean seasonal water turbidity decreased at all sites by 49–80%; this was accompanied by growth of submergent plants in shallow, sheltered areas including the vicinity of cattails at the vegetated site. This drop in turbidity was not significant in the second year after exclusion at the open water and lagoon sites, with turbidity levels declining by only 26–54% of 1993–1994 values; only the vegetated site showed a sustained decrease in turbidity and persistent growth of submergent plants. At the vegetated site, increased clarity was concurrent with a significant reduction in edible algal biomass and an increased representation of large zooplankton grazers and substrate-associated cladocerans. At the open water site, a spring clear-water phase was evident during the first year of exclusion and this coincided with the unusual appearance of a large population of *Daphnia*. Compared to the other sites, the lagoon remained relatively turbid throughout the study. Results of this study indicate that the response of lower trophic levels to biomanipulation was variable from site-to-site and contributed to the co-existence of two alternative states in the marsh. In vegetated areas, water clarity was maintained by a positive feedback system between zooplankton and submergent macrophytes in the first 2 years following exclusion. We suggest that both benthivore removal (to reduce bioturbation) and planktivore reductions (to produce top down effects) were required to produce clear water and allow submersed macrophyte growth. Although carp removal likely contributed to a 45% reduction in turbidity, an unusual climactic event in 1997, resulting in delayed fish spawning in the marsh, temporarily reduced zooplanktivory and favoured zooplankton grazing-induced water clarity improvements.

1. Introduction

Use of biomanipulation to force a switch from turbid, phytoplankton-dominated lakes to clear-water, macrophyte-dominated systems is a well documented restoration strategy for shallow freshwater lakes (see Moss et al., 1996; Scheffer, 1998). Despite the large number of cases documenting the switch between these two alternative states, it has often been dif-

ficult to distinguish between two possible mechanisms that lead to the initial increase in light penetration: 1) reduction in sediment resuspension by removal of benthivorous fish such as common carp (*Cyprinus carpio*) or bream (*Abramis brama*) (e.g. Meijer et al., 1990), or 2) trophic cascade-induced clarity through removal of planktivores with subsequent increase in top-down control of phytoplankton by zooplankton (e.g. Ozimek et al., 1990; van Donk et

al., 1990; Hanson & Butler, 1994). In either case, successful biomanipulations have been followed rapidly by increased water transparency, and the development of submersed aquatic vegetation throughout the lake.

The stability of the clear-water state has also been difficult to predict (Scheffer, 1998) and may be due to differences among lakes with respect to interactions at the lower trophic levels. For example, establishment of aquatic vegetation may help maintain water clarity in some lakes by stabilizing the sediment and reducing sediment resuspension by wind (Hamilton & Mitchell, 1997). It may also suppress algal growth through competition for nitrogen (Ozimek et al., 1990; van Donk et al., 1990) and some macrophyte taxa contain chemicals which can have an allelopathic effect on algae (e.g. Wium-Andersen et al., 1982). Increase in macrophyte cover can also provide refugia for large-bodied zooplankton grazers such as *Daphnia*, and this has been used to explain the shift in zooplankton community from rotifers and small-bodied cladocerans to larger-bodied forms following biomanipulation (Hansen & Jeppesen, 1992; Hanson & Butler, 1994) with enhanced top-down control of algae (Timms & Moss, 1984; Schriver et al., 1995). Clearly, the outcome of biomanipulation, both in terms of degree of success and stability of the altered state, can be affected by any number of these factors, and it is becoming increasingly important to understand the different roles played by these forcing variables so that effective management strategies can be devised.

Although the theory of alternative stable states has been applied widely to shallow eutrophic lakes in Europe (80% of reported biomanipulations in Drenner & Hambright, 1999), it has not received as much attention in North America, and has seldom been applied to coastal wetlands of the Laurentian Great Lakes, even though these wetlands are similar to shallow lakes in a number of ways. First, like shallow lakes, they are highly influenced by anthropogenic stressors such as urban and agricultural runoff (Crosbie & Chow-Fraser, 1999). Secondly, loss of submergent vegetation in these wetlands has been blamed on increased nutrient and sediment loads from developing watersheds, as well as sediment resuspension from benthivorous fish such as the common carp, *Cyprinus carpio* (Whillans, 1996; Chow-Fraser, 1998, 1999). However, there are also key differences between shallow lakes and wetlands, notably with respect to hydrology and seasonal fish migrations. For example, unlike most shallow lakes, coastal wetlands are subject to large-lake processes, including long-term and seasonal fluctuations in water level (Maynard & Wilcox, 1996). In Cootes Paradise Marsh (Lake Ontario), where mean depth is 0.7 m, water levels have fluctuated by more than a meter over an 8-to-10-year cycle, and by more than 0.5 m seasonally (about 15% of the marsh routinely dries up by the end of the summer) (Chow-Fraser et al., 1998; Chow-Fraser, 1999). In addition, the connectedness between large lakes and coastal wetlands allows seasonal migrations by the fish community. Some fish species use wetlands for only part of their life (e.g. spawning, feeding, or nursery area) and are present only seasonally, while others are permanent residents (Jude & Pappas, 1992). Hence, the fish community in coastal wetlands tends to vary substantially from year to year.

Because of such seasonal variations, as well as site-to-site differences with respect water turbidity (Chow-Fraser, 1998) and the zooplankton community (Lougheed & Chow-Fraser, 1998), coastal wetlands might be expected to exhibit highly variable temporal and spatial responses to biomanipulation. Although spatially variable responses to fish removal have been observed within large, shallow European lakes (e.g. Meijer & Hosper, 1997), studies have yet to provide comparative statistical analyses of changes in water quality, phytoplankton and zooplankton among several sites and explain how these site-to-site differences are maintained within a single system. Such a comparison is necessary for predicting the effectiveness of biomanipulation in triggering the switch to a clear-water state when temporally and spatially variable ecosystems are being restored. In this paper, we describe contemporaneous changes in lower trophic levels at three characteristically different sites in Cootes Paradise Marsh, a degraded urban coastal marsh of Lake Ontario, from which carp have been actively excluded since 1997 (Wilcox & Whillans, 1999). The overall goal of this paper is to evaluate the impact of benthivore removal on water quality and plankton communities, paying particular attention to site-to-site variations in the response. Our results should indicate the effectiveness of carp exclusion as a restoration strategy in a spatially variable marsh.

2. Study site

Compared with the large number of biomanipulation studies on shallow lakes, there have only been a few studies on Great Lakes coastal wetlands, which have mainly been confined to small-scale enclosure

experiments (Havens, 1991; Lougheed et al., 1998). Fortunately, recent attempts in ecosystem restoration through the Binational Great Lakes Remedial Action Plans (see Krantzberg et al., 1997) have provided a rare opportunity to formally test biomanipulation theory in these wetlands. The restoration of Cootes Paradise Marsh is one of the most ambitious restoration projects in the Great Lakes basin, designed to restore aquatic vegetation through a carp exclusion scheme (Hamilton Harbour Remedial Action Plan Stage 2, 1992; Wilcox & Whillans, 1999).

Cootes Paradise is a 250-ha drowned river-mouth marsh located at the westernmost point of Lake Ontario (43°N, 79°W) (Figure 1) that is managed by the Royal Botanical Gardens (Burlington, ON, Canada). At the turn of the century, a diverse community of emergent and submergent vegetation covered 90 percent of the marsh; however, by the 1970's only 15% of the marsh retained cover, primarily cattails (*Typha* sp.) and manna grass (*Glyceria* sp.). The loss of emergents has been attributed primarily to increased water levels, while submergent loss has been blamed on decreased water clarity resulting from sediment resuspension from wind and carp activity, as well as excessive inputs of nutrients from sewage and runoff (Chow-Fraser, 1998).

Changes in the fish and macrophyte communities following carp exclusion are the subject of a manuscript in preparation (see Lougheed et al., 2001); however, a few preliminary trends are reported here. Prior to biomanipulation, common carp existed at 700 kg/ha in the vegetated areas of Cootes Paradise Marsh (Lundholm & Simser, 1999). The seasonal migration of fish such as carp in and out of the marsh in the spring and fall facilitated the exclusion of these migrating species via the construction of a fishway at the outlet of Cootes Paradise (see Figure 1) during the winter of 1997. The fishway used 5-cm wide grating to physically exclude large fish from the marsh (see Wilcox & Whillans, 1999). Fish not capable of passing through the grating were manually processed such that all fish other than carp were released into the marsh, whereas carp were returned to waters outside Cootes Paradise. This effectively prevented large carp (>30 cm) from entering the marsh after February 1997. Carp biomass, estimated from monthly surveys of four 50-meter electrofishing transects, declined by greater than 90% in 1997 and an additional 7% (relative to 1996 levels) in 1998 (T. Theÿsmeÿer, Royal Botanical Gardens, pers. comm.). Immediately following carp exclusion, submergent vegeta-

tion, primarily *Potamogeton pectinatus*, became established in shallow and sheltered areas of the marsh, notably in the vicinity of established cattail beds (2570 submergent stems/ha in June 1997; Lundholm & Simser, 1999). In the second year following exclusion, submergent plant density increased substantially in these areas (34,100 submergent stems/ha in June 1998; T. Smith, Royal Botanical Gardens, pers. comm.); however, the open and exposed sections of the marsh remained essentially devoid of vegetation throughout the study period (Lundholm & Simser, 1999).

3. Methods

3.1. *Sampling and counting methods*

We present water turbidity data collected for 3 years prior to carp exclusion (1993–94, 1996) and 4 years following exclusion (1997–2000) to illustrate long-term trends in water clarity (NOTE: there was no monitoring program in 1995); the remainder of the data analysis, including water chemistry, phytoplankton and zooplankton, represent 2 years pre-exclusion (1993–94) and 2 years post-exclusion (1997–98). Samples were collected bi-weekly from mid-May to late August from three sites, all approximately 1 km apart (Figure 1). There was a relatively deep open water site near the marsh outflow (mean depth ranges from 97–127 cm); a shallow lagoon site that historically received loadings from the Dundas Sewage Treatment Plant (depth 43–69 cm); and a vegetated site within the cattails beds of a marsh inlet (depth 23–49 cm). Following exclusion, there were also patches of submersed macrophytes in the vicinity of the vegetated site; however, the sampling location remained within the cattail beds. Depth and selected water quality characteristics from each site are summarized in Table 1. All sites were sampled 8 times per year for zooplankton and water quality parameters with the exception of the vegetated site in 1993 ($n = 7$) and 1994 ($n = 7$) and the lagoon site in 1998 ($n = 6$) because access was restricted due to factors beyond our control.

All samples for water, zooplankton and phytoplankton analyses were collected from the middle of the water column at each site. Water and zooplankton were analyzed as summarized in Lougheed & Chow-Fraser (1998). For statistical and graphical analyses, zooplankton biomass (μg/L) is shown in dry weight and taxa were grouped into the fol-
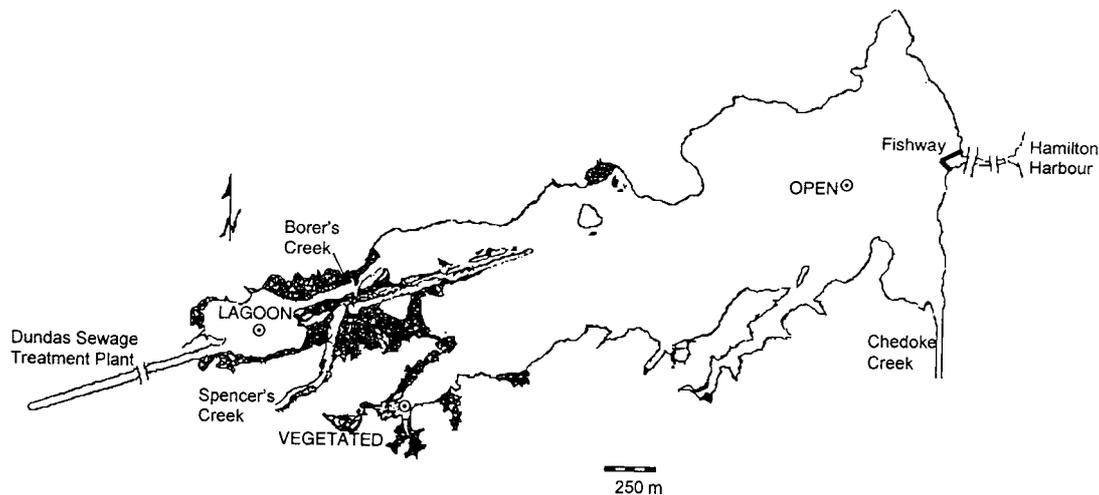
Figure 1. Location of sampling sites (LAGOON, VEGETATED and OPEN) in Cootes Paradise Marsh. Shaded areas indicate the presence of emergent vegetation throughout the study period.

Table 1. Means of bi-weekly sampling trips from mid-May to late August each year before (1993 and 1994) and after (1997 and 1998) carp exclusion for selected water quality variables.

	1993	1994	1997	1998
OPEN WATER				
Depth(cm)	127	98	114	95
Turbidity (NTU)	74	60	26	44
TP(μg/L)	157	126	121	282
TNN (μg/L)	671	513	388	650
LAGOON				
Depth(cm)	69	43	53	58
Turbidity (NTU)	71	91	36	51
TP(μg/L)	288	364	272	436
TNN (μg/L)	3486	4117	5095	3950
VEGETATED				
Depth(cm)	49	23	33	27
Turbidity (NTU)	24	43	11	11
TP(μg/L)	198	197	231	265
TNN (μg/L)	483	329	300	906

lowing categories: microcladocerans (<300 μm), medium cladocerans (300–600 μm), macrocladocerans (*Daphnia*; >600 μm), herbivorous rotifers, nauplii and copepodids, cyclopoid copepods, predaceous rotifers and substrate-associated cladocerans (*Simocephalus exspinosus* and chydorid cladocerans). The published length-filtering rate equation of Chow-Fraser & Knoechel (1985) was used to calculate cladoceran grazing rate (mL filtered/L/day), while all rotifer species were assigned an identical grazing rate, regardless of length or taxa, based on the *in situ* experimental results of Bogdan et al. (1980). Results are presented using a relatively low rotifer grazing rate (0.05 mL/day); however, similar trends were observed using a rotifer grazing rate of 0.15 mL/day.

Phytoplankton samples were collected using a 1-L Van Dorn bottle and preserved with Lugol's iodine in the field. Subsamples of 5-mL were settled for 24-hours in algal settling chambers, with very concentrated samples diluted by 10 to 20 times with distilled water. Algal cells and colonies were identified using up to 400× magnification and measured along one full transect of each settled slide under a phase microscope at 200× magnification. The entire slide was also surveyed for large cells and colonies. Algal bio-volumes were calculated by approximation to geometric shapes, and expressed as biomass (μg/L). Taxa were divided into algal groups (blue-greens, greens, euglenoids, chrysophytes, diatoms, cryptophytes and dinoflagellates) and either edible (<30 μm) or inedible (>30 μm) size classes after Chow-Fraser & Knoechel (1985).

3.2. *Statistical analyses*

Statistical analyses were performed using SAS.Jmp software (SAS Institute Inc., Cary, N.C., version 3.1.5). Comparisons of mean water quality variables, phytoplankton biomass and zooplankton biomass between years and clusters were analyzed with

an analysis of variance (ANOVA) followed by Tukey-Kramer multiple comparisons at the 95% significance level. These data were $\log_{10}$-transformed to normalize the distribution. Where relevant, yearly data were divided into early summer and late summer sampling trips. The division point was selected as July 9 for all years, to ensure 4 sample dates before and after this date for all those sites visited 8 times per year.

4. Results

4.1. *Water quality*

Table 1 summarizes selected mean water quality variables for each of the sites during 1993–94 and 1997–98. All sites were generally eutrophic and turbid (Total phosphorus: TP = 121–435 μg/L; Total nitrate: TNN = 300–5095 μg/L; Turbidity = 10.7–91 NTU). The lagoon site usually experienced higher turbidity, nutrient and algal levels relative to the other sites. At the vegetated site, water turbidity for the two years immediately following exclusion was significantly reduced by 55 to 80% relative to all pre-exclusion years (Figure 2). We could not sample the vegetated site in 1999 as low water levels resulted in the marsh drying up in these shallower vegetated areas; however, in 2000, water turbidity increased slightly to a level significantly different from 1996 only. Post-exclusion turbidity at the open water and lagoon sites was more variable. In 1997, turbidity at these 2 sites was reduced by greater than 49% relative to pre-exclusion years. This decrease was significant at the open water site. In the subsequent three years (1998–2000), turbidity at these two sites was not significantly different from levels observed prior to exclusion.

By comparing carp-less enclosures and an unenclosed site in the marsh, Lougheed et al., (1998) predicted that water turbidity would be reduced by 45% following carp exclusion. The dashed lines on Figure 2 represent a 45% reduction relative to the maximum and minimum seasonal mean turbidity observed in 1994, 1994 or 1996. Turbidity values at all sites following exclusion closely approximated these predicted ranges, with the exception of the open water site in 1999, where low water levels likely promoted increased wind resuspension of sediment in this exposed location. There were no significant differences between pre- and post-exclusion years for either TP or TNN concentrations; although, at the open water site, TP was significantly higher in 1998 relative to all other years (ANOVA, Tukey–Kramer, $p < 0.05$).
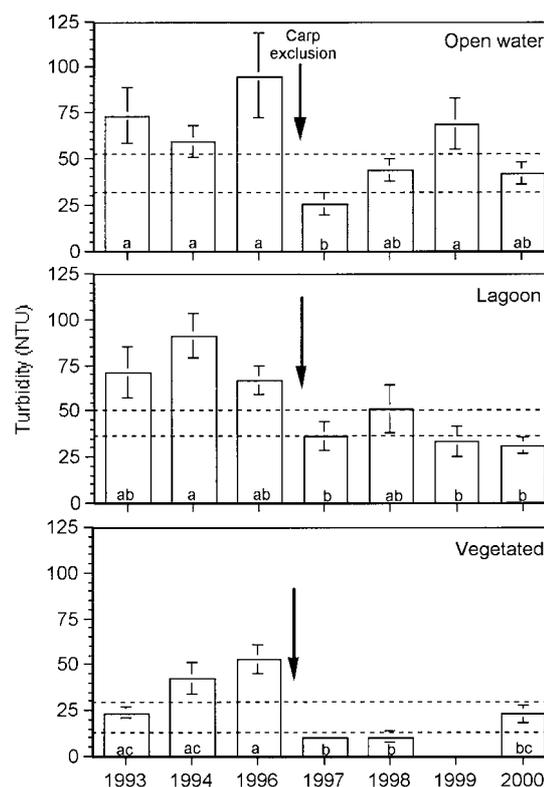

Figure 2. Comparison of mean turbidity levels prior to (1993–94, 1996) and following (1997–2000) carp exclusion at three sites in Cootes Paradise Marsh. Dashed lines represent the range of turbidity expected following carp exclusion as predicted by enclosure experiments (45% reduction relative to pre-exclusion years; Lougheed & Chow-Fraser, 1998). Letters at base of histogram bars indicate statistical similarities (ANOVA, Tukey–Kramer, $p > 0.05$).

4.2. *Phytoplankton*

Marsh-wide, there was not an obvious change in the species composition of phytoplankton observed following carp exclusion, with 79 to 88 taxa identified in 1993–94 and 73 to 84 identified in 1997–98 (see Chow-Fraser et al. (1998) for species list). The phytoplankton community throughout the marsh was generally dominated by cryptophytes, diatoms, euglenoids and green algae.

Comparison of algal groups divided into edible and inedible size classes at each site revealed no statistically significant differences in mean taxonomic composition between 1993 and 1994. After exclusion, however, there were some notable changes. Mean seasonal total and edible phytoplankton biomass was significantly reduced at the vegetated site for both years following carp exclusion (Figure 3; ANOVA, Tukey–Kramer; $p < 0.005$), while there were no
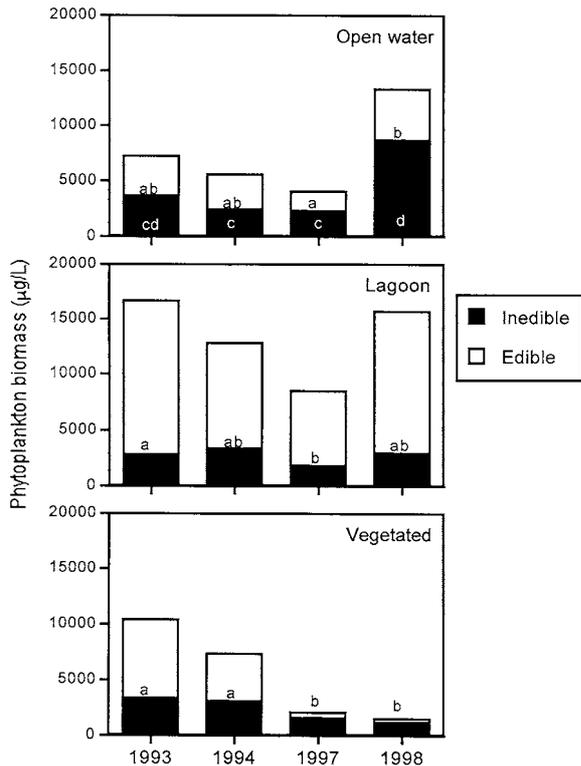
Figure 3. Comparison of mean seasonal total, edible and inedible phytoplankton biomass prior to (1993 & 1994) and following (1997 & 1998) carp exclusion at three sites in Cootes Paradise Marsh. Letters indicate statistical similarity between years (ANOVA, Tukey–Kramer, $p < 0.05$) for edible (ab) or inedible (cd) phytoplankton.

consistent changes in mean seasonal phytoplankton biomass observed at the other 2 sites. There was, however, a significant increase in total, edible and inedible phytoplankton at the open water site in 1998 (ANOVA, Tukey–Kramer, $p < 0.05$). In addition, there was a significant (ANOVA; Tukey–Kramer; $p < 0.005$) decline in euglenoids at the open water site in 1998, as well as significantly higher (ANOVA; Tukey–Kramer; $p < 0.005$) contribution of blue-green algae to the late summer community at this site. There was also an increase in cryptophyte biomass at both the open water (ANOVA; Tukey–Kramer; $p < 0.005$) and lagoon sites ($p > 0.05$) in early summer 1998.

4.3. *Zooplankton and zooplankton grazing*

The total number of zooplankton species in the marsh increased following carp exclusion from 27 species (1993–1994) to 40 species (1997–1998). Individually, only the vegetated site showed a sustained increase in species richness, from less than 26 to more than 32 species. This increase included both an increase in rotifers (9 new species) and cladocerans (6 new species). A complete list of zooplankton species found pre-exclusion can be found in Lougheed & Chow-Fraser (1998). New cladoceran species included: *Camptocercus macrurus, Ceriodaphnia reticulata, Chydorus sphaericus, Daphnia galeata mendotae, Pleuroxus denticulatus, Pleuroxus procurvatus.* New rotifers were: *Euchlanis* sp., *Lepadella* sp., *Monostyla cornuta, M. quadridentata, Mytilina* sp., *Notholca* sp., *Platyias quadricornus, Ploesoma* sp., *Trichocerca elongata).* All the new rotifers encountered in the marsh post-exclusion were found at the vegetated site, with 4 new species observed at the open water site. The lagoon site showed the greatest increase in the number of cladoceran taxa, including 5 taxa that were new to the marsh as well as 3 taxa previously observed at the other sites. In addition, the open water and vegetated sites were each were home to 5 new cladoceran species.

Comparison of zooplankton composition revealed no striking differences between pre-exclusion years, except at the lagoon site (Figure 4) where micro-grazers dominated in 1993 and cyclopoids dominated in 1994. Post-exclusion, there was a notable increase in the occurrence of large-bodied zooplankton at vegetated and open sites (Figure 5). At the open water site, *Daphnia* biomass in 1997 was significantly higher than in pre-exclusion years (ANOVA, Tukey–Kramer, $p < 0.05$), when *Daphnia* never occurred above a level of 3 individuals/L. These *Daphnia* reached a level of 530 individuals/L (4000 μg/L) in June 1997 before the population crashed abruptly at the start of July (Figure 4). This unusual seasonal trend was not repeated in 1998. Similarly, at the vegetated site, the biomass of *Daphnia* was significantly greater in early summer 1997 than it was in early summer of pre-exclusion years (ANOVA, Tukey–Kramer, $p < 0.05$); although this represented a much lower biomass (maximum 32 *Daphnia*/L) than that seen at the open water site. The only apparent sustained change in the zooplankton community following carp exclusion was the increased biomass of substrate-associated cladocerans (e.g. *Simocephalus exspinosus*) at the vegetated site in both post-exclusion years relative to both pre-exclusion years (Figure 5; ANOVA, Tukey–Kramer, $p < 0.05$). This population was at its greatest in mid- to late-summer (Figure 4) after submergent plants become established. Cyclopoid biomass was numerically higher in 1998 at the open water site,
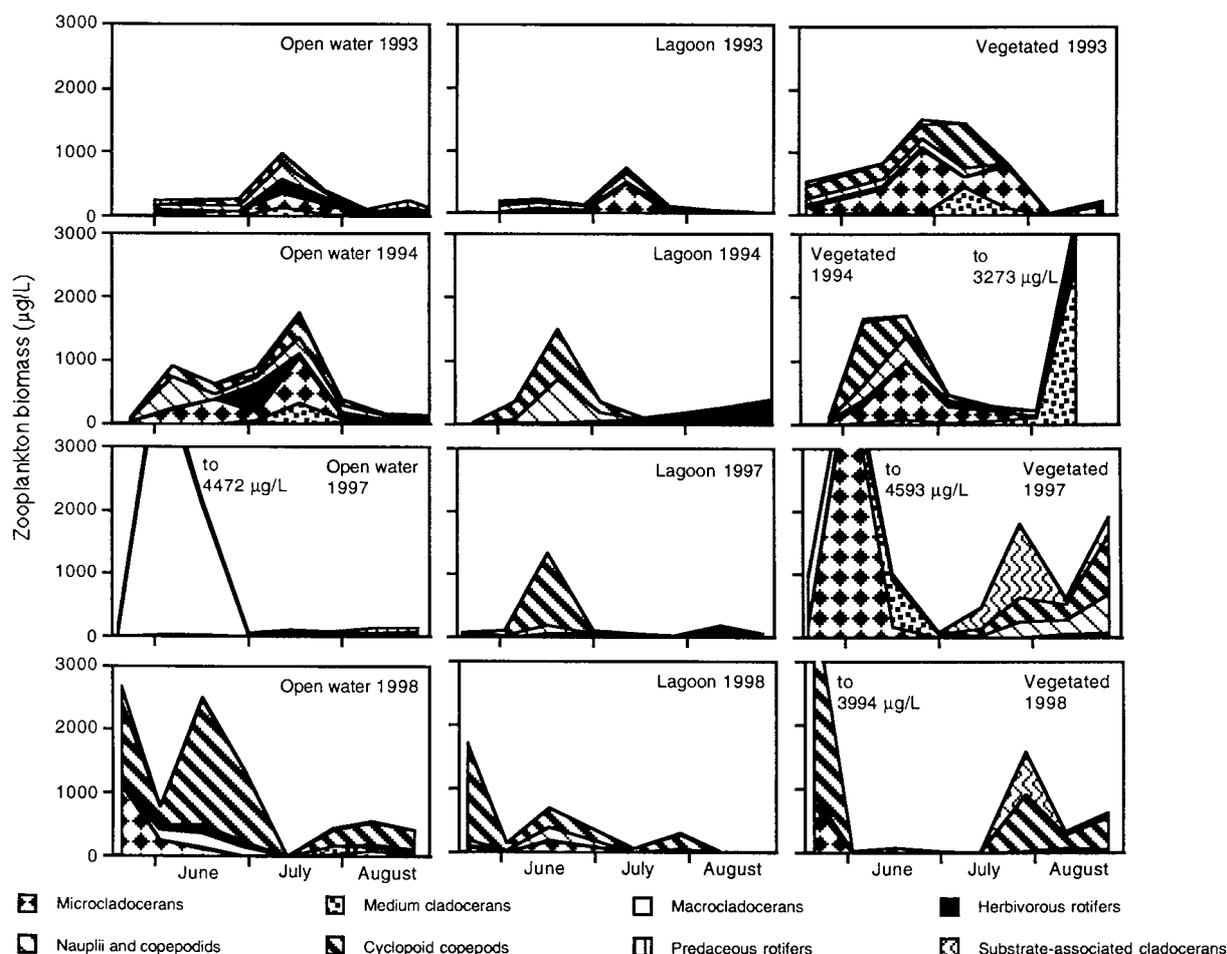
Figure 4. Seasonal patterns in biomass (μg/L) of zooplankton taxa before carp exclusion (1993 & 1994; top two rows) and after carp exclusion (1997 & 1998; bottom two rows) at three representative sites in the marsh (OPEN: left column; LAGOON: middle column; VEGETATED: right column).

although these values were only significantly higher when compared to 1993 and 1997 data (ANOVA, Tukey–Kramer, $p < 0.05$). Finally, there was a significant reduction in herbivorous rotifer biomass at the lagoon site in 1998 relative to previous years (ANOVA, Tukey–Kramer, $p < 0.05$).

The community grazing rate tended to be lowest at the lagoon site (Figure 6), which was largely dominated by herbivorous rotifers and predaceous copepods, as compared to the open or vegetated sites, which had a greater proportion of cladoceran grazers. Mean zooplankton grazing rates were not significantly different between pre- and post-exclusion years (ANOVA, Tukey–Kramer, $p < 0.05$) at any of the study sites; however in 1997, the zooplankton communities at the open and vegetated sites were filtering

>850 mL/day on average, with maximum grazing rates of 4840 mL/day and 2780 mL/day, respectively, observed during the June peak in zooplankton biomass. The only other occasion when values as high as these were observed was in August 1994 at the vegetated site when zooplankton were concentrated in 10 cm of water at the summer's end.

The relationship between edible phytoplankton biomass and zooplankton grazing was examined for all site-year comparisons, and was significant only for the open water and vegetated sites in 1997, where >55% of the variation in edible phytoplankton biomass throughout the season could be explained by zooplankton grazing (Figure 7). Both these sites exhibited a large peak in herbivorous zooplankton biomass in early summer, coincident with low edible
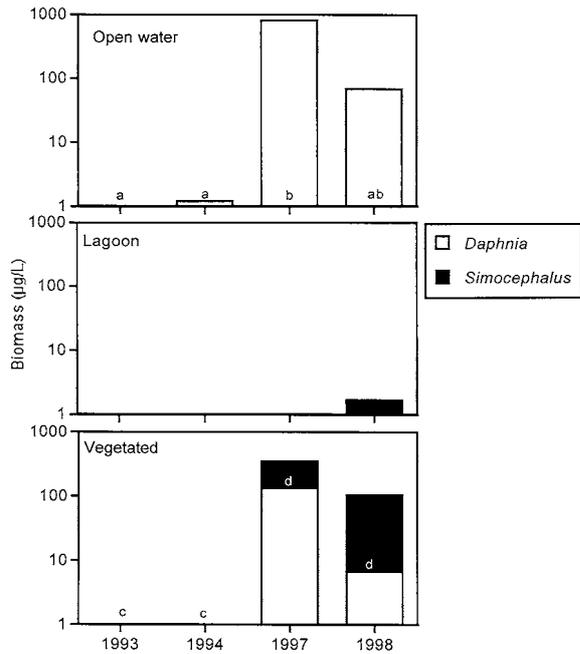
Figure 5. Comparison of mean seasonal biomass of large cladoceran grazers (>600 μm mean body length), including *Daphnia* sp. and *Simocephalus exspinosus* biomass prior to (1993 & 1994) and following (1997 & 1998) carp exclusion at three sites in Cootes Paradise Marsh. Letters indicate statistical similarity between years (ANOVA, Tukey–Kramer, $p < 0.05$) for or *Daphnia* (ab) or *Simocephalus* (cd) populations.

phytoplankton biomass, followed by a slight increase in phytoplankton levels upon the zooplankton decline (Figure 8).

5. Discussion

Using a series of enclosure experiments Lougheed et al. (1998) predicted that the exclusion of large carp from shallow, non-vegetated areas of Cootes Paradise would at most increase water clarity by 45% compared to pre-exclusion levels; however, the initial results in 1997 showed an improvement of 49 to 80%. Assuming 45% accurately reflects the decrease in sediment resuspension due to carp exclusion, then an additional 4 to 35% remains unexplained. We attribute this greater than expected increase in water clarity to a zooplankton-mediated spring clear-water phase in the first year following carp exclusion. Zooplankton grazing increased water clarity sufficiently to promote the establishment of submergent plants in shallow, sheltered areas which, in turn, prolonged the clear-water period. We suggest that this
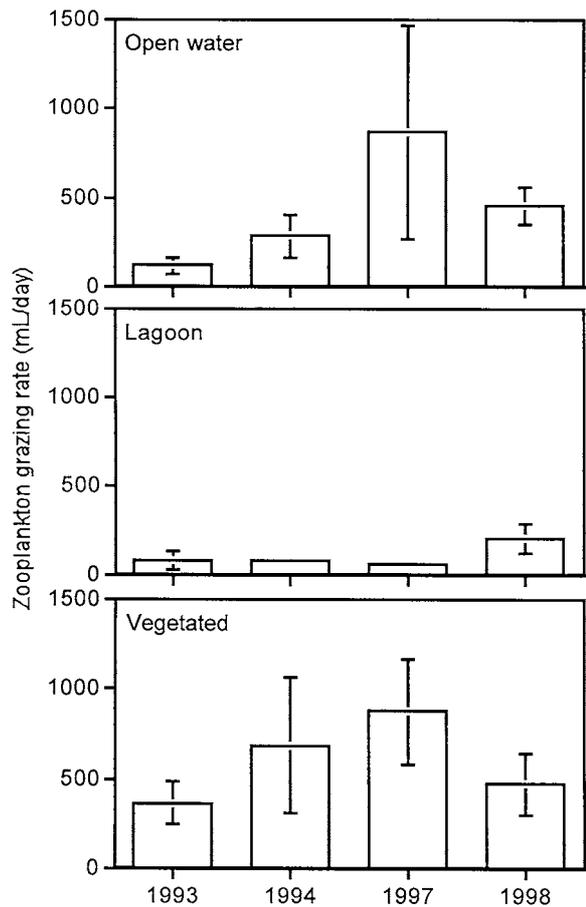

Figure 6. Comparison of mean zooplankton grazing rates (mL filtered/L/day) prior to (1993 & 1994) and following (1997 & 1998) carp exclusion at three sites in Cootes Paradise Marsh.

unusual zooplankton population bloom resulted from an unexpected, temporary removal of zooplanktivory due to the delayed production of young-of-the-year (YOY) fish (T. Theijsmeijer, Royal Botanical Gardens, pers. comm.) after an unseasonably cool spring in 1997. Fish community changes are currently the topic of investigation elsewhere (Lougheed et al., 2001).

An important finding in this study was that the three sites within the marsh followed different trajectories following biomanipulation due to different mechanisms acting at the lower trophic levels. Water clarity and macrophyte growth improved most in those areas of the marsh that were least degraded (i.e. areas with emergent vegetation), whereas the other sites remained relatively turbid and devoid of vegetation or only exhibited temporary changes in water clarity. This confirms Chow-Fraser's (1998) assertion that without further remedial measures, factors such as
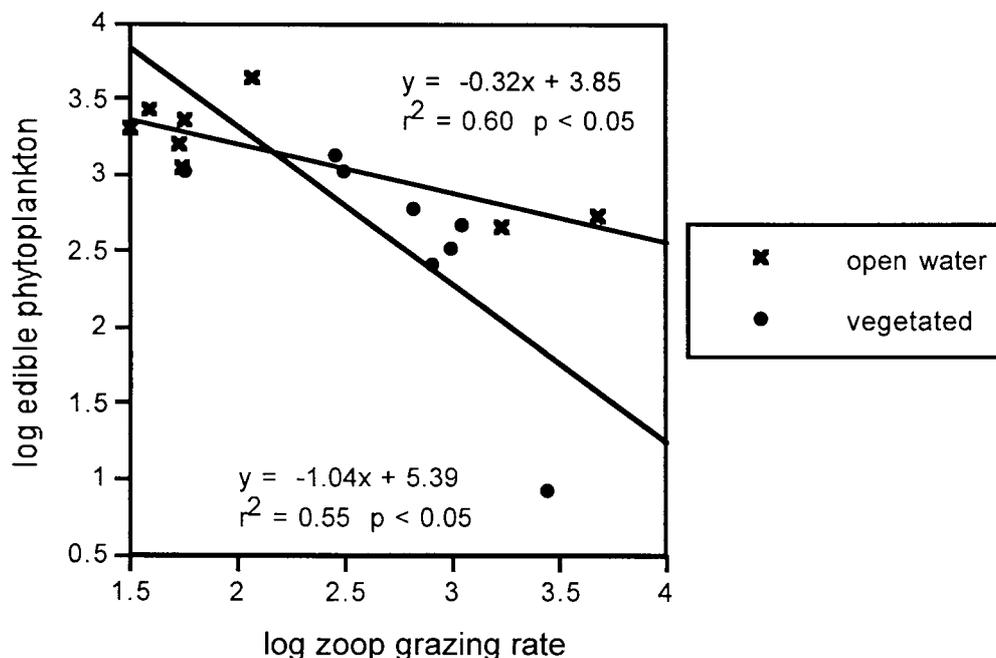
Figure 7. Significant relationships between edible phytoplankton biomass and zooplankton grazing rate at 2 sites in Cootes Paradise Marsh sampled bi-weekly over the summer of 1997.

wind and wave action, high sediment loading and high algal biomass will likely continue to keep much of the marsh in a relatively turbid state.

The occurrence of a spring clear-water phase due to cladoceran grazing, typified by reduced algal biomass, a reduced proportion of small particles and increased *Daphnia* biomass, has been noted in nutrient-rich lakes (Lampert et al., 1986; Ozimek et al., 1990; Hanson & Butler, 1994). The open water site in Cootes Paradise was in an exposed location approximately 0.5 km from any shoreline or vegetated habitat and near the outlet to Hamilton Harbour. In May 1997, *Daphnia galeata mendotae*, a species previously unrecorded in the marsh, entered from the relatively cool and clear harbour (Chow-Fraser, unpubl. data), rapidly peaked in population size at the open water site, and then crashed abruptly. This crash was followed immediately by the rise in phytoplankton biomass (Figure 8). During the *Daphnia* bloom, the water cleared and the bottom (130 cm) was illuminated for approximately a week in early summer 1997. By using the published length-filtering rate equation of Chow-Fraser & Knoechel (1985), we estimate that at this peak, *Daphnia* (400 *Daphnia*/L) were filtering the water column almost 5 times a day (4.84 L filtered/L/day). By comparison, in the second

year following exclusion (1998) when YOY fish actually appeared earlier than expected (T. Theijsmeijer, Royal Botanical Gardens, pers. comm.) due to an unusually warm spring, we did not see any proliferation of *Daphnia*, nor any evidence of a clear-water phase. Apparently, without a sustained decrease in zooplanktivory (natural or induced), this spring clear-water phase is not likely to be repeated at the open water site.

Although it appeared that the open water site returned to pre-exclusion conditions in 1998, several changes occurred at the lower trophic levels which illustrate that the communities at this site remained in a state of transition following carp exclusion. Consistent with other studies in which cyclopoids tended to dominate when faced with increased fish predation (Schriver et al., 1995), cyclopoid copepods contributed substantially to the zooplankton biomass at the open water site in the second year following biomanipulation (1998), when YOY fish actually appeared earlier than expected. Cyclopoid predominance may occur in spite of the presence of sufficient edible algae for cladoceran grazers (Schriver et al., 1995), because they are better than cladocerans at escaping predators. Changes in predation pressure may also have played a role in structuring the phytoplankton community. Fol-
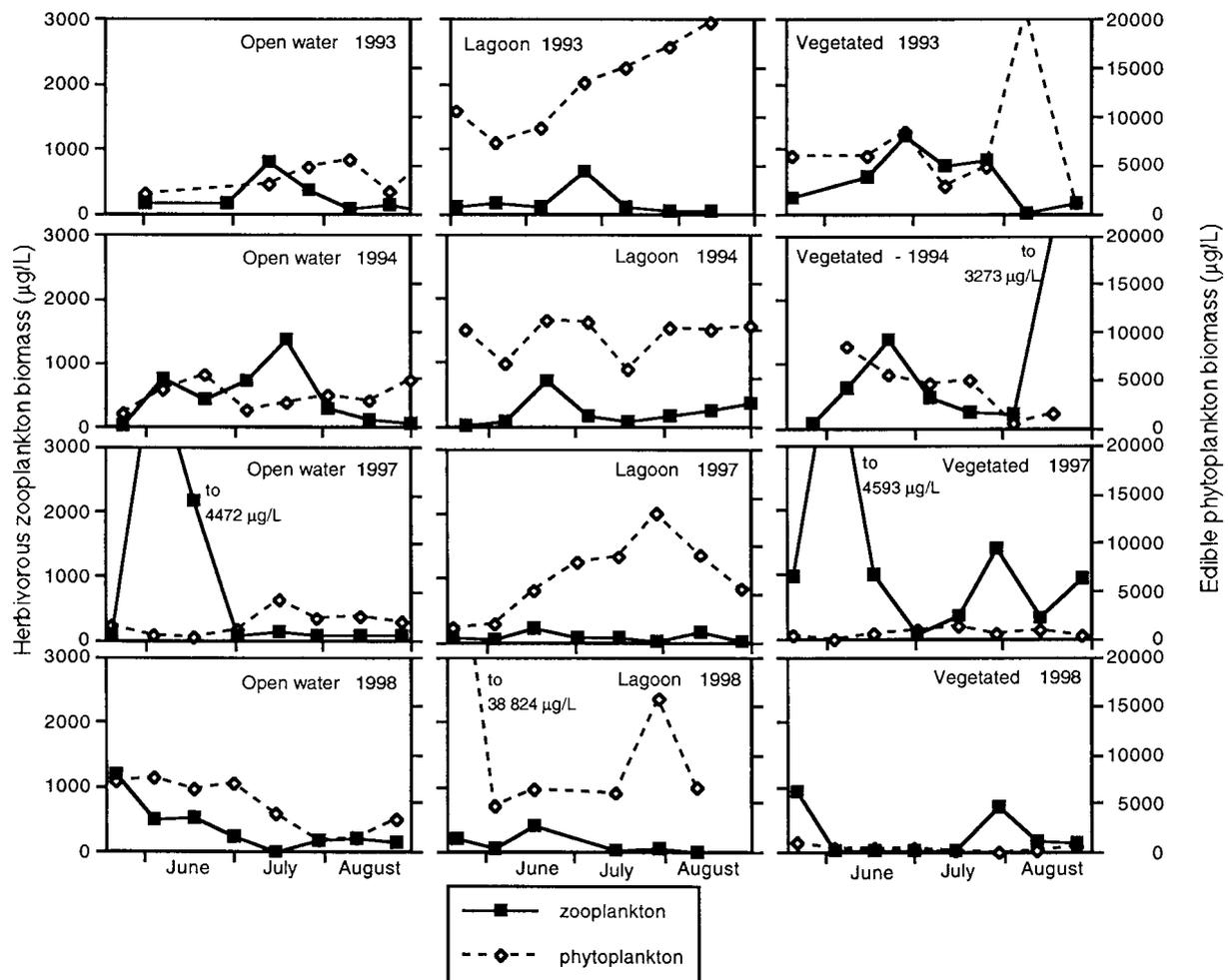
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Figure 8. Seasonal patterns in biomass of herbivorous zooplankton and edible phytoplankton before carp exclusion (1993 & 1994; top two rows) and after carp exclusion (1997 & 1998; bottom two rows) at three representative sites in the marsh (OPEN: left column; LAGOON: middle column; VEGETATED: right column).

lowing periods of intense zooplankton grazing, some studies have shown an increase in cryptophyte biomass (e.g. Hanson & Butler, 1994; Schriver et al., 1995), such as that observed in early summer 1998 at the open water and lagoon sites. Chow-Fraser et al. (1998) noted that increased eutrophication in Cootes Paradise through the 1970's resulted in an increased proportion of phytoplankton capable of heterotrophic uptake and tolerant of low light environments (euglenoids and cryptophytes). Although euglenoids appear to have been reduced following exclusion at the open water site, cryptophytes still contribute substantially to the population, indicating that increases in clarity were insufficient to reduce the competitive advantage of these taxa.

Like the open water site, there was significantly higher biomass of *Daphnia* in early summer 1997 at the vegetated site, although the spring peak in herbivorous zooplankton biomass was composed primarily of *Bosmina* (Figure 4; 4000 *Bosmina*/L; 30 *Daphnia*/L). This resulted in a substantially lower community grazing rate relative to the open water site; however, zooplankton were still capable of filtering the water column nearly three times per day (2.78 L filtered/L/day) in June 1997. In fact, greater than 55% of the variation in edible phytoplankton biomass at the open and vegetated sites in 1997 can be explained by estimations of zooplankton grazing rates (Figure 7). Although some authors have suggested that reduced bioturbation of nutrient-laden sediment, rather than

zooplankton grazing, may be more important in controlling algal biomass and water turbidity in shallow, hypereutrophic systems (Horpilla & Kairesalo, 1990; Havens, 1991), reduced algal biomass at these two sites in the absence of nutrient reductions argues strongly against this hypothesis.

The vegetated site maintained an increase in clarity for 2 years following biomanipulation, due in part to the development of submersed macrophytes in the vicinity of cattail beds; this resurgence in vegetation also occurred in other shallow and sheltered regions of the marsh (Lundholm & Simser, 1999). Macrophytes may contribute to the maintenance of clarity by stabilizing sediment (Hamilton & Mitchell, 1997), competing with phytoplankton for nitrogen (Ozimek et al., 1990; van Donk et al., 1990), preventing algal growth through allelopathy (Wium-Andersen et al., 1982) and providing zooplankton refugia against predation (Timms & Moss, 1984). For example, a mid-summer peak in the biomass of substrate-associated cladocerans coincided with a slight reduction in edible biomass levels at this site in 1997 and 1998 (Figures 4 and 8). Because of the relative isolation of the vegetated site (see Figure 1) and reduced outflow from this inlet except during storm events, the submersed macrophyte beds had only a localized effect on water clarity and the distribution of the zooplankton community (Scheffer, 1998). These submergent macrophytes (especially turbidity-tolerant canopy-forming taxa such as *P. pectinatus*) were able to persist despite the lack of a clear-water phase in the spring of 1998; however, more recent data show that the submergent macrophyte population is now in decline (Project Paradise Update 2000, Royal Botanical Gardens, 680 Plains Rd. W, Burlington, Ontario, Canada).

The post-exclusion increase in large-bodied zooplankton such as *Daphnia* and *Simocephalus* at the vegetated site had been predicted by Lougheed & Chow-Fraser (1998). This rise in abundance coincided with a significant reduction in the biomass of edible algae, especially edible green algae, and may be partially attributed to an increase in submersed macrophytes in the vicinity of the cattail beds which may have provided better habitat for zooplankton grazers. Isolated emergent macrophyte beds (*Typha* sp.) in the shallow inlets and bays of Cootes Paradise have historically provided refugia for larger zooplankton grazers (Kay, 1949; Lougheed & Chow-Fraser, 1998; Chow-Fraser et al., 1998) which had contributed to moderate decreases in edible phytoplankton biomass relative to adjacent open

water areas (Chow-Fraser et al., 1998); however, zooplankton were unable to noticeably control algal standing crop in vegetated areas until submergent plants became established after the reduction in carp activity and the zooplankton-mediated spring clear-water phase. This agrees with the suggestions of other studies which showed that large herbivorous cladocerans increased water clarity when they were provided with macrophyte refugia from predation (Timms & Moss, 1984; Schriver et al., 1995).

The increased diversity of habitats in submerged vegetation has been associated with an increased diversity of zooplankton species (Pennak, 1966; Paterson, 1993; Gaiser & Lang, 1998), especially plant-associated taxa such as *Simocephalus* and some chydorids, (Pennak, 1966; Timms & Moss, 1984; Gaiser & Lang, 1998) or taxa associated with detritus and sediment (e.g. *Pleuroxus*) (Fryer, 1968). Our results definitely support these findings. Of the three study sites, only the vegetated site showed a sustained increase in species richness, from less than 26 to more than 32 species, including 9 new rotifer species and 5 new cladoceran species. Of these 14 new taxa, at least 8 are known to frequent vegetated environments, including the rotifers *Euchlanis*, *Lepadella*, *Monostyla quadridentata*, *Mytilina* and *Trichocerca elongata* (Pennak, 1966) and the cladocerans *Pleuroxus*, *Ceriodaphnia* and *Chydorus* (Pennak, 1966; Quade, 1969, Beklioglu & Moss, 1996; Lougheed & Chow-Fraser, in press).

We suggest that, following carp exclusion, the open water and vegetated sites represented 2 alternative states existing in one system. The trophic state of these two sites was relatively similar, with no significant differences between mean TP or TNN levels observed for the open (TP = 171.5 μg/L; TNN = 555.3 μg/L) and vegetated sites (TP = 222.7 μg/L; TNN = 504.5 μg/L). However, using data from 1998 for illustrative purposes, the open water site was turbid (44 NTU) and algal dominated (13.3 mg/L phytoplankton; 1100 stems/ha submersed macrophytes), while the vegetated site represented the clear (11 NTU), macrophyte-dominated (34100 stems/ha; 1.4 mg/L phytoplankton) state. While we observed these differences for 2 years following carp exclusion, the stability of the macrophyte-dominated state in isolated regions of Cootes Paradise is uncertain, especially given that Jeppesen et al. (1990) have suggested that above a phosphorus level of 150 μg/L, the macrophyte-dominated state cannot be maintained over the long term. In particular, with increased

eutrophication there is higher predation pressure on zooplankton grazers by an abundant planktivorous fish population and water clarity is insufficient to allow submergent plant colonization.

The lagoon, which was hydrologically separate from the open water and vegetated sites, also appeared to have been less affected by the biomanipulation. Mean seasonal TP levels were always greater than 270 μg/L, therefore above the level required for the long-term stability of biomanipulation efforts (Jeppesen et al., 1990). In addition, 2 additional conditions necessary for stabilization of a clear-water, macrophyte dominated system were also absent from this site: low nitrate concentration and presence of large grazers (Jeppesen et al., 1990; Moss et al., 1996). In systems dominated by aquatic vegetation, phytoplankton may be nitrogen limited as plants remove nitrogen from the water column and provide the alternating aerobic and anaerobic conditions required for denitrification (Scheffer, 1998). The concentration of nitrate nitrogen is extremely high at this site (Table 1) owing to aeration of ammonia in the effluent discharged from the Dundas Sewage Treatment Plant (Chow-Fraser et al., 1998). The rich source of nitrate in the sewage effluent essentially ensures that algae are never nitrogen limited in the lagoon and consequently aquatic plants never gain a competitive advantage. This is not as much of a concern in other areas of the marsh because nitrate concentration decreases by an order of magnitude (Chow-Fraser et al., 1998) as water flows east towards Hamilton Harbour and is diluted by inflows from Spencer's Creek and Borer's Creek (see Figure 1).

The absence of large grazers at the lagoon site may be partially attributable to the high turbidity at this site, as elevated turbidity can mechanically interfere with cladoceran feeding (e.g. Kirk & Gilbert, 1990); the appearance of eight new species of cladoceran grazers following carp exclusion suggests that the zooplankton community in the lagoon may have responded to a slight, although not significant, reduction in mean seasonal turbidity from >70 NTU (before) to <51 NTU (after). We suggest that this establishment of larger zooplankton may have been limited by water turbidity rather than food for two reasons: (1) the reduction in turbidity was not accompanied by a change in algal biomass and (2) edible phytoplankton contributed on average greater than 75% of the total algal biomass at this site in each year studied (Figures 4 and 7). It is difficult to separate the direct effects of reduced turbidity from those that are indirect (i.e. macrophyte growth)

without the use of experimental enclosures; however, marsh-wide increases in the number of medium and large cladoceran species (even at unvegetated sites) following exclusion suggests that the reduced turbidity may have conferred a competitive ability to those species adapted to a less turbid environment.

The improved light environment in shallow and sheltered regions of the marsh was coincident with a reduction in the growth of planktonic algae; however, this increased clarity together with the nutrient-rich sediment, appear to be promoting the growth of benthic algal blooms (primarily *Spirogyra* sp.) (V. Lougheed, pers. obs.) which have not been reported in the marsh since the 1940's (Chow-Fraser et al., 1998). This is consistent with other Great Lakes studies in which filamentous green benthic algae have been shown to increase following improvements in the light environment (e.g., Lowe & Pillsbury, 1995). These changes may have important implications for the flow of energy through the benthic food web in Cootes Paradise Marsh and should be further investigated.

5.1. *Conclusions and management implications*

These results detail the mechanisms acting at lower trophic levels that promoted the maintenance of two alternative states: a turbid, algal-dominated state and a clear-water, macrophyte-dominated state (e.g. Moss et al., 1996; Scheffer, 1998), within a single ecosystem that is temporally and spatially variable. Many trophic interactions, both human-induced and natural, played a role in these changes. The exclusion of benthivorous carp to reduce sediment resuspension (Meijer et al., 1990; Lougheed et al., 1998) likely contributed to a 45% reduction in water turbidity. This increased clarity, in conjunction with the natural delay in the arrival of planktivorous YOY fish (T. Theÿsmeÿer, Royal Botanical Gardens, pers. comm.) promoted the presence of large grazers in the first year of biomanipulation. This initiated a spring clear-water phase (e.g. Lampert et al., 1986; Hanson & Butler, 1994) which promoted macrophyte growth in shallow, sheltered areas of the marsh. The establishment of submersed macrophytes at the vegetated site subsequently promoted water clarity due, in part, to provision of better habitat for large zooplankton grazers (Timms & Moss, 1984). Conversely, a combination of wind-induced and algal turbidity, as well as nutrient enrichment (at the lagoon site) all combined to suppress the growth of submergent macrophytes and large zooplankton and

consequently kept both the open water site and lagoon site in a relatively, turbid state.

Due to the dynamic nature of Great Lakes coastal wetlands, Cootes Paradise Marsh will need to be continually monitored over the next decade to determine the ultimate effect of the carp exclusion and other restorative efforts. For example, in 1999 the Laurentian Great Lakes experienced the lowest water levels seen since the 1960's, nearly half a metre lower than levels recorded in 1997 and 1998. Ground surveys and aerial photos revealed that emergent vegetation expanded quickly into newly available habitat in Cootes Paradise Marsh (unpubl. data) at the expense of submergent macrophyte habitat. The number of submergent plants in the marsh declined by approximately half that seen in 1998 (Project Paradise Update, 2000, Royal Botanical Gardens, 680 Plains Rd. W, Burlington, Ontario, CANADA). In 2000, water levels returned to near-average levels; however, submersed macrophytes remained less abundant and, in the absence of these plants, water turbidity in the vegetated areas nearly doubled.

It is unclear whether any significant improvements in water clarity would have been observed without the extraordinary zooplankton grazing rates and the subsequent establishment of submersed macrophytes. Despite the fact that carp activity was a primary contributing factor to high water turbidity in the marsh prior to exclusion, wind-related resuspension and internal nutrient loading remain important agents of water quality degradation. These data confirm Lougheed et al.'s (1998) assertion that wetland managers must consider all factors that may contribute to increases in water turbidity and nutrient concentrations to ensure that the desired response will be obtained in marsh restoration programs. Although improvements in water clarity and submergent plant growth were observed in shallow, isolated areas of the marsh, the long-term stability of the biomanipulation remains uncertain, especially given the elevated nutrient levels and the high biomass of planktivorous fish which is likely contributing to the reduced populations of large zooplankton grazers.

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