Factors that regulate the zooplankton community structure of a turbid, hypereutrophic Great Lakes wetland

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Abstract: We sampled zooplankton from mid-May to early September over 2 years to study the spatial and seasonal distribution of animals in a large urban wetland of Lake Ontario. Samples were from several habitat types including open water, vegetated areas, fast-flow areas, and a sewage lagoon. Mean seasonal densities ranged from 17 individuals/L (5 μg/L) in fast-flow areas to 1800 individuals/L (1100 μg/L) in low-flow, highly vegetated areas. All of our sites were dominated by herbivorous rotifers (e.g., *Brachionus* sp., *Polyarthra* sp., *Keratella* sp.), small herbivorous cladocerans (*Bosmina longirostris*; mean length <300 μm), cyclopoid nauplii, and medium-sized cladocerans (e.g., *Moina micrura*; mean length 300–600 μm), which were absent from the most eutrophic sites. The high levels of inorganic suspended solids in the marsh appeared to select against large filter feeders such as *Daphnia* and allowed smaller zooplankton to dominate. Multivariate analyses indicated that the zooplankton distribution was related to flow rate, extent of macrophyte cover, and level of site degradation. If the forthcoming carp (*Cyprinus carpio*) exclusion from Cootes Paradise Marsh results in increased macrophyte growth, we predict that zooplankton biomass will increase and that the zooplankton community may shift to larger forms.

Résumé : Pour étudier la distribution spatiale et temporelle des espèces animales d'un grand marais urbain du lac Ontario, nous en avons échantillonné le zooplancton de la mi-mai au début de septembre pendant 2 ans. Les échantillons ont été prélevés dans divers habitats : eaux libres, zones de végétation, zones de fort courant et étang d'eaux usées. Les densités moyennes saisonnières allaient de 17 sujets/L (5 μg/L), dans les zones d'eaux de fort courant, à 1800 sujets/L (1100 μg/L) dans les zones de faible courant, à végétation dense. Dans tous les sites échantillonnés dominaient les rotifères herbivores (p. ex. *Brachionus* sp., *Polyarthra* sp., *Keratella* sp.), les petits cladocères herbivores (p. ex. *Bosmina longirostris*, longueur moyenne inférieure à 300 μm), les nauplius de cyclopoïdés et les cladocères de taille moyenne (p. ex. *Moina micrura*, longueur moyenne de 300–600 μm), qui n'étaient pas présents dans la plupart des sites les plus eutrophes. Les fortes quantités de matières inorganiques en suspension mesurées dans le marais semblaient défavoriser les gros organismes filtreurs comme les *Daphnia* et permettre aux petits organismes de dominer le zooplancton. D'après les analyses multivariables, la distribution du zooplancton serait liée au débit des eaux, à l'étendue de la couverture de macrophytes et au degré de dégradation du site. Si l'élimination prochaine de la carpe (*Cyprinus carpio*) du marais Cootes Paradise donne lieu à une croissance accrue des macrophytes, nous pensons que la biomasse du zooplancton augmentera et que sa composition pourrait changer en faveur d'organismes de plus grande taille.
[Traduit par la Rédaction]

Introduction

Wetlands are highly productive and complex systems with links to both the watershed and the open water that provide diverse habitats to a variety of resident and migratory aquatic life such as fish (Jude and Pappas 1992) and waterfowl (Prince et al. 1992). In the Laurentian Great Lakes basin, many of these habitats are being degraded by nutrient and sediment load from the watershed, fluctuating water levels, as well as the activities of the common carp (*Cyprinus carpio*) (Whillans 1996). Variability in abiotic factors, as well as the patchy distribution of aquatic vegetation, contribute to seasonal and spatial variability in water quality characteristics and the amount of available habitat for fish and aquatic invertebrates.

Throughout the Great Lakes basin, a number of restoration projects has been initiated to improve water quality and increase macrophyte growth in degraded wetlands (Cootes Paradise Marsh, Hamilton; Second Marsh, Oshawa; Toronto Harbour, Toronto; Metzger Marsh, Lake Erie). In many of these projects, managers have put much of the blame on the presence of large populations of the common carp, which are thought to cause water turbidity and uproot aquatic vegetation through their spawning and feeding activities. This assumption is based on studies that have shown that the removal of other benthivorous fish communities has caused an increase in water clarity (Hanson and Butler 1990; Meijer et al. 1990*a*, 1990*b*) and an associated reduction in nutrient levels (Havens 1991, 1993; Breukelaar et al. 1994; Cline et al. 1994) that ultimately led to an improvement in plant growth (Hanson and Butler 1990; Meijer et al. 1990*a*). Some studies have found increased zooplankton biomass and mean body size (Hanson and Butler 1990; Havens 1993), while others have found no effect on zooplankton (Meijer et al. 1990a) from these manipulations.

An understanding of the complex abiotic and biotic components that control the dynamics of lower trophic levels in wetlands is necessary to assist in the planning of remedial actions aimed at increasing and (or) saving aquatic habitat. Zooplankton are an important part of Great Lakes food webs,

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providing a vital link between primary producers and the higher trophic levels, as well as contributing substantially to the detritus. Despite their pivotal role, very little research has been carried out on the ecology of these invertebrates, especially those in Great Lakes coastal wetlands (Krieger 1992).

Although little is known regarding the zooplankton communities in wetland ecosystems, comparatively more work has been done on zooplankton dynamics in lake ecosystems. These studies suggest that zooplankton communities are structured by biotic components, such as the effects of macrophyte refugia (Timms and Moss 1984; Hansen and Jeppesen 1992; Schriver et al. 1995), fish predation (Brooks and Dodson 1965; Cristoffersen et al. 1993; Ronneberger et al. 1993), and food availability (Starkweather and Bogdan 1980; McCauley and Kalff 1981; Stemberger 1981; Chow-Fraser and Knoechel 1985; Chow-Fraser 1986; Zurek and Bucka 1994), as well as abiotic components such as turbidity (Zettler and Carter 1986; Hart 1988, 1990; Kirk and Gilbert 1990; Kirk 1991), nutrient status (Bays and Crisman 1983; Hanson and Peters 1983; Pace 1986), and temperature (Galkovskaja 1987; Hart 1988; Gulati et al. 1992). Given that these factors are highly variable through time and space, it is not surprising that a great deal of spatial and temporal variation in zooplankton community structure and abundance has also been reported in Great Lakes wetlands such as Old Woman's Creek Estuary on Lake Erie (Krieger and Klarer 1991, 1992), the Bay of Quinte marshes of eastern Lake Ontario (Cooley et al. 1986) and Saginaw Bay, Lake Huron (Bridgeman et al. 1995).

In this 2-year study, we examined the zooplankton community composition and dynamics of Cootes Paradise Marsh, a turbid, hypereutrophic Great Lakes wetland with a focus on the factors that structure this community. We used canonical correlation analysis to determine the key environmental variables that control zooplankton biomass in the marsh. Results from this 2-year survey are used to formulate predictions for the marsh-wide carp exclusion that is currently taking place as part of the Hamilton Harbour Remedial Action Plan (HHRAP). These valuable baseline data allow us to generate recommendations for the monitoring program that will be used to evaluate the success of the remedial actions and ultimately allow comparison with the post-exclusion zooplankton community.

Methods

Study site

Cootes Paradise is a 250-ha drowned river-mouth marsh, located at the western end of Lake Ontario (Fig. 1). It has been severely degraded by eutrophication, high water turbidity and water level fluctuations that are out of synchrony with the growth requirements of aquatic vegetation (HHRAP 1992). The marsh is part of the Hamilton Harbour watershed, which was designated an area of concern by the International Joint Commission in 1987 and is the site of a large-scale restoration as part of the HHRAP. Only 15% of the marsh is now covered by aquatic vegetation, mainly cattails (*Typha* spp.) and manna grass (*Glyceria* sp.) (unpublished data). Eutrophication has resulted from the discharge of primary-treated sewage (1919 to the early 1960s) from the Dundas sewage treatment plant (STP) at the western end of the marsh and continues to be a problem today because of internal loading, inputs from several combined sewer overflows, and inputs from the two main tributaries, Spencer and Chedoke Creeks (Chow-Fraser et al. 1996). Both creeks and run-off also contribute high sediment load from the watershed. It is suggested that, in Cootes Paradise Marsh, this sediment is kept in suspension by the prevailing winds and the feeding and spawning activities of bottom-feeding fish such as the common carp (HHRAP 1992).

Although water-quality monitoring has been taking place in Cootes Paradise Marsh for the past 20 years, this is the first extensive study on zooplankton community structure since the 1940s, when the marsh was more than half covered by vegetation and had mean summer Secchi depths two times higher than those of present day (41 cm (Kay 1949) vs. 19 cm: this study; site 1). In this study, six sampling sites (See Fig. 1; Nos. 1, 12, 3, 4, 5, and 6) were established along the long axis of the marsh, ranging from the open water sites near Hamilton Harbour to the Dundas STP. A seventh long-term site (No. 7) was located in Spencer Creek, which enters the marsh at the southwest end. In addition to these sites, there were five more sites (8, 9, 10, 13, 16) in or near the embayments and remnant marsh areas of Cootes Paradise. Mean water quality characteristics of these sites for 1993 and 1994 are reported in Table 1. Using Ward's clustering procedure, P. Chow-Fraser (unpublished data) has grouped these sites according to similarities in their water quality characteristics. Sites 1 and 12, the open-water sites, were most similar to site 13, which is located at the outskirts of Westdale Cut. Sites 9 and 10, located near vegetated sites in Mac Landing, were also similar, while the two vegetated sites, Nos. 8 and 16, were grouped together. West Pond (site 5), a former sewage lagoon, was the most unique among the in-marsh sites being the most eutrophic and turbid (Table 1). Among those sites flowing into the marsh, sites exposed to the flowing water entering the marsh via Spencer Creek, such as the delta (site 3), the Desjardins Canal (site 4), and in the creek itself (site 7), were most similar. Site 6, located on the outskirts of the marsh at the STP outfall was unique compared with all other sites. Based on these clusters of water quality parameters, we selected five sites representative of the range of variation within the marsh (Nos. 1, 3, 5, 8, and 9) on which to concentrate our zooplankton surveys and analyzed samples collected biweekly in 1993 and 1994 (seven or eight samples per site per year). For the remainder of this paper, we will refer to site 1 as open water, site 3 as the delta, site 5 as West Pond, site 8 as the vegetated site, and site 9 as near vegetation (~10 m from cattails). We also include information on other sites (Nos. 4, 6, 7, 10, 12, 13, and 16) that had been sampled monthly in 1993 (three or four samples per site) to illustrate the variety of zooplankton communities in the marsh.

Sample methods

Water and zooplankton samples were collected from mid-May to the beginning of September (when the marsh dried up at the western end) in 1993 and 1994. Because of the shallow depth of this system and high level of wind-induced mixing (see Table 1 for wind speed; see also Sager 1996), all samples were taken from the middle of the water column. Zooplankton was collected using a 5-L Schindler–Patalas trap with a 63-μm Nitex mesh cup; high suspended sediment levels in the marsh did not make it feasible to use a smaller mesh. Samples were preserved immediately in 4% sugar–formalin. Subsamples of at least 100 organisms, including at least 20 large organisms (>300 μm mean length) were identified and counted under a dissecting microscope at 40× magnification. The whole sample was also surveyed for large and rare organisms. Initial identification was aided by a phase-contrast microscope at 200–400×. Measurements of all organisms were made with the aid of the Bioscan Optimas image analysis system. Lengths were not corrected for the effect of preservative (Campbell and Chow-Fraser 1995), but shrinkage in rotifers and cyclopoids, which formed the majority of zooplankton in our samples, were assumed to be negligible.

Water samples were collected using a 1-L Van Dorn bottle. Water quality variables such as total phosphorus (TP) and total nitrogen (TN) were determined using Hach reagents according to Hach protocols and standard methods (APHA 1992). Suspended solids (TSS) were also determined using standard methods (APHA 1992).

Fig. 1. Location of sampling sites in Cootes Paradise Marsh, Lake Ontario; larger dots indicate the representative sites (see text for details); arrows indicate the inflows and outflows of the marsh; and shaded areas indicate the presence of emergent vegetation.

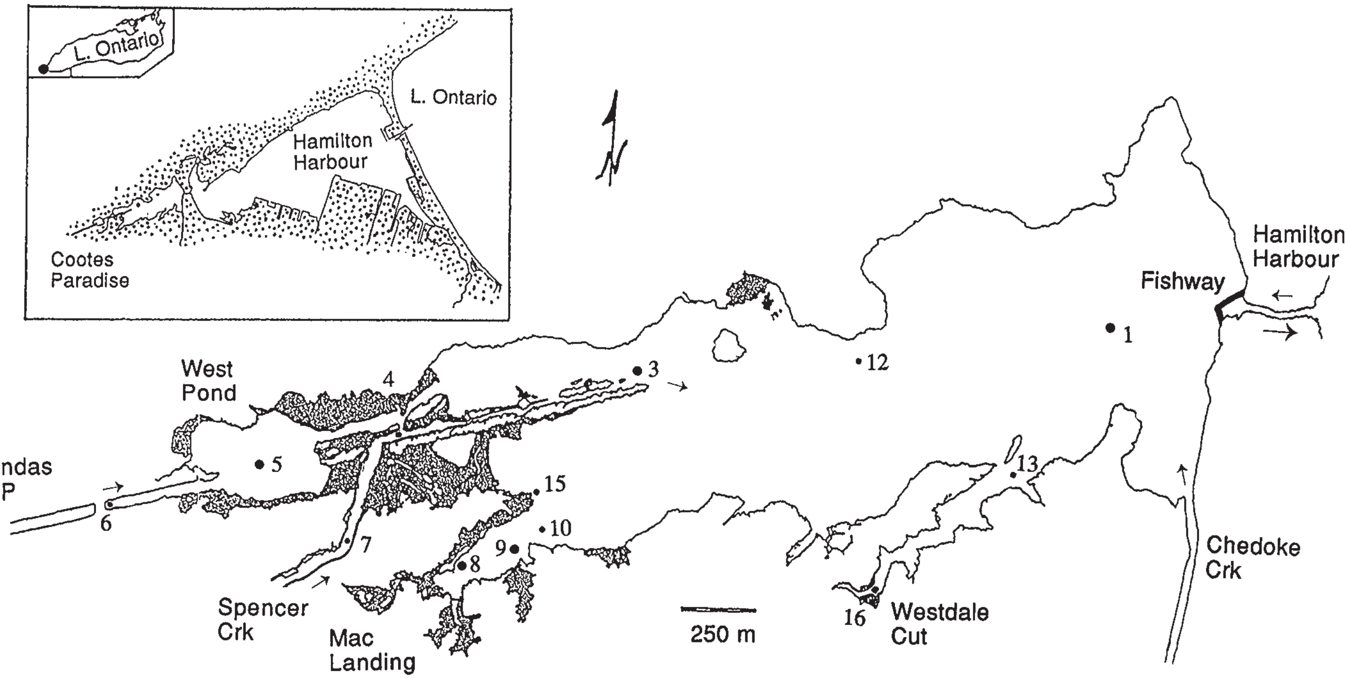


Table 1. Mean water quality and physical variables at 12 sampling sites in Cootes Paradise Marsh over the summers of 1993 and 1994 from mid-May to mid-September.

Site	*n*	Wind (m/s)	Depth (cm)	Temperature (°C)	TP (µg/L)	TN (µg/L)	CHL*a* (µg/L)	TSS (mg/L)	Secchi (cm)	Flow[a]	Plants[a]
1	20	3	109	21	144	3 222	39	57	19	N	N
3	19	1	75	19	97	3 492	18	60	26	Y	N
4	19	1	77	17	84	3 052	12	49	23	Y	N
5	18	3	54	22	315	7 558	146	105	13	N	N
6	18	1	163	20	174	11 570	34	27	43	Y	N
7	18	1	130	17	49	2 509	4	44	44	Y	N
8	16	1	38	23	216	3 091	27	79	20	N	Y
9	18	2	46	22	209	3 372	52	76	16	N	Y
10	18	3	51	22	149	3 377	57	86	16	N	N
12	20	2	72	21	157	2 770	51	56	19	N	N
13	18	2	122	21	187	3 095	50	69	18	N	N
16	8	0	31	21	592	3 287	8	94	20	N	Y

Note: Site 16 was only sampled in 1993.

[a] Y, Yes (present); N, no (absent).

Temperature was determined using an H2O® Hydrolab and Scout® monitor; water depth and Secchi depth were measured using a 20 cm diameter Secchi disc. Chlorophyll *a* (CHL*a*) was extracted using 90% acetone and a 1-h extraction period in the freezer; absorbance readings were taken with a Milton Roy spectrophotometer. Results in this study have been corrected for phaeopigments by acidification (Likens and Wetzel 1991). Additional variables not included in this study because of their correlation with other variables or their lack of in-marsh variability (soluble reactive phosphorus, total available nitrogen (TAN), total nitrate nitrogen (TNN), pH, dissolved oxygen, turbidity) have also been collected, and this information is available from the second author.

Rotifer identification was based on Chengalath et al. (1971) and Stemberger (1979), while crustacean identification was based on Balcer et al. (1984), Pennak (1989), and Thorp and Covich (1991). Identification was to the level of species for all common organisms except *Asplanchna* and *Polyarthra*, which were to genus, *Acanthocyclops vernalis* and *Ectocyclops phalerutus*, which were grouped together as cyclopoid copepods in counting, and all copepod nauplii. Total abundance and biomass for each sample were first calculated on an individual basis, then combined for species and functional group total.

We used published length–weight relationships and dry-weight estimates from Dumont et al. (1975) and Malley et al. (1989) to estimate dry weight for the zooplankton in this study. Bottrel et al. (1976), Geller and Muller (1985), and Malley et al. (1989) have cautioned against using borrowed relationships because of seasonal and lake-to-lake variations; however, because of the time-consuming nature of dry-weight determination, we used published values and assumed the error due to sampling variability was greater than that due to the length–weight regressions. We ensured that any equations and dry-weight estimates were used for organisms in the same length range. To minimize errors, equations taken from Malley et al. (1989)

Table 2. Frequency (in percent) of occurrence of each zooplankton species for the whole marsh (total frequency) and for three representative sites from mid-May to early September of 1993 and 1994.

	Total frequency	1993			1994		
		Open water	West Pond	Vegetation	Open water	West Pond	Vegetation
Rotifera							
Asplanchna sp.	72	71	86	71	75	62	71
Brachionus angularis	58	71	71	71	50	50	57
Brachionus bidentata	12	14	0	14	0	50	0
Brachionus calyciflorus	80	100	100	57	75	75	86
Brachionus caudatus	60	100	43	43	38	75	29
Brachionus diversicornus	25	43	14	29	12	12	0
Brachionus havanaensis	12	14	0	14	0	0	0
Brachionus quadridentatus	9	0	14	29	0	0	14
Brachionus rubens	6	0	0	0	0	0	29
Brachionus urceolaris	45	14	71	43	0	75	57
Filinia longiseta	55	43	57	57	62	38	57
Filinia brachiata	1	0	1	0	0	0	0
Kellicotia sp.	0	0	0	0	25	0	14
Keratella cochlearis	35	29	14	14	75	12	71
Keratella quadrata	41	57	43	43	38	0	57
Lecane luna	6	0	0	57	0	0	0
Monostyla bulla	4	0	0	0	0	12	29
Notholca sp.	1	0	0	0	0	0	0
Platyias patulus	3	0	0	0	0	0	29
Polyarthra sp.	77	71	43	86	88	88	86
Trichocerca cylindrica	20	57	43	14	0	12	0
Cladocera							
Bosmina longirostris	90	100	86	100	100	38	100
Diaphanosoma birgei	19	14	14	0	25	50	29
Daphnia retrocurva	8	14	0	0	50	0	0
Kurzia sp.	4	0	0	29	0	12	0
Leydigia sp.	1	0	0	0	0	0	0
Macrothrix sp.	9	14	0	14	0	0	29
Moina micrura	54	71	29	71	62	62	71
Scapholeberis sp.	12	14	0	43	0	0	100
Simocephalus sp.	1	0	0	14	0	0	0
Copepoda							
Nauplii	97	100	100	100	100	100	100
Cyclopoid copepods	90	100	86	86	100	88	100
Diaptomus minutus	9	29	0	29	12	0	0
N (no. samples included)	101	7	7	7	8	8	7

Note: Frequency of occurrence is defined as (number of sites where a species occurs/number of sites sampled (N)) × 100.

were from an artificially eutrophied lake (Lake 227). Given the scarcity of information on rotifer biomass, dry-weight estimates used from Dumont et al. (1975) were largely averages of biomass values obtained from a variety of locations. In certain cases (not for any common species) where specific dry weight values were not available, estimations were made by comparison with similar species.

Statistical analyses

All calculations and statistical analyses were performed using SAS JMP (SAS Institute Inc. 1992), and graphical analysis was performed using Cricket Graph III. Canonical correlation analysis was used to summarize the relationship between environmental and response variables by finding linear combinations of these variables that have the highest possible between-set correlation. For details on canonical correlation analysis, see Gittens (1980) and ter Braak (1990, 1995). This multivariate analysis has been used successfully in other studies to determine the environmental variables that control plankton production in lake ecosystems (Munawar and Wilson 1978; Varis et al. 1989; Varis 1991). In this study, canonical correlation was used in conjunction with descriptions of the dynamics and composition of the zooplankton community to identify the relationship between the key variables in each data set. This analysis was performed on two different data sets: (*i*) data from the representative sites (Nos. 1, 3, 5, 8, 9) sampled biweekly in 1993 and (*ii*) a similar data set from 1994.

Concentrations of TN, TP, CHL*a* and TSS, physical variables such as temperature and depth, and variables representing proximity to macrophytes and water flow were entered as independent variables; the biomass of respective functional taxa were entered as the dependent variables. Zooplankton taxa with a low frequency of occurrence were excluded (i.e., macrograzers). Water flow was recorded as either absent (no observable flow) or present (visible flow) to represent the overall hydrologic character of the site over the season and was not based on measured flow rates. We classified sites according to proximity to macrophytes as follows: 1, >20 m from plants; 2, <10 m from

Table 3. Minimum, mean, and maximum total zooplankton biomass (μg/L) at 12 sampling sites in Cootes Paradise sampled *n* times from mid-May to early September of 1993 and 1994.

	1993				1994			
Site	*n*	Minimum	Mean	Maximum	*n*	Minimum	Mean	Maximum
1	7	5	327	979	8	64	611	1765
3	7	3	102	239	8	1	130	517
4	4	24	38	55	—			
5	7	33	207	715	8	21	392	1494
6	3	85	787	2137	—			
7	4	3	5	5	—			
8	7	22	767	1507	7	77	1109	3273
9	7	34	577	1656	8	133	628	1346
10	4	96	588	974	—			
12	4	69	666	1721	—			
13	4	57	719	1228	—			
16	4	64	1064	2242	—			

Table 4. Minimum, mean, and maximum total zooplankton abundance (individuals/L) at 12 sampling sites in Cootes Paradise sampled *n* times from mid-May to early September of 1993 and 1994.

	1993				1994			
Site	*n*	Minimum	Mean	Maximum	*n*	Minimum	Mean	Maximum
1	7	14	786	1941	8	85	1331	3278
3	7	33	225	592	8	6	385	2169
4	4	44	122	246	—			
5	7	185	582	1400	8	38	1050	2607
6	3	256	2504	6858	—			
7	4	16	17	18	—			
8	7	76	1226	3525	7	233	1800	3472
9	7	110	1249	2120	8	347	1422	3066
10	4	88	1547	2566	—			
12	4	204	1323	2376	—			
13	4	103	1512	2369	—			
16	4	124	1463	4060	—			

plants. All data were standardized to zero mean and unit variance, and the zooplankton data were normalized using a transformation of $\log(x + 1)$. The correlation of the zooplankton taxa and environmental variables with the canonical variates of the first two canonical axes were plotted in canonical biplots, where the loadings from axis 2 were plotted against the loadings from axis 1.

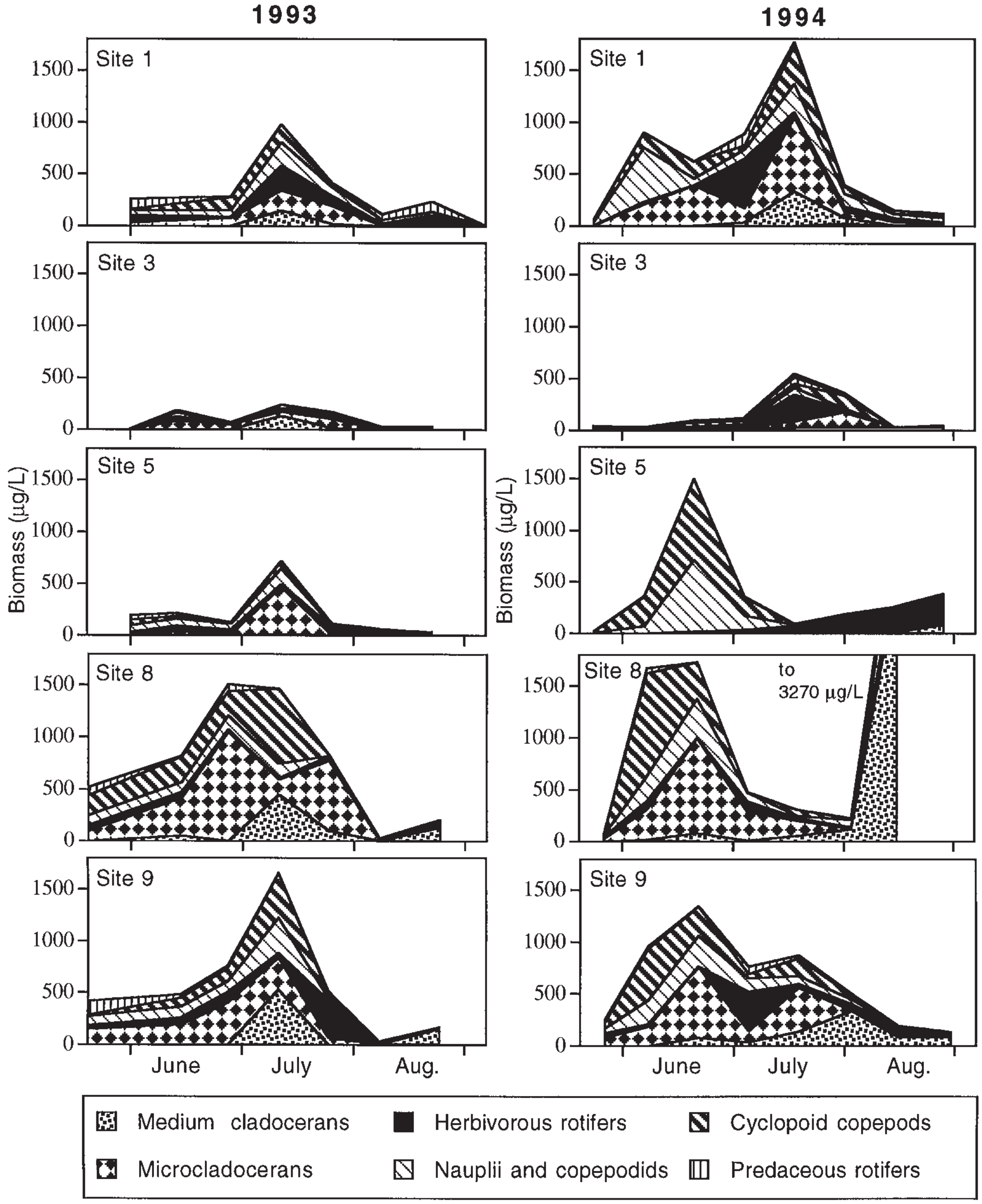
Results

Zooplankton community structure

Common species of zooplankton in Cootes Paradise Marsh (frequency of occurrence >50%) included the rotifers *Asplanchna* sp., *Brachionus angularis*, *B. calyciflorus*, *B. caudatus*, *Filinia longiseta*, and *Polyarthra* sp.; the cladocerans *Bosmina longirostris* and *Moina micrura*; the cyclopoid copepods *Acanthocyclops vernalis* and *Ectocyclops phalerutus*; and copepod nauplii (Table 2). The rotifers contributed the largest numbers of species (22) followed by cladocerans (9) and copepods (3). We analyzed the relative distribution of the zooplankton by grouping them according to their size-specific functional role in the ecosystem rather than by taxonomic affiliation. Herbivorous rotifers included all rotifers except *Asplanchna*, which was classified as a predaceous rotifer. Other grazers were grouped either as microcladocerans (<300 μm mean length), medium cladocerans (300–600 μm mean length), macrograzers (>600 μm mean length), or nauplii and copepodids. The term microcladocerans was used to represent *Bosmina*; medium cladocerans included species such as *Moina*, *Diaphanosoma*, and *Scapholeberis*; while macrograzers consisted of *Daphnia* and *Diaptomus*. Cyclopoid predators included *Acanthocyclops* and *Ectocyclops*.

Mean total biomass and abundance tended to be lowest at the flowing sites associated with Spencer Creek (Nos. 3, 4, 7) (Tables 3 and 4). Low to moderate biomass and abundance were observed for the more turbid and eutrophic open-water site (No. 5), followed by other open-water sites (Nos. 1, 10, 12), as well as the near-vegetation site (No. 9). A vegetated site (No. 8) and a less exposed, open-water site (No. 13) had moderate to high abundances and biomass. The highest biomass levels were seen at a vegetated site near a combined sewer overflow outfall (No. 16), while the highest abundances were seen at the STP outfall (No. 6). Differences in sampling frequency should be noted (*n*; Tables 3 and 4). It should also be noted that site 16 could not be sampled in 1994 because of experimental manipulations in Westdale Cut. Mean total zooplankton biomass and densities were generally higher in

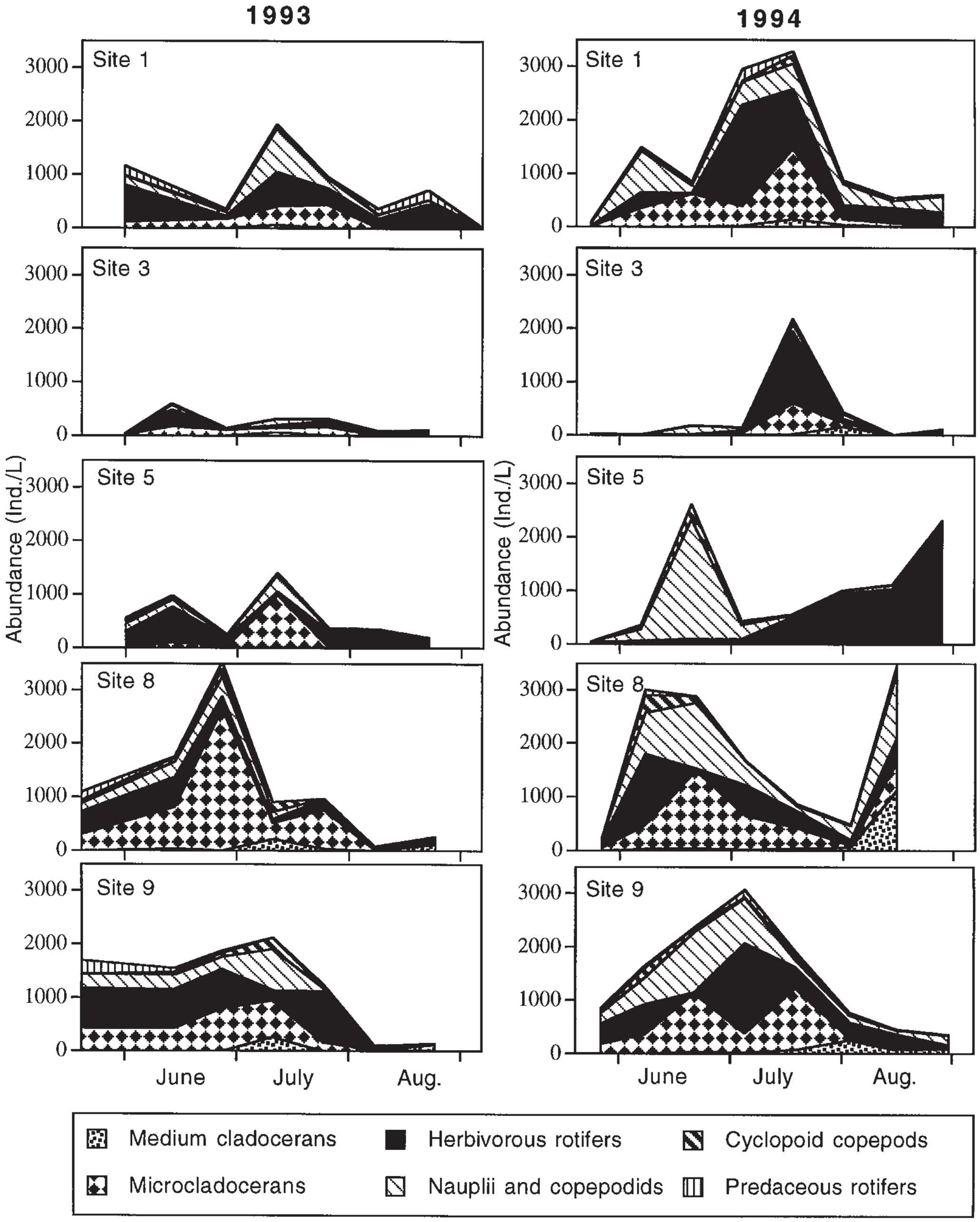
Fig. 2. Changes in the biomass (µg/L) of zooplankton taxa over the summers of 1993 (left column) and 1994 (right column) at five representative sites in the marsh (sites 1, 3, 5, 8, and 9).



1994 compared with 1993 (Tables 3 and 4), although there were no significant differences between years (ANOVA, $p > 0.05$).

Although peaks in zooplankton biomass and abundance occurred at different times in 1993 versus 1994, there were no striking differences in zooplankton composition between years, except at site 5 (Figs. 2 and 3). The most unique distribution pattern was associated with this site, a turbid and eutrophic sewage lagoon, where medium cladocerans were virtually absent, and the total biomass and abundance of zooplankton was relatively low. There was also relatively low zooplankton levels at site 3, the flowing water site; however, zooplankton composition at this site was not obviously different from the other sites sampled biweekly (Figs. 2 and 3). The other flowing sites (Nos. 4, 7, 6), which were sampled at a much lower frequency, had a disproportionate representation of herbivorous rotifers, with site 6, the most eutrophic of the flowing sites, having a species composition intermediate between that of the riverine (No. 7) and sewage lagoon (No. 5) sites (Fig. 4). By comparison, greater total biomass and abundance was observed throughout the summer at the open-water site (No. 1) and inside (No. 8) or near (No. 9) the vegetation (Figs. 2 and 3). Proportionally (Fig. 4), site 8 had relatively low levels of herbivorous rotifers, as did the other site found inside the vegetation (No. 16), although otherwise the zooplankton communities at these two sites were very different from each other.

Fig. 3. Changes in the density (individuals/L) of zooplankton taxa over the summers of 1993 (left column) and 1994 (right column) at five representative sites in the marsh (sites 1, 3, 5, 8, and 9).



All other sites in the marsh (Nos. 1, 9, 10, 12, 13) had similar zooplankton compositions (Figs. 2–4). One notable difference was that, although not visible in the graphics presentations, macrograzers occurred almost exclusively at site 1 but at very low densities (1–3 individuals/L).

Predictors of zooplankton community structure.
Canonical correlation analysis effectively summarized the patterns of variation in the zooplankton and environmental data; the first two axes explained 71 and 83% of the variation in the data set for 1993 and 1994, respectively, and the correlation between taxa and environmental data varied from 67 to 93% (Table 5).

The distribution of environmental variables along the first two canonical axes revealed several prominent trends in the data set, which were maintained between years (Figs. 5*a* and 5*b*) and which can be interpreted based on water quality differences between sites and years. Variables indicating trophic state, such as TP, TN, and CHL*a*, were closely correlated; however, the correlation of TP and TN to the axes, as indicated by the length of the vector, was stronger in 1994. In 1994, TSS was also correlated with these variables, while in 1993 the correlation of TSS with the axes was very weak. The weakness of these associations in 1993 was likely due to the high water levels seen in this year (Fig. 6), which diluted nutrient and turbidity effects for most of the season (P. Chow-Fraser,

Fig 4. Mean relative proportion (percent biomass) of zooplankton taxa at all sites sampled monthly in the marsh in 1993.

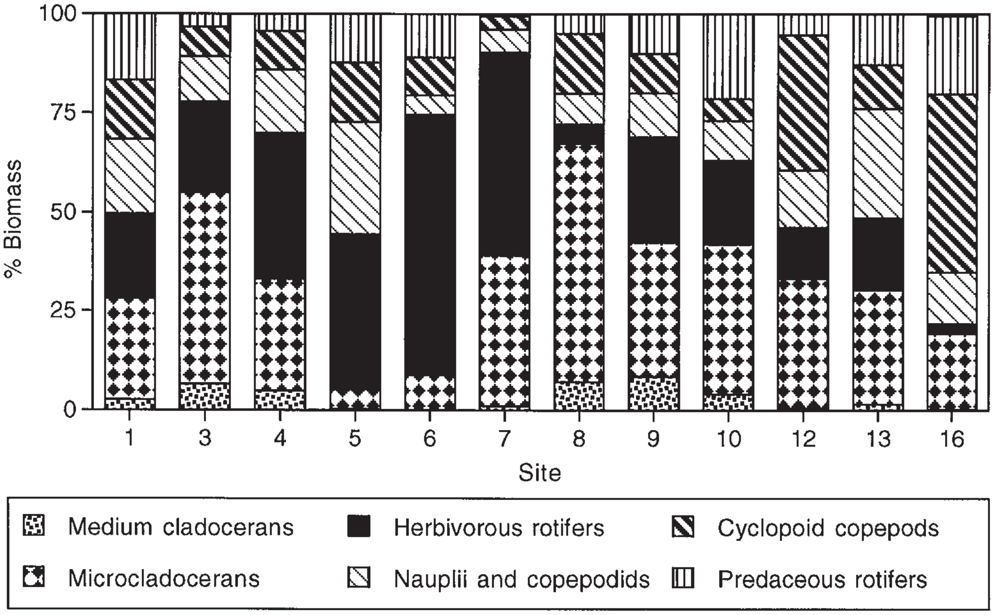


Table 5. Table showing the characteristics of the first four canonical correlation axes.

Canonical axis	Cumulative proportion of sum of eigenvalues	Canonical r^2
	1993	
1	0.51	0.93
2	0.71	0.85
3	0.86	0.81
4	0.96	0.75
	1994	
1	0.65	0.86
2	0.83	0.67
3	0.92	0.54
4	0.96	0.39

unpublished data) and resulted in much weaker relationships between these three variables (TP, TN, CHL*a*, TSS). In both years, these trophic state variables did not reach midsummer maxima and, therefore, in the canonical analysis were not correlated with temperature in either year. The generally warmer environment at the shallow, vegetated site (Table 1) was reflected in a positive correlation between plants and temperature; however, site 5 was also relatively warm, and therefore, the vector for temperature tended to fall partway between plants and the variables indicative of degradation. In 1993, plants were negatively correlated with the variables associated with trophic state; however, in 1994, there was no correlation between these variables. As expected, the water flow was negatively correlated with temperature and plants.

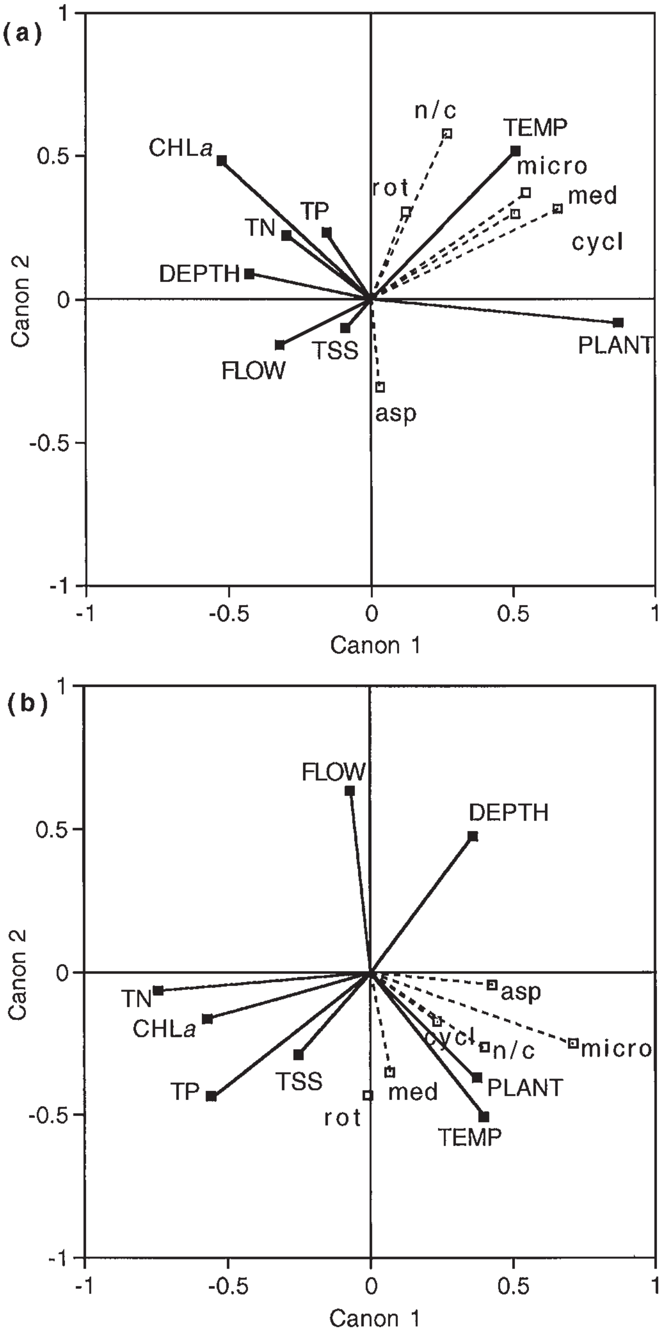
With few exceptions, in both 1993 and 1994, all zooplankton taxa tended to be positively correlated with each other. In general, all taxa were positively correlated with temperature and plants; however, microcladocerans, medium cladocerans, and cyclopoids were consistently most strongly correlated with these variables. This is to be expected given the midsummer maxima in biomass of these taxa, most notably at the vegetated site (No. 8). The exceptions to this generality were predaceous rotifers, which occurred at lower temperatures in the spring of 1993, and were negatively correlated to their prey, herbivorous rotifers and nauplii. The negative correlation of most taxa with nutrients and turbidity is expected, since the site that was most consistently eutrophic (No. 5) had relatively low biomass of zooplankton. Similarly, given the overall low biomass at the flowing site (No. 3), all taxa were negatively correlated with flow.

Discussion

Marshes are temporally and spatially dynamic systems that are highly variable with respect to water flow, water depth, distribution of aquatic vegetation, and the concentration of nutrients and suspended solids. This study is one of the first to link such variation to taxonomic composition and biomass structure of zooplankton in a Great Lakes coastal wetland.

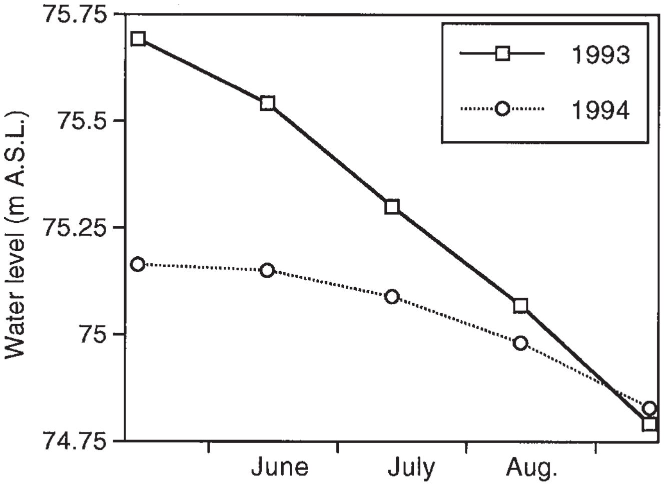
Macrophytes are known to play an important role in the ecology of zooplankton in the littoral regions of lakes. Studies in a shallow, eutrophic Danish lake showed that an increase in macrophyte cover changed the zooplankton community from rotifers to larger cladocerans (Hansen and Jeppesen 1992). In Cootes Paradise, the reduced proportion of rotifers at the vegetated site (No. 8) suggests that, in the presence of aquatic macrophytes, rotifers were outcompeted by other taxa. Sensitivity to fish predation is known to decrease with increased macrophyte cover, since cladocerans use macrophytes as refugia against predation. This allows larger zooplankton to hide during the day and horizontally migrate out of the weeds at night to graze (Timms and Moss 1984). In more eutrophic systems, macrophyte protection from fish predation may allow grazers to increase their population size sufficiently to control phytoplankton growth (Schriver et al. 1995). We suggest that the relatively low chlorophyll *a* levels in the vegetated site (Table 1) relative to most other sites is evidence that grazing

Fig. 5. Biplot display (axis 2 versus axis 1) of the canonical loadings of environmental variables (solid line) and zooplankton taxa (broken line) for (*a*) 1993 and (*b*) 1994. CHL*a*, Chlorophyll *a*; PLANT, proximity to aquatic macrophytes; TEMP, temperature; TN, total nitrogen, TP, total phosphorus; TSS, total suspended solids; asp, predaceous rotifers; cycl, cyclopoid copepods; rot, herbivorous rotifers; micro, microcladocerans; med, medium cladocerans; n/c, nauplii and copepodids.



zooplankton were preferentially using macrophyte cover, presumably as refugia. Preliminary studies (Chow-Fraser et al. 1998) in a different area of the marsh (site 15: cattail beds north of site 10) indicate that phytoplankton biomass increased while large herbivore biomass decreased with distance (up to 15 m away) from the cattail beds.

Fig. 6. Change in mean monthly water level from May to September for 1993 (solid line) and 1994 (broken line).



We confirm the findings of Krieger and Klarer (1991), who reported that sites near the marsh outflow have zooplankton assemblages that are more similar to that in the receiving waters. Aerial photos tracking turbidity patterns in Cootes Paradise Marsh have indicated that the exchange of water between the marsh and the receiving water, Hamilton Harbour, can be reversed and is dependent on watershed inputs and wind direction (P. Chow-Fraser, unpublished data). In this study, the intrusion of harbour water into the marsh on some dates was supported by a reduction in pH, temperature, and suspended solids at site 1 that was consistent with the harbour water. *Daphnia* were found nearly exclusively at the open-water site (No. 1) near the marsh outflow, coincident with the presence of moderately high numbers of *D. retrocurva* in Hamilton Harbour (unpublished data), and we suggest that they were carried via intrusion from the harbour. We speculate that the presence of macrograzers, such as *Daphnia*, in the open waters of Cootes Paradise Marsh may be transient and not representative of self-sustaining populations. The only other location in the marsh where *Daphnia* have been found is at the vegetated site (No. 15) north of site 10, which was sampled for the first time in 1996 and where *Daphnia* were also found at a very low density (1 individual/L) during the midsummer peak in biomass. The existence of low densities of several species of *Daphnia* (*D. longispina*, *D. retrocurva*, *D. parvula*) in remote vegetated areas suggests that *Daphnia* may become a more prominent grazer once the marsh is restored to a macrophyte-dominated system.

The consistently low biomass of medium cladocerans and macrograzers in the marsh suggests the presence of factors inhibiting the survival of these larger grazers. Grazing by large filter feeders is generally thought to be inhibited in highly turbid systems (Hart 1988; Kirk and Gilbert 1990; Kirk 1991) or systems with blue-green alga blooms (Chow-Fraser and Sprules 1986). Unlike other hypereutrophic systems, where blue-green alga blooms occur frequently, Cootes Paradise has no such blooms because of the high TN:TP ratio (P. Chow-Fraser, unpublished data); however, Cootes is an extremely turbid system, with turbidity levels 10–20 times higher than those reported for other studies. In the 1940s, when the water was on average twice as clear as present day, many species of *Daphnia* were found associated with the submergent and emergent vegetated areas of the marsh (Kay 1949). This suggests that reduced macrophyte cover and mechanical interference due to increased turbidity through time may have been responsible for the low numbers of *Daphnia* in Cootes Paradise. That *Moina*, a genus known to be tolerant of turbidity, was the most abundant large herbivore in the marsh, is consistent with the literature (*M. brachiata*; Hart 1988), which indicates that high turbidity selects for this medium-sized cladoceran. The relative absence of large herbivores at the most degraded site (No. 5), in combination with the highest turbidity levels, is in support of this; however, overall low zooplankton biomass of all taxa suggests that additional factors, besides turbidity and the absence of vegetation, may also have been important at this site.

Zooplankton distribution and biomass may also be structured by differences in food availability. Zooplankton are known to have specific food and food-size preferences (Starkweather and Bogdan 1980; McCauley and Kalff 1981; Stemberger 1981; Chow-Fraser and Knoechel 1985; Chow-Fraser 1986; Zurek and Bucka 1994). As in other Great Lakes wetlands (Klarer and Millie 1994), the species composition and total biomass of phytoplankton is highly variable seasonally and from site-to-site in Cootes Paradise Marsh (P. Chow-Fraser, unpublished data), which is consistent with the results seen for water quality and zooplankton. Although it appears, from chlorophyll *a* values alone, that site 5 was the most food-rich site and, therefore, should have a higher biomass of zooplankton, much of the phytoplankton biomass at this site consisted of large, flagellated phytoplankton (>30 μm), including both euglenoids and large cryptomonads (Chow-Fraser et al. 1998), which were likely inedible to those smaller organisms able to withstand the high levels of turbidity at this site.

In conclusion, it appears that zooplankton community dynamics in Cootes Paradise Marsh are primarily structured by proximity to macrophytes and water turbidity, while zooplankton at sites on the outskirts of the marsh were further influenced by flowing water. Differences in food availability and predation pressure likely also played a role in structuring the zooplankton communities. Although there does not appear to be a direct relationship between body size and marsh fertility, larger bodied zooplankton may be disadvantaged by high water turbidity in the absence of vegetation, while smaller zooplankton taxa may be constrained by the effect of hyper-eutrophication on the phytoplankton community.

One of the goals of the HHRAP is to exclude carp from Cootes Paradise Marsh and thereby increase macrophyte growth and improve water quality. There is, however, little experimental evidence that clearly links the exclusion of large carp from degraded Great Lakes wetlands with water clarity or quality improvements sufficient to allow the establishment of a healthy marsh community, including emergent and submergent macrophytes. Further research on these issues, such as that by Lougheed et al. (1998) will contribute valuable knowledge to wetland managers on those conditions necessary for Great Lakes wetlands to start recovering from years of abuse.

From this premanipulation study of the zooplankton in Cootes Paradise, we can predict that increased emergent macrophyte growth in existing or colonized areas of the marsh will increase the total zooplankton biomass and shift the zooplankton community to larger bodied forms, irrespective of any change in predation pressure arising from the biomanipulation. Similarly, based on past conditions in the marsh (Kay 1949), we can predict that the introduction of submergent macrophytes may also allow larger grazers to persist. The monitoring program following carp exclusion should focus on those sites that are most likely to be affected, in particular the vegetated areas (No. 8) and the near-vegetated areas (No. 9), where emergent macrophytes may become established. Large- to medium-sized zooplankton may also have an increased competitive advantage at the open-water sites (Nos. 1 and 5), where reductions in turbidity and internal loading in the absence of macrophyte growth may occur; however, at these exposed and unvegetated sites the effect of wind in stirring up nutrient-rich bottom sediment may be of further concern. Zooplankton communities in flowing water sites at the marsh inputs will probably not change in response to carp exclusion but are more likely to be altered by watershed or sewage treatment plant alterations.

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