Ecological Applications, 12(2), 2002, pp. 474–486

DEVELOPMENT AND USE OF A ZOOPLANKTON INDEX OF WETLAND QUALITY IN THE LAURENTIAN GREAT LAKES BASIN

VANESSA L. LOUGHEED[1] AND PATRICIA CHOW-FRASER

McMaster University, Department of Biology, Hamilton, Ontario, Canada L8S 4K1

Abstract. Recent interest in biological monitoring as an ecosystem assessment tool has stimulated the development of a number of biotic indices designed to aid in the evaluation of ecosystem integrity; however, zooplankton have rarely been included in biomonitoring schemes. We developed a wetland zooplankton index (WZI) based on water quality and zooplankton associations with aquatic vegetation (emergent, submergent, and floating-leaf) that could be used to assess wetland quality, in particular in marshes of the Laurentian Great Lakes basin. Seventy coastal and inland marshes were sampled during 1995–2000; these ranged from pristine, macrophyte-dominated systems, to highly degraded systems containing only a fringe of emergent vegetation. The index was developed based on the results of a partial canonical correspondence analysis (pCCA), which indicated that plant-associated taxa such as chydorid and macrothricid cladocerans were common in high-quality wetlands, while more open-water, pollution-tolerant taxa (e.g., *Brachionus*, *Moina*) dominated degraded wetlands. The WZI was found to be more useful than indices of diversity (H', species richness) and measures of community structure (mean cladoceran size, total abundance) for indicating wetland quality. Furthermore, an independent test of the WZI in a coastal wetland of the Great Lakes, Cootes Paradise Marsh, correctly detected moderate improvements in water quality following carp exclusion. Since wetlands used in this study covered a wide environmental and geographic range, the index should be broadly applicable to wetlands in the Laurentian Great Lakes basin, while further research is required to confirm its suitability in other regions and other vegetated habitats.

Key words: biomonitoring index; Laurentian Great Lakes basin; partial canonical correspondence analysis (pCCA); restoration; wetland zooplankton index (WZI); wetlands; zooplankton.

INTRODUCTION

The utilization of biological monitoring in assessing ecosystem integrity has received more and more attention in recent years. A growing number of studies have reported on the use of fish (e.g., Karr 1981, Minns et al. 1994), macroinvertebrates (e.g., Lenat 1993, Burton et al. 1999), diatoms (e.g., Kelly and Whitton 1995), and periphyton (e.g., McCormick and Stevenson 1998) to detect habitat degradation in a variety of geographic locations and ecosystem types. In the Laurentian Great Lakes, the development and selection of indicators of ecosystem health was one of the primary challenges given to the scientific community during the 1996 State of the Lakes Ecosystem Conference (SOLEC; a biennial conference hosted by the Canadian and U.S. governments to examine issues concerning the Laurentian Great Lakes) (Bertram and Statler-Salt 1999).

Wetlands are ecologically and economically important ecosystems that are being rapidly lost and degraded. Whillans (1982) estimated that heavily settled areas of the lower Great Lakes have lost 75% of their wetland area, with some areas experiencing 100% loss. Many of the remaining wetlands have become degraded by exotic benthivorous common carp (*Cyprinus carpio*) and changes in land use patterns over the past several decades, both of which have increased water turbidity and nutrient concentrations (Whillans 1996, Chow-Fraser 1998, 1999). To track these changes in ecosystem quality and quantity, managers require simple, robust indicators that can be applied across the basin by many environmental agencies. We propose to use zooplankton, and their association with macrophytes and relevant water quality variables, to indicate the quality of marshes in the Great Lakes basin.

Although zooplankton are known to respond quickly to environmental conditions (Schindler 1987), only a few attempts have been made to use the zooplankton community to indicate quality of aquatic ecosystems (Gannon and Stemberger 1978, Sládecek 1983, Stemberger and Lazorchak 1994, Gaiser and Lang 1998). Our rationale for choosing zooplankton was three-fold. First, there are well-documented plant-associated zooplankton taxa whose presence in a system is highly dependent on the presence of submersed macrophytes (Quade 1969, Paterson 1993). Hence, the taxonomic composition of the zooplankton community should reflect the presence and distribution of submergent plants in the wetland. Second, zooplankton taxa often have different preferences for trophic state (Berzins and Bertilsson 1989, Berzins and Pejler 1989) and water clarity

Manuscript received 10 November 2000; revised 2 May 2001; accepted 16 May 2001; final version received 11 July 2001.

[1] Present address: Department of Zoology, Michigan State University, East Lansing, Michigan 48824-1115 USA. E-mail: loughee2@msu.edu

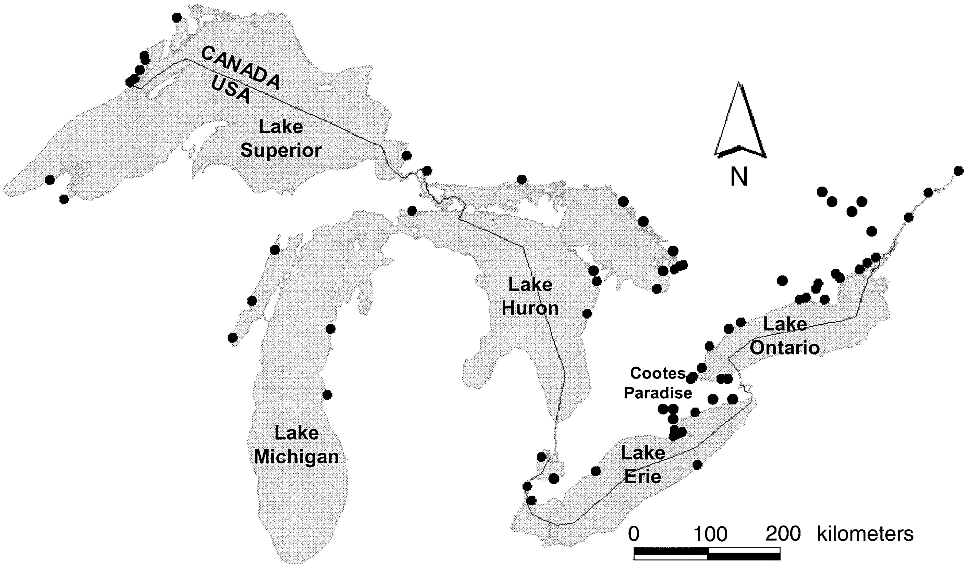

FIG. 1. Map of Great Lakes region showing the location of 70 wetlands sampled during 1995–2000, including the location of Cootes Paradise Marsh (Lake Ontario).

(Lougheed and Chow-Fraser 1998), and therefore species replacement will also occur with water quality degradation. Finally, since the species richness of submersed macrophytes declines as marshes become eutrophic and degraded (Crosbie and Chow-Fraser 1999; Lougheed et al. 2001), we hypothesize that the zooplankton community should reflect changes in the plant community as we proceed along the trophic–degradation gradient.

In general, biotic indices integrate the sensitivity of several taxonomic groups to environmental conditions (e.g., acidity, degree of degradation) into a single index value. These indices are particularly useful in situations where data must be statistically analyzed and conveyed to nonbiologists. In particular, a biotic index that could track changes over the short term (i.e., several years) would be a useful tool for evaluating restoration techniques such as the recent and costly exclusion of carp from Great Lakes coastal wetlands (e.g., Cootes Paradise Marsh in Lake Ontario, Metzgers Marsh in Lake Erie) (Lougheed et al. 1998, Wilcox and Whillans 1999). A common criticism is that these indices may oversimplify effects on the community in question, especially when organisms are grouped into higher taxonomic groups, where responses of individual members may vary greatly (Sládecek 1983, Gaiser and Lang 1998). However, we feel that these integrative indices are superior to measures that result in loss of species-specific information (e.g., diversity) or those that rely only on a select number of taxa (e.g., indicator species).

The objectives of this study were to develop a wetland zooplankton index (WZI) based on water quality and observed associations of zooplankton with aquatic vegetation that can be used to assess wetland quality; to compare this biotic index with commonly used indicators of community quality such as the Shannon-Wiener species diversity index; and to evaluate the ability of the WZI to assess the response of a degraded coastal wetland of Lake Ontario (Cootes Paradise Marsh) to carp exclusion as a restoration technique.

METHODS

Water and zooplankton samples were collected from 70 marshes in the Great Lakes basin during 1995–2000. Wetlands ranged from St. Lawrence River sites within Ontario, down to the Windsor–Detroit area and Lake St. Clair, then up to Lake Superior (Fig. 1). Fifty-four of these were coastal marshes (lying within 2 km of Great Lakes shoreline or connecting channels, but not separated hydrologically from the lakes due to dams or waterfalls) of the upper (Lake Huron, Lake Michigan, and Lake Superior) and lower (Lake Ontario, Lake Erie) lakes, while the remaining 16 were inland wetlands located within the Great Lakes–St. Lawrence River basin. Coastal wetlands are subjected to unique hydrological phenomena relative to more protected inland systems; however, we included both coastal and inland systems in this study to (1) broaden our disturbance gradient since almost all coastal wetlands in southern Ontario have been disturbed to a certain degree, and (2) ensure the results were broadly applicable to both coastal and inland wetlands.

All wetlands were visited at least once in midsummer (mid-June–end of July), while a subset were also visited in early summer (May–mid-June) and/or late summer (August). Zooplankton samples collected in midsummer constituted two-thirds of all samples included in this study. To ensure consistent measurements of both water quality and zooplankton communities, both of which have been shown to be affected by storm events (Krieger and Klarer 1991, Chow-Fraser 1999), wetlands were generally visited no sooner than 48 h following a rain event.

We characterized the plankton communities within four different habitat types in each wetland: open water 10 m from the outermost edge of aquatic plants (OPEN 10 m), open water 3 m from aquatic plants (OPEN 3 m), within submergent plant beds (>5 stems/m^2; SUB) and within or immediately adjacent to emergent aquatic vegetation (EM). When submergent or emergent beds were absent or inaccessible, plankton below floating aquatics were sampled (FLTG). The species richness of submergent plants in each wetland was determined as described in Lougheed et al. (1998).

All water samples were collected from the middle of the water column at the OPEN 3-m site. Because of the large site-to-site, year-to-year, and seasonal variation in water levels, which are characteristic of Great Lakes coastal marshes (Maynard and Wilcox 1997, Chow-Fraser 1999), water depths in this study range 5–260 cm, depending on wetland site, time of year, and the sampling year in question. Water samples were analyzed according to standard methods (American Public Health Association 1992) for total phosphorus (TP), total nitrogen (TN) (sum of total kjeldahl nitrogen [TKN] and total nitrate nitrogen [TNN]), and total suspended solids (TSS). Following digestion by potassium persulfate, TP was analyzed according to Murphy and Riley (1962) and measured on a Milton Roy spectrophotometer (Thermo Spectronic, Rochester, New York, USA). Nitrogen analyses (TKN and TNN) were performed using Hach protocols and Hach reagents (Hach Company 1989) and measured on a Hach DR2000 spectrophotometer (Hach, Loveland, Colorado, USA). Planktonic chlorophyll-*a* (CHL-*a*) was filtered onto Whatman GF/C filters (Whatman, Clifton, New Jersey, USA) and extracted using 90% acetone with a one-hour extraction period. Absorbance measurements were made with a Milton Roy spectrophotometer, and results were corrected for phaeopigments by acidification. Temperature, pH, dissolved oxygen, and conductivity were determined using a H2O Hydrolab multiprobe and Scout monitor (Hydrolab, Austin, Texas, USA).

All zooplankton samples were collected from the middle of the water column at each of the habitat site types (where available). Zooplankton at open-water sites were collected using a five-liter Schindler-Patalas trap (Schindler 1969), while zooplankton in vegetation were collected using a one-liter beaker inverted three times into adjacent areas of vegetation for a total sample volume of three liters. All samples were filtered through 64-μm mesh Nitex screen (Sefar America, Depew, New York, USA), back washed into 60-mL bottles and preserved in 4% sugar–formalin. Samples were thoroughly mixed and subsampled to obtain at ≥100 animals. Abundances and lengths of all animals present in the subsamples were recorded, but biomass could not be determined because of the absence of published length–mass relationships for many of the taxa encountered. Copepods were identified to suborder only (i.e., cyclopoids, calanoids, harpacticoids), and therefore we report on their abundances, but exclude them from all subsequent, more species-specific analyses. Rotifer identification was based on Stemberger (1979), whereas crustacean identification was based on Balcer et al. (1984), Pennak (1989), and Thorp and Covich (1991).

All statistical analyses were performed using SAS.Jmp software (version 3.1.5, SAS Institute, Cary, North Carolina, USA), with the exception of canonical correspondence analysis, which was performed using CANOCO 4.0 (ter Braak and Smilauer 1998), and the Shannon-Wiener diversity index, which was calculated using MVSP (version 3.1, Kovach Computing Services, Ithaca, New York, USA).

Multivariate statistical analyses

Canonical correspondence analysis (CCA) is a useful technique when species data have been collected over a suitably large habitat range to display a unimodal relationship to the measured environmental variables (Jongman et al. 1995). It has been used by many authors to relate the distribution of zooplankton taxa to their environment (e.g., Hessen et al. 1995, Romo et al. 1996, Attayde and Bozelli 1998). Canonical correspondence analysis maximizes the separation of species optima along synthetic axes representing the primary environmental gradients in the data set. To confirm that CCA was an appropriate model for this data set, we first entered the species abundance data into a detrended correspondence analysis (CANOCO 4.0, not shown), which revealed sufficiently large gradient lengths (>4 SD) to indicate that zooplankton distributions in this study showed a clear unimodal response along the environmental gradient (ter Braak and Smilauer 1998). Then, because samples were collected over a four-month period, we performed a partial CCA (pCCA) instead of a regular CCA, which eliminated background variation due to the covariable time (i.e., day of the year; Jongman et al. 1995, ter Braak and Verdonschot 1995).

Environmental parameters entered into the pCCA analysis included continuous variables such as: TP, TN, TSS, chlorophyll-*a* (CHL-*a*), temperature (TEMP), dissolved oxygen (DO), pH, conductivity (COND), and latitude (LATITUDE; measured as decimal degrees), along with more qualitative variables that described habitat type: SUB, EM, FLTG (within submergent, emergent, and floating-leaf macrophyte beds, respectively), OPEN 3 m, and OPEN 10 m (open water 3 m and 10 m away from macrophyte beds, respectively). All continuous environmental variables were $\log_{10}$-transformed (excluding pH) to approximate normal distributions and standardized to zero mean and unit variance.

Although our analyses included rare zooplankton taxa, we confirmed in a preliminary analysis that the general conclusions were unaffected when rare taxa were removed prior to running the pCCA. Zooplankton abundances were $\log_{10}$-transformed ($\log(x + 1)$) to normalize the data and reduce the sample variance. Statistical significance of the pCCA was determined using Monte Carlo permutations (199 random permutations; ter Braak and Smilauer 1998).

Development of the wetland zooplankton index

The wetland zooplankton index (WZI) was developed based on trends observed in the pCCA, which will be discussed in detail in the *Results.* We assigned ''optimum'' (U) and ''tolerance'' (T) values (ter Braak and Verdonschot 1995) to each grouping that emerged from the pCCA as a suitable taxonomic unit (referred to henceforth as ''taxon''). For this purpose, we ran a pCCA (not shown) using collapsed taxonomic groupings instead of individual species; it is important to note that the environmental and species trends displayed by this pCCA were virtually identical to those of the species-specific pCCA (Fig. 2). Each taxonomic group was assigned a weight that indicated its optimum along the pCCA axis 1, where 1 = most tolerant of degraded conditions and 5 = most intolerant of degraded conditions. The weighted standard deviations of the taxon scores on the pCCA axis 1 were then used to indicate tolerance, that is, whether the taxon had a narrow (3), intermediate (2), or broad (1) niche breadth. Accordingly, those taxa given higher tolerance weights occurred across very narrow ranges and were therefore assumed to be better indicators of specific environmental conditions than taxa that were more ubiquitous. Very rare taxa (those that occurred in <10% of the wetlands) were assigned a low tolerance score, because their sparse distribution could not be used reliably to reflect specific environmental conditions.

The index was calculated using weighted averages in the following equation (Zelinka and Marvan 1961, Lenat 1993, Kelly and Whitton 1995):

$$\mathrm{WZI} = \frac{\sum_{i=1}^{n} Y_i T_i U_i}{\sum_{i=1}^{n} Y_i T_i}$$

where Y_i is the abundance or presence of species i, T_i is the tolerance (1–3), and U_i is the optimum (1–5). The index can therefore range from one (indicative of low quality) to five (indicative of high-quality wetland). The index was labeled $\mathrm{WZI}_{\text{P-A}}$ when presence/absence data were used to calculate index values, whereas WZI indicates the index calculated based on zooplankton abundances.

Assessment of marsh restoration

Cootes Paradise Marsh is a degraded 250-ha drowned river mouth marsh located at the western end of Lake Ontario (43° N, 79° W) (see Fig. 1). Carp have been physically excluded from the marsh since the winter of 1997 by the Cootes Paradise Fishway (Wilcox and Whillans 1999; Lougheed and Chow-Fraser, *in press*). In the on-going long-term study of Cootes Paradise Marsh (see Chow-Fraser 1999; Lougheed and Chow-Fraser, *in press*), three sites in the marsh were sampled biweekly over the summer (May–August, inclusive) for two years prior to carp exclusion (1993 and 1994) and two years following (1997 and 1999). Two sites were classified as OPEN 10-m sites: a relatively deep open water site near the marsh outflow (mean depth ranged from 97–127 cm) and a shallow lagoon site that historically received loadings from the Dundas Sewage Treatment Plant (depth 43–69 cm). The third site was an emergent site (EM) within the cattail beds of a marsh inlet (depth 23–49 cm). In total, 90 samples of zooplankton were enumerated and identified from these sites over the four years, but none of these was used in the pCCA or the subsequent development of the WZI. These data were used to evaluate the usefulness of the WZI in tracking site-specific changes in marsh quality following marsh exclusion and to compare the WZI with other measures of zooplankton community structure.

RESULTS

Environmental variation

Wetlands in this study represented a wide range of conditions from oligotrophic to extremely hypereutrophic (Table 1). The principal components analysis (PCA) identified which environmental parameters explained the greatest amount of variation in the data set. Nearly 50% of the variation in the continuous environmental variables was explained by principal components axis 1. Principal component (PC) axis 1 was significantly ($P < 0.0001$) and positively correlated with variables that are indicative of the nutrient status (TP, $r = 0.82$; TN, $r = 0.74$; see *Methods* for variable definitions), particulate content (TSS, $r = 0.86$; CHL-*a*, $r = 0.84$), and ionic strength (COND, $r = 0.76$) of the water, but negatively correlated with LATITUDE ($r = -0.68$). Therefore, PC axis 1 generally contrasted degraded wetlands in highly developed southern latitudes of the lower Great Lakes with high-quality wetlands of central and northern Ontario.

Zooplankton composition

In all, 60 cladoceran species and 78 rotifer species were identified in these wetland samples. Less than half of all species (34 rotifers and 27 cladocerans) occurred commonly (defined as occurring in >10 % of wetlands; bolded values in the Appendix). Very few occurred in >50% of the wetlands sampled, and these included the rotifers *Asplanchna* sp., *Keratella cochlearis*, and *Polyarthra* sp. Common cladocerans included *Scapholeberis kingi*, *Simocephalus exspinosus*, *Sida crystallina*,

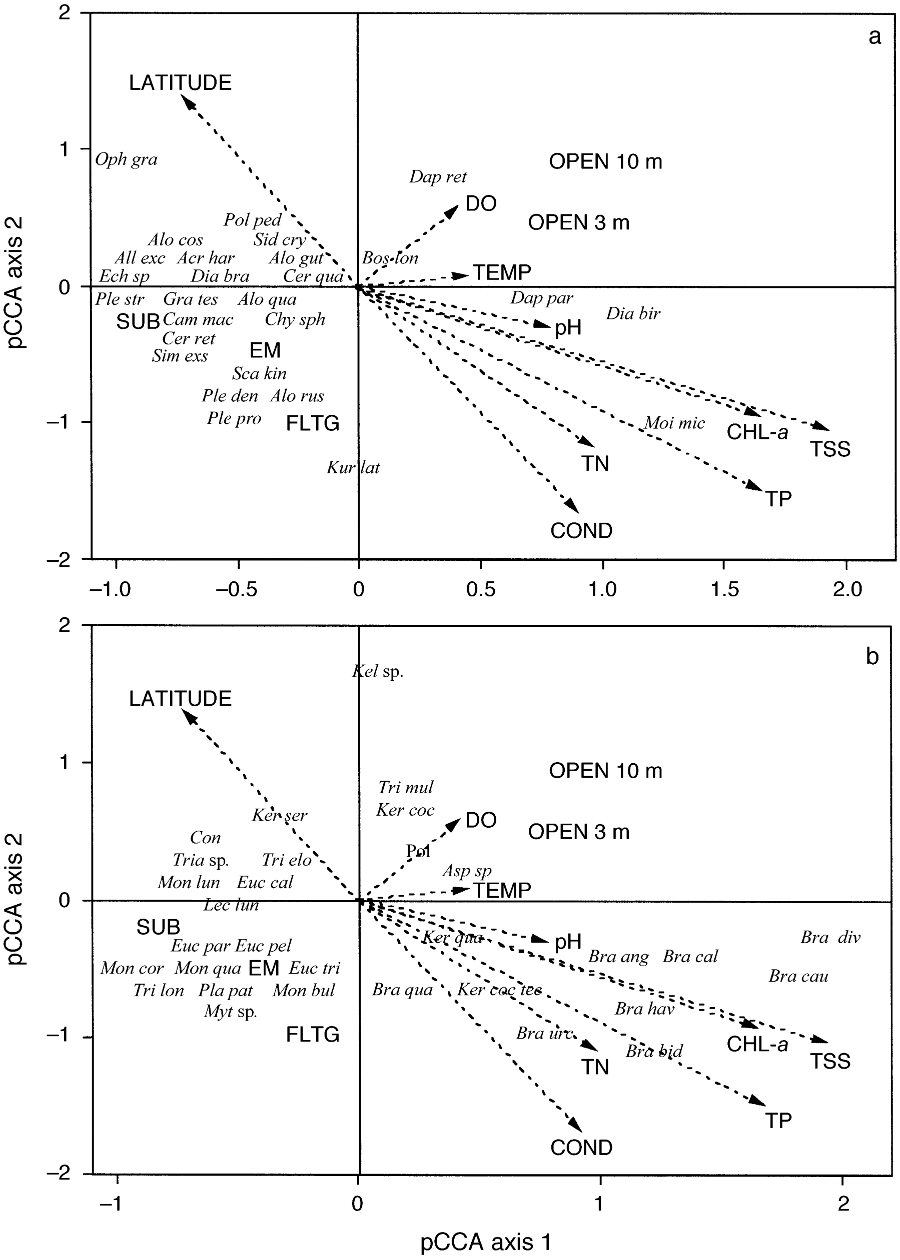

FIG. 2. Bi-plot of the partial canonical correspondence analysis (pCCA; axis 1 vs. axis 2) separated into (a) cladoceran, and (b) rotifer taxa. A complete list of cladocerans and rotifers observed in the 70 wetland sites appears in the Appendix.

Bosmina longirostris, and three chydorids (*Camptocercus macrurus, Chydorus sphaericus, Pleuroxus denticulatus*). There were few differences in the zooplankton communities observed in coastal vs. inland wetlands. Seven rare rotifers and seven rare cladocerans were found only in inland sites, while only three taxa (*Diaphanosoma birgei, Moina micrura, Brachionus caudatus*) that could be classified as common were absent from inland wetlands (see the Appendix).

Relative to the open water sites, the vegetated sites tended to have greater species richness, abundances, Shannon-Wiener diversity (H'), and larger mean size of cladocerans (Table 2). In particular, there was disproportionate representation of larger taxa in vegetated sites including Chydoridae, Daphnidae (but not *Daphnia*), Sididae, and Macrothricidae. By comparison, rotifers and *Bosmina* formed a greater proportion of organisms encountered at open-water sites. Both mature and immature forms of copepods tended to occur with greater abundances within the vegetation.

TABLE 1. Means and ranges (and in-text abbreviations) of environmental variables observed at 70 wetlands in the Great Lakes basin.

Variable	Mean	Range
Total phosphorus (TP; μg/L)	117	13–959
Total nitrogen (TN; μg/L)	2911	572–13000
Total suspended solids (TSS; mg/L)	25.0	0.1–283
Chlorophyll-*a* (CHL-*a*; μg/L)	29.7	0–396
Temperature (TEMP; °C)	22.5	11.5–30
Dissolved oxygen (DO; mg/L)	8.43	1.5–20
pH	7.6	6.0–9.4
Conductivity (COND; μS/cm)	400	38–1387

Partial canonical correspondence analysis (pCCA)

Bi-plots of the first two pCCA axes are found in Fig. 2; for clarity, data corresponding to rotifers and cladocerans are shown in separate bi-plots (Fig. 2a, b). These figures explain 52% of the variation in zooplankton distribution along the first two synthetic environmental axes. The significance of each of the environmental variables in explaining the distribution of zooplankton species was assessed using the forward selection procedure of CANOCO. All variables were significant at the $P < 0.05$ level. The most important predictors of zooplankton distribution, as indicated by their correlation with pCCA axis 1 were TSS (0.534), TP (0.531), CHL-*a* (0.445) and the presence of submergent vegetation (SUB) (−0.364), or open water 3 m away (0.347). Because all water quality data were collected at the OPEN 3-m site, this axis does not reflect differences in water quality between open water and vegetated sites in any individual wetland; instead, it indicates that heavily vegetated wetlands have clearer water and a unique zooplankton community, whereas wetlands with sparse macrophyte distribution tend to be more turbid, and are associated with taxa that are more typically found in limnetic ecosystems. By comparison, the second axis of the pCCA, which distinguished urbanized wetlands, which occur primarily in southern Ontario, from more pristine northerly wetlands, was highly correlated with LATITUDE (0.435), COND (−0.521), and TP (−0.374).

To reduce clutter, we have plotted only the common (occurring in >10% of wetlands) rotifer and cladoceran taxa on the bi-plots, using the first three letters of the genus and species as labels (Fig. 2). Species of the same rotifer genera tended to show similar environmental preferences along pCCA axis 1 (e.g., *Monostyla* in Fig. 2b) as did species of cladocerans (e.g., *Alona* in Fig. 2a). Wetlands that had clear water with substantial submersed aquatic vegetation tended to be associated with specific rotifer genera. For example, all eight species of *Monostyla* encountered in this study tended to occur within submersed macrophyte beds. Similarly, nine of 11 species of *Lecane*, six of seven species of *Euchlanis*, all five species of *Lepadella*, four of five species of *Trichocerca*, and less speciose taxa

TABLE 2. Comparison of means (1 SE) of zooplankton community structure at five habitat types.

Structure	OPEN 10 m	OPEN 3 m	EM	SUB	FLTG	Stats ($P < 0.05$)
N	55	105	94	68	10	
Species richness	7.78 (0.38)	8.82 (0.35)	11.61 (0.44)	12.71 (0.57)	12 (1.35)	S, E > 10, 3; F > 10
H′	1.08 (0.05)	1.17 (0.05)	1.48 (0.06)	1.58 (0.06)	1.50 (0.18)	S, E > 10, 3
Mean cladoceran size (μm)	291 (35)	388 (22)	522 (24)	526 (27)	457 (71)	S, E > 10, 3
Abundance (no. animals/L)						
Rotifers	492 (106)	251 (50)	195 (35)	257 (48)	221 (121)	NS
Cladocerans	138 (27)	157 (42)	603 (234)	211 (38)	328 (160)	S, E > 3
Copepods and copepodids	54 (18)	41 (9)	134 (26)	220 (40)	220 (81)	F, S, E > 10, 3; S > E
Nauplii	121 (25)	149 (39)	183 (37)	235 (50)	460 (253)	S > 10, 3
Abundance (%; excluding copepods)						
Rotifers	57 (5)	59 (3)	44 (3)	50 (3)	39 (9)	E < 3
Chydoridae	4 (3)	6 (2)	15 (2)	22 (2)	28 (6)	F, E, S, > 3, 10; S > E
Daphnidae	5 (3)	7 (2)	16 (2)	11 (2)	13 (5)	E > 3, 10
Sididae	1 (1)	2 (1)	3 (1)	3 (1)	5 (2)	NS
Macrothricidae	0	0	1 (1)	1 (1)	1 (1)	NS
Bosmididae	31 (4)	23 (3)	19 (3)	11 (3)	10 (8)	S < 10, 3
Other cladocerans	4 (0)	1 (0)	2 (0)	2 (0)	3 (0)	NS
WZI	2.85 (0.07)	3.10 (0.06)	3.50 (0.06)	3.77 (0.06)	3.49 (0.26)	S, E > 3, 10
WZI_{P-A}	3.16 (0.08)	3.54 (0.07)	3.95 (0.06)	4.20 (0.04)	3.77 (0.23)	S, E > 3, 10; F > 10

Notes: Statistical comparisons (Stats) are the results of an analysis of variance followed by Tukey-Kramer multiple comparisons ($P < 0.05$). Habitat sites are defined as follows: OPEN 10 m, open water 10 m from the outermost edge of aquatic plants; OPEN 3 m, open water 3 m from aquatic plants; EM, within or immediately adjacent to emergent aquatic vegetation; SUB, within submergent plant beds (>5 stems/m^2), FLTG, plankton below floating aquatics were sampled when submergent or emergent beds were absent or inaccessible. The habitat sites are abbreviated as 10, 3, E, S, and F, respectively, in the "Stats" column.

such as *Platyias* sp. and *Mytilina* sp. were commonly found associated with submergent vegetation. Species of cladocerans that were well represented in heavily vegetated wetlands included 25 of 28 species of chydorids encountered in this study, seven of eight species of macrothricids, *Simocephalus* sp., *Polyphemus pediculus*, *Sida crystallina*, *Diaphanosoma brachyurum*, *Scapholeberis kingi*, and *Ceriodaphnia* sp. By comparison, there were only a few taxa tolerant of highly degraded, sparsely vegetated wetlands, and these included all 10 species of *Brachionus*, *Filinia*, *Asplanchna*, *Polyarthra* and six of seven species of *Keratella*; cladoceran species that were found consistently in degraded wetlands included both species of *Moina*, all four species of *Daphnia*, and the bosminids, *Bosmina longirostris* and *Eubosmina coregoni*.

Development of wetland zooplankton index (WZI)

Before calculating the WZI, we reduced the total number of taxa in our data set by grouping species of the same genus according to their location on the first axis of the pCCA bi-plot (Table 3). Grouping taxa together has a practical benefit, because some taxa (e.g., chydorids) are difficult to key to species. An index based on genera would require less training and time than one requiring species-specific identification. There were, however, some taxa with unique habitat requirements that could not be grouped together. Although most of the chydorids were similarly intolerant of degraded conditions and occurred far to the left of the origin (0,0) on pCCA axis 1 (Fig. 2a), several (e.g., *Kurzia*, *Monospilus*, and *Leydigia*; Table 3) were more tolerant of degraded conditions, and accordingly their positions in the bi-plot occurred more centrally or further to the right-hand side of pCCA axis 1. These formed a separate group (Table 3).

Optimum (U; center of distribution) and tolerance (T; range of distribution) values were determined for each taxon based on a pCCA using these collapsed taxonomic groupings (Table 3). The location of a taxon on pCCA axis 1 represented its center of distribution along this primary synthetic axis formed by several key environmental variables. Details of the assignment of U and T are outlined in the *Methods.* In general, taxa tolerant of degraded conditions (U = 1–2) had broader tolerance (T = 1), while those less tolerant (U = 4–5) often had narrower tolerances (T = 3) (Table 3).

We calculated WZI values for zooplankton communities in each of the habitat types in the 70 wetlands. Aquatic vegetation was an important determinant of the WZI, since WZI values from sites containing submergent and/or emergent vegetation were significantly higher than those associated with open water (Table 2). In fact, the WZI increased significantly with the species richness of submerged macrophytes observed in each of these wetlands (Fig. 3; r^2 = 0.32, P < 0.0001), leveling off at ~10 species of submergent plants and a WZI value of 4. This is not unexpected, given the significant relationship between submergent plants species richness and wetland water quality (Crosbie and Chow-Fraser 1999; Lougheed et al. 2001).

To compare the WZI with more standard measures of zooplankton community structure, we correlated it and four other indices (Shannon-Wiener diversity index

TABLE 3. Optimum (U) and tolerance (T) of zooplankton taxa.

Taxon/species	U	T
Rotifers		
Anuropsis sp.	3	1†
Ascomorpha sp.	1	1†
Asplanchna sp.	2	1
Brachionus sp.	2	1
Cephalodella sp.	3	1†
Collotheca sp.	5	2
Conochiloides	4	2
Euchlanis sp.	4	2
Filinia sp.	1	1
Gastropus sp.	2	1†
Hexarthra sp.	1	1†
Kellicotia sp.	3	3
Keratella sp.	3	1
Lecane sp.	5	2
Lepadella sp.	4	2
Lophocaris sp.	2	1†
Macrochaetus sp.	4	1†
Monostyla sp.	5	2
Mytilina sp.	5	3
Notholca sp.	3	1†
Platyias sp.	4	2
Ploesoma sp.	4	2
Polyarthra sp.	3	1
Pompholyx sp.	1	1†
Scaridium sp.	5	1†
Testudinella sp.	4	2
Trichocerca sp.	4	2
Trichotria sp.	5	2
Chydoridae	4	2
Kurzia latissima‡	3	3
Leydigia leydigit‡	1	1†
Monospilus dispar‡	2	1†
Macrothricidae	5	3
Illiocryptus sordidus‡	1	1†
Daphnidae		
Ceriodaphnia sp.	4	2
Daphnia sp.	2	2
Megafenestra sp.	2	1†
Scapholeberis kingi	4	2
Simocephalus sp.	5	3
Sididae		
Diaphanosoma birgei	1	2
D. brachyurum	5	2
Latona parviremis	4	1†
Latonopsis occidentalis	5	1†
Sida crystallina	5	3
Bosminidae	3	1
Additional species		
Polyphemus pediculus	5	3
Leptodora kindti	1	1†
Moina sp.	1	1
Holopedium gibberum	3	1†

† Taxa that occurred in <10% of wetlands were automatically given a tolerance value of 1.
‡ These species represent exceptions to the Chydoridae and Macrothricidae groupings.

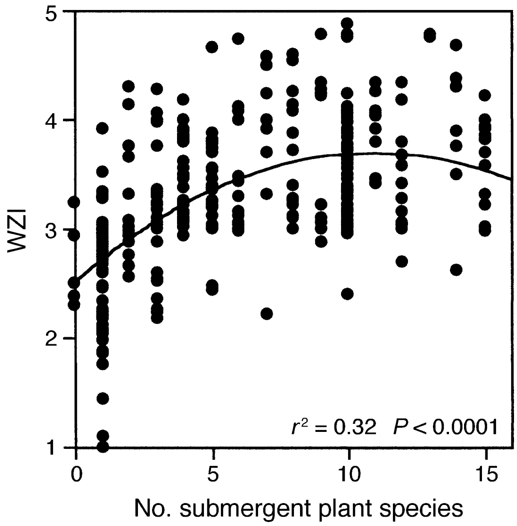

FIG. 3. Relationship between wetland zooplankton index (WZI) values and submergent plant species richness for 70 wetlands in the Great Lakes basin.

(H'), species richness, total zooplankton abundance, mean cladoceran size) with principal components analysis (PCA) axis 1 as the independent variable. The WZI correlated more highly with PCA axis 1 (Fig. 4a; $r^2 = 0.25$, $P < 0.05$), than did Shannon-Wiener diversity index, H' (Fig. 4c; $P > 0.05$), $\log_{10}$(zooplankton abundance) (Fig. 4d; $r^2 = 0.13$, $P < 0.05$), mean size of cladocerans (Fig. 4e; $P > 0.05$), or species richness (Fig. 4f; $P > 0.05$). The WZI also consistently explained more variation in regressions with variables such as total phosphorus (TP; $r^2 = 0.18$, $P < 0.05$), CHL-*a* ($r^2 = 0.20$, $P < 0.05$), and total suspended solids (TSS; $r^2 = 0.19$, $P < 0.05$), compared with the other measures.

We also used this principal components axis to compare the WZI calculated based on abundances vs. the index values calculated from presence/absence data (WZI_{P-A}; Fig. 4b). The slopes of the lines were not statistically different (ANCOVA; $P > 0.05$), but comparison of the intercepts indicated that the WZI_{P-A} values were ~0.4 units greater than the corresponding WZI at any given PCA axis 1 value (intercept = 3.74 and 3.32, respectively; ANCOVA; $P < 0.05$).

Case study: Cootes Paradise

Lougheed and Chow-Fraser (*in press*) described how water clarity increased and submersed macrophytes became established in shallow, sheltered, vegetated areas of Cootes Paradise Marsh (1997 and 1998) after most of the large carp were excluded in the spring of 1997. These changes at the vegetated site were concomitant with a significant reduction in edible algal biomass and increased representation of large zooplankton grazers and substrate-associated cladocerans. By contrast, open-water areas in the marsh remained turbid and devoid of vegetation and only exhibited temporary or nonsignificant changes in water clarity; there were also fewer changes in the zooplankton community at the open-water sites.

We calculated WZI and WZI_{P-A} values for three different sites in the marsh (i.e., vegetated, lagoon, and open-water; see *Methods*) for each of two years prior to carp exclusion (1993 and 1994) and two years following carp exclusion (1997 and 1998). Fig. 5 compares the WZI_{P-A} values calculated for each site–year combination in Cootes Paradise to other Lake Ontario coastal marshes. Trends were no different if the WZI was used as opposed to the $WZI_{P-A.}$ There were no consistent significant differences seen between both pre- and postexclusion years at the open water sites, although the WZI_{P-A} tended to be higher in 1998 than in one (lagoon) or both (open-water) pre-exclusion years. By comparison, the mean for the vegetated site increased significantly in both years following exclusion (ANOVA; Tukey-Kramer, $P < 0.05$). Despite these significant increases, however, the average summer index values did not generally exceed the mean for all other Lake Ontario wetlands and were still considerably lower than the WZI_{P-A} value observed at a nearby reference wetland (Fig. 5).

While the WZI correctly detected moderate improvements in water quality following carp exclusion, there were no significant differences observed at any of the sites between pre- and postexclusion years with respect to species richness, cladoceran body length or rotifer and cladoceran abundance. In fact, contrary to expectations, the Shannon-Wiener index of diversity was significantly reduced at the vegetated site following carp exclusion (ANOVA; Tukey-Kramer, $P < 0.05$).

DISCUSSION

We developed an index based on water quality, macrophyte habitat, and distribution of zooplankton that can be used to evaluate wetland quality across the Great Lakes basin. This index design method could be extrapolated to other systems and thus aid in tracking restoration and degradation of vegetated aquatic habitats. Because the database we used to develop this index included a broad range of wetland quality (Table 1), wetland types (i.e., lacustrine, riverine, palustrine), and geomorphological settings (e.g., open shoreline, river delta, barrier beach) (Maynard and Wilcox 1997, Chow-Fraser and Albert 1999), we are confident that it will have wide applicability.

Wetlands in our database fall on a continuum: at one extreme are turbid, eutrophic, and algae-rich systems with few, if any, submersed macrophytes; at the other extreme are high-quality wetlands that are relatively clear, oligotrophic with abundant and diverse submergent macrophyte beds (Table 1; Lougheed et al. 2001). This gradient in wetland quality was accompanied by a predictable change in the taxonomic composition of the zooplankton community, as indicated by the pCCA,

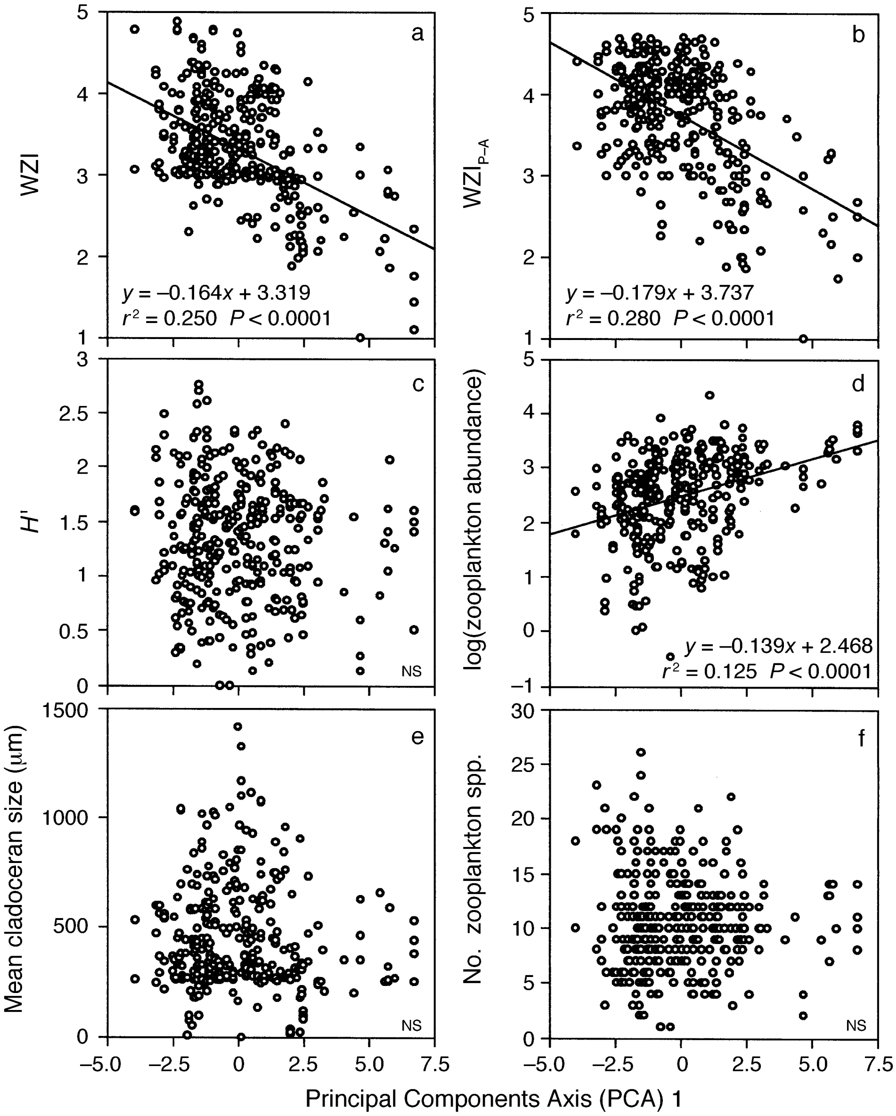

FIG. 4. Role of principal components axis 1 in explaining variation in several measures of zooplankton community structure: (a) WZI, (b) $WZI_{P\text{-}A}$, (c) H', (d) log(total zooplankton abundance), (e) mean size of cladocerans (µm), and (f) species richness of rotifers and cladocerans.

which showed that plant-associated taxa dominated high-quality wetlands while more pollution-tolerant taxa dominated degraded wetlands. Results from the few published studies on zooplankton in Great Lakes wetlands (Krieger 1992) are consistent with our findings. For example, Krieger and Klarer (1991) and Lougheed and Chow-Fraser (1998) also found *Diaphanosoma birgei*, *Moina micrura*, and Bosminids occurring in degraded wetlands of the lower lakes, while other authors found plant-associated cladocerans such as macrothricids, chydorids, *Simocephalus*, and *Sida* occurring in relatively pristine Lake Huron (Cardinale et al. 1998, Gathman et al. 1999) and Lake Erie wetlands (Campbell 1993, Botts 1999). Similar species trends have also been reported in prairie pothole wetlands (Gaiser and Lang 1998).

The 1987 revision to the Great Lakes Water Quality Agreement (GLWQA) acknowledges the importance of biological systems in the monitoring and assessment of the Great Lakes ecosystem and endorses an ecosystem approach. The selection of appropriate indicators of ecosystem health for coastal wetlands of the Great Lakes is required to accurately illustrate that changes in environmental quality are accompanied by ecological changes. The wetland zooplankton index (WZI) is a more useful indicator of wetland degradation and restoration than indices of diversity (H', species richness) and measures of community structure (mean size,

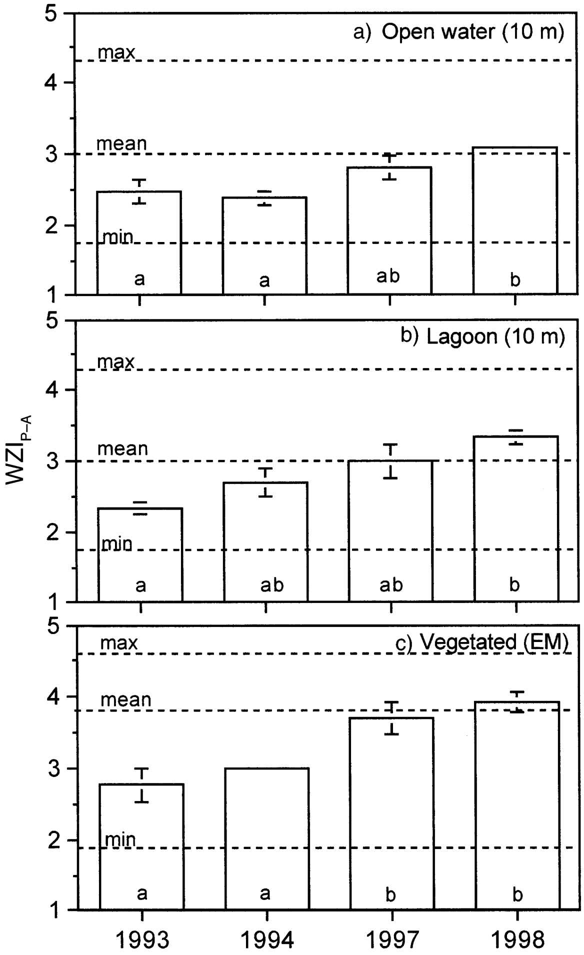

FIG. 5. Comparison of WZI_{P-A} values before (1993 and 1994) and after (1997 and 1998) carp exclusion from three sites: (a) open water, (b) lagoon, and (c) vegetated sites in Cootes Paradise Marsh. The minimum, mean, and maximum WZI_{P-A} (WZI using presence/absence data) values observed at similar habitat types are indicated by dashed lines: (a) and (b) OPEN 10 m, and (c) EM in Lake Ontario. The maximum values indicate those obtained from the least disturbed reference site in Lake Ontario. Letters indicate statistical similarity between years (ANOVA; Tukey-Kramer, $P < 0.05$).

total abundance), likely because the latter ignore taxon-specific information. Moreover, some simpler zooplankton indices, which are based on ratios of taxonomic groups, are also inferior. For example, the ratio of calanoid to cyclopoid copepods plus cladocerans (Gannon and Stemberger 1978), or of calanoids to cyclopoids (Derevenskaya and Mingasova 2000), which have been used to indicate lake quality, cannot be applied here, because >75% of these wetlands, including many of the more oligotrophic systems, did not have calanoids present. Indices based on only a few genera (e.g., ratio of *Brachionus* to *Trichocerca*; Sládecek 1983) are also inappropriate, as they cannot describe conditions at sites where both these taxa are absent, which in this case represents nearly half of all sites sampled.

The strong relationship between WZI values and wetland degradation is due to several factors, of which the most obvious are the presence of submersed macrophytes (Quade 1969, Cyr and Downing 1988, Paterson 1993), trophic state (Berzins and Bertilsson 1989, Berzins and Pejler 1989), and water clarity (Lougheed and Chow-Fraser 1998). All three factors played a primary role in the construction of the index. However, the index development largely ignored geographic location (i.e., latitude) and degree of development in the watershed, which loaded significantly on the second axis of the pCCA. Other authors have also shown that the wetland environments in the upper and lower lakes are unique, due largely to differences in climate, geology, and exposure (Smith et al. 1991), and that this has important consequences for the macrophyte community (Minc 1997; Lougheed et al. 2001). In fact, both the abundance and species richness of rotifers and cladocerans varied inversely with latitude ($r^2 = 0.05$; $P < 0.0001$), with 57 of the 138 zooplankton taxa identified in this study absent from the upper lakes (see the Appendix). Consequently, we advise against the indiscriminate comparison of WZI values across lakes or latitudes and suggest that comparisons be made to a least disturbed reference wetland in each lake or region, some examples of which are listed in Table 4.

In using this index to assess wetland quality, we have four methodological recommendations. First, this index should be applied cautiously to wetlands that are dominated by taxa identified as rare indicator species (Table 3), as well as taxa that had been grouped with other species into a single taxon because of their rare occurrence (see the Appendix). Grouping species into genera and larger taxonomic divisions might ease identification, but also obscure important differences in habitat preferences of useful indicator species (e.g., Sládecek 1983, Gaiser and Lang 1998). Future studies should focus on collecting sufficient information on "rare" taxa so that corresponding optimum and tolerance values can be updated, and criteria for inclusion of taxa into larger groups could be confirmed. Fortunately, the WZI gives zero weight to absent species of rotifers and cladocerans, in order to ensure that wetlands will not be misclassified simply because they are located outside the geographic home range of a particular taxon, due to seasonal variability in species occurrences or due to differences in sampling effort.

Second, it is important to restrict comparisons to samples from similar habitat types. For the purpose of among marsh comparisons, we recommend that WZI values be based on samples collected from vegetated (emergent, submergent) or near-vegetated (OPEN 3 m) sites. Not only are these sites often located in waters that are accessible by wading, thereby reducing the extra labor required with launching a boat, but samples collected from open-water (10-m) sites underrepresent

TABLE 4. Maximum WZI_{P-A} values from three different habitat types at the least disturbed sites visited in this study (suggested reference wetlands) in all five Great Lakes and four inland sites in the basin.

Lake	Wetland†	Latitude (N)	Longitude (W)	OPEN 3 m	EM	SUB
Lake Ontario	Hay Bay (ON)	44°10′30″	76°55′30″	4.3	4.6	4.5
Lake Erie	Long Pt Complex (ON)	42°35′00″	80°23′00″	4.1	4.4	4.5
	Presque Isle (PA)	42°09′37″	80°05′56″	4.1	4.4	3.9
	Turkey Creek (ON)	42°14′08″	83°05′07″	4.1	4.5	4.6
Lake Huron	Spanish River (ON)	46°12′00″	82°21′00″	3.8	4.2	4.3
	Sturgeon Bay (ON)	44°44′00″	79°44′00″	4.3	4.5	3.9
Lake Michigan	Escanaba River (WI)	45°42′26″	89°04′48″	4.2	4.4	4.6
	Pentwater River (MI)	43°45′38″	86°24′0.6″	4.2	4.4	4.7
Lake Superior	Pine Bay (ON)	48°03′00″	89°31′00″	3.3	4.7	4.5
	West Fish Creek (WI)	46°35′11″	90°56′50″	4.0	3.8	4.5
Inland	Big Creek (ON)	42°57′20″	80°26′50″	4.7	4.5	4.3
	Indian River (ON)	44°14′00″	78°09′00″	4.4	4.6	4.6
	Tay River (ON)	44°52′45″	76°10′30″	4.5	4.6	4.7
	Wye Marsh (ON)	44°42′00″	79°51′00″	3.7	4.5	4.2

Note: Habitat sites are defined as follows: OPEN 3 m, open water 3 m from aquatic plants; EM, within or immediately adjacent to emergent aquatic vegetation; SUB, within submergent plant beds (>5 stems/m^2).

† ON, Ontario, Canada; PA, Pennsylvania, USA; WI, Wisconsin, USA; MI, Michigan, USA.

the range of taxa encountered at sites closer to vegetation and will result in a much lower WZI value.

Third, sampling in riverine systems should be done in as sheltered a location as possible to ensure a comprehensive species list and a WZI value that reflects the true value of the marsh habitat. Wetland zooplankton index values may be reduced considerably in more riverine sites as the flush out of resident water due to storm runoff may eliminate or severely reduce the abundance of many zooplankton taxa (V. L. Lougheed, *unpublished data*). An impoverished zooplankton community may persist for weeks or months following a severe runoff event, and only a few species may return to their prestorm abundance (Krieger and Klarer 1991).

Finally, wetlands are not only spatially variable, but wetland communities can also exhibit high temporal variability, due to seasonal and interannual differences in water level (Chow-Fraser et al. 1998), sediment and nutrient inflows (Chow-Fraser 1999), temperature (Lougheed and Chow-Fraser, *in press*) and species dynamics (e.g., Lougheed and Chow-Fraser 1998). Consequently, seasonal and year-to-year variation in WZI values is not surprising, and a seasonal or year-to-year range of ~1.0 can be expected between the lowest and highest calculated WZI value for any given site in a wetland (V. L. Lougheed, *unpublished data*). To accurately assess marsh restoration efforts, we advise that a biweekly sampling regime be established. If this is not feasible, then sampling should take place in mid- to late summer, as zooplankton dependent on submergent plants for habitat may not appear until this vegetation becomes established in midsummer.

The WZI rapidly tracked site-specific improvements in Cootes Paradise Marsh following implementation of carp exclusion in the spring of 1997. Lougheed and Chow-Fraser (*in press*) used a statistical approach to evaluate changes in water quality and the response of the zooplankton and phytoplankton communities, and found that only the vegetated site exhibited an immediate positive response to remedial actions, whereas the more open-water sites changed only slightly. We arrived at the same conclusions using the WZI; in addition, we were able to compare the WZI of Cootes Paradise to a reference wetland in Lake Ontario (Hay Bay) and the mean WZI of all Lake Ontario wetlands to illustrate that following carp exclusion, the zooplankton community in several areas of Cootes Paradise Marsh was representative of a moderate quality system.

Zooplankton have often been overlooked as biomonitors of environmental quality, but, as we have demonstrated, the zooplankton community varies predictably with wetland quality and responds quickly to changes in the environment. Consequently, these microinvertebrates should be included as important components of biological monitoring protocols. The index that we have developed should be broadly applicable to wetlands in the Great Lakes basin, but further research is required to confirm its suitability in other regions and other vegetated habitats. We suggest that the WZI should not be used as a sole indicator of wetland quality, but as a complement to water quality information and surveys of other trophic levels where possible. To determine the most cost-effective and accurate combination of methods for the routine assessment of wetland quality, more effort should be directed at comparing the utility of the WZI with other indices based on fish (index of biotic integrity [IBI]; Minns et al. 1994), benthos (IBI; Burton et al. 1999), periphyton, and macrophytes and in constructing a more comprehensive index representing the overall ecological integrity of wetland ecosystems (Karr 1991, Keddy et al. 1993).

ACKNOWLEDGMENTS

We are grateful to many people for their help in locating and sampling these wetlands, especially B. Crosbie, R. Haas, C. MacIsaac, S. McNair, C. Moulder, and B. Reich. This research was funded by an Ontario Graduate Scholarship to

V. L. Lougheed, the J. F. Harvey and H. S. Harvey Travel Scholarship to V. L. Lougheed, a private donation from B. D. L. Bennett and a research grant to P. Chow-Fraser from the Great Lakes Fisheries Commission. Research in Cootes Paradise Marsh was funded in part by a research grant to P. Chow-Fraser from the McMaster Eco-Research Program for Hamilton Harbour, and a National Sciences and Engineering Research Council of Canada operating grant.

Literature Cited

American Public Health Association. 1992. Standard methods for the examination of water and wastewater. 18th edition. American Public Health Association. Washington, D.C., USA.

Attayde, J. L., and R. L. Bozelli. 1998. Assessing the indicator properties of zooplankton assemblages to disturbance gradients by canonical correspondence analysis. Canadian Journal of Fisheries and Aquatic Sciences **55**:1789–1797.

Balcer, M. D., N. L. Korda, and S. I. Dodson. 1984. Zooplankton of the Great Lakes. University of Wisconsin Press, Madison, Wisconsin, USA.

Bertram, P., and N. Statler-Salt. 1999. Selection of indicators for Great Lakes basin ecosystem health. Environment Canada and U.S. Environmental Protection Agency. State of the Lakes Ecosystem Conference 1998. [Online, URL: ⟨www.cciw.ca/solec⟩.].

Berzins, B., and J. Bertilsson. 1989. On limnic micro-crustaceans and trophic degree. Hydrobiologia **185**:95–100.

Berzins, B., and B. Pejler. 1989. Rotifer occurrence and trophic degree. Hydrobiologia **182**:171–180.

Botts, P. S. 1999. Lake Erie coastal wetlands: a review and case study of Presque Isle invertebrates. Pages 995–1012 *in* D. P. Batzer, R. B. Rader, and S. A. Wissinger, editors. Invertebrates in freshwater wetlands of North America. John Wiley & Sons, Canada.

Burton, T. M., D. G. Uzarski, J. P. Gathman, J. A. Genet, B. E. Keas, and C. A. Stricker. 1999. Development of a preliminary invertebrate index of biotic integrity for Lake Huron coastal wetlands. Wetlands **19**:869–882.

Campbell, J. M. 1993. The cladoceran species of inshore habitats of Lake Erie at Presque Isle. Journal of the Pennsylvania Academy of Science **67**:115–119.

Cardinale, B. J., V. J. Brady, and T. M. Burton. 1998. Changes in the abundance and diversity of coastal wetland fauna from the open water/macrophyte edge towards shore. Wetlands Ecology and Management **6**:59–68.

Chow-Fraser, P. 1998. A conceptual model to aid restoration of Cootes Paradise Marsh, a degraded coastal wetland of Lake Ontario, Canada. Wetland Ecology and Management **6**:43–57.

Chow-Fraser, P. 1999. Seasonal, interannual and spatial variability in the concentrations of total suspended solids in a degraded coastal wetland of Lake Ontario. Journal of Great Lakes Research **25**:799–813.

Chow-Fraser, P., and D. A. Albert. 1999. Coastal wetland ecosystems: biodiversity investment areas. Environment Canada and U.S. Environmental Protection Agency. State of the Lakes Ecosystem Conference 1998. [Online, URL: ⟨www.cciw.ca/solec⟩.].

Chow-Fraser, P., V. Lougheed, V. Le Thiec, B. Crosbie, L. Simser, and J. Lord. 1998. Long-term response of the biotic community to fluctuating water levels and changes in water quality in Cootes Paradise Marsh, a degraded coastal wetland of Lake Ontario. Wetland Ecology and Management **6**:19–42.

Crosbie, B., and P. Chow-Fraser. 1999. Percentage land use in the watershed determines the water and sediment quality of 22 marshes in the Great Lakes basin. Canadian Journal of Fisheries and Aquatic Sciences **56**:1781–1791.

Cyr, H., and J. A. Downing. 1988. Empirical relationships of phytomacrofaunal abundance to plant biomass and macrophyte bed characteristics. Canadian Journal of Fisheries and Aquatic Sciences **45**:976–984.

Derevenskaya, O. Yu., and N. M. Mingazova. 2000. Communities of zooplankton in lakes in the course of their contamination and restoration. Hydrobiological Journal **36**: 1–7.

Gaiser, E. E., and K. L. Lang. 1998. Distribution of cladoceran zooplankton among prairie pothole wetlands in northwest Iowa. Lake and Reservoir Management **14**:37–51.

Gannon, J. E., and R. S. Stemberger. 1978. Zooplankton (especially crustaceans and rotifers) as indicators of water quality. Transactions of the American Microscopal Society **97**:16–35.

Gathman, J. P., T. M. Burton, and B. J. Armitage. 1999. Coastal wetlands of the upper Great Lakes: distribution of invertebrate communities in response to environmental variation. Pages 949–994 *in* D. P. Batzer, R. B. Rader, and S. A. Wissinger, editors. Invertebrates in freshwater wetlands of North America. John Wiley & Sons, Canada.

Hessen, D. O., B. A. Faafeng, and T. Andersen. 1995. Replacement of herbivore zooplankton species along gradients of ecosystem productivity and fish predation pressure. Canadian Journal of Fisheries and Aquatic Sciences **52**: 733–742.

Jongman, R. H. G., C. J. F. ter Braak, and O. F. R. van Tongeren. 1995. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, UK.

Karr, J. R. 1981. Assessment of biotic integrity using fish communities. Fisheries **6**:21–27.

Karr, J. R. 1991. Biological integrity: a long-neglected aspect of water resource management. Ecological Applications **1**: 66–84.

Keddy, P. A., H. T. Lee, and I. C. Wisheu. 1993. Choosing indicators of ecosystem integrity: wetlands as a model system. Pages 61–79 *in* S. Woodley, J. Kay, and G. Francis, editors. Ecological integrity and the management of ecosystems. St. Lucie Press, Delray Beach, Florida, USA.

Kelly, M. G., and B. A. Whitton. 1995. The trophic diatom index: a new index for monitoring eutrophication in rivers. Journal of Applied Phycology **7**:433–444.

Krieger, K. A. 1992. The ecology of invertebrates in Great Lakes coastal wetlands: current knowledge and research needs. Journal of Great Lakes Research **18**:634–650.

Krieger, K. A., and D. M. Klarer. 1991. Zooplankton dynamics in a Great Lakes coastal marsh. Journal of Great Lakes Research **17**:255–269.

Lenat, D. R. 1993. A biotic index for the southeastern United States: derivation and list of tolerance values, with criteria for assigning water-quality ratings. Journal of North American Benthological Society **12**:279–290.

Lougheed, V. L., and P. Chow-Fraser. 1998. Factors that regulate the zooplankton community structure of a turbid, hypereutrophic Great Lakes wetland. Canadian Journal of Fisheries and Aquatic Sciences **55**:150–161.

Lougheed, V. L., and P. Chow-Fraser. *In press.* Spatial variability in the response of lower trophic levels after biomanipulation in a freshwater marsh. Journal of Aquatic Ecosystem Stress and Recovery.

Lougheed, V. L., B. Crosbie, and P. Chow-Fraser. 1998. Predictions on the effect of common carp (*Cyprinus carpio*) exclusion on water quality, zooplankton and submergent macrophytes in a Great Lakes wetland. Canadian Journal of Fisheries and Aquatic Sciences **55**:1189–1197.

Lougheed, V. L., B. Crosbie, and P. Chow-Fraser. 2001. Primary determinants of macrophyte community structure in 62 marshes across the Great Lakes basin: latitude, land use & water quality effects. Canadian Journal of Fisheries and Aquatic Sciences **58**:1603–1612.

Maynard, L., and D. Wilcox. 1997. Coastal wetlands of the Great Lakes: background paper for the State of the Lake

Conference (SOLEC). Environment Canada and U.S. Environmental Protection Agency EPA 905-D-96-001c, Chicago, Illinois, USA, and Toronto, Canada.

McCormick, P. V., and R. J. Stevenson. 1998. Periphyton as a tool for ecological assessment and management in the Florida Everglades. Journal of Phycology **34**:726–733.

Minc, L. D. 1997. Great Lakes coastal wetlands: an overview of controlling abiotic factors, regional distribution and species composition. A report submitted to the Michigan Natural Features Inventory. December 1997. Funded by EPA Great Lakes National Program Office (Federal Grant GL9 95810-02) through The Nature Conservancy's Great Lakes program office, East Lansing, Michigan, USA.

Minns, C. K., V. W. Cairns, R. G. Randall, and J. E. Moore. 1994. An index of biotic integrity (IBI) for fish assemblages in the littoral zone of Great Lakes' Areas of Concern. Canadian Journal of Fisheries and Aquatic Sciences **51**: 1804–1822.

Murphy, J., and J. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta **27**:31–36.

Paterson, M. 1993. The distribution of microcrustacea in the littoral zone of a freshwater lake. Hydrobiologia **263**:173–183.

Pennak, R. W. 1989. Freshwater invertebrates of the United States. John Wiley & Sons, New York, New York, USA.

Quade, H. W. 1969. Cladoceran faunas associated with aquatic macrophytes in some lakes in northwestern Minnesota. Ecology **50**:170–179.

Romo, S., E. van Donk, R. Gylstra, and R. Gulati. 1996. A multivariate analysis of phytoplankton and food web changes in a shallow biomanipulated lake. Freshwater Biology **36**:683–696.

Schindler, D. W. 1969. Two useful devices for vertical plankton and water sampling. Journal of the Fisheries Research Board of Canada **26**:1948–1955.

Schindler, D. W. 1987. Detecting ecosystem responses to anthropogenic stress. Canadian Journal of Fisheries and Aquatic Sciences **44**(Suppl. 1):6–25.

Sládecek, V. 1983. Rotifers as indicators of water quality. Hydrobiologia **100**:169–201.

Smith, P. G. R., V. Glooschenko, and D. A. Hagen. 1991. Coastal wetlands of the three Canadian Great Lakes: inventory, current conservation initiatives, and patterns of variation. Canadian Journal of Fisheries and Aquatic Sciences **48**:1581–1594.

Stemberger, R. S. 1979. A guide to rotifers of the Laurentian Great Lakes. United States Environmental Protection Agency, Office of Research and Development, Environmental Information Centre, Cincinnati, Ohio, USA.

Stemberger, R. S., and J. M. Lazorchak. 1994. Zooplankton assemblage responses to disturbance gradients. Canadian Journal of Fisheries and Aquatic Sciences **51**:2435–2447.

ter Braak, C. J. F., and P. Smilauer. 1998. CANOCO reference manual and user's guide to CANOCO for Windows: software for canonical community ordination (version 4). Microcomputer Power, Ithaca, New York, New York, USA.

ter Braak, C. J. F., and P. F. M. Verdonschot. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences **57**:255–289.

Thorp, J. H., and Covich, A. P. 1991. Ecology and classification of North American freshwater invertebrates. Academic Press, San Diego, California, USA.

Whillans, T. H. 1982. Changes in the marsh area along the Canadian shore of Lake Ontario. Journal of Great Lakes Research **8**:570–577.

Whillans, T. H. 1996. Historic and comparative perspectives on rehabilitation of marshes as habitat for fish in the lower Great Lakes basin. Canadian Journal of Fisheries and Aquatic Sciences **53**(Suppl. 1):56–66.

Wilcox, D. A., and T. H. Whillans. 1999. Techniques for restoration of disturbed coastal wetlands of the Great Lakes. Wetlands **19**:835–857.

Zelinka, M., and P. Marvan. 1961. Zur Prazisierung der biologischen Klassifikation des Reinheit fliessender Gewässer. Archive für Hydrobiologie **57**:389–407.

APPENDIX

A complete list of cladocerans and rotifers observed at 70 wetlands in the Great Lakes basin is available in ESA's Electronic Data Archive: *Ecological Archives* A012-004-A1.