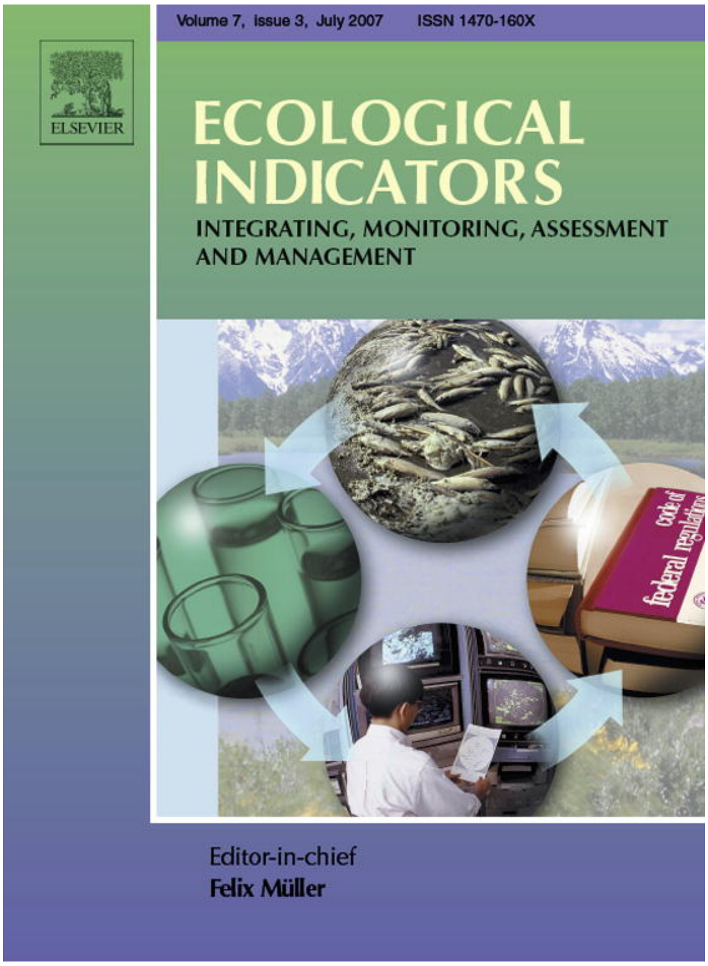
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Evaluation of geographic, geomorphic and human influences on Great Lakes wetland indicators: A multi-assemblage approach

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Abstract

Developing effective indicators of ecological condition requires calibration to determine the geographic range and ecosystem type appropriate for each indicator. Here, we demonstrate an approach for evaluating the relative influence of geography, geomorphology and human disturbance on patterns of variation in biotic indicators derived from multiple assemblages for ecosystems that span broad spatial scales. To accomplish this, we collected abundance information on six biotic assemblages (birds, fish, amphibians, aquatic macroinvertebrates, wetland vegetation, and diatoms) from over 450 locations along U.S. shorelines throughout each of the Great Lakes during 2002–2004. Sixty-six candidate taxon- and function-based indicators analyzed using hierarchical variance partitioning revealed that geographic (lake) rather than geomorphic factors (wetland type) had the greatest influence on the proportion of variance explained across all indicators, and that a significant portion of the variance was also related to response to human disturbance. Wetland vegetation, fish and bird indicators were the most, and macroinvertebrates the least, responsive to human disturbance. Proportion of rock bass, *Carex lasiocarpa*, and stephanodiscoid diatoms, as well as the presence of spring peepers and the number of insectivorous birds were among the indicators that responded most strongly to a human disturbance index, suggesting they have good potential as indicators of Great Lakes coastal wetland condition. Ecoprovince, wetland type, and indicator type (taxa vs function based) explained relatively little variance. Variance patterns for macroinvertebrates and birds were least concordant with those of other assemblages, while diatoms and amphibians, and fish and wetland vegetation were the most concordant assemblage pairs. Our results strongly suggest it will not be possible to develop effective indicators of Great Lakes coastal wetland condition without accounting for differences among

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lakes and their important interactions. This is one of the first attempts to show how ecological indicators of human disturbance vary over a broad spatial scale in wetlands.

Keywords: Great Lakes coastal wetlands; Biotic assemblages; Ecological condition indicators; Diatoms; Wetland vegetation; Aquatic macroinvertebrates; Amphibians; Fish; Birds; Hierarchical variance partitioning; Biogeography; Geomorphology

1. Introduction

Indicators of ecological condition are increasingly recognized as important tools for the management of aquatic ecosystems (Blöch, 1999; NRC, 2000; U.S.EPA, 2001; Environment Canada and U.S.EPA, 2003; Niemi et al., 2004). Development of effective indicators of ecological condition requires study sites be properly classified and indicators be calibrated to identify the geographic range and ecosystem type most appropriate for their application (Karr and Chu, 1999; Seegert, 2001; U.S.EPA, 2002a,b,c; Niemi and McDonald, 2004). Classification of habitat types and calibration of variables have been shown to be important in the development of biotic condition indices (Karr et al., 1986; Simon and Lyons, 1995; Hughes et al., 1998), the RIVPACS (River In Vertebrate Prediction and Classification System) model in the United Kingdom (Wright, 2000), the AQEM Project in Europe (Buffagni et al., 2001) and other indicator metrics for streams (Smith et al., 1999; Bailey et al., 2001), but have not been evaluated fully as part of indicator development for wetlands or most other ecosystem types.

Development of ecological indicators has received considerable attention in the North American Great Lakes, particularly for assessing the condition of coastal waters (Keough and Griffin, 1994; Maynard and Wilcox, 1997; Environment Canada and U.S.EPA, 2003; Lawson, 2004). Because they are central features of the land–water interface, coastal wetlands are a key component of these assessments. Due to their heterogenous nature and limited study, it has been difficult to identify effective indicators for coastal wetlands (Lawson, 2004). Most indicators proposed for Great Lakes coastal wetlands remain untested and uncalibrated, especially across the full range of natural environmental variation that is present in the Great Lakes (Burton et al., 1999; Randall and Minns, 2002; Environment Canada and U.S.EPA, 2003; Wilcox et al., 2002; Albert and Minc, 2004; Uzarski et al., 2004).

We investigated the relative importance of physiographic and biogeographic factors for many potential Great Lakes coastal wetland indicators using a multi-taxa approach. Indicators are typically developed with a single taxon or single assemblage focus (Schulze et al., 2004), but a multi-taxa approach can provide a more comprehensive assessment of anthropogenic influences (Mensing et al., 1998; O'Connor et al., 2000; Bryce and Hughes, 2003; Fore, 2003; Schulze et al., 2004) and an opportunity to examine concordance in patterns of response among the indicators (Jackson and Harvey, 1993; Allen et al., 1999a,b). We evaluated indicators from a study designed to develop and test indicators of ecological condition for coastal ecosystems in the Great Lakes (Niemi et al., 2004; Danz et al., 2005).

We had three main goals for this study. The first was to examine the relative importance of geographic, geomorphic and human disturbance influences on indicator responses. Geographic factors are important sources of variation because of differences in species distributions and climate-related factors across a region as large as the Great Lakes. Where geographically-based differences were detected, we analyzed whether ecoprovince (broad spatial scale) as defined by Keys et al. (1995) or the individual Great Lakes (finer spatial scale) consistently had a stronger influence. Ecoprovince classification accounts for differences in climate, vegetation and physiography between regions (Keys et al., 1995). Moreover, indicator responses often vary by wetland type because of differences in hydrogeomorphology among different types of wetlands (Keough et al., 1999; Albert and Minc, 2004). Hydrogeomorphic context can have an important influence on water chemistry, residence times and connectivity to the adjacent Great Lake and its associated watershed (Trebitz et al., 2002). In both inland lakes and wet meadows adjacent to the Great Lakes, position in the watershed and landscape context have been linked to food web alterations, species richness and invertebrate and bird abundances (Lewis and Magnuson, 2000; Riera et al., 2000; Riffel et al., 2003).

Our second goal was to compare the responses of taxon- and function-based indicators. Functional indicators are those based on species traits rather than taxonomy (Keddy, 1992). Because species distributions reflect many factors, such as climate and vegetation patterns, which are unrelated to human disturbance, responses of taxon-level indicators to disturbance can be difficult to distinguish from geographic influences. Functional classes of organisms include taxonomic or ecological variants that replace one another across habitats or geographic regions, potentially providing advantages over individual species as indicators (Terborgh and Robinson, 1986; Keddy, 1992; Austen et al., 1994). However, differences in geographic influences on species and functional indicators will depend on the species selected and should be less pronounced for species with basin-wide distributions. We also expected that the response of functional indicators to human disturbance would be less confounded by wetland geomorphic type than taxon-based indicators because species distributions seem most likely to be driven by species-specific habitat preferences (Reavie and Smol, 1997; Naugle et al., 1999; Marks, 2003; Tanner et al., 2004; Wei et al., 2004; Price et al., 2005).

Our third goal was to examine the concordance in response to anthropogenic stress among indicators from different biotic assemblages. Examining concordance can highlight redundancy among indicator responses, help assess the relative utility of particular indicators, and provide insight into ecological processes influencing particular assemblages (Allen et al., 1999a,b; Paszkowski and Tonn, 2000). For instance, because fish, macroinvertebrates and diatoms are constrained to the aquatic portions of their watersheds, indicators from these assemblages may respond to a similar suite of disturbances and, therefore, may have more concordant response patterns. Where concordance of response is high among indicators or assemblages, there is redundant information provided about ecological condition. So, understanding concordance is pertinent to decisions about cost- and information-effectiveness of various combinations of indicators (Yoder and DeShon, 2003).

In addition to considering how geographic and geomorphic factors need to be incorporated into indicator development, the approach we present here provides a means of evaluating which species and functional groups have the best individual potential as indicators of environmental stress in the Great Lakes coastal zone, as well as for other ecosystems being evaluated across broad spatial scales. This paper is intended to demonstrate an approach rather than serve as an exhaustive evaluation of all potential indicators and sources of variation. It is not intended to provide an estimate of those indicators that best represent the overall biological integrity of Great Lakes coastal ecosystems, although results from this paper should contribute to those estimates in the near future.

2. Methods

2.1. Data sources, study area and survey methods

The larger study that the data used here were derived from was based on a single integrated conceptual framework. The framework was a modification of the ecological risk assessment paradigm used by the U.S.EPA and had the ultimate goal of providing recommendations on a suite of hierarchically-structured indicators useful for making informed management decisions about Great Lakes coastal ecosystems (Niemi et al., 2004; Danz et al., 2005). Common methodologies were used to collect abundance information on bird, fish, amphibian, aquatic macroinvertebrate, wetland vegetation, and diatom assemblages from over 450 coastal locations along U.S. shorelines throughout each of the five Great Lakes. The Great Lakes are located along the U.S. and Canadian border (Fig. 1), have a total drainage area of over 500,000 km^2 hold nearly 20% of the world's freshwater. Climate, geology, soils, hydrology, lake processes, human influences and biotic communities vary greatly across the basin and even within lakes (Government of Canada and U.S.EPA, 1995), but in general there is a north temperate climate throughout, a heavily forested, more pristine landscape in northern regions and an agricultural, more populated and more industrialized landscape in the south. Although six

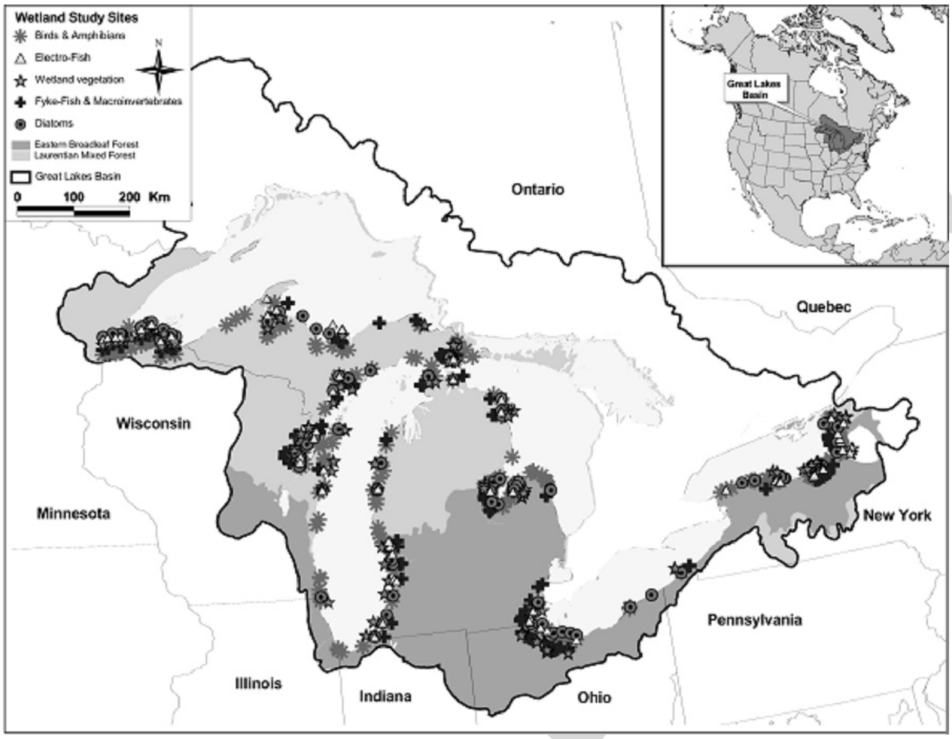

Fig. 1. Map of sampling locations in the Great Lakes for each of the assemblages (some sampling points have been moved slightly to reduce overlap and improve clarity).

ecosystem types were sampled as part of the larger project (Danz et al., 2005), for this paper we focus only on responses within three wetland types, river-influenced, protected, and open-coastal, as defined by Keough et al. (1999).

2.1.1. Indicator selection criteria

Eight to ten candidate indicators from each of the six assemblages that were sampled were selected by the co-authors most familiar with particular assemblages (Table 1). Indicators were selected based on criteria recommended by Hughes et al. (1998) and O'Connor et al. (2000). These included indicators that (1) were known or thought to be responsive to human disturbance, (2) represented ecologically important species or functions, (3) were sampled effectively (low intra-site variance), and (4) were limited in redundancy with other indicators selected from that assemblage. We also attempted to maximize similarity in the types of functional indicators examined for each assemblage by selecting indicators representing the following guilds when feasible: (1) stress tolerance (e.g. turbidity tolerance), (2) reproductive strategy (e.g. nest-guarding), (3) mobility (e.g. motility), and (4) trophic (e.g. insectivores). In addition, at least one compositional metric (taxonomic richness, diversity, abundance) was included for each assemblage.

The number of wetlands sampled varied by assemblage (Table 1), but all groups sampled at least 25% of the 276 wetlands that met our selection criteria (herbaceous, sufficient size (>4 ha), publicly accessible, and surface water connection to the Great Lakes for the fish groups). Birds and amphibians were sampled at >75% of the possible wetlands. Sites were spread across the Great Lakes and approximately evenly distributed among the Laurentian Mixed Forest Ecoprovince (LMF) in the northern lakes and Eastern Broadleaf Forest Ecoprovince (EBF) in the southern lakes (Fig. 1). The two ecoprovinces differ in climate, physiography, and the degree and types of human disturbance (Danz et al., in press). The EBF has a longer history of human occupation, a higher human population density, and a watershed with a higher proportion of agriculture and greater atmospheric deposition than the LMF (Danz et al., in press).

Table 1
List of indicators, indicator classes, sample sizes, *I* (independent variance explained) values, rank *I* values and significance of the *I* values associated with the four main effects based on hierarchical partition modeling results

Indicator	Indicator code	Indicator class	Number of wetlands	Wetland type		Lake		Eco-province		HDI	
				I	Rank	*I*	Rank	*I*	Rank	*I*	Rank
Diatoms			65 (21 coastal, 20 protected, 24 riverine)								
Shannon-Wiener diversity (ln)	Shanwien	Compositional		0.02	2	0.16[a]	1	0.01	3	0.02	2
% Motile	Motile	Functional guild		0.00	4	0.11	1	0.02	3	0.06[a]	2
% Planktonic	Plankton	Functional guild		0.02	3	0.16[a]	1	0.04	2	0.01	4
Lange-Bertalot index	Lanberti	Functional guild		0.03	3	0.16[a]	1	0.01	4	0.08[a]	2
Trophic diatom index	Trophdi	Functional guild		0.12[a]	2	0.29[a]	1	0.05	4	0.10[a]	3
% Stephanodiscoids	Stephano	Species		0.02	4	0.22[a]	2	0.11[a]	3	**0.26**[a]	1
% *Achnanthidium minutissimum* complex	Achnanth	Species		0.01	4	0.12	2	0.05[a]	3	**0.15**[a]	1
% *Staurosira/ Staurosirella/ Pseudostaurosira*	Ssp	Species		0.03	3	0.29[a]	1	0.06[a]	2	0.03	4
% *Cocconeis*	Coccneis	Species		0.03	2	0.24[a]	1	0.00	4	0.01	3
% *Planothidium*	Planothi	Species		0.08	1	0.07	2	0.01	4	0.04[a]	3
Wetland vegetation			90 (26 coastal, 29 protected, 35 riverine)								
Species richness (number of taxa)	Sprichn	Compositional		0.06	3	0.10[a]	1	0.07[a]	2	0.04	4
% Native taxa	Propnati	Functional guild		0.04	4	0.17[a]	1	0.08[a]	3	**0.16**[a]	2
% Invasive taxa	Propinv	Functional guild		0.02	4	0.26[a]	1	0.11[a]	3	**0.22**[a]	2
% Wetland obligate taxa	Propobli	Functional guild		0.07[a]	2	0.27[a]	1	0.01	4	0.03	3
% cover *Carex stricta*	Carestri	Species		0.02	4	0.10[a]	2	0.12[a]	1	0.10[a]	3
% cover *Carex lasiocarpa*	Carevaam	Species		0.01	4	0.11[a]	2	0.10[a]	3	**0.31**[a]	1
% cover *Sparganium eurycarpum*	Spareury	Species		0.10[a]	2	0.20[a]	1	0.01	3	0.01	4
% cover *Phragmites australis*	Phraaust	Species		0.05	3	0.18[a]	1	0.03	4	0.09[a]	2
% cover *Typha angustifolia* and *Typha* × *glauca*	Typhinv	Species		0.03	4	0.14[a]	2	0.04[a]	3	**0.15**[a]	1
Macroinvertebrates			75 (24 coastal, 20 protected, 31 riverine)								
Lowest taxonomic unit richness	Lturich	Compositional		0.20[a]	2	0.21[a]	1	0.01	3	0.00	4
% Burrowers	Burrow	Functional guild		0.08[a]	2	0.11[a]	1	0.02	4	0.02	3
% Clingers	Clinger	Functional guild		0.03	2	0.19[a]	1	0.01	4	0.01	3

% Predators	Predator	Functional guild		0.04	2	0.06	1	0.01	3	0.00	4
% Insect filter-gatherers	Filt_gath	Functional guild		0.04	2	0.06	1	0.01	4	0.03	3
% *Caenis* spp.	Caenis	Species		0.12[a]	1	0.08	2	0.02	4	0.04[a]	3
% *Coenagrion*/*Enallagma* spp.	Coenenal	Species		0.09[a]	2	0.17[a]	1	0.01	3	0.00	4
% *Oecetis* spp.	Oecetis	Species		0.10[a]	1	0.04	2	0.01	3	0.01	4
% *Aeshna* spp.	Aeshna	Species		0.10[a]	1	0.04	2	0.02	3	0.02	4
% *Procloeon*/*Callibaetis* spp.	Proccall	Species		0.00	4	0.03	3	0.05[a]	1	0.04	2
Amphibians			211 (62 coastal, 78 protected, 71 riverine)								
Species richness	Sprich	Compositional		0.02	3	0.16[a]	1	0.01	4	0.02[a]	2
Species richness of tree frogs	TrFrogSp	Compositional		0.01	4	0.19[a]	1	0.13[a]	3	0.14[a]	2
Species richness of Ranids	RanidSp	Compositional		0.01	4	0.22[a]	1	0.02	2	0.01	3
Species richness of early spring breeders	SpfrogSp	Compositional		0.03[a]	2	0.05[a]	1	0.01	3	0.01	4
Presence–absence of *Bufo americanus*	Amto	Species		3.68[a]	2	14.32[a]	1	0.57	4	2.11[a]	3
Presence–absence of *Rana clamitans*	Grfr	Species		0.31	4	12.55[a]	1	0.32	3	1.71	2
Presence–absence of *Hyla versicolor*	Grtf	Species		3.54[a]		21.84[a]	1	7.70[a]	3	7.83[a]	2
Presence–absence of *Pseudacris crucifer*	Sppe	Species		1.73	44	13.01[a]	2	10.15[a]	3	**18.00**[a]	1
Fish—electrofishing			57 (28 protected, 29 riverine)								
Native species richness	Natnmsp	Compositional		0.09[a]	1	0.08	2	0.00	4	0.01	3
% Large fish (>200 mm average adult size)	Large	Functional guild		0.04	4	0.37[a]	1	0.05	3	0.07[a]	2
% Nest-guarding spawners	Nestguar	Functional guild		0.06	4	0.30[a]	1	0.07[a]	3	**0.19**[a]	2
% Intolerant of turbidity	Intolera	Functional guild		0.01	4	0.10	2	0.05	3	**0.17**[a]	1
% Top carnivores as adults	Topcarn	Functional guild		0.03	2	0.37[a]	1	0.00	4	0.01	3
% *Lepomis macrochirus*	Bluegill	Species		0.00	4	0.22[a]	1	0.18[a]	2	0.08[a]	3
% *Ameiurus nebulosus*	Brwnbull	Species		0.03	2	0.24[a]	1	0.03	3	0.03	4
% *Cyprinus carpio* and *Carassius auratus*	Carpgold	Species		0.05	4	0.30[a]	1	0.06	3	**0.20**[a]	2
% *Notemigonus chrysoleucus*	Goldshin	Species		0.00	4	0.50[a]	1	0.03	3	0.06	2
% *Ambloplites rupestris*	Rockbass	Species		0.01	4	0.12[a]	2	0.10[a]	3	**0.33**[a]	1

Table 1 (*Continued*)

Indicator	Indicator code	Indicator class	Number of wetlands	Wetland type		Lake		Eco-province		HDI	
				I	Rank	*I*	Rank	*I*	Rank	*I*	Rank
Fish—fyke-netting			80 (27 coastal, 23 protected, 30 riverine)								
Native species richness	Natnmsp	Compositional		0.04	1	0.02	2	0.01	3	0.01	3
% Large fish (>200 mm average adult size)	Large	Functional guild		0.00	4	0.08	1	0.00	3	0.01	2
% Nest-guarding spawners	Nestguar	Functional guild		0.05	2	0.08	1	0.00	3	0.00	3
% Intolerant of turbidity	Intolera	Functional guild		0.01	4	0.04	1	0.02	3	0.02	2
% Top carnivores as adults	Topcarn	Functional guild		0.02	2	0.07	1	0.01	3	0.00	4
% *Lepomis macrochirus*	Bluegill	Species		0.04	4	0.12[a]	2	0.10[a]	3	**0.21**[a]	1
% *Ameiurus nebulosus*	Brwnbull	Species		0.02	4	0.07	1	0.06[a]	2	0.04	3
% *Cyprinus carpio* and *Carassius auratus*	Carpgold	Species		0.07[a]	3	0.17[a]	1	0.04[a]	4	**0.16**[a]	2
% *Notemigonus chrysoleucus*	Goldshin	Species		0.18[a]	1	0.14[a]	2	0.02	4	0.03	3
% *Ambloplites rupestris*	Rockbass	Species		0.08[a]	4	0.10[a]	2	0.08[a]	3	0.13[a]	1
Birds			223 (66 coastal, 84 protected, 73 riverine)								
No. of Individuals	Tot_individs	Compositional		0.01	4	0.06[a]	2	0.04[a]	3	**0.21**[a]	1
No. of Short-distance migrants	Sdm	Functional guild		0.01	4	0.04[a]	3	0.04[a]	2	**0.17**[a]	1
No. of Long-distance migrants	Ldm	Functional guild		0.02	2	0.10[a]	1	0.01	4	0.02[a]	3
No. of Wetland obligates	Wo	Functional guild		0.01	2	0.03	1	0.00	4	0.01	3
No. of Aerial foragers	Af	Functional guild		0.02	3	0.06[a]	1	0.01	4	0.06[a]	2
No. of Insectivores	Insectivore	Functional guild		0.01	4	0.05[a]	2	0.03[a]	3	**0.20**[a]	1
No. of *Geothlypis trichas*	COYE	Species		0.00	4	0.08[a]	1	0.04[a]	2	0.01	3
No. of *Dendroica petechia*	YWAR	Species		0.00	4	0.03	2	0.01	3	0.03[a]	1
No. of *Cistothorus platensis*	SEWR	Species		0.00	4	0.04	1	0.03[a]	2	0.02[a]	3

[a] Significant *Z*-scores, $p \leq 0.05$ from Monte Carlo simulations; because of the presence–absence form of amphibian species data, log-likelihoods are presented rather than r^2-values; indicators with ≥15% variance explained by the HDI highlighted in bold.

Sites were selected using a stratified random design to span multiple human disturbance gradients (Danz et al., 2005) and we used an integrated measure of anthropogenic stress to characterize human disturbance (Danz et al., in press) that was based on a variety of publicly available geographic information system (GIS) data sources related to agriculture, atmospheric deposition, land cover, human population, and point source pollution in the Great Lakes Basin. A total of 149 disturbance-related variables were quantified with ArcGIS and ArcView software and analyzed in a principal components analysis to quantify the generalized human disturbance index (HDI) we used for this study (Danz et al., 2005; Danz et al., in press; Johnston et al., in press).

2.1.2. Diatoms

Diatoms have good potential as indicators because they are ubiquitous and diverse, yet individual taxa tend to have narrow environmental tolerances and respond rapidly to stressors such as nutrient and salinity inputs, siltation, and invasive species (Stoermer and Smol, 1999; Stevenson, 2001; Wehr and Sheath, 2003). We examined one compositional and four functional diatom indicators based on data collected at 65 wetlands (Fig. 1): Shannon-Wiener species diversity, proportion of motile diatoms (e.g. *Navicula*, *Nitzschia*), proportion of planktonic diatoms, the Lange-Bertalot Index (LBI, an indicator of saprobity, Lange-Bertalot, 1979) and the trophic diatom index (TDI, a measure of eutrophication in rivers, Kelly and Whitton, 1995). We also examined five taxonomic indicators measured as proportional abundances: stephanodiscoid taxa (species in the current or former *Stephanodiscus* genus, generally considered indicators of eutrophication), the *Achnanthidium minutissimum* complex (among the most common taxa in the Great Lakes), total *Staurosira*, *Staurosirella*, and *Pseudostaurosira* (a group of small, araphid benthic taxa, formerly in the genus *Fragilaria*, found throughout the Great Lakes), *Cocconeis* (an epiphytic genus) and *Planothidium* (a common periphytic genus) (Table 1). Both benthic and sedimented diatoms were sampled and processed as described by Reavie et al. (2006).

2.1.3. Wetland vegetation

Vegetation is often an excellent indicator of the physical and chemical condition of wetlands (Adamus and Brandt, 1990; Galatowitsch et al., 1999b; Lopez and Fennessy, 2002; Mensing et al., 1998; Stein and Ambrose, 1998), and is beginning to be used as such in studies of Great Lakes wetlands (Wilcox et al., 2002; Timmermans and Craigie, 2003; Albert and Minc, 2004). The fixed position of individual plants simplifies sampling and increases the likelihood that indicators based on vegetation are spatially coincident with *in situ* stressors. Emergent vegetation is also visible above water, making it easier to observe gradients and monitor by remote sensing (Lopez et al., 2004). We examined one compositional and three functional indicators that have been proposed in the literature (Bertram and Stadler-Salt, 1998; Galatowitsch et al., 1999a; Simon et al., 2001; Wilcox et al., 2002) based on data collected at 90 wetlands (Fig. 1): species richness, proportion of native taxa, proportion of invasive taxa, and proportion of obligate wetland taxa. We examined five taxonomic indicators, expressed as average percent cover per wetland: three native species, *Carex lasiocarpa*, *Carex stricta*, and *Sparganium eurycarpum*, and two invasive taxa, *Phragmites australis*, and "invasive *Typha*" (*Typha angustifolia* + *Typha* × *glauca*). The selected taxa each occurred in at least 45% of the wetlands sampled and represent a range of habitat preferences and sensitivities to disturbance.

Vegetation was sampled in 1 m^2 quadrats distributed along randomly placed transects within emergent and wet meadow areas (Bourdaghs et al., in press). Transect length and target number of sample plots were determined in proportion to the size of the wetland to be sampled (20 plots/60 ha, minimum transect length = 40 m, minimum plots/site = 8, average plots/site = 21). Plot locations were established in the field by dividing each transect into 20 m segments and randomly locating a plot in each segment using a random number table. Within each quadrat all vascular plants were identified to the lowest taxonomic division possible, using the Integrated Taxonomic Information System (ITIS, http://www.itis.usda.gov) as the taxonomic authority. Cover was estimated visually for each taxon using modified Braun-Blanquet cover classes (ASTM, 1997). Ten plant species were considered invasive: *Butomus umbellatus*, *Frangula alnus*, *Hydrocharis morsus-ranae*, *Lythrum salicaria*, *Myriophyllum spicatum*, *Phalaris arundinacea*, *P. australis*, *Potamogeton* *crispus*, *T. angustifolia* and *Typha* × *glauca*. Wetland indicator status (obligate, facultative) was determined for each species using federal lists for U.S. Fish and Wildlife Service Regions 1 and 3 (Reed, 1988).

2.1.4. Macroinvertebrates

Aquatic macroinvertebrates have long been used as indicators of environmental conditions (e.g. Hilsenhoff, 1987; Rosenberg and Resh, 1993). They are species-rich, respond to a broad range of environmental conditions, and are relatively immobile and live in close contact with both bottom sediments and the water column, thereby having the potential for exposure to stresses via both sediment and aqueous pathways. We examined taxonomic richness, and four function- and five taxon-based indicators, all quantified as proportional abundances based on data from 75 wetlands (Fig. 1). The four function-based indicators were burrowers, clingers, predators, and insect filter-gatherers (Merritt and Cummins, 1996; Thorp and Covich, 2001), all of which have been used as indicators of condition in streams and inland wetlands, and have been proposed as index of biotic integrity metrics in the Great Lakes (Uzarski et al., 2004). The five taxon-based indicators were *Caenis* spp. (soft-sediment inhabitants), *Coenagrion*/*Enallagma* spp. (restricted to vegetation), *Oecetis* spp. (hard-substrate inhabitants), *Aeshna* spp. (long-lived predator species), and *Procloeon* + *Callibaetis* spp. (short-lived genera, one or the other of which would be expected in most coastal wetlands).

Macroinvertebrates were sampled from the three dominant habitats in each wetland as determined from shoreline and nearshore substrate type, extent and composition of riparian and aquatic vegetation, and anthropogenic impacts. Samples were collected along two to six transects set perpendicular to depth contours, depending on the size of the wetland. D-framed nets (250 μm mesh) were swept through aquatic vegetation for 30 s. Samples were collected in duplicate at the midpoint of two depth zones along each transect, the emergent zone (defined as depths less than 50 cm) and the submergent zone (depths 50–100 cm). Samples were rinsed over 250 μm mesh sieves and preserved in Kahle's preservative, then size-fractioned using a standard sieve series (4 mm, 1 mm, 500 and 250 μm). Each size-fraction was completely examined under 6× magnification (size-fractioning increased sample processing efficiency by reducing the variability of particle sizes being examined). Macroinvertebrates from each size-fraction were identified to lowest practical taxonomic unit (typically to genus for non-dipteran insects, family for Diptera, and order or family for other invertebrates). Abundances were summed across sieve size fractions to get the number of each taxon per sample.

2.1.5. Amphibians

Amphibians have only recently received attention as indicators of ecological condition worldwide (Houlahan et al., 2000) and in Great Lakes coastal wetlands (Weeber and Vallianatos, 2000; Timmermans and Craigie, 2003; Grabas et al., 2004). However, their sensitivity to habitat loss and pollution and concerns over declines in their populations (Hecnar, 2004; Alford and Richards, 1999) suggests they are good candidates for condition indicators. The four amphibian compositional indicators we examined were overall species richness, richness of tree frogs (gray tree frogs, *Hyla versicolor* and *H. chrysoscelis*, and spring peepers, *Pseudacris crucifer*), richness of Ranids (bull frog, *Rana catesbeiana*, green frog, *R. clamitans*, mink frog, *R. septentrionalis*, leopard frog, *R. pipiens*, pickerel frog, *R. palustris*, wood frog, *R. sylvatica*), and richness of early spring breeders (Western chorus frog, *Pseudacris triseriata*, Boreal chorus frog, *P. maculata*, leopard frog, spring peeper, and wood frog). The four species indicators we examined were based on presence–absence across all site visits and included American toad (*Bufo americanus*), green frog, gray tree frog, and spring peeper. We conducted amphibian calling surveys at most of the same points ($n = 211$) sampled for birds following guidelines outlined by the Marsh Monitoring Program (Weeber and Vallianatos, 2000, and see http://www.bsc-eoc.org/mmpmain.html).

2.1.6. Fish

Fish have long been included as key indicators in assessment of biotic integrity in streams (e.g. Karr et al., 1986; Lyons and Wang, 1996) and to a lesser degree in lakes (Fabrizio et al., 1995; Whittier, 1999; Schulz et al., 1999) and estuaries (Jordan et al., 1991; Deegan et al., 1997). Fish have received little attention as wetland indicators, but their ecological significance in Great Lakes coastal wetlands (Jude and Pappas,

1992) has recently generated interest (Wilcox et al., 2002; Timmermans and Craigie, 2003; Grabas et al., 2004; Uzarski et al., 2005). The five species indicators we examined were bluegills (*Lepomis macrochirus*), brown bullheads (*Ameiurus nebulosus*), carp (*Cyprinus carpio*) + goldfish (*Carassius auratus*), golden shiner (*Notemigonus chrysoleucus*), and rock bass (*Ambloplites rupestris*). We also examined native species richness and four functional indicators based on proportional abundances: large fish (>200 mm median adult size, as per Becker, 1983—a surrogate for longevity and mobility), nest-guarding spawners (a high-investment reproductive strategy, Balon, 1975), turbidity-intolerant fish and fish that are top carnivores as adults (consume primarily fish, crayfish, frogs, and large insects; Becker, 1983).

Fish were sampled with both boat-mounted electro fishing gear (electro-fish) and fyke-nets (fyke-fish). The two methods were used by separate field crews that overlapped at 35 sites. We analyzed these data sets separately, but the same indicators were computed for each. Fyke-nets were fished at the same wetlands where macroinvertebrates were sampled and a few additional sites ($n = 80$), while electrofishing was completed at 58 sites. Fish were identified primarily using taxonomic descriptions in Becker (1983), counted and released. All data were standardized for effort as catch per net-night (fyke-nets) or catch per minute fished (electrofishing).

2.1.7. Birds

Birds have been used as indicators of ecological condition because they are sensitive to changes in land-use (Forman et al., 1976; Brooks et al., 1991; Niemi et al., 2004), habitat conditions (Wilcove and Terborgh, 1984; Riffel et al., 2003), and chemical contaminants (Frederick et al., 2004). They have been used in the development of forest (O'Connell et al., 1998), riparian (Bryce et al., 2002), grassland (Browder et al., 2002), rangeland (Bradford et al., 1998) and stream (Bryce et al., 2002) condition indices and are beginning to receive attention in Great Lakes wetland assessments (Weeber and Vallianatos, 2000; Timmermans and Craigie, 2003; Grabas et al., 2004). We examined total number of individuals and numbers of individuals comprising five functional guilds: short-distance migrants (wintering in southern or coastal U.S.; Keast, 1980), long-distance migrants (wintering in the West Indies, southern Mexico, or Central and South America), wetland obligate species (Riffel et al., 2003), aerial foragers (Ehrlich et al., 1988), and insectivores (Ehrlich et al., 1988). We also examined three species indicators (number per species): common yellowthroats (*Geothlypis trichas*), yellow warblers (*Dendroica petechia*), and sedge wrens (*Cistothorus platensis*). Surveys were conducted by trained observers (Hanowski and Niemi, 1995) at 223 wetlands during June and early July in 2000, 2001 and 2002 using the Marsh Monitoring Workshop wetland breeding bird survey protocol (Ribic et al., 1999). Additional details are in Hanowski et al. (in press) and see http://www.bsc-eoc.org/mmpmain.html.

2.2. Data analysis

2.2.1. Hierarchical variance partitioning

We used hierarchical partitioning (HP) (Chevan and Sutherland, 1991; Christensen, 1992) to evaluate the independent influence of geomorphic, geographic and human disturbance effects on the 66 response variables. In HP the goal is to compare the influence of each predictor variable on a response over a hierarchy of all possible 2^N models for N predictors instead of identifying a single best model (MacNally, 2000, 2002). The importance of each predictor is estimated by averaging the increase in model fit over all models in which a predictor occurs. Conceptually, HP can be used in a variety of multiple regression settings (e.g. normal linear regression, logistic, Poisson) with any goodness of fit measure (e.g. R^2, log-likelihood).

We used the hier.part package (Walsh and MacNally, 2004) in the statistical software R version 2.0.1 (R Development Core Team, 2004) to carry out HP for each response using four main effects: (1) wetland geomorphic type (three levels), (2) Great Lake (five levels), (3) ecoprovince (two levels) and (4) the HDI from Danz et al. (in press). This index combines information about agriculture, atmospheric deposition, human population, land use and point sources to broadly reflect the intensity of disturbance for coastal watersheds in the U.S. Great Lakes basin. Because we used four main effects, the HP utilized 2^4 or 16 models.

For the four responses representing presence–absence of amphibian species, we specified logistic regression models and used log-likelihood to measure goodness of fit. For the remaining 62 continuous response variables, we added the minimum non-zero value to all observations for variables with a minimum of zero and then found the Box-Cox power transformation with power parameter lambda between −3 and +3 that maximized the log-likelihood in the four-effects models (SAS Institute Inc., 2004). The transformed values were then used as responses in HP specifying a general linear model and R^2 as the measure of fit. Significance of the independent contribution to variance (I) for the four predictors was assessed using Z-scores from a comparison of the observed I's to I's resulting from 200 permutations on randomized data (MacNally, 2002). Because we were interested in the potential importance of interactions, we wrote code in SAS (hier.part accomodates only a limited number of effects) to assess the strength of all two-way interactions ($n = 6$ per indicator, $66 \times 6 = 396$ interactions overall) based only on the proportional contribution to variance explained over and above the contributions of the main effects that comprised them. All two-way interactions with significant variance contributions were tallied by assemblage and examined for ecological relevance by comparing means and slopes from appropriate plots.

2.2.2. Evaluating geographic, geomorphic and human influences

The HP results were evaluated using one-way analysis of variance (ANOVA) to determine if there were statistically significant differences in the mean proportion of variance explained (raw I's) or proportion of explained variance (relative I's) associated with the four main variance components (lake, ecoprovince, wetland type and HDI) across all indicators, by biotic assemblage and by indicator type. Differences between species and functional indicator average raw and relative I values were evaluated by assemblage and across all assemblages.

2.2.3. Examination of concordance patterns

Concordance in the response among indicators from the different assemblages was evaluated three ways: (1) by examining plots of ANOVA results; (2) by calculating Pearson correlation coefficients between assemblages for averages of the raw I and relative I values associated with each main effect in the variance partitioning for each variable; and (3) by ordinating the matrix (raw I averages only) used to estimate correlations with non-metric multidimensional scaling to provide a two-dimensional representation of similarities in response among assemblages (McCune and Mefford, 1997). For the correlations, I values were averaged across all indicators from a particular assemblage and Pearson correlations were calculated in a pair-wise fashion for each two-way combination of assemblage-types.

3. Results

3.1. Evaluation of geographic, geomorphic and human influences—main effects

Hierarchical partition models revealed that lake had the strongest influence among the four main effects across all indicators (Table 1 and Fig. 2) and by

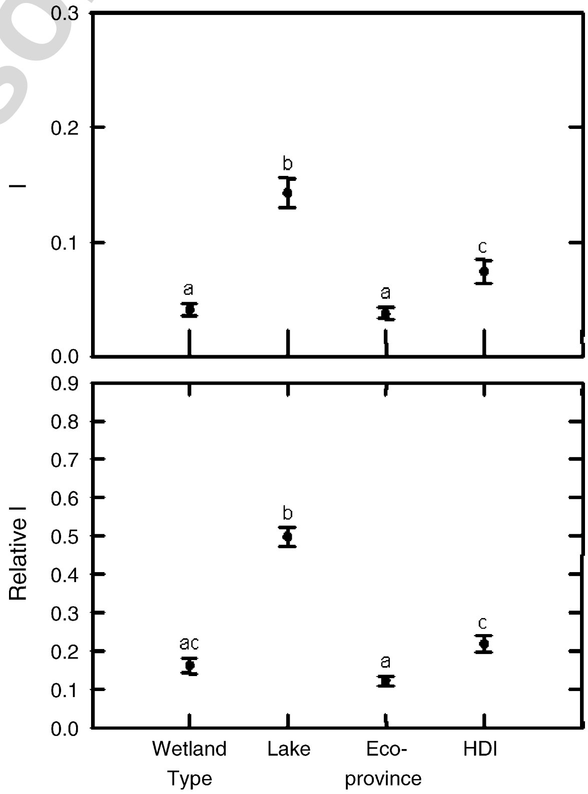

Fig. 2. Mean (±1 S.E.) proportion of variance explained (raw I's) and explained variance (relative I's) associated with the four main variance components (lake, ecoprovince, wetland type and HDI) across all indicators. Significance of differences in means based on ANOVA of hierarchical variance partition modeling results (means with no letters in common were significantly different, $p \leq 0.05$).

assemblage (Table 1 and Fig. 3). Both the raw and relative *I*'s were highest for lake and lowest for ecoprovince across all indicators ($p < 0.001$). Responsiveness to the HDI accounted for the second highest contribution to variance explained, but this contribution was significantly less than the variation accounted for by lake ($p < 0.001$). Ranking the variation explained by the four main effects revealed a similar pattern with 44 of the indicators most influenced by lake, 13 by HDI, 7 by wetland type and only 2 by ecoprovince (Table 2).

Although lake was clearly the most influential factor overall (Fig. 2 and Table 2), responses varied considerably among the various biotic assemblages. Indicators derived from electro-fish, diatoms, wetland vegetation and amphibians had the most variance

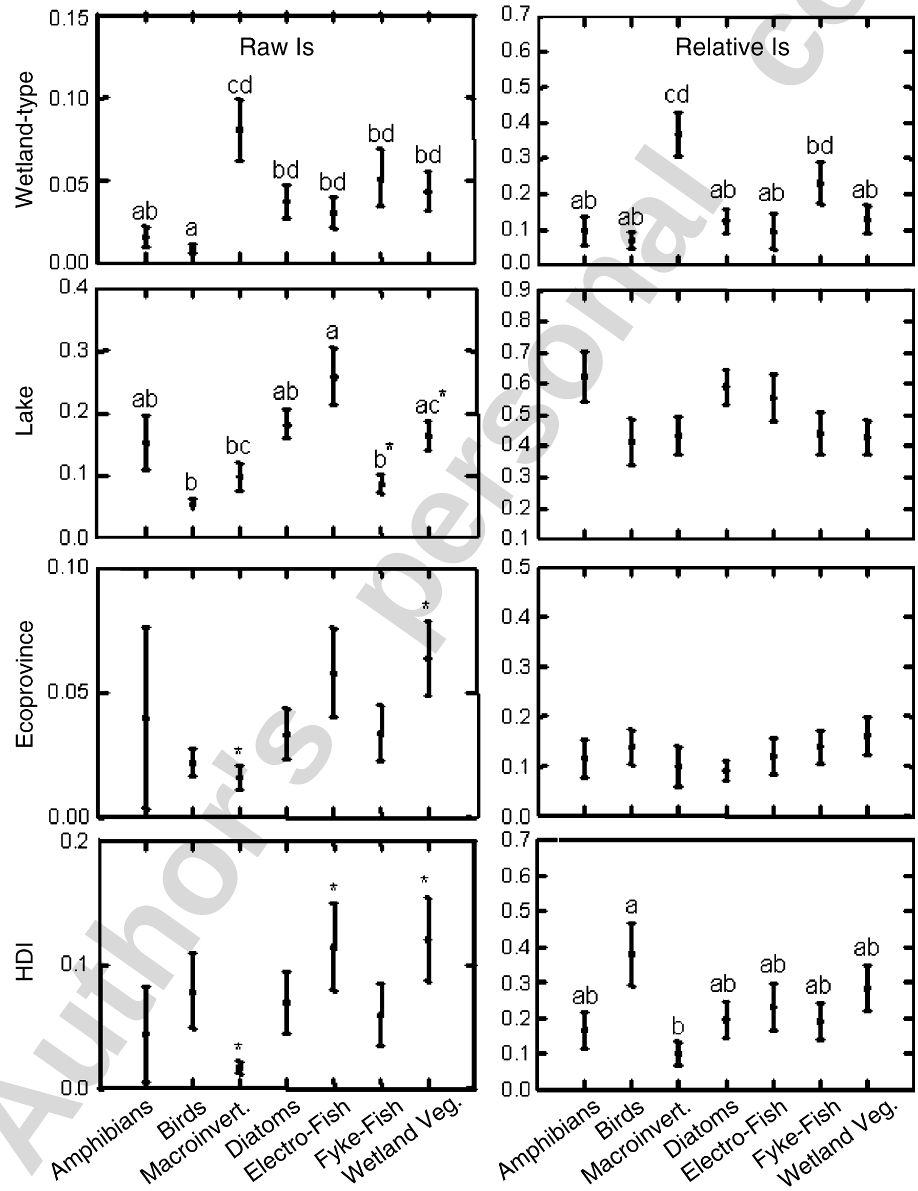

Fig. 3. Mean (±1 S.E.) proportion of variance explained (raw *I*'s) and explained variance (relative *I*'s) associated with the four main variance components (lake, ecoprovince, wetland type and HDI) by biotic assemblage. Significance of differences in means based on ANOVA of hierarchical variance partition modeling results (means with no letters in common were significantly different, $p < 0.05$; '*' indicates non-overlapping 95% confidence intervals).

Table 2
Number of indicators with highest ranked proportion of variance explained associated with the four main effects (lake, ecoprovince, wetland type and HDI) across all indicators, by assemblage, and by indicator type

Indicator category	Wetland type	Lake	Ecoprovince	HDI
All indicators	7	44	2	13
By assemblage				
Amphibians	0	7	0	1
Birds	0	5	0	4
Macroinvertebrates	3	6	1	0
Diatoms	1	7	0	2
Electro-fish	1	7	0	2
Fyke-fish	2	6	0	2
Wetland vegetation	0	6	1	2
By indicator-type				
Compositional	2	7	0	1
Functional guild	0	21	0	3
Species	5	16	2	9

explained by lake, macroinvertebrates the most by wetland type, and electro-fish, wetland vegetation and birds the most related to the HDI (ANOVA, $p < 0.05$, Figs. 3 and 4). Ecoprovince explained relatively little variance for any of the assemblages (Table 2), and was particularly insignificant with respect to the relative I's ($p > 0.7$, Figs. 3 and 4).

Monte Carlo p-values for each indicator and the number of indicators that had the highest ranked proportion of variance explained by wetland type revealed that macroinvertebrates were the only assemblage that varied greatly by wetland type (Tables 1 and 2). Six of the 10 macroinvertebrate indicators had significantly different levels of variance explained by wetland type, while only one responded significantly to the HDI. In contrast, all of the amphibian and wetland vegetation indicators and most of the diatom, bird and electro-fish indicators had significant levels of variance explained by lake and also had a majority of indicators responding significantly to the HDI ($p < 0.05$, Table 1). Over half of the wetland vegetation and bird indicators had significant differences by ecoprovince, while fyke-fish were the only group of indicators about equally responsive to the different main effects. However, fyke-fish had among the lowest total number of significant Z-scores (second only to macroinvertebrates) across all main effects (Table 1). Examination of patterns in the relative I's for each of the indicators (Fig. 4) yielded similar results.

Sixteen indicators had at least 15% of total variance explained by response to disturbance ($p \leq 0.05$, Table 1). The I values (maximum likelihood for amphibian species) for rock bass and carp-goldfish (electro-fish), *C. lasiocarpa* and invasive taxa (wetland vegetation), stephanodiscoids (diatoms), number of individual and insectivorous birds, bluegill (fyke-fish), and spring peepers (amphibians) were all 0.20 or higher (or 18.00 maximum likelihood) for the HDI. However, despite the significant relationship to the HDI, carp-goldfish had more variance explained by lake (Table 1).

3.2. *Evaluation of geographic, geomorphic and human influences—interactions*

Nearly 90% (352 of 396) of two-way interactions were not statistically significant and explained low amounts of variance above and beyond the main effect. Significant interactions tended to include the lake main effect; seven of the 62 indicators had significant ($p \leq 0.05$) and strong (accounted for >5% of variance explained) lake × wetland type and HDI × lake interactions (Table 3). There were also some significant and strong HDI × ecoprovince, HDI × wetland type, and ecoprovince × wetland type interactions (Table 3), but in terms of the amount of variance explained, interactions that included lake were clearly more prevalent. Nine of the 10 strongest interactions (based on I values) included a lake term and the six strongest were all lake × wetland type interactions (Table 4). The fact that four of the strongest lake by wetland type interactions were associated with fish indicators suggests this type of interaction maybe especially important when developing indicators based on fish data (Table 4).

We plotted examples of some of the typical significant interactions to highlight the complexities that should be considered in any final selection of indicators of ecological condition for Great Lakes coastal wetlands. Significant interactions with the HDI often resulted from very short disturbance gradients in opposite ends of the basin; Lake Superior wetlands are confined to the low end of the disturbance gradient, while wetlands in Lakes Erie and Ontario are on the

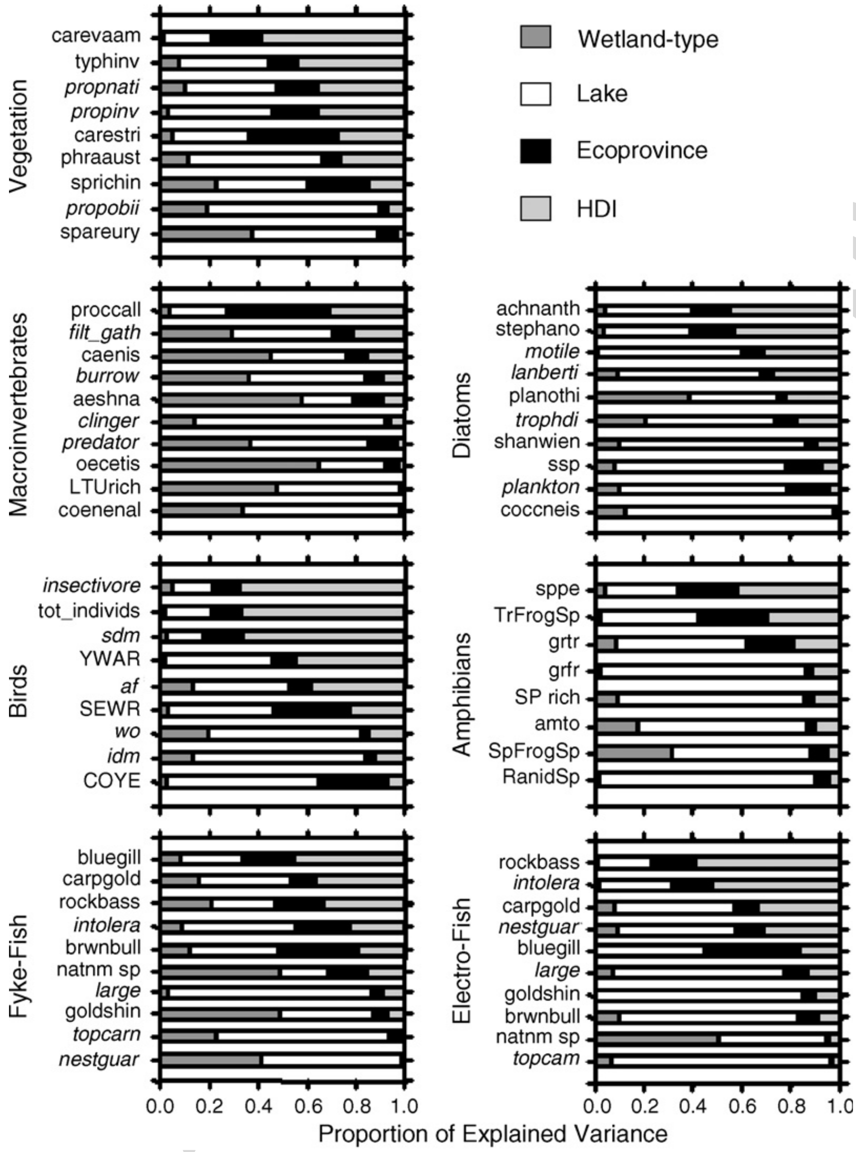

Fig. 4. Proportion of explained independent variance (relative I's) associated with the four main variance components (lake, ecoprovince, wetland type and HDI) for each indicator based on hierarchical variance partition modeling. Indicators organized by biotic assemblage and ordered by the amount of variance attributed to the HDI (functional indicators italicized; see Table 1 for explanation of indicator abbreviations).

high end of the disturbance gradient (Fig. 5). Wetland sites in Lakes Huron and Michigan spanned the disturbance gradient more fully. The significant province × disturbance interaction for short-distance migrant birds (Fig. 5a) illustrates a general increase in abundance with disturbance, with a flattening of the curve at the upper end of the disturbance gradient. It will be difficult to conclude whether the pattern is best explained by a separate slopes model (i.e. a significant interaction), by a single slope for both provinces combined (dotted line in Fig. 5a), or possibly by a non-linear response across the entire basin. Results for the trophic diatom index (Fig. 5b) illustrated different relationships to disturbance for individual lakes; especially for Lakes Erie, Ontario and Superior. Interactions that included wetland type were quite varied, but some were simply due to magnitude differences among ecoprovinces or lakes (e.g. Fig. 6a). Others resulted from abundance reversals among wetland types, making it more difficult to be confident

Table 3
Number of significant two-way interactions ($p \leq 0.05$; those that accounted for $\geq 5\%$ of variance explained in parentheses) based on hierarchical partition modeling for each biotic assemblage (species indicators excluded from amphibian totals because presence–absence data format was incompatible with the general linear models that were used to assess interactions)

Assemblage	Interaction					
	Lake by wetland type	Ecoprovince by wetland type	Ecoprovince by lake	HDI by wetland type	HDI by lake	HDI by ecoprovince
Amphibians	0	0	0	0	2 (1)	2 (1)
Birds	2 (1)	1 (0)	1 (0)	1 (0)	2 (0)	4 (2)
Macroinvertebrates	1 (1)	1 (1)	1 (0)	2 (2)	2 (2)	0
Diatoms	0	0	0	1 (1)	2 (2)	0
Electro-fish	2 (1)	2 (0)	1 (1)	1 (0)	1 (1)	1 (0)
Fyke-fish	3 (3)	0	1 (0)	0	0	0
Wetland vegetation	1 (1)	3 (2)	0	0	2 (1)	1 (0)
Total	9 (7)	7 (3)	4 (1)	5 (3)	11 (7)	8 (3)

of ecological relevance. Sampling variability, random error or real ecological differences all offer plausible explanations for these sorts of patterns.

3.3. Evaluation of geographic, geomorphic and human influences—species versus functional indicators

In contrast to the variance partitioning differences observed among assemblages, there were no striking differences among the different indicator types (functional, compositional or species). There was a slightly higher mean proportion of explained variance associated with ecoprovince across all species indicators compared with indicators representing compositional or functional guilds (ANOVA, $p = 0.05$, Fig. 7). Functional and compositional indicators did account for 28 of 44 indicators with the highest ranked lake influences, suggesting functional indicators were more affected at this spatial scale. In contrast, species indicators frequently had the most variance explained by wetland type or the HDI (Table 2).

There were also few differences between functional and species indicators by assemblage. However, based on the proportion of variance explained, bird guilds were more affected by wetland type (ANOVA, $p = 0.04$) than bird species, and fyke-fish species indicators were more affected by lake, ecoprovince and HDI differences (ANOVA, $p \leq 0.02$) than fyke-fish functional indicators. No other function versus species comparisons were statistically significant by assemblage; however, with the exception of bird and wetland vegetation indicators, species indicators tended to have more variance explained by ecoprovince and the HDI than functional indicators (Table 1).

Table 4
Significant interactions ($p \leq 0.05$) that explained the 10 greatest proportions of variance (I) across all indicators

Indicator	Assemblage	Interaction	I
% Intolerant of turbidity	Fyke-fish	Lake × wetland type	0.26
% Nest-guarding spawners	Fyke-fish	Lake × wetland type	0.25
% Top carnivores	Fyke-fish	Lake × wetland type	0.21
% *Oecetis* spp.	Macroinvertebrates	Lake × wetland type	0.21
% Rock bass	Electro-fish	Lake × wetland type	0.14
% Cover *S. eurycarpum*	Wetland vegetation	Lake × wetland type	0.11
% Insect filter-gatherers	Macroinvertebrates	HDI × lake	0.11
% Intolerant of turbidity	Electro-fish	HDI × lake	0.1
Species richness	Amphibians	HDI × lake	0.08
Species richness of early spring breeders	Amphibians	HDI × ecoprovince	0.08

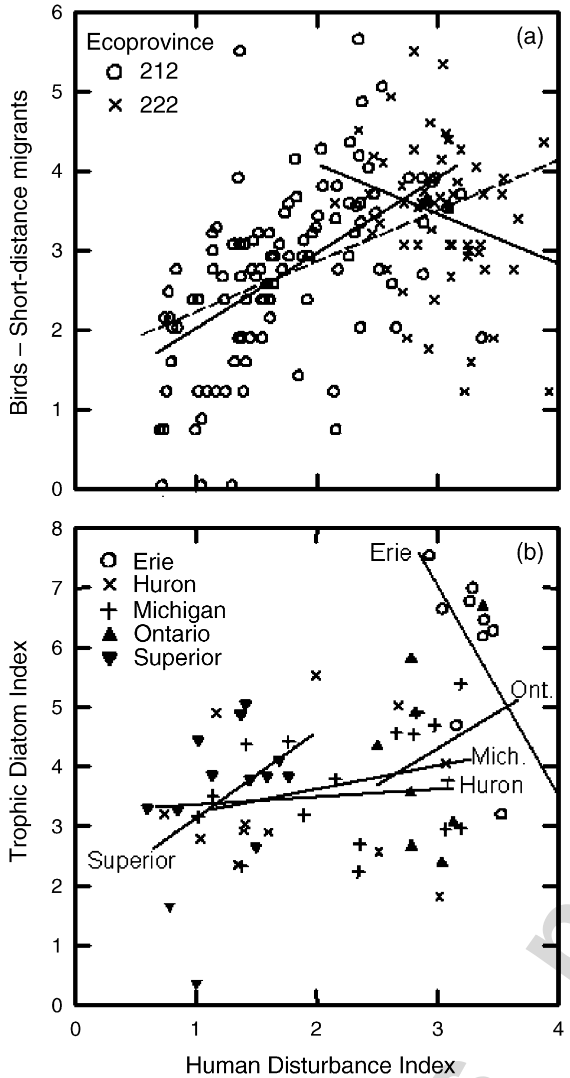

Fig. 5. Plots of Box-Cox transformed values for short distance migrant birds as an example of a typical significant HDI × ecoprovince interaction (a) and for the trophic diatom index as an example of a typical HDI × lake interaction (b) identified with hierarchical partition models. In panel (a) the dashed line represents a linear fit to all data and the solid lines represent the fit by ecoprovince. In panel (b) the lines represent a linear fit for each lake.

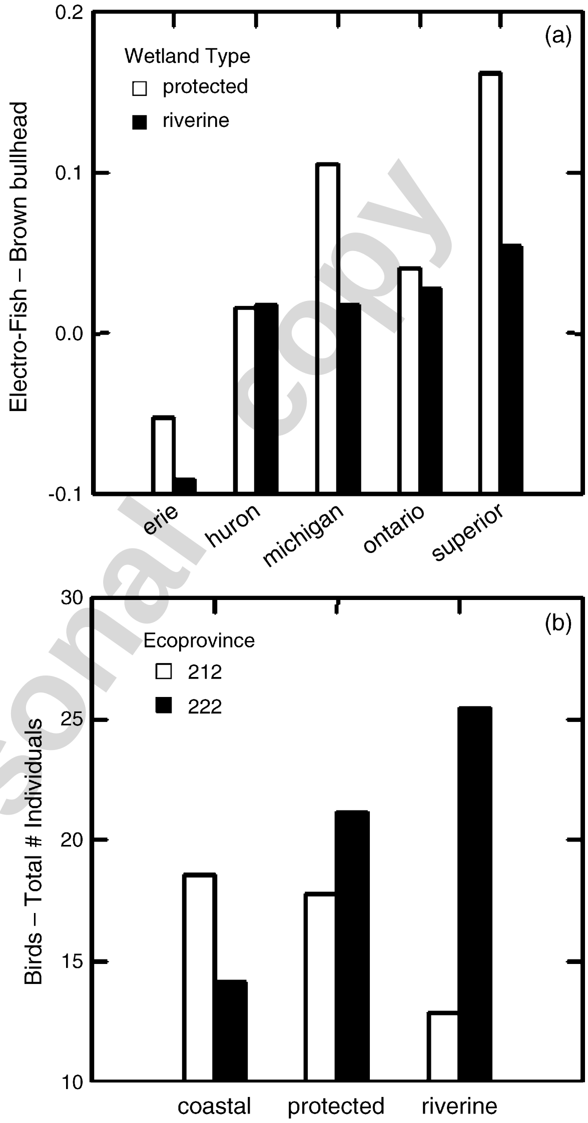

Fig. 6. Least-squares means for electro fished brown bullheads as an example of a typical significant lake × wetland type interaction (a) and for total number of birds as an example of a typical ecoprovince × wetland type interaction (b) identified with hierarchical partition models.

3.4. Examination of concordance patterns

Patterns in the ANOVA responses among assemblages revealed many similarities in the way variance was partitioned among indicators for different assemblages. For example, wetland vegetation and bird indicators varied markedly with respect to lake, ecoprovince and HDI, while electro-fish, diatom and amphibian indicators were most influenced by lake and HDI. Macroinvertebrate variation was greatest among wetland types and fyke-fish variation was relatively low across all of the main experimental design factors. Correlations among the average *I*'s associated with the main effects for each assemblage revealed additional patterns of concordance. Average diatom, electro-fish and amphibian variance partitions were similar for both raw and relative *I*'s ($r \geq 0.98$, $p < 0.05$), as they were for wetland vegetation and electro-fish ($r \geq 0.96$, $p < 0.05$, Table 5). Patterns in the raw and relative *I*'s were least correlated between

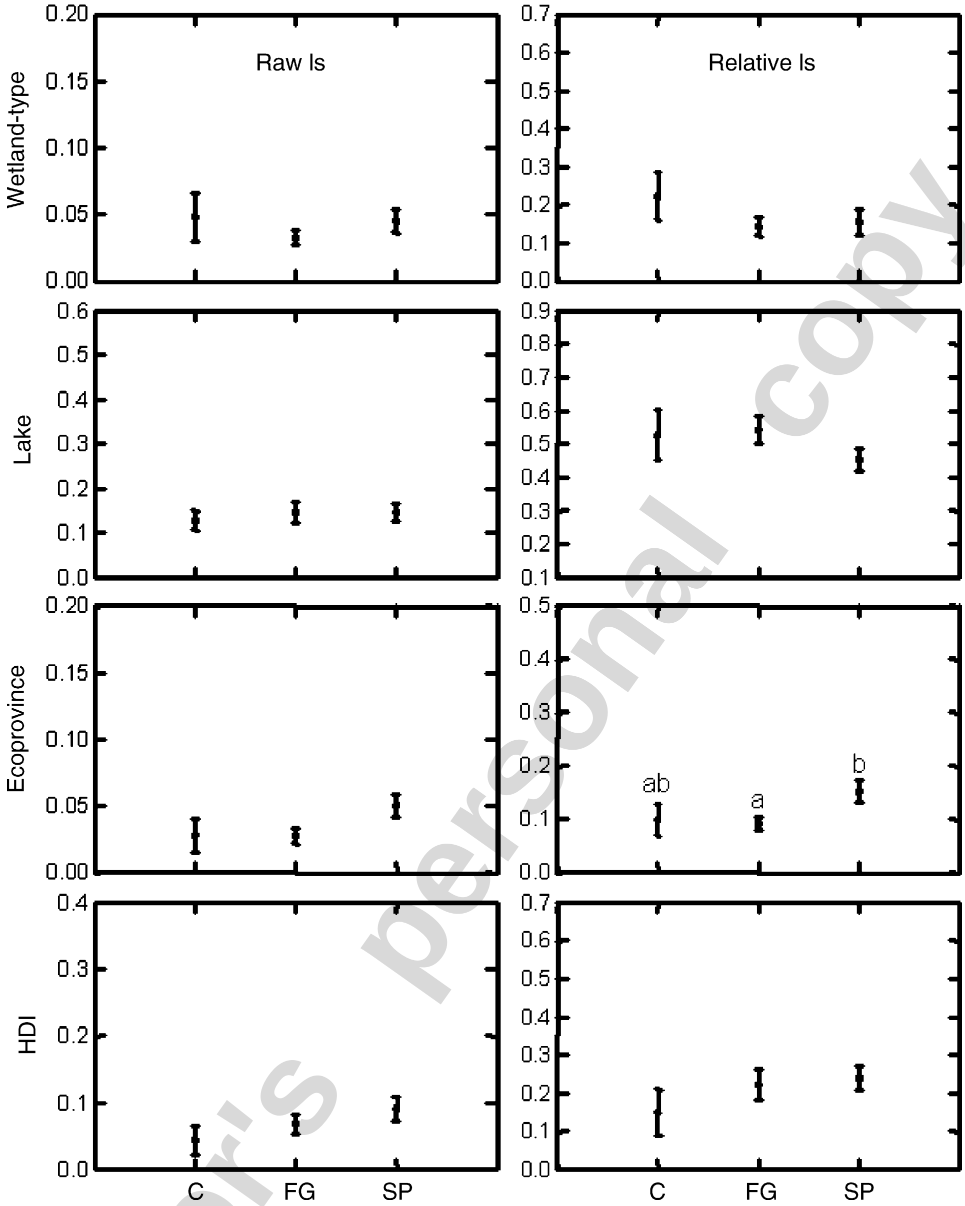

Fig. 7. Mean ($\pm$ 1 S.E.) proportion of variance explained (raw I's) and explained variance (relative I's) associated with the four main variance components (lake, ecoprovince, wetland type and HDI) by indicator type (compositional [C], functional guild [FG], and species [SP]). Significance of differences in means based on ANOVA of hierarchical variance partition modeling results (means with no letters in common were significantly different, $p < 0.05$).

birds and macroinvertebrates; the correlation between their raw I's was -0.24, the only negative correlation we observed (Table 5). The two assemblages least correlated with all other assemblages based on a mean correlation across all pair-wise comparisons were macroinvertebrates ($r = 0.39$, raw I's; $r = 0.52$, relative I's) and birds ($r = 0.43$, raw I's; $r = 0.64$, relative I's). Most of the concordance patterns apparent through examination of pair-wise correlations were also apparent in the visual representation of these relationships through ordination (Fig. 8). Macroinvertebrates and birds were least similar to other assemblages, and electro-fish, wetland vegetation, diatoms and amphibians were the most similar in ordination space. Ordination results also indicated that diatoms and amphibians, and electro-fish and wetland vegetation

Table 5
Pearson correlation matrices based on the proportion independent variance explained (raw I's) and the proportion of independent explained variance (relative I's) for the four main effects from hierarchical partition modeling averaged across all indicators for each assemblage

Raw I's	Relative I's						
	Amphibians	Birds	Macro-invertebrates	Diatoms	Electro-fish	Fyke-fish	Wetland vegetation
Amphibians	–	0.72	0.63	**0.99***	**0.99***	**0.95***	0.93
Birds	0.41	–	0.07	0.75	0.82	0.57	0.92
Macroinvertebrates	0.54	−0.24	–	0.65	0.54	0.84	0.39
Diatoms	**0.98***	0.48	0.61	–	**0.99***	**0.96***	0.94
Electro-fish	**0.98***	0.58	0.48	**0.99***	–	0.91	**0.98***
Fyke-fish	0.84	0.54	0.68	0.94	0.90	–	0.83
Wetland vegetation	0.88	0.79	0.29	0.92	**0.96***	0.83	–

Significant correlations for each matrix, $p \leq 0.05$, in bold type and denoted with '*'.

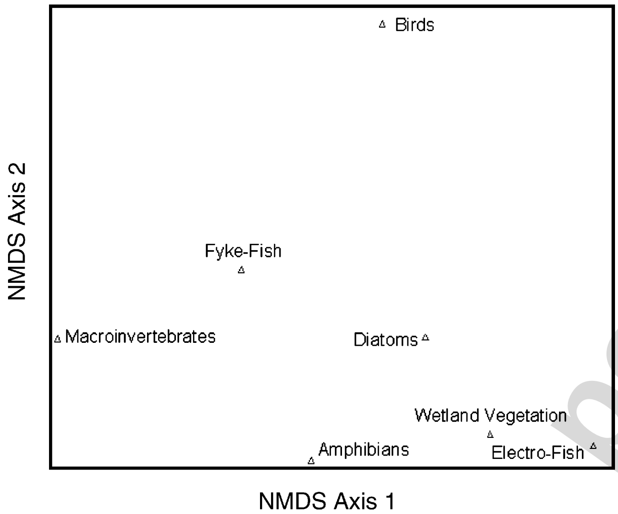

Fig. 8. Non-metric multidimensional scaling ordination based on the proportion independent variance explained (raw I's) for the four main effects from hierarchical partition modeling averaged across all indicators for each assemblage (average I's by assemblage were rows and main effects were columns in the ordination matrix).

were the two pairs of assemblages with the most similar response patterns.

4. Discussion

4.1. Evaluating geographic, geomorphic and human influences—overall patterns

Variance partitioning of geographic, geomorphic and human influences on ecological indicators of coastal wetland condition has important implications for indicator development in the Great Lakes. Foremost of these implications was the predominant influence of individual lakes. The largest portion of the variance in our data set was attributable to variation across lakes and the majority of important interactions were also driven by lake influences (lake × wetland type and HDI × lake interactions). These results strongly suggest it will be difficult to develop effective indicators of Great Lakes coastal wetland condition without considering differences among lakes and their important interactions. For some indicators, this may necessitate developing or calibrating indicators on a lake-by-lake basis. Other possibilities include accounting for the variance associated with lake and using the residual values or covariates to develop indicators (O'Connor et al., 2000; Fore, 2003; King et al., 2005), or stratifying data by covariates and developing indicators within strata (Uzarski et al., 2005). Accounting for lake × HDI interactions may be particularly important because levels and types of disturbance differ widely by lake (Danz et al., in press). Thus, lake-specific criteria maybe necessary for estimating the condition of each lake. These results are consistent with the differences in climate, geology, physical and chemical characteristics as well as productivity among lakes (e.g. Dobson et al., 1974; Government of Canada and U.S.EPA, 1995); however, previous indicator work in the Great Lakes has not sampled broadly or intensively enough to quantify the importance and magnitude of lake-specific indicators.

Although lake influences were the most important in our study, response to our integrated general human disturbance index was also important. The influence of human disturbance varied dramatically among indicators, but we identified a number of indicators that have good potential as indicators of environmental stress across a wide range of conditions in the Great Lakes. These include abundance of rock bass, *C. lasiocarpa*, stephanodiscoid diatoms, bluegills, and carp/goldfish; the prevalence of invasive wetland vegetation taxa; the abundance of insectivorous birds and total number of individual birds; and presence or absence of spring peepers. Some of these (or slight variants) have been identified previously as having good potential for indicating condition of Great Lakes coastal wetlands (Wilcox et al., 2002; Timmermans and Craigie, 2003; Albert and Minc, 2004; Grabas et al., 2004; Uzarski et al., 2005), but *C. lasiocarpa*, stephanodiscoid diatoms, and insectivorous birds have not. Although it was not the primary purpose of this analysis, identification of a suite of indicators that are effective across the Great Lakes Basin and applicable across wetland types would be desirable for large-scale monitoring programs and would facilitate tracking changes in ecological condition across the basin (Uzarski et al., 2005).

Understanding versatility, applicability and responsiveness is considered critical for effective indicator development (Jackson et al., 2000; Dale and Beyeler, 2001; Niemi et al., 2004). Perhaps not surprisingly, many of the taxa we found to have the broadest potential as indicators are from groups that have characteristically high mobility and/or broad geographic ranges. Many of the taxa that were least responsive to human disturbance were macroinvertebrates. Only one of the macroinvertebrate indicators (*Caenis* spp.) had a significant amount of variance explained by the HDI as a main effect and this accounted for only 4% of total variance. This was surprising given the sensitivity to various land-use disturbances observed for macroinvertebrates in other wetland studies (e.g. Mensing et al., 1998; Uzarski et al., 2004) and in streams (e.g. Fore, 2003). Based on the prevalence of strong influences associated with wetland type in the HP models, it may be that local factors play a key role for macroinvertebrates in Great Lakes wetlands. Local environmental variables are critical to the distribution of aquatic taxa (substrate type and water chemistry) (e.g. Jackson and Harvey, 1993; Bryce and Hughes, 2003; Johnson et al., 2004). These are important factors that vary by wetland-type (Keough et al., 1999; Albert and Minc, 2004; Trebitz et al., 2002, 2005) and lake (e.g. Dobson et al., 1974). Variance attributable to local variables can be accommodated by appropriately stratifying sampling efforts. For example, Uzarski et al. (2004) developed invertebrate indicators applicable across fringing wetlands in Lakes Michigan and Huron by restricting sampling to plant zones common to all wetlands.

Although physical, vegetation and other biotic characteristics have been shown to differ markedly among ecoprovinces in the Great Lakes (Keys et al., 1995), only about a third of the indicators we examined were significantly influenced by ecoprovince. The two ecoprovinces in the Great Lakes Basin essentially contrast Lake Superior, Lake Huron, and northern Lake Michigan, with southern Lake Michigan, Lake Erie and Lake Ontario (Fig. 1), and thus would be expected to capture many of the biogeographic factors that differ among the lakes (latitude, longitude, position in the watershed), albeit on a coarser scale. Accounting for this source of variation was important for many of the indicators associated with wetland vegetation, bird, and fish assemblages because more than half of wetland vegetation and bird indicators and four of the 10 fyke-fish indicators had a significant amount of variance explained by ecoprovince. Ecoprovince explained greater than 10% of total variance for some indicators (e.g. *C. stricta*, bluegills, stephanodiscoid diatoms) suggesting these could not be used effectively without accounting for this variation. Ecoprovincial influences on the response of biota to disturbance have not been well-studied in the Great Lakes, but indications are that they may still be important to consider (Brazner et al., 2005; Hanowski et al., in press; Price et al., 2005).

Interactions involving ecoprovince were relatively common. These interactions will need to be examined carefully in any final selection of indicators. In many cases, we found that the interactions may have been driven by experimental artifacts (e.g. relatively short disturbance gradients in some lakes), differences in magnitude of response rather than direction, or potentially random variation rather than real effects. The fact that the longest gradients such as those found in Lakes Huron and Michigan, which range widely in latitude tended to have similar slopes suggests that shorter gradients probably contributed to the detection of some interactions. Another explanation is that response patterns in Lakes Erie and Ontario tended to have shallower slopes because most of the coastal wetlands within these lakes are highly disturbed (Danz et al., in press), resulting in minimal variance within these lakes or threshold effects in the responses. Moreover, our stressor characterization is a generalized index of human disturbance. Since interactions are likely to be disturbance-dependent (Fore, 2003; Bryce and Hughes, 2003), future studies will need to focus on interactions associated with specific types of disturbance.

4.2. Evaluation of geographic, geomorphic and human influences—species versus functional indicators

While we thought that functional indicators might perform better than taxon-based indicators (Keddy, 1992; Austen et al., 1994), taxon-based indicators were slightly more responsive to the HDI and less influenced by lake than were function-based indicators. However, the differences were not pronounced. This result may have been influenced by our choice of indicators (e.g. many species selected had basin-wide distributions). Nevertheless, our results provide no compelling reason to expect that functional indicators will respond more clearly across a human disturbance gradient than taxon-based indicators. The lack of strong differences between taxon-based and functional indicators may have been related to different sizes and mobilities of the taxa considered. Combining organisms of different size or mobility into a common functional indicator integrates disturbance influences across different spatial scales for different organisms (Allen et al., 1999a) and may result in ambiguous responses for the entire guild if individual species responses offset one another (Holland et al., 2004).

4.3. Examination of concordance patterns

Our expectations that fish and diatom and bird and wetland vegetation indicator responses would be concordant were relatively well supported by the correlation and ordination results, although the level of concordance depended on the way variance was characterized (i.e. raw or relative *I*'s). The lack of concordance between macroinvertebrates and other groups was unexpected given their similarity in response in a number of other studies (Jackson and Harvey, 1993; Mensing et al., 1998; Allen et al., 1999a; Wang and Lyons, 2003). Reasons for this are unclear, but this result indicates that patterns in macroinvertebrate response to human disturbance in coastal wetlands maybe atypical of their responses in lakes, inland wetlands, and streams. The similarity in amphibian variance patterns to those of diatom, wetland vegetation and electro-fish variance patterns suggests that amphibians were affected by both aquatic and riparian influences since aquatic influences (e.g. dissolved nutrients, habitat structure) are likely to determine patterns in diatoms and fish, and riparian conditions that were likely to have influenced wetland vegetation (Saab, 1999; Johnston, 2003; Riffel et al., 2003). Concordance in wetland vegetation and fish indicators may have resulted from the important role wetland vegetation plays as a component of fish habitat (e.g. Brazner and Beals, 1997; Uzarski et al., 2005). Concordance among the responses of these assemblages to land-use disturbance in wetland drainages (Mensing et al., 1998) provides additional support for the idea that the responses of these two groups may be linked in wetland habitats. Differences in the patterns of variation between electro- and fyke-fish were also noteworthy in that the two capture methods provided a unique view of the response of fish assemblage indicators. This highlights the importance of understanding the bias associated with different sampling methods (e.g. Hayes, 1989; Reash, 1999) and indicates it may be important to calibrate indicator criteria and scores for particular methods (Deegan et al., 1997; Simon and Sanders, 1999).

There is considerable evidence that certain assemblages are more responsive to specific kinds of human disturbance (e.g. Mensing et al., 1998; O'Connor et al., 2000; Fore, 2003; Bryce and Hughes, 2003) or scales of disturbance characterization (O'Connor et al., 2000; Holland et al., 2004) resulting in patterns of concordance that are disturbance- (Mensing et al., 1998; Fore, 2003) or scale-specific (Mensing et al., 1998; Allen et al., 1999a). Although some of the results to date regarding the response patterns of particular assemblages have been contradictory (e.g. Jackson and Harvey, 1993; Mensing et al., 1998; Allen et al., 1999a; Paszkowski and Tonn, 2000; Fore, 2003), it is clear that future efforts need to be focused on identifying how to summarize and integrate differences in responsiveness of indicators when disturbance is characterized at different scales (e.g. local versus regional), or for specific (e.g. agriculture or urban land use) rather than general disturbance gradients.

The similarity in responses of some assemblages (e.g. wetland vegetation and electro-fish) suggests these assemblages may be providing redundant information about the ecological condition of coastal wetlands. The lack of similarity in response of birds and macroinvertebrates to most other assemblages and to each other suggests indicators from these assemblages carry the least redundant information, at least for the indicators we examined. These results are pertinent to decisions about cost- and information-effectiveness of various combinations of indicators (Yoder and DeShon, 2003). For example, because diatom and amphibian responses appear to partition the variance in similar ways, one might consider limiting sampling to one of these two assemblages. However, similar variance partitioning does not necessarily imply fully redundant evaluations of ecological condition. A large part of the value of using indicators from multiple assemblages relates to their diagnostic potential, so eliminating indicators from certain assemblages would need to be done with caution to avoid sacrificing diagnostic capability (Yoder and Rankin, 1995; Norton et al., 2000).

5. Conclusions

Partitioning the variance among different stress components and over a hierarchy of spatial scales has been deemed a critical step in the development of new ecological indicators (Jackson et al., 2000; Paul, 2003; Niemi et al., 2004). Our results provide some of the answers necessary for taking this "critical step" towards developing indicators for Great Lakes coastal wetlands. The overall purpose of our approach was to explore the variation and concordance among different biotic variables to a general human disturbance gradient, identify important covariables, and provide a means of evaluating which assemblages and which taxa within those assemblages have potential as indicators for coastal wetlands in the Great Lakes region. Indicators with wide applicability may be easy and cost effective to implement as well as provide comparative data for evaluating changes over time. Our results should also contribute to the process of selecting a suite of indicators that have potential for inclusion in a multi-metric/multi-assemblage index of coastal wetland condition. To date, this type of index has been lacking for Great Lakes coastal wetlands despite a high level of interest among resource agencies (Keough and Griffin, 1994; U.S.EPA, 2002a; Environment Canada and U.S.EPA, 2003; Lawson, 2004). Examination of the large-scale factors affecting the response of indicators from a broad array of biotic assemblages to a general human disturbance gradient provided an excellent starting point. Working from a single integrated conceptual framework, common methodologies applied across the entire basin and a carefully interpersed sampling design (Niemi et al., 2004; Danz et al., 2005), we found evidence of important differences in indicators across lakes and other geographic and geomorphic circumstances. We also found strong concordances in variation among biological assemblages sampled contemporaneously across the Great Lakes basin. This is one of the first attempts to show how variation in ecological indicators of human disturbance vary at this scale for wetland ecosystems. More refined assessments of ecological condition for Great Lakes coastal systems are forthcoming.

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