

**Are Anurans of Great Lakes Coastal Wetlands Reliable
Indicators of Ecological Condition?**

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ABSTRACT. *Frogs and toads (anurans) are sensitive to a variety of anthropogenic stressors and are widely suggested as indicators of ecological condition. We surveyed 220 coastal wetlands along the U.S. shores of the Laurentian Great Lakes and quantified relationships between presence of anuran species and degree of anthropogenic disturbance. Results were used to derive explicit, functional relationships between environmental condition and anuran occurrences. These functions were subsequently used to calculate a multi-species indicator of ecological condition at other (novel) wetlands. Of 14 anuran species observed, spring peeper (Pseudacris crucifer) exhibited the strongest and most consistent relationship with environmental condition across the entire study area. Other species exhibited significant relationships with the environmental gradient, but the direction of association varied geographically or the overall species abundance was very low (e.g., mink frog, Rana septentrionalis). Even if applied to separate ecological provinces (Laurentian Mixed Forest or Eastern Deciduous Forest), multi-species estimates of wetland condition based on anurans are not much better indicators of human disturbance than are indices based solely on occurrence of spring peeper. Nevertheless, indicators grounded in explicit relationships with environmental stress are superior to traditional measures (e.g., species richness) that combine species with different responses to the stress gradient. At least one anuran species (spring peeper) can contribute meaningfully to the assessment of ecological condition in Great Lakes coastal wetlands; its value as an indicator will be improved if it can be combined with information from other wetland species such as birds, fishes, and vascular plants.*

INDEX WORDS: *Amphibians, frogs, biological indicator, ecological condition, coastal wetlands, Great Lakes.*

INTRODUCTION

Coastal wetlands of the Great Lakes are used as breeding habitat by at least 14 species of frogs and toads, many of which occur widely across the entire region (Hecnar 2004, Price *et al.* 2005). The Great Lakes basin also contains ten percent of the U.S. human population and has been heavily affected by human activities (Niemi *et al.* 2006). Land use and landscape changes within the basin have been particularly dramatic, especially the conversion of wetlands to agricultural, urban, and industrial land uses (Brazner 1997, Detenbeck *et al.* 1999). Point and non-point pollution (Marsalek and Ng 1989, Nature Conservancy 1994), exotic species (Brazner *et al.* 1998, Herrick and Wolf 2005), and hydrological modifications (Meadows *et al.* 2005), among other factors, also affect the condition of Great Lakes wetlands and likely influence amphibian distributions in the coastal zone.

Amphibians have several physiological and ecological traits that imply sensitivity to anthropogenic disturbance (Vitt *et al.* 1990). Their thin, semi-permeable skin readily absorbs moisture (Duellman and Trueb 1986), facilitating the uptake of toxicants, pollutants, and other contaminants from the environment (Bishop and Gendron 1998, DeGarady and Halbrook 2006), especially when those substances are contained in water. Many amphibians exhibit a bi-phasic life cycle, depending on aquatic habitat for reproduction and larval development, and terrestrial habitat for adult growth, hibernation, foraging, and dispersal. The use of multiple habitats potentially exposes amphibians to a greater range of environmental and anthropogenic stresses at various spatial scales (Johnson *et al.* 2002) than would be expected for organisms using only terrestrial or aquatic habitats. Several studies document the sensitivity of amphibians to landscape-scale anthropogenic threats, such as habitat fragmentation (Kolozsvary and Swihart 1999, Knutson *et al.* 2000, Willson and Dorcas 2003), whereas other studies highlight

importance of local-scale factors such as hydroperiod (Pechmann *et al.* 1989), and introduced predators (Hecnar and M'Closkey 1997, Adams 1999). These characteristics suggest that amphibians may be excellent indicators of overall ecological condition.

Although several studies have identified relationships between the presence and/or abundance of anuran species and specific environmental stressors, few have tested whether amphibians can serve as effective indicators of overall ecological condition. Noss (1990) and Niemi and McDonald (2005) suggest one of the roles of an ecological indicator should be to measure the response of an ecosystem to a wide range of anthropogenic disturbances. We used field data collected in Great Lakes coastal wetlands to evaluate the relationship between presence of anuran species and degree of anthropogenic disturbance. We subsequently used these biotic response (BR) relationships to calculate a multi-species indicator of ecological condition for 13 coastal wetlands that were not included in the development of species-disturbance relationships. Comparisons of our index of ecological condition (IEC) based on amphibian occurrences with the actual degrees of disturbance or stress provided a test of the utility of amphibians as reliable ecological indicators in the Great Lakes coastal zone.

METHODS

Study Sites

We surveyed anurans at 351 sampling points in 220 coastal wetland complexes along the U.S. shores of Lakes Erie, Huron, Michigan, Ontario, and Superior (Niemi *et al.* 2006). The 220 coastal wetlands represented a random sample of coastal wetlands along a multivariate gradient of disturbance (Danz *et al.* 2005). Study sites consisted of individual wetlands or geographically connected wetland complexes (range = approximately 1 ha to 945 ha of wetland habitat, mean = 48.1 ha, SE = 7.1) within two ecoregions (Albert 1995); the Laurentian Mixed Forest Province in

the north (n = 122) and the Eastern Broadleaf Forest Province in the south (n = 98). Three wetland types were sampled including open coastal wetlands, riverine-influenced wetlands, and barrier-protected wetlands within 1 km of the Great Lakes shoreline (Keough *et al.* 1999). All wetlands had plant communities typical of marshes, sedge meadows, wet meadows, or shrub swamp (Eggers and Reed 1987). We did not conduct surveys in forested wetlands.

Anuran Calling Surveys

We used calling surveys following the Marsh Monitoring Program protocol (Weeber and Vallianatos 2000) to collect presence/absence (i.e., detected/non-detected) data for anurans on three separate evenings in spring and summer of either 2002 or 2003. Survey 1 was conducted primarily in April when overnight air temperatures were ≥ 5 °C; Survey 2 was conducted in late May when overnight air temperatures were ≥ 10 °C; and Survey 3 was conducted in early July on nights when air temperatures were ≥ 17 °C. Surveys began approximately ½ hour after sunset and lasted no later than midnight. At each sampling point, observers listened for 3 minutes and noted the presence of all vocalizing anurans. Surveys were only conducted when weather conditions were favorable to anuran detection (e.g., wind speed < 20 km/hr and no heavy precipitation). Most wetland complexes were sampled with one point; however, larger complexes were sampled with up to three sampling points. We considered a species present at a wetland point if it was detected during one or more of the sampling periods.

Analysis

We employed the probability indicator method (Howe *et al.* 2007, Howe *et al.* this issue) to calculate an index of ecological condition (IEC) for anurans at each wetland sample point. The probability indicator method uses a *biotic response* (BR) function (*species-specific sensitivity/detectability* (SSD) function in Howe *et al.* 2007), defined as the quantitative

relationship between the wetland's environmental condition (C_{env}) and a four parameter function reflecting the species' response to variation in condition, its overall ubiquity in the region, and its ease of detection. This function is expressed as

$$P_i(C) = \beta_{i,1} + \beta_{i,2} \frac{e^{\beta_{i,4}(C - \beta_{i,3})}}{1 + e^{\beta_{i,4}(C - \beta_{i,3})}} \quad (1)$$

where $\beta_{i,1}$ equals the lowest probability of observing species i (across all values of $C = C_{env}$ between $-\infty$ and ∞), $\beta_{i,2}$ equals the difference between highest and lowest probabilities of observing species i (across all values of C between $-\infty$ and ∞), $\beta_{i,3}$ equals the condition (C) where $P = \beta_{i,1} + \frac{1}{2} \beta_{i,2}$, and $\beta_{i,4}$ is a measure of the steepness of the function at $\beta_{i,3}$. These parameters can be estimated from expert opinion or, more desirably, from field data. In this study, we derived parameters from field observations of anurans among sites with different levels of anthropogenic disturbance.

The anthropogenic disturbance or stress gradient, which we called the *environmental gradient*, was determined from a suite of 39 independent environmental variables (Table 1), including 1) seven statistically important principal components from a previous multivariate analysis of human impacts (e.g., pesticide applications, point sources of chemical and air pollution, human population density) in the drainage areas of shoreline segments associated with our wetland sample points (Danz *et al.* 2005); 2) land cover variables (e.g., proportion residential land use, proportion cultivated land) within 100 m, 500 m, 1 km, and 5 km from the center of the wetland, based on analysis of Landsat 5 and Landsat 7 imagery (30 m x 30 m pixels), primarily from 2001 (Wolter *et al.* 2006); and 3) land cover variables (e.g., proportion natural land, proportion wetland cover) within the wetland or wetland complex itself. A geographic information system (ArcGIS 9.1; ESRI 2005) was used to calculate the land cover variables,

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including proportions of industrial, road, residential, cultivated, natural (e.g., forest), and wetland land cover (Table 1). Principal component analysis (PCA) was used to summarize these 39 variables. Scores from interpretable principal component axes were combined into a single index of environmental condition (C_{env}) by adding the scores for each axis, weighted according to the percent variation explained by the axis. As a result, the gradient of environmental condition (C_{env}) enabled us to order sample sites from those most affected by humans ($C_{env} = 0$; e.g., high human population densities, low proportion of natural land cover) to those least impacted by humans ($C_{env} = 10$; e.g., low levels of pesticide use, high proportion of natural land cover). This gradient differs from the environmental stress gradient of Danz et al. (2005) and related applications because we have placed more emphasis on specific land cover variables.

We used the environmental gradient to develop BR functions for seven anuran species. Previous studies (Lehtinen *et al.* 1999, Johnson *et al.* 2002) have suggested that species habitat relationships may vary between different ecological provinces; to account for these differences we developed separate BR functions for the Laurentian Mixed Forest Province and the Eastern Broadleaf Forest Province. Identical to Howe *et al.* (this issue), we grouped wetland sample sites into categories of 0.5 units (0-0.5, 0.5-1.0, etc.) ranging from highly affected by humans ($C_{env} = 0$) to minimally impacted ($C_{env} = 10$). Results from categories with fewer than five wetland sites were combined with the adjacent category having the fewest sites. The midpoint of the range of C_{env} for each category was used as the corresponding value of environmental condition. We defined the observed probability of occurrence for each species in each category as the proportion of sample points where the species was detected. We estimated parameters of the best-fit BR functions by iteration (Hilborn and Mangel 1997), minimizing the lack-of-fit (LOF) expression:

$$\sum_{n=1}^N [p_{in} - P_i(C_n)]^2 / [P_i(C_n) * (1 - P_i(C_n))] \quad (2)$$

where N is the total number categories, p_n is the species' observed frequency (i.e., proportion) of occurrence in the n th category, and $P_i(C_n)$ is the expected probability of occurrence from equation 1, given the set of parameter values and the environmental condition of site n based on the independent environmental variables ($C = C_{env}$). To derive parameter estimates of $\beta_{i,1}$, $\beta_{i,2}$, $\beta_{i,3}$, and $\beta_{i,4}$ the Solver tool of Microsoft Excel was used to minimize Expression 2, subject to the constraints that $\beta_{i,1}$ and $0 \leq \beta_{i,2} \leq 1$, $0 \leq \beta_{i,3} \leq 10$, and $0 \leq P_i(C_n) \leq 1$. We also limited the steepness parameter ($\beta_{i,4}$) to values between -1 and 1 to avoid pronounced “tails” of the function near $C_{env} = 0$ and $C_{env} = 10$.

We estimated site-specific indices of ecological condition (IEC) using a probabilistic method that maximizes; 1) the probabilities of finding species that were observed, and 2) the probabilities of not finding species that were not observed. Specifically, estimates of IEC (= C in Equation 3) were derived by iteration, maximizing the likelihood function:

$$\sum_{observed} \log(P_i(C)) + \sum_{unobserved} \log(1 - P_i(C)). \quad (3)$$

The first sum represents the expected probabilities of finding species observed at the point (based on BR functions), whereas the second sum represents the expected probabilities of not finding species that were not observed at the point. The iterative process derives the value of IEC (=C in Equation 3) that best “fits” the observed data. In other words, we seek a value of IEC that maximizes the product of the probabilities of having observed/not observed each species at the site. For computational reasons, the maximization is applied to the sum of the logarithms. Species that exhibited poor fit to the best BR function (LOF from Equation 2 > 2.0) were

excluded from the analysis. Expected probabilities of occurrence (or non-occurrence) were calculated using BR functions for the appropriate ecological province.

To test the reliability of anuran-based indicators for coastal wetlands, we excluded 13 sites (nine in the Laurentian Mixed Forest Province and four in the Eastern Deciduous Forest Province) from the derivation of BR functions. We then compared calculated values of IEC for these sites based on anuran occurrences with the previously derived values of C_{env} based on land use and human activities (Table 1).

Linear regression was used to compare estimates of IEC for the 13 reserved sites with corresponding measures of C_{env} . If anuran species are consistently associated with the degree of anthropogenic disturbance, then the slope of IEC versus C_{env} should be close to 1 with a y-intercept of $x = 0$. Deviations from this 1:1 relationship suggest additional factors, other than those used to derive our anthropogenic disturbance gradient, are influencing anuran occurrences in Great Lakes coastal wetlands.

RESULTS

The PCA of environmental variables identified five interpretable axes of variation among wetland complexes. These principal component axes (eigenvectors) accounted for 68% of the variance in the original 39 environmental variables (Howe *et al.* this issue). We rotated the first principal component axis to correspond with the proportion natural vegetation within 1 km of the wetland center. This principal component accounted for approximately 24% of the variation and was strongly correlated (positively) with proportion of residential land cover at all distances (100 m, 500 m, 1 km, and 5 km) and total road length within 5 km. Strong negative correlations with principal component 1 included the proportion of natural vegetation within all distances from the wetland center and the proportion of wetland vegetation, especially at 100 m and 5 km. Together,

scores from the first five principal components (all with eigenvalues > 2.0) effectively separated large wetlands surrounded by extensive natural vegetation from smaller wetlands surrounded by more disturbed (agricultural, residential, and industrial) land uses. To construct our gradient of environmental stress, we adjusted the PCA scores by: 1) reversing the signs of scores on principal components one, two, three, and five so they formed consistent gradients ranging from maximally stressed to minimally stressed conditions (component four was already positively scaled from maximally to minimally stressed condition so did not have to be adjusted); 2) converting the scores to a standardized scale (0-10); and 3) weighting the standard scores by the % variation associated with the corresponding PCA axis. We added the five principal component scores to yield a single gradient of environmental condition ranging from 0 = highly degraded, to 10 = minimally degraded (Howe *et al.*, this issue).

We recorded 14 anuran species at the 220 Great Lakes coastal wetland complexes (Fig. 1).

Spring peeper was the most commonly reported species, followed by green frog (*Rana clamitans*), gray treefrogs (*Hyla versicolor* and *Hyla chrysoscelis*), American toad (*Bufo americanus*), northern leopard frog (*Rana pipiens*), chorus frog (*Pseudacris maculata* and *triseriata*), bullfrog (*Rana catesbeiana*), wood frog (*Rana sylvatica*), and mink frog (*Rana septentrionalis*). Other species recorded were Fowler's toad (*Bufo fowleri*), pickerel frog (*Rana palustris*), and northern cricket frog (*Acris crepitans*); these 3 species were not included in our indicator analysis because they were detected at ≤ 5 sampling points.

Relationships among species occurrences and the environmental gradient varied among anuran species and ecological province (Figs. 2 and 3, Tables 2 and 3). The strongest positive response to environmental condition (reverse of anthropogenic disturbance or stress) was exhibited by the spring peeper, the only species that displayed a consistently positive relationship

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with environmental condition in both ecological provinces (Figs. 2a, 3a). Wood frog and mink frog also displayed a strong positive response to the environmental gradient, but both species were found primarily in the Laurentian Mixed Forest Province. Other anurans displayed a positive relationship with the environmental gradient in one ecological province, but a negative relationship in the other province (Figs. 2 and 3). Because individual species showed both positive and negative relationships with anthropogenic stress, anuran species richness did not exhibit a consistent relationship with the environmental gradient used in our analysis (Fig. 4).

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The correlation between environmental condition (C_{env}) and anuran-based condition (IEC) was not strong ($r = 0.26$, $p > 0.10$) (Fig. 5). When we excluded wetland sites where only a single

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anuran species had been recorded (circles in Fig. 5), the correlation improved substantially ($r = 0.62$), but the relationship was still marginally insignificant ($0.05 < p < 0.10$). Note that species exhibiting BR functions with poor fit ($LOF > 2.0$) to the anthropogenic disturbance gradient in a particular ecological province were not used to calculate the index of ecological condition (IEC).

DISCUSSION

Frog and toad species in Great Lakes coastal wetlands exhibited both positive and negative relationships to our independently derived environmental gradient (Table 2, Fig. 2, Fig. 3). Consequently, anuran species richness is a poor indicator of ecological condition in Great Lakes coastal wetlands. Additionally, several species including green frog, gray treefrog, and American toad, showed a different relationship with the environmental gradient in the northern Laurentian Mixed Forest Province than in the more southern Eastern Deciduous Forest Province. Only spring peeper displayed a positive relationship with the environmental gradient in both ecological provinces.

Noss (1990) has suggested that in order to provide an early warning of change biological indicators should be sufficiently sensitive to environmental stress, distributed over broad geographic areas, and continuously exposed to a wide range of stressors. Indeed, we found at least five species of anurans (Fig. 1) widely distributed throughout the Great Lakes basin. However, our results suggest that only spring peepers appear to provide a geographically consistent environmental signal over a wide range of stresses, and even for this species the relationship was not identical in the Laurentian Mixed Forest and Eastern Deciduous Forest Ecological Provinces. Knutson *et al.* (1999) also recommended the spring peeper as an indicator of forest health in the Midwest U.S. Gibbs (1998), however, noted the spring peeper occurs in areas with a high degree of forest fragmentation in the northeastern U.S. We detected spring peepers in wetlands with relatively poor environmental condition, but the probability of occurrence was much greater in high-quality wetlands. Additionally, we found that spring peepers had a lower overall probability of occurrence at high-quality wetlands in the southern ecological province than in the northern province.

Other species of anurans might also be useful indicators of environmental stress, but their signal to environmental condition must be treated cautiously, especially with reference to geographical context. Our results suggest that ecological province influenced the relationship between probability of anuran occurrence and environmental condition (i.e., anthropogenic stress). Several possible explanations for this exist, including competitive or predatory factors (Lehtinen *et al.* 1999, Knutson *et al.* 2000, Johnson *et al.* 2002), historic land use patterns (Hecnar and M'Closkey 1998), and/or temporal persistence of wetlands and wetland types (e.g., permanent versus ephemeral) in the larger landscape (Vos and Stumpel 1995, Semlitsch and Bodie 1998). Regional patterns of biogeography likely also influence this relationship as some

species, such as mink frogs, occur only in the Laurentian Mixed Forest Province (Harding 1997). In the Great Lakes basin, urban land and agricultural land constitute a relatively larger area in the Eastern Deciduous Forest Province than in the Laurentian Mixed Forest Province (Wolter *et al.* 2006). Similarly, overall coastal wetland loss and modification (e.g., creation of dikes) also are greater in the southern than in the northern portion of the Great Lakes. This suggests different stressors or degrees of stress might affect anuran distributions in the two ecological provinces, even though these species occur across the entire Great Lakes basin.

Based on weak and somewhat inconsistent relationships between anuran species occurrences and anthropogenic disturbance, multi-species estimates of ecological condition based on anurans (IEC) did not closely correspond to the independently derived environmental gradient (Fig. 5). This does not imply these frogs and toads are insensitive to anthropogenic stress, but such findings suggest that anurans may not consistently respond to environmental variables traditionally associated with intensity of human land use and habitat modification (i.e., the variables used in this study). Our estimates of ecological condition using amphibian species presence and absence were better predictors of environmental condition when we excluded sites where only a single species was recorded, suggesting anurans might be too infrequent overall (compared with birds, for example) to serve as reliable biotic indicators in Great Lakes coastal wetlands. Fortunately, the probability-based indicator approach described here and elsewhere (Howe *et al.* 2007) readily allows species of different taxa to be combined in the estimation of ecological condition. Once parameters of an explicit biotic response (BR) function have been derived or defined, any species can be included in the iterative estimation of an index of ecological condition (IEC).

The diverse life-history strategies of amphibians may inhibit their utility as large-scale indicators of ecological condition. Some species may be sensitive to specific environmental stresses but insensitive to other stresses, especially those reflected by landscape variables at the scales measured here. For example, many anuran species have been shown to be sensitive to urbanization (Knutson *et al.* 1999, Lehtinen *et al.* 1999, Price *et al.* 2005, Rubbo and Kiesecker 2005), yet these same species are able to occupy wetlands and reproduce in significantly modified landscapes, particularly those dominated by agricultural land (Knutson *et al.* 2004). Our stressor gradient covered a broad range of variation, including nearly pristine coastal wetlands and highly industrial urban environments. This broad range, coupled with the extensive geographic area of our study sites (even within each ecological province), might have obscured important relationships between environmental stress and anuran distributions.

The spatial scale at which the environmental variables are collected might also influence the relationship between environmental condition and anuran occurrences. In our study, we incorporated variables collected at various spatial scales, ranging from a 100 m radius to a 5 km radius surrounding the sampling point. Price *et al.* (2005) evaluated anuran-habitat relationships in Great Lakes coastal wetlands at various spatial scales, including measurements collected within the wetland sampling area. They found that habitat models for several species performed best at large geographic scales (e.g., 3 km radius or greater). The presence of chorus frogs, however, was best explained by habitat variables at the wetland survey locality (500 m radius); models developed at larger spatial scales performed poorly for this species. Such patterns may be related to the spatial scale at which a species interacts with its environment. Knutson *et al.* (2004) and others have found that pond factors are more important than landscape variables in explaining amphibian species richness and reproductive success. They suggest that predation by

fish was primarily responsible for these patterns. However, several studies (e.g., Beebee 1985, Hecnar and M'Closkey 1998, Price *et al.* 2005) emphasize that landscape scale variables are also important predictors of some species. A more detailed analysis of condition that incorporates both local and landscape-scale variables in our environmental gradient might improve some of our BR models and therefore provide a more reliable means for indicating ecological condition.

The complex geography of amphibian populations also suggests that caution may be necessary in using anurans as ecological indicators in the Great Lakes coastal zone. Many pond-breeding amphibian populations appear to be structured as metapopulations, where breeding habitats form discrete patches within the broader landscape (Marsh and Trenham 2001). In Great Lakes coastal wetlands, it is likely that distribution and extent of amphibian breeding habitat change with Great Lakes water levels, ultimately influencing the distribution of frogs in the coastal zone. Wilcox *et al.* (2002) demonstrated that water levels can strongly affect the distributions and response of organisms to wetland condition. During our anuran surveys, the average water levels of the Great Lakes were at the lowest level in over 25 years (NOAA 2006). The low water levels created extensive shoreline marshes in some regions (i.e., Green Bay and Saginaw Bay), which may have provided anuran breeding habitats that were not present when water levels were higher. High water levels in the Great Lakes likely subject amphibians to wave action, storm surges, and predation, causing different distribution patterns than the patterns we observed. Creating BR models for each anuran species during high and low water levels might be necessary to effectively use anurans as indicators of Great Lakes coastal wetland condition.

The inconsistent responses of anurans to our environmental gradient also might reflect imperfect detection of species during our surveys (MacKenzie *et al.* 2002). Although we conducted calling surveys using a standardized protocol on nights favorable to anuran detection,

few anuran species are so conspicuous that they are always detected at such surveys. Environmental factors, observer experience, and survey protocol have been shown to influence anuran detection probabilities (Pierce and Gutzwiller 2004, Weir *et al.* 2005, Gooch *et al.* 2006). Additionally, the frequency and duration of some species' vocalizations (i.e., spring peeper), may influence detection of other species with lower frequency calls (i.e., northern leopard frogs). Methods other than calling surveys (i.e., drift fences, larval surveys, etc.) may be required to detect species that are inadequately detected with auditory surveys (Crouch and Paton 2002). Future studies using anurans as indicators should incorporate species-specific detection probabilities into indicator development.

In summary, this investigation provides one of the first critical assessments of anuran-based ecological indicators. Our results emphasize that anurans, particularly spring peepers, can contribute to the assessment of ecological condition in Great Lakes coastal wetlands. To employ other species, however, geographic context (e.g., ecological province) and perhaps other factors must be taken into account. Derivation of our IEC was relatively ineffective when only one or a few species were present at sites of interest, suggesting amphibians might be best used when combined with data from other taxa, such as birds. Additionally, calculation of IECs might require different BR functions for different geographic regions, different landscape types, and perhaps even different Great Lakes water levels.

ACKNOWLEDGMENTS

This research was supported by a grant from the U.S. EPA's Science to Achieve Results Estuarine and Great Lakes program through funding to the Great Lakes Environmental Indicators (GLEI) project (U.S. EPA agreement EPA/R-8286750), and a grant from the National Aeronautics and Space Administration (NAG5-11262). Although the research described in this

article has been funded in part by the U.S. EPA, it has not been subjected to the agency's required peer and policy review and therefore does not necessarily reflect the views of the agency, and no official endorsement should be inferred. SJP was also supported by the Zoological Society of Milwaukee, Davidson College biology department, and National Science Foundation grants (DBI-0139153 and DEB-0347326) to Michael E. Dorcas. The Cofrin Center for Biodiversity, University of Wisconsin-Green Bay, and the Natural Resource Research Institute, University of Minnesota Duluth also provided financial, technical, and logistical support. We gratefully acknowledge other scientists involved with the GLEI project, especially V. Brady, T. Brown, J. Brazner, N. Danz, C. Johnson, L. Johnson, T. Hollenhorst, P. Wolter, D. Marks, and the many trained investigators who helped in field surveys. Michael E. Dorcas, Stephen J. Hecnar, and Melinda Knutson provided comments that greatly improved this manuscript. This is contribution number xxx of the Center for Water and the Environment, Natural Resources Research Institute, University of Minnesota Duluth.

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TABLE 1. Variables used to define an environmental stress gradient for wetland bird survey sites. Numbers give the first five eigenvectors (scaled to standard deviations) from PCA using the correlation matrix. First eight variables are derived from previous PCA analysis incorporating categories of variables associated with the drainage area of the shoreline segment (segment-shed) surrounding the wetland complex (Danz et al. 2005). Land cover classes were determined by Wolter and others at NRRI, UMN Duluth (Wolter et al. 2006) and combined into six general categories (industrial, roads, residential, cultivated, natural, wetland). Proportions of land cover in each category were determined by GIS analysis for areas within 100 m, 500 m, 1 km, and 5 km of the centroid of the wetland complex, excluding open water.

Variable	Eigenvector				
	1	2	3	4	5
Agricultural PC 1 (Danz <i>et al.</i> 2005)	0.412	0.530	0.062	0.226	-0.222
Atmospheric deposition PC 1 (Danz <i>et al.</i> 2005)	0.309	0.328	0.283	0.226	-0.266
Atmospheric deposition PC 2 (Danz <i>et al.</i> 2005)	0.135	-0.318	-0.110	0.290	-0.017
Point source pollution PC 1 (Danz <i>et al.</i> 2005)	0.232	0.141	0.024	-0.011	-0.232
Point source pollution PC 2 (Danz <i>et al.</i> 2005)	0.032	-0.159	0.018	0.089	-0.025
Soil type PC 1 (Danz <i>et al.</i> 2005)	-0.255	-0.359	-0.237	0.039	0.289
Soil type PC 1 (Danz <i>et al.</i> 2005)	-0.126	0.109	0.000	-0.282	-0.014
Urbanization PC 1 (Danz <i>et al.</i> 2005)	0.675	-0.197	-0.030	0.101	0.103
Prop. industrial land in wetland complex	0.299	-0.247	-0.069	-0.726	0.123
Prop. road area in wetland complex	0.081	0.049	0.199	0.183	0.736
Prop. residential land use in wetland complex	0.632	-0.674	-0.104	0.169	0.130
Prop. cultivated land in wetland complex	0.258	0.701	0.247	-0.181	-0.016
Prop. natural land cover in wetland complex	-0.219	-0.502	0.581	0.100	-0.371
Prop. wetland land cover in wetland complex	-0.409	0.160	-0.728	0.183	-0.151

Prop. industrial land use w/in 100 m	0.424	-0.367	-0.150	-0.725	0.097
Prop. road area within 100 m	0.267	-0.021	0.326	0.154	0.721
Prop. residential land use within 100 m	0.731	-0.092	-0.076	0.252	0.154
Prop. cultivated land within 100 m	0.304	0.749	0.290	-0.206	0.003
Prop. natural land cover within 100 m	-0.373	-0.560	0.579	0.086	-0.341
Prop. wetland land cover within 100 m	-0.428	0.185	-0.814	0.169	-0.077
Prop. industrial land use w/in 500 m	0.513	-0.408	-0.235	-0.649	0.017
Prop. road area within 500 m	0.614	-0.245	0.213	0.249	0.380
Prop. residential land use within 500 m	0.780	-0.212	-0.110	0.327	0.047
Prop. cultivated land within 500 m	0.346	0.820	0.299	-0.180	-0.008
Prop. natural land cover within 500 m	-0.588	-0.570	0.487	0.087	-0.145
Prop. wetland land cover within 500 m	-0.399	0.220	-0.841	0.139	0.038
Prop. industrial land use w/in 1 km	0.553	-0.422	-0.266	-0.543	-0.041
Prop. road area within 1 km	0.715	-0.315	0.075	0.268	0.109
Prop. residential land use within 1 km	0.779	-0.258	-0.143	0.316	-0.029
Prop. cultivated land within 1 km	0.328	0.845	0.247	-0.148	-0.020
Prop. natural land cover within 1 km	-0.666	-0.562	0.394	0.055	-0.018
Prop. wetland land cover within 1 km	-0.389	0.207	-0.814	0.102	0.053
Prop. industrial land use w/in 5 km	0.574	-0.412	-0.336	-0.118	-0.201
Prop. road area within 5 km	0.720	-0.369	-0.221	0.136	-0.226
Prop. residential land use within 5 km	0.723	-0.337	-0.230	0.179	-0.238
Prop. cultivated land within 5 km	0.301	0.800	0.176	0.026	-0.135
Prop. natural land cover within 5 km	-0.653	-0.551	0.175	-0.083	0.231
Prop. wetland land cover within 5 km	-0.423	0.094	-0.597	-0.026	0.204
Total road length within 5 km	0.744	-0.300	-0.239	0.054	-0.305

TABLE 2. *Anuran species used to estimate ecological condition in Great Lakes coastal wetlands in the Laurentian Mixed Forest Ecological Province. List includes the most commonly observed species in decreasing order of sensitivity across a stress gradient (C_{env}) based on intensity of human activities (environmental stress). Values of β_1 , β_2 , β_3 , and β_4 correspond to estimates of the parameters in Equation 1. Species with negative β_4 are more likely to occur in sites with poor condition. LOF is the lack-of-fit statistic described in Equation 2. The quantity $|P(10)-P(0)|$ describes the absolute difference in probabilities of a species' presence at poorest quality ($C_{env} = 0$) versus highest quality ($C_{env} = 10$) sites. Scientific names of species are given in text.*

Common Name	β_1	β_2	β_3	β_4	LOF	$ P(10)-P(0) $
Spring peeper	0.07	0.87	0.62	0.91	0.54	0.55
Leopard frog	0.19	1.00	-0.30	-1.00	0.99	0.43
Gray Treefrog(s)	0.69	1.00	-0.92	-1.00	1.91	0.28
Green frog	0.47	1.00	-1.00	-0.95	0.81	0.28
Chorus frog	0.00	0.25	5.49	-1.00	0.53	0.25
Wood frog	0.00	0.30	0.57	1.00	1.87	0.19
Mink frog	0.00	0.15	7.26	1.00	0.44	0.14

TABLE 3. *Anuran species used to estimate ecological condition in Great Lakes coastal wetlands in the Eastern Deciduous Forest Ecological Province. List includes the most commonly observed species in decreasing order of sensitivity across a stress gradient (C_{env}) based on intensity of human activities (environmental stress). Values of β_1 , β_2 , β_3 , and β_4 correspond to estimates of the parameters in Equation 1. Species with negative β_4 are more likely to occur in sites with poor condition. LOF is the lack-of-fit statistic described in Equation 2. The quantity $|P(10)-P(0)|$ describes the absolute difference in probabilities of a species' presence at poorest quality ($C_{env} = 0$) versus. highest quality ($C_{env} = 10$) sites. Scientific names of species are given in text.*

Common Name	β_1	β_2	β_3	β_4	LOF	$ P(10)-P(0) $
Spring Peeper	0.00	0.81	3.10	0.26	0.63	0.44
Bullfrog	0.00	0.45	8.16	-1.00	1.84	0.39
American Toad	0.10	0.30	5.91	-1.00	1.17	0.29
Gray Treefrog(s)	0.30	0.29	3.61	1.00	0.84	0.29
Leopard Frog	0.00	0.43	0.18	1.00	0.77	0.23
Green Frog	0.49	0.21	2.42	1.00	2.71	0.19
Chorus Frog	0.00	0.51	2.74	0.08	1.40	0.10

FIG. 1. Distribution of anuran species in field samples (three calling surveys during spring and early summer) at coastal wetlands in the Eastern Deciduous Forest Ecological Province (n = 201) and Laurentian Mixed Forest Ecological Province (n = 200).

FIG. 2. Biotic response functions for a) spring peeper, b) green frog, c) gray treefrog, and d) American toad from Great Lakes coastal wetlands of the Laurentian Mixed Forest Ecological Province. Environmental condition (x-axis) represents the gradient of environmental disturbance, ranging from most impacted (0) to least impacted (10). Y-axis represents the proportion of points where the species was recorded among wetlands representing 15 categories (0 - 0.63, 0.63-1.00, 1.00-2.25, etc.)

FIG. 3. Biotic response functions for a) spring peeper, b) green frog, c) gray treefrog, and d) American toad from Great Lakes coastal wetlands of the Eastern Deciduous Forest Ecological Province. Environmental condition (x-axis) represents the gradient of environmental disturbance, ranging from most impacted (0) to least impacted (10). Y-axis represents the proportion of points where the species was recorded among wetlands representing 12 categories (0.6 – 1.50, 1.5-2.00, 2.00-2.50, etc.)

FIG. 4. Relationship between environmental condition and the mean number anuran species. Sites from the Laurentian Mixed Forest Ecological Province and the Eastern Deciduous Forest Ecological Province are plotted separately.

FIG. 5. Relationship between environmental condition based on environmental variables and ecological (biotic) condition based on occurrences of anuran species in coastal wetlands of the Great Lakes. Ecological condition was derived from the probabilistic method described in text, given biotic response functions for the appropriate ecological province. Sites indicated by circles were characterized by only a single anuran species.

FIG. 1

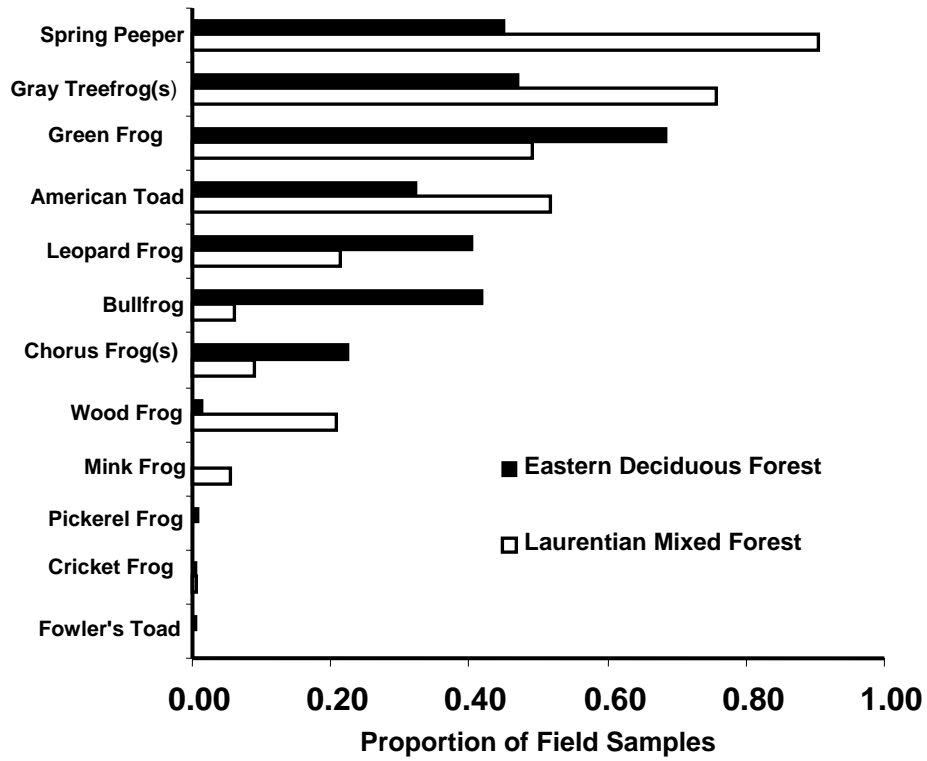


FIG. 2

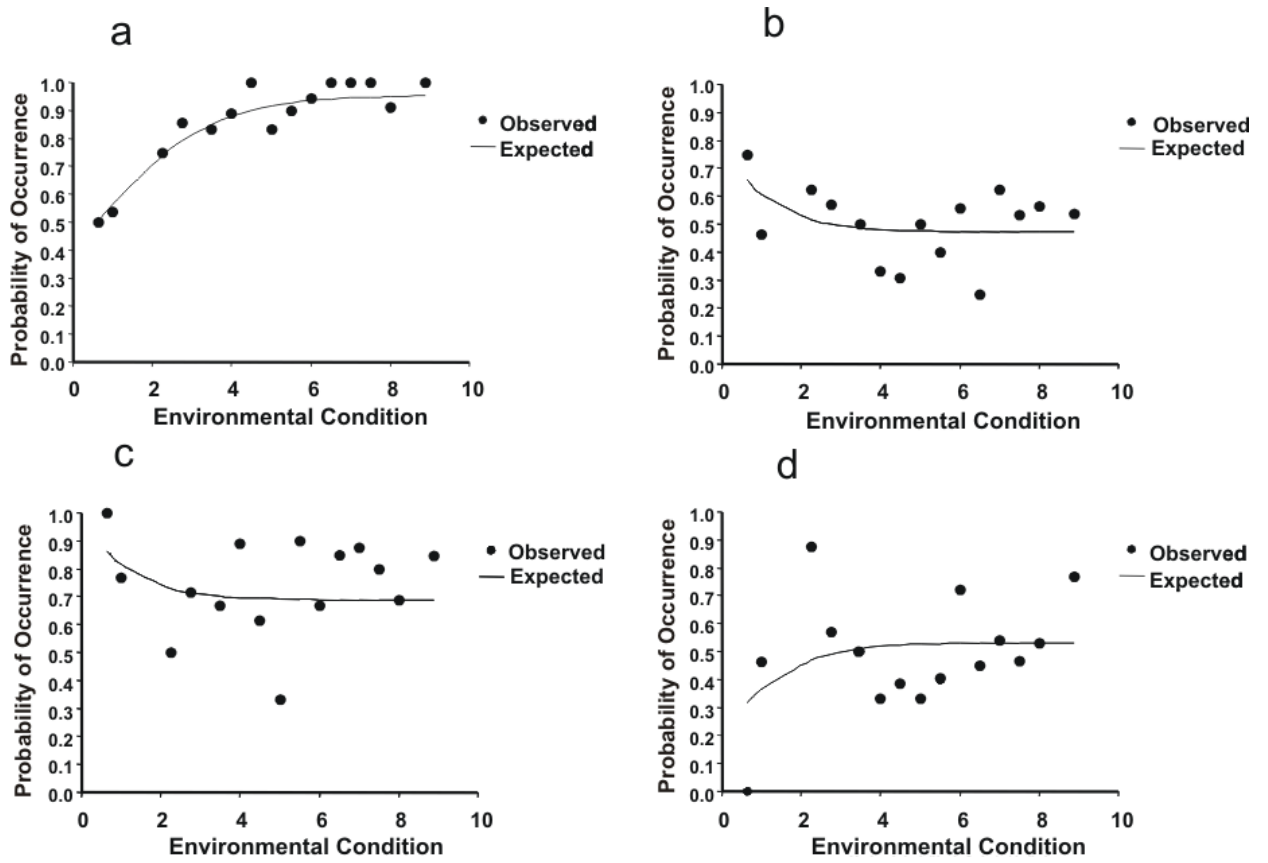


FIG. 3

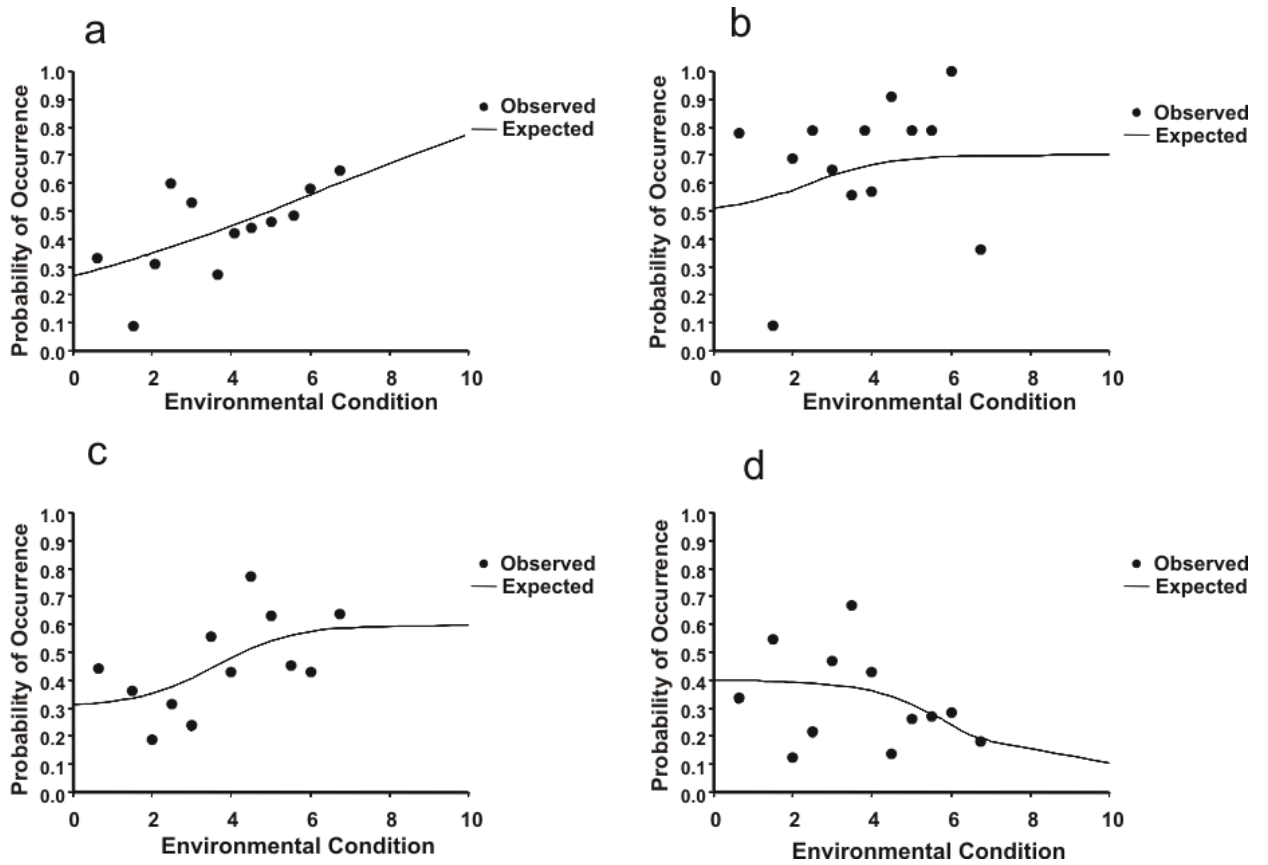


FIG. 4

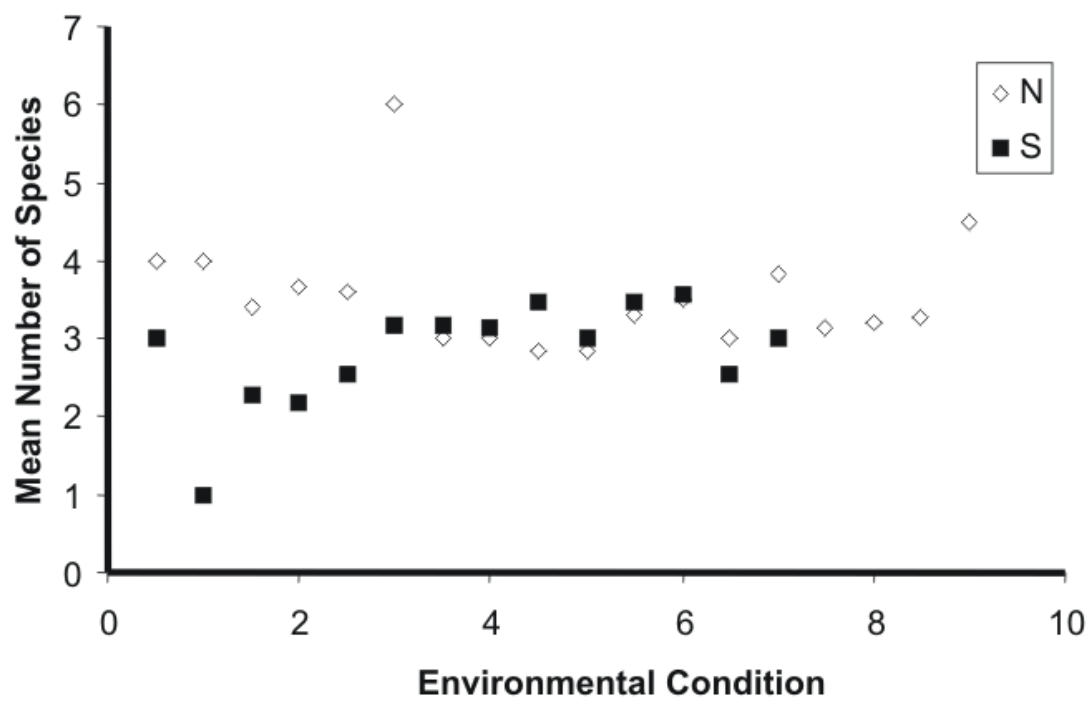


FIG. 5

