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Research Article

The importance of spatial scale for conservation and assessment of anuran populations in coastal wetlands of the western Great Lakes, USA

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Abstract

Distributions of pond-breeding amphibians may be influenced by habitat factors at different spatial scales. We used anuran calling surveys to investigate the association between 5 anuran species and habitat variables measured within 100, 500, 1000, and 3000 m of sampling points at 63 coastal wetlands along the US shores of Lake Michigan and Lake Huron. Stepwise logistic regression was used to create predictive models for each species at each spatial scale. Our results confirm the view that habitat variables at multiple scales influence frog distributions, but the strength of predictive models was significantly affected by the spatial scale at which habitat variables were derived. Remotely sensed habitat variables within a 3000 m radius were among the most effective predictors of occurrence for American toad (*Bufo americanus*), eastern gray treefrog (*Hyla versicolor*), spring peeper (*Pseudacris crucifer*), and green frog (*Rana clamitans melanota*). The western chorus frog (*Pseudacris triseriata*) was predicted most effectively by variables derived within a 500 m radius. For the most part, these anurans exhibited species-specific responses to habitat variables; however the suite of landscape-scale variables associated with urban land use appeared in all species' regression models. Associations with landscape-scale variables coupled with well-documented habitat needs at local breeding sites suggest that conservation and assessment of frogs and toads in coastal wetlands should consider the influence of habitat variables at multiple spatial scales.

Introduction

Amphibians typically require multiple habitats throughout their life, including aquatic habitat for breeding and larval growth and terrestrial habitat for adult growth, foraging, hibernation, and dispersal. Distribution patterns of amphibians therefore may be influenced by habitat factors at several spatial scales. At a breeding pond, amphibian distributions are influenced by pond hydroperiod (Collins and Wilbur 1979), type and amount of vegetation surrounding the breeding site (Hecnar and M'Closkey 1998; Munger et al. 1998; Skelly et al. 1999), presence of fish and/or other predators

(Semlitsch 1988; Lawler et al. 1999; Semlitsch 2000) and water chemistry (Glooschenko et al. 1992; Hecnar and M'Closkey 1996). Studies of amphibian metapopulation dynamics (Gill 1978; Sjögren-Gulve and Ray 1996; Pope et al. 2000) and analysis of adjacent non-breeding habitat (Dodd and Cade 1998; Semlitsch 1998; Guerry and Hunter 2002; Semlitsch and Bodie 2003; Gibbons 2003) indicate that landscape-scale habitat variables influence local amphibian distributions. Correlations between landscape metrics and amphibian presence or species richness emphasize the detrimental effects of anthropogenic habitat fragmentation, degradation, destruction, and conversion (Hecnar and M'Closkey 1998; Knutson et al. 1999; Kolozsvary and Swihart 1999; Lehtinen et al. 1999; Joly et al. 2001; Johnson et al. 2002). Because habitat destruction is a primary cause of amphibian declines and local extinctions (Dodd and Smith 2003), knowledge of amphibian–habitat associations at both local and landscape scales should be important components of amphibian conservation measures.

The coastal zone of the western Great Lakes region is an important habitat for amphibians (Pentecost and Vogt 1976; Maynard and Wilcox 1997). Historically, many areas of the Great Lakes shoreline supported vast and diverse wetlands, which likely provided extensive breeding sites for salamanders and frogs. Areas adjacent to the coastal wetlands were primarily forested (Bailey 1995), and were probably important amphibian habitat during the non-breeding season. Coastal regions of the Great Lakes have been extensively modified since European settlement. Currently, most forests along the coastline have been converted to agricultural land or urban areas, and the majority of wetlands have been lost (Dodge and Kavetsky 1995; Environment Canada 1995; Mitsch and Gosselink 2000). Bosley (1978), for example, estimated that coastal wetlands along the southern and western shores of Green Bay, Wisconsin, USA have been reduced in area by 60–75% from historic times. Besides changes in land use, coastal wetlands are threatened by numerous anthropogenic activities, such as hydrological modifications (Whillans 1979), point and non-point pollution (Nature Conservancy 1994), invasion of exotic species (Whillans 1979; Brazner 1997; Brazner and Jenson 1999), and climate change (Hartman 1990; Mortsch 1998). The variety of disturbances has likely affected amphibians and their coastal habitat, yet few, if any, studies have focused on identifying amphibian–habitat associations in the Great Lakes coastal environment (Maynard and Wilcox 1997; Hecnar 2004).

We sampled anurans in coastal wetlands along the US shores of Lake Michigan and Lake Huron and related the presence or absence of five anuran species to land cover variables at multiple spatial scales. Our objectives were: (1) to determine the most effective spatial scale for predicting occurrences of anuran species and (2) to identify specific variables associated with anuran species' distributions in the Great Lakes coastal environment. Results provide meaningful information for anuran conservation efforts and will help wetland managers interpret the significance of amphibian population changes in the Great Lakes coastal region.

Methods

Study sites

We surveyed anurans at 63 coastal wetlands along the US shores of Lake Michigan and Lake Huron (Figure 1). Study sites were identified according to a stratified random scheme along a multivariate gradient of disturbance (Danz et al. in press). Each study site was part of a 'segment-shed', defined as the drainage area or watershed associated with a segment of the Great Lakes coastline. Segment-sheds were bounded by shoreline points midway between adjacent second order and higher streams. From these points, watershed boundaries were generated by GIS analysis of elevation data. We compiled a large array of data associated with potential environmental stressors (e.g., agricultural runoff, human population density, toxic chemical releases, etc.) for each segment-shed. We used principal components analysis to summarize stressor gradients and selected study sites so that samples were distributed across the stressor gradients.

Study sites represented three wetland habitat types: (1) shoreline emergent wetlands, (2) riverine-influenced wetlands, and (3) protected (inland) wetlands within 1 km of the shoreline. All study wetlands were dominated by plants typical of marshes, sedge meadows, wet meadows, or shrub swamps (e.g., *Typha*, *Scirpus*, and *Carex* spp., *Phragmites australis*, *Alnus rugosa)*. We deter-

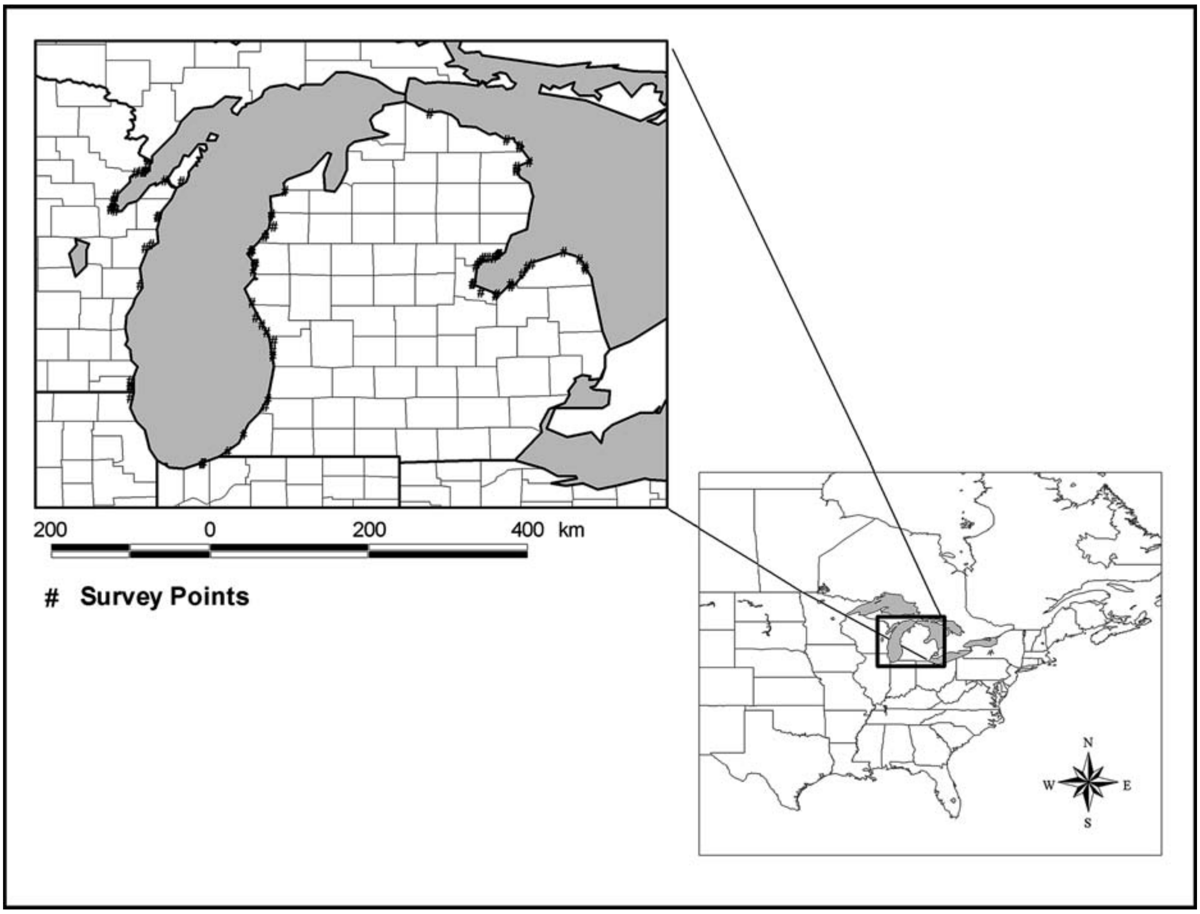

Figure 1. Location of sampling points ($n = 93$) on the shores of Lake Michigan and Lake Huron. At each sampling point anuran calling surveys were performed and wetland habitat variables were measured. Each point also served as the centroid from which landscape data were collected.

mined survey points within the selected study sites prior to the sampling period using United States Geological Survey (USGS) topographic maps, digital orthophotographs and notes from ground truthing. Between 1 and 3 points were sampled in each wetland, depending on accessibility and wetland size. All points were separated by a minimum of 500 m to eliminate double counting of frogs. Altogether 93 sampling points were visited within the 63 wetlands.

Anuran sampling techniques

We surveyed frogs and toads at each sampling point on three separate evenings between April 2002 and mid-July 2002. All sampling points were surveyed using half-circle anuran calling surveys, consistent with the methods developed by the Marsh Monitoring Program (Weeber and Vallianatos 2000). We scheduled each visit to coincide with the onset of seasonal conditions: (1) when overnight ambient air temperatures ≥5 °C, (2) when overnight ambient air temperatures ≥10 °C, and (3) when overnight ambient air temperatures ≥17 °C. Surveys were only conducted when weather was optimal. Weather conditions recorded during each visit include temperature, precipitation, cloud cover, and wind speed. Surveys began 1 half-hour after sunset and were conducted through the night if weather conditions remained favorable. At each sampling point the observers listened for 3 min and identified all vocalizing anuran species.

Twelve anuran species occur in the western Great Lakes region (Harding 1997); we narrowed our focus to include species that are easily detected by calling surveys, have somewhat prolonged breeding seasons (> 1 month), and are widely distributed throughout the western Great Lakes. Our analysis includes the American toad (*Bufo americanus*), western chorus frog (*Pseudacris triseriata*), northern spring peeper (*Pseudacris crucifer*), eastern gray treefrog (*Hyla versicolor*), and green frog (*Rana clamitans melanota*). Western chorus frogs are extremely rare in northeastern Wisconsin (Casper 1996), and therefore sampling points in this region were excluded from chorus frog analyses.

Habitat analyses

We analyzed habitat characteristics at multiple scales, where scale is defined as the spatial resolution at which patterns were measured (Morrison and Hall 2002). The smallest scale (local) was the area within the 100 m half-circle (1.6 ha) anuran sampling plot. More extensive (landscape) scales include the circular areas within 500 (78.5 ha), 1000 (314.2 ha), and 3000 m (2827.4 ha) of the anuran sampling point.

During June 2002, SJP and DRM collected field data for habitat analysis at the 100 m scale. Within a 100 m half-circle area we conducted a time-efficient habitat survey similar to that used by the Marsh Monitoring Program (Weeber and Vallianatos 2000). Specifically we (1) visually estimated the percent coverage of 12 major vegetation/habitat types at the wetland and (2) categorized specific habitat attributes pertaining to the wetland such as nearest road type and wetland size (Weeber and Vallianatos 2000). Habitat types were based on the physical structure of the vegetation. These attributes, along with a Shannon–Wiener Evenness index (1949), served as variables for the local scale wetland predictive models (Table 1). Several related variables (habitat 'richness,' habitat dominance) were not included because they were highly correlated with the Shannon–Wiener Evenness index.

We determined the landscape cover classes using a combination of Landsat Thematic Mapper (TM) satellite data, USGS National Land Cover Data (NLCD), digital orthophotographs, and notes collected during ground truthing. The NLCD, which served as our base map, was derived from early to mid-1990's Landsat TM data. It uses a 21-class land cover classification scheme based on the Anderson land-use and land-cover classification applied over the entire United States (USGS 2002). We used ArcView 3.2 (ESRI 1996) to create 3000 m radius buffers centered on anuran sampling points and imported these buffers into ERDAS IMAGINE 8.4 (ERDAS 1999). We subsequently used ERDAS IMAGINE to evaluate and re-classify vegetation in individual pixels of the NLCD layer. For each anuran sampling point, we modified the area within the 3000 m radius buffer on the NLCD image based on the differences between the NLCD image and our ancillary data sources, which included the current Landsat TM data, digital orthophotographs, and notes acquired through ground truthing. We reduced the 21 land cover classes present on the original NLCD image to 9 cover classes: (1) water, (2) developed land, (3) barren land, (4) forested upland, (5) herbaceous upland, (6) agricultural land, (7) ur-

Table 1. Variables recorded for our local habitat analysis. The majority of variables were collected as relative areas in the defined 100 m half-circle area.

Variable	Units
Water	Proportion
Submergent vegetation	Proportion
Floating vegetation	Proportion
Cattail/bur-reed	Proportion
Grasses/sedge	Proportion
Giant reed grass	Proportion
Rushes	Proportion
Shrubs	Proportion
Exposed/barren ground such as sand or rock	Proportion
Forest including coniferous and deciduous trees	Proportion
Anthropogenic cover including driveways, roads, etc.	Proportion
Recreational grass (i.e. lawn)	Proportion
Shannon–Wiener Evenness	Index (0–1)
Wetland size	Ordinal (tiny (1.5–2.5 ha), small (2.5–5 ha), medium (5–25 ha), or large (25–50 ha))
Wetland type	Ordinal (coastal, riverine, or protected)
Nearest road type	Ordinal (highway, paved road, gravel, or dirt)

ban/recreational grassland, (8) woody wetland, and (9) emergent herbaceous wetland.

Once classification was complete, we created two additional circular buffers (500 and 1000 m) in ArcView 3.2. Again, these buffers were imported into ERDAS 8.4, giving us a total of 3 buffers (500, 1000, and 3000 m) for each classified site. We clipped each image according to the buffer size using the Area of Interest (AOI) tool in ERDAS 8.4. Each clipped image was saved as a new raster file, providing three datasets corresponding to the different buffer sizes. We used APACK 2.22 software (Mladenoff and DeZonia 2001) to calculate 96 metrics for each spatial scale.

Landscape metrics were screened using Pearson's correlation coefficients (SAS 8.0, SAS Institute 1999) to remove colinearity and to reduce the total number of variables. If two variables were highly correlated ($|r| > 0.6$), only 1 of them was retained based on its perceived biological relevance and ease of interpretation. This process generated a set of 33 relatively independent variables (Table 2). Since an objective of this study was to examine the effects of spatial scale on amphibian habitat relationships, landscape level independent variables were consistent through all spatial scales.

Statistical Analyses

We used logistic regression (Hosmer and Lemeshow 1989) to assess anuran–habitat associations at each scale (SAS 8.0, SAS Institute 1999). Both wetland characteristics and landscape-scale variables were used as independent variables and the presence/absence of each anuran was used as the dependent variables. If a species was detected in at least 1 of the counts it was considered present at that site, otherwise it was considered absent. We used a stepwise procedure with an inclusion/removal cutoff of $p = 0.15$ (Hosmer and Lemeshow 1989). Inclusion cutoffs less than 0.15 are not recommended, as this may result in the exclusion of important variables from the model (Bendel and Afifi 1977; Costanza and Afifi 1979).

Given that many of our sites were separated by only 500 m, landscape-scale data were not independent due to overlapping buffer areas. The

Table 2. Landscape metrics calculated by APACK 2.22 landscape analysis software as described by Mladenoff and DeZonia (2001). Metrics can pertain to a cover class, the composite area within a buffer, or both. This table represents a subset (33 out of 96 metrics) that was found to be not highly correlated ($|r| < 0.6$). Refer to Mladenoff and DeZonia (2001) for equations for each metric.

Metrics	Abbreviation	Definition	Units
Connectivity between circular patches[a]	CCI	A gravity-based metric that can be used to estimate habitat fragmentation. Lower values indicate a mosaic of small patches whose edge-to-edge distances are relatively far apart. Higher values suggest a mosaic of large patches whose edge-to-edge distances are relatively close together	Unitless value
Edge density[b,c]	ED	A measure that represents the total edge length of a cover type divided by the total landscape area	Meters/hectare
Edge distribution Evenness[b]	EDE	A measure that estimates the evenness of the distribution of edge types upon a landscape. Edge is defined as the border between two neighboring cells of different cover types	Index (0–1)
Fractal (Box) dimension[b]	FBD	A measure of the fractal dimension of the landscape using the box counting method. Ranges from 1.0 for maps made up of patches whose outlines are very regular or straight to 2.0 for maps made of patches whose outlines are irregular	Index (1–2)
Average patch perimeter/area ratio[a,b]	PA	The average perimeter ratio for all patches present	Meters/hectare
Relative area[a]	RA	The proportion of the landscape area populated by the particular cover type	Proportion
Shannon–Wiener Evenness[b]	SWE	The relative diversity of the landscape as described by Shannon and Weaver (1949). SWE is reported as the measured diversity of the landscape divided by the maximum possible diversity for the landscape	Index (0–1)

[a] Metrics pertaining to the 9 landscape cover classes.

[b] Metrics pertaining to a composite buffer area (e.g., 500, 1000, 3000 m).

[c] Only the metric regarding the cover class water was included.

lack of independence violates an assumption of logistic regression and could result in spatial autocorrelation between sampling points (Klute et al. 2002). To improve the degree of spatial independence among samples and minimize spatial autocorrelation, we used a restricted randomization method to create multiple subsets of our sampling points. Each subset contained only sampling points that were separated by a minimum of 6 km, which is twice the extent of the largest buffer radius (3000 m). Altogether 30 unique subsets of sampling points were created. The sampling points in each subset were the same across different spatial scales. This method not only addressed the independence assumption, but also allowed us to assess the robustness and variability associated with each logistic regression model at each spatial scale.

McFadden's ρ^2 was used to judge goodness-of-fit for logistic regression models. McFadden's ρ^2 is a transformation of the likelihood ratio statistic intended to mimic R^2 values of linear regression. Similar to R^2, McFadden's ρ^2 ranges from 0 to 1, with ρ^2 values closer to 1 indicating better model fit. We considered a McFadden's $\rho^2 \geq 0.20$ as satisfactory model fit (Hensher and Johnson 1981). All ρ^2 values that were larger than 0.10 were significant at the $p < 0.01$ level; therefore all models with satisfactory ρ^2 values were also highly significant. The scale-specific McFadden's ρ^2 values were used to detect the scale at which model predictions were most successful.

We used GraphPad Prism 4.0 (GraphPad Software Inc. 2003) to perform a Friedman's test (Bradley 1968), a non-parametric alternative to repeated measures analysis of variance, on the McFadden's ρ^2 values. Our objective was to determine if spatial scales differed significantly in their ability to predict anuran species' occurrences. Dunn's post test (Daniel 1990) was used to group the scales according to their relative ability to predict anuran species' occurrences.

The relative importance of habitat variables was illustrated by tallying the incidence of each significant variable in logistic regression models at each scale for each species. For a particular species, each variable had the potential to occur in 30 models at a spatial scale. Because we used an inclusion/removal cutoff of $p = 0.15$, a variable could occur in 4.5 models simply by chance. We only consider variables to be important predictors of an anuran species if they were present in ≥ 5 models at a given spatial scale.

Results

At least 1 of the 5 focal anuran species was detected at 81 of the 93 sampling points. The spring peeper was detected at 55 of these points, followed by the green frog at 44, eastern gray treefrog at 35, and American toad at 34. The western chorus frog was found at 18 sites of the 71 within its range. Other species not included in our analysis but detected in coastal wetlands included the northern leopard frog (*Rana pipiens*) at 18 sampling points, wood frog (*Rana sylvatica*) at 15, bullfrog (*Rana catesbeiana*) at 2, and Blanchard's cricket frog (*Acris crepitans blanchardi*) at 1.

We performed 120 logistic regression models (30 subsets * 4 spatial scales) for each of the 5 focal anurans. The success of predictive models (based on McFadden's ρ^2 values) among subsets of sites were highly variable (Figure 2a–e). For example, although variables at the 500 m spatial scale were most effective at predicting the occurrence of the western chorus frog, ρ^2 values ranged from 0.088 to 0.963 among the 30 sub-samples. Despite this variability, comparisons among spatial scales yielded statistically significant differences in the ability of landscape variables to predict anuran species' occurrences (Table 3).

American toad occurrences were best predicted by variables at the 3000 and 100 m spatial scales ($p \leq 0.05$, Dunn's post test), although only 46.7% of the predictive models met the standard for acceptance (McFadden's $\rho^2 \geq 0.20$) at the 100 m spatial scale (Table 3). The relative area of developed land within the 3000 m radius showed a strong negative influence on American toad occurrences in coastal wetlands; this variable contributed significantly to 26 of 30 logistic regression models (Table 4d). The relative area of forested upland and fractal (box) dimension of all cover classes at the 3000 m scale also were negatively associated with American toad occurrence. Herbaceous upland was a significant contributor in 16 of 30 models at the 3000 m scale and was always positively associated with American toad occurrence. At the 100 m scale, American toads also were positively associated with the relative area of grass/sedge cover and negatively associated with

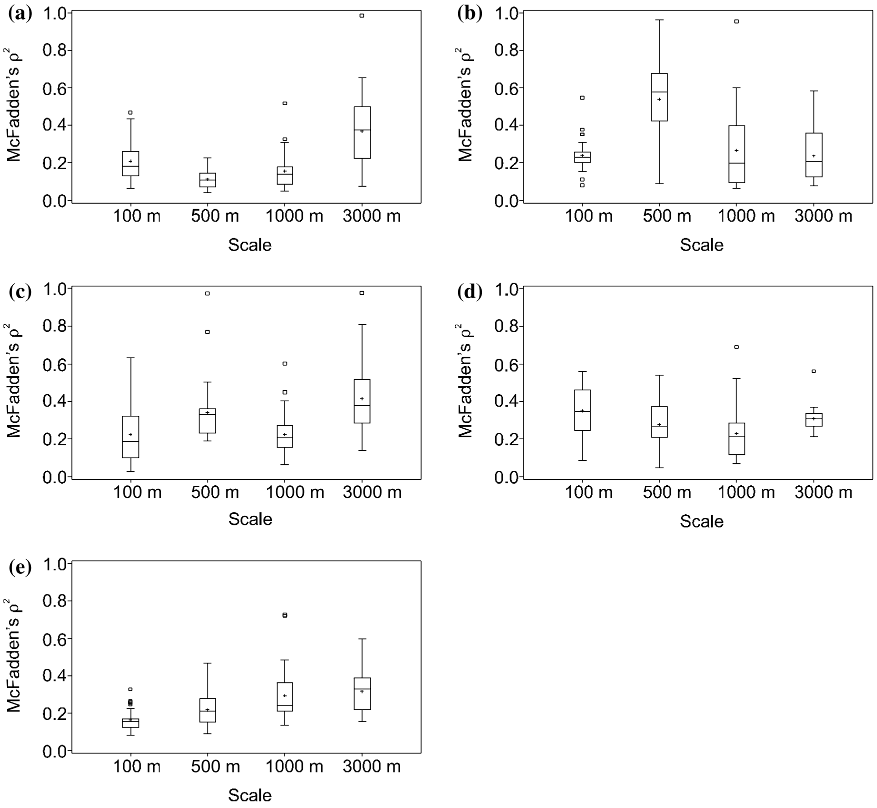

Figure 2. Box and whisker plots of the McFadden's ρ^2 values from logistic regression models for (a) American toad, (b) western chorus frog, (c) northern spring peeper, (d) eastern gray treefrog, and (e) green frog. The top and bottom edges of each box are located at the 75th and 25th percentiles respectively, while the center horizontal line is at the 50th percentile (median) and the mean is represented by a hash mark (SAS 8.0, SAS Institute 1999). Whiskers extend to the maximum and minimum ρ^2 values within 1.5 interquartile ranges and outliers (beyond 1.5 interquartile ranges) are represented by squares. We constructed one model based on each data subset ($n = 30$) for each species ($n = 5$) at each spatial scale ($n = 4$) for a total of 600 logistic regression models.

the relative area of forest and Shannon–Wiener Evenness (Table 4a).

The western chorus frog was the only anuran to have variables at a single scale (500 m) yield significantly better McFadden's ρ^2 values than models using variables from other spatial scales ($p \leq 0.05$, Dunn's post test, Table 3). Five variables were associated with chorus frog occurrence at the 500 m scale (Table 4b). Emergent herbaceous wetland with a high perimeter to area ratio was positively associated with chorus frogs in 28 of 30 logistic regression models. Edge density of water was the strongest negative association with chorus frog occurrences.

Variables at the 100, 500, and 3000 m spatial scales were not significantly different in their ability to predict the occurrences of eastern gray treefrogs ($p \leq 0.05$, Dunn's post test) (Table 3). Six variables were associated with eastern gray treefrog occurrence at the local scale (100 m) (Table 4a), notably wetland type, the relative area of grass/sedge cover (positive) and the relative area of forest (negative). The relative area of forested upland and fractal (box) dimension of all cover classes were positively associated with gray treefrog occurrences at the 500 m scale (Table 4b), suggesting that gray treefrogs prefer highly irregular cover class patches dispersed throughout large areas of forest. At the 3000 m scale, eastern gray treefrogs were strongly associated (negatively) with the relative area of urban/recreational grassland, which was identified in 20 models (Table 4d).

Spring peeper occurrences were best predicted by variables at the 3000 and 500 m spatial scales ($p \leq 0.05$, Dunn's post test) (Table 3). The spring peeper was associated with seven variables at the

Table 3. Results of nonparametric Friedman's test (Bradley 1968) comparing the predictive success (McFadden's ρ^2 of habitat variables measured at different spatial scales). We consider McFadden's $\rho^2 \geq 0.20$ as acceptable model fit (Hensher and Johnson 1981).

Common name (Friedman's test statistic)	Scale (m)	Rank sum	Dunn's grouping			Percent acceptable models
American toad	3000	104	A			80.0
(S = 32.12**)	100	80	A			46.7
	1000	67		B		20.0
	500	49		B		10.0
Gray treefrog	100	88	A			90.0
(S = 14.12*)	3000	82	A			100.0
	500	77	A			76.7
	1000	53		B		53.3
Spring peeper	3000	96	A			83.3
(S = 24.12**)	500	88	A			93.3
	100	61		B		50.0
	1000	55		B		53.3
Chorus frog	500	109	A			96.7
(S = 31.18**)	3000	66		B		50.0
	100	64		B		76.7
	1000	61		B		50.0
Green frog	3000	98	A			83.3
(S = 28.20**)	1000	84	A	B		76.7
	500	71		B	C	53.3
	100	47			C	23.3

* $p < 0.01$
** $p < 0.001$

3000 m scale including a positive association with relative area of forested upland and a negative association with developed land (Table 4d). Of the five variables associated with spring peepers at the 500 m scale, the relative area of woody wetland appeared in every logistic regression model (Table 4b). Other variables commonly associated with spring peepers at the 500 m scale included fractal (box) dimension of all cover classes and relative area of forested upland. Both variables were positively associated with spring peeper occurrences.

Landscape metrics at the 1000 and 3000 m scales were the most effective predictors of green frog occurrences ($p \leq 0.05$, Dunn's post test, Table 3). The green frog was associated with eight variables at the 3000 m scale and 10 at the 1000 m scale (Tables 4d and 4c). Green frog occurrence was negatively influenced by urban/recreational grassland and the relative area of developed land at the 3000 and 1000 m spatial scales, respectively. At the 3000 m scale, the perimeter-to-area ratio of water was included in 17 models.

Discussion

Our findings support the view that factors operating at multiple spatial scales influence the distribution of anurans. In general, variables associated with larger geographic scales (particularly 500 and 3000 m from the survey point) predicted the occurrence of anurans better than the local scale variables measured within 100 m of the survey point in Great Lakes coastal areas. Associations with landscape-scale variables highlight an important aspect of amphibian ecology: anurans require both aquatic and terrestrial habitats to complete their life cycles. Due to these multiple habitat requirements, the area needed to accurately predict species' occurrences must include both non-breeding and breeding habitats. Yet, all landscape scales did not perform identically in predicting occurrences of anuran species. These differences likely reflect species-specific habitat preferences and amphibian population dynamics.

Associations with variables measured at the 500 m scale suggest that the condition and type of habitat adjacent to coastal wetlands may be particularly important to some species. Many amphibian species have specific non-breeding habitat preferences. For example, eastern gray treefrogs and spring peepers spend the majority of their lives in forests or wooded wetlands after the breeding season (Harding 1997). In our analysis, both eastern gray treefrogs and spring peepers exhibited strong associations with these variables at the 500 m scale. The western chorus frog was also predicted effectively by variables at the 500 m scale. Chorus frogs often breed in roadside ditches, marshes and other ephemeral wetland habitats (Wright and Wright 1949; Vogt 1981; Harding 1997) and remain close to their breeding sites throughout the year (Kramer 1973). In the Great Lakes coastal zone, western chorus frog occurrence was consistently associated positively with a high perimeter-to-area ratio of emergent wetlands and negatively with edge density of water. Species that were poorly predicted by variables at the 500 m scale, like the American toad and green frog, may be less specific in their habitat requirements in and near breeding sites. Alternatively, the habitat associations of these species might integrate a broader landscape context because individuals are more mobile and encounter a greater variety of habitat conditions during their lifetime.

Table 4. Habitat variables at the (a) 100 m, (b) 500 m, (c) 1000 m, and d) 3000 m spatial scales strongly associated with the occurrences of 5 anuran species in coastal wetlands of the western Great Lakes. Importance was judged by the frequency that a variable was present in logistic regression models. Tallies (number of models) for variables occurring in ≥ 5 models are included along with their influence (+ or –) on each anuran. Abbreviations for habitat variables are described in Table 2.

Habitat Variables	American toad	Chorus frog	Spring peeper	Gray treefrog	Green frog	Total
(a) 100 m						
Wetland type	–	28	11	28	–	67
RA – grass/sedge	13+	–	–	17+	–	30
RA – forest	14–	–	–	12–	–	26
RA – submergent vegetation	–	–	–	–	23+	23
RA – rush	13+	–	–	–	–	13
RA – giant reed	–	–	13–	–	–	13
Wetland size	–	–	–	12	–	12
RA – urban/recreational grassland	–	11+	–	–	–	11
SWE	10–	–	–	–	–	10
RA – cattail/bur-reed	–	–	–	10–	–	10
RA – water	–	–	–	10+	–	10
(b) 500 m						
RA – forested upland	–	–	16+	19+	22+	57
FDB – all cover classes	–	–	20+	23+	–	43
PA – developed land	12–	8–	13–	–	–	33
RA – herbaceous planted/cultivated	–	11+	–	10+	10+	31
RA – woody wetland	–	–	30+	–	–	30
PA – emergent herbaceous wetland	–	28+	–	–	–	28
ED – water	–	26–	–	–	–	26
RA – barren land	6–	–	–	–	14–	20
PA – herbaceous upland	–	–	–	18–	–	18
RA – emergent herbaceous wetland	8+	–	–	–	–	8
RA – herbaceous upland	–	–	–	7–	–	7
PA – woody wetland	–	–	6+	–	–	6
PA – all cover classes	–	–	–	5–	–	5
CCI – herbaceous upland	–	5+	–	–	–	5
(c) 1000 m						
RA – developed land	–	–	10–	17–	13–	40
RA – woody wetland	–	–	19+	–	5–	24
FDB – all cover classes	–	6+	6–	–	12–	24
PA – developed land	23–	–	–	–	–	23
RA – forested upland	–	–	19+	–	–	19
PA – barren land	–	9–	–	–	7+	16
PA – herbaceous upland	–	–	–	15–	–	15
PA – forested upland	–	–	–	12–	–	12
ED – water	–	12–	–	–	–	12
RA – urban/recreational grassland	–	–	–	–	11–	11
RA – herbaceous planted/cultivated land	–	–	–	5+	6+	11
RA – emergent herbaceous wetland	–	–	–	–	10+	10
PA – herbaceous planted/cultivated land	–	–	–	5–	5–	10
PA – emergent herbaceous wetland	–	10+	–	–	–	10
EDE – all cover classes	–	–	–	8–	–	8
CCI – herbaceous planted/cultivated	–	8+	–	–	–	8
PA – water	–	–	–	–	7+	7
CCI – forested upland	–	–	–	–	7+	7
CCI – water	–	7+	–	–	–	7
RA – barren land	–	–	5+	–	–	5
ED – all cover classes	–	5+	–	–	–	5
(d) 3000 m						
RA – developed land	26–	–	13–	11–	7–	57
PA – urban/recreational grassland	–	–	6–	20–	19–	45
RA – forested upland	16–	–	18+	–	–	34

Table 4. (contd).

Habitat Variables	American toad	Chorus frog	Spring peeper	Gray treefrog	Green frog	Total
PA – water	9+	–	5+	–	17+	31
SWE – all cover classes	–	17–	–	12–	–	29
FDB – all cover classes	21–	–	7–	–	–	28
RA – urban/recreational grassland	–	–	6–	–	20–	26
CCI – herbaceous upland	–	18+	–	–	–	18
RA – herbaceous upland	14+	–	–	–	–	14
PA – woody wetland	–	–	–	–	11+	11
PA – developed land	10–	–	–	–	–	10
RA – woody wetland	–	–	10+	–	–	10
PA – herbaceous planted/cultivated land	7–	–	–	–	–	7
PA – emergent herbaceous wetland	–	7+	–	–	–	7
ED – water	–	–	–	–	7–	7
RA – herbaceous planted/cultivated land	–	–	–	6–	–	6
PA – herbaceous upland	–	–	–	5–	–	5
PA – barren land	–	–	–	–	5+	5
ED – all cover classes	–	–	–	–	5–	5

Associations with variables at large spatial scales also may reflect amphibian population dynamics. Amphibians that require both terrestrial and aquatic habitat often occur in a set of populations connected via dispersal (metapopulation) within a large geographic area (Hanski and Simberloff 1997; Dodd and Smith 2003). Amphibian metapopulation dynamics are influenced by the number of individual amphibians dispersing among breeding sites (Sjögren 1991) and by the density and distribution of wetlands in the landscape (Semlitsch and Bodie 1998; Semlitsch 2000). Most adult amphibians exhibit very low dispersal rates and display fidelity to the site where they first reproduce (Oldham 1966; Gill 1978; Berven and Grudzien 1990 but see Perret et al. 2003). Dispersal between local populations mainly occurs in juveniles (Schroeder 1976; Berven and Grudzien 1990). Juvenile dispersal capabilities, which are influenced by both physiological constraints (Sinch 1990) and characteristics of the landscape (deMaynadier and Hunter 1999; Marsh and Trenham 2001; Rothermel and Semlitsch 2002; Squire and Newman 2002), determine the scales at which amphibian metapopulation dynamics operate. Juvenile dispersal is necessary for the continued functioning of amphibian metapopulation dynamics because it permits the recolonization of locally extinct or declining populations (Brown and Kodric-Brown 1977).

Recolonization may be particularly important for anuran persistence in Great Lakes coastal wetlands, where water levels fluctuate hourly, seasonally, and yearly (Keough et al. 1999). These natural water level fluctuations change the type of coastal community, which influences the animal species inhabiting coastal wetlands (Harris et al. 1981; Maynard and Wilcox 1997; Keough et al. 1999). During 2002, the average water levels of Lake Michigan and Lake Huron had been at the lowest point in over 25 years (NOAA 2002). The coastal wetlands we surveyed were characterized by patches of open water scattered within large expanses of emergent vegetation. The emergent vegetation effectively isolated amphibian breeding sites from the Great Lakes. During periods of high water, aquatic submergent plant communities (e.g., *Najas flexilis*, *Vallisneria americana*, *Zizania aquatica*, *Myriophyllum spicatum)* and open water areas may dominate the wetland community. Shoreline wetlands may be non-existent and other wetlands in the coastal zone may be frequently connected to the Great Lakes. This would subject amphibians to increased predation from fish, wave action, and storm surges and could result in local population extinctions due to poor breeding habitat.

Periodic extinctions due to high water could be overcome by immigration from neighboring populations. However, cover types that impede recolonization may be particularly detrimental. All anurans in our analysis displayed negative associations with developed land or urban/recreational grassland. Previous landscape scale studies have also revealed that urbanization is negatively correlated with amphibian abundance or occurrence (Gibbs 1998; Hecnar and M'Closkey 1998;

Knutson et al. 1999; Lehtinen et al. 1999). Urbanization contributes to the complete loss of habitat which can eventually lead to local population extinction; however the infrastructure and other anthropogenic characteristics of urbanized landscapes also influence anuran distributions. In particular, habitat fragmentation caused by roads can reduce amphibian abundance and isolate populations by impeding amphibian movements across landscapes (Fahrig et al. 1995; Ashley and Robinson 1996; Findlay and Houlahan 1997; Carr and Fahrig 2001). Reh and Seitz (1990) and Hitchings and Beebee (1997) have shown that genetic divergence among populations is positively correlated with urban development in the surrounding landscape. Human-subsidized predators and exotic species are often more prolific in urbanized areas (Richter and Azous 1995). Great Lakes coastal areas continue to experience habitat changes due to human activities, primarily in the form of shoreline cottage development and urban sprawl (Maynard and Wilcox 1997); in many places, these changes are likely to threaten the persistence of amphibian populations.

Other anthropogenic variables may also influence the distribution of anurans among coastal wetlands. A recent study in the Midwest showed that old fields hinder the dispersal abilities of juvenile amphibians by causing increased mortality due to higher temperatures and lack of moist microhabitats (Rothermel and Semlitsch 2002). In our study, herbaceous planted/cultivated land showed both negative and positive associations with different anuran species, perhaps reflecting different habitat preferences or sensitivities to agricultural settings. Drainage ditches and other habitat modifications may serve as dispersal corridors or replace natural wetlands in agricultural landscapes (Schroeder 1976; Reh and Seitz 1990).

The habitat associations revealed by our analysis do not necessarily imply direct cause–effect relationships between environmental conditions and anuran populations, but they nevertheless provide interpretable predictors of occurrences at several spatial scales of reference. Unmeasured factors such as water chemistry and presence of predators surely are important for survival of anurans in coastal wetlands, but these variables are often difficult to measure and change on a day-to-day or short term basis due to the dynamic nature of the coastal environment (Keough et al. 1999). Habitat suitability of anurans might also be judged by a measure other than presence–absence, such as population density or reproductive success, especially since anurans may persist in habitats that have recently become degraded. Additionally, the short-term duration of this study might have limited our ability to detect all species present. However, the five species in our analysis have fairly long breeding seasons, and therefore they are likely to have been detected during at least one survey period.

This multi-scale investigation of anuran–habitat associations in Great Lakes coastal wetlands underscores the importance of scale for the conservation and assessment of anuran populations. Our results concur with other studies (Beebee 1985; Pavignano et al. 1990; Hecnar and M'Closkey 1998, Johnson et al. 2002) suggesting that factors at both the landscape and local-scale can affect amphibian occurrences, but landscape-scale variables often are better predictors than local wetland characteristics. Variables measured at one landscape scale did not adequately predict occurrences of all species, and models constructed at several spatial scales of reference were needed to identify the most effective predictors of anuran occurrence. The most appropriate scales for evaluating anuran–habitat associations will differ among species due to differences in core habitat needs, life histories and perhaps population structure. In nearly every case, populations of anurans in coastal wetlands of the western Great Lakes appear to be sensitive to anthropogenic effects of urbanization.

Our findings suggest that surveys of anuran populations can contribute significantly to assessments of ecological condition in the Great Lakes coastal zone. Although amphibians represent only part of the ecological picture, their presence reflects habitat conditions over a rather large range of spatial scales. Some species are sensitive to local conditions while others respond to more extensive landscape-scale variables. A multi-species or multimetric index (Karr 1981; Simon 2003) that includes frogs and toads therefore will address several important dimensions of ecological condition. In other words, because these species are sensitive to human impacts at multiple scales, assessment of anuran populations should be included in long-term monitoring of human impacts on Great Lakes ecosystems.

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