ORIGINAL PAPER

Great Lakes coastal wetland habitat use by seven turtle species: influences of wetland type, vegetation, and abiotic conditions

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Received: 15 February 2011/Accepted: 30 November 2011/Published online: 14 December 2011 © Springer Science+Business Media B.V. 2011

Abstract Great Lakes coastal wetlands are important habitats for turtles but few studies have looked at factors driving community structure in these systems. We evaluated the effects of wetland type, vegetation, and abiotic conditions on turtle communities for 56 wetlands in Lakes Huron, Michigan, and Superior with data collected during the summers of 2000–2008. Overall, 1,366 turtles representing seven species were captured using fyke nets. For the majority of species, catches were highest in drowned river mouth wetlands In addition, turtles tended to be more abundant in water lilies, submersed aquatic vegetation, and cattails

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Institute for Great Lakes Research, CMU Biological Station, Department of Biology, Central Michigan University, Brooks Hall 217, Mt. Pleasant, MI 48859, USA compared to bulrush. We also found positive correlations between catches of four of the species as well as total turtle catch and turtle species richness with a human disturbance gradient. These correlations suggest that turtles may be able to utilize coastal wetland areas that are inhospitable to fish because of hypoxic conditions. Our results show the importance Great Lakes coastal wetlands to turtles, and stress the need for managers to take into account turtle populations when preparing conservation and restoration strategies.

Keywords Coastal wetlands · Great Lakes · Turtles · Community composition · *Chelydra serpentine* · *Chrysemys picta* · *Graptemys geographica* · *Emydoidea blandingii* · *Apalone spinifera* · *Trachemys scripta* · *Sternotherus odoratus*

Introduction

Aquatic turtles can play a significant role in lake, stream, and wetland ecosystems due to their large biomass per area (Iverson 1982) and their ability to feed at various trophic levels (Alexander 1943). The Great Lakes region contains 11 different species of freshwater turtles (Harding 1997), which is a greater diversity than many other parts of North and South America (Stephens and Weins 2003). Turtles can form

important linkages within aquatic habitats (e.g., lakestream, wetland-pelagic) and between terrestrial and aquatic environments due to their different habitat requirements for basking, feeding, mating, nesting, and hibernation (Bodie and Semlitsch 2000; Congdon et al. 1994; Congdon and Gibbons 1996; Klemens 2000).

The complex habitat requirements of turtles, especially their need for suitable aquatic-terrestrial habitat corridors, make aquatic turtle populations especially vulnerable to anthropogenic impacts (Burke and Gibbons 1995; DeCatanzaro and Chow-Fraser 2010). Road mortality, in particular, has been implicated in population declines and male-biased sex ratios for a number of freshwater turtle species (Aresco 2005; DeCatanzaro and Chow-Fraser 2010; Gibbs and Steen 2005; Steen and Gibbs 2004). Nest predation by mammals such as raccoons (*Procyon lotor*), which are often associated with anthropogenic stressors, is another significant source of mortality (Marchand et al. 2002). Finally, most freshwater turtle species are long-lived, making them susceptible to bioaccumulative toxicants which can further impact their populations (Bishop et al. 1998; Bishop and Gendron 1998). However, despite their importance in aquatic food webs, their vulnerability to anthropogenic stressors, and their observed population declines, turtles remain largely overlooked in aquatic ecosystem research relative to other faunal groups (Bishop and Gendron 1998; Bodie and Semlitsch 2000). In the Laurentian Great Lakes region specifically, very little information is available to explain turtle abundance or habitat preference in coastal wetland habitats (e.g., Burton and Uzarski 2009; Tran et al. 2007). DeCatanzaro and Chow-Fraser (2010) recently explored turtle abundances in relation to anthropogenic disturbance in coastal wetlands of Georgian Bay, Lake Huron and Lakes Erie and Ontario. Our study also explores relationships between turtle populations and anthropogenic disturbance but focuses on coastal wetlands of Lakes Michigan, Superior, and Huron.

There is growing consensus among scientists and resource managers that coastal wetlands are a critical component of the Great Lakes ecosystem (Bouchard 2007; Jude et al. 2005; Lake Michigan LaMP 2008; GLRCS 2005; Uzarski et al. 2005). However, over 50% of pre-settlement coastal wetland area has been lost, with losses exceeding 95% in some locations (Brazner and Beals 1997; Comer et al. 1995; Krieger et al. 1992; Whillans 1982). Many remaining wetlands suffer from fragmentation (Gyekis 2006; Uzarski et al. 2009), nutrient and sediment loading (Uzarski et al. 2005), and invasive species (Jude et al. 2005). In addition to turtles, Great Lakes coastal wetlands provide critical habitat for more than 80 species of fish (Jude and Pappas 1992; Uzarski et al. 2005), over 260 macroinvertebrate taxa (Burton et al. 2002; Cardinale et al. 1998; Cooper et al. 2007; Gathman et al. 1999), at least 20 mammal species, 80-90 bird species (Prince et al. 1992; Prince and Flegel 1995; Weeber and Vallianatos 2000), and at least 20 amphibian species (Burton and Uzarski 2009; Weeber and Vallianatos 2000). While turtles are a key component of coastal wetland food webs, it remains unclear how they interact with other faunal groups or respond to chemical and physical stressors since little research has been devoted to turtles. Furthermore, conservation strategies for Great Lakes coastal habitats rarely include turtles explicitly due to the lack of habitat preference and distributional data available for this group.

Our goal in this study was to describe habitat preferences and relative abundances of seven turtle species in Great Lakes coastal wetlands using incidental catch from an 8-year fish monitoring dataset that included wetlands of Lakes Michigan, Huron, and Superior. Turtles were documented as by-catch during the monitoring efforts and we used these data to explore turtle distributions among three coastal wetland types and six vegetation types to determine predominant patterns in wetland habitat use by the seven species. We also compared turtle distributions to gradients in ambient chemical and physical conditions to further explain patterns in habitat use and identify relationships between turtle populations and human disturbance. Our working hypothesis was that turtle distributions would vary by both wetland type and dominant vegetation type and that catches of at least some species would correlate with human disturbance and system productivity.

Methods

Study sites

We analyzed turtle by-catch data from 56 wetlands located along the Michigan shoreline of Lakes Fig. 1 Map of the state of Michigan within its location with the contiguous United States showing locations of wetlands where turtle communities where sampled (as by-catch) between 2000 and 2008. At each location, multiple vegetation types were sampled if available



Michigan, Huron, and Superior (Fig. 1). All sampling was conducted during the summer (July to September) from 2000 to 2008, though no sampling was conducted in 2007. Three wetland types were sampled; drowned river mouths (n = 17), protected embayments (n = 14), and fringing exposed (n = 25), which were characterized according to Albert (2003), Albert and Minc (2001), and Keough et al. (1999). Drowned river mouth wetlands occur where tributary rivers widen to form a broad wetland complex before discharging into a coastal lake or a Great Lake (Albert 2003; Cooper et al. 2007). Drowned river mouth wetlands are hydrologically influenced by the adjacent Great Lake because they are connected via channels but are protected from Great Lake wave energy, which allows deep organic matter accumulation (Keough et al. 1999; Albert 2003; Nelson et al. 2009). Protected embayment wetlands occur among rock/till complexes where shoreline morphology protects shallow lacustrine habitat from wind and wave energy, allowing emergent vegetation to persist (Keough et al. 1999; Albert 2003). The protected embayment wetlands that we sampled all had a direct surface water connection to the adjacent Great Lake. Fringing exposed wetlands form where gradually sloping bathymetry or geomorphic features such as sand bars provide enough protection from wave energy for emergent vegetation to persist but are generally subject to more hydrologic energy than protected embayments which results in very little organic matter accumulation in the emergent zone of these wetlands (Keough et al. 1999; Albert 2003). The three wetland types we sampled represent a gradient of increasing exposure to wave energy and longshore currents from drowned river mouths (virtually no wave or longshore current energy), to protected embayments (moderate wave and current energy), to fringing exposed wetlands (heavily influenced by waves and currents) (Albert 2003; Uzarski et al. 2009).

Our sampling protocol was designed for monitoring coastal wetland fish communities (e.g., Cooper et al. 2007, 2009; Uzarski et al. 2005) and specific study objectives varied throughout the 8-year period. However, sampling methodology remained consistent and followed Great Lakes Coastal Wetlands Consortium protocols (GLCWC 2008). Our criteria for choosing specific areas to sample within each wetland included: sufficient depth (0.2-1.0 m) and inundated area for sampling with fyke nets (approximately 200 m²), a well-developed plant community, and access by boat. Within each wetland, sampling was stratified by 'vegetation zones' which were near-monodominant stands of given plant types (i.e., >75% coverage; Burton et al. 2004; Uzarski et al. 2005). Vegetation zone types included: Nuphar advena and Nyphaea oderata (hereafter: 'lily'), Typha spp. (hereafter: 'cattail'), Schoenoplectus spp. (hereafter: 'bulrush'), Sparganium spp. (hereafter: 'bur reed'), Peltandra virginica (hereafter: 'arrow arum'), and submersed aquatic vegetation (hereafter: 'SAV'). The majority of SAV consisted of dense beds of Myriophyllum spicatum, though most SAV beds also contained Ceratophyllum demersum and several species of Potamogeton, especially Potamogeton crispus. In wetlands where multiple vegetation types were available, we sampled each of them, which resulted in 81 unique locations over the study period (mean of 1.5 vegetation zones per wetland). Stratifying our sampling by vegetation type was necessary to meet the original study objectives (fish monitoring) but also allowed us to explore patterns in turtle distributions among both vegetation and wetland type.

Sampling

Two sizes of fyke nets were used, depending on water depth. Small nets had 0.5-m tall \times 1-m wide mouths and were set in 30 to 50-cm deep water. Large nets had 1-m \times 1-m mouths and were set in 50–100-cm deep water. Both net sizes had 4.8 mm mesh (bar measurement) and leads that extended 7.3 m from the middle of the mouth of each net. Wings extended 1.8 m from each side of the mouth of each net at approximately 45° to the lead. Nets were set either within the vegetation zone of interest or just outside the vegetation zone with the lead extending into the habitat (Brazner and Beals 1997; Brazner et al. 1998; Uzarski et al. 2005). A portion of the cod-end of each net was suspended above the water surface to allow captured turtles access to the atmosphere. Upon hauling nets, turtles were identified to species, enumerated on site, and released immediately. Others have also found fyke nets to be an effective method for capturing aquatic turtles (DeCatanzaro and Chow-Fraser 2010; Dreslik and Phillips 2005; Vogt 1980).

During each sampling trip, a minimum of three unbaited nets were set overnight (12-24 h) within each vegetation zone. We considered a 'net-night' to equal one net set for one night and our 8-year dataset contained a total of 725 net-nights. For locations that were visited multiple times, the same general wetland area was sampled each time (i.e., the same vegetation zone was sampled), though specific net locations varied somewhat. Since a few wetlands were sampled more frequently than others (e.g., some locations were sampled annually while others were sampled only once over the 8 years), there was the potential for locations that were sampled multiple times to have inflated power in our analyses. To account for this, we standardized the dataset so that each vegetation zone within each wetland was represented by average turtle catches per net-night, which included all years that a location was sampled. In total, 81 sampling locations (i.e., vegetation zones) distributed across 56 coastal wetlands were sampled at least once during the period.

Abiotic conditions

To characterize ambient conditions, basic chemical and physical parameters were measured during each site visit, except in 2000. Water samples for analysis of soluble reactive phosphorus (SRP), nitrate, ammonium, sulfate, chloride, and total alkalinity were collected in 1-l acid-washed polyethylene bottles. Temperature, dissolved oxygen (DO), turbidity, pH, and specific conductance were measured in situ using either a HydroLab DataSonde 4a (Hach Corporation, Loveland, Colorado) or a Yellow Springs Instruments (Yellow Springs, Ohio) model 6600. Samples and in situ measurements were collected at mid-depth prior to setting fyke nets. Analytical and quality assurance/ quality control procedures followed protocols recommended by APHA (American Public Health Association) (1998). Additionally, in 2003 and 2006, thickness of the organic sediment layer was measured at a subset of locations (n = 26) by gently pushing a wooden meter stick into the sediment until a firm layer was reached.

Statistical analysis

Turtle catch data did not approximate normal distributions so we used nonparametric statistical tests to identify and explain the predominant patterns in our dataset. We tested whether the catch per net-night of each turtle species, the total number of turtles captured, or turtle species richness differed among wetland types or vegetation types using one-way Kruskal-Wallis tests. When significant effects were found, we made post-hoc pair-wise comparisons using Mann-Whitney U-tests to identify which wetland or vegetation types differed. Species richness was calculated as the total number of species observed in each vegetation zone over the entire study period. We applied a Bonferroni correction to each family of tests to control for the increased risk of Type-1 error due to multiple comparisons by dividing an alpha of 0.05 by the number of comparisons being conducted in each set of analyses. For example, for each set of nine Kruskal-Wallis tests used to compare catches of each species, total turtle catch, and species richness among vegetation types and wetland types, we divided our a priori alpha of 0.05 by 9 to yield an adjusted alpha of 0.006. Then, for post-hoc Mann-Whitney U-tests, we divided alpha by the number of comparisons made for each family of tests (i.e., 3 post-hoc wetland type comparisons yielded an adjusted alpha of 0.017 while 15 post-hoc vegetation type comparisons yielded an adjusted alpha of 0.003).

To identify patterns in ambient chemical/physical conditions that could potentially provide insight into turtle distributions, we conducted principal components analysis (PCA) on the correlation matrix of the eleven abiotic variables. This technique was used to summarize the 11 abiotic variables into synthetic axes representing trends in overall wetland conditions. We recognized that some of the individual variables may not be important in structuring turtle communities directly (e.g., specific conductance, alkalinity). However, by combining all 11 variables into principal components, the most general trends in abiotic conditions could be explored as potentially influencing turtle distributions. For the PCA and subsequent comparisons with the turtle community, we included each set of observations made over the eight sampling years (n = 150). In other words, if a location was sampled in multiple years, data from each separate year were included in the PCA. We chose to use this larger chemical/physical dataset in an effort to maximize the statistical power of our exploratory turtle-abiotic analyses. To determine which variables loaded most heavily into each principal component, we compared eigenvector values. We then calculated Spearman rank-order correlation coefficients between PC scoresrepresenting ambient chemical/physical conditionsand turtle catches and species richness. Since our turtle data were acquired from a fish monitoring database, we also explored the relationship between PC scores and total fish CPUE for comparison to turtle catches. Additionally, since relationships between abiotic conditions and turtle communities may have been confounded by wetland type (e.g., if abiotic conditions and turtle communities both varied by wetland type), we conducted separate PCAs for each wetland type and compared the resulting PC scores to turtle catches and species richness within each wetland type separately.

Observations on the thickness of the organic sediment layer were available for only 26 locations so this variable was not included in the PCAs. Instead, we calculated Spearman rank-order correlation coefficients between organic sediment thickness and catch per net-night for each species as well as total species richness.

Kruskal–Wallis and Mann–Whitney *U*-tests as well as Spearman rank-order correlation coefficients were calculated using MyStat version 12 (Systat Software Incorporated, Chicago, Illinois). Critical values for Spearman rank-order correlations followed Ramsey (1988). Principal component analyses were conducted using SAS version 9.1 (SAS Institute, Cary, North Carolina).

Results

Turtle catches

A total of 1,366 turtles representing seven species were captured over the eight sampling years (Fig. 2). Species included: common snapping (*Chelydra serpentina*), painted (*Chrysemys picta*), map (*Graptemys geographica*), Blanding's (*Emydoidea blandingii*), spiny softshell (*Apalone spinifera*), red-eared slider (*Trachemys scripta*), and musk (*Sternotherus odoratus*).

Drowned river mouth, protected embayment, and fringing exposed wetlands contained at least one turtle



Fig. 2 Mean (+SE) turtle catch net-night⁻¹ for seven species in three wetland types (**a**) and six vegetation types (**b**) sampled between 2000 and 2008

in 57, 32, and 8% of nets respectively. We found significant differences in catch per net-night among wetland types for all species except Blandings, redeared slider and spiny softshell turtles (Table 1; Fig. 2). We also found significant differences in total catch and species richness among wetland types (Table 1). Subsequent pair-wise Mann-Whitney U-tests revealed that catches of map, musk, painted, and common snapping turtles as well as species richness and total abundance were all greater in drowned river mouth wetlands than fringing exposed wetlands. Map and common snapping turtles were also greater in drowned river mouth than protected embayment wetlands (Table 1). Additionally, catches of painted turtles as well as total turtle catch and species richness were higher in protected embayment wetlands than fringing exposed wetlands (Table 1).

We found significant differences in catch per netnight among vegetation types for all species except Blanding's and red-eared slider turtles (Table 2; Fig. 2). We also found significant differences among vegetation types for total catch and species richness. Pair-wise Mann–Whitney *U*-tests revealed a number of differences between vegetation types (Table 2) and, in general, turtles tended to be more abundant in water

Table 1 Kruskal–Wallis and Mann–Whitney *U*-test *P* values comparing turtle catch net-night⁻¹ for seven species as well as total turtle catch and species richness among wetland types (drowned river mouth [n = 41], DR; fringing exposed [n = 26], FE; protected embayment [n = 14], PE)

	Kruskal– Wallis	DR > FE	DR > PE	PE > FE
Blanding's	0.044	_	_	_
Мар	<0.001	<0.001	0.005	1.000
Musk	0.004	0.007	0.044	1.000
Painted	<0.001	<0.001	0.703	0.001
Red-eared	0.069	-	_	-
Common snapping	<0.001	<0.001	0.002	0.479
Spiny softshell	0.077	-	_	-
Total catch	<0.001	<0.001	0.050	0.001
Species richness	<0.001	<0.001	0.028	0.003

Kruskal–Wallis tests were conducted first and if significant differences were detected, Mann–Whitney *U*-tests were conducted post-hoc to identify specific differences. Values that are less than our Bonferroni-corrected alpha (P = 0.006 for Kruskal–Wallis tests and P = 0.017 for post-hoc Mann–Whitney *U*-tests) are bolded

lilies, submersed aquatic vegetation, and cattails compared to bulrush (Table 2; Fig. 2). Note that for these analyses we excluded observations from eight locations because they did not fit into one of our six discrete vegetation categories (i.e., they were mixed vegetation zones).

Abiotic conditions and turtles

Principal components analysis of abiotic variables revealed a gradient of increasing anthropogenic disturbance/productivity in principal component (PC) 1. This gradient included increasing specific conductance, chloride, and alkalinity and decreasing dissolved oxygen, temperature, and pH along PC 1, which explained 27.7% of the variance in the correlation matrix (Table 3). Principal components analysis of abiotic variables from each individual wetland type revealed similar gradients of increasing specific conductance, chloride, and alkalinity in PC 1 (Table 3) suggesting that these trends represented the most prominent pattern in water quality in all three wetland types.

Table 2 Kruskal–Wallis and Mann–Whitney *U*-test *P* values comparing turtle catch net-night⁻¹ for seven species as well as total turtle catch and species richness among vegetation types

		Map	Blanding's	Musk	Painted	Red- eared	Common snapping	Spiny softshell	Total catch	Species richness
Kruskal–Wallis tests										
		<0.001	0.151	0.002	0.006	0.897	<0.001	<0.001	0.001	<0.001
Pair-wise Mann–Whitne	ey U-tests									
Lily $(n = 15)$	Arrow arum	0.045	-	0.166	0.326	_	0.087	0.291	0.182	0.082
	SAV	0.029	-	0.656	0.197	-	1.000	0.042	0.330	0.168
	Bulrush	0.002	-	<0.001	0.005	-	<0.001	0.021	0.002	0.001
	Bur reed	0.282	-	0.106	0.215	_	0.259	0.402	0.113	0.156
	Cattail	0.797	-	0.251	0.373	_	0.974	0.291	0.897	0.360
Arrow arum $(n = 8)$	SAV	0.003	_	0.472	0.068	_	0.044	0.030	0.052	0.007
	Bulrush	0.517	-	0.027	0.148	_	0.222	1.000	0.305	0.524
	Bur reed	0.206	-	0.429	0.546	_	0.721	1.000	0.763	0.878
	Cattail	0.064	-	0.927	0.742	_	0.203	1.000	0.185	0.237
SAV $(n = 6)$	Bulrush	<0.001	-	<0.001	0.001	_	<0.001	<0.001	0.001	<0.001
	Bur reed	0.021	-	0.176	0.065	_	0.065	0.077	0.044	0.016
	Cattail	0.026	_	0.472	0.117	_	0.696	0.030	0.272	0.018
Bulrush ($n = 39$)	Bur reed	0.253	_	1.000	0.489	_	0.072	1.000	0.527	0.419
	Cattail	0.012	_	0.027	0.438	_	<0.001	1.000	0.007	0.012
Bur-reed $(n = 5)$	Cattail	0.371	-	0.429	0.758	-	0.314	1.000	0.210	0.410

Kruskal–Wallis tests were conducted first and if significant differences were detected, Mann–Whitney *U*-tests were conducted posthoc to identify specific differences. Values that are less than our Bonferroni-corrected alpha (P = 0.006 for Kruskal–Wallis tests and P = 0.003 for post-hoc Mann–Whitney *U*-tests) are bolded

Principal Component 1 scores from the PCA of all wetland data were positively and significantly correlated with catches of map (Spearman r = 0.328, P < 0.01), musk (Spearman r = 0.341, P < 0.01), painted (Spearman r = 0.328, P < 0.01), common snapping (Spearman r = 0.459, P < 0.001), and all turtles (Spearman r = 0.402, P < 0.001), as well as species richness (Fig. 3). Catches of Blanding's and spiny softshell turtles did not correlate with PC 1 scores. No analyses were done on red-eared slider abundances because only 6 were captured. In contrast to turtle catches, the correlation between PC 1 and total fish CPUE was negative and significant (Spearman r = -0.205, P < 0.01).

Within fringing exposed wetlands alone, total turtle catch and species richness correlated positively and significantly with PC 1 of the fringing exposed wetland PCA (P < 0.01); painted and common snapping turtle catches also correlated positively, though marginally (0.05 < P < 0.10), with PC 1 of this analysis. Within drowned river mouth wetlands alone,

musk, painted, and common snapping turtle catches as well as total turtle catch and species richness all correlated positively and significantly (P < 0.05) with PC 1 of the drowned river mouth PCA. No significant correlations were found between abiotic conditions and turtle catches or species richness in the protected embayment wetlands when analyzed separately.

In the 26 wetland locations where organic sediment depth was measured, organic depth was positively correlated with catches of map (P < 0.01), musk (P < 0.01), painted (P < 0.001), and common snapping (P < 0.001) turtles as well as total turtle catch (P < 0.001) and species richness (P < 0.01).

Discussion

As in many other shallow freshwater ecosystems, turtles in Great Lakes coastal wetlands have been largely overlooked by researchers. By using turtle by-catch data from an 8-year fish monitoring dataset,

	All wetlands	Drowned river mouths	Protected embayments	Fringing exposed
Variance explained	27.7%	28.2%	32.3%	25.7%
Eigenvector values				
Specific conductance	0.531	0.527	0.502	0.539
Chloride	0.466	0.484	0.486	0.457
Alkalinity	0.416	0.396	0.447	0.375
Nitrate	0.302	0.233	-0.134	0.239
Turbidity	0.287	0.366	0.401	0.030
Sulfate	0.231	0.209	0.287	0.152
Ammonium	0.231	0.256	0.058	0.198
Soluble reactive P	0.056	-0.065	-0.127	0.058
pH	-0.064	0.102	-0.001	-0.303
Temperature	-0.101	-0.055	0.050	0.149
Dissolved oxygen	-0.172	-0.129	0.172	-0.350

 Table 3
 Variance explained by and eigenvector values for the first principal component from four different principal component analyses

The first principal component analysis was conducted on abiotic data from all wetlands (n = 150). Subsequent analyses were conducted on abiotic data from drowned river mouths only (n = 78), protected embayments only (n = 25), and fringing exposed wetlands only (n = 47). Abiotic variables are arranged from high to low principal component 1 values from the analysis of all wetlands



Fig. 3 Relationship between turtle species richness and principal component 1 from a principal components analysis of 11chemical and physical variables. Principal component 1 explained 27.7% of the variance in the chemical and physical dataset and represented a gradient from sites with relatively high dissolved oxygen, temperature, and pH to sites with relatively high specific conductance, chloride, and alkalinity. *Shapes* of points represent wetland types (*triangle*, drowned river mouth; *circle*, protected embayment; *square*, fringing exposed)

we found substantial numbers of turtles in all three coastal wetland types sampled. However, turtle catch and species richness were both significantly greater in drowned river mouth wetlands than fringing exposed systems. In addition, catches of two species were greater in drowned river mouth wetlands than protected embayment wetlands. Consistent with these differences in turtle community structure were a number of chemical and geomorphic differences between the three wetland types. Because of their geomorphology, drowned river mouth wetlands generally are exposed to very little wave action and retain more benthic organic matter than embayment or fringing wetlands which are exposed to greater wave energy and have relatively inorganic substrates (Jude et al. 2005; Keough et al. 1999; Nelson et al. 2009). Drowned river mouth wetlands are also influenced by the associated tributary river which largely determines the fluvial geomorphology of these systems and can be a source of nutrients, fine organic matter, and coarse woody debris. Thus, drowned river mouth wetlands along the Great Lakes shoreline tend to have greater heterogeneity of benthic substrates, more fine organic matter, and more course woody debris than protected embayment or fringing exposed wetlands (Albert 2003; Albert and Minc 2001; Minc 1997). Thick accumulations of organic matter, which are characteristic of drowned river mouth wetlands, provide winter hibernation habitat for many Great Lakes turtles (Ernst et al. 1994; Harding 1997). Flooding from rivers also leaves large deposits of soft sand on the riparian zones which are important turtle nesting sites (Ernst et al. 1994; Harding 1997) and the large woody debris that is characteristic of drowned river mouth systems provides basking sites. We hypothesize that the greater catches of turtles that we found in drowned river mouth wetlands resulted from a combination of greater habitat heterogeneity, protection from wave energy, and increased number of basking, hibernation, and nesting sites in these systems relative to the other wetland types.

In addition to differences by wetland type, we found that turtle communities differed by dominant macrophyte species. While we collected most turtle species in all vegetation types, we found the highest abundances in lily, SAV and cattail and the lowest abundances in bulrush. In Great Lake coastal wetlands, macrophyte community structure is largely driven by hydrology (e.g., exposure to wave energy, water level regime, tributary velocity), water clarity, nutrient loading, and latitude (Keddy and Reznicek 1986; Lougheed et al. 2001; Wilcox and Xie 2007). Our findings are largely consistent with other studies showing that both turtle and fish community structure is often closely associated with vegetation type in Great Lakes wetlands (Brazner and Beals 1997; DeCatanzaro and Chow-Fraser 2010; Minns et al. 1994; Uzarski et al. 2005).

Principal component 1 of a PCA on wetland chemical/physical data can be interpreted as gradients of both anthropogenic disturbance (Uzarski et al. 2005) and natural productivity (Snodgrass et al. 1996). Our PCAs revealed gradients of increasing anthropogenic disturbance and productivity as evidenced by increasing specific conductance, chloride, and nitrate, and decreasing dissolved oxygen along the first PC in each analysis. Specific conductance and chloride were likely elevated in certain wetlands due to runoff of road salt and discharges of wastewater effluent. Nitrate was likely elevated in some areas due to both wastewater effluent and agricultural runoff. Dissolved oxygen tended to be low in the more disturbed/ productive areas, likely due to increased organic matter deposition and decomposition associated with areas of high nutrient loading. Drowned river mouth systems tend to be naturally more productive than coastal fringing wetlands even in the absence of anthropogenic disturbance because of the high inputs of allochthonous material and minimal flushing of organic matter (Jude et al. 2005; Nelson et al. 2009). This naturally high productivity can become further exacerbated if the watershed draining into the drowned river mouth wetland complex receives high nutrient inputs. Total turtle catch, species richness, and catches of four of the species all correlated positively with PC 1 (i.e., increasing human disturbance and productivity) when data from all wetland types were included. Total turtle catch, species richness, and catches of a number of the species also correlated with PC 1 from analyses conducted for both drowned river mouth and fringing exposed wetlands alone. Others have also found that painted turtles increased in abundance in more disturbed wetlands (DeCatanzaro and Chow-Fraser 2010; Lindeman 1996). The positive relationship between turtle communities and anthropogenic disturbance could result from the high productivity in these systems. For example, some turtles may be keying in on wetland habitats with high nutrient loads to exploit the high primary and secondary productivity within these areas (Lindeman 1996). Lindeman (1996) proposed that high painted turtle abundance in wastewater lagoons was a result of turtle diets in those habitats consisting mainly of highcalorie Chironomidae larvae and pupae, which can persist in extremely degraded habitats (e.g., Coffman and Ferrington 1996). Therefore, our results and others suggest that some freshwater turtles are resistant to certain anthropogenic stressors and may actually benefit from moderate nutrient loading by taking advantage of the high productivity in these areas. However, an important caveat to emphasize is that while turtles seem capable of inhabiting anthropogenically disturbed systems, populations can also suffer from direct human-caused impacts such as road mortality (Aresco 2005; DeCatanzaro and Chow-Fraser 2010; Gibbs and Steen 2005; Steen and Gibbs 2004) and indirect perturbations such as nest predation by raccoons, which can thrive in human-altered habitats (Marchand et al. 2002). Although we did not directly assess the effects of human activities on turtle abundances, others have found that turtle populations decline when they are closer to roads (DeCatanzaro and Chow-Fraser 2010; Gibbs and Steen 2005; Steen and Gibbs 2004). Because of this, we propose that turtle populations are most likely highest in areas of high productivity and low road density.

In Great Lakes coastal wetlands, thick layers of organic sediment can form in areas with high levels of

primary productivity (i.e., 'eutrophic habitats') and little water movement. In turn, these thick organic deposits can cause extreme fluctuations in water column dissolved oxygen (Nelson et al. 2009). The positive correlations we found between organic sediment depth and catches of four of the turtle species as well as total turtle catch and species richness suggest that turtles are exploiting habitats that may be unsuitable for most fish at some times of the day because of hypoxic conditions (Nürnberg 1995). Fish species richness and abundance often decline in a predictable manner as systems become more eutrophic and accumulate more organic sediment until only the most hypoxia-tolerant fish are able to persist (Bond 1996; Nürnberg 1995). For example, at one of our most degraded wetlands, Cooper et al. (2009) collected a total of 51 fish in 9 net-nights (5.67 fish/net-night) comprising 3 species, yet we captured 158 turtles (17.6 turtles/net-night) in that system at the same time. The fish species that Cooper et al. (2009) collected; bluntnose minnow (Pimephales notatus), bowfin (Amia calva), and brook stickleback (Culaea inconstans) are all hypoxia-tolerant fish (Becker 1983). The increasing abundance of turtles in highly eutrophic and anthropogenically disturbed systems that we observed represents a hypoxia-tolerant organism taking advantage of coastal habitats that are unsuitable for most fish species. Furthermore, the negative correlation that we observed between PC 1 and fish CPUE is consistent with this observation. The loss of fish from disturbed and highly eutrophic habitats likely has a minimal effect on turtles because of their omnivorous feeding habits and since fish typically make up a small portion of turtle diets (Lagler 1943). Accordingly, turtles are likely important in linking coastal wetlands to adjacent aquatic habitats, a service that would otherwise disappear when fish are lost.

Native freshwater turtle populations are facing many threats globally, including loss of suitable habitat and increased predation due to habitat alteration (Burke and Gibbons 1995; Marchand et al. 2002). We found six native species, including the Blanding's, a species of concern in the state of Michigan, while only a single non-native species, the red-eared slider, was collected. Because of the apparent importance of coastal wetland habitats for native turtles, we suggest that conservation strategies for coastal habitats include turtles specifically. In addition, ongoing monitoring programs in Great Lakes coastal wetlands should include assessments of turtle communities, especially since current monitoring efforts often include fyke netting for fish which also effectively capture turtles. Though our study represents one of the first broad analyses of turtle communities in wetlands of Lakes Michigan, Huron, and Superior, tracking trends in turtle populations by utilizing by-catch data from ongoing wetland monitoring efforts will likely lead to a much better understanding of the factors that shape their distributions. Conservation and restoration strategies for Great Lakes coastal habitats should include turtles explicitly since they are abundant in these habitats, have potential value in biomonitoring programs, and perform important ecological rolls.

Acknowledgments Funding for the various fish sampling projects came from the Great Lakes Commission, Great Lakes Protection Fund, Michigan Department of Environmental Quality, Michigan Department of Natural Resources, U.S. Environmental Protection Agency, and the U.S. Fish and Wildlife Service. Dr. Thomas Burton and Dr. Carl Ruetz III provided valuable guidance and insight on many of these projects. We thank members of the Uzarski, Burton, and Ruetz labs for assistance with fish sampling and chemical analyses.

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