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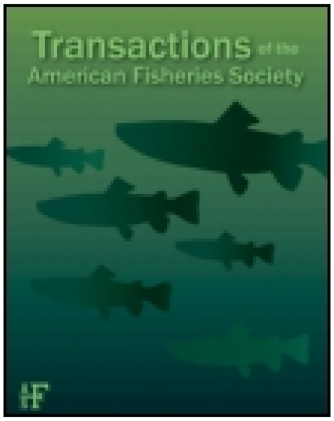

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ARTICLE

Coastal Wetland Support of Great Lakes Fisheries: Progress from Concept to Quantification

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Abstract

Fishery support is recognized as a valuable ecosystem service provided by aquatic systems, but it is harder to quantify than to describe conceptually. In this paper, we combine data on fish inhabiting Great Lakes coastal wetlands (GLCWs) with information on commercial and recreational harvest and the piscivore forage base to develop quantitative understanding of the multiple species involved in direct and indirect fishery support of this complex fishery. We then examine patterns of species co-occurrence and life history and relationships to GLCW conditions in order to identify fishery support metrics useful in aggregating species patterns and evaluating management outcomes. Our criteria for wetland prevalence (≥10% occurrence) and fishery importance (≥1% of recreational or commercial harvest in one or more of the Great Lakes or having a major forage fish role) yielded 21 wetland-using, fishery-relevant species representing multiple taxonomic groups and life history attributes. Wetland-using species are estimated to make up half the biomass and 60% of the dollar value of the fish landed commercially and ~80% of the fish numbers harvested recreationally. All of the GLCWs studied supported species of interest to recreational and commercial fishers but with widely varying composition. A few key habitat characteristics (e.g., vegetation structure) are broadly predictive of the types of sport and panfish present, with more degraded GLCWs generally supporting abundant but lower-value taxa (rough-fish species) and less degraded GLCWs supporting fewer but higher-value taxa (sport and panfish species). No single taxonomic or functional metric seems adequate to capture the diversity of fishery-relevant species supported by GLCWs; fishery support needs to be understood and managed in a multimetric context.

Ecosystem services accounting allows actual or potential environmental changes to be evaluated in terms of their likely effects on humans (National Research Council 2005; Farber et al. 2006; Palmer and Filoso 2009). Fishery support is a prominent ecosystem service attributed to aquatic systems and refers to providing spawning, foraging, and refuge habitat to species that are exploited for recreational fishing or commercial harvest (Holmlund and Hammer 1999; Barbier et al. 2011). Unfortunately, while fishery support is readily understood as a concept, how best to actually measure complex cases of fishery support is far from established. The sources of complexity in fishery support can arise from a number of factors, including the diversity of fish species and human user groups involved and the spatial extent and connectivity of the ecosystem (Barbier et al. 2011; Engle 2011; Tallis et al. 2012).

Coastal wetlands in the Laurentian Great Lakes exemplify a complex fishery support situation. Great Lakes coastal wetlands (GLCWs) are used by a large suite of fish species, including many with recognized sport and commercial importance (Jaworski and Raphael 1978; Jude and Pappas 1992; Sierszen et al. 2012b), whose high biological productivity and diversity contribute to food webs extending across a much broader nearshore zone (Wetzel 1992; Brazner et al. 2000; Vadeboncoeur et al. 2011). Human user groups in the Great Lakes value diverse aspects of the fishery, including biomass and dockside value (commercial harvesters), trophy size (sport anglers), and catchability and eating quality (family and

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subsistence fishers). As with coastal habitats elsewhere (Able 2005; Manson et al. 2005; Jordan et al. 2012), the spatial scale over which GLCW fishery support plays out is complicated because the various fish species can move among GLCWs and other habitats on a seasonal, ontogenetic, or facultative basis and because fishing activities often take place outside the GLCWs themselves and are assessed and managed over broad spatial scales (e.g., Brazner et al. 2001; Murphy et al. 2012).

Among the questions that need to be addressed to develop fishery support metrics for such complex situations are which species to include, what kinds of measurement endpoints are informative, and how to establish the linkage between specific ecosystems and the broader spatial scales over which ecological services are realized. There is also the question of how fishery support metrics relate to ecosystem conditions and potential management actions. This is a subject of considerable current interest for Great Lakes coastal habitats, since the ongoing Great Lakes Restoration Initiative (GLRI 2010) is supporting expanded efforts to remediate environmental impacts and improve ecological condition. Many GLRI projects are directed at the coastal margin, which is most directly affected by shoreline development (e.g., urbanization and hydrologic alteration) and watershed-derived stressors such as sedimentation and nutrient loading (Vadeboncoeur et al. 2011; Niemi et al. 2007; Allan et al. 2013). Developing quantifiable metrics of fishery support would provide a basis for prioritizing management actions and tracking the benefits of such restoration projects (Wainger and Mazzotta 2011).

Ideally, fishery support accounting would work with endpoints that can be quantified as a standing stock or a rate (growth or production) per unit area (Bell 1997; Wainger and Boyd 2009; Engle 2011) as a basis for evaluating changes in fishable biomass or size. However, growth or production data are time-consuming to collect and thus rarely obtained in synoptic surveys. Rather, the typical fish survey produces count and occurrence data from a standardized sampling effort meant to index assemblage composition and the relative abundance of species. Establishing endpoints of value to human users (e.g., the presence of a target species) can be sufficient to link an ecosystem condition with an ecological outcome (e.g., improved habitat for that species) for which human preferences can be measured (Wainger and Mazzotta 2011). Index data may therefore be useful for fishery service accounting and can offer a robust avenue for evaluating fish–habitat relationships because of their ability to smooth over some of the variability due to sampling gear, location, and time (Steen et al. 2008). Community-level analyses of such index data have shown that GLCW fish composition is substantially affected by habitat and watershed conditions (e.g., Brazner and Beals 1997; Seilheimer and Chow-Fraser 2007; Arend and Bain 2008; Trebitz et al. 2009a). However, species composition data must be translated into metrics of fishery support to predict the ecosystem services implications of proposed management actions affecting GLCWs. To date, analyses focusing on fishery-relevant species and endpoints are lacking for GLCWs.

Our goals in this paper are to add quantitative detail toward understanding which Great Lakes species are both fishery relevant and wetland users and to ascertain their patterns of co-occurrence and life history in order to identify multispecies fishery support metrics that are useful in differentiating among GLCW types and conditions. We speak of GLCWs as providing "direct" fishery support when they harbor species that are sought, caught, and harvested by commercial harvesters or recreational anglers (whether the fish are captured in the wetland or elsewhere) and as providing "indirect" fishery support when they harbor forage fish available for consumption by other fishes inhabiting the broader nearshore zone. Our approach was to combine recreational and commercial harvest data with GLCW survey data to identify fishery-relevant, wetland-using species; to examine their exploitation and life history patterns to determine how multispecies fishery support can be decomposed into more homogeneous and measurable components; and finally to examine relationships to GLCW condition in order to identify metrics that are useful in tracking ecosystem service changes associated with habitat degradation and restoration.

We acknowledge that our approach does not address some of the recalcitrant questions related to fish habitat, such the extent to which GLCWs are essential and what portion of the harvested biomass or production can be attributed to them (Rose 2000; Able 2005; Levin and Stunz 2005; Rosenfield and Hatfield 2011). Also, we focus exclusively on the supply side of fishery support ecosystem services and do not address the equally complex problem of assigning values to the benefits that humans derive from a fishery (e.g., Whitehead et al. 2005; Brander et al. 2006; Spangenberg and Settele 2010). Nevertheless, our analysis constitutes substantial progress in refining our understanding of the associations between GLCWs and the multiple fishery-relevant species that inhabit them, thereby moving fishery support from a purely conceptual basis toward operationally applicability. The issues discussed in the context of GLCWs are equally relevant to complex cases of fishery support in other aquatic ecosystem types and locations (e.g., salt marshes, seagrass beds, and mangroves: Manson et al. 2005; Sheaves 2009; Engle 2011; Vasconcelos et al. 2011).

METHODS

Our analyses of patterns for fishery-relevant, wetland-using fish species relies primarily on data from 58 GLCWs surveyed via electrofishing over the summers of 2002–2004 (details in Trebitz et al. 2009a). This data set included lacustrine, riverine, and protected-type GLCWs on all five Great Lakes, with sites being chosen to span a gradient of agricultural use and urbanization in the watershed (Danz et al. 2005). Our sampling was conducted from mid to late summer, as is typical of GLCW fish surveys. Fish were sampled at five to seven separate locations per wetland (standardized 10-min electrofishing effort per station, or 50–70 min of effort per wetland). The sampling effort was distributed proportionally to the available vegetated and open-water habitat. Catches were enumerated by species and by age-class (young-of-year, yearling, or adult) based on size distributions. Supporting water quality and habitat data were also collected.

Establishing wetland use and fishery importance.—We operationally defined species that are both wetland using and fishery relevant as those that we found in at least 10% of the GLCWs surveyed that also met certain recreational and commercial harvest thresholds. The 10% occurrence criterion was to ensure that we only included species with sufficient data that their distribution and prevalence patterns could be assessed. For additional perspective, we compiled published species data from ichthyoplankton surveys of GLCWs. Such data demonstrate spawning and nursery use of GLCWs and are especially relevant for fish species not detected in adult and juvenile summer surveys owing to sampling gear (typically fyke nets or electrofishing) or temporal biases. Because we found larval fish data for relatively few GLCWs and mostly reported in general terms (e.g., presence only, spatially aggregated), we did not set a criterion for occurrence frequency in listing species (but applied the same harvest thresholds).

We identified wetland-using species having direct fishery importance using recent recreational and commercial fishing data compiled by various management agencies (Table 1). We classified the harvest level for each species in each lake into four tiers: "dominant" for species making up a larger percentage of the harvest than any other species; "major" for those comprising $\geq$10% of the total; "minor" for those comprising 1.0–10% of the total; and "trace" for those comprising $<$1.0% of the total, based on the number harvested in recreational fishing and the biomass landed in commercial fishing. We used tiers rather than actual quantities because of the large range in productivity across the lakes and the variation in assessment methods and spatial and temporal coverage among data sources (Table 1). A species had to attain at least minor recreational or commercial harvest in at least one lake to be retained in our analyses. When fishery data were aggregated across taxa (e.g., "sunfish" rather than individual species), we applied the harvest level to all potential species meeting the criteria of $\geq$10% occurrence in GLCWs. For the commercial fishing data, we also computed the average price and percent of the total biomass and dollar value attributable to each species. To do so, we summed U.S. and Canadian data without regard to year, assuming that among-year differences were unimportant. No currency conversion was applied, since the exchange rate lay between US\$0.95 and \$1.05 per Canadian dollar for all of 2011 and 2012. We did not attempt to assign a dollar value to species of recreational importance given the much greater complexity of evaluating recreational enjoyment as opposed to commercial values and landings (e.g., Gordon et al. 1973; Provencher and Bishop 1997).

We identified fish species having indirect fishery importance in the Great Lakes (i.e., as forage for sport fish) as those wetland-using species that are significant components of coastal predator diets or pelagic prey fish surveys, based on the scientific literature. We excluded sedentary, demersal species (e.g., sculpins) because they are unlikely to move (and thus transfer energy) between GLCWs and nearshore environments even if prevalent in both habitats.

Evaluating wetland associations.—We characterized GLCW associations for the wetland-using, fishery-relevant species using our own survey data and life history information from the literature. First, general distribution and prevalence patterns were evaluated to determine which fishery-relevant species are most commonly encountered, how many such species typically occur, and how their composition varies across GLCWs. Then, to address the extent to which GLCW condition affects fishery support, relationships between the species and wetland environmental characteristics were examined at two spatial scales: the wetland scale and the scale of sampling locations within wetlands (hereafter, station scale). Finally, we examined the patterns in various potential summary metrics of fishery support suggested by the taxonomic and life history patterns for the fishery-relevant species.

At the wetland scale, the relationships of species to categorical environmental variables were analyzed by means of box plots and analysis of variance (ANOVA) and relationships to numerical environmental variables were analyzed by linear regression. We also computed the richness of the fishery-relevant species in four categories: sport fish, panfish, rough fish, and forage fish. Patterns in the assemblage of fishery-relevant species were examined using nonmetric multidimensional scaling (NMDS) ordination, with Bray–Curtis similarity as the distance metric. To facilitate graphical depiction of fish composition patterns, we focused on results from a two-dimensional ordination (a three-dimensional ordination explained only 7% more variability). The ordinations combined all age-classes, since trial ordinations that examined young-of-year and juvenile–adult fish separately were qualitatively similar. Overlay vectors to the ordination were generated for the individual species, for richness for the four species categories, and for the environmental variables by computing the Pearson correlation between each of these variables and the first and second ordination axis scores and using the resulting values as x- and y-coordinates for the endpoints of the vectors radiating from the origin. Encounter probability (the percent of sampling locations within each GLCW at which a species was captured) was used as the species-level variable for all of the wetland-scale analyses because encounter probability is interpretable in terms of fishing opportunity and presents a useful compromise between high-variability abundance data and low-information occurrence data (Sheaves et al. 2012).

TABLE 1. Sources and details for fishery harvest data. The commercial data are comprehensive, whereas the recreational data are from surveys with varying focal species, user groups, and temporal and spatial coverage. The recreational data are on a number basis unless stated otherwise.

Source	Lake (area)	Year	Details
		Commercial	
OMNR 2013a	Erie (Canada)	2012	All landings, biomass and dollar value
OMNR 2013b	Huron (Canada)	2012	All landings, biomass and dollar value
OMNR 2013c	Ontario (Canada)	2012	All landings, biomass and dollar value
OMNR 2013d	Superior (Canada)	2011	All landings, biomass and dollar value
NMFS database[a]	Five lakes (U.S.)	2011	All landings, biomass and dollar value
		Recreational	
OMNR 2013a	Erie (Canada)	2012	Angler diaries
Ohio DNR 2012	Erie (Ohio)	2011	Creel: boat fishing only, selected species
MDNR database[b]	Huron (Saginaw Bay)	2011	Creel and charter reporting: ice, boat, shore fishing
Breidert 2011	Michigan (U.S.)	2010	Biomass basis
Hanson 2012	Michigan: (U.S.)	2011	Creel: recreational anglers, selected species
Masterson and Eggold 2012	Michigan (Wisconsin)	2011	Creel, charter reporting, mail survey: boat and shore fishing, selected species
Lantry and Eckert 2012	Ontario (New York)	2011	Creel: boat fishing only
Zunker 2013	Superior (Wisconsin)	2012	Creel and charter reporting; ice and boat fishing
DFO 2008[c]	Four lakes (Canada)	2005	Mail survey

[a]Available: www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/other-specialized-programs/great-lakes-landings/index.
[b]Available: www.dnr.state.mi.us/CharterCreel/Default.aspx.
[c]Included despite data age because it was most recent Canada-side data available for three of the lakes.

At the station scale, the relationships of species to categorical environmental variables were analyzed graphically and by cross-tabulation, while the relationships to numerical environmental variables were analyzed via logistic regression. Station-scale analyses were pursued only for species with enough data for this to be meaningful, operationally defined as species found in ≥25% of the GLCWs, in all five Great Lakes, and for which we caught ≥100 individuals. Station-scale analyses used presence/absence as the data format and only included GLCWs in which the species was found, so that absences reflected station characteristics rather than broader distribution patterns. We did not use abundance data (e.g., catch per effort) for these analyses because they often fail to meet distributional assumptions (Francis et al. 2005; Valavanis et al. 2008) and lead to a more complicated hierarchical data structure for stations nested within wetlands (Wagner et al. 2006). For species with enough data (at least five presences per predictor variable), station-scale analyses were conducted separately for young-of-year and for older fish (juveniles and adults combined), so that differences across life stages could be examined.

Wetland-scale and station-scale analyses focused on a small set of the available environmental variables chosen a priori to have relevance to fish, minimal collinearity, and potential for manipulation by GLCW restoration or management. The numerical variables (measured at the station scale, averaged to the wetland scale) were turbidity (nephelometric turbidity units; an index of water clarity), fetch (m [$\log_{10}$ transformed]; an index of wind-and-wave exposure), sediment density (g/cm^3; higher densities are sandier), and a submerged- and floating-leaf vegetation structure index (higher levels indicate denser cover and more growth forms; Brazner and Beals 1997); see Trebitz et al. (2009a) for computation details on all these variables. We also considered one categorical descriptor at the wetland scale (protected, riverine, or lacustrine wetland; Albert et al. 2005) and one at the station scale (channelized, lake-like, or backbay station; Trebitz et al. 2009a). For the ordination analyses only, we included additional environmental variables (as overlay vectors) to provide a more comprehensive picture of GLCW conditions. These were plankton chlorophyll *a* (an index of water clarity and productivity), three anthropogenic disturbance metrics (percent natural land cover in the watershed, percent natural land cover in the 100-m buffer around the GLCW, and an agricultural intensity index calculated from county and 8-digit HUC data; Danz et al. 2005), and two additional vegetation structure metrics (the maximum depth of submerged plant growth and a nuisance plant density index based primarily on the emergent taxa *Phragmites* (common reeds), *Typha* (cattails), and purple loosestrife *Lythrum salicaria*; Trebitz and Taylor 2007). Two potentially fish-relevant environmental variables that we did not include were dissolved oxygen (since earlier work had shown that it explains GLCW fish composition only at very small spatial scales, e.g., among vegetation beds; Trebitz et al.

2009b); and water temperature. Water temperature is confounded with a latitudinal anthropogenic disturbance gradient across the Great Lakes basin (population density and agricultural intensity both increase to the south; Trebitz et al. 2009a), and the basinwide distribution of the fish species considered here suggests that water temperature is not the primary driver of their abundance patterns.

Finally, we examined potential guild-level fishery support metrics (e.g., groupings based on species composition or traits such as sport fish or warmwater species), with the goal of identifying metrics that usefully aggregate species-specific information while preserving patterns relevant to different human user groups and GLCW conditions. We depict the results with radar plots (polar coordinate plots in which points are specified by angle and distance from the origin rather than the usual *x*- and *y*-values), with the level of the fishery support metric given by the distance from the origin and the angle matching that of the GLCW in the earlier NMDS ordination. The guild metrics were constructed by summing encounter probabilities across the relevant species using adults only for taxonomic combinations (to focus on harvestable fish) but all life stages for life history combinations (the usual procedure in computing fish guild metrics for biotic integrity analyses; Fausch et al. 1990). We obtained a macrohabitat classification from an analysis of Great Lakes fish species done by Jude and Pappas (1992), with the groupings that we used being "coastal" (their rankings of 32–66), "weak wetland" (their rankings of 67–90), and "strong wetland" (their rankings of 90–113). We compiled life history information relevant to wetland affinity (i.e., littoral tendency, substrate preference, vegetation use, and thermal preference) from Becker (1983), Coker et al. (2001), and Lane et al. (1996a, 1996b). We classified fish as obligate wetland users if they rely on aquatic vegetation to spawn or for nursery habitat and as facultative wetland users otherwise.

RESULTS

Wetland-Using Species of Direct Fishery Importance

We identified 18 fish species (Table 2) that had at least a 10% frequency of occurrence in GLCWs (our criteria for wetland using) and that made up at least 1% of the recreational or commercial harvest in one or more Great Lakes (our criteria for direct fishery importance). Collectively, these species made up 48% of the landed biomass and accounted for 63% of the dollar value of all species harvested commercially across the Great Lakes in 2011 or 2012 (Table 3), as estimated from

TABLE 2. Great Lakes coastal wetland–using fishes with direct importance to recreational or commercial fishing, organized by general fishing category. Importance by lake (E = Erie, H = Huron, M = Michigan, O = Ontario, and S = Superior) is coded as follows: dominant (largest percentage of the harvest of any species) = bold with asterisks; major (>10% of the harvest) = bold and underlined; minor (1–10% of the harvest) = ordinary type; and trace (<1% of the harvest) = in parentheses. The basis is biomass for commercial harvests but numbers for recreational harvests.

Species	Commercial importance					Recreational importance				
Sport fish										
Channel Catfish	E	H	(M)			(E)	H		O	(S)
Largemouth Bass						E	H		O	S
Northern Pike		(H)		O	(S)	(E)	H	(M)	(O)	S
Smallmouth Bass	(E)	(H)				E	**<u>H</u>**	M	O	S
Yellow Perch	***E***	H	(M)	***O***	(S)	***E***	***H***	***M***	***O***	**<u>S</u>**
Walleye[a]	**<u>E</u>**	H	(M)	O	(S)	E	**<u>H</u>**	M	**<u>O</u>**	***S***
White Bass	**<u>E</u>**	(H)	(M)	(O)		E	(H)			
White Perch	E	(H)	(M)	O		(E)	(H)	(M)		
Panfish										
Black Crappie[b]		(H)		O		(E)	H	(M)	**<u>O</u>**	(S)
Rock Bass	(E)	(H)		O		(E)	**<u>H</u>**		O	
Sunfish (3 species)[c]	(E)			**<u>O</u>**		E	H	(M)	O	
Rough fish										
Black/Brown Bullhead[d]	(E)	(H)		O						
Common Carp	E	(H)	(M)	(O)						
Freshwater Drum	E	(H)		O		(E)	(H)			
Gizzard Shad	(E)									
White Sucker	(E)	(H)		O			(H)			

[a]Walleyes dominate the Canadian side of Lake Superior harvest only.
[b]Black Crappies meet our GLCW prevalence criteria but White Crappies do not; the fishery harvest data do not differentiate between the two species.
[c]Sunfish meeting the GLCW prevalence criteria and of interest to anglers are Pumpkinseeds, Bluegills, and Green Sunfish; some fishery harvest sources differentiate among the species but others do not.
[d]Black and Brown Bullheads are difficult to differentiate (Rutkayová et al. 2013) and thus are combined in our data.

TABLE 3. Percentages of Great Lakes–wide total commercially landed biomass and dollar value and average prices for wetland-using species. Numbers reflect combined NMFS and OMNR data for 2011 or 2012 across all five Great Lakes. Species are listed in order of decreasing percent biomass or price.

Species	% Biomass	% Dollar value	Price ($/kg)
Sport fish			
Yellow Perch	18.2	36.0	5.16
Walleye	10.6	18.5	4.55
White Bass	8.0	4.3	1.40
White Perch	6.0	2.8	1.21
Channel Catfish	1.7	0.5	0.76
Northern Pike	0.1	<0.1	0.58
Panfish			
Black Crappie	<0.1	<0.1	7.20
Sunfish (3 species)	0.1	0.1	2.79
Rock Bass	<0.1	<0.1	1.17
Rough fish			
Freshwater Drum	1.7	0.3	0.41
Common Carp	1.3	0.3	0.56
Black/Brown Bullhead	0.2	0.1	0.74
White Sucker	<0.1	<0.1	0.20
Gizzard Shad	0.1	<0.1	0.07
All of above species	48.0	62.9	

NOAA and OMNR databases and reports (Table 1). The total biomass of wetland-using species landed commercially exceeded 11,000 metric tons, with the vast majority coming from Lake Erie. The total number of fish from wetland-using species harvested recreationally in just Canadian waters in 2005 exceeded 4 million, with roughly half of those coming from Lake Erie (Table 4). The percentage of the commercial harvest accounted for by wetland-using species varied widely among lakes (>70% in Lakes Erie and Ontario, ~10% in Lake Huron, ≤1.0% in Lakes Michigan and Superior), but the majority of the recreational harvest was due to wetland-using species in all the lakes (Table 4).

Yellow Perch *Perca flavescens* is the most important wetland-using species for Great Lakes fisheries. The species is ubiquitous in GLCWs, occurring more frequently than any other fishery-relevant species (Brazner and Beals 1997; Seilheimer and Chow-Fraser 2007; Arend and Bain 2008; Trebitz et al. 2009a). Yellow Perch comprised 32% of the total fish harvested recreationally across Canadian Great Lakes waters in 2005 (DFO 2008)—a rate three times higher than that of any other species. Yellow Perch also comprised 36% of the dollar value and 18% of the biomass landed in commercial fisheries across all five Great Lakes in 2010–2011 (Table 3)—a dollar value higher than that of any other species and a landed biomass second only to that of Lake Whitefish *Coregonus clupeaformis*. Yellow Perch are particularly important to commercial fishing in Lakes Erie and Ontario (>25% of the harvested biomass) and to recreational fishing in Lakes Erie and Huron (>75% of the harvest; DFO 2008; Ohio DNR 2012; OMNR 2013a), but they also make up at least 25% of

TABLE 4. Estimated percentages of the total recreational and commercial harvest across the Great Lakes comprised of the wetland-using fish species from Table 2. Commercial harvests reflect combined NMFS and OMNR data for 2011 and 2012; recreational harvest data are from a Canada-side 2005 survey (DFO 2008) that does not cover Lake Michigan (cross-lake comparisons for more recent recreational fishing data are difficult because of variations in methodology).

	Commercial harvest		Recreational harvest	
Lake	Biomass (metric tons)	Percent	Number (thousands)	Percent
Erie	10,313	72.2	2,248,469	95
Huron	407	11.1	1,022,878	71
Michigan	28	1.0		
Ontario	184	84.0	803,739	76
Superior	1.6	<0.1	237,861	61
All 5 lakes	10,933	48.0	4,312,947	82

the recreational harvest in portions of Lakes Michigan, Ontario, and Superior (Lantry and Eckert 2012; Hanson 2012; Masterson and Eggold 2012; Zunker 2013).

Seventeen other wetland-using species are important fishery targets in the Great Lakes. Walleye *Sander vitreus* have major recreational importance in three of the lakes (Table 2) and comprised 11% of the commercial biomass and 19% of the dollar value in 2010–2011 (Table 3). White Bass *Morone chrysops* and White Perch *Morone americana* each exceeded 5% of the landed biomass and 2% of the dollar value, with commercial landings coming from four lakes and recreational harvests in three lakes (Tables 2, 3). Channel Catfish *Ictalurus punctatus* are commercially landed in three lakes and recreationally harvested in four of them (Table 2). Smallmouth Bass *Micropterus dolomieu* and Northern Pike *Esox lucius* have recreational importance in all five lakes as well as some commercial harvest (Table 2). The Largemouth Bass *Micropterus salmoides* is the only wetland-using sport fish lacking commercial importance, but it is harvested recreationally in four lakes (Table 2). Rock Bass *Ambloplites rupestris*, Black Crappie *Pomoxis nigromaculatus*, and sunfish *Lepomis* spp. each attain major recreational or commercial importance in at least one lake and are harvested in several more (Table 2). The sunfish species of most interest to recreational anglers are Pumpkinseed *L. gibbosus* and Bluegill *L. macrochirus*, but large Green Sunfish *L. cyanellus* are also fished (Becker 1983). Four wetland-using rough-fish species attain at least minor commercial importance in Lakes Erie or Ontario, although rough-fish harvests only reach trace levels in Lakes Huron and Michigan (Table 2). Some Freshwater Drum *Aplodinotus grunniens* and White Sucker *Catostomus commersonii* are also recreationally harvested, while bullheads (*Ameiurus* spp.) and Common Carp *Cyprinus carpio* are commercially harvested only. Gizzard Shad *Dorosoma cepedianum* are commercially harvested only in Lake Erie and only at trace levels (i.e., below our 1.0% criterion); however, we include this species in Table 2 because of its numerical dominance in the GLCWs of Lake Erie and its role in indirect fishery support.

Wetland-Using Species of Indirect Fishery Importance

We identified five wetland-using, mobile, small-bodied fish species capable of providing indirect fishery support as forage for nearshore piscivores. These are Yellow Perch and Gizzard Shad (already in Table 2), plus Spottail Shiner *Notropis hudsonius*, Emerald Shiner *Notropis atherinoides*, and Alewife *Alosa pseudoharengus*, which have 40, 32, and 28% frequencies of occurrence, respectively, in our GLCW data set. Alewife, Emerald Shiner, Spottail Shiner, and young-of-year Yellow Perch are considered important pelagic forage species in multiple Great Lakes, while young-of-year Gizzard Shad are important in Lake Erie (Jude and Tesar 1985; Knight and Vondracek 1993; Rand and Stewart 1998; Zhao et al. 2013; J. S. Schaeffer, T. P. O'Brien, and S. Lenart [paper presented at the Great Lakes Fish Commission, Lake Huron Committee meeting, 2012]). Yellow Perch and Gizzard Shad thus provide both indirect fishery support (as young of year) and direct fishery support (as adults).

Larval Surveys as Additional Evidence for Wetland Use

All of the species classified as wetland using based on regular occurrence in adult and juvenile fish surveys were also found in GLCWs as larvae. Importantly, additional species were found as larvae that rarely or never appear in adult and juvenile surveys. Most notable among these from a fishery perspective are *Coregonus* species and Rainbow Smelt *Osmerus mordax*. Rainbow Smelt ranks third (after Yellow Perch) in commercially landed biomass across the Great Lakes according to NMFS and OMNR data, with harvests being particularly important in Lake Erie (24%), and attains major recreational harvest in Lake Superior (DFO 2008; Zunker 2013). Identification of larval *Coregonus* to species is difficult (Auer 1982), but those from GLCWs likely include Lake Whitefish and Cisco *C. artedi*, since these are the most widespread and shallow-water oriented of the coregonines (Scott and Crossman 1973; Gamble et al. 2011). Lake Whitefish represent the largest portion (biomass) of the species harvested commercially from Lakes Michigan, Huron, and Superior and experience some recreational harvest, whereas Ciscoes dominate the commercial harvest in Lake Ontario and are a close second to Lake Whitefish in Lake Superior (NMFS and OMNR data; DFO 2008; Zunker 2013). The other fishery-relevant species caught as larvae (Table 5) but not reported in Table 2 are rough fishes with only trace commercial importance (Bowfin *Amia calva*, Quillback *Carpiodes cyprinus*, Bigmouth Buffalo *Ictiobus cyprinellus*, and Burbot *Lota lota*).

Wetland Prevalence and Life History Patterns for Fishery-Relevant Species

Among the 21 species caught in our survey and identified as providing direct or indirect fishery support, the highest GLCW occurrence rates are for Yellow Perch (>90%), followed by Pumpkinseed, White Sucker, and Common Carp (each >70%) and Largemouth Bass, Northern Pike, Bullheads, Rock Bass, and Bluegill (each ≥60%; Table 6). Twenty of the twenty-one species were found in GLCWs in all five Great Lakes. Gizzard Shad were not found in Lake Superior but nevertheless were more numerous across all 58 GLCWs combined that any other species (due to extremely high catches in Lake Erie); Yellow Perch were the next most numerically abundant species across the data set. We caught at least one of the eight sport fish species in every GLCW, with some wetlands yielding as many as six (Table 7). The average richness of sport fish exceeded three in the GLCWs of all lakes except Lake Huron, where the average was only 2.3. All GLCWs harbored at least one of the five panfish species, with the average between two and three in all lakes. All GLCWs also

TABLE 5. Fishery-relevant species for which larvae have been documented in GLCWs within various lakes. The taxonomic resolution is to the least common denominator across studies. All studies commenced sampling in April or May, continued for at least 2 months, and used fine-mesh pushed or towed nets (except Cooper et al. 2012, which used light traps).

Species	Erie[a]	Huron[b]	Michigan[c]	Ontario[d]	Superior[e]
Found regularly as adults or juveniles:					
Black/Brown Bullhead	xx		xx	xx	xx
Channel Catfish	xx				xx
Alewife/Gizzard Shad	xx	xx	xx	xx	
Black Crappie	xx	xx	xx	xx	xx
Common Carp/Goldfish	xx	xx	xx	xx	xx
Freshwater Drum	xx	xx		xx	xx
Largemouth Bass		xx	xx		
Northern Pike		xx	xx	xx	xx
Rainbow Smelt	xx	xx		xx	xx
Rock Bass		xx	xx	xx	xx
Smallmouth Bass		xx	xx	xx	xx
Sunfish	xx	xx	xx	xx	xx
Yellow Perch	xx	xx	xx	xx	xx
Walleye	xx				xx
White/Longnose Sucker[f]	xx	xx	xx	xx	xx
White Perch/White Bass	xx			xx	xx
Not found regularly as adults or juveniles:					
Bigmouth Buffalo	xx				
Bowfin			xx		
Burbot		xx	xx		xx
Cisco/Lake Whitefish	xx	xx	xx		xx
Quillback	xx				
Rainbow Smelt	xx	xx		xx	xx

[a]Ohio shore GLCWs: Cooper et al. (1981); Mizera et al. (1981); Johnson (1989); Krupa (2003).
[b]Les Cheneaux Islands and Saginaw Bay area GLCWs: O'Gorman (1983); Höök et al. (2001); Cooper et al. (2012).
[c]Two Michigan shore GLCWs: Jude et al. (1981); Chubb and Liston (1986).
[d]New York shore and Toronto area GLCWs: Lewis and Patch (1982); Klumb et al. (2003).
[e]Wisconsin shore GLCWs: Tanner et al. (2004); Hoffman et al. (2012); Hoffman, unpublished.
[f] Longnose Suckers *Catostomus catostomus* are not fishery relevant. They are listed here only because they cannot be differntiated from White Suckers as larvae.

harbored at least one of the five rough-fish species, with the average richness being substantially higher in Lake Erie than in the other lakes (Table 7). The average richness of forage species was lowest in Lake Huron GLCWs (Table 7). The richnesses of sport, pan-, rough-, and forage fish were essentially uncorrelated (all $r < 0.3$).

The 21 fish species vary considerably in the life history traits relevant to understanding their use of GLCWs and in the potential for developing guild metrics relevant to fishery support. Eleven are classified as having a warm thermal preference, but there are also 9 having cool thermal preference and one each having cold–cool and cold preferences (Table 6). All of the species are somewhat or predominantly littoral, but 11 are coastal associated and only 10 weakly or strongly wetland associated. Only four of the species are obligate wetland users (requiring vegetation for spawning or nurseries), although most have vegetation affinity (Table 6). Among the nine species with ≥50% occurrence in the GLCWs, the one consistent trait is that all are littoral with moderate or high vegetation affinity (Table 6). None of the pelagic forage species exhibits a warm thermal preference or obligate wetland use, which is to be expected. There was little congruence among the various dimensions along which life history can be classified (Table 6). For example, the thermal guild categories did not align consistently with the habitat association categories, nor did wetland dependency align with the life history categories; and obligate vegetation spawners like Northern Pike and Common Carp were classified as coastal associated rather than wetland associated based on their macrohabitat use patterns.

Environmental Associations for Fishery-Relevant Species

Ordinations of encounter probability data produced species vectors radiating throughout the ordination space (Figure 1), reflecting considerable variation in the makeup of fishery-relevant species across GLCWs. The two-dimensional ordination depicted had a stress of 0.20 and explained 79% of the among-wetland variability. The GLCWs from Lakes Superior,

TABLE 6. Summary of life history traits for 24 coastal wetland–using species of direct or indirect fishery relevance, in order of percent occurrence in our GLCW survey. See text for categorization details.

Species	Occurrence (%)	Thermal guild	Macrohabitat association	Wetland use	Wetland-related life history
Sport fish					
Yellow Perch	93	Cool	Coastal	Facultative	Often littoral, moderate veg affinity
Largemouth Bass	67	Warm	Weak wet	Obligate	Littoral, high veg affinity
Northern Pike	67	Cool	Coastal	Obligate	Littoral, high veg affinity
Smallmouth Bass	38	Warm	Coastal	Facultative	Often littoral, but only sparse veg
Walleye	28	Cool	Coastal	Facultative	Often littoral, but low veg affinity
White Perch	14	Warm	Weak wet	Facultative	Somewhat littoral
White Bass	10	Warm	Strong wet	Facultative	Somewhat littoral, age-0 veg affinity
Channel Catfish	10	Warm	Coastal	Facultative	Somewhat littoral, low veg affinity
Panfish					
Pumpkinseed	79	Warm	Weak wet	Obligate	Littoral, high veg affinity
Rock Bass	64	Cool	Weak wet	Facultative	Littoral, age-0 veg affinity
Bluegill	60	Warm	Weak wet	Facultative	Littoral, high veg affinity
Black Crappie	33	Cool	Coastal	Facultative	Littoral, high veg affinity
Green Sunfish	16	Warm	Strong wet	Facultative	Littoral, high veg affinity
Rough fish					
White Sucker	72	Cool	Coastal	Facultative	Littoral, age-0 veg affinity
Common Carp	71	Warm	Coastal	Obligate	Littoral, high veg affinity
Black/Brown Bullhead	67	Warm	Strong wet	Facultative	Littoral, high veg affinity
Gizzard Shad	33	Cool	Weak wet	Facultative	Littoral, high veg affinity
Freshwater Drum	22	Warm	Weak wet	Facultative	Somewhat littoral, age-0 veg affinity
Forage fish					
Yellow Perch[a]	93	Cool	Coastal	Facultative	Often littoral, moderate veg affinity
Spottail Shiner	40	Cold–cool	Coastal	Facultative	Age-0 veg affinity, adults pelagic/littoral
Gizzard Shad[a]	33	Cool	Weak wet	Facultative	Littoral, high veg affinity
Emerald Shiner	32	Cool	Coastal	Facultative	Age-0 veg affinity, adults pelagic/littoral
Alewife	28	Cold	Coastal	Facultative	Littoral, low veg affinity

[a]The entries for Yellow Perch and Gizzard Shad are repeated under forage fish due to the dual roles of these species.

Ontario, and Erie each form a cluster, whereas those from Lakes Michigan and Huron span much more ordination space, indicating more diverse composition (Figure 1). All species ordinated were found in at least four of the five Great Lakes, so the ordination reflects prevalence patterns rather than simply extent of range. Overlay vectors suggest a primary axis of variation related to eutrophication and anthropogenic disturbance (highest values in the lower left quadrant) and a secondary axis related to substrate type and vegetation structure (highest values in the upper left and right quadrants; Figure 1). Rough-fish richness and three of the five rough-fish species were oriented toward eutrophication–disturbance. Forage-fish richness and two of the five forage species also aligned with the eutrophication–disturbance axis, while one

TABLE 7. Mean wetland-scale richness (ranges in parentheses) of groups of fishery-relevant species, summarized by lake. Table 6 lists the species contributing to each group.

Lake	Number of wetlands	Sport fish	Panfish	Rough fish	Forage fish
Erie	6	3.3 (2–5)	2.8 (2–4)	4.3 (3–6)	3.5 (2–5)
Huron	6	2.3 (1–3)	2.5 (1–4)	2.5 (1–4)	1.5 (0–3)
Michigan	17	3.2 (1–6)	2.4 (1–4)	3.2 (1–6)	2.1 (0–4)
Ontario	12	3.2 (2–4)	2.8 (2–4)	3.0 (2–4)	2.0 (1–3)
Superior	17	3.2 (2–5)	2.2 (1–4)	2.0 (1–3)	2.2 (1–4)
All 5 lakes	58	3.1 (1–6)	2.5 (1–4)	2.8 (1–6)	2.2 (0–5)

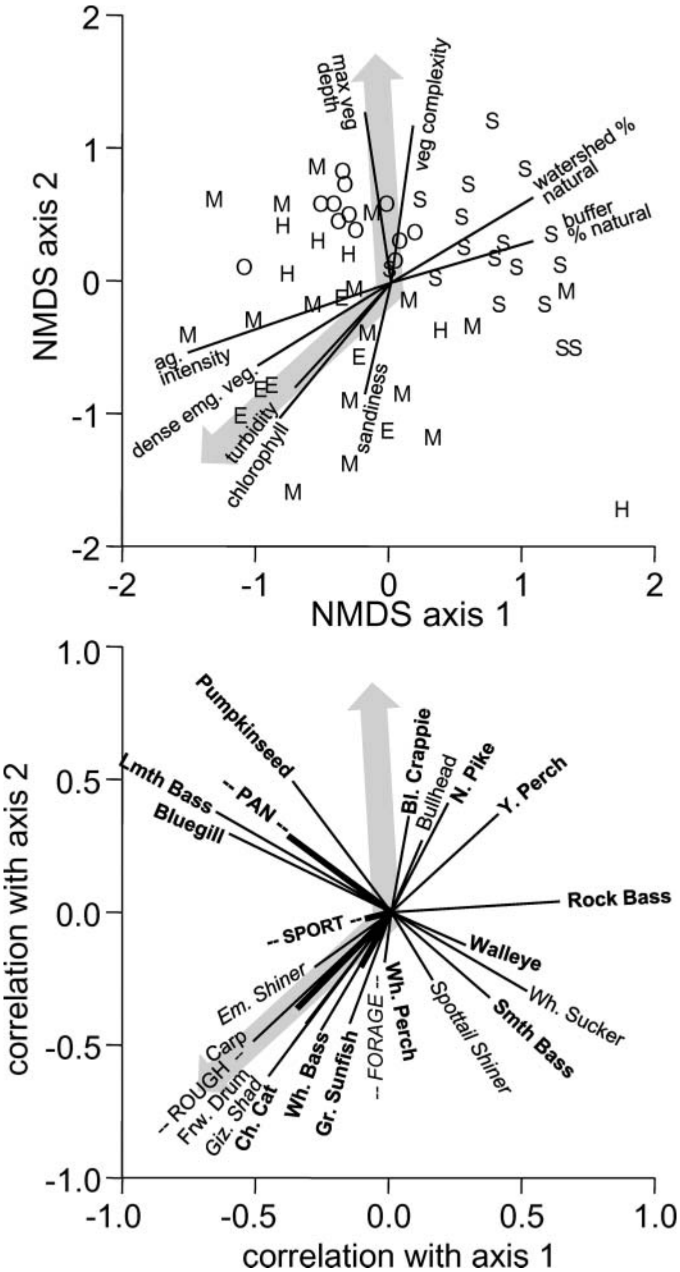

FIGURE 1. NMDS ordination of wetland-scale encounter probability for 24 fishery-relevant species. The top panel shows the positions of GLCWs coded by lake (E = Erie, H = Huron, M = Michigan, O = Ontario, and S = Superior) overlain with vectors showing the correlation with environmental variables. The bottom panel shows overlay vectors for all species (thin lines) except Alewifes (for which the vector is too short to depict) as well as group richness (thick lines), with the names of sport fish and panfish in bold, those of rough fish in ordinary type, and those of forage fish in italics. In both panels the wide gray arrows summarize the two general axes of environmental variation, the one oriented to the lower left being related to eutrophication and anthropogenic disturbance and the other being related to vegetation structure.

species (Alewife) was uncorrelated with the ordination. Panfish richness and three of the five panfish species aligned with increasing vegetation structure. Sport fish richness had little correlation with the ordination because of the disparate orientations of the component species.

The results of analyses relating individual species to environmental variables broadly reflected the patterns in the ordination but revealed further details relevant to how GLCW condition affects fishery support. Species ordinating in the upper left quadrant consistently had positive responses to vegetation structure at both wetland and station scales (Table 8), highlighting this as an influential environmental variable. Despite a strong association between turbidity and the overall eutrophication–disturbance gradient, negative associations to turbidity were few (Table 8), which is consistent with a general tolerance for turbidity by GLCW fish species (Trebitz et al. 2007). Fetch and sediment density ("sandiness") were rarely predictors at the wetland scale but were at the station scale for several species (Table 8). There were few differences among GLCW types (lacustrine, protected, or riverine) in species encounter probabilities, but more species had presence/absence patterns related to station type (lakelike, backbay, or channel; Table 8). Several species showed contrasting station-scale response patterns between life stages, with young-of-year tending to be more open-area oriented than older fish based on station type and fetch relationships (e.g., Largemouth Bass, Yellow Perch, Rock Bass, White Sucker, and Common Carp; Table 8).

Potential Guild Metrics of Fishery Support

Radar plots suggest that fishing-related groupings have some potential for organizing GLCW fishery support patterns. Encounter rates for adult sport fish were highest in GLCWs in the upper, well-vegetated radar plot quadrants (Figure 2a), and those for adults of the three panfish species of most interest to anglers (Black Crappie, Bluegill, and Pumpkinseed) were highest in GLCWs in the upper left quadrants (Figure 2b). Encounter rates for adult rough fish (mostly of interest to commercial fishing) were highest in GLCWs in the lower left, eutrophic–disturbed quadrant (Figure 2c). Only some of the potential taxonomic aggregations usefully distinguished among GLCWs. Encounter rates for adult Smallmouth Bass and Largemouth Bass were highest in upper left quadrant GLCWs (Figure 2d), but those for percids (Walleye and Yellow Perch) were distributed more or less evenly across the radar-plot space while those for adult *Morone* spp. (White Bass and White Perch) were nonzero in only a few GLCWs (not shown).

Groupings based on life history traits do not have much potential to organize fishery-support differences among GLCWs. The GLCW points were more or less uniformly distributed across the radar plots for the groupings of direct fishery-support species illustrated (wetland-associated species, obligate wetland spawners, species with a warm thermal preference, and vegetation-associated sport and panfish; Figure 3) as well as for other trait-based

TABLE 8. Wetland- and station-scale environmental associations, presented clockwise by species position within the ordination. The up and down arrows indicate positive and negative responses, respectively, with arrow thickness indicating significance (thin: $P < 0.05$; thick: $P < 0.005$) for the numerical predictors (Turb = turbidity, Veg = vegetation structure, fetch, and Sand = sediment density). Station-scale analyses are presented by age-group: 0 (young of year), older (juveniles and adults), all, or na (insufficient data). Three species—Alewife, Walleye, and White Perch—are not listed because there were no significant predictors for them.

	Wetland-scale predictors					Station-scale predictors					
Species	GLCW type	Turb	Veg	Fetch	Sand	Age	Station type	Turb	Veg	Fetch	Sand
Upper left quadrant											
Bluegill			↑			Older	Backbay↑		⬇	↑	
Largemouth Bass			⬆			0	Channel↓		⬇	⬇	
						Older					
Pumpkinseed			⬆			Older	Lakelike↑		↑	↑	↓
Age-0 sunfish[a]			⬆			0	Lakelike↑		⬇		⬇
Upper right quadrant											
Black Crappie						All	Backbay↓				
Northern Pike	Lacustrine↓		↑			0					
						Older					
Black/Brown Bullhead					⬇	0					↓
						Older	Channel↓				⬇
Yellow Perch		↓	↑			0	Lakelike↑		↑	↑	
						Older		⬇	⬆		
Rock Bass		↓				0					
						Older	Lakelike↓			⬇	↑
Lower right quadrant											
White Sucker						0					
						Older	Lakelike↓			⬇	⬇
Smallmouth Bass	Protected↓	↓	↓			0			↓		
						Older			↓		↓
Spottail Shiner			↓	↓	↓	All	Backbay↓		↓	↑	
Lower left quadrant											
Green Sunfish			↓			na					
Channel Catfish	Riverine↑					na					
White Bass		⬆				na					
Gizzard Shad		⬆	↑			na					
Freshwater Drum		⬆			↑	na					
Common Carp		⬆		⬆		0	Backbay↓	↓	⬇	↑	
						Older	Lakelike↓	↑			
Emerald Shiner		⬆				All	Backbay↓		↓		

[a] Bluegill and Pumpkinseed combined.

combinations examined (not illustrated), and trial plots summing just adults rather than all life stages were no clearer. For forage species, there was a pattern of higher encounters with vegetation-associated species in lower left quadrant GLCWs driven largely by Gizzard Shad (not shown), but other useful life history trait–related patterns were not evident.

DISCUSSION

Our goals were to refine our understanding of which Great Lakes species are both fishery relevant and wetland using, to examine their patterns of co-occurrence and life history with an eye toward developing useful metrics for multispecies fishery support, and to examine the relationships between GLCW condition and fishery support in the context of potential management actions. We discuss our progress toward each of these goals below.

Prominent Fishery-Relevant, Wetland-Using Species

We identified eight sport fish, five panfish, and five roughfish species meeting the criteria of having at least 10% occurrence across GLCWs and representing at least 1% of the

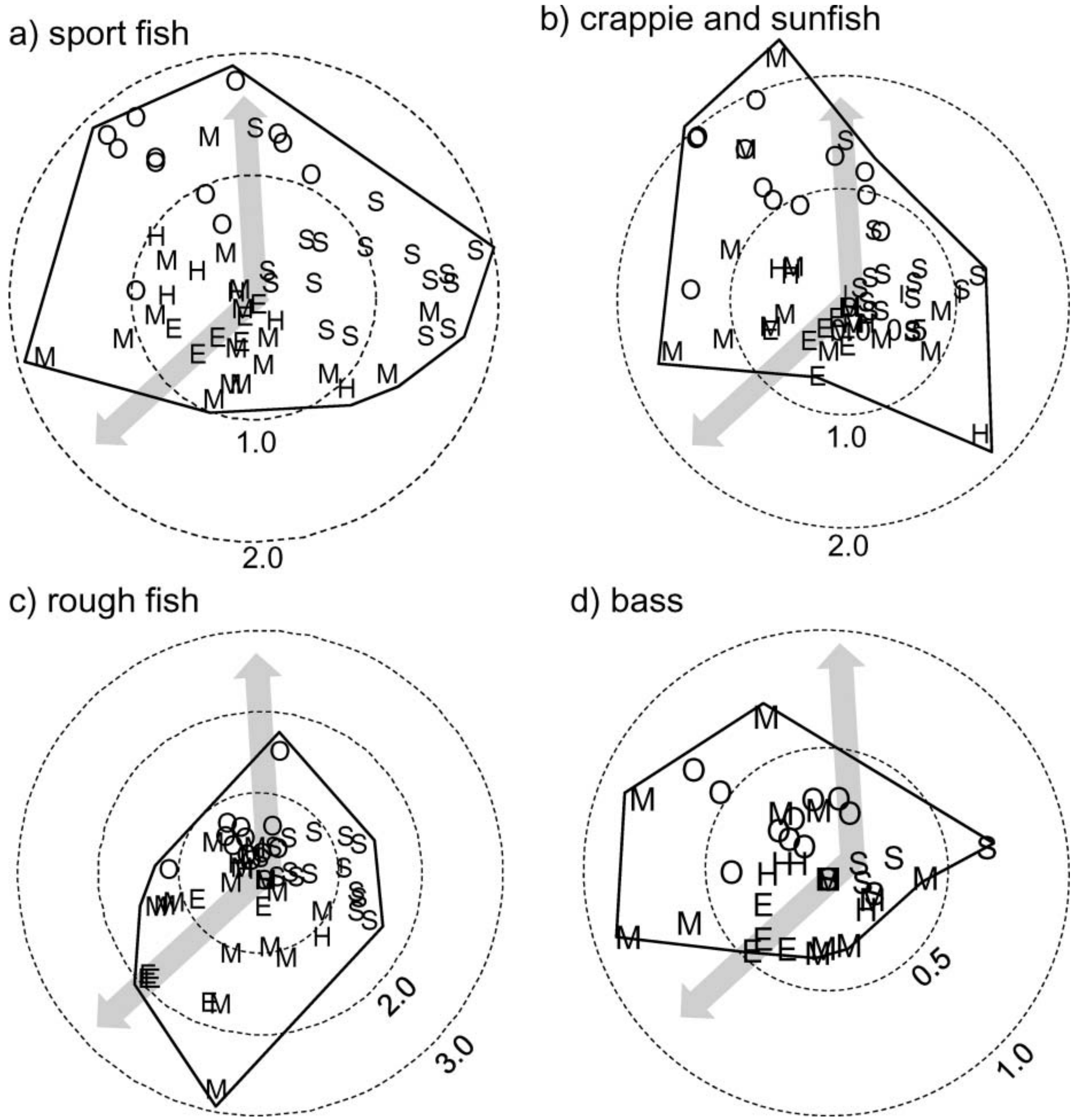

FIGURE 2. Radar plots showing the summed probabilities of encountering an adult fish in various taxonomic or fishing-relevance categories. Panel **(a)** shows any of eight sport fish species, panel **(b)** Black Crappies, Bluegills, and Pumpkinseeds, panel **(c)** any of five rough-fish species, and panel **(d)** Largemouth and Smallmouth Bass. The GLCWs (letter symbols) are plotted at the same angles from the origin as in the ordination but with the radial distance reflecting the encounter probability (further from the origin = higher probability). The rings show the distance scale, the polygons enclose the extent of the data points, and the wide gray arrows indicate the two general axes of environmental variation from the ordination.

recreational or commercial harvest in at least one lake, thereby adding quantitative detail to the long-recognized importance of GLCWs in supporting fishery-relevant species (Jaworski and Raphael 1978; Herdendorf et al. 1981; Jude and Pappas 1992). While Yellow Perch is the most prominent wetland-using species in terms of sport and commercial importance, other wetland-using species popular with recreational anglers include Largemouth Bass, Smallmouth Bass, Walleye, Northern Pike, Channel Catfish, Black Crappie, Bluegill, and Pumpkinseed, while almost all of the rough-fish species landed commercially in the Great Lakes are users of GLCWs.

Estimates that ∼50% of the commercial harvest (biomass) and >80% of the recreational harvest (numbers) across the Great Lakes are comprised of species that use wetlands suggest that the GLCW role in direct fishery support is large. Simply combining fishery harvest data with information on wetland use is obviously insufficient to quantify the portion deriving from wetland-driven recruitment or productivity,

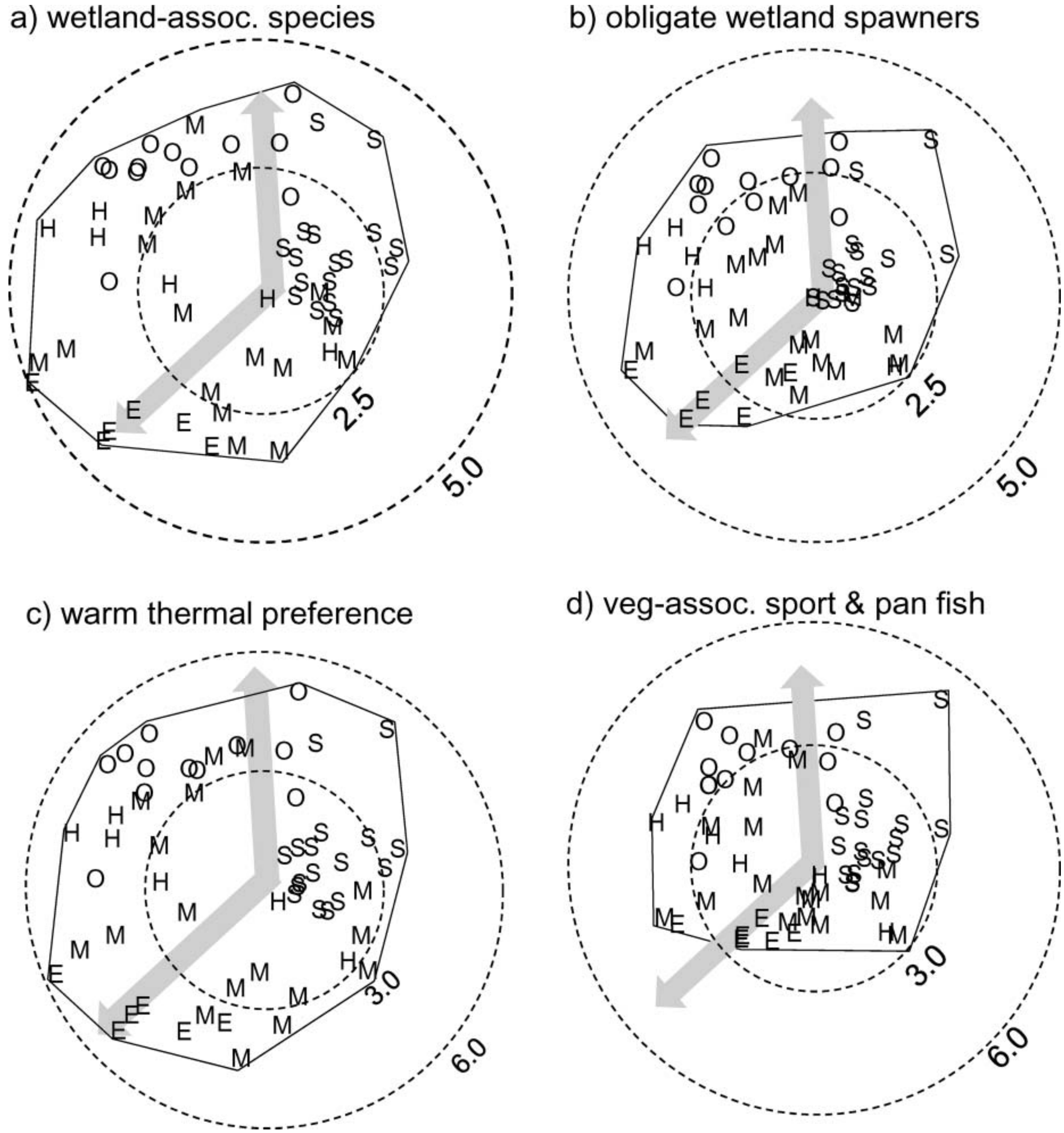

FIGURE 3. Radar plots showing the summed probabilities of encountering any life stage of a species with direct fishery importance in various life history categories derived from Table 5. Panel **(a)** shows species having a weak or strong wetland association, panel **(b)** species that are obligate wetland spawners, panel **(c)** species having a warm thermal preference, and panel **(d)** sport fish or panfish with high or young-of-year vegetation affinity. See Figure 2 for additional details.

especially since the harvested species also use other coastal habitats. However, the GLCW contribution is likely substantial based on the high areal productivity of wetlands. Shallow-water habitat in the Great Lakes is a small portion of the total lake area (~3%), and an even smaller portion is littoral (i.e., vegetated; Wetzel 1992); yet littoral habitat is estimated to represent 14–37% of the basinwide primary productivity, with areal productivity in areas with mixed submerged, floating, and emergent vegetation (i.e., wetlands) more than five times that of littoral habitats having only submerged vegetation (Brazner et al. 2000). Furthermore, a positive correlation between lakewide wetland area and Great Lakes commercial fish harvest has been reported (Brazner et al. 2000).

The GLCWs also provide indirect fishery support for sport fish species that may not use them directly. Wetland-using forage species, notably Emerald Shiner, Spottail Shiner, Gizzard Shad, and Alewife, are important diet items for nearshore pelagic predators such as salmonids (e.g., Brandt 1986; Jude et al. 1987). Also, the harvest data compiled in this paper do not include fish caught for sale as live bait, another indirect contribution to Great Lakes fisheries (baitfish species include White Sucker, Emerald Shiner, and Spottail Shiner; Kerr 2012).

Almost all of the species commercially harvested from the Great Lakes are destined for human consumption (T. Goniea, Michigan Department of Natural Resources, T. Johnson, Ontario Ministry of Natural Resources, and R. Kinnunen, Michigan Sea Grant, personal communications). Sport and panfish sold as restaurant and retail-counter fare bring higher prices and make up more of the harvest on a dollar basis than a biomass basis, whereas rough fish sold in ethnic food markets bring lower prices and make up more of the harvest on a biomass basis than a dollar basis (Table 3). Gizzard Shad is the exception (it is sold primarily as crab bait), explaining the lower price for it than all the other commercial species. Harvest data, however, have limitations for representing fish value, particularly for recreational fishing. For example, angler interest in fishing for Largemouth and Smallmouth Bass and Northern Pike is higher than the harvest suggests (because of catch-and-release regulations and anglers' persisting even when their success is low; Bence and Smith 1999; DFO 2008; USFWS and USCB 2012), whereas the harvest of White Perch and White Bass is more opportunistic than targeted (Ohio DNR 2012). Great Lakes recreational fishery data probably underestimate the importance of sunfish and crappie species because assessments tend to emphasize the ice-free season and large-boat access points. Shore-based anglers report a greater tendency to seek sunfish than do boat-based anglers (Palla 2011), and at least in Lake Superior crappie tend to be targets in ice-fishing rather than summer angling (J. Lindgren, Minnesota Department of Natural Resources, personal communication). A national-scale angler preference survey (USFWS and USCB 2012) found that sunfish and crappie were broadly popular fishing targets even though the largest fishing-related expenditures (e.g., guide services and multiday trips) were directed at sport fish.

Our list of wetland-using species providing fishery support is conservative. For example, the recreationally important Muskellunge *Esox masquinongy* and the commercially harvested Bigmouth Buffalo are obligate vegetation spawners and thus wetland dependent, but they were omitted because of their low occurrence in our survey (~5%). Goldfish *Carassius auratus* and some redhorse sucker species (*Moxostoma* spp.) meet our wetland prevalence criterion but were not included because their commercial harvest is low. Quillback have commercial importance in Lake Erie but their occurrence was only 6% in our cross-lake survey. Surveys targeting distribution patterns on a lake-specific scale might include these species (e.g., Bigmouth Buffalo and Quillback occur frequently in Lake Erie GLCWs). Our compilation of larval fish data suggests that additional species might meet the criteria for being wetland-using if GLCW fish surveys were better timed to detect species for which the adults are present only briefly (e.g., in spring) to breed. Given their large commercial importance, finding *Coregonus* species and Rainbow Smelt in GLCWs as larvae but not at older life stages points to a potentially very important but poorly documented fishery support.

With respect to indirect fishery support, we only included species that are prominent in pelagic forage fish surveys or predator diet studies. We suspect these forage fish surveys underestimate the contribution of species that stay in very shallow waters, as this is an environment not easily sampled. Yellow Perch, for example, are not reported as being present in recent nearshore forage fish assessments for Lake Superior (e.g., Johnson et al. 2004; Gamble et al. 2011) despite being numerically dominant in a study of exchange between a Lake Superior GLCW and the adjacent nearshore area (Brazner et al. 2001). Brazner et al. (2001) also found frequent wetland–nearshore exchange for forage-sized Golden Shiner *Notemigonus crysoleucas* and Blacknose Shiner *Notropis heterolepis*, additional common GLCW species that likely provide some indirect fishery support. Stable isotope and otolith microelement analyses offer tools for getting at exchanges and habitat use patterns (Brazner et al. 2004; Hoffman et al., in press), but studies relevant to addressing fishery support in the Great Lakes are just beginning.

Useful Summary Metrics of GLCW Fishery Support?

The wetland-using, fishery-relevant species vary considerably in life history traits and environmental associations. While this means that GLCWs across a broad geographic and condition gradient are capable of providing meaningful fishery support, it also raises the problem of how to best quantify that support across species and fishery categories in order to ascertain the important patterns. We are not aware of good solutions to this problem in the fishery support literature; studies typically focus on a single fishery segment and either look at species (sometimes genera or families) one at a time or at very broad aggregations of catch (e.g., Manson et al. 2005; Vasconcelos et al. 2011; Sheaves et al. 2012; Blandon and zu Ermgassen 2014; Seitz et al. 2014). We saw the problem of quantifying multispecies, multi–user group fishery support as analogous to that of translating the concept of biological integrity into measurable indicators (e.g., Karr and Chu 1999), which led us to explore metrics based on taxonomic and functional groupings similar to those that have proven to be of value in biological integrity assessment.

Metrics that combine species that are related taxonomically or that are defined in terms of fishery user groups have some potential for organizing GLCW fishery support patterns. Radar plots depicting among-wetland patterns in encounter probability (i.e., the percentage of sampling locations where a species occurred) show some clear spatial patterns, especially for sport and rough-fish species; however, efforts to aggregate fishery-relevant species via encounter probability summation had variable success. Combining the three panfish species of most interest to anglers (Bluegill, Pumpkinseed, and Black Crappie) conveniently also combined species with similar orientations in the ordination while excluding the opposing Rock Bass and Green Sunfish and produced a strong signal in the radar plots. However, Yellow Perch and Walleye (i.e., the Percidae) were not nearly as useful in the radar plots when combined despite their having similar orientations in the ordination and potentially similar appeal to anglers. Quantification based on richness was generally not helpful because combining enough species to obtain adequate range resulted in species with opposing occurrence patterns trading off in the calculations. For example, the orientation of the vectors for sport fish species was so diverse that overall sport fish richness had no meaningful pattern.

Functional metrics of the type generally included in fish-based biotic integrity indices (Fausch et al. 1990; Simon 1998) were generally not useful in organizing patterns of fishery support. Tolerance metrics did not discern among GLCWs because all of the fishery-relevant species are at least moderately tolerant of turbidity (Trebitz et al. 2007) and otherwise adapted to a wide variety of water quality conditions (Jude and Pappas 1992). Dietary categories essentially duplicated categorizing by fishing type, since the sport fish are piscivores, the panfish feed primarily on macroinvertebrates, and the rough fish are largely omnivores. Spawning guild metrics also did little to move classification beyond taxonomic and fishery groupings; for example, nest guarding is characteristic of both bass and sunfish. Even summarizing species encounter probabilities within life history traits related directly to the use of GLCWs (e.g., thermal preference, vegetation association, and wetland dependence; Table 6) did little to organize the patterns of fishery support, as evidenced by point clouds with no obvious spatial bias in the radar plots (Figure 3).

Are "Wetland Dependence" and "Poster-Child Species" Useful?

The presence of charismatic species may serve as public-friendly endpoints that people can readily value. For this reason and because single-species fisheries are more tractable to quantify, studies of fishery support have tended to focus on individual taxa for which both exploitation and habitat associations are well understood (e.g., penaeid shrimp in estuaries and mangroves; salmon *Oncorhynchus* spp. in Pacific Northwest coastal zone, blue crabs *Callinectes sapidus* in seagrass beds; Manson et al. 2005; Engle 2011; Jordan et al. 2012). Were we to nominate a representative fishery-support species for GLCWs, Yellow Perch is an obvious candidate given its high abundance and frequency of occurrence, its prominence in commercial and sport harvests, and its role as a forage species. However, Yellow Perch are not restricted to wetland environments either by life history or prevalence (they are equally abundant in nearshore/beach and GLCW habitats; Brazner and Beals 1997), and recent studies suggest that the species separates into primarily wetland-resident and primarily lake-resident populations having only weak connectivity (Janetski et al. 2013; Schoen 2013). Thus, while GLCW-derived Yellow Perch are known to play an ecological role in the Great Lakes, the species does not demonstrate that GLCWs are necessary to support Great Lakes fisheries.

In fact, the concept of wetland dependence among Great Lakes fish species is not a good match with GLCW use (as Table 6 illustrates). Fish have ontogeny and plasticity in habitat use that make essential fish habitat difficult to quantify (e.g., Levin and Stunz 2005; Kimirei et al. 2011), and even for species for which certain habitats are crucial those habitats may be neither limiting nor ones in which much time is spent (Minns et al. 1996; Rosenfield 2003). Thus, there is a need to characterize the interactions between GLCWs and other nearshore habitats analogous to that recognized for other coastal habitats (e.g., mangroves and salt marshes) in the context of the coastal ecosystem mosaic (Manson et al. 2005; Sheaves 2009). Furthermore, there is geographic variability in the Great Lakes with respect to how strongly fish species are wetland associated, as discrete GLCWs provide the only littoral habitat in some areas (e.g., Lake Superior) whereas entire coastal regions are littoral in character elsewhere (e.g., western Lake Erie and Green Bay). Nevertheless, the evidence of the spawning of multiple fishery-relevant species in GLCWs demonstrates that these habitats do contribute to overall fish populations and the use of multiple habitats (including GLCWs) for spawning–rearing can be a valuable risk-hedging strategy. Acknowledging that the spatial scale over which fishery-relevant species and their fisheries operate extends well beyond the GLCWs is not at odds with valuing GLCWs for fishery support. Increased attention to quantifying the spatial distribution of fishing effort and harvest would help establish the link between GLCW availability/condition and fishery support.

Focusing on "poster child" species or life history traits thought to coincide with wetland dependence (e.g., an affinity for quiescent or warm water, vegetated habitat, and organic substrates) sells short the diversity of fishery-relevant species that GLCWs support. The alternative is to embrace this diversity by evaluating entire suites of species despite the complexity this entails and by continuing to work toward useful multimetric characterization of fishery support. Species-specific assessments should be chosen for their value in understanding wetland–lake connectivity and the effects of ecological conditions. For example, despite the lack of clear wetland dependence or a requirement for vegetation on the part of Yellow Perch, the within-wetland encounter rates for this species were strongly and negatively correlated with the anthropogenic disturbance gradient in our ordination, making it a potentially useful indicator species.

GLCW Fishery Support in Relation to Wetland Characteristics and Condition

Great Lakes coastal wetlands are naturally heterogeneous, with differences in hydromorphology, substrate type, and vegetation structure leading to broad differences in the fish communities supported. The natural variability in GLCWs can generally be described as a continuum ranging from those in sheltered settings that tend to be deep and morphologically complex with organic sediments and vegetation that is abundant and diverse in form to those in exposed settings that tend to be shallower and morphologically simpler with sandier substrates and vegetation that is sparser and more monotypic. Like coastal ecosystems worldwide, GLCWs are also subject to stressors stemming from shoreline and watershed land-use practices (nutrient and sediment inputs, shoreline hardening, hydrologic alteration, recreational overuse, and the proliferation of nuisance species) that affect their physical and biological structures. Changes particularly relevant to fish assemblages include declining water clarity, degraded vegetation, and altered trophic pathways (Whillans 1996; Deegan 2002; Jude et al. 2005; Seitz et al. 2014).

Evans et al. (1987) characterize the overall productivity of lakes as depending on nutrient and energy inputs but the distribution of that production as driven by habitat conditions and biotic interactions. The same can be said of support for fish in GLCWs, as is readily apparent in our ordination of fishery-relevant species. As the most eutrophic and most littoral of the Great Lakes, Lake Erie would be expected to support the largest number and biomass of littoral fish. However, the fish composition in that lake is strongly biased toward rough-fish species of lesser commercial value and limited recreational interest. The GLCWs in other eutrophic settings (e.g., Green Bay and Saginaw Bay) are similar to those of Lake Erie with respect to species composition. In less eutrophic, less disturbed areas of the Great Lakes, yields of wetland-using, fishery-relevant species are lower but distributed more toward the sport and panfish species that bring high dockside prices and recreational interest. Depending on the characteristics of the individual GLCWs (and the broader biogeography), the fishery-relevant species supported are likely to divide into a warmer-water, phytophilic group (e.g., sunfish, Largemouth Bass, Black Crappie, and Northern Pike) and a cooler-water, lithophilic group (e.g., Smallmouth Bass, Walleye, and Rock Bass), although some species like Yellow Perch are prevalent in both.

These patterns suggest some ability to manage the nature of fishery support in GLCWs through protection and restoration. In a broad sense, anything that ameliorates degraded vegetation structure in GLCWs is likely to enhance conditions for the more desirable panfish and sport fish species. Poor water clarity resulting from nutrient and sediment loading is strongly implicated in the loss of the structurally diverse vegetation (Lougheed et al. 2001; Albert and Minc 2004) that is important to many sport and pan fish species (Randall et al. 1996; Smokorowski and Pratt 2007) and in shifting energy flow from benthic pathways and visual feeders (often sport and panfish) toward planktonic pathways and tactile/filter feeders (often rough fish; Sierszen et al. 2012a). As is evident from the “dense emergent vegetation” vector in our ordination (Figure 1), the proliferation of invasive plant species such as *Typha* and *Phragmites* is associated with nutrient loading and hydrologic alteration (Frieswyk and Zedler 2007; Tulbure and Johnston 2010) and can negatively affect the habitat for ambush piscivores such as Northern Pike and Largemouth Bass. Shoreline clearing and hardening are also associated with degraded vegetation structure in GLCWs (e.g., Trebitz et al. 2009b; Uzarski et al. 2009) and tend to reduce spawning habitat (Reed and Pereira 2009). Disruption of the normal connectivity between GLCWs and the adjacent lakes is another condition that is detrimental to support for fishery-relevant species (Johnson et al. 1997; Jude et al. 2005). Restoring hydrologic connectivity is a major thrust of restoration on marine coasts (e.g., Montalto and Steenhuis 2004) and is expected to enhance the number and size of fishery-relevant species in GLCWs (Bouvier et al. 2009). Nutrient and sediment control, invasive plant removal, and the reversal of shoreline hardening and hydrologic alterations are all part of the suite of restoration efforts currently proposed in the Great Lakes coastal areas (GLRI 2010), some with the express purpose of improving fisheries.

As a tangible example of potential restoration outcomes, consider the differences in fishery-relevant species encounter rates between the GLCWs within Lake Michigan that ordinated in a quadrant associated with high anthropogenic disturbance (lower left) and those associated with well-developed vegetation structure (upper left and right). While the among-GLCW variability is considerable, restoration actions that alter the vegetation structure from that typical of disturbed wetlands to that typical of well-vegetated wetlands could lead to an approximate doubling of the encounter rate for fishable-size (adult) bass, crappie, and sunfish but a halving of that for rough fish (Figure 4). This would clearly benefit recreational anglers, who value bass and panfish but have little interest in rough fish; for commercial fishing the shift away from rough fish and toward panfish would bring reduced landed biomass but higher dockside values. There was no difference in Yellow Perch encounter rates between the above GLCW groups, but other studies suggest that water quality improvements (especially in lacustrine coastal wetlands) would also roughly double the abundance of Yellow Perch (Leach et al. 1977; Parker et al. 2012). We chose Lake Michigan deliberately for the above example because its coastline spans the broadest disturbance gradient within the Great Lakes (Niemi et al. 2007) and the GLCW groups being compared are geographically and morphologically similar enough that shifts in ordination position between them are plausible. Predictions of restoration outcomes within some of the other Great Lakes are more difficult due to their less-prominent disturbance gradients (less “signal”

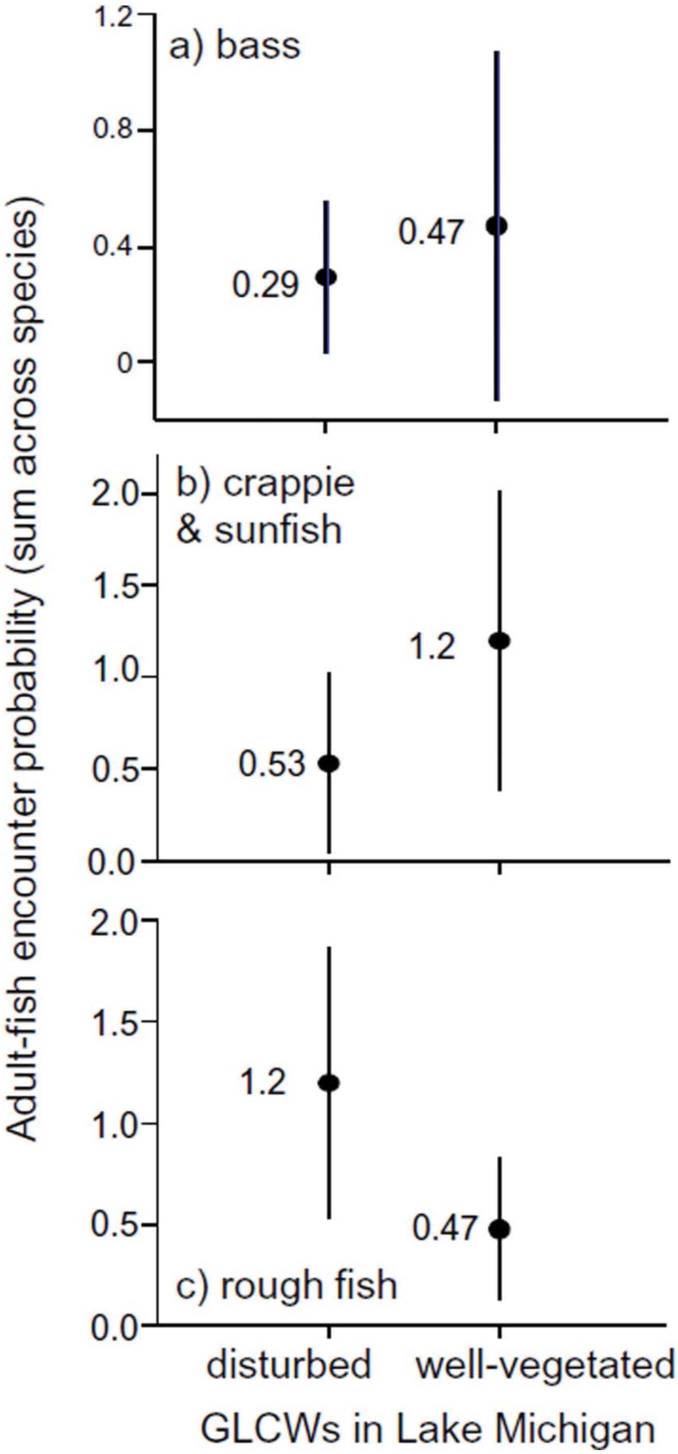

FIGURE 4. Comparison of encounter probabilities among Lake Michigan GLCWs falling into the disturbed (lower left; $N = 8$) ordination quadrant with ones falling into the well-vegetated (upper left and upper right; $N = 4$) ordination quadrants from Figure 1 for **(a)** Largemouth or Smallmouth Bass, **(b)** Black Crappies, Bluegills, or Pumpkinseeds, and **(c)** the five rough-fish species. The circles denote averages and the vertical bars 95% confidence intervals.

relative to "noise"). Ultimately, developing a framework for assessing the responses of fishery-relevant species on a regional scale is desirable because the cumulative effect of small-scale habitat degradation can be substantial impact over broader coastal regions (Jordan et al. 2009) and because habitat protection and restoration maintain fish communities and the diversity of fishing opportunities across broader scales than just individual ecosystems (Rahel 2002; Sheaves 2009).

Summary and Conclusions

Great Lakes coastal wetlands exemplify a complex fishery support situation. At least 21 fish species that are directly harvested or that serve as prey for other harvested species are regular users of GLCWs; they represent diverse taxonomic groups and life history traits; and they are fished for by multiple human user groups well beyond the GLCWs themselves. Our criteria of a minimum level of GLCW use and fishery importance make this list of species conservative; including species with more biogeographically restricted distributions or temporal use patterns not picked up by summer adult/juvenile fish surveys (e.g., larvae) would reveal additional fishery-relevant species supported by GLCWs. We have shown that synoptic survey data reveal patterns in fishery-relevant species associated with differences in the physical environments and ecological conditions of GLCWs that can be interpreted in terms of differences in fishing opportunity. For example, we can predict that management actions that lead to improved vegetation structure by controlling nutrient loading and other anthropogenic stressors will increase the rates of encounter with wetland-associated pan- and sport fish while lowering those with rough fish. Quantifying fishery support for GLCWs and other complex situations (such as those found in marine coastal ecosystems) is usefully viewed as a multispecies, multimetric problem that synoptic survey data can help solve. Our estimates that ~50% of the commercial and ~80% of the recreational fishery harvest in the Great Lakes is accounted for by wetland-using species would benefit from additional studies linking roving fish and spatially distributed fisheries back to GLCWs. The key information needs closely parallel those expressed for understanding fishery support in other coastal habitats (e.g., Able et al. 2005; Manson et al. 2005) and include fishery harvest data with higher spatial and temporal resolutions in order to match the ecologically relevant scales of habitat use; better data on fish origins and movements; and data documenting differential growth, mortality, and recruitment among alternative habitats.

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REFERENCES

Able, K. W. 2005. A reexamination of fish estuarine dependence: evidence for connectivity between estuarine and ocean habitats. Estuarine, Coastal, and Shelf Science 64:5–17.

Albert, D. A., and L. D. Minc. 2004. Plants as regional indicators of Great Lakes coastal wetland health. Aquatic Ecosystem Health Management 7:233–247.

Albert, D. A., D. A. Wilcox, J. W. Ingram, and T. A. Thompson. 2005. Hydrogeomorphic classification for Great Lakes coastal wetlands. Journal of Great Lakes Research 31(Supplement 1):129–46.

Allan, J. D., P. B. McIntyre, S. D. P. Smith, B. S. Halpern, G. Boyer, A. Buchsbaum, A. Burton, L. Campbell, L. Chadderton, J. Ciborowski, P. Doran, T. Eder, D. M. Infante, L. B. Johnson, C. G. Joseph, A. L. Marino, A. Prusevich, J. Read, J. Rose, E. Rutherford, S. Sowa, and A. D. Steinman. 2013. Joint analysis of stressors and ecosystems services to enhance restoration effectiveness. Proceedings of the National Academy of Sciences of the USA 110:372–377.

Arend, K. K., and M. B. Bain. 2008. Fish communities in coastal freshwater ecosystems: the role of the physical and chemical setting. BMC Ecology [online serial] 8:23.

Auer, N. A. 1982. Identification of larval fishes of the Great Lakes basin with emphasis on the Lake Michigan drainage. Great Lakes Fishery Commission, Special Publication 82-3, Ann Arbor, Michigan.

Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier, and B. R. Silliman. 2011. The value of estuarine and coastal ecosystem services. Ecological Monographs 81:169–193.

Becker, G. C. 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison.

Bell, F. W. 1997. The economic valuation of saltwater marsh supporting marine recreational fishing in the southeastern United States. Ecological Economics 21:243–254.

Bence, J. R., and K. D. Smith. 1999. An overview of recreational fisheries of the Great Lakes. Pages 259–305 *in* W. W. Taylor and C. P. Ferreri, editors. Great Lakes fishery policy and management: a binational perspective. Michigan State University Press, East Lansing.

Blandon, A., and P. S. E. zu Ermgassen. 2014. Quantitative estimate of commercial fish enhancement by seagrass habitat in southern Australia. Estuarine, Coastal, and Shelf Science 141:1–8.

Bouvier, L. D., K. Cottenie, and S. E. Doka. 2009. Aquatic connectivity and fish metacommunities in wetlands of the lower Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 66:933–948.

Brander, L. M., R. J. Florax, and J. E. Vermaat. 2006. The empirics of wetland valuation: a comprehensive summary and a meta-analysis of the literature. Environmental Resource Economics 33:223–250.

Brandt, S. B. 1986. Food of trout and salmon in Lake Ontario. Journal of Great Lakes Research 12:200–205.

Brazner, J. C., and E. W. Beals. 1997. Patterns in fish assemblages from coastal wetland and beach habitat in Green Bay, Lake Michigan: a multivariate analysis of abiotic and biotic forcing factors. Canadian Journal of Fisheries and Aquatic Sciences 54:1743–1761.

Brazner, J. C., S. E. Campana, D. K. Tanner, and S. T. Schram. 2004. Reconstructing habitat use and wetland nursery origin of Yellow Perch from Lake Superior using otolith elemental analysis. Journal of Great Lakes Research 30:492–507.

Brazner, J. C., M. E. Sierszen, J. R. Keough, and D. K. Tanner. 2000. Assessing the ecological importance of coastal wetlands in a large-lake context. Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen 27:1950–1961.

Brazner, J. C., D. K. Tanner, and J. A. Morrice. 2001. Fish-mediated nutrient and energy exchange between a Lake Superior coastal wetland and its adjacent bay. Journal of Great Lakes Research 27:98–111.

Breidert, B. 2011. Harvest of fishes from Lake Michigan during 2010. Report to Great Lakes Fishery Commission, Lake Michigan Committee, Ann Arbor, Michigan.

Chubb, S. L., and C. R. Liston. 1986. Density and distribution of larval fishes in Pentwater Marsh, a coastal wetland on Lake Michigan. Journal of Great Lakes Research 12:332–343.

Coker, G. A., C. B. Portt, and C. K. Minns. 2001. Morphological and ecological characteristics of Canadian freshwater fishes. Canadian Manuscript Report of Fisheries Aquatic Sciences 2554.

Cooper, C. L., W. C. Bartholomew, C. R. Herdendorf, J. M. Reutter, and F. L. Snyder. 1981. Limnetic larval fish of the Maumee and Sandusky River estuaries. Journal of Great Lakes Research 7:51–54.

Cooper, M. J., K. F. Gyekis, and D. G. Uzarski. 2012. Edge effects on abiotic conditions, zooplankton, macroinvertebrates, and larval fishes in Great Lakes fringing marshes. Journal of Great Lakes Research 38:142–151.

Danz, N. P., R. R. Regal, G. J. Niemi, V. J. Brady, T. Hollenhorst, L. B. Johnson, G. E. Host, J. M. Hanowski, C. A. Johnston, T. Brown, J. Kingston, and J. R. Kelly. 2005. Environmentally stratified sampling design for the development of Great Lakes environmental indicators. Environmental Monitoring and Assessment 102:41–65.

Deegan, L. A. 2002. Lessons learned: the effects of nutrient enrichment on the support of nekton by seagrass and salt marsh ecosystems. Estuaries 25:727–742.

DFO (Department of Fisheries and Oceans). 2008. Survey of recreational fishing in Canada: selected results for the Great Lakes fishery 2005. DFO, Ottawa.

Engle, V. D. 2011. Estimating the provision of ecosystem services by Gulf of Mexico coastal wetlands. Wetlands 31:179–193.

Evans, D. O., B. A. Henderson, N. J. Bax, T. R. Marshall, R. T. Oglesby, and W. J. Christie. 1987. Concepts and methods of community ecology applied to freshwater fisheries management. Canadian Journal of Fisheries and Aquatic Sciences 44(Supplement):S448–S470.

Farber, S., R. Costanza, D. L. Childers, K. Erickson, K. Gross, M. Grove, C. S. Hopkinson, J. Kahn, S. Pincetl, A. Troy, P. Warren, and M. Wilson. 2006. Linking ecology and economics for ecosystem management. Bioscience 56:121–133.

Fausch, K. D., J. Lyons, J. R. Karr, and P. L. Angermeyer. 1990. Fish communities as indicators of environmental degradation. Pages 123–144 *in* S. M. Adams, editor. Biological indicators of stress in fish. American Fisheries Society, Symposium 8, Bethesda, Maryland.

Francis, M. P., M. A. Morrison, J. Leathwick, C. Walsh, and C. Middleton. 2005. Predictive models of small fish presence and abundance in northern New Zealand harbours. Estuarine, Coastal, and Shelf Science 64:419–435.

Frieswyk, C. B., and J. B. Zedler. 2007. Vegetation change in Great Lakes coastal wetlands: deviation from the historical cycle. Journal of Great Lakes Research 33:366–380.

Gamble, A. E., T. R. Hrabik, J. D. Stockwell, and D. L. Yule. 2011. Trophic connections in Lake Superior, part II. The nearshore fish community. Journal of Great Lakes Research 37:550–560.

GLRI (Great Lakes Restoration Initiative). 2010. Great Lakes Restoration Initiative action plan, FY2010–FY2014. Available: greatlakesrestoration.us/pdfs/glri_actionplan.pdf. (January 2015).

Gordon, D., D. W. Chapman, and T. C. Bjornn. 1973. Economic evaluations of sport fisheries: what do they mean? Transactions of the American Fishery Society 102:293–311.

Hanson, D. 2012. 2011 Lake Michigan recreational fishery trends by region. Lake Michigan Committee Meeting, Windsor, Ontario. Available: http://www.in.gov/dnr/fishwild/files/fw-Lake_Michigan_Recreational_Creel_Report_2011.pdf. (January 2015).

Herdendorf, C. E., S. M. Hartley, and M. D. Barnes, editors. 1981. Fish and wildlife resources of the Great Lakes coastal wetlands within the United States, volume 1. Overview. U.S. Fish and Wildlife Service Report FWS/OBS-81/02-v1.

Hoffman, J. C., J. R. Kelly, G. S. Peterson, and A. M. Cotter. In press. Landscape-scale food webs of fish nursery habitat along a river–coast mixing zone. Estuaries and Coasts. DOI: 10.1007/s12237-014-9880-8.

Hoffman, J. C., J. R. Kelly, G. S. Peterson, A. M. Cotter, M. A. Starry, and M. E. Sierszen. 2012. Using δ^{15}N in fish larvae as an indicator of watershed sources of anthropogenic nitrogen: response at multiple spatial scales. Estuaries and Coasts 35:1453–1467.

Holmlund, C., and M. Hammer. 1999. Ecosystem services generated by fish populations. Ecological Economics 29:253–368.

Höök, T. O., N. M. Eagan, and P. W. Webb. 2001. Habitat and human influences on larval fish assemblages in northern Lake Huron coastal marsh bays. Wetlands 21:281–291.

Janetski, D. J., C. R. Ruetz, Y. Bhagat, and D. F. Clapp. 2013. Recruitment dynamics of age-0 Yellow Perch in a drowned river mouth lake: assessing synchrony with nearshore Lake Michigan. Transactions of the American Fisheries Society 142:505–514.

Jaworski, E., and C. N. Raphael. 1978. Fish, wildlife, and recreational values of Michigan's coastal wetlands. Report to Michigan Department of Natural Resources, Ypsilanti.

Johnson, D. L. 1989. Lake Erie wetlands: fisheries considerations. Pages 257–273 *in* K. A. Krieger, editor. Lake Erie estuarine systems: issues, resources, status, and management. National Oceanic and Atmospheric Administration, Estuary-of-the-Month Seminar Series 14, Washington, D.C..

Johnson, D. L., W. E. Lynch, and T. W. Morrison. 1997. Fish communities in a diked Lake Erie wetland and an adjacent undiked area. Wetlands 17:43–54.

Johnson, T. B., M. H. Hoff, A. S. Trebitz, C. R. Bronte, T. D. Corry, J. F. Kitchell, S. T. Lozano, D. M. Mason, J. V. Scharold, S. T. Schram, and D. R. Schreiner. 2004. Spatial patterns in assemblage structures of pelagic forage fish and zooplankton in western Lake Superior. Journal of Great Lakes Research 30(Supplement 1):395–406.

Jordan, S. J., T. O. O'Higgins, and J. A. Dittmar. 2012. Ecosystem services of coastal habitats and fisheries: multiscale ecological and economic models in support of ecosystem-based management. Marine Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 4:573–586.

Jordan, S. J., L. M. Smith, and J. A. Nestlerode. 2009. Cumulative effects of coastal habitat alterations on fishery resources: towards prediction at regional scales. Ecology and Society [online serial] 14(1):16.

Jude, D., D. Albert, D. G. Uzarski, and J. Brazner. 2005. Lake Michigan's coastal wetlands: distribution, biological components with emphasis on fish, and threats. Pages 439–477 *in* T. Edsall and M. Munawar, editors. State of Lake Michigan: ecology, health, and management. Backhuys Publishers, Ann Arbor, Michigan.

Jude, D. J., and J. Pappas. 1992. Fish utilization of Great Lakes coastal wetlands. Journal of Great Lakes Research 18:651–672.

Jude, D. J., T. L. Rutecki, C. P. Madenjian, G. E. Noguchi, P. P. Schneeberger, S. A. Klinger, G. G. Godun, and M. H. Winnel. 1981. The physical, chemical, and biological nature of Pigeon Lake, a Lake Michigan coastal lake. University of Michigan, Great Lakes Research Division, Special Report 78, Ann Arbor.

Jude, D. J., and F. J. Tesar. 1985. Recent changes in the inshore forage fish of Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 42:1154–1157.

Jude, D. J., F. J. Tesar, S. F. Deboe, and T. J. Miller. 1987. Diet and selection of major prey species by Lake Michigan salmonines, 1973–1982. Transactions of the American Fisheries Society 116:677–691.

Karr, J. R., and E. W. Chu. 1999. Restoring life in running waters: better biological monitoring. Island Press, Washington, D.C.

Kerr, S. J. 2012. The management of bait in Ontario: a review. Ontario Ministry of Natural Resources, Peterborough.

Kimirei, I. A., I. Nagelkerken, B. Griffioen, C. Wagner, and Y. D. Mgaya. 2011. Ontogenetic habitat use by mangrove/seagrass-associated coral reef fishes shows flexibility in time and space. Estuarine, Coastal, and Shelf Science 92:47–58.

Klumb, R. A., L. G. Rudstam, E. L. Mills, C. P. Schneider, and P. M. Sawyko. 2003. Importance of Lake Ontario embayments and nearshore habitats as nurseries for larval fishes with emphasis on Alewife (*Alosa pseudoharengus*). Journal of Great Lakes Research 29:181–198.

Knight, R. L., and B. Vondracek. 1993. Changes in prey fish populations in western Lake Erie, 1969–88, as related to Walleye, *Stizostedion vitreum*, predation. Canadian Journal of Fisheries and Aquatic Sciences 50:1289–1298.

Krupa, K. A. 2003. Larval fish exchange between Lake Erie and a coastal marsh. Master's thesis. Ohio State University, Columbus.

Lane, J. A., C. B. Portt, and C. K. Minns. 1996a. Nursery habitat characteristics of Great Lakes fishes. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2338.

Lane, J. A., C. B. Portt, and C. K. Minns. 1996b. Spawning habitat characteristics of Great Lakes fishes. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2368.

Lantry, J. R., and T. H. Eckert. 2012. 2011 Lake Ontario fishing boat survey. New York State Department of Environmental Conservation, Albany.

Leach, J. H., M. G. Johnson, J. R. M. Kelso, J. Hartmann, W. Nümann, and B. Entz. 1977. Responses of percid fishes and their habitats to eutrophication. Journal of the Fisheries Research Board of Canada 34:1964–1971.

Levin, P. S., and G. W. Stunz. 2005. Habitat triage for exploited fishes: can we identify essential "essential fish habitat"? Estuarine, Coastal, and Shelf Science 64:70–78.

Lewis, L. M., and S. P. Patch. 1982. Lake Ontario shoreline protection study report: Sage Creek Marsh. U.S. Fish and Wildlife Service, Cortland, New York.

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

Manson, F. J., N. R. Loneragan, G. A. Skilleter, and S. R. Phinn. 2005. An evaluation of the evidence for linkages between mangroves and fisheries: a synthesis of the literature and identification of research directions. Oceanography and Marine Biology: an Annual Review 43:485–515.

Masterson, C., and B. Eggold. 2012. Wisconsin's 2011 open-water sportfishing effort and harvest from Lake Michigan and Green Bay. Wisconsin Department of Natural Resources, Publication FH-830-12, Milwaukee.

Minns, C. K., R. G. Randall, J. E. Moore, and V. W. Cairns. 1996. A model simulating the impact of habitat supply limits on Northern Pike, *Esox lucius*, in Hamilton Harbour, Lake Ontario. Canadian Journal of Fisheries and Aquatic Sciences 53(Supplement 1):20–34.

Mizera, J. J., C. L. Cooper, and C. E. Herdendorf. 1981. Limnetic larval fish in the nearshore zone of the western basin of Lake Erie. Journal of Great Lakes Research 7:62–64.

Montalto, F. A., and T. S. Steenhuis. 2004. The link between hydrology and restoration of tidal marshes in the New York–New Jersey estuary. Wetlands 24:414–425.

Murphy, S., N. Collins, S. E. Doka, and B. J. Fryer. 2012. Evidence of Yellow Perch, Largemouth Bass, and Pumpkinseed metapopulations in coastal embayments of Lake Ontario. Environmental Biology of Fishes 95:213–226.

National Research Council. 2005. Valuing ecosystem services: towards better environmental decision making. National Academies Press, Washington, D.C.

Niemi, G. J., J. R. Kelly, and N. P. Danz. 2007. Environmental indicators for the coastal region of the North American Great Lakes: introduction and prospectus. Journal of Great Lakes Research 33(Supplement 3):1–12.

O'Gorman, R. 1983. Distribution and abundance of larval fish in the nearshore waters of western Lake Huron. Journal of Great Lakes Research 9:14–22.

Ohio DNR (Department of Natural Resources). 2012. Ohio's Lake Erie fisheries 2011. Ohio DNR, Federal Aid in Fish Restoration, Project f-69-P, Annual Status Report, Fairport and Sandusky.

OMNR (Ontario Ministry of Natural Resources). 2013a. 2012 status of major stocks. OMNR, Wheatley.

OMNR (Ontario Ministry of Natural Resources). 2013b. Lake Huron commercial fishing summary for 2012. OMNR, Owen Sound.

OMNR (Ontario Ministry of Natural Resources). 2013c. Lake Ontario fish communities and fisheries: 2012 annual report of the Lake Ontario management unit. OMNR, Picton.

OMNR (Ontario Ministry of Natural Resources). 2013d. Lake Superior commercial fishing summary for 2011. OMNR, Lake Superior Report TR-LSA-2013-nn, Owen Sound.

Palla, J. S. 2011. Lake Michigan 2010 creel survey report. Indiana Department of Natural Resources, Indianapolis.

Palmer, M. A., and S. Filoso. 2009. Restoration of ecosystem services for environmental markets. Science 325:575–576.

Parker, A. D., M. J. Cooper, C. R. Ruetz, D. P. Coulter, and D. G. Uzarski. 2012. Chemical and physical factors associated with Yellow Perch abundance in Great Lakes coastal wetlands: patterns within and among wetland types. Wetlands Ecology and Management 20:137–150.

Provencher, B., and R. C. Bishop. 1997. An estimable dynamic model of recreation behavior with an application to Great Lakes angling. Journal of Environmental Economics and Management 33:107–127.

Rahel, F. J. 2002. Homogenization of freshwater faunas. Annual Reviews in Ecology and Systematics 33:291–315.

Rand, P. S., and D. J. Stewart. 1998. Dynamics of salmonine diets and foraging in Lake Ontario, 1983–1993: a test of a bioenergetic model prediction. Canadian Journal of Fisheries and Aquatic Sciences 55:307–317.

Randall, R. G., C. K. Minns, V. W. Cairns, and J. E. Moore. 1996. The relationship between an index of fish production and submerged macrophytes and other habitat features at three littoral areas in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 53(Supplement 1):35–44.

Reed, J. R., and D. L. Pereira. 2009. Relationship between shoreline development and nest site selection by Black Crappie and Largemouth Bass. North American Journal of Fisheries Management 29:943–948.

Rose, K. R. 2000. Why are quantitative relationships between environmental quality and fish populations so elusive? Ecological Applications 10:367–385.

Rosenfield, J. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. Transactions of the American Fisheries Society 132:953–968.

Rosenfield, J. S., and T. Hatfield. 2011. Information needs for assessing critical habitat of freshwater fish. Canadian Journal of Fisheries and Aquatic Sciences 63:683–698.

Rutkayová, J., R. Biskup, R. Harant, V. Šlechta, and J. Koščoet, 2013. *Ameiurus melas* (Black Bullhead): morphological characteristics of new introduced species and its comparison with *Ameiurus nebulosus* (Brown Bullhead). Reviews in Fish Biology and Fisheries 23:51–68.

Schoen, L. S. 2013. Wetland–nearshore habitat coupling in the Great Lakes: reconstructing fish movements among Great Lakes coastal wetlands. Master's thesis. Central Michigan University, Mount Pleasant.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Ottawa.

Seilheimer, T. S., and P. Chow-Fraser. 2007. Application of the wetland fish index to northern Great Lakes marshes, with emphasis on Georgian Bay coastal wetlands. Journal of Great Lakes Research 33(Supplement 3):154–171.

Seitz, R. D., H. Wennhage, U. Bergström, R. N. Lipcius, and T. Ysebaert. 2014. Ecological value of coastal habitats for commercially and ecologically important species. ICES Journal of Marine Science 71:648–665.

Sheaves, M. 2009. Consequences of ecological connectivity: the coastal ecosystem mosaic. Marine Ecology Progress Series 391:107–115.

Sheaves, M., R. Johnston, and R. M. Connolly. 2012. Fish assemblages as indicators of estuary ecosystem health. Wetlands Ecology and Management 20:477–490.

Sierszen, M. E., J. C. Brazner, A. M. Cotter, J. A. Morrice, G. S. Peterson, and A. S. Trebitz. 2012a. Watershed and lake influences on the energetic base of coastal wetland food webs across the Great Lakes basin. Journal of Great Lakes Research 38:418–428.

Sierszen, M. E., J. A. Morrice, A. S. Trebitz, and J. C. Hoffman. 2012b. A review of selected ecosystems services provided by coastal wetlands of the Laurentian Great Lakes. Aquatic Ecosystem Health Management 15:92–106.

Simon, T. P. 1998. Assessing the sustainability and biological integrity of water resources using fish communities. CRC Press, Boca Raton, Florida.

Smokorowski, K. E., and T. C. Pratt. 2007. Effect of change in physical structure and cover on fish and fish habitat in freshwater ecosystems: a review and meta-analysis. Environmental Reviews 15:12–41.

Spangenberg, J. H., and J. Settele. 2010. Precisely incorrect? Monetising the value of ecosystem services. Ecological Complexity 7:327–337.

Steen, P. J., T. G. Zorn, P. W. Seelbach, and J. S. Schaeffer. 2008. Classification tree models for predicting distribution of Michigan stream fish from landscape variables. Transactions of the American Fisheries Society 137:976–996.

Tallis, H., S. E. Lester, M. Ruckelshaus, M. Plummer, K. McLeod, A. Guerry, S. Andelman, M. Caldwell, M. Conte, S. Copps, D. Fox, R. Fujita, S. Gaines, G. Gelfenbaum, B. Gold, P. Kareiva, C. Kim, K. Lee, M. Papenfus, S. Redman, B. Silliman, L. Wainger, and C. White. 2012. New metrics for managing and sustaining the ocean's bounty. Marine Policy 36:303–306.

Tanner, D. K., J. C. Brazner, V. J. Brady, and R. R. Regal. 2004. Habitat associations of larval fish in a Lake Superior coastal wetland. Journal of Great Lakes Research 30:349–359.

Trebitz, A. S., J. C. Brazner, V. J. Brady, R. Axler, and D. K. Tanner. 2007. Turbidity tolerances of Great Lakes coastal wetland fishes. North American Journal of Fisheries Management 27:619–633.

Trebitz, A. S., J. C. Brazner, N. P. Danz, M. S. Pearson, G. S. Peterson, D. K. Tanner, D. L. Taylor, C. W. West, and T. Hollenhorst. 2009a. Geographic, anthropogenic, and habitat influences on Great Lakes coastal wetland fish assemblages. Canadian Journal of Fisheries and Aquatic Sciences 66:1328–1342.

Trebitz, A. S., J. C. Brazner, M. S. Pearson, G. S. Peterson, D. K. Tanner, and D. L. Taylor. 2009b. Patterns in habitat and fish assemblages within Great Lakes coastal wetlands and implications for sampling design. Canadian Journal of Fisheries and Aquatic Sciences 66:1343–1354.

Trebitz, A. S., and D. L. Taylor. 2007. Exotic and invasive aquatic plants in Great Lakes coastal wetlands: distribution and relation to watershed land use and plant richness and cover. Journal of Great Lakes Research 33:705–721.

Tulbure, M. G., and C. A. Johnston. 2010. Environmental conditions promoting nonnative *Phragmites australis* expansion in Great Lakes coastal wetlands. Wetlands 30:577–587.

USFWS (U.S. Fish and Wildlife Service) and USCB (U.S. Census Bureau). 2012. 2011 National survey of fishing, hunting, and wildlife-associated recreation. USFWS and USCB, Report FHW/11-NAT, Washington, D.C.

Uzarski, D. G., T. M. Burton, R. E. Kolar, and M. J. Cooper. 2009. The ecological impacts of fragmentation and vegetation removal in Lake Huron's coastal wetlands. Aquatic Ecosystem Health and Management 12:45–62.

Valavanis, V. D., G. J. Pierce, A. F. Zuur, A. Palialexis, A. Saveliev, I. Katara, and J. Wang. 2008. Modelling essential fish habitat based on remote sensing, spatial analysis, and GIS. Hydrobiologia 612:5–20.

Vadeboncoeur, Y., P. McIntyre, and M. J. Vander Zanden. 2011. Borders of biodiversity: life at the edge of the world's large lakes. BioScience 61:526–537.

Vasconcelos, R. P., P. Reis-Santos, M. J. Costa, and H. N. Cabral. 2011. Connectivity between estuaries and marine environment: integrating metrics to assess estuarine function. Ecological Indicators 11:1123–1133.

Wagner, T., D. B. Hayes, and M. T. Bremigan. 2006. Accounting for multilevel data structures in fisheries data using mixed models. Fisheries 31:180–187.

Wainger, L. A., and J. W. Boyd. 2009. Valuing ecosystem services. Pages 92–111 *in* K. McLeod and H. Leslie, editors. Ecosystem-based management for the oceans. Island Press, Washington, D.C.

Wainger, L., and M. Mazzotta. 2011. Realizing the potential of ecosystem services: a framework for relating ecological changes to economic benefits. Environmental Management 48:710–733.

Wetzel, R. G. 1992. Wetlands as metabolic gates. Journal of Great Lakes Research 18:529–532.

Whillans, T. H. 1996. Historic and comparative perspectives on rehabilitation of marshes as habitat for fish in the lower Great Lakes basin. Canadian Journal of Fisheries and Aquatic Sciences 53(Supplement 1):58–66.

Whitehead, J. C., P. A. Groothuis, R. Southwick, and P. Foster-Turley. 2005. Measuring the economic benefits of Saginaw Bay coastal marsh with revealed and stated preference methods. Journal of Great Lakes Research 35:430–437.

Zhao, Y., P. M. Kocovsky, and C. P. Madenjian. 2013. Development of a stock–recruitment model and assessment of biological reference points for the Lake Erie Walleye fishery. North American Journal of Fishery Management 33:956–964.

Zunker, C. 2013. Wisconsin's 2012 Lake Superior creel survey report. Wisconsin Department of Natural Resources, Bayfield.