



Spatial and temporal dynamics of nearshore fish communities in Lake Michigan and Lake Huron



William W. Fetzer^{a,*}, Brian M. Roth^a, Dana M. Infante^a, David F. Clapp^b, Randall M. Claramunt^b, David G. Fielder^c, Danielle K. Forsyth^d, Ji X. He^c, Tammy J. Newcomb^e, Catherine M. Riseng^f, Kevin E. Wehrly^d, Troy G. Zorn^g

^a Department of Fisheries and Wildlife, Michigan State University, 480 Wilson Road, East Lansing, MI 48824, USA

^b Charlevoix Fisheries Research Station, Michigan Department of Natural Resources, 96 Grant Street, Charlevoix, MI 49720, USA

^c Alpena Fisheries Research Station, Michigan Department of Natural Resources, 160 E. Fletcher Street, Alpena, MI 49707, USA

^d Institute for Fisheries Research, Michigan Department of Natural Resources and University of Michigan, 1109 N. University Avenue, Ann Arbor, MI 48109, USA

^e Lansing Office, Michigan Department of Natural Resources, 525 W. Allegan Street, Lansing, MI 48909, USA

^f School of Natural Resources and Environment, University of Michigan, 440 Church Street, Ann Arbor, MI 48109, USA

^g Marquette Fisheries Research Station, Department of Natural Resources, 484 Cherry Creek Road, Marquette, MI 49855, USA

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ABSTRACT

Ecosystem changes across the Great Lakes have increased the importance of understanding the role of nearshore zones (<30 m depth) in lake-wide dynamics. We evaluated spatiotemporal dynamics of nearshore fish communities in the Michigan waters of the Great Lakes, focusing on Lakes Huron and Michigan, using multiple long-term gill net surveys. We assessed temporal dynamics of nearshore fish community composition, metrics of species diversity, and catch-per-unit-effort (CPUE) of key fish species across fifteen nearshore areas in exposed coastlines and coastal embayments. Permutation multivariate analyses of variance demonstrated significant differences in the composition of fish communities between sites. Canonical correspondence analyses indicated this was driven by differences between exposed coastlines and coastal embayments, which differed in productivity, depth, temperature, and the relative composition of fish from thermal and eutrophication tolerance guilds. Dissimilarities of fish communities among locations were primarily driven by differences in the relative abundance of a few numerous, ubiquitous species that represent only a small subset of total species richness. Analyses of diversity profiles via Hill numbers indicated that species composition was unevenly distributed within nearshore fish communities and was dominated by approximately five species within a location. Warm- and cool-water species richness generally increased over time. While CPUE of most species decreased, some top predators increased at some locations. These results highlight that local environmental conditions, such as temperature and productivity, drive nearshore fish community heterogeneity, requiring that researchers and managers use caution when extrapolating local trends to the wider range of environmental conditions found at broader scales.

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Introduction

Coastal and nearshore ecosystems are complex, heterogeneous freshwater and marine environments that provide valuable ecosystem services for humans (Barbier et al., 2011) and critical habitats for many organisms. Coastal and nearshore ecosystems are also some of the most heavily used and threatened ecosystems globally (Lotze et al., 2006; Worm et al., 2006). Common drivers of ecosystem change for coastal and nearshore ecosystems include climate change, eutrophication, altered hydrological regimes, invasive species, overharvest, and

coastal development, such as dredging, shoreline hardening, and beach grooming (Barbier et al., 2011). These anthropogenic drivers can reduce the social, economic, and ecologic value of coastal and nearshore ecosystems by altering ecosystem processes, which reduces their capacity to provide raw materials, erosion control, maintenance of fisheries, tourism, recreation, and other ecosystem services. Anthropogenic drivers can also reduce the ecological integrity of coastal and nearshore ecosystems; however, characterizing broad scale heterogeneity of ecosystem and fish community changes remains challenging despite recent progress (Ludsin et al., 2001; Uzarski et al., 2005; Trebitz et al., 2009; Bhagat and Ruetz, 2011; Larson et al., 2013; Ivan et al., 2014; Janetski and Ruetz, 2015).

Nearshore ecosystems in the Great Lakes Basin are typically defined by the 30 m depth contour (Edsall and Charlton, 1997) and comprise

* Corresponding author at: Wisconsin Department of Natural Resources, 101 S. Webster St, Madison, WI, 5703, USA.

E-mail address: william.fetzer@wisconsin.gov (W.W. Fetzer).

many habitat types, including wetlands, river estuaries, drowned river mouths, protected bays, rocks, sand, and vegetation beds, all of which differ in their physical, chemical, and biological properties (Uzarski et al., 2005; Wang et al., 2015). Over the past century, nearshore habitats underwent dramatic ecological changes similar to those experienced in coastal and nearshore areas across the globe (Seelbach et al., 2013). These include changes in thermal profiles and trophic state which are expected to exert a strong influence on spatial and temporal fish community dynamics (Wehrly et al., 2012). Thermal profiles indicate a warming trend, driven by a longer duration of summer stratification (McCormick and Fahnenstiel, 1999) and warmer summer surface water temperatures (Dobiesz and Lester, 2009). Dynamics of trophic status are more heterogeneous. Initially, trophic status increased via cultural eutrophication; however, reductions in nutrient loadings and introductions of dreissenid mussels increased the complex mosaic of primary production in nearshore habitats. At lake-wide scales, primary production shifted from offshore to nearshore habitats (Hecky et al., 2004; Vanderploeg et al., 2010), but at regional and local scales, changes in the trophic status of nearshore habitats were more variable.

Despite significant efforts to characterize offshore fish community responses to anthropogenic drivers (e.g., changes in productivity, introductions of non-native species, etc.; Madenjian et al., 2002; Bronte et al., 2003; Mills et al., 2003; Dobiesz et al., 2005; Bunnell et al., 2014), attempts to characterize spatial and temporal dynamics of nearshore fish community dynamics have proved challenging. Previous attempts have primarily focused on spatial dynamics (Uzarski et al., 2005; Trebitz et al., 2009), temporal dynamics (Ludsin et al., 2001; Ivan et al., 2014), or very nearshore areas (Bhagat and Ruetz, 2011; Larson et al., 2013; Janetski and Ruetz, 2015), while attempts to characterize spatial and temporal fish community dynamics across multiple habitat types and broad scales are limited. Over the long-term, fish communities have responded to improved water quality by shifting community composition to include a greater proportion of species that are moderately-tolerant and intolerant to eutrophication (Ludsin et al., 2001; Ivan et al., 2014). Across spatial scales, fish communities are structured by physical, chemical, and biological drivers (Uzarski et al., 2005; Trebitz et al., 2009), suggesting that spatial variation in the effects of anthropogenic perturbations on environmental conditions could limit the ability to extrapolate local observations to broader scales. For instance, environmental context can influence how ecological perturbations influence patterns of fish community dynamics in nearshore habitats and lead to inconsistencies across broader scales. Developing a mechanistic understanding of why fish community responses to ecosystem perturbations are often inconsistent remains difficult, but could be improved by assessing the magnitude of fish community responses along environmental gradients, such as productivity or temperature.

Many challenges exist to characterize broad-scale spatial and temporal ecological dynamics in coastal and nearshore habitats. In general, there is a lack of lake-wide monitoring programs for nearshore habitats, and sampling tends to be fragmented across multiple federal, state, tribal, and academic assessment programs. Without cohesive monitoring, information sharing can be limited and data deemed incompatible for comparisons across space and time. Scale-dependent differences in physical, chemical, and biological conditions, in addition to geographic differences in the relative importance of multiple anthropogenic drivers, also make it difficult to identify the appropriate grain and extent of analyses. This lack of a spatiotemporal framework limits our ability to identify which ecosystems are most susceptible to perturbations, which species are most susceptible to anthropogenic drivers, and which drivers of ecosystem change have the strongest effect on ecological dynamics. By identifying how environmental conditions and species traits mediate resilience to ecosystem perturbations, conservation and management strategies can be developed to address the ecological perturbations that pose the greatest risk to coastal and nearshore ecosystems. However, development of these strategies is contingent upon our ability to extrapolate results from a subset of locations to broad spatiotemporal

scales through a mechanistic, theoretical framework (i.e., environmental gradients).

Several basin-level projects have recently mapped environmental conditions (Great Lakes Aquatic Habitat Framework; Wang et al., 2015) and stressors (Great Lakes Environmental Assessment and Mapping project; Allan et al., 2013) to identify and prioritize restoration and preservation objectives across the Great Lakes; however, both of these projects currently lack fish community data. Our study lays the groundwork for future inclusion of fish community data into these mapping efforts by investigating both spatial and temporal dynamics of nearshore fish assemblages in the Michigan waters of the Great Lakes. Specifically, our approach was to conduct analyses of existing data sets to quantify spatial and temporal heterogeneity of fish communities in nearshore ecosystems by: 1) defining nearshore fish community assemblages across broad spatial scales and relating these to environmental conditions (e.g., depth, temperature, and productivity), 2) assessing temporal dynamics of community composition within individual sites by comparing metrics of species diversity and the relative contribution of eutrophication tolerance and thermal guilds to total species richness, and 3) determining temporal and spatial trends of individual species to identify if particular species demonstrate local or regional trends in abundance. We hypothesized that fish community structure would be heterogeneous across locations, but asynchronous spatiotemporal fluctuations in abundant, cosmopolitan species will drive dissimilarity among sites (Mathews and Marsh-Mathews, 2016). We also hypothesized that, over time, the number of species intolerant to eutrophication (e.g., sensitive to low dissolved oxygen and high productivity) and warm-water species would increase, while the number of species tolerant to eutrophication and cold-water species would decline (Ludsin et al., 2001; Ivan et al., 2014) based on observed environmental changes in the Great Lakes (Dobiesz and Lester, 2009). Finally, we predicted these changes would be driven by abundance trends of individual species at specific locations.

Methods

Study site description

The Michigan Department of Natural Resources (MDNR) maintains four field stations that are responsible for conducting fish community surveys across the Michigan waters of the Great Lakes. In general, individual field stations focus survey efforts within an individual lake (e.g., Alpena — Lake Huron, Charlevoix — Lake Michigan, Marquette — Lake Superior, and Lake St. Clair — Lake St. Clair and Lake Erie). Sampling protocols vary and a variety of gears are deployed to monitor fish populations, including gill nets, bottom trawls, mid-water trawls, trapnets, and creel surveys. To date, coordination to standardize sampling across surveys and locations has been limited. As a result, experimental design, gear design and size, and data management were location-specific to retain comparability within, and not across surveys. This, however, made large-scale comparisons more difficult. To overcome this challenge and ensure the greatest potential for cross-site comparisons, we limited our analyses to only the gill net datasets (Table 1). Across field stations, gill nets consisted of similar mesh sizes (Table 2) and were typically fished for a similar duration of time (e.g., overnight). Additionally, gill nets are a passive gear and less likely to have catchability affected by the specific vessel used to employ them in a fish community survey (Zale et al., 2012), contrary to trawls, the second most common and widespread gear used by the MDNR.

We increased comparability within the time series of individual surveys by limiting analyses only to years when a consistent gill net configuration was used and only including those sites that were sampled in all years of the time series, when possible. Additionally, gill net catch was converted to a standardized catch per unit effort (CPUE) for each sampling event within a survey, typically based on a catch per net night or catch per defined length of gill net (Table 2). For most surveys, sampling

Table 1
Survey descriptions for MDNR gill net datasets.

Location	Lake	Shoreline type	Timing of survey	Years
Les Cheneaux Islands ^a	Lake Huron	Coastal embayment	September–October	1969–2012
Bays de Noc ^b	Lake Michigan	Coastal embayment	August–October	1989–2012
Saginaw Bay ^c	Lake Huron	Coastal embayment	September	1996–2012
St. Mary's River ^d	Lake Huron	Coastal embayment	August	1975, 1979, 1987, 2002, 2006
South Haven ^e	Lake Michigan	Exposed coastline	April–June	2002–2012
Saugatuck ^e	Lake Michigan	Exposed coastline	April–June	2002–2012
Grand Haven ^e	Lake Michigan	Exposed coastline	April–June	2002–2012
Arcadia ^e	Lake Michigan	Exposed coastline	April–June	2002–2010, 2012
Leland ^e	Lake Michigan	Exposed coastline	April–June	2002–2009, 2012
Charlevoix ^e	Lake Michigan	Exposed coastline	April–June	2002–2007, 2012
Grindstone City ^f	Lake Huron	Exposed coastline	May–June	1977–2014
AuSable ^f	Lake Huron	Exposed coastline	May–June	1979–2012
Sturgeon Point ^f	Lake Huron	Exposed coastline	May–June	1995–2014
Thunder Bay ^f	Lake Huron	Exposed coastline	May–June	1995–2014
Presque Isle ^f	Lake Huron	Exposed coastline	May–June	1991–2014

^a Fielder (2008).^b Schneeberger (2000).^c Fielder and Thomas (2014).^d Fielder et al. (2007).^e Schneeberger et al. (1998) and Makauskas and Clapp (2012).^f He and Bence (2007).

events that occurred at depths >30 m (100 ft) were removed to limit the analyses to those sites that represent nearshore fish community dynamics (Edsall and Charlton, 1997). Several sampling events were included from early in the Lake Huron time series where the minimum depth was <30 m and maximum depth was <35 m because multiple net sets were pooled.

Fifteen locations from six different surveys remained following removal of data from inconsistently sampled sites or years when net configurations differed from the rest of the time series (Tables 1, 2; Fig. 1). Survey design differed across locations, but typically sampled the same depths and locations across years (see citations in Table 1 for more details). Four surveys were located in coastal embayments or river corridors. These included: Saginaw Bay, Lake Huron; Les Cheneaux Islands, Lake Huron; Big and Little Bay de Noc (Bays de Noc), Lake Michigan; and St. Marys River (Lake Superior and Lake Huron corridor). Six sites were along the eastern shoreline of Lake Michigan and five sites were along the western shoreline of Lake Huron. These eleven sites sampled exposed coastlines that are not associated with an embayment. Mesh sizes were consistent across time within a location and were similar across surveys, though some differences were present at the upper and lower sizes of meshes fished (Table 2). Time series duration differed across sites, and the number of years when consistent data were available ranged from five to 40 years (Table 1).

At each location, GLAHF provided temperature, productivity, and depth (m) data (Table 3; Wang et al., 2015). To calculate environmental metrics, latitude and longitude for every sampling event within a survey were incorporated into GLAHF's hierarchical spatial framework to create a convex hull containing all sampling locations. Environmental data from all grid cells contained within a convex hull were extracted from GLAHF's spatial database and used to calculate each metric. Temperature was summarized as annual cumulative degree days (CDD) for all days when surface temperatures were above 10 °C (averaged annually from 1995 to 2013). Chlorophyll *a* was measured as µg/L (average from 2008 to 2013).

Spatial structure

We tested for spatial differences in nearshore fish community structure using multivariate analyses of species matrices for each year data were collected at a site. For each survey, the total annual catch for each species was calculated by summing the catch from all sampling events remaining after filtering inconsistent sampling events and standardizing for effort. Years were not pooled within individual sites. To improve consistency and remove the effect of varying effort across sites/surveys on absolute catch rates, total annual catch of each species was converted to a proportion of the total annual catch. A permutation

Table 2
Gear descriptions for MDNR gillnet datasets. Mesh sizes correspond to stretch-mesh.

Location	# sampling events	Depth sampled (m)	Net length (m)	Height (m)	Mesh sizes (mm)
Les Cheneaux Islands	171.7 ^a	1–8.5	305	1.8	38, 51, 64, 76, 89, 102, 114, 127, 140, 152
Bays de Noc	363	1.8–3.0	18.3	1.8	25, 38, 51, 64, 76, 102
Saginaw Bay	204	1.5–9.0	305	1.8	38, 51, 57, 64, 70, 76, 83, 89, 102, 114, 127
St. Marys River	182	Unknown	305 (366 ^b)	1.8	38, 51, 64, 76, 89, 102, 114, 127, 140, 152 ^b
South Haven	68	9.0–30.0	610	1.8	38, 51, 64, 76, 89, 102, 114, 127, 140, 152
Saugatuck	66	9.0–30.0	610	1.8	38, 51, 64, 76, 89, 102, 114, 127, 140, 152
Grand Haven	65	9.0–30.0	610	1.8	38, 51, 64, 76, 89, 102, 114, 127, 140, 152
Arcadia	60	9.0–30.0	610	1.8	38, 51, 64, 76, 89, 102, 114, 127, 140, 152
Leland	54	9.0–30.0	610	1.8	38, 51, 64, 76, 89, 102, 114, 127, 140, 152
Charlevoix	41	9.0–30.0	610	1.8	38, 51, 64, 76, 89, 102, 114, 127, 140, 152
Grindstone City	280.8 ^a	5.8–35.0 ^c	275	1.8	51, 64, 76, 89, 102, 114, 127, 140, 152
AuSable	155.7 ^a	9.4–34.4 ^c	275	1.8	51, 64, 76, 89, 102, 114, 127, 140, 152
Sturgeon Point	53.1 ^a	7.9–35.4 ^c	275	1.8	51, 64, 76, 89, 102, 114, 127, 140, 152
Thunder Bay	79.2 ^a	8.2–32.3 ^c	275	1.8	51, 64, 76, 89, 102, 114, 127, 140, 152
Presque Isle	124.2 ^a	9.1–32.3 ^c	275	1.8	51, 64, 76, 89, 102, 114, 127, 140, 152

^a Early data reported as length of nets not number. Number of nets represents each time 1000' of net were set.^b 38, 127, 140, and 152 were added in 2002. Length of net declined from 1200' to 1000' in 2002 also.^c Sites were included if the minimum depth was <30 m and maximum depth was <35 m.



Fig. 1. Map of sampling locations across coastal Great Lakes habitats. Polygons are drawn around all sampling events to indicate the area sampled by each survey.

multivariate analysis of variance (PERMANOVA) test was used to test for differences in the centroid of the distance matrix for each survey in an analysis of variance experimental design using permutation methods (e.g., Bray–Curtis; Anderson, 2001). Observed data were compared to 1000 random permutations to determine if community structure was significantly different across surveys. Canonical Correspondence Analyses (CCA) was used to visualize differences between locations on two dimensions, ordinate the species associated with the grouping of individual years across surveys, and relate species composition to environmental predictors (e.g., depth, chlorophyll *a*, and CDD). The proximity of individual years within the plot indicates their degree of similarity. Similarity percentages (SIMPER) were calculated for each pairwise comparison of all sampling locations to identify the species that contributed the greatest amount to dissimilarity between sites. Species were considered important contributors to dissimilarity by sequentially adding the largest contributors until a cumulative dissimilarity of 90%

was reached. All species remaining after the 90% cutoff was reached were considered unimportant because they contributed little to dissimilarity between sites. All analyses were done using the ‘vegan’ package in R (Oksanen et al., 2013; R Core Team, 2013).

Temporal diversity trends

Within individual locations, species richness trends were deconstructed to assess temporal trends in specific ecological guilds by grouping species according to eutrophication tolerance and thermal guilds. We defined species as tolerant, moderately tolerant, and intolerant to eutrophication (following Ludsins et al., 2001; Grabarkiewicz and Davis, 2008; Kornis et al., 2012; Ivan et al., 2014) or warm-, cool-, and cold-water based on classifications available in the literature (Table 4; Becker, 1983; Coker et al., 2001; Hasnain et al., 2010; Froese and Pauly, 2015).

Table 3
Depth, cumulative degree days (CDD), and chlorophyll *a* (Chl *a*) for all study sites.

Location	Depth (m)	CDD (C)	Chl <i>a</i> (µg/L)
Les Cheneaux Islands	1.5	2153.4	3.9
Bays de Noc	5.3	2905.2	6.5
Saginaw Bay	5.7	3332.8	11.2
St. Marys River	7.4	2502.1	4.5
South Haven	20.2	3260.3	0.9
Saugatuck	20.6	3197.0	1.3
Grand Haven	22.5	3078.4	2.1
Arcadia	23.4	2618.0	1.0
Leland	25.0	2643.8	0.7
Charlevoix	41.4	2686.1	1.0
Grindstone City	15.0	2869.0	1.5
AuSable	21.5	2670.8	0.8
Sturgeon Point	16.1	2551.9	0.6
Thunder Bay	14.6	2517.1	0.9
Presque Isle	29.2	2330.2	0.4

We also tested for significant temporal trends in fish community structure using different “orders” of Hill numbers ($q = 0, 1, 2$; Hill, 1973) to assess both total species richness and the effect of species relative abundances on evenness within communities by creating a diversity profile. As the “orders” of Hill numbers increase, species relative abundances become increasingly important in affecting Hill number calculation by taking into account how evenly individual species are spread across the community (Gotelli and Chao, 2013). Hill numbers (qD) are calculated by their “order” q based on the equation:

$${}^qD = \left(\sum_{i=1}^S p_i^q \right)^{1/(1-q)}$$

where p_i is the relative abundance of species i and S is the total number of species in the community. At $q = 0$, relative abundances of species are not considered, therefore, this metric represents simply species richness. A Hill number at $q = 1$, represents the number of “typical species” in the community. At $q = 1$, the Hill number is undefined, therefore its limit as q approaches 1 is used, represented as the exponent of the Shannon diversity index. When $q = 2$, abundant species are weighed more heavily and the resulting Hill number represents the number of “abundant species” and is equal to the inverse of Simpson’s diversity index. Combined, these metrics provide complementary indices to assess how fish communities are structured over time both in terms of absolute diversity and evenness through a diversity profile. When communities are evenly distributed, Hill numbers of $q = 0, 1, 2$ will be similar; however, when species within communities are unevenly distributed, Hill numbers of $q = 1$ and $q = 2$ will be lower than the $q = 0$. Hill numbers of $q = 1$ and $q = 2$ will increase in similarity as evenness decreases (see Gotelli and Chao, 2013 for further description). Linear regression was used to test for significant changes in species richness metrics and Hill numbers over time for individual surveys locations.

Species-specific trends

In addition to fish community dynamics, we explored CPUE trends for species of management importance across surveys. Species selected included apex predators (lake trout, walleye, northern pike, smallmouth bass, burbot), important prey fish or intermediate predators (yellow perch, alewife, lake whitefish, rainbow smelt), and a wide-spread benthivore (common white sucker). We limit our analyses to include only those surveys where a species was consistently captured. To reduce heteroscedasticity in the datasets, we log-transformed the CPUE plus one (e.g., $\ln(\text{CPUE} + 1)$). Temporal trends in transformed catch rates were detected with linear regressions calculated for each survey where a species was commonly captured.

Results

Community dynamics across space

Fish communities within coastal habitats of the Michigan waters of the Great Lakes were clearly differentiated by unique species assemblages among locations. The PERMANOVA test indicated that location was a significant predictor of fish community centroids ($F_{14,255} = 47.28, p < 0.001$). Coastal fish community separation was strongest between shoreline types (coastal embayments versus exposed coastlines), though additional separation was only visible within coastal embayments (Fig. 2). This indicated that the composition of fish communities in exposed coastlines of Lake Michigan and Lake Huron were very similar. Separation between shoreline types was primarily driven by productivity (chlorophyll *a*) and depth, while separation within shoreline types was primarily driven by thermal profiles (CDD; Fig. 2).

Separation between shoreline types was primarily driven by the dominance of warm- and cool-water species in coastal embayments, while exposed coastlines in eastern Lake Michigan and western Lake Huron sites were dominated by cold-water species that were intolerant to eutrophication. Pair-wise comparisons through the SIMPER analyses identified individual species driving dissimilarity within and across shoreline types. Within shoreline types, abundant, ubiquitous species drove dissimilarity among sites based on site-specific differences in their relative abundances. Warm and cool-water species and those tolerant and moderately tolerant to eutrophication drove dissimilarity within embayment sites (Figs. 2, 3, 4). These species included yellow perch, white sucker, northern pike, walleye, rock bass, brown bullhead, and small mouth bass (Table 5). The fish community in Saginaw Bay contained unique warm-water, tolerant species such as freshwater drum, white bass, goldfish, and longnose gar, among others (Fig. 2). In contrast, the Les Cheneaux Islands samples contained a mix of warm- and cool-water species with moderate tolerances, such as bowfin, largemouth bass, northern pike, rock bass, and pumpkinseed. Bays de Noc, which sits intermediate to Saginaw Bay and Les Cheneaux Islands on the CCA plot, were dominated by a mix of warm-water, tolerant species (e.g., small mouth bass, common carp) and cool-water, moderately-tolerant species (e.g., common shiner, trout perch).

Eastern Lake Michigan and western Lake Huron sites were comprised of cold-water, intolerant species and included alewife, lake trout, round whitefish, lake whitefish, longnose sucker, and burbot. Eastern Lake Michigan sites were slightly segregated by latitude, as eutrophic-tolerant and warm-water species present at southern sites, particularly yellow perch were not present at northern sites (Figs. 2, 3, 4). This division occurs between Grand Haven and Arcadia, as northern sites were oriented toward the most positive end of Coordinate 1, and southern sites related to Coordinate 1 more negatively (Fig. 2). This separation roughly corresponds to Muskegon, MI. Western Lake Huron sites were dominated by cold- and cool-water species, with a greater prevalence of walleye near sites located near Saginaw Bay.

Community dynamics in time

Temporal trends in species richness and diversity indices (Hill numbers) were heterogeneous across nearshore Great Lake sites. Eutrophication tolerance guilds showed different patterns of species richness changes across locations. Intolerant species richness tended to decline or remained stable at most sites (Table 6; Fig. 3); though we did detect a significant increase in the Les Cheneaux Islands. Moderately tolerant and tolerant species richness remained stable or increased in most embayments and coastal Lake Michigan, but significantly decreased in the Bays de Noc and several coastal Lake Huron sites (Table 6; Fig. 3). Warm-water species increased or remained stable, while cold-water species either declined or remained stable (Table 6; Fig. 4). Cool-water

Table 4
Fish species, species codes, and ecological guilds of fish captured in MDNR nearshore gill net surveys. Numbers of years each species are captured within a survey are indicated (total number of years per survey are present in parenthesis). Eutrophication tolerance guilds include tolerant (T), moderately tolerant (M), and intolerant (I).

Species	Scientific name	Species code	Guild		Coastal embayments				Exposed coastlines – Lake Michigan						Exposed coastlines – Lake Huron				
			Tolerance ^a	Thermal ^b	Les Cheneaux Is. (40)	Bays de Noc (25)	Saginaw Bay (17)	St. Marys River (5)	South Haven (11)	Saugatuck (11)	Grand Haven (11)	Arcadia (10)	Leland (9)	Charlevoix (7)	Grindstone City (30)	AuSable (38)	Sturgeon Pt. (20)	Thunder Bay (20)	Presque Is. (16)
Alewife	<i>Alosa pseudoharengus</i>	aw	M	Cold	13	15	2	5	9	6	7	10	9	6	16	21	3	8	3
Alligator gar	<i>Atractosteus spatula</i>	ag	T	Warm				2											
Atlantic salmon	<i>Salmo salar</i>	as	I	Cold															1
Black crappie	<i>Pomoxis nigromaculatus</i>	bc	T	Warm	4		2	2											
Bloater	<i>Coregonus hoyi</i>	bl	I	Cold				1	5	4	1	6	8	7	1				
Bowfin	<i>Amia calva</i>	bo	M	Warm	23		2	3											
Brook trout	<i>Salvelinus fontinalis</i>	br	I	Cold	12	1	2	1											
Brown bullhead	<i>Ameiurus nebulosus</i>	bb	T	Warm	38	12	1	5											
Brown trout	<i>Salmo trutta trutta</i>	bt	M	Cold		2		2	2	2		2				1			
Burbot	<i>Lota lota</i>	bu	I	Cold	16		4	3	6	10	7	10	9	6	29	16	15	19	14
Channel catfish	<i>Ictalurus punctatus</i>	cc	M	Warm	2		17	3	2	9					1	1	1	1	
Chinook salmon	<i>Oncorhynchus tshawytscha</i>	ch	M	Cold	12	4	5	4	5	2	5	3	4		4	9		6	2
Coho salmon	<i>Oncorhynchus kisutch</i>	co	M	Cold	3	1		2	3	1									
Common carp	<i>Cyprinus carpio</i>	ca	T	Warm	14	9	16	4											
Common shiner	<i>Luxilus cornutus</i>	cs	M	Cool		8							1						
Common white sucker	<i>Catostomus commersonii</i>	ws	T	Cool	40	19	17	5	11	7	11	5	9	7	17	13	2	4	1
Eurasian ruffe	<i>Gymnocephalus cernua</i>	er	T	Cool		1													
Freshwater drum	<i>Aplodinotus grunniens</i>	fd	M	Warm	1	6	17	3		3	2								
Gizzard shad	<i>Dorosoma cepedianum</i>	gz	M	Cool	8	15	17	3	2	3	2	3							
Golden redhorse	<i>Moxostoma erythrurum</i>	gr	M	Warm		2		1											
Goldfish	<i>Carassius auratus</i>	gf	T	Warm			5												
Lake chub	<i>Couesius plumbeus</i>	lc	M	Cold									3	2					
Lake herring	<i>Coregonus artedii</i>	lh	I	Cold	28			5	3				1	1		4		1	
Lake sturgeon	<i>Acipenser fulvescens</i>	ls	M	Cool				4	2	5	3	3							
Lake trout	<i>Salvelinus namaycush</i>	lt	I	Cold	13		3	2	11	11	11	10	9	7	30	38	20	20	16
Lake whitefish	<i>Coregonus clupeaformis</i>	lw	I	Cold	9	2	3	5	11	11	11	10	9	6	26	36	13	20	12
Largemouth bass	<i>Micropterus salmoides</i>	lb	M	Warm	4	2		1											
Logperch	<i>Percina caprodes</i>	lp	M	Cool		1													
Longnose gar	<i>Lepisosteus osseus</i>	lg	M	Warm	2	4	16	2											
Longnose sucker	<i>Catostomus catostomus</i>	ln	M	Cool	4		5	5	11	11	11	10	9	7	25	13	11	14	14

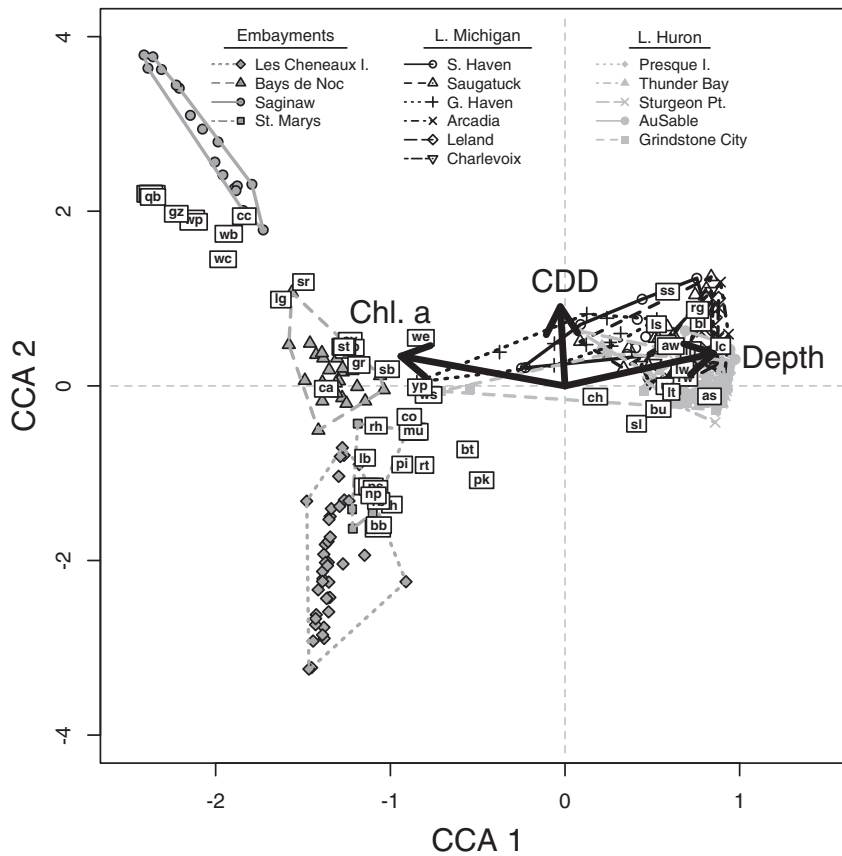


Fig. 2. NMDS ordination of fish communities across locations. NMDS was derived using a Bray-Curtis distance matrix, and resulted in a final stress of 0.12. Species codes are based on those presented in Table 2.

species remained stable or increased in embayments and coastal Lake Michigan, but remained stable or declined in coastal Lake Huron.

Temporal changes in diversity indices (Hill numbers) were primarily limited to sites in Lake Huron. Seven sites showed significant changes in total species richness ($q = 0$; Table 6; Fig. 5). Total species richness increased in the Les Cheneaux Islands and Saugatuck, but decreased in the Bays de Noc and several coastal Lake Huron sites. These patterns were fairly consistent with overall trends of species richness based on ecological guilds (Table 6). Overall, total species richness was similar across all sites, except St. Marys River (Fig. 5), which tended to be higher, and coastal Lake Huron sites, which tended to be lower. The number of “typical species” ($q = 1$) and “abundant species” ($q = 2$) was similar across all sites (Fig. 5) and generally remained stable over time. Only the Les Cheneaux Islands showed a significant increase in the number of “typical species,” though the slope of this line was small (0.03 species per year; ESM Table S3; Fig. 5) and was likely a function of the longer time series at this location. At several coastal Lake Huron sites, the number of “typical” and “dominant” species declined.

Trends in species of management importance

Trends in relevant species varied by species and by site. Overall, CPUE tended to be fairly stable for most species and sites; and, if significant trends were detected, the directionality tended to be consistent across locations for most species (Tables 7, 8; ESM Table S4; ESM Figs. S7–S16). Despite the high degree of heterogeneity across species and sites, several trends emerged from our regression analysis.

Catch-per-unit-effort patterns in top predators were stable or tended to increase over the duration of the time series for most species, except burbot and lake trout in coastal Lake Huron. Lake trout CPUE increased significantly at three sites (Table 7), two of which were on the

eastern shore of Lake Michigan (South Haven and Saugatuck). However, these increases were offset by either significantly negative trends (Leland) or flat trajectories at the other sites in eastern Lake Michigan (ESM Table S4; ESM Fig. S7), offering a mixed view of lake trout dynamics in Lake Michigan. Lake trout CPUE significantly declined at four Lake Huron sites. Walleye, smallmouth bass, and northern pike were only frequently captured at the four embayment sites, though walleye were occasionally sampled in coastal Lake Huron. Walleye CPUE significantly increased in both the Les Cheneaux Islands and Saginaw Bay, remained stable at the Bays de Noc and the St. Marys River, and declined in three coastal Lake Huron sites (Table 7; ESM Table S4; ESM Fig. S8). Northern pike CPUE was stable at three sites where they are captured, and significantly declined in the St. Marys River (Table 6; ESM Table S4; ESM Fig. S9). Smallmouth bass CPUE significantly increased in the Les Cheneaux Islands (Table 7), but showed no significant trends at the Bays de Noc, Saginaw Bay, and the St. Marys River (ESM Table S4, ESM Fig. S10). Burbot were observed in both embayments and coastal habitat types. When present in embayments, burbot CPUE significantly decreased in two sites (Les Cheneaux Islands, Saginaw Bay) or showed no trend (St. Marys River; Table 7; ESM Table S4; ESM Fig. S11). In exposed coastlines, CPUE of burbot was stable or increased across coastal Lake Michigan sites, but declined in four coastal Lake Huron sites (Table 7; ESM Table S4; ESM Fig. S11).

All of the prey species and intermediate predators investigated were stable or declined at sites monitored by the MDNR (Table 8). Yellow perch and alewife CPUE declined significantly in the Bays de Noc and most coastal Lake Huron sites (Table 8), but showed no significant trends at other locations (ESM Table S4; ESM Fig. S12, S13). Lake whitefish CPUE significantly declined at Grand Haven, Charlevoix, and all coastal Lake Huron sites (Table 8), while all other sites showed no change (ESM Table S4; ESM Fig. S14). Significant declines in rainbow

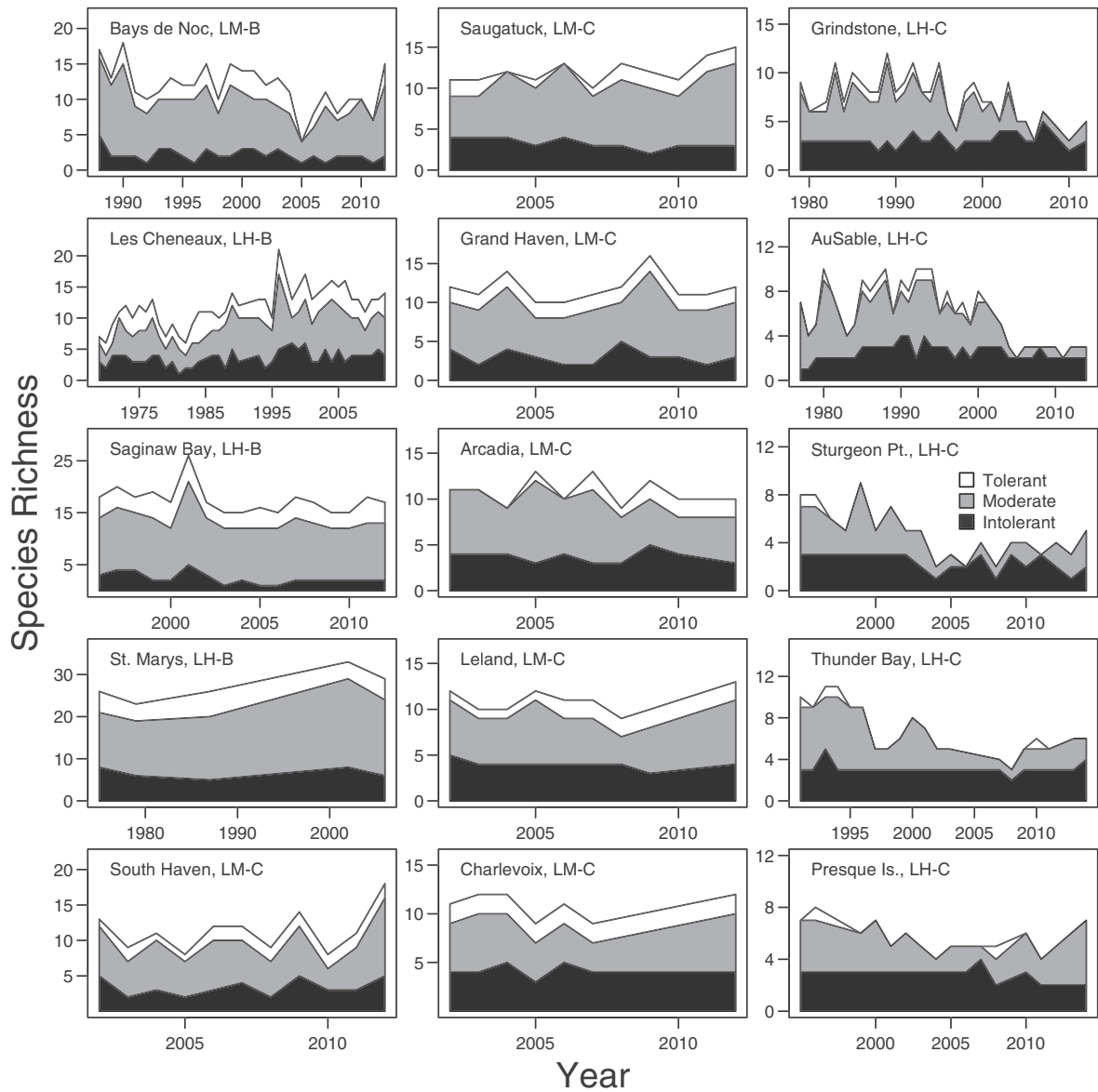


Fig. 3. Trends in species richness based on eutrophication guilds at 15 sites around the Great Lakes. Habitat type (embayment – B; exposed coastline – C) and lake (Lake Huron – LH; Lake Michigan – LM) are indicated for each site. Trends for individual guilds are presented in ESM Figs. S1–S3. Regression coefficients and model results are found in ESM Table S1.

smelt CPUE were observed at South Haven, Saugatuck, Grand Haven, the Bays de Noc, Grindstone City, AuSable, Thunder Bay, and Presque Isle (Table 8), but remained stable at all other sites (ESM Table S4; ESM Fig. S15). White sucker CPUE showed a strong decline in the Bays de Noc and coastal Lake Huron sites (Table 8; ESM Fig. S16), while all other sites showed no significant change (ESM Table S4; ESM Fig. S16).

Discussion

Our results demonstrate heterogeneity in species assemblages across shoreline type (e.g., exposed coastlines vs. embayments), but suggest that within specific shoreline types, species assemblages and community dynamics may be more homogenous than previously suspected. Dissimilarity in fish species assemblages, both across and within habitat types is strongly related to productivity, depth, and thermal profiles which alter the composition of fish species from different ecological guilds (e.g., eutrophication tolerance and thermal). This supports previous research showing ecosystem productivity and temperature are important factors driving fish community dynamics across broad scales (Wehrly et al., 2012). Interestingly, these differences across

sites are primarily driven by a few ubiquitous and relatively abundant species, as community evenness across all sites was low and dominated by a small subset of total species richness. Our analyses build on previous analyses of coastal and nearshore (<30 m) fish community dynamics in the Great Lakes that focused on community and diversity patterns at shorter time scales or smaller spatial regions (Ludsin et al., 2001; Uzarski et al., 2005; Trebitz et al., 2009; Bhagat and Ruetz, 2011; Larson et al., 2013; Ivan et al., 2014; Janetski and Ruetz, 2015) and allow us to draw generalization by quantifying heterogeneity of spatial and temporal dynamics across a wide range of locations.

Nearshore heterogeneity and homogeneity

High habitat heterogeneity in nearshore ecosystems makes it challenging to assess ecological dynamics across spatial scales, despite providing important ecosystem services (Barbier et al., 2011) and maintaining high levels of biodiversity (Vadeboncoeur et al., 2011). In the Great Lakes, previous attempts to characterize heterogeneity of nearshore fish community assemblages have focused on wetlands and drowned river mouths (e.g., Minns et al., 1994; Uzarski et al., 2005;

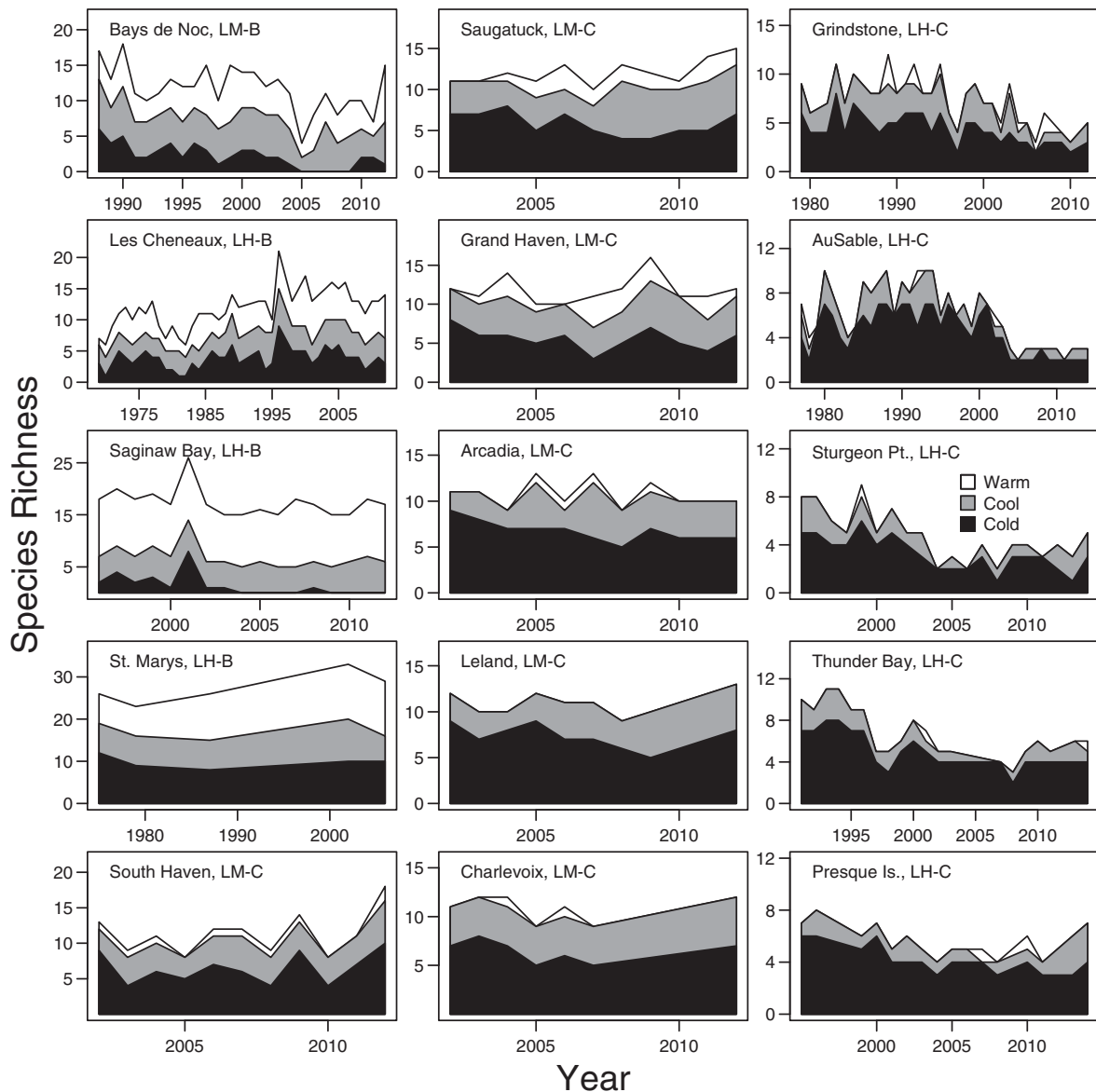


Fig. 4. Trends in species richness based on thermal guilds at 15 sites around the Great Lakes. Habitat type (embayment – B; exposed coastline – C) and lake (Lake Huron – LH; Lake Michigan – LM) are indicated for each site. Trends for individual guilds are presented in ESM Figs. S4–S6. Regression coefficients and model results are found in ESM Table S2.

Bhagat and Ruetz, 2011; Janetski and Ruetz, 2015), while coastal habitats not directly associated with very nearshore habitats (>5 m) are generally lacking in broad scale analyses despite their connections to both offshore and shoreline habitats. Our analyses support previous observations that heterogeneity in nearshore fish community assemblages is high, as evident by the lack of overlap between shoreline types in our ordination plot (Fig. 2). However, we also observed several consistent patterns across all sites in our study that suggest commonalities in drivers of ecological structure and function in nearshore ecosystems.

Separation of fish community assemblages in our study sites clearly occurred between exposed coastlines and coastal embayments driven primarily by chlorophyll *a* and depth, while thermal profiles (i.e., CDD) drove separation within shoreline types. Though previous research suggests differences in the timing of sampling between shoreline types may have influenced this separation (Bhagat and Ruetz, 2011), the complete lack of community overlap indicates that the observed separation is likely representative of true differences and not an artifact of sampling. Exposed coastlines are characterized by communities dominated by cold-water species intolerant to eutrophication (Figs. 2, 3, 4) that reflect both environmental conditions within these areas and

their connectivity to offshore habitats. Coastal embayments are dominated by warm- and cool-water species that are moderately tolerant or tolerant of eutrophication (Figs. 2, 3, 4). Within shoreline types, the degree of fish community heterogeneity appears to reflect local environmental conditions. Coastal exposed sites within our study showed a much higher degree of overlap in fish assemblages than those in coastal embayments. Though latitudinal gradients in environmental conditions (e.g., productivity and temperature) likely have some influence on the fish community (Janetski and Ruetz, 2015), in general, exposed coastlines are comprised of a very similar species complex. In contrast, coastal embayments show little overlap across locations (Fig. 2). This strong separation reflects the greater variation in environmental conditions across these locations, including very different ranges in temperature, productivity, connectivity to offshore habitats, local habitat diversity, and many other environmental factors (Wang et al., 2015). Future analyses should explicitly evaluate these features to further define associations between and among nearshore fish communities.

Despite spatial differences in fish assemblages both within and across shoreline types, our metric of dissimilarity across sites is primarily driven by the relative abundance of the most abundant and

Table 5

Dominant species driving dissimilarity across sites. Species were considered important contributors to dissimilarity by sequentially adding the largest contributors until a cumulative dissimilarity of 90% was reached. The number of times a species was identified as important in pair-wise comparisons among the sites we investigated is presented in parentheses. Pair-wise comparisons are presented as comparisons within and across habitat type. Habitat types included coastal embayments (bays) and exposed coastlines (coast) from Lake Huron and Lake Michigan.

Comparison	Species
Bay to bay (6)	Northern Pike (6), Smallmouth Bass (6), Walleye (6), White Sucker (6), Yellow Perch (6), Brown Bullhead (5), Rock Bass (5), Alewife (4), Lake Herring (4), White Perch (4).
Bay to coast (44)	Lake Trout (44), Yellow Perch (44), White Sucker (35), Walleye (33), Northern Pike (32), Round Whitefish (32), Lake Whitefish (30), Alewife (29), Longnose Sucker (28), Rock Bass (23).
Lake Huron Coast (10)	Burbot (10), Lake Trout (10), Lake Whitefish (10), Round Whitefish (10), Walleye (7), Alewife (6), Longnose Sucker (6).
Lake Michigan Coast (15)	Alewife (15), Lake Trout (15), Longnose Sucker (14), Round Whitefish (14), Yellow Perch (14), Lake Whitefish (13), White Sucker (10).
Huron-Michigan Coast (30)	Alewife (30), Lake Trout (30), Round Whitefish (28), Lake Whitefish (27), Longnose Sucker (26), Yellow Perch (22), Burbot (16), White Sucker (15).
All pairwise comparisons (105)	Lake Trout (99), Yellow Perch (90), Alewife (84), Round Whitefish (84), Lake Whitefish (80), Longnose Sucker (75), White Sucker (66), Walleye (52).

ubiquitous species across all surveys (e.g., yellow perch, alewife, lake trout, longnose sucker, white sucker, lake whitefish, round whitefish, and walleye; Table 4). SIMPER analyses demonstrate that dissimilarities within a single shoreline type are consistently driven by the relative abundance of a few, dominant species across all pair-wise comparisons (Table 5). Dissimilarities across shoreline types are more complex, and are driven by both species that are ubiquitous and abundant across both habitats and species that are only abundant in one habitat. Not surprisingly, rare species drive most heterogeneity in the species found across sites. These patterns indicate species turnover likely plays a larger role than nestedness in driving beta diversity across nearshore fish communities (Baselga, 2010).

Diversity profiles (Hill numbers) indicate low evenness across fish communities in both exposed coastlines and coastal embayments, and provide further evidence that nearshore fish communities are dominated by a few species within each site (Bhagat and Ruetz, 2011; Janetski and Ruetz, 2015). Hill numbers showed a large drop from $q = 0$ to $q = 1$, but a small difference between $q = 1$ and $q = 2$. This indicates a large difference in total species richness and the number of “typical

species,” but little difference between the number of “typical species” and the number of “abundant species” (Gotelli and Chao, 2013). Overall, species richness may be higher in nearshore habitats relative to offshore habitats, but most fish species within nearshore communities are rare. However, rare and dominant species are not static, and their abundances can change in response to management actions or ecological perturbations that make a location more or less favorable over time. For example, walleye and smallmouth bass were initially absent or uncommon in the Les Cheneaux Islands during the 1970s and 1980s, but have increased beginning in the 1990s. Concurrently, burbot populations have declined. If rare species are able to fill niches left unoccupied by declining abundances of previously dominant species, higher species richness in nearshore ecosystems may make these communities more resilient through turnover and portfolio effects (Lyons et al., 2005; Schindler et al., 2010). Therefore, despite dominance of only a few species in coastal habitats, rare species may also play an important role in the long-term ecological dynamics within these habitats.

Contrary to our a priori expectations, species richness ($q = 0$) was fairly consistent across all sites, but highest in the St. Marys River. The St. Marys River includes both lentic and lotic areas throughout the river corridor and survey collections reflect this higher diversity of habitat types, and to a lesser extent additional effort relative to other sites (Fielder et al., 2007). Other surveys focus on open water habitats that likely have lower local habitat diversity, especially in exposed coastlines, which reduces the range of ecological niches present.

Species richness trends

Temperature and productivity are known to be important factors determining fish community assemblages (Ludsin et al., 2001; Wehrly et al., 2012), and may drive spatial heterogeneity in Lakes Michigan and Huron nearshore habitats. Across the Great Lakes basin, both of these factors have changed throughout the duration of our study: mid-summer water temperatures and water clarity (a proxy for productivity) have been increasing (Dobiesz and Lester, 2009; Pothoven et al., 2016). Our analyses of temporal trends in species richness for eutrophication tolerance and thermal guilds suggest that fish communities in nearshore habitats are responding to these changes. Across all sites, warm-water species richness is significantly increasing or remaining stable, while cold water species richness is significantly declining or remaining stable (Table 6). Declines in cold-water species were present in three coastal embayments (Les Cheneaux, Bays du Noc, and Saginaw Bay), which are more likely to be isolated from cold-water refuges. We suspect the declines in cold-water species richness in coastal Lake Huron sites was likely due to trophic dynamics associated with the collapse of alewife and other deepwater demersal species (Riley et al.,

Table 6

Summary table of temporal trends in Hill numbers and species richness based on ecological guilds. Significant positive (+) and negative (–) trends were identified based on an $\alpha = 0.05$. Regression coefficients and model results are found in ESM Table S1–S3.

Site	Hill numbers			Eutrophication tolerance			Thermal tolerance		
	q = 0	q = 1	q = 2	Intolerant	Moderate	Tolerant	Warm	Cool	Cold
Les Cheneaux	+	+		+	+	+	+	+	–
Bays de Noc	–				–				–
Saginaw Bay				–					–
St. Marys					+		+		
South Haven						+		+	
Saugatuck	+			–	+		+	+	
Grand Haven									
Arcadia						+			–
Leland						+			
Charlevoix								+	
Grindstone City	–				–	–		–	–
AuSable	–	–			–			–	–
Sturgeon Pt.	–			–	–	–			–
Thunder Bay	–	–	–		–			–	–
Presque Is.		–	–						–

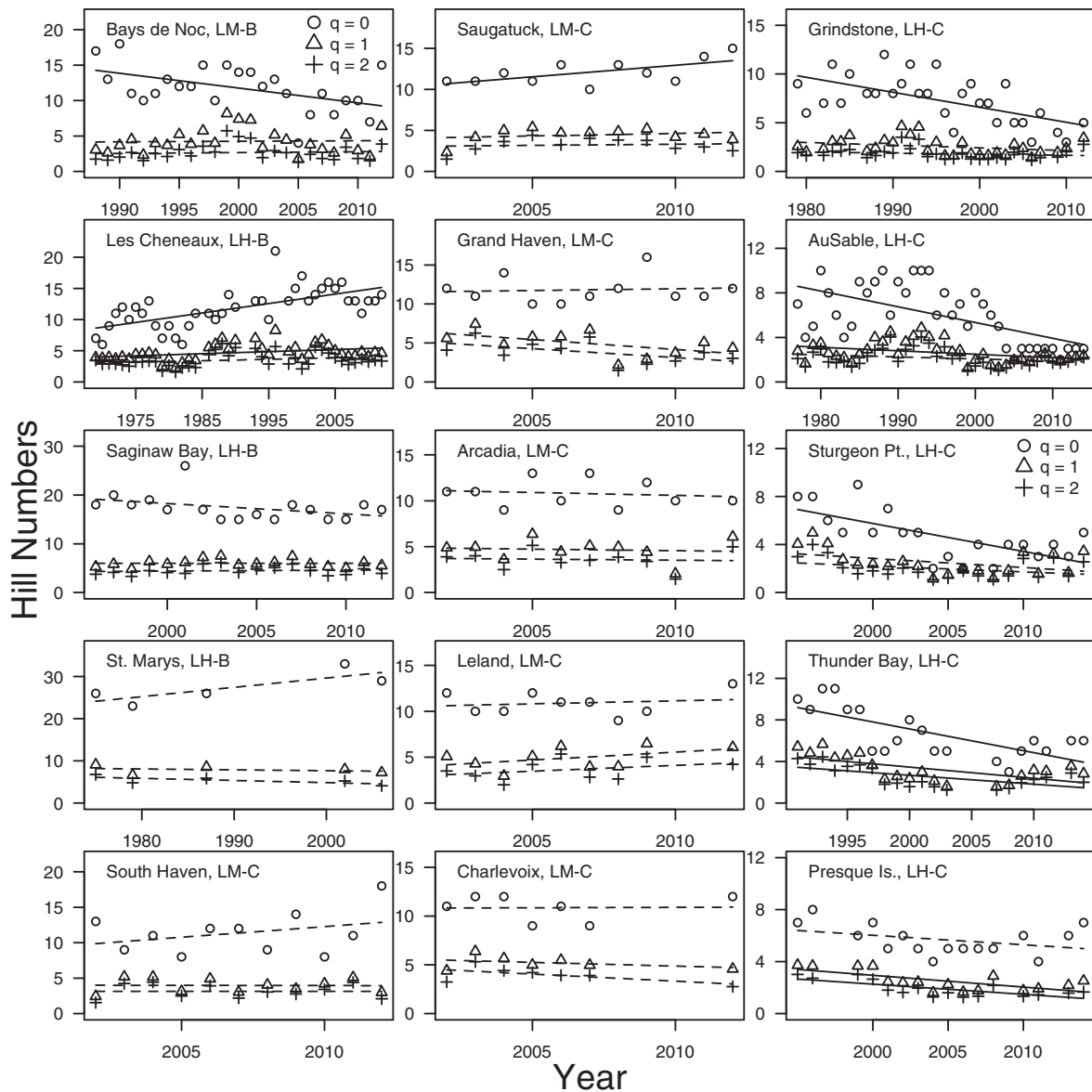


Fig. 5. Trends in Hill numbers ($q = 0, 1, 2$) at 15 sites around the Great Lakes. Habitat type (embayment – B; exposed coastline – C) and lake (Lake Huron – LH; Lake Michigan – LM) are indicated for each site. Significant trends are denoted with solid lines. Note different y-axis scaling across panels. Regression coefficients and model results are found in ESM Table S3.

2008) and subsequent decline of non-native salmonids that has been documented extensively in the literature (Bunnell et al., 2014; Kao et al., 2016) and not a lack of suitable cold water habitat in these areas which occur adjacent to offshore habitats with ample cold water. Longer summer stratification (McCormick and Fahnenstiel, 1999) and warmer summer surface water temperatures (Dobiesz and Lester, 2009) are likely benefiting warm- and cool-water species. These species are expected to continue increasing in abundance as climate forecasts predict temperatures will continue to rise in nearshore habitats (Trumpickas et al., 2009), but this could also aid in the establishment or expansion of non-native species (Mandrak, 1989).

Differentiating the effects of changing temperature and productivity remains challenging. Across all sites, the number of species intolerant to eutrophication are generally declining or remaining stable (except Les Cheneaux Islands), while the number of moderately tolerant and tolerant species are increasing or remaining stable (except the Bays de Noc and coastal Lake Huron; Table 6). These trends are inconsistent with existing temporal studies of nearshore fish community changes (Ludsin et al., 2001; Ivan et al., 2014) and broad-scale patterns in productivity across the Great Lakes (Dobiesz and Lester, 2009). Our a priori

expectation was that intolerant species would increase as water quality increased at many of these coastal sites (sensu Ludsin et al., 2001); however, we did not consider a priori that tolerance to eutrophication and thermal guilds are correlated. For instance, species intolerant to eutrophication are predominantly cold-water species (nine out of 13), while all the tolerant species are either warm- (seven out of 12) or cool-water species (five out of 12). Overlap between eutrophication tolerance and thermal guilds is less consistent within intermediate guilds, as moderately tolerant species are comprised of warm- (13 out of 38), cool- (12 out of 38), and cold-water species (13 out of 38). We observed that thermal guilds are more restrictive than eutrophication tolerance guilds, highlighting the importance of temperature as a factor driving fish physiology and, ultimately, their distributions (Whitney et al., 2016). Warming coastal temperatures will make environmental conditions more suitable to warm-water fish, but increasing water quality is less likely to negatively affect fish tolerant to eutrophication. Conversely, cold-water species are less likely to persist with warming temperatures, despite improvements in water quality.

We suspect changing climate is one of the dominant factors driving species richness changes across sites in Lake Michigan and coastal

Table 7

Summary table of temporal trends in top predator species of management importance catch-per-unit-effort. Significant positive (+) and negative (–) trends were identified based on $\alpha = 0.05$.

Species	Location	Trend	Slope	F statistic	DF	p-Value
Lake trout	Les Cheneaux	+	0.01	9.43	1, 38	<0.01
	South Haven	+	0.14	17.38	1, 9	<0.01
	Saugatuck	+	0.13	42.67	1, 9	<0.001
	Leland	–	–0.07	22.12	1, 7	<0.01
	Grindstone City	–	–0.08	72.91	1, 28	<0.001
Walleye	AuSable	–	–0.06	19.87	1, 36	<0.001
	Sturgeon Point	–	–0.08	17.76	1, 18	<0.001
	Thunder Bay	+	0.08	28.70	1, 18	<0.001
	Les Cheneaux	+	0.02	51.73	1, 38	<0.001
	Saginaw Bay	+	0.10	29.48	1, 15	<0.001
Northern pike	AuSable	+	0.01	15.96	1, 36	<0.001
	Sturgeon Point	+	0.02	21.37	1, 18	<0.001
	Presque Isle	+	0.01	6.99	1, 14	0.02
	St. Marys	–	–0.05	13.52	1, 3	0.03
	Smallmouth bass	+	0.03	69.00	1, 38	<0.001
Burbot	Les Cheneaux	–	–0.01	4.47	1, 38	0.04
	Saginaw Bay	–	–0.01	11.36	1, 15	<0.01
	South Haven	+	0.08	8.65	1, 9	0.02
	Grindstone City	–	–0.04	24.85	1, 28	<0.001
	Sturgeon Point	–	–0.05	20.84	1, 18	<0.001
	Thunder Bay	–	–0.06	29.29	1, 18	<0.001
	Presque Isle	–	–0.04	20.73	1, 14	<0.001

embayments, while food web responses following the collapse of alewife is the dominant factor in exposed coastlines of Lake Huron. The response of fish communities to changing climate is generally slow (Lynch et al., 2016), while the collapse of a dominant prey population, by definition, can lead to rapid shifts in fish community dynamics (Kao et al., 2016). We suspect this explains differences in fish community dynamics in exposed coastlines of Lake Michigan and Lake Huron. Though productivity has declined in both systems, alewife populations only crashed

Table 8

Summary table of temporal trends in intermediate predator and prey species of management importance catch-per-unit-effort. Significant positive (+) and negative (–) trends were identified based on $\alpha = 0.05$.

Species	Location	Trend	Slope	F statistic	DF	p-Value
Yellow perch	Bays de Noc	–	–0.03	6.64	1, 23	0.02
	Grindstone City	–	–0.11	72.99	1, 28	<0.001
	AuSable	–	–0.01	19.03	1, 36	<0.001
	Sturgeon Point	–	–0.04	13.58	1, 18	<0.001
	Thunder Bay	–	–0.02	15.23	1, 18	<0.001
Alewife	Bays de Noc	–	–0.02	15.62	1, 23	<0.001
	Grindstone City	–	–0.03	5.19	1, 28	0.03
	AuSable	–	–0.02	7.18	1, 36	0.01
	Sturgeon Point	–	–0.01	9.08	1, 18	<0.01
	Thunder Bay	–	–0.06	16.71	1, 18	<0.001
Lake whitefish	Presque Isle	–	–0.01	7.91	1, 14	0.01
	Grand Haven	–	–0.28	10.60	1, 9	<0.01
	Charlevoix	–	–0.16	10.77	1, 5	0.02
	Grindstone City	–	–0.03	6.87	1, 28	0.01
	AuSable	–	–0.03	6.79	1, 36	0.01
Rainbow smelt	Sturgeon Point	–	–0.02	10.82	1, 18	<0.01
	Thunder Bay	–	–0.11	46.45	1, 18	<0.001
	Presque Isle	–	–0.10	28.37	1, 14	<0.001
	Bays de Noc	–	–0.01	5.13	1, 23	0.03
	South Haven	–	–0.23	5.05	1, 9	0.05
White sucker	Saugatuck	–	–0.34	19.19	1, 9	<0.01
	Grand Haven	–	–0.32	10.05	1, 9	0.01
	Grindstone City	–	–0.01	7.13	1, 28	0.01
	AuSable	–	–0.01	13.45	1, 36	<0.001
	Thunder Bay	–	–0.01	7.25	1, 18	0.01
White sucker	Presque Isle	–	–0.01	13.39	1, 14	<0.01
	Bays de Noc	–	–0.02	36.46	1, 23	<0.001
	Grindstone City	–	–0.02	8.93	1, 28	<0.01
	AuSable	–	–0.01	2.14	1, 36	0.15
	Sturgeon Point	–	–0.01	4.69	1, 18	0.04
	Thunder Bay	–	–0.01	4.18	1, 18	0.06
	Presque Isle	–	0.00	2.70	1, 14	0.12

in Lake Huron. Changes in species richness appear to be occurring slowly in Lake Michigan (e.g., more warm-water species) and we suspect this is driven by gradually warming water temperatures in nearshore areas (Trumpickas et al., 2009). However, in Lake Huron, previously documented food web changes have been dramatic (e.g., the crash of alewife and subsequent decline of non-native salmonids; Kao et al., 2016), which has likely had a particularly negative impact on cold-water species that are intolerant to eutrophication, as well as, CPUE of individual species. We suspect subtle climate driven changes are also likely occurring in Lake Huron, but hypothesize that these gradual changes are overshadowed by the dramatic changes following alewife collapse. Interestingly, declines in species richness appeared to occur prior to the alewife crash, and reflect similar observations made in deepwater demersal habitats (Riley et al., 2008). This could suggest that a decrease in species richness may be a signal of food web reconfiguration.

Results of our study are inconsistent with two previous studies on coastal and nearshore fish community dynamics; however, these studies focused solely on eutrophication tolerance guilds and did not consider thermal guilds (Ludsin et al., 2001; Ivan et al., 2014). Both studies were conducted in areas where water quality improved significantly throughout the duration of the study (e.g., Lake Erie and Saginaw Bay). The number of species tolerant to eutrophication tended to decrease, while the number of species intolerant to eutrophication tended to increase. Interestingly, Ivan et al. (2014) and our study both included Saginaw Bay as a study location; however, trends in species richness did not follow similar patterns across the two studies. We suspect this is primarily driven by gear differences across studies. Both the Ivan et al. (2014) and Ludsin et al. (2001) studies analyzed fish community data collected with ~10.7 m headrope bottom trawl, while our study used data collected with gill nets ranging in mesh size from 25 mm to 152 mm. These gears sample different components of the fish community (Zale et al., 2012; Fielder and Thomas, 2014). Trawls tend to capture smaller fish, making most species vulnerable to capture during early life stages, while gill nets tend to only capture fish that grow to relatively large sizes during juvenile and adult life stages. This is supported by differences in species richness across the two studies. Ivan et al. (2014) captured 59 species, while our entire study only captured 63 across all sites and only 36 in Saginaw Bay. These differences highlight the value gained by employing both gear types, which can detect changes in fish communities at different time scales. Trawls allow rapid detection of shifts in recruitment dynamics and changes in the relative abundance of fish that do not obtain large sizes. Shifts in the composition of gill net surveys occur at much slower time scales because they are based on both the mortality rates of long-lived species and recruitment of young fish into the gear. For instance, freshwater drum can live up to 72 years (Pereira et al., 1995). Over time, differences between trawl and gill net species richness may become more consistent as the adult fish community catches up with the rapid fish community changes observed in the trawl survey (Ivan et al., 2014).

Food web linkages

Our analyses of relevant species support recent trends observed in offshore habitats of the Great Lakes, and suggest top down and bottom up processes are important for driving ecological dynamics in both nearshore and offshore habitats (Bunnell et al., 2014). Top predators across our surveys generally remained stable or increased across locations, though some exceptions do occur (most notably northern pike, burbot, and lake trout in coastal Lake Huron). Concurrently, all prey fish showed significant declines in CPUE or remained stable. Though the role of other factors in driving these trends should not be understated (e.g., changes in productivity and temperature), additional research is needed to gauge the influence of top predators on prey trends in nearshore habitats. Previous analyses, conducted in offshore habitats (Tsehaye et al., 2014), should: 1) assess the aggregate biomass of

predators relative to prey, 2) evaluate the capacity of prey fish to meet consumptive demands of predators in nearshore ecosystems, and 3) determine how predator foraging responds to changes in prey abundances. Our analyses of coastal Lake Huron sites suggest regime shifts in offshore habitats can have strong influences on nearshore fish communities which exhibited similar declines in diversity (Riley et al., 2008; Kao et al., 2016), and suggest more research is needed to understand food web interactions between nearshore and offshore habitats. Further monitoring of populations and food web interactions in nearshore habitats are necessary to better characterize the trophic ecology of these species and evaluate their capacity to integrate resources across multiple energy pathways (Turschak et al., 2014; He et al., 2015).

Decreases in prey fish populations are also likely to be driven by widespread changes in productivity and water clarity patterns across both nearshore and offshore habitats of the Great Lakes (Bunnell et al., 2014). Changes in primary production have reduced zooplankton abundance and biomass across the Great Lakes (e.g., Barbiero et al., 2009), and could represent a recruitment bottleneck for many predator and prey fish during early life history stages. These life stages may also be more vulnerable to predation pressure if the detection capabilities of predators and prey respond asymmetrically to changing water clarity (Utne-Palm, 2002). Clearly, additional research is needed to evaluate how changing environmental conditions influence both bottom-up and top-down drivers of recruitment and population dynamics of key prey species in nearshore habitats.

Trends in relevant species also highlight the necessity to develop additional population models across a wider range of species and locations. These could provide more robust information about demographic rates (e.g., recruitment, growth, and mortality) beyond what can be inferred from trends in CPUE, and aid in the development of a mechanistic understanding of what drives population dynamics of nearshore fish species (Wilberg et al., 2005; Fielder and Bence, 2014). Additionally, several of our detected trends could be statistical type I errors due to the large number of statistical tests performed in our analyses. Though consistent directional trends across sites suggest this likely has minimal effect on the ability to draw conclusions from our results, further confidence could be gained through the development of more rigorous population models, evaluation of non-linear trends over time, and more focused analyses on factors driving changes in diversity metrics at individual sites.

Management implications and recommendations

There has been a growing need to develop a better understanding of nearshore ecological dynamics and integrate this information with our knowledge of offshore ecosystem structure and function. This need has been driven by broad scale ecological changes across the Great Lakes basin, including shifting productivity from offshore into nearshore environments from invasive species impacts (Hecky et al., 2004; Vanderploeg et al., 2010). Meeting this need is challenging because these habitats have not been studied in a systematic and comprehensive fashion compared to pelagic habitats or omitted altogether in the case of most coastal nearshore environments. Most of the investment in nearshore monitoring has been in embayments, while assessment of exposed coastlines have mostly been in the form of shallow water gill net sets targeting offshore fish communities. Our findings show that exposed coastlines are more characteristic of main basin cold-water fish communities. Increasingly, they appear as if they may be more aptly described as the edges of the main basin open water as opposed to more typical warm- and cool-water fish communities typified by coastal embayments. Current investment in nearshore surveys in exposed coastlines may be adequately apportioned, and managers will need to decide how relevant nearshore fish communities in these habitats are to overall management goals. Outside of the scope of our work is the degree to which coastal nearshore habitats may serve as spawning and nursery grounds for some species, especially open-water prey and

predator species (Höök et al., 2008; Altenritter et al., 2013). Such life stages and species may not be vulnerable to gill net gear and not well represented in our analyses. Thus, these habitats may play an important role in overall ecological dynamics, but additional research with new, targeted sampling may be required to more fully assess their importance.

If the goal for managers is a more holistic ecosystem-based approach to Great Lakes management, then we offer the following recommendations for assessment and analysis to achieve that goal. Our analyses represent a first step toward integrating nearshore fisheries datasets with existing spatial frameworks (e.g., GLAHF). We recommend further integration of fisheries datasets with both environmental conditions (Great Lakes Aquatic Habitat Framework; Wang et al., 2015) and ecosystem perturbations (Great Lakes Environmental Assessment and Mapping project; Allan et al., 2013) to determine how environmental conditions mediate local, regional, and basin-scale patterns of fish community responses to ecological perturbations. This effort should focus on: 1) identifying habitats that lead to high fish diversity and production rates across the Great Lakes basin, 2) identifying environmental attributes necessary to achieve diverse conservation objectives, and 3) improving the ability to forecast how fish production and diversity will respond to restoration initiatives. Secondly, improved indicators of nearshore fish community dynamics should be developed and incorporated into the Environmental Protection Agency's "State of Lakes" and the Great Lakes Fishery Commission's "State of the Lakes" reports. For instance, segregating the fish community into ecologically relevant guilds (e.g., eutrophication and thermal tolerance) provides a valuable, straightforward whole fish community metric that easily communicates spatial and temporal changes within these habitats and is less sensitive to inconsistent sampling across locations. This would prioritize needs and data gaps in assessment and understanding of nearshore fish communities and potentially increase funding for focused and purposeful routine sampling of these areas.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jglr.2016.12.003>.

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