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## Seasonal habitat-use differences among Lake Erie's walleye stocks

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### ABSTRACT

Understanding the spatial ecology and habitat-use of Lake Erie's commercially important walleye (*Sander vitreus*) population is imperative due to their large-scale seasonal migrations (>400 km) exposing them to five different jurisdictions in the USA and Canada. The objective of this study was to determine the habitat selected by walleye throughout the year and across Lake Erie. Here, we used acoustic telemetry to estimate walleye occurrence at three lake depth categories that were pertinent to biology (e.g., spawning) and management (e.g., quota allocation). Detection data from 851 adults during five continuous years identified consistent seasonal fluctuations in habitat selection across western (WB) and eastern (EB) basin walleye stocks. Sex-specific differences were also found during spawning periods (March–May) when males showed a stronger affinity to shallow waters <6 m than females. Also, EB stocks selected these shallow waters longer than WB stocks, likely due to differences in thermal patterns between basins. Deep water (>13 m) was readily selected between spring and winter (>6 months/year) for most WB and EB walleye despite stock-specific migration patterns. This study provides novel information about the space use patterns of one of the most economically important fish in North America at spatial and temporal scales relevant to management.

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### Introduction

Studying movements and distribution of fishes have both contributed to our understanding of fundamental aspects of ecology such as reproduction, mortality, predation risks, resource use, ontogeny, competition, and migration (Hussey et al., 2015; Hays et al., 2016). Further, knowledge of fish movement patterns can play an important role in conservation and management (Crossin et al., 2017; McGowan et al., 2017). For example, acoustic telemetry provided information to help re-establish important fishing grounds of Greenland halibut (*Reinhardtius hippoglossoides*) in the Canadian Arctic that were altered, in part, by historical sea ice changes (Hussey et al., 2017). Similarly, walleye (*Sander vitreus*) harvest limits in Lake Huron were changed after acoustic telemetry

showed extensive movements throughout the lake after spawning (Hayden et al., 2014; Krueger et al., 2018). Inherent value exists for natural resource managers to consider and incorporate relevant information concerning movements, spatial distribution, and habitat-use of species with economic, ecological, or conservation value (Cooke et al., 2016; Brooks et al., 2019).

Species that undertake large-scale movements are intrinsically more difficult to manage due to the spatial scale in which they occur (Wilhelm et al., 2014) and because they often cross jurisdictional management boundaries. Nevertheless, management tools exist to mitigate these limitations. For example, marine protected areas have been established in the Caribbean to protect species, such as the Nassau grouper (*Epinephelus striatus*), that annually migrate thousands of kilometers to the same area to spawn (Sadovy de Mitcheson and Colin, 2012). Movement of fishes across jurisdictional boundaries can also be problematic because regulations and priorities may not be ubiquitous across the range of

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the species (Miller and Munro, 2004; Pracheil et al., 2012; Song et al., 2017). Interjurisdictional co-operation is, therefore, important to ensure conservation of shared resources, especially for species that are vulnerable to overexploitation (e.g., predictable migrations to spawning grounds).

Lake Erie's walleye population provides an example of a migratory fish that has benefitted from inter-jurisdictional management (Hatch et al., 1987; Knight, 1997; Vandergoot et al., 2019). During the mid-1900s, walleye populations in Lake Erie crashed due to a combination of overfishing, habitat loss, and pollution (Regier et al., 1969). Thanks to increased efforts during the 1970s to curtail overexploitation and pollution, along with a commitment to inter-jurisdictional fishery management by the states (USA) and province (Canada) surrounding Lake Erie, walleye rebounded during the late 1970s and have since supported one of the largest freshwater fisheries in the world (Hatch et al., 1987; Vandergoot et al., 2019). Lake Erie's walleye fisheries are currently managed through an annual total allowable catch (TAC), which is the number of fish that can be safely harvested without jeopardizing the sustainability of the population (Kayle et al., 2015). Each year, the TAC is established through consensus by the Great Lakes Fishery Commission's Lake Erie Committee (LEC), and subsequently allocated among jurisdictions based on the amount of suitable adult walleye habitat – defined as surface area of waters with  $\leq 13$  m depth – in each applicable jurisdiction (Michigan: 5.3%; Ohio: 51.4%; Ontario: 43.4%) (Kutkuhn et al., 1976; STC, 2007; Kayle et al., 2015).

Walleye spawn in tributaries and on open-water reefs throughout Lake Erie, with the largest spawning populations in the western basin (WB) (DuFour et al., 2015; Kayle et al., 2015) and smaller populations occurring in the central (CB) and eastern (EB) basins (Zhao et al., 2011; Stepien et al., 2018). Post-spawn, WB walleye travel extensively within Lake Erie (Wang et al., 2007; Vandergoot and Brenden, 2014; Raby et al., 2018) and sometimes move between Great Lakes (Brenden et al., 2015; Hayden et al., 2019), while EB walleye tend to remain within the EB (Zhao et al., 2011). Despite extensive mixing between populations in the EB, particularly during the summer (Zhao et al., 2011), ' $\leq 13$  m walleye habitat' quotas are allocated for the WB and CB of Lake Erie (management units 1–3; Fig. 1), whereas the EB (management units 4–5; Fig. 1) is managed as a separate entity by local managers. Across the lake, high inter-annual fidelity to specific spawning areas (hereafter termed 'stocks') exists (Chen, 2016; Hayden et al., 2018); however, walleye stocks are typically consid-

ered as being either WB or EB aggregated groups for management purposes (Kayle et al., 2015).

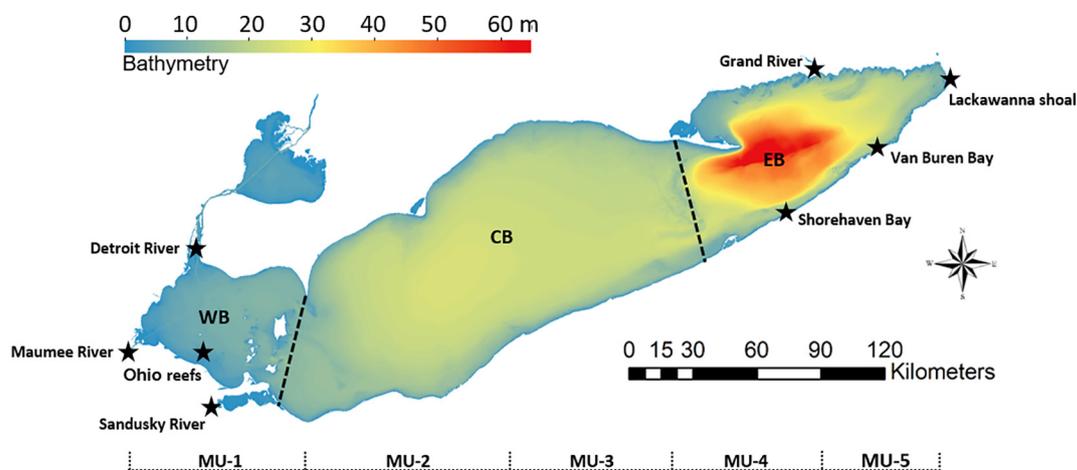
Although large-scale seasonal movements of walleye have been reported in the Great Lakes, a lack of knowledge exists concerning the habitats or areas selected by walleye across the year. For instance, little is known about potential differences in broad-scale habitat-use between WB and EB populations, or among stocks within a given basin. Further, differences among biological characteristics such as sex, size, and age likely play an important part in determining habitat-use because of distinct reproductive, physiological, or energetic requirements (Wang et al. 2007; Pritt et al., 2013; Raby et al., 2018). Understanding spatial and temporal patterns in habitat-use can help contribute to management decision-making to ensure the long-term sustainability of the walleye fishery by providing important baseline information regarding current habitat-use patterns. In turn, this can be used to evaluate current management strategies, improve fishery yields, and understand potential changes in the future (e.g., climate-related trends).

The purpose of this study was to assess year-round habitat-use of different walleye spawning stocks throughout Lake Erie. A large-scale array of acoustic receivers (>300) maintained throughout Lake Erie between 2013 and 2018 enabled the observation of movements of >850 telemetered walleye. Receivers were deployed across depth gradients in Lake Erie and used to determine habitat selectivity at monthly intervals across three depth categories of biological and management significance. The main research questions were: (1) what depth strata were selected by walleye throughout the year?; (2) did WB and EB stocks show similar depth selection patterns despite differences in their migration patterns?; and (3) were there stock, age, size, or sex associated with depth selectivity?

## Methods

### Study area and acoustic arrays

The movements of walleye were monitored in Lake Erie, the shallowest, smallest lake in the Laurentian Great Lakes by volume. Lake Erie has a surface area of  $\sim 26,000$  km<sup>2</sup> and borders Canada (Ontario) and USA (Michigan, Ohio, Pennsylvania, and New York). Water from lakes Superior, Huron, and Michigan enter the west end of Lake Erie via the Detroit River and exit via the Niagara River at the east end of the lake. Lake Erie is divided into three main areas based on limnological characteristics: the WB, central basin



**Fig. 1.** Bathymetric map of study area including approximate locations of walleye stocks and divisions (dotted black line) between the western basin (WB), central basin (CB), and eastern basin (EB). Management Units (MU) for Lake Erie walleye are also indicated by vertical divisions (divisions are approximate).

(CB), and EB (Fig. 1). The WB, a eutrophic-mesotrophic area, is bordered by Michigan, Ohio, and Ontario. The WB is the shallowest section of the lake rarely reaching 15 m deep and is prone to extensive summer warming and in some years harmful algal blooms (Michalak et al., 2013). The mesotrophic CB is the largest section of Lake Erie surrounded by Ontario, Ohio, and Pennsylvania, and primarily consists of depths between 13 and 22 m (Fig. 1). Summer temperatures are cooler than in the WB; however, hypoxic/anoxic bottom conditions can persist during summer, largely due to influx of primary production from the WB and low volume of hypolimnion in summer (Lam et al., 2006). Finally, the mesotrophic-oligotrophic EB is bordered by Ontario, Pennsylvania, and New York, and includes the deepest parts of Lake Erie, up to 64 m. Off-shore oligotrophic waters in the EB tend to be well-mixed in the shallow epilimnion during the summer with a deep, cold, and oxygenated hypolimnion. Nearshore shallow mesotrophic areas are highly productive but consist of relatively small area compared to the WB (Fig. 1; Ryan et al., 1999).

Acoustic receivers (69 kHz; Vemco Ltd, Innovasea, Bedford, Nova Scotia) were deployed throughout Lake Erie and its tributaries beginning in 2011 as part of the Great Lakes Acoustic Telemetry Observation System (GLATOS; Krueger et al., 2018). Receivers were moored on the lake bottom with the hydrophone facing upwards enabling detection of tagged individuals throughout the water column within their detection range – (see below, as well as Heupel et al. (2006) and Hussey et al. (2015) for more information about acoustic telemetry). The number, location, and deployment period of receivers (i.e., seasonal vs. year-round deployments) varied between and within years (Fig. 2) due to project-specific objectives, but the minimum and maximum number of receivers deployed monthly during 2013–2018 (i.e., the years of interest for this study) ranged from 82 to 413. The non-seasonal receiver arrays transitioned from lines to grids beginning in mid-2016 (see Kraus et al., 2018).

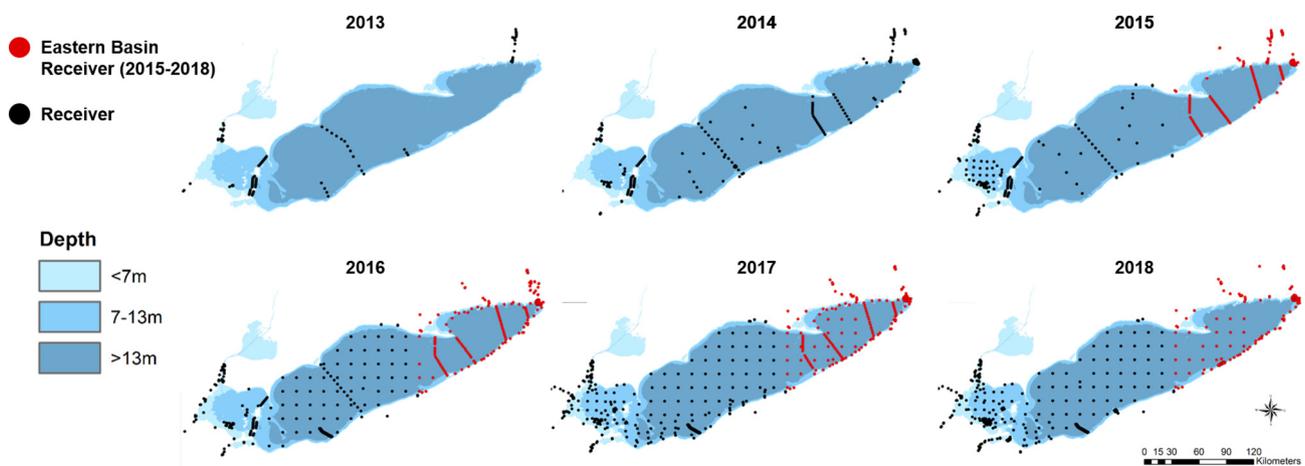
### Walleye tagging

Walleye collection and tagging occurred as part of a large collaboration among academic and government institutions in the western and eastern basins of Lake Erie in the spring spawning period during 2011–2018 (Fig. 1). Limited receiver coverage existed in the WB during 2011 and 2012, but coverage expanded throughout Lake Erie beginning in 2013, therefore only detection data from 2013 to 2018 (including individuals tagged in previous years) were

used in this analysis. Fish from eight unique stocks were tagged including four from the WB (Ohio reefs, Detroit River, Sandusky River, and Maumee River) and four from the EB (Grand River (Ontario), Van Buren Bay, Shorehaven Bay, and an in-lake shoal adjacent to Lackawanna, N.Y.). Fish from tributary populations were collected via boat electrofishing, and open-water reef/shoal populations were sampled via short-set (i.e., < 2 hrs) gillnets, trapnets, or occasionally electrofishing. Post-capture, walleye were held in large flow-through tanks at the capture site (i.e., on land or aboard a large vessel) for tagging. Acoustic transmitters were surgically implanted using established methods for walleye (Cooke et al., 2011; Schoonyan et al., 2017). Fish were sedated immediately before surgery by a brief exposure to pulsed direct current (30 V, 100 Hz, and 25% duty cycle) from a Portable Electroanesthesia System unit (Smith-Root, Inc., Vancouver, Washington, USA; Vandergoot et al., 2011). Acoustic transmitters (V16-4H, 16 mm diameter, 86 mm long, 24 g, estimated battery life = 1.5 – 4.5 years; Vemco Ltd, Innovasea, Bedford, Nova Scotia) were implanted intracoelomically via a small (~3 cm) ventral incision, which was closed with two or three absorbable monofilament sutures. After surgery (<5 min procedure), walleye recovered in flow-through tanks until suitable for release (i.e., regained and maintained equilibrium; <15 min between tagging and release). Each fish's total length (cm) was measured and sex determined during tagging by visually examining extruded gametes. The age-at-capture of individuals was estimated using thin-sectioned fin rays (Kocovsky and Carline, 2000; Fischer and Koch, 2017). If fin rays were not able to provide an age estimate (e.g., thin-section missing annuli near base), age was estimated using year-specific age-length keys (Isermann and Knight, 2005). All sampling and handling of fish during this study were carried out in accordance with guidelines for the care and use of fishes by the American Fisheries Society (<http://fisheries.org/docs/wp/Guidelines-for-Use-of-Fishes.pdf>).

### Data analysis

All data analyses were conducted in R version 3.5.2 (R Core Team, 2018). Common biases and limitations of acoustic telemetry studies were addressed before analyses began. For example, false detections (e.g., Simpfendorfer et al., 2015), dropped/expelled tags, and apparent mortality events were filtered out of the final dataset for analyses. Only individuals with a minimum detection period (i.e., time between first and last detection) of 30 days, as well as



**Fig. 2.** Map of study location (Lake Erie) with receiver locations segregated by study year. Note that receiver presence varied within each year, and these maps represent the maximum number of unique stations throughout the year for illustrative clarity. Within-year variation in the receiver array is accounted for in the analyses.

at least 15 unique days of detections, were included. If the time between consecutive detections at each receiver station for an individual was less than the minimum transmission rate, both detections were identified as false detections and removed. Similarly, detections between adjacent receivers that exceeded the maximum detection range of receivers (10 km; Hayden et al., 2016) and maximum prolonged swimming speed of walleye (1.2 m/s; Scruton et al., 1998) were removed. If an individual was consistently detected on only one receiver for an extended amount of time (i.e., >3 months) and was not detected at a different receiver > 1 km away afterwards, the individual was considered dead (or its tag had been dropped) and the affected detections were removed. Pertinent to the goals of the study, if individuals never departed the riverine system they were tagged in, they were not included in further analyses.

Detection data between July 2013–June 2018 were used to create individual detection histories in both spawning and non-spawning periods. Specifically, walleye tagged in the WB yielded adequate data between July 2013–June 2018, while walleye tagged in the EB yielded adequate data between June 2015–June 2018. To visualize migration patterns, monthly proportions of individuals (years pooled) occurring in each of the three basins were plotted.

To address the three main objectives of this study regarding habitat selection, a selectivity index approach was used, in which the water's bottom depth where walleye were detected was quantified relative to available habitat provided by the receiver array. It is important to note that the transmitters in this study did not have pressure sensors, so depth strata investigations refer to the depth of the receiver that detected tagged fish (not the depth of the individual specifically). Our selectivity approach was selected because receiver deployments were not equitably distributed across the three depth ranges and because receiver locations changed intermittently during the study. Each detection was given a bottom depth value equivalent to that of the receiver it was detected on. The bottom depth (m) at each receiver station was estimated based on bathymetric charts (<https://www.ngdc.noaa.gov/mgg/great-lakes/erie.html>) or in-field observations at time of deployment. The validity of this approach was tested because individuals are not necessarily co-located with a receiver for each detection (i.e., dependent on detection range). A sensitivity analysis was conducted with a random subset of the detection data (WB ~5% of total dataset; EB ~10% of total dataset) that compared the receiver location depth and the depth of a randomized point within the expected detection range. Based on Hayden et al. (2016) and previous testing in Lake Erie, two detection ranges were selected (500 m and 1000 m) that best represented the maximum distances of most detections from a receiver (e.g., 0–500 m and 0–1000 m). To determine how well receiver depth matched with randomized depths at the same receiver, the proportion of detections that resulted in the same depth strata designation (see below) was calculated. In WB walleye detections, the receiver depth and randomized-location depth were within the same depth strata designation between 93 and 99% (500 m range; <7m: 96%, 7–13 m: 93%, >13 m: 99%) and 90–99% (1000 m range; <7m: 93%, 7–13 m: 90%, >13 m: 99%) of detections. In EB walleye detections, depths were within the same strata between 91 and 99% (500 m range; <7m: 92%, 7–13 m: 91%, >13 m: 99%) and 83–91% (1000 m range; <7m: 87%, 7–13 m: 83%, >13 m: 91%) of detections. We acknowledge that some depths were likely mis-categorized based on this method given that detection ranges can vary both spatially (e.g., Euclidean distance between animal and receiver) and temporally (e.g., environmental fluctuations; Hayden et al., 2016; Klinard et al., 2019), but we expected the effect to be minimal given the above results. The three depth strata used to examine walleye habitat selection were selected as follows: <7m – when spawning in rivers and at reefs occurs (Vandergoot et al., 2010); 7–13 m – to represent behaviour inde-

pendent of spawning and equal to or below the management established 13 m cut-off; and >13 m – behaviour above the 13 m cut-off. We acknowledge that the '13 m walleye habitat' definition is not necessarily perceived or enforced as a strict rule, however its use in this study enabled the integration of biological patterns relative to management considerations.

Selectivity indexes were calculated to examine differences in depth strata used by tagged walleye relative to depth strata available (based on receiver deployments). Jacobs (1974) and Chesson (1978) selectivity indices were initially investigated; however, given the similarity of output only Chesson's output was included. Chesson's selectivity index ( $\alpha$ ) provides an empirical representation of resource use relative to availability of that resource within the environment, as follows:

$$\alpha = \frac{r_i/p_i}{\sum (r_i/p_i)} \quad (1)$$

where  $r_i$  is the proportion of detections within depth strata  $i$  and  $p_i$  is the proportion of receivers available at depth  $i$ . Chesson indices were calculated for each individual and month combination in relation to the three depth strata (<7m, 7–13 m, >13 m). The proportion of detections ( $r_i$ ) at each depth was calculated monthly by averaging depths every two hours for each individual. This two-hour binning was done to help reduce the effect of receiver clusters deployed near each other (i.e., otherwise detections may be over-inflated). The proportion of receivers available in the environment ( $p_i$ ) was determined by calculating the number of receivers present at each depth interval every 30 min throughout the month. These 30-min binned periods were used to account for receivers that were added or removed during that month, thus, avoiding over- or under-estimation of receivers available. Only receivers present during the detection period of each individual were included in the calculation of  $p_i$ . All receivers in Lake Erie and affiliated rivers were included in the analysis of WB walleye (except when conditions above were not met) based on the lake-wide distribution of WB walleye, while receivers used in the EB walleye analysis were filtered to only include receivers in the EB (Fig. 1) due to their limited movement outside this area (Zhao et al., 2011; Vandergoot and Brenden, 2014). Values of  $\alpha$  range from 0 to 1, with values >1/number of depth intervals indicating positive selection for that depth and values <1/number of depth intervals indicating avoidance. Therefore, in this study, the selectivity cut-off was  $\alpha = 0.33$  (i.e., 1/3 depth intervals). Habitat availability was based on areas where receivers were present as opposed to the proportion of depth strata throughout the lake. This approach was necessary because it was not possible to detect tagged individuals outside the range or presence of receivers. Otherwise, comparisons with habitat availability throughout the lake (i.e., in areas where receivers were not present) would be biased. The main limitation of the selectivity approach was that subjective depth categories (although relevant to biology and management) needed to be selected to represent the unbalanced deployments and that selectivity patterns reflect where receivers were deployed as opposed to potential trends throughout all parts of Lake Erie.

Finally, a generalized additive mixed-effect model (GAMM) approach using the *bam* function from the 'mgcv' package (Wood, 2017; see also Pedersen et al., 2019) was used to explore depth selectivity in Lake Erie with monthly Chesson indices for each individual as the response variable (research question #1). A model comparison approach was used to test whether EB and WB depth selection differed across monthly Chesson indices (research question #2). Similar comparisons were made between stocks within each basin due to the broad-scale movements described above. Another level of comparisons was tested within each stock for sex differences, as well as age and size (TL)

differences within-sex (or pooled if sexes were not different) (research question #3). Age and size were treated as categorical variables for simplicity and included two levels: age (<8 yrs and  $\geq$  8 yrs) and size (female: <65 cm and  $\geq$  65 cm total length; male: <55 cm and  $\geq$  55 cm total length). All walleye tagged were sexually mature (i.e., fish were collected on spawning grounds during the spawning period); therefore, these groupings were selected less on biological significance and more on even division among the data.

For each explanatory variable (i.e., basin, stock, sex, age, and size), the GAMM approach consisted of testing for differences between a test model and a null model using the *compareML* function from the “itsadug” package (van Rij et al., 2017), following similar methods as Sósokuthy (2017). The test model consisted of the parametric explanatory variable in question (e.g., *sex*), an overall monthly smooth of the Chesson index (e.g.,  $s(\text{month})$ ), a smooth capturing the difference between the explanatory variable levels (e.g.,  $s(\text{month}, \text{by} = \text{sex})$ ), and individual smooths accounting for the random variable Fish ID (e.g., different smooths for each individual;  $s(\text{month}, \text{Fish ID})$ ). The null model excluded the parametric term and difference smooth. Significant differences (alpha = 0.05) indicated whether models with and without separated variable levels (e.g., *sex* combined versus male/female separated) differed. Visual inspection of test model plots were used to explore specifically where (i.e., which months) differences existed. Random smooths (e.g.,  $bs=fs'$ ) were incorporated into each model to account for by-group variation in non-linear effects (Wood, 2017). A basis function of 12 (i.e., # of knots in smoothers;  $k = 12$ ) was selected for all smoothers to incorporate the expected monthly variability in Chesson index values throughout the year and across all stocks. A monthly autocorrelation structure was also added to the models by applying correlation parameter estimates (i.e., rho argument) based on the test model (Baayen et al., 2018). Individual GAMM comparisons were not made *post-hoc* (e.g., between two specific stocks) because basin-specific investigations were a priority. Instead, smoother plots were used to visually assess and describe monthly among-group differences as needed. All years were pooled because exploratory analyses showed relatively high similarity within stocks across years and because a broad overview of depth selectivity was preferred based on study objectives.

## Results

After filtering, data from 851 walleye were incorporated into the present analysis, including 521 (Male: 286, Female: 235; >18 million detections) individuals from the four WB stocks and 330

(Male: 244, Female: 86; >8 million detections) individuals from the four EB stocks (Table 1). No evidence of expelled tags existed and few suspected mortality events (i.e., consistent detections on a single receiver through time) were visible based on data filtering. Some fishery captures reflecting mortality were reported and natural mortality undoubtedly occurred for some individuals outside of receiver detection ranges prior to the end of the transmitter battery life. Mean estimated age at tagging was between 5.6 and 10.9 years across all 8 stocks (and sexes), while mean total length was between 51.6 and 67.4 cm (Table 1). Females had a larger size-at-age than males.

### Effect of tagging basin

The proportion of walleye moving among basins (years pooled) was similar among stocks within a basin (Fig. 3). For WB walleye, residence within the WB was highest during March and April (the spawning season), and decreased during the summer (i.e., June to September) before increasing again at the end of the year (Fig. 3a). During the summer, most fish were located in the CB (30–80%), while the EB was visited by ~10–30% of the tagged fish (Fig. 3a). By contrast, EB-tagged walleye primarily remained in the EB throughout the year with 80–100% of individuals remaining in the same basin they were tagged (Fig. 3b).

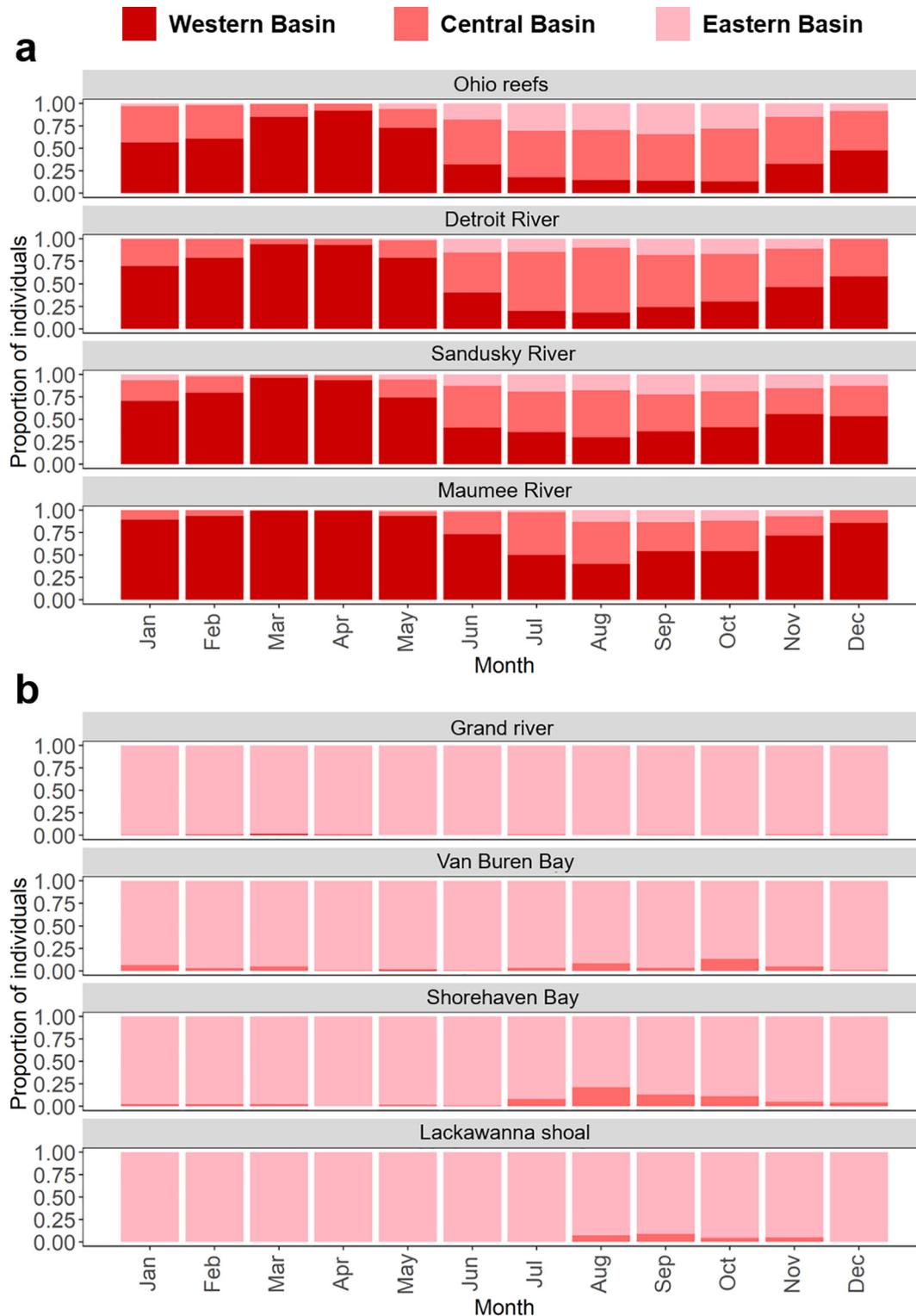
Comparative GAMMs showed that, despite general similarities, walleye tagged in the WB and EB had different depth selection patterns for all three depth strata (<7 m, 7–13 m, >13 m:  $p < 0.001$ ; Fig. 4a). For the <7 m category, EB walleye had a positive selection (Chesson index >0.33) that extended for a longer period (i.e., March to May) relative to their WB counterparts (i.e., March to April). As a result, Chesson indices (CIs) were lower for EB walleye in the 7–13 m category during this period and into summer. Both WB and EB walleye selected for the >13 m category (deeper than the management agencies' definition of walleye habitat) during summer; however, WB walleye had higher CIs that extended beyond summer into the fall and winter (Fig. 4a). During this period, EB tagged walleye more strongly selected depths of 7–13 m (Fig. 4a). Overall, walleye tagged in the WB and EB tended to avoid waters shallower than 13 m between June – October and June – August, respectively.

### Effect of spawning stock

Western basin walleye stocks differed in their depth selection across months for the three depth strata evaluated ( $p < 0.001$ ; Table 2, Fig. 4b); nevertheless, similarities existed across stocks. Specifically, CIs peaked above 0.33 (i.e., positive selection) between February and April for depth <7 m, and stocks avoided that depth

**Table 1**  
Biometrics for walleye tracked using acoustic telemetry from various spawning stocks in the western and eastern basins of Lake Erie during 2013–2018.

Basin	Stock	Sex	Number of individuals	Mean ( $\pm$ SE) age at tagging	Range in age estimates	Mean ( $\pm$ SE) total length (cm) at tagging	Range in total length (cm)
Western Basin	Ohio reefs	M	195	8.5 $\pm$ 0.2	2–19	55.3 $\pm$ 0.1	38.1–68.0
		F	113	7.9 $\pm$ 0.2	3–14	64.5 $\pm$ 0.1	47.6–75.9
	Detroit River	M	35	7.2 $\pm$ 0.4	4–16	54.8 $\pm$ 0.1	47.6–61.2
		F	25	6.5 $\pm$ 0.4	3–10	60.2 $\pm$ 0.1	50–74.4
	Sandusky River	M	41	5.6 $\pm$ 0.3	3–11	51.6 $\pm$ 0.1	42.0–63.1
		F	63	6.3 $\pm$ 0.3	3–13	59.0 $\pm$ 0.1	47.5–73.9
	Maumee River	M	15	7.5 $\pm$ 0.7	3–13	54.3 $\pm$ 0.1	46.1–59.5
		F	34	7.1 $\pm$ 0.4	3–10	61.8 $\pm$ 0.1	51.8–70.2
Eastern Basin	Grand River	M	63	9.4 $\pm$ 0.3	4–15	58.5 $\pm$ 0.1	46.3–70.0
		F	52	10.9 $\pm$ 0.2	7–16	67.4 $\pm$ 0.1	53.0–79.5
	Van Buren Bay	M	56	8.3 $\pm$ 0.3	4–12	57.0 $\pm$ 0.1	47.6–74.3
		F	34	8.8 $\pm$ 0.4	3–13	63.9 $\pm$ 0.1	46.0–75.9
	Shorehaven Bay	M	67	7.8 $\pm$ 0.4	3–17	53.7 $\pm$ 0.1	44.5–64.8
	Lackawanna shoal	M	58	7.9 $\pm$ 0.3	4–13	54.2 $\pm$ 0.1	45.5–64.4

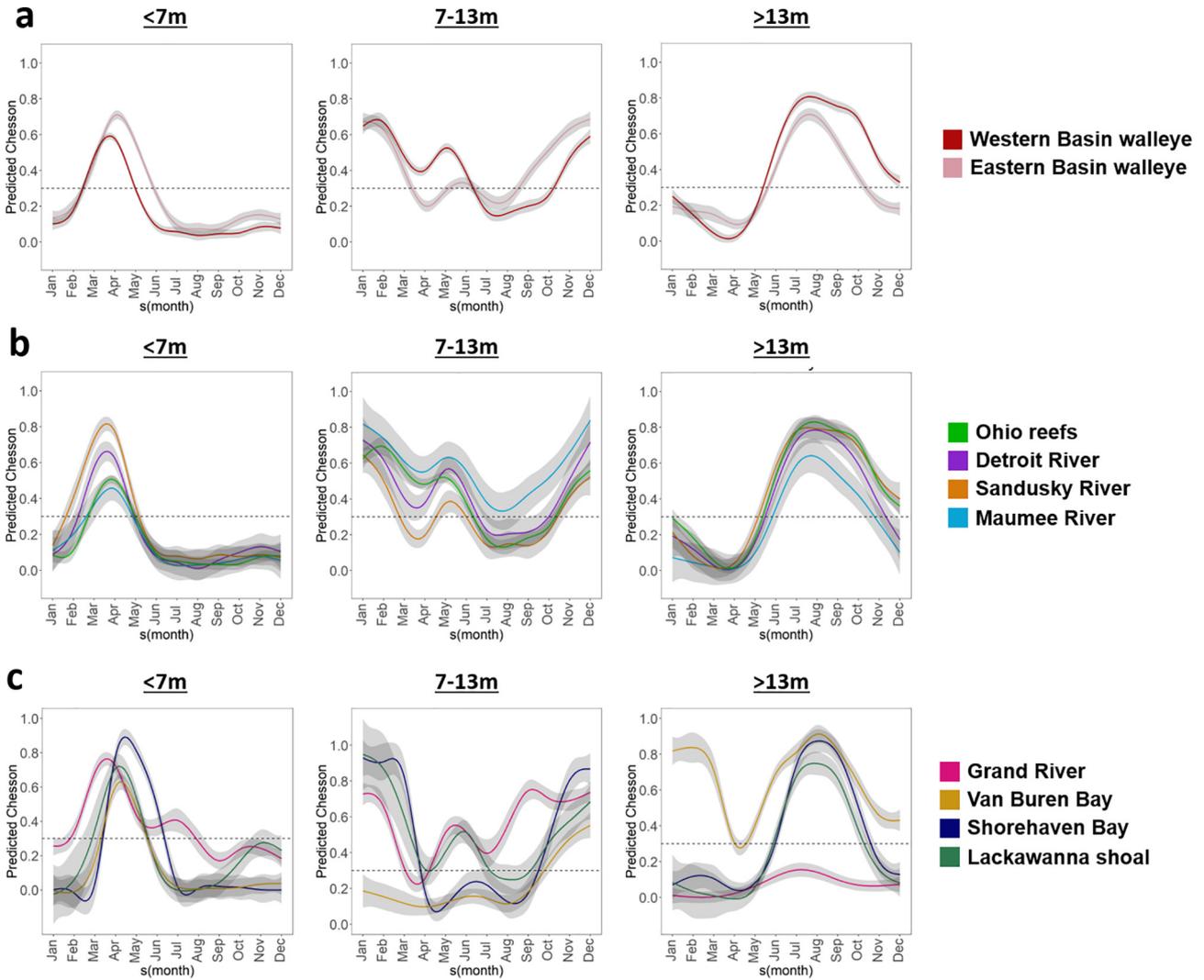


**Fig. 3.** Monthly proportion of individuals (years pooled) occurring in the three basins. For western basin fish (a), the basin reached by each individual (each month) that was furthest to the east was used. Among eastern basin stocks (b), the basin reached by each individual (each month) that was furthest to the west was used.

stratum in all other months (Fig. 4b). The 7–13 m stratum had high CIs (>0.5) during winter (Nov–Feb) for each stock, but CIs dropped afterwards until April, before increasing in May and June, and finally staying low from July through October (Fig. 4b). Despite these seasonal troughs, Maumee River walleye still typically selected for the 7–13 m depth (CIs >0.33), whereas Ohio reefs and Detroit River walleye showed avoidance of this depth strata

during summer; Sandusky River fish avoided 7–13 m during March–April and July–October troughs. Finally, all stocks tended to avoid waters deeper than 13 m between January and May but selected for these areas June to November (Fig. 4b).

With exception of the spring spawning period and in contrast to WB walleye, EB walleye showed different habitat selection patterns throughout the year (Table 3; Fig. 4c). During the spawning



**Fig. 4.** Monthly GAMM plots from western basin (WB) and eastern basin (EB) walleye (a – all stocks combined), and stock-specific smoothers for WB (b) and EB (c) walleye in Lake Erie indicating the level of affinity (Chesson index > 0.33 = preference; Chesson index < 0.33 = avoidance) for the three depth strata. The selectivity cut-off (Chesson index = 0.33) is identified by the grey dotted horizontal line. Confidence intervals are outlined in grey. Statistical tests between null and test model including all stocks from each basin and depth stratum were significant ( $\alpha = 0.05$ ).

**Table 2**

P-values for comparisons between test and null GAMM models among three depth strata in each western basin stock of Lake Erie testing for differences in sex, age, and size of walleye. P-values are included with a corresponding \* where significant ( $\alpha = 0.05$ ). Age and size results are separated for males and females when sex was significantly different.

Stock		<7m	7–13m	>13m
Ohio reefs	Sex	<0.001*	<0.001*	<0.001*
		<i>Males</i>	<i>Males</i>	<i>Males</i>
		<i>Females</i>	<i>Females</i>	<i>Females</i>
	Age	0.011*	0.297	<0.001*
	Size	0.003*	0.734	<0.001*
Detroit River	Sex	<0.001*	<0.001*	0.002*
		<i>Males</i>	<i>Males</i>	<i>Males</i>
		<i>Females</i>	<i>Females</i>	<i>Females</i>
	Age	0.975	0.359	0.021*
	Size	0.940	0.652	0.998
Sandusky River	Sex	0.017*	0.891	0.698
		<i>Males</i>	<i>Sex combined</i>	<i>Sex combined</i>
		<i>Females</i>	<i>Females</i>	<i>Females</i>
	Age	0.543	0.675	0.131
	Size	0.281	0.022*	0.219
Maumee River	Sex	0.028*	0.009*	<0.001*
		<i>Males</i>	<i>Males</i>	<i>Males</i>
		<i>Females</i>	<i>Females</i>	<i>Females</i>
	Age	0.693	0.026*	0.994
	Size	0.508	0.011*	0.973
				0.024*
				0.998

period (March-May), habitat <7 m depth was selected for by all stocks; however, these peaks were more varied temporally than among WB stocks (e.g., between March-April for Grand River,

April-May for Van Buren Bay and Lackawanna shoal, and Apr-Jun for Shorehaven Bay; Fig. 4c). Grand River, Shorehaven Bay, and Lackawanna shoal walleye appeared to prefer depths of 7–13 m

**Table 3**  
P-values for comparisons between test and null GAMM models among three depth strata in each eastern basin stock of Lake Erie testing for differences in sex, age, and size of walleye. P-values are included with a corresponding \* where significant ( $\alpha = 0.05$ ). Age and size results are separated for males and females when sex was significantly different.

Stock		<7m		7–13m		>13m	
Grand River	Sex	0.755		0.348		<0.001*	
		Males	Females	Males	Females	Males	Females
	Age	0.001*		0.005*		0.006*	0.013*
Van Buren Bay	Size	<0.001*		<0.001*		0.021*	0.007*
	Sex	<0.001*		<0.001*		<0.001*	
		Males	Females	Males	Females	Males	Females
Shorehaven Bay	Age	<0.001*	0.876	0.033*	<0.001*	0.002*	0.093
	Size	0.197	0.199	<0.001*	0.027*	<0.001*	0.012*
	Sex	NA		NA		NA	
Lackawanna shoal		Sex combined		Sex combined		Sex combined	
	Age	0.036*		0.835		0.005*	
	Size	0.020*		0.800		0.010*	
Lackawanna shoal	Sex	NA		NA		NA	
		Sex combined		Sex combined		Sex combined	
	Age	0.929		0.990		0.823	
	Size	0.443		0.915		0.512	

throughout the year with exception of the spring spawning period (March and April) and some periods during the summer. Van Buren Bay walleye tended to reside in the waters deeper than 13 m throughout the year except during spring (when in <7 m depth, presumably to spawn; Fig. 4c). Grand River fish avoided waters >13 m throughout the year, while the other stocks selected these deep areas during the summer.

#### Effect of sex

Male and female walleye tagged in the WB showed sex- and stock-specific habitat-use patterns throughout the year (Table 2; Fig. 5). The main exception to this generalization was for Sandusky River walleye where males and females used the same habitat for most of the year (Table 2, Fig. 5). For the <7 m depth stratum, all stocks demonstrated relatively similar selection patterns, but males typically had higher CIs between February and May than females (Fig. 5). For the 7–13 m depth stratum, females typically had higher CIs in March and April compared to males, which often avoided 7–13 m (and selected for <7 m) during this period. Finally, for the >13 m depth stratum in pooled stocks (and Ohio reefs/Detroit River), females had higher CIs across most months, whereas Sandusky River males and females were similar, and Maumee River males appeared to use this depth more regularly during summer than females (Fig. 5).

In the EB, female and male depth use at <7 m and 7–13 m was similar for Grand River walleye, with the only difference occurring in water >13 m during early summer (June through August); however, both sexes still avoided this depth (Table 3, Fig. 6). Depth use for Van Buren Bay walleye differed between sexes at each depth stratum (Table 3, Fig. 6). Van Buren Bay males showed more variation than females in depth selection, in part due to the strong selection by males for <7 m in April and May; nevertheless, deep water (>13 m) was selected throughout the year by both sexes (Fig. 6).

#### Effect of fish age and size

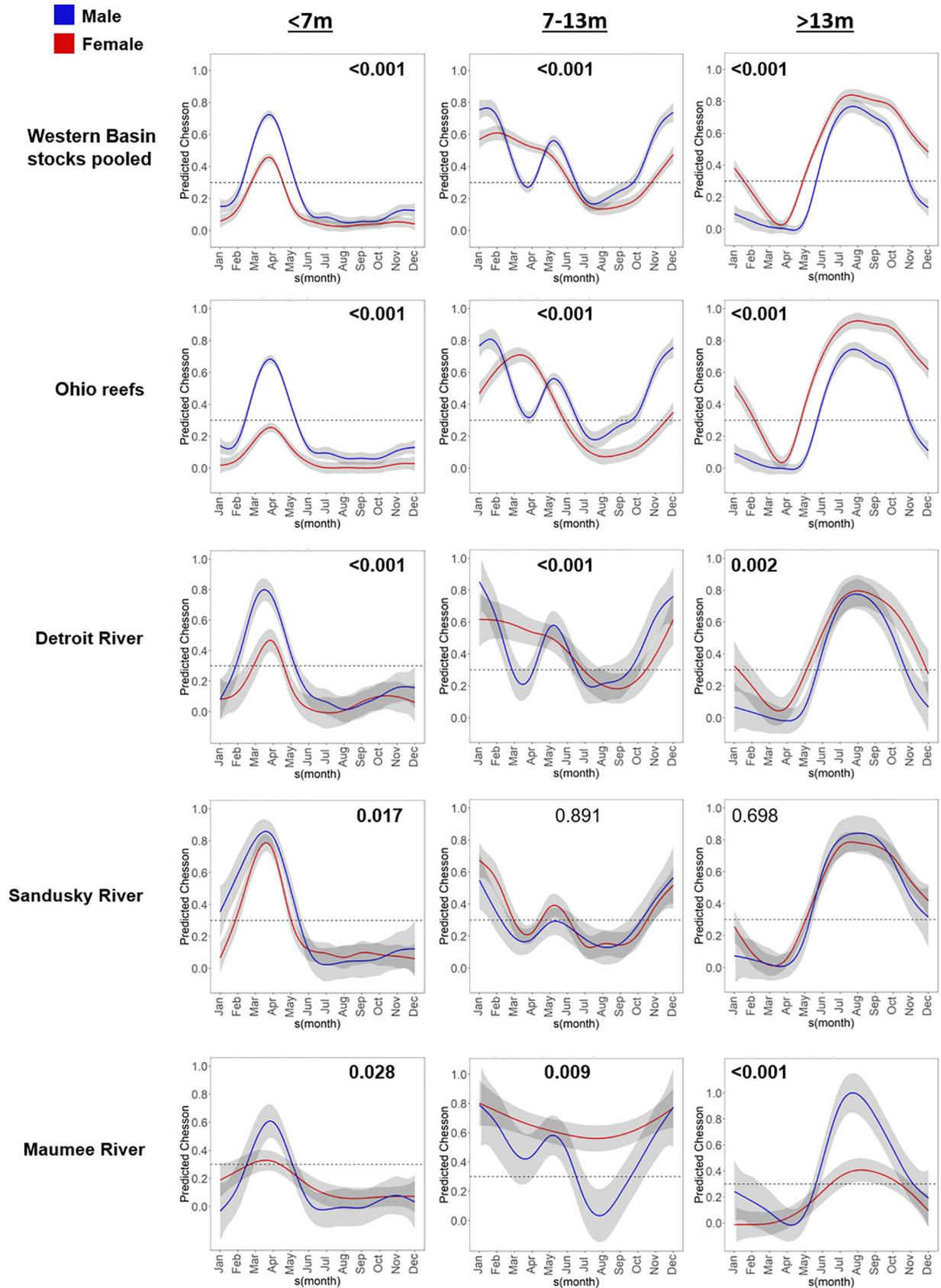
Although several individual spawning stocks displayed differences in the depth habitat occupied among the different age and size categories evaluated (Table 2), the overall habitat selection patterns were similar. For example, small (<55 cm) and large (>55 cm) male and female walleye from the Ohio Reefs showed similar habitat selection patterns throughout the year regardless of depth strata (Fig. S1). Similar habitat selection patterns were also observed for young (<8 years) and old ( $\geq 8$  years) walleye

(Fig. S1). Given the infrequent and minor differences between age and size, the predicted habitat selection models are presented in supplementary materials (Figs. S1–S8) without further description.

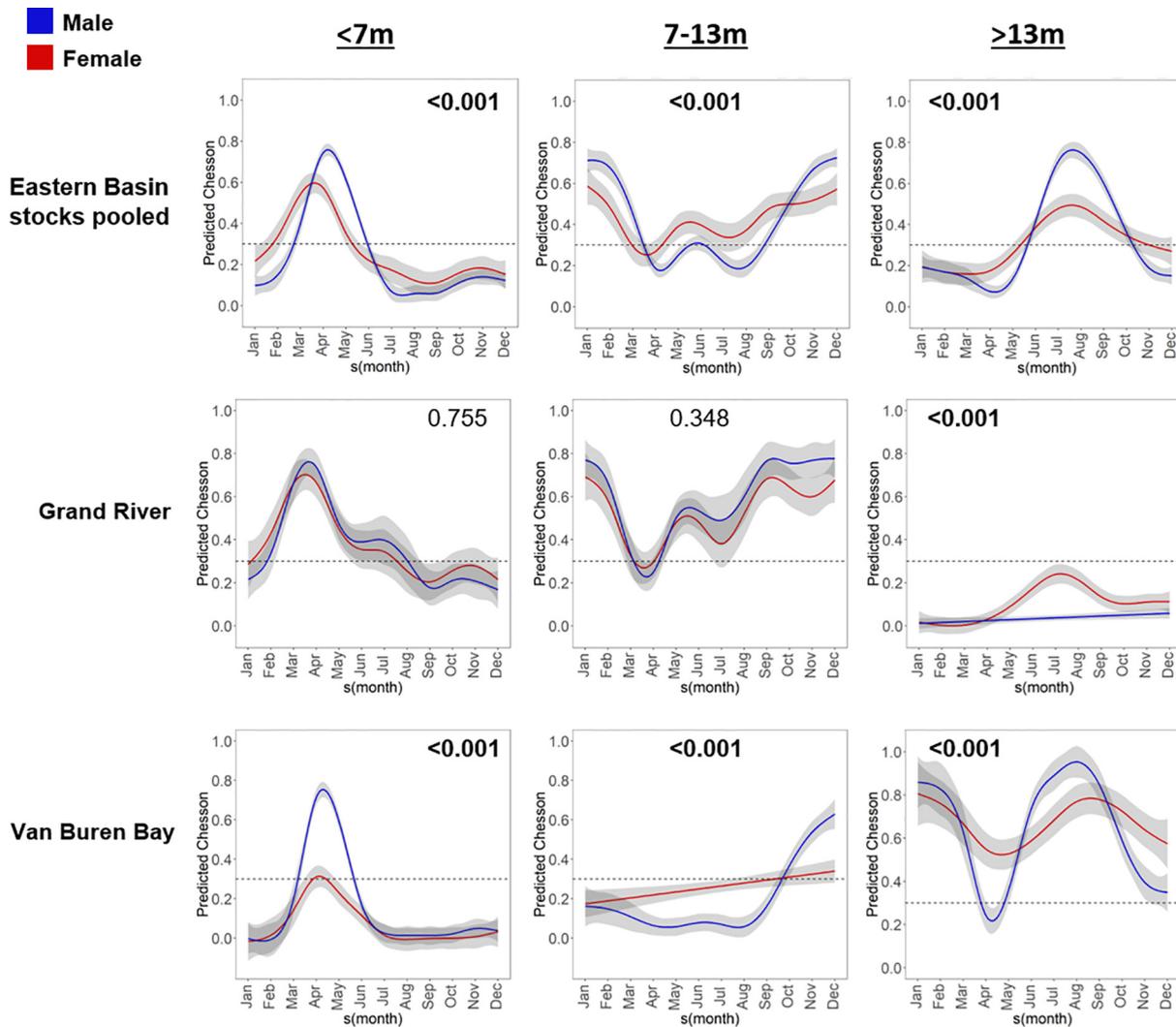
## Discussion

The results of our study identified differing walleye habitat-use among basins of origin, stocks, and sexes throughout the year in Lake Erie. For instance, WB walleye had a stronger preference for the >13 m depth-strata than their EB counterparts outside of the spawning period (June – February). Generally, individual WB stocks had similar monthly habitat selectivity patterns across depth-strata, whereas considerable variation in habitat selection existed among EB stocks. Nevertheless, some EB stocks (e.g., Lackawanna shoal) had similar overall trends compared to WB stocks. These findings, particularly the strong selection by WB and EB stocks for depth-strata >13 m during non-spawning periods, provide fishery managers with an improved understanding of how mature walleye select specific habitats throughout Lake Erie.

Walleye from Lake Erie's western and eastern basins showed stark differences in their large-scale movements; specifically, WB walleye often made movements to the east up to ~400 km, while EB walleye remained more local (although far within-basin movements were often made). These findings are consistent with previous work examining their spatial ecology (Wang et al., 2007; Zhao et al., 2011; Vandergoot and Brenden, 2014; Raby et al., 2018). Furthermore, our results suggested that these populations also differed in their habitat selection patterns. These differences appeared to be at least partially driven by each basin's distinct spawning period and subsequent migrations. The WB warms more quickly during the spring than the EB due to shallower waters, leading to a seasonally earlier period in which spawning occurs. In contrast, temperatures remain well below optimum for spawning in the EB until late April or early May (J. Robinson, unpublished data). Water temperatures quickly rise in the WB above thermal optimum for adult walleye (>23 °C; Barton and Barry, 2011), likely stimulating eastward movement (Raby et al., 2018). The temporally longer affinity of WB walleye to deeper waters (>13 m) after spring compared to EB walleye represents greater time spent away from the WB in more energetically beneficial CB or EB waters (Kershner et al., 1999; Madenjian et al., 2018). Greater time spent foraging in the productive eastern areas of Lake Erie during summer, fall, and early winter may in turn support rapid gonadal development that is nearly complete by the end of the calendar year (Malison et al., 1994; Malison and Held, 1996). Despite these



**Fig. 5.** Monthly sex-specific GAMM plots from western basin walleye stocks (combined and stock-specific) in Lake Erie indicating the level of affinity (Chesson index > 0.33 = preference; Chesson index < 0.33 = avoidance) for the three depth strata. The selectivity cut-off (Chesson index = 0.33) is identified by the grey dotted horizontal line. Confidence intervals are outlined in grey. P-values from null and test model comparisons are included and bolded when sexes significantly differed ( $\alpha = 0.05$ ).



**Fig. 6.** Monthly sex-specific GAMM plots from eastern basin walleye stocks (combined and stock-specific) in Lake Erie indicating the level of affinity (Chesson index  $> 0.33$  = preference; Chesson index  $< 0.33$  = avoidance) for the three depth strata. The selectivity cut-off (Chesson index = 0.33) is identified by the grey dotted horizontal line. Confidence intervals are outlined in grey. P-values from null and test model comparisons are included and bolded when sexes significantly differed ( $\alpha = 0.05$ ).

different thermal regimes, walleye from both basins showed similar timing in selection for shallow waters during late winter, which suggests that an external cue such as photoperiod may play a role in pre-spawn behavior of walleye. A greater temporal resolution beyond the scope of this study would be required to investigate fine-scale trends in staging or other pre-spawning behaviour (see [Bade et al., 2019](#)).

Along with distinguishing migration patterns between walleye from the eastern and western basins, the information presented here provided novel insights into habitat selection (i.e., depth-strata) throughout the year for walleye from multiple spawning populations. Generally, WB stocks demonstrated similar patterns in depth habitat selection throughout the year, while EB stocks showed more variability in habitat selection patterns. The most obvious example of EB variability was the Grand River population, where walleye either appeared to reside within the river year-round or made short (30–50 km) movements along the north shore to the west of the river mouth. These observations were consistent with previous research using traditional mark-recapture techniques (T. MacDougall, unpublished data). By contrast, Van Buren Bay walleye readily used the  $>13$  m depth stratum outside of the spawning period, similar to WB stocks. The strong selection for 7–13 m waters between October and March by EB walleye demon-

strated importance of this depth habitat considering the relatively small area and narrow margin dividing shallow ( $\leq 13$  m) from deep ( $>13$  m) waters along the southern shore of eastern Lake Erie. Stock- or group-specific spatial behaviour has been similarly shown in Atlantic cod (*Gadus morhua*) which have distinctive spatial affinity based on stock, maintaining population integrity at a spatial scale  $<20$  km when overwintering in eastern Canada ([Campana et al., 1999](#)). Lake sturgeon (*Acipenser fulvescens*) in the Great Lakes also show within-population variation in migration patterns and habitat-use, segregating into several distinct groups after spawning in rivers ([Kessel et al., 2018](#)). The greater variation in monthly habitat selection among EB stocks may reflect the lower productivity throughout the year in the EB compared to the WB, resulting in stock-specific foraging and thermoregulatory strategies to maximize fitness. Receiver configuration in the WB was different from the EB throughout the study; therefore, differences in selectivity between wider-ranging WB walleye and EB walleye may, in part, be influenced by receiver availability.

The results presented here also provide an initial glimpse into the spatial mixing among stocks in summer and autumn that occurs in the CB and EB, which may be useful to fishery management. For instance, our results suggested that EB stocks had a stronger preference for intermediate depth-strata (i.e., 7–13 m)

during late summer and early autumn, while WB stocks more strongly selected for the >13 m depth-strata. This result suggested differential spatial occupancy patterns between the larger WB and smaller EB populations. Such differences may lead to differential exploitation of WB and EB stocks by commercial and recreational fisheries, and varying availability to fishery-independent surveys that use experimental gillnets set at varying depths.

Sex-specific differences in habitat selection were also evident in our data. Like many fishes, male walleye arrive at spawning grounds earlier and stay later than females in both riverine and open-lake spawning populations (Pritt et al., 2013; Bade et al., 2019). These sex-specific spawning behaviors are likely driving seasonal differences in habitat selection not only for the <7 m depth strata, but also differences in the deep habitat categories as well. For example, although waters >13 m were selected for by the Van Buren Bay stock throughout most of the year, only males appeared to spend a substantial amount of time in shallow waters, presumably for spawning. After spawning, WB females departed for the CB earlier than males during 2014 and 2015 and were 1.8 times more likely to be detected in the EB than were males (Raby et al., 2018), which is reflected in the earlier peaks in positive selection for habitat >7 m across most WB stocks. Previous observations that large (old) females were more likely than males to move into the eastern CB and EB (Wang et al., 2007) where favorable forage and thermal habitat exist may help explain elevated preferences for deeper waters relative to males. The extended time of females in deep waters, especially within the less-exploited EB may protect these fish from mortality and support future sustainability of the walleye fishery.

No evidence existed to support major size- or age-specific differences in habitat selection. One possible explanation for this observation is that all fish tagged here were sexually mature. Immature walleye often remain in the WB for longer periods than mature individuals in this study (M. Faust, unpublished data). Similarly, a limited fishery for immature walleye (<age 4) exists in the nearshore waters (<7 m) of the EB during the summer months (J. Robinson, unpublished data). Consequently, sampling a greater age range in future studies, particularly immature walleye, would help derive the importance of, and affinity for, deep waters to Lake Erie population. The inclusion of immature walleye in this analysis would likely shift selectivity for waters  $\leq 13$  m more positively during summer, reflecting more accurately the fish that are targeted by the fishery during that period. Nevertheless, Ohio reefs (93% of WB larvae, DuFour et al., 2015) in the WB and Van Buren Bay (65% of EB adults, Zhao et al., 2011) in the EB support two of the largest spawning populations in Lake Erie; therefore habitat-use patterns of mature walleye depicted in this study are relevant for management as they reflect a significant portion of population-wide trends throughout Lake Erie.

The definition of suitable walleye habitat consisting of waters  $\leq 13$  m deep to allocate TAC among jurisdictions for the WB walleye population (Kutkuhn et al., 1976; STC, 2007; Kayle et al., 2015) was not supported by our data. Many EB and WB stocks selected depths >13 m for half the year, which coincided with the highest harvest months. Recent studies also suggested that walleye use habitat beyond the 13 m definition. For example, an analysis of hydroacoustic data during autumn in Lake Erie's CB showed that large targets, inferred to be walleye, occurred in the deepest sampling layers (i.e., 10–15 m) across all sampling conditions (e.g., day vs. night, large vs. small vessel; DuFour et al., 2018). Similarly, a subset ( $n = 20$ ) of walleye from this study were tagged with pressure-sensing acoustic transmitters and showed a mean estimated swimming depth during stratification of 13.3 m (Gorman et al., 2019). Based on fisheries-independent gillnet data collected annually across Lake Erie during August–November 1989–2010, Pandit et al. (2013) concluded that estimates of suit-

able habitat differed between basins and between juvenile and adult walleye. Furthermore, they concluded that the current 13 m definition overestimated the amount of habitat available in the western basin and underestimated habitat available to walleye in the eastern basin. However, spatio-temporally limited gillnet sampling effort (i.e., during August in eastern basin and October in western and west-central basins) limited any further inferences about walleye habitat in Lake Erie.

Despite the apparent disconnect between the management definition of suitable habitat and what walleye appear to use, there is no indication that current walleye quota allocations in Lake Erie are flawed based on the past sustained natural recruitment, strong yields by both commercial and recreational fisheries, and minimal conflict among jurisdictions on Lake Erie (Kayle et al., 2015). Therefore, a rigorous evaluation of quota allocation procedures for Lake Erie's spatially structured, multi-jurisdictional fisheries may not be necessary unless stock-specific demographic or socio-economic issues arise. Although individual stocks are aggregated into either WB or EB groups for management, managers have recognized the need to pursue a more holistic approach of assessment and management of walleye in Lake Erie (Kayle et al. 2015). DuFour et al. (2015) described the benefits of maintaining a diverse portfolio of walleye stocks, and in recent years, managers have increasingly more information at their disposal. For instance, a recent study used restriction site-associated DNA sequencing of >12,000 polymorphic loci to examine genetic stock structure among Lake Erie's walleye stocks and were able to classify walleye back to their basin of origin with >95% accuracy (Chen et al., 2019). Techniques such as this, combined with an improved understanding of individual stock movement patterns across a range of age- and size-classes, may facilitate steps toward a more complete understanding of fisheries performance relative to walleye spatial ecology, along with a true lake-wide assessment and management process.

## Conclusion

The findings of this study support previous research on basin- and sex-related migration patterns, and expanded knowledge about stock-specific habitat-use at a scale not previously known. Estimates of habitat selectivity across all months provided new information about the timing of movements among stocks, between sexes, and age/size categories. The consistency among WB and some EB stocks' use of various depth-strata throughout the year suggests that at least from a broad-scale habitat-use perspective, aggregating populations for management is reasonable, although distinct spawning seasons still need to be considered. Nevertheless, much additional work remains; for instance, future analysis should strive to examine whether walleye from different stocks show different spatial use patterns outside of the spawning season, despite similar depth-strata, resulting in differential exploitation patterns. For example, does one walleye stock move north from USA into Canadian waters where commercial exploitation dominates relative to other southern stocks that may remain to be exploited by the recreational fishery in the United States? Furthermore, future research should help pinpoint the specific variables that cause the large-scale space-use differences between WB and EB walleye. As suggested by Raby et al. (2018), seasonal movements outside of the WB may be associated with increased foraging opportunities (Biesinger et al., 2017), behavioural thermoregulation to avoid warm WB waters during the summer (Wang et al., 2007), high competitive pressure (Hartman and Margraf, 1992), selective fishing pressure against individuals that remain in WB during summer (where fishing effort is highest; Wills et al., 2018), reduced habitat quality (e.g., harmful algal blooms; Michalak et al., 2013), social cues, or genetic predisposi-

tion. These variables and resultant behaviour in face of increasing environmental change could have important implications for spatial management of exploitation of specific stocks throughout Lake Erie.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jglr.2020.03.014>.

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