Site fidelity and seasonal habitat preferences of largemouth bass (*Micropterus salmoides*) in a temperate regulated reservoir

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Abstract A wide range of fish species navigate and return to previously selected habitats across time scales ranging from days to years. While this ability may be challenged in anthropogenically disturbed systems, such as temperate regulated reservoirs, where littoral freezing/drying may alter critical habitats, no work has yet been conducted to determine if fish within these systems are able to home to specific habitats. In addition, most studies have examined site fidelity over a limited time scale. In this study we investigated the long-term movement and habitat utilization of largemouth bass *Micropterus salmoides* (Lacépède, 1802) using a combination of radio telemetry and habitat mapping across nine consecutive seasons in a winter drawdown reservoir to examine seasonal population- and individual-level spatial clustering and site fidelity. Largemouth bass navigated across large distances through spatially and temporally disturbed habitat with exceptional inter-annual site fidelity during winter, spring, and summer. Drawdown constrained the availability of preferred winter habitat, concentrated fish, and rendered them potentially vulnerable to overexploitation, predation, and competition. Adaptive drawdown protocols should be developed that incorporate temporally and spatially resolved fish movement data, and variables such as available critical habitat, which are essential for maintaining fish population stability in temperate regulated reservoirs.

Keywords Reservoir drawdown, Largemouth bass, Habitat preferences, Site fidelity, Seasonal homing

Introduction

A wide range of both marine and freshwater fish species are known to exhibit site fidelity and are able to navigate and return to previously selected habitats of various types across time scales ranging from days to years. Recent studies have revealed return migrations to marine pelagic home ranges by tiger sharks *Galeocerdo cuvier* (Péronlesueur, 1822) (Lea et al., 2015), homing to summer feeding sites by Pacific halibut *Hippoglossus stenolepis* Schmidt, 1904 (Loher, 2008), and movement to spawning aggregation sites by common coral trout *Plectropomus leopardus* (Lacépède, 1802) (Bunt & Kingsford, 2014). In freshwater, three-spined stickleback *Gasterosteus aculeatus* Linnaeus, 1758 have been shown to return to home ranges in ditches (Ward et al., 2013), while wild and hatchery lake trout *Salvelinus namaycush* (Walbaum, 1792) home to shoal spawning sites within the Great Lakes (Binder et al., 2016), and rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) home to natal spawning sites within tributaries (Biette et al., 1981).

Habitat characteristics determine the strategies used for navigation as well as the likelihood of homing success (Odling-Smee & Braithwaite, 2003). While the environmental cues underlying linear riverine migrations such as odour (olfaction) and unidirectional flow (rheotaxis) are highly guiding and straightforward (Bett & Hinch, 2015), lacustrine migrations may require different sets of cues including the use of spatial information and landmarks to facilitate navigation across open habitats with complex and disjunct flow and stratification patterns (Braithwaite & De Perera, 2006; Rogers & Bergersen, 1995). Anthropogenically disturbed lacustrine systems, such as regulated reservoirs, may therefore further challenge fish navigation and homing abilities to previously selected habitats (i.e., philopatry). In regulated reservoirs, natural water level fluctuations are replaced by artificially managed drawdown and refill periods to meet various objectives including, but not limited to, hydroelectric power generation, wastewater dilution (Bradford & Heinonen, 2008), and the provision of storage capacity to offset downstream flooding impacts. Extreme water level fluctuations and the consequent littoral freezing/drying that occurs in some temperate reservoirs has the potential to disrupt spawning areas and other critical habitats and resources (Carmignani & Roy, 2017; Hirsch et al. 2017). In addition to drying, the physical disturbance of littoral habitat caused by drawdown, such as increased turbidity (Hirsch et al., 2017), can have lasting carry-over effects, and may alter the reliability of navigation cues (e.g., chemosensory and visual) used to relocate key spawning and/or summer home range habitats. Despite the habitat disruption and potential associated influence on fish movement, habitat selection, and site fidelity, no work has yet been conducted to determine if fish are able to navigate effectively and home to specific habitats in temperate reservoirs with water level regulation.

One of the most intensively managed and recreationally important reservoir fish species is largemouth bass. In northern temperate systems, largemouth bass are known to utilize distinct seasonal habitats and typically migrate in autumn and spring to and from common overwintering and individual summer home range areas (Lewis & Flickinger, 1967; Hanson et al., 2007; Hasler et al., 2009). In the winter, large aggregations are formed in less complex, deeper water habitat (Hanson et al., 2007; Rogers, 1998). These areas provide thermal refuge and likely reduce the risk of adult overwinter mortality (Rogers, 1998; Westhoff et al., 2016). Though not yet widely appreciated, the availability of high-quality overwintering habitat is likely critical for population stability and successful recruitment (Suski & Ridgway, 2009), and may also be a limiting factor in many fall and winter drawdown reservoirs where much of the affected lake becomes air-exposed during winter months. In the study system examined here (Lake Eugenia, Ontario, Canada), water levels have historically been drawn down by approximately 2 m in the fall/winter and refilled to full pool by April. With an average depth of 1.5 m, the majority of the lake, similar to other shallow reservoir lakes, is rendered unavailable to resident fishes during the winter and littoral areas used during other seasons become highly impacted.

Only three studies investigating largemouth bass site fidelity in regulated reservoirs or systems could be found, all of which were conducted short-term. During early experiments with fish telemetry, Warden & Lorio (1975) showed that fish rapidly returned to littoral areas in the fall after re-flooding of a Mississippi reservoir with summer drawdown. Waters & Noble (2004) showed nest site re-occupation in a reservoir in Puerto Rico with frequent year-round water level fluctuations. In the same year, Karchesky & Bennett (2004) noted that fish returned to areas of original capture after spring refill of a run-of-the-river reservoir in Idaho, with this study focused on overwintering habitat use. Only one of these studies tracked the same fish for a full year, with tags lasting only an average of 14 days in earlier work, and in studies from 2004 the total project durations were 18 months and 11 months, respectively. These time frames are consistent with other studies, as most researchers who have examined site fidelity have often done so during a single year, within a single season, using mark-recapture and translocation (e.g., Hodgson et al., 1998; Ridgway & Shuter, 1996; but see Lewis & Flickinger, 1967).

The goal of this study was to build upon previous work and to investigate long-term movement and habitat utilization patterns as well as fill knowledge gaps related to the inter-annual multi-seasonal homing ability of fish in (temperate) regulated reservoirs. To this end we both conducted a radio-telemetry study of largemouth bass across nine seasons with repeated winter drawdowns, from the summer of 2015 to the summer of 2017, and also performed a translocation experiment to further assess site fidelity to critical overwintering habitat. Using the collected data we explored the degree of both population- and individual-level spatial clustering (i.e., distribution) and site fidelity among largemouth bass in Lake Eugenia across seasons and between years. We expected high degrees of clustering and fidelity in the winter at both population- and individual-levels, with fish aggregations located in the same overwintering area each year. In the summer we expected limited population clustering yet high individual site fidelity and clustering, with fish occuppying individual home ranges distributed throughout the lake.

Methodology

Study Site

Lake Eugenia (44.3254287N, -80.491047W) is a reservoir created in 1916 by the Hydro Electric Power Commission of Ontario (now Ontario Power Generation, OPG) and is located in the municipality of Grey Highlands, Ontario, Canada at an elevation of 433 m above sea level (ASL). At full pool, the surface area is 6.425 km^2 and the maximum depth is 12.2 m with average depth approximately 1.5 m. The lake has historically been drawn down by approximately 2 m in the fall/winter (mean = 2.4 m, 2014-2015, OPG unpub. data), reducing its surface area by more than half, and is refilled to full pool by early April. The Beaver River feeds the reservoir from the south-east, with flow exiting the reservoir from two major outflows, Wodehouse Creek to the north-west and the Beaver River to the south-west. Prior to the early 1980's, Lake Eugenia supported a cold-water fish community dominated by rainbow trout, brook trout *Salvelinus fontinalis* (Mitchill, 1814), brown trout *Salmo trutta* Linnaeus, 1758, and yellow perch *Perca flavescens* (Mitchill, 1814). However, the lake has since been colonized by warm-water species that comprise the majority of the recreational fishery including largemouth bass, smallmouth bass *Micropterus dolomieu* Lacépède, 1802, rock bass *Ambloplites rupestris* (Rafinesque, 1817), common carp *Cyprinus carpio* Linnaeus, 1758, and sunfish *Lepomis* spp..

Lake Eugenia is a well populated cottage lake with extensively developed shorelines and is popular for recreational angling. As such, metal signs were posted at access points around the lake to inform the public of this study, and to encourage anglers to practice catch and release. Signs posted around the lake also offered a reward to anglers who reported the location of any captures of tagged fish. To assist with fish relocalization, particularly by anglers, as well as to assist with habitat mapping (see below), a map of the lake was subdivided into 203 numbered 200 m x 200 m quadrats and was posted online at a website shown on the signs.

Radio Telemetry and Translocation

Twenty-seven adult largemouth bass were captured with either angling or boat electrofishing in August and September 2015 from various quadrats across the lake. Each fish was externally anchor-tagged and then anesthetized in a 50 ppm induction bath of clove oil and ethanol in a 1:9 ratio. Upon loss of equilibrium fish were weighed (g), measured (total length (TL), mm) and transferred to a surgical tank with a maintenance dose of anesthetic (25 ppm). Each fish was surgically implanted with a coded radio transmitter (150.660-150.740 MHz, 40 mm x 12 mm, 8 g in air, 3.5 g in water, battery life expectancy ~3 years; SigmaEight Inc., Aurora, Ontario) with a 10 mm incision closed with braided silk suture. Fish recovered in a holding tank with fresh lake water before being released at their site of capture.

Fish were tracked from August 16, 2015 to September 10, 2017, using a four-element Yagi antenna and a digital receiver with pulse-code discrimination software (Lotek SRX_400; Lotek Wireless Inc., Newmarket, Ontario). A total of 49 tracking sessions were conducted across seasons, with 7 in summer and 6 in fall 2015, 3 in winter, 6 in spring, 10 in summer, and 9 in fall 2016, and 3 in winter, 1 in spring, and 4 in summer 2017. Spring relocations were considered those occurring between March 20 - June 19/20, summer relocations were considered those between June 20/21 - September 21/22, fall relocations were between September 22/23 - December 20/21, and winter relocations were from December 21/22 -

March 19. Prior to thick ice formation, fish were tracked on the lake using motorized watercraft (22 ft pontoon boat, 16 ft aluminum motorboat) and by foot along the shoreline. During the winter, fish were tracked by truck, snowmobile, and by foot, both from shore and on the lake ice. Fish locations were determined using triangulation (accuracy 3-50 m). Upon fish code identification (<100 m detection range) either a Universal Transverse Mercator (UTM) coordinate or quadrat number was recorded. In rare instances when only the relevant quadrat was recorded as a fish location, the GPS of the quadrat centroid was assigned as the location.

A translocation experiment was also conducted to further explore the strength of site fidelity in the lake. Three additional largemouth bass were angled from the bay in which overwintering occurred on November 6, 2016 (during lake drawdown) and were transported ~2.4 km in a 142 L aerated cooler by boat to the south-eastern shoreline (44.316389 N, -80.489444 W). Fish were tagged, anesthetized, measured (g), weighed (TL, mm) and implanted with coded radio transmitters as described above, and released at this location after recovery. A total of 12 out of the 49 tracking sessions were conducted from the time translocated individuals were tagged until summer 2017, including four that occurred during fall 2016.

Habitat Mapping

Maps depicting full pool and winter drawdown habitat availability were created for Lake Eugenia. The ArcMap Aerial Imagery base map layer was used to identify habitat features within the lake at full pool (Maxar (WV02) imagery captured on October 24, 2014; ArcMap 10.7.1 World_Imagery [MapServer] Low Resolution 15 m Imagery, 0.6 m resolution). Habitat features were visually identified by color and texture at a consistent scale of reference at each quadrat (1:3390; Fitzgerald et al., 2006). Aquatic habitat polygons were then traced manually as custom freeform shapefiles in ESRI ArcMap Desktop software by a single individual highly familiar with Lake Eugenia's morphology and habitat structure. The following littoral aquatic habitat features were delineated from aerial imagery: submerged aquatic vegetation (SAV), coarse woody habitat (CWH), and shoals. Areas without these features were assumed to contain predominantly exposed substrate, the main habitat type throughout the lake, and were assigned as such during accuracy calculations. To determine the difference in water depth and remaining lake surface area and habitat between full pool and drawdown lake conditions, lake depth isopleth polygons for the 1.5 m depth stratum were created using NOAA Raster Navigational Charts (NOAA RNC®) bathymetric maps, and were used as a proxy for winter drawdown water level. Note that as SAV presence was calculated based on early fall imagery, distribution was assumed to be at its maximum, with the difference between full pool and winter maps reflecting the change imposed by drawdown (i.e., water level) rather than seasonal die-back.

Seven variable-length (average: 434.6 ± 346.6 m) underwater video transects were conducted on November 10, 2019, and were used for field validation of habitat classifications. A GoPro HERO4 Session (1080p; GoPro Inc., California) waterproof video camera was deployed from the side of a boat to capture video footage of the lake bottom. All transects were limited to depths <4.5 m where the lake bottom was clearly visible from the side of a boat. GPS-linked routes were recorded during transect surveys using mobile GPS software (Gaia GPS, California, USA) that marked unique GPS points every ~2 m. GPS points were extracted from each transect route and still video frames were linked with GPS points by matching timestamps. Viable still frames (n = 285) were analyzed to identify predominant habitat type (SAV, CWH, shoal, exposed substrate) at GPS points according to estimated percent coverage. When coverage was <25%, habitats were classified as exposed substrate (adapted from Fitzgerald et al. 2006). Habitat data classified from video transects were used to calculate overall and producer's accuracy of the manually classified full pool habitat map. Overall accuracy was calculated as the number of correctly manually classified points divided by the total number of field validation points analyzed and producer's accuracy, a habitat-specific measure, was calculated by dividing the number of correctly manually classified points within each habitat classification by the total number of field validation points analyzed for that habitat class (Stehman 1997).

Statistical Analysis

Initial post-tagging movement of radio-tagged fish was measured based on the Euclidean distance between the GPS locations (in m) of their pre-tagging location of capture and their first post-tag relocation. Population lake-wide distribution or spatial clustering ($Pop_{cluster}$) was calculated as the distance between the average location used by the population in the season for each year and the location of each individual, with smaller distances indicating concentrated grouping and larger distances indicating more dispersed grouping (n = 42 and 17 spring 2016 and 2017, 60, 69 and 14 summer 2015, 2016 and 2017, 22 and 87 fall 2015 and 2016 and 16 and 23 winter 2016 and 2017, respectively). Individual-level clustering ($Ind_{cluster}$) was calculated as the distance between the average location used by an individual in the season for each year and each relocation of that individual. At least two data points were required per season and year for this calculation (n = 10 and 0 fish in spring 2016 and 2017, 19, 16 and 2 fish in summer 2015, 2016 and 2017, 5 and 21 fish in fall 2015 and 2016 and 3 and 6 fish in winter 2016 and 2017, respectively; 267 data points total). As one-way analysis of variance assumptions of normality and homogeneity of variance were often violated even after data transformation, Kruskal-Wallis rank sum tests were used to determine differences between seasons in $Pop_{cluster}$ and $Ind_{cluster}$, followed by pairwise Wilcoxon rank sum comparisons if significant. Secondarily, potential differences in clustering between years for each season were explored using a series of Kruskal-Wallis tests for each metric. Inter-annual seasonal site fidelity was also calculated at both the population- ($Pop_{fidelity}$) and individual-level ($Ind_{fidelity}$) as the distance between the season-specific average location for the population or of each individual between years. Significant inter-seasonal differences for $Ind_{fidelity}$ were determined with a Kruskal-Wallis test and Wilcoxon pairwise comparisons. For $Ind_{fidelity}$, at least one data point in each of two years for a particular season were required (n = 12, 22, 14 and 9 fish in the spring, summer, fall and winter, respectively). Significant inter-seasonal differences for $Pop_{fidelity}$ were determined with a G-test for goodness-of-fit with the DescTools package (Andri et al., 2020) in R Version 3.6.3 (R Core Team, 2020). All localizations of each fish were included in the above analyses (i.e., initial capture, tracking and angler recapture data); translocated fish were not included.

As with the greater radio-tagged population, the initial movement of translocated individuals was based on the Euclidean distance between the GPS locations of their pre-tagging location of capture, their first post-translocation relocation, and the release point. Within-season fidelity was computed for each fish as the Euclidean distance between the overwintering area and the average GPS point of all post-translocation relocations within the fall of 2016. With the exception of the above G-test, all reported analyses of radiotelemetry and translocation movement, spatial clustering and fidelity data were performed with base functions within R Version 3.2.1 (R Core Team, 2015). All results were considered significant at $\alpha<0.05$.

In order to investigate seasonal preferences in fish habitat, each quadrat was first characterized by the average depth and percent area represented by CWH, SAV, and shoals (habitat delineation adapted from Fitzgerald et al. 2006) during both full pool and drawdown conditions. As structural habitat features could overlap within a quadrat, values could add to greater than 100%. Each tracked or angler reported fish location was then assigned a value for each of the habitat features and depth based on the selected quadrat and season. Seasonal habitat utilization was calculated by averaging the assigned quadrat-specific habitat values for each fish, per season. Seasonal depth utilization was calculated by computing the proportion of locations per season located within each 1 m depth stratum using average quadrat depth as a proxy for fish location depth. As few quadrats measured greater than 5 m in depth, depths 5 m and above were binned into a single category group. Seasonal habitat and depth utilization were then compared to full pool (for spring, summer, fall) and drawdown (for winter) lake-wide habitat and depth availabilities. Preference curves were computed by dividing utilization by availability for each season or depth bin and standardizing these values by the highest computed preference, such that the highest seasonal habitat and depth preference value was equal to 1 (Bunt et al., 2013).

Results

Radiotelemetry and Translocation

Radio-tagged largemouth bass measured between 364 and 502 mm (average ± SD: 407 ± 34 mm) and weighed between 771 and 2268 g (average ± SD: 1102 ± 365 g). Translocated fish measured 427 ± 43 mm and weighed 1210 ± 346 g. Fish were relocated a total of 323 times throughout the duration of the study with an average of 12 relocations per individual, plus an additional 20 relocations of translocated fish, with an average of 7 relocations per individual. A total of 12 angler recaptures were reported throughout the study period with 11 that included the quadrat of capture (Table 1).

Nineteen of the 27 radio-tagged fish were first relocated within a month of when they were tagged and released. These fish were tracked an average of 543 m (range: 0 - 2596 m) from their pre-tag location with sixteen individuals initially relocated within 500 m. The remaining eight fish were first relocated in a different season and/or year. Different regions of Lake Eugenia were used across seasons (Fig. 1), with members of the population significantly more spatially distributed across the lake in the spring and summer and spatially aggregated in the winter (Fig. 2a; $Pop_{cluster}$: $H_{(3)} = 118.540$, $P < 0.001$). Despite aggregation and decreased large-scale movements in the winter, largemouth bass were observed 2.4 km away from the overwintering area on one occasion on December 10 2015 and were tracked patrolling the overwintering area during the day in schools under the ice on January 21 2018 (see Supplemental Material Video SA and SB). The degree of seasonal clustering differed significantly between years for both spring ($H_{(1)} = 5.267$, $P = 0.022$; average distances 1145 m and 1450 m) and fall ($H_{(1)} = 34.777$, $P < 0.001$; average distances 1354 m and 628 m), and only slightly for both summer ($H_{(2)} = 6.376$, $P = 0.041$; average distances 1222 m, 1099 m and 1025 m) and winter ($H_{(1)} = 4.002$, $P = 0.045$; average distances 289 m and 242 m). Seventy-four percent of all tracked fish were detected in the main ~11 ha (calculated as a 375 m circle) overwintering bay at least once.

The degree of inter-annual fidelity also varied seasonally at the population-level ($Pop_{fidelity}$: $G_{(3)} = 707.510$, $P < 0.001$). The average location used by the tagged population was most similar during the winter with location centres differing by only 143 m between years, followed by summer where location centres differed by an average of 384 m between years (range: 54 - 571 m). Inter-annual differences between average seasonal locations were highest for the spring and fall, with 666 m and 917 m between average locations used between years, respectively.

While the population as a whole was distributed across different regions of Lake Eugenia in the spring and summer, this was not the case for individual fish (e.g., fish 17 in Fig. 1). Instead, as expected, individuals utilized particular localized areas of the lake in both the summer and winter significantly more so than in the fall and spring (Fig. 2b; $Ind_{cluster}$: $H_{(3)} = 21.590$, $P < 0.001$), with the greater population-level spread in the summer due to specific individuals selecting different areas rather than any one fish moving widely around the lake. Here, the degree of seasonal clustering was not significantly different between years for any season, with the average individual clustering distance 548 m and 487 m in fall 2015 and 2016, respectively ($H_{(1)}=0.734$, $P = 0.391$), 252 m, 253 m and 109 m in summer 2015, 2016 and 2017, respectively ($H_{(2)} = 0.914$, $P = 0.633$) and 141 m and 120 m in winter 2016 and 2017, respectively ($H_{(1)} = 0.437$, $P = 0.509$). No individual clustering could be computed for spring 2017.

As at the population-level, inter-annual individual-level fidelity was highest for both winter and summer and least in the fall, and significantly different between the seasons (Fig. 2c; $Ind_{fidelity}$: $H_{(3)} = 8.076$, $P = 0.044$). While 21% of fish returned to within 200 m (size of one quadrat) and 29% within 400 m (two quadrats) of their previous year's average location in the fall, 33% and 58% returned to within these distances between years in the spring, 23% and 59% in the summer and 44% and 89% (8/9 fish) returned to within these distances in the winter, with the remaining fish returning to areas that were only 418 m apart between years. Of note, and as can be visualized in Figure 1 for fish 17, fish often used areas of Lake Eugenia in the spring and summer that were completely dry each winter after the reservoir drawdown. Fourty-three of the 59 total spring detections (73%) and 86 of the 143 total summer detections (60%) occurred within such

Table 1 Vital statistics and number of total relocations of each fish during each season and year. Su is summer, F fall, W winter and Sp spring and T are translocated fish, TL is total length. The total number of relocations is shown with the number from angler recaptures indicated by the number of asterisks. All other relocations are from mobile tracking.

			Relocations								
			2015		2016				2017		
Tag	TL (mm)	Mass (g)	Su	F	W	Sp	Su	F	W	Sp	Su
1	371	862	3			1	1	4	1	1	
2	387	907	2			3	1*	1			
3	400	1089	2	1	1	2	1	4	1		
4	406	1089	2	1		1	3*	4		1	2
5	384	907	1	1	2		3	2	1	1	
6	458	2132	2	1		1	2	4	1	1	1
7	364	771	2		1	1	4**	1	1		
8	388	907	1	1		2		5			
9	431	1315	2	1	1	1	3	4	2	1	1
10	372	771	1		1	1		2	2	1	
11	380	862	1	2*			5	5		1	1
12	395	998	2	1		2	4	3	3	1	1
13	427	1043	1			1					
14	368	771	2	2*	1	1					
15	502	2268	1				6	4	1	1	1
16	441	1179	2		1	1	5	6	2	1	1
17	444	1179	3	2	2	5	6*	7	1	1	2
18	394	862	3	3*	1		4	5		1	1
19	448	1225	1		1	1		4		1	
20	386	998			1	4	4	4	2		
21	422	1134		1		3	1	3	1		
22	409	1179		1		1	2	3	1	1	
23	375	862				2	1*				
24	376	907					2	2		1	
25	391	862		2	1	5	7*				1
26	425	1179		1		2	3	5		1	1
27	442	1497			2	1	1	5	3	1	1
		Total	34	21	16	42	69	87	23	17	14
1T	417	1134						2	2	1	
2T	474	1588						6	1	1	1*
3T	390	907						3	1	1	1

quadrats, with only 7 fish in the spring (12 localizations) and 8 fish in the summer (34 localizations) using locations that were submerged across all seasons.

Fidelity to overwintering locations was also demonstrated by the movements of translocated fish. Fish 1T and 2T were first relocated 4 days post-release 1.78 km and 2.60 km from the release point and only 650 m and 210 m from their capture location, respectively. Fish 3T was first relocated 12 days post-release 1.79 km from the release point and 650 m from the capture location. Fish showed a high degree of within-season site fidelity, with the average location used throughout the rest of fall 2016 differing by an average of only 374 m (range: 230 - 500 m) from their initial point of capture.

Habitat Characteristics and Preference

Aerial imagery-based habitat mapping agreed with analyzed video transect points (n = 285) with 66% overall accuracy, based on predominant habitat types (SAV, CWH, exposed substrate and shoal). Producer's accuracy values for exposed substrate, SAV, and shoals were 81% (n = 185), 50% (n = 74), and 100% (n = 5), respectively. CWH in the north-eastern basin was poorly characterized by aerial imagery delineation (0/21 CWH-dominated transect points were classified by aerial imagery). Dense macrophyte beds shadowed CWH in this

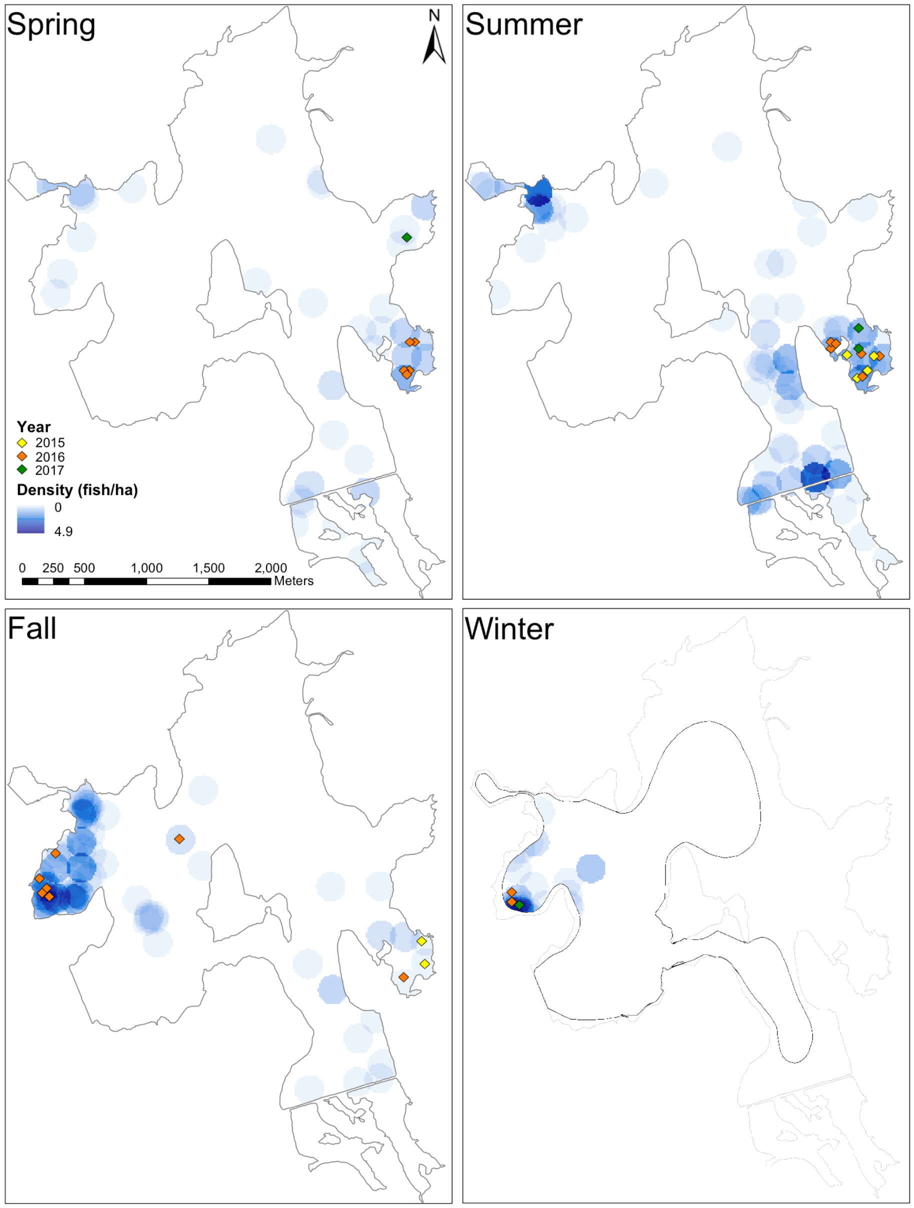

Fig. 1 Spatial distribution and density of the tagged population of largemouth bass across seasons among all years in Lake Eugenia based on telemetric locations. Inter-annual seasonal positions for a single largemouth bass, fish 17, are included (filled diamonds) to illustrate individual movement patterns. Within the winter panel, the dark outline indicates lake surface area with the lighter outline illustrating the lake footprint.

bay and rendered it less visible in available aerial imagery. However, habitat delineations outside of this basin agreed well with video transect data (82% overall accuracy with the north-eastern basin excluded, n = 147).

Aquatic habitat in the lake varied widely. The shallower regions of the lake (eastern and southern basins) were largely dominated by contiguous beds of SAV (*Potamogeton richardsonii* (Bennet) Rydberg and *Vallisneria* spp., with *Ceratophyllum demersum* Linnaeus prevalent in the shallower southern bays), complex CWH, and large shoals (Fig. 3). The deeper western basins were more bathymetrically

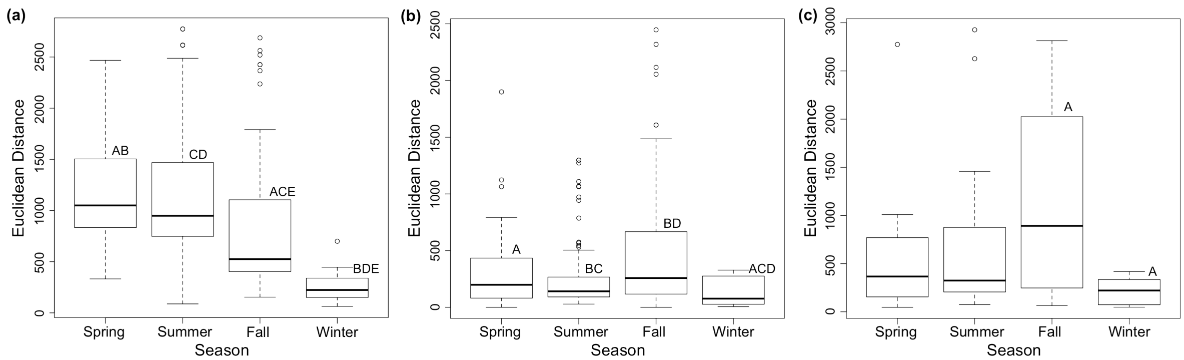

Fig. 2 (a) Population-level spatial clustering ($Pop_{cluster}$), (b) individual-level spatial clustering ($Ind_{cluster}$) and (c) individual-level site fidelity ($Ind_{fidelity}$) by season based on Euclidean distances of GPS locations and/or inter-annual distributional epicenters. Matching letters denote a significant difference at $\alpha<0.05$ based on Wilcoxon pairwise comparisons.

complex, but contained only sparse discontinuous SAV beds, occasional shoals, and intermittent CWH. While mapped SAV indicated locations of dense vegetation beds, during the summer sparse submerged vegetation was also prevalent throughout the lake. CWH in the form of extensive stump fields and fallen timber characterized the southern and eastern extents of the lake (Fig. 3a). Water levels fluctuated between 434 and 432 m ASL during the study period (OPG, unpublished data). Mean winter water levels were 1.7 m lower than mean summer water levels, with minimum water levels in February across 2016 and 2017 (Fig. 3c; average: 432.1 ± 0.2 m). The deepest area in the lake was near the dam (approx. 12 m); however, deep cut channels that traced the thalweg of the original riverbed, as well as the outflow to the power generation station, provided most of the deep-water habitat. At full pool in the summer Lake Eugenia measured 6.32 km^2, and after drawdown only 2.93 km^2 remained submerged (Fig. 3b). This represented a 54% loss in area which lead to a reduction in the amount of mapped CWH available in the winter by nearly 100%, mapped shoal habitat by 66%, and the area mapped during maximum SAV by 57%. The bathymetric gradients in the western bays were reduced during winter, leading to the emergence of relatively large flats with intermittent SAV.

Shoals and SAV were utilized and preferred most during summer months. Utilization and preference for shoal habitat remained low in spring, fall, and winter, while SAV was the most utilized habitat type across seasons, relative to availability. Winter habitat preferences indicated SAV as a potentially important structural habitat type (Fig. 4a-c). Utilization of CWH decreased as seasons progressed from spring to winter, concomitant with seasonal decreases in availability related to drawdown. Largemouth bass occupied a wide range of available depths throughout all seasons with peaks at 0-1 m (spring) and 2-3 m (spring, summer, fall, winter). In winter, the preference for areas with depths between 2-3 m was higher than for any other depth range, and in any other season (Fig 4. d-g).

Discussion

This study represents not only the first investigation into long-term inter-annual year-round seasonal site fidelity in a regulated reservoir, but also provides the first evidence of seasonal homing in a north-temperate largemouth bass population. Individual fish displayed both strong fidelity to spring and summer habitat, the majority of which was dewatered each winter, as well as strong homing to a specific overwintering location. The importance of overwintering habitat for largemouth bass in the regulated reservoir was also demonstrated by high degrees of population aggregation and was underscored by the movement of translocated fish. Coupled with the seasonal habitat preferences and availability limitations identified here, our results suggest that policies and protocols related to drawdown should address local reservoir ecology and may require adaptive

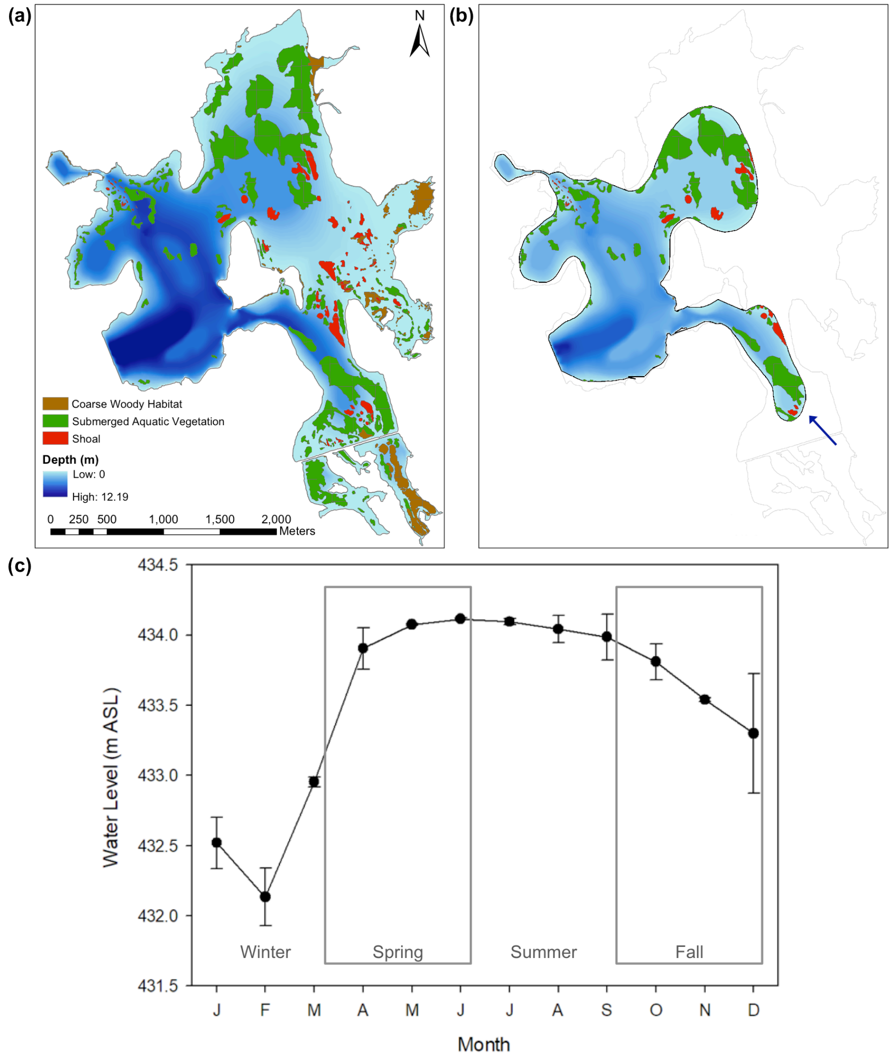

Fig. 3 Detailed habitat and bathymetric maps and seasonal water level data showing (a) full pool, (b) drawdown (winter) aquatic habitat characteristics and (c) average monthly water levels in Lake Eugenia. The blue arrow in (b) indicates the location of continuous inflow from the upper Beaver River and the dark outline indicates lake surface area with the lighter outline illustrating the lake footprint. Data in (c) are the mean ± SD monthly water levels over the duration of the study period, August 2015 - September 2017 with seasonal relocation time periods denoted.

implementation to reach desired fisheries production objectives in addition to providing services such as flood control.

Fall and Overwinter Site Selection, Fidelity, and the Potential Impacts of Drawdown

Unlike in other seasons, largemouth bass did not exhibit site fidelity to, or spatial clustering in, any specific locations in the fall at either the population- or individual-levels. Instead, detections revealed lake-wide travel during this season as fish returned from their individual specific summer home ranges to the population-wide, common overwintering area. Different degrees of population clustering, as well as the lesser population fidelity, found between years for this season were likely due to differences in tracking dates between years, with tracking conducted twice in September, four times in October and once in November in fall 2015; however, three times in October, five times in November and once in December in fall 2016. Fish were more clustered in 2016 as they were likely tracked when they were already closer to the

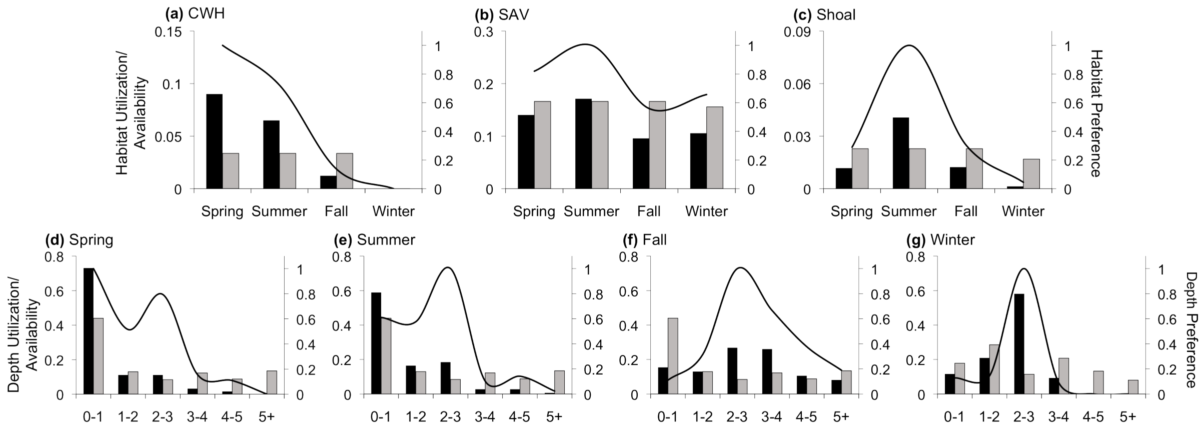

Fig. 4 Structural habitat utilization (black bars), availability (grey bars) and preference curves across seasons (a-c) and depth utilization (black bars), availability (grey bars) and preference curves across seasons (d-g) for largemouth bass in Lake Eugenia.

common overwintering location (see Limitations below regarding tracking frequency). The fact that fish migrated between summer and winter locations in autumn is consistent with previous telemetry work in both regulated (e.g., Karchesky & Bennett, 2004) and unregulated (e.g., Hanson et al., 2007) systems. During migration, fish utilized the deepest habitats compared to any season and had the least preference for any type of littoral structure. While it is therefore unlikely that bass used unique littoral features to navigate, as suggested by Rogers & Bergersen (1995), all three translocated fish quickly moved back to the overwintering bay likely through an entrained process triggered in response to a fixed suite of environmental cues such as flow, temperature, and dissolved oxygen which are important factors for bass overwintering (Karchesky & Bennett, 2004; Hasler et al., 2009; Suski & Ridgway, 2009).

The habitat most strongly preferred by largemouth bass, the 2-3 m depth stratum, was strongly affected by winter drawdown. Drawdown decreased the total area of Lake Eugenia by 54% and the total area of available habitat in this preferred depth range specifically by nearly 30%. As expected, the greatest degree of population- and individual-level spatial clustering and site fidelity was found during the winter, with fish likely concentrated in the limited areas with available winter habitat, especially during maximum drawdown in February. Note however that winter aggregations, like with autumn migration, have been reported for largemouth bass in both regulated (e.g., Rogers, 1998; Karchesky & Bennett, 2004) as well as unregulated (e.g., Carlson 1992; Hanson et al., 2007) systems. The severity of the drawdown and habitat limitation within Lake Eugenia, however, may have concentrated fish to an even greater extent than they would have otherwise. Within Karchesky & Bennett (2004), for example, drawdown reduced the surface area of the system by only 11% with 18 of the 19 tagged bass occupying two primary overwintering areas, while five overwintering areas were idenitified in the unregulated system in the study by Carlson (1992). While generalist piscivores like largemouth bass are expected to succeed in winter drawdown scenarios (Carmignani & Roy, 2017), the removal of preferred and potentially ideal habitat is likely to lead to density-dependent population regulation with far-reaching impacts on fish survival and annual recruitment, amplifying the strength of inter- and intra-specific interactions (Pitlo, 1992; Post et al., 1998; Raborn et al. 2004). Indeed, fall and winter aggregations of largemouth bass in northern lakes have been associated with intensified cannibalism by adult fish on young-of-the-year (Post et al., 1998) that may decrease recruitment and limit population stability.

Spring and Summer Site Fidelity following Selection for Predictable Habitat Features

The degree of population spatial clustering was low and individual site fidelity relatively high for fish with respect to both spring spawning site and summer home range selection. Seasons differed in the level of population fidelity and individual clustering, with both lower in the spring than that found in the summer. This result stemmed from the fact that the spring period in Lake Eugenia included not only the use of spawning sites but also the movement (migration) of fish from overwintering areas to such locations; also similar to previous telemetry findings from regulated (e.g., Karchesky & Bennett, 2004) and unregulated (e.g., Ridgway, 2002; Hanson et al., 2007) systems. Interestingly, lake refill appeared to play a primary role in triggering this movement as we noted the departure of bass from overwintering locations as soon as the lake refilled in early April, regardless of apparent insufficient warmth (<6^{o}C) prior to this point. In Lake Eugenia fish returned to and selected spawning sites, the majority of which were in areas previously dry and potentially disturbed for up to 4 months during the winter drawdown period. Both movement from overwintering sites and successful reproduction may therefore be controlled more strongly by lake water level when refill is delayed (Kallemeyn, 1987). Although never previously documented in northern populations of largemouth bass, the individual spring site fidelity found here may not have been altogether dissimilar from that found in an undisturbed, temperate smallmouth bass population studied by Ridgway et al. (1991) in which 81% of male fish were found within 200 m of the spawning site used the previous year. In contrast, fidelity within this study included information from an unknown ratio of males to females and spring data included the movement from overwintering locations. Note that as with the fall migration, the different degrees of population clustering, as well as lesser population fidelity, found between years for spring was likely at least partially due to differences in tracking between years. Tracking was conducted three times in April, twice in May and once in June in 2016 however only once in June in 2017. Fish were more clustered in 2016 as they were likely tracked while beginning to move from the common overwintering location in April and were already distributed throughout the lake near individual spawning areas in June.

Fish were located predominantly in shallow, littoral areas with complex structural habitat (SAV, CWH, shoals) during both spring as well as the peak period of growth for northern populations of largemouth bass in the summer (Brown & Murphy, 2004; Ostrand et al., 2005). However, deeper areas near weedlines and drop-offs were also selected more strongly relative to availability in the summer. As drawdown has been shown to prevent the establishment and decrease the cover of stemmed macrophytes (Sutela et al., 2013; Wilcox & Meeker, 1991) as well as decrease littoral macroinvertebrate prey abundance (Haxton & Findlay, 2008; Trottier et al., 2019), the availability of optimal spawning and summer home range habitats may be limited by drawdown degradation. Combined with the relatively high individual site fidelity across both spring and summer, this suggests that ideal habitat may be limited and of increased importance for bass in regulated reservoirs. Indeed the higher individual spatial clustering observed in the summer may be the product of territoriality and protection of limited optimal habitat (Ridgway et al., 1991), with fish again using familiar areas, the majority of which were previously dry during the winter. The return of largemouth bass to specific seasonal habitats was not impeded by littoral disturbance within this study and thus fish may have either committed home range features to memory or mechanistic navigation cues (e.g., olfaction, vision, electrolocation, audition, water movement; Braithwaite & De Perera, 2006) may be independently identified year after year.

Limitations and Other Implications for Management

While this work has shown that largemouth bass can now be added to the list of species known to facultatively navigate and home across large distances with exceptional inter-annual seasonal site fidelity, there were several limitations with this project. Firstly, there was not an effective control, or perhaps more ideally, a before-after drawdown design. Either would have allowed for a greater understanding of the degree to which our observed spatial clustering and fidelity were a function of largemouth bass ecology in general, or specific to populations residing within regulated reservoirs. Comparison would have allowed us to establish, for example, whether observed overwintering patterns were a function of relegation to limited habitat areas caused by drawdown, or if in fact, fish would have selected habitat and aggregated in the same way (i.e., location, degree) even if Lake Eugenia was not a regulated system. The second limitation of this study is with respect to our overall tracking frequency as well as between year seasonal tracking consistency. Without a doubt the frequency with which tracking was conducted meant that captured localizations provided only a snapshot of the total movement of fish throughout the lake. Nonetheless we feel that our data produced an accurate description of the distribution and that increased sampling frequency would not have changed the relative seasonal patterns of clustering or fidelity observed. Indeed a greater number of tracking sessions in the winter would not have revealed any less overwintering aggregation, nor would more tracking sessions in the spring or fall have found more clustering, but instead only further exposed the lake-wide migrations between summer and winter areas. The greatest number of tracking sessions took place in summer 2016 and the degree of population- and individual-level clustering was no less strong than in other studied summers. While greater sampling date consistency may have reduced some of the noted between-year variation within our dataset, the relative seasonal patterns would again not have changed.

Continuing to improve and expand our understanding of how reservoir management and drawdown influences the homing capacities of various fish species will allow for the development of improved management strategies and may identify opportunities for limiting potential over-exploitation and promoting species coexistence (McMeans et al., 2020). Indeed here winter drawdown resulted in seasonal habitat limitation that constrained overwintering habitat availability and likely concentrated fish into aggregations that intensified interactions (e.g., competition for space and food, predation) and made fish dramatically more susceptible to harvest. Winter aggregations formed more than a month before the provincially mandated closure of the recreational sport fishery at Lake Eugenia in each year of this study. The understanding of seasonal homing and distribution of largemouth bass gained here could be used to predict the effects of changes in critical habitats and refine harvest regulations and season closure dates to prevent potential over-exploitation at identified aggregation sites.

While the benefits afforded by lake and reservoir drawdown for downstream flood control are well established and will be inarguably more important as extreme weather events become more common, policies and protocols related to drawdown are generally applied without assessing the benefit or need for flood control with respect to specific systems and have been largely unchanged or re-evaluated for over a century. Operational guidelines are currently derived from regional water management plans that may be developed into more adaptive strategies that address policy objectives and site-specific flow regulation requirements. Effective fisheries management plans should incorporate knowledge acquired from temporally and spatially resolved fish movement data that factor in variables such as lake bathymetry and available critical habitat, both of which are essential for maintaining the stability of fish populations in temperate regulated reservoirs.

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Author contributions CB, BJ and TF conceived the ideas, CB designed methodology; CB and TF collected the field data; BJ and TF organized and analysed the data; TF and LR created and analyzed the habitat and depth maps; CB, BJ and TF interpreted results and wrote the manuscript; LR and BM contributed to the manuscript

Data availability Data will be made available upon reasonable request.

Conflict of interest The authors have no conflict of interest.

Ethical approval Collection and tagging of Largemouth Bass was performed under a licence to collect fish for scientific purposes issued by the Ontario Ministry of Natural Resources and Forestry (Licence No. 1080776).

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Supplementary Material

Video SA: Multi-species underwater video including largemouth bass patrolling 2.4 km away from the overwintering area on December 10 2015

Available online at: www.biotactic.com/LG1.mp4

Video SB: A school of largemouth bass swims slowly toward the camera in a v-formation under the ice at the primary overwintering area identified in Lake Eugenia on January 21 2018

Available online at: www.biotactic.com/LG2.mp4