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RESEARCH ARTICLE

Space use and residency patterns of largemouth bass relative to a freshwater protected area

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Abstract
Fish movement patterns are an essential consideration for the design of effective freshwater protected areas. The Rideau waterway system (Ontario, Canada) is home to some of the oldest single-resource freshwater protected areas (FPAs) in Ontario (> 70 years active). Initially, these FPAs were intended to provide holistic protection to the heavily exploited largemouth bass, but since their establishment, little is known regarding their protective capacity. Using a passive acoustic telemetry network, we measured how site fidelity varied with body size and across seasons in largemouth bass within one Rideau waterway FPA. Collectively, 50 bass were tracked for an average of 227 days, with some individuals tracked upwards of 744 days. Tagged fish spent on average 55% of their time at liberty within the FPA, with occupancy rates exceeding 85% for some individuals. Most of the tagged fish displayed cyclical movement behaviour between the FPA and non-protected areas, largely corresponding with known life-history stages. Largemouth bass occupancy was highest in the spring–summer seasons (i.e. reproductive period), with a sharp decline during the autumn that sustained through the winter. FPA occupancy varied with body size, with large fish (> 430 mm) using the FPA more extensively. Our findings show that this Rideau waterway FPA provides temporal protection from exploitation to a highly targeted sportfish, especially during their reproductive period, likely providing major conservation benefits. These findings also highlight the value of considering the habitat requirements of a species across life stages to inform effective FPA design.

Keywords Telemetry · Movement · Occupancy · Resource-management · Conservation

Introduction

Declines in freshwater biodiversity highlight the need for more effective conservation strategies to safeguard exploited species from over harvest as well as other adverse human-use impacts (Reid et al. 2019; Tickner et al. 2020). Management actions in the form of freshwater protected areas (FPAs), which restrict/prohibit human-use activities within a designated area, have been garnering attention as a potential strategy to benefit freshwater biodiversity (Ashley et al. 2003; Abell et al. 2007; Cooke et al. 2023). Similar to marine protected areas (MPAs), the objectives of FPAs are often to protect biodiversity within entire ecosystems; however, resource-based FPAs that target a single species for protection are common (Saunders et al. 2002; Zolderdo et al. 2019). Specifically, the establishment of FPAs to protect economically valuable species (e.g. largemouth bass, *Micropterus salmoides* [Lacépède, 1802]) are amongst the most common in North America. However, the effectiveness and utility of FPAs are still largely debated (Abell et al. 2007; Hedges et al. 2010). Unlike protected areas in the marine environment, FPAs are often small in size, seasonal and/or obscurely placed within lakes and rivers (Hermoso et al. 2016) and have, in some cases, been installed without consideration of the movement behaviours of the target fish species to be protected. These factors have resulted in

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mixed-resource management outcomes and, as a consequence, have created a paucity in the use of FPAs in resource regulation (Abell et al. 2007; Acreman et al. 2020).

Understanding the movement behaviours of fishes is highly valuable for effective FPA design and management (e.g. FPA size, location, habitat coverage relative to individual movement patterns as in Schlosser 1991). For example, understanding the movement dynamics of a species can help evaluate whether an FPA is sufficiently large to encompass the majority of an animal's home range, how the level of protection varies across seasons and in relation to life-history strategies of both target and non-target species, and whether reproduction occurs within the protected area boundaries. A useful and powerful technique to evaluate movement dynamics of fishes in, and around, protected areas can be achieved through the use of passive acoustic telemetry. Passive acoustic telemetry utilizes a network of submerged autonomous receivers that record the presence of animals fitted with an acoustic transmitter (Donaldson et al. 2014). This fisheries-independent tracking technique functions continuously (i.e. 24 h/day), providing fine-scale movement data that is generally unobtainable through traditional mark–recapture techniques and/or active tracking (Reyier et al. 2020). Telemetry techniques have been commonly used to investigate migration patterns and site fidelity of fishes within, and adjacent to, MPAs, which has provided vital information for guiding the development of certain MPAs to maximize conservation benefits (Knip et al. 2012; Lea et al. 2016; Reyier et al. 2020). At present, similar information for FPAs is lacking (Loury et al. 2018).

Within Ontario there are over 600 designated FPAs, although only a few of these provide year-round protection (2020 Ontario Recreational Fishing Regulations). Some of these FPAs are created for holistic biodiversity protection purposes, but the majority are based on single-resource protection (i.e. designed for one species). The Rideau waterway system (Ontario, Canada) is home to some of the oldest FPAs in Ontario. Established more than 70 years ago (circa 1940s), these year-round intra-lake FPAs were intended as a means to protect the viability of the largemouth bass fishery that was suffering from heavy exploitation through excessive recreational harvest (Ontario Department of Game and Fisheries Monthly Bulletin 1939). Remarkably, these FPAs were created prior to contemporary understanding of source-sink dynamics. In addition to the use of FPAs as a management strategy, the largemouth bass fishery in the Rideau Waterway system is managed through conventional harvest quotas and seasonal closure periods (i.e. the largemouth bass fishery is closed from 15 December until the third Saturday in June within Rideau waterway system). Recent research has shown that these FPAs have positively benefitted largemouth bass through supporting larger population densities within the protected area boundaries (Zolderdo et al. 2019). Furthermore, largemouth bass inside the FPAs are believed to exhibit basal phenotypes that have not been influenced by fisheries-induced selection pressure, such as high-performance metabolic phenotypes, increased reproductive effort and reduced stress responsiveness (Cooke et al. 2017; Twardek et al. 2017; Zolderdo et al. 2023). Collectively, these results indicate some degree of protective capacity enabling FPA populations to maintain a more natural state relative to unprotected individuals outside of the FPA that have been influenced by humans through harvest and exploitation (Hessenauer et al. 2015; Louison et al. 2017). Thus, intra-lake FPAs may provide a refuge to protect against fisheries-induced selection. However, the level of protective capacity across seasons and life-history stages has not been quantified.

Using passive acoustic telemetry, we quantified the seasonal and annual movement dynamics of adult and subadult largemouth bass within, and adjacent to, the Big Rideau Lake (BRL) FPA for the first time since its establishment in the 1940s. Specifically, the objectives of this study were to assess how site fidelity within the FPA varied in relation to body size, as well as to evaluate the protective capacity of the FPA through quantifying how often, and when, fish tagged within the FPA stayed within its boundaries. Resolving largemouth bass movement dynamics across seasons and life stages will help to assist in the design and management needs of future FPAs intended to protect this heavily targeted sportfish.

Methods

Study area

All fish tagging was conducted within the Ministry of Natural Resources and Forestry (MNRF) designated FPA on Big Rideau Lake (44.728977° N, 76.177343° W). The FPA serves as a strict fisheries exclusion zone and is regularly patrolled and respected by anglers. Relative to Big Rideau Lake, which has a surface area of 45.36 km^2, the FPA covers a surface area of 0.57 km^2 (1.26% of the total surface area). The FPA is relatively shallow, with depths ranging from 0.5 to 2.5 m. The FPA has known spawning and nursery habitat for largemouth bass and a single, narrow entrance/exit canal approximately 40 m at its narrowest constriction point through which all fish must pass if they enter or exit the FPA (Figs. 1, 2). There is little to no boat traffic that occurs within the FPA boundaries due to it being a fisheries exclusion zone, coupled with the shallow habitat conditions that are not conducive to recreational boating. Furthermore, there is limited shoreline development with only two seasonal residences constructed within the protected area boundaries.

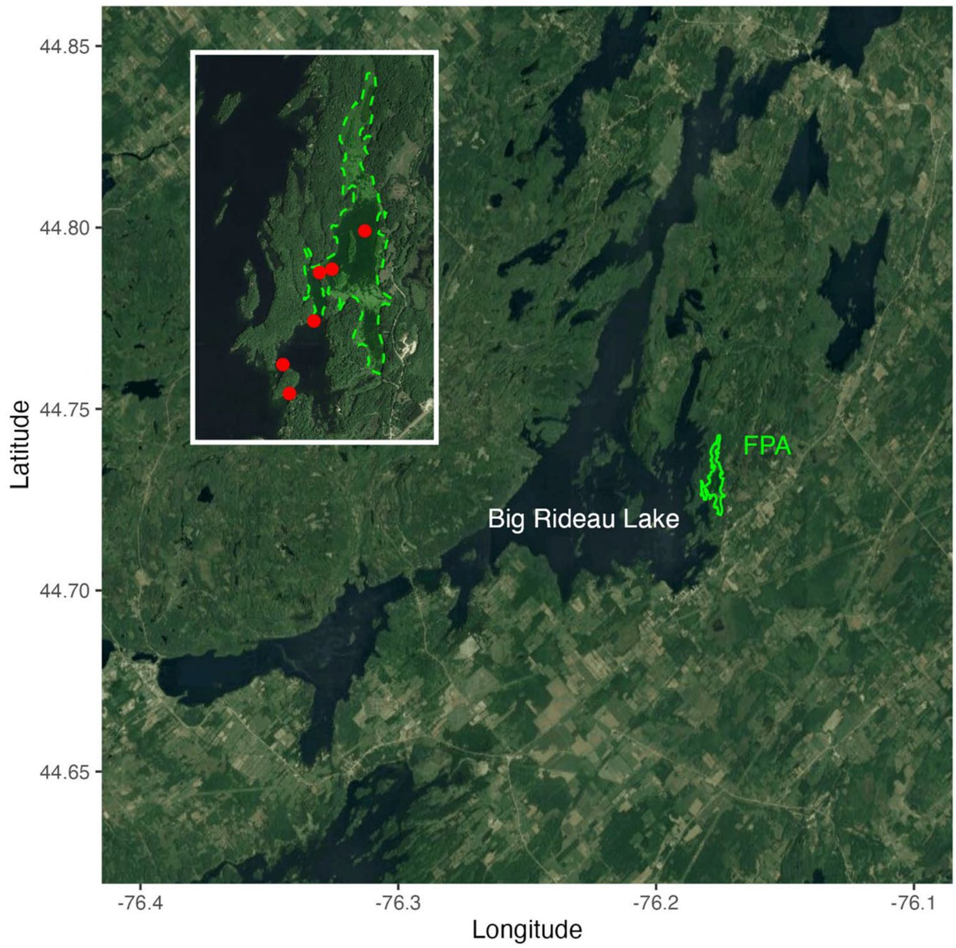

Fig. 1 Map of Big Rideau Lake with the freshwater protected area (FPA) outlined with a solid-green line. A close up view of the FPA is shown inside the white box, with the FPA boundaries outlined with a green-dashed line. The telemetry receiver locations are represented by the red dots both inside and outside of the FPA (Color figure online)

Fish tagging

Fifty largemouth bass, comprising both adults and subadults (size range from 130 to 475 mm in total length), were collected from inside of the FPA boundaries, and implanted with one of three sizes of acoustic transmitters (Lotek Wireless Inc., ON, Canada; Table 1). All fish were captured within the Big Rideau Lake FPA during the summer of 2015 (June–September) using rod-and-reel angling ($n=33$) or electrofishing ($n=17$). Upon capture, fish were subjected to an initial assessment including the length measurement and an inspection of any external indications of injury or disease. If fish looked unhealthy and/or showed signs of injury, they were immediately released. Following initial assessments, fish were placed onto a foam-lined surgery table aboard the research vessel. The surgery tables were equipped with an independent water pump and water reservoir, which enabled a continuous flow of fresh oxygenated water to be passed over the gills during the surgical procedure, minimizing air-exposure and 'out-of-water' handling time. Fish were held in place on the surgery table using a pair of DC-electrified fish handling gloves with a standard voltage output of ~32 V and five current settings (4, 6.3, 10, 16 and 25 mA; Smith-Root Inc., Washington, USA; 2016). Current settings were established by beginning at the lowest setting and then incrementally increasing the current strength until tetany was observed and then returning to one setting lower, which induced a safe electro-anaesthesia (i.e. muscle relaxation, normal ventilation, loss of equilibrium and reduced reactivity; see Abrams et al. 2018 for more detail). Once fish were safely immobilized, a ~25 mm longitudinal incision was made on the ventral side of the fish between the pectoral fins and the cloaca. A sterilized (betadine) acoustic transmitter was inserted into the coelom through the incision, which was then closed using a 3-0 monofilament suture (PDS II polydioxanone suture; violet monofilament, 3-0). Surgical tools were sterilized in a diluted solution of betadine between each surgery. A new pair of nitrile gloves were used for each surgery. Surgery times ranged between 3 and 6 min, with the same surgeon conducting all surgeries. Following tag implantation, fish were allowed to recover in coolers filled with fresh lake water. After a brief recovery period (5–10 min), fish were released near their site of capture. All tag types emitted a coded signal frequency of

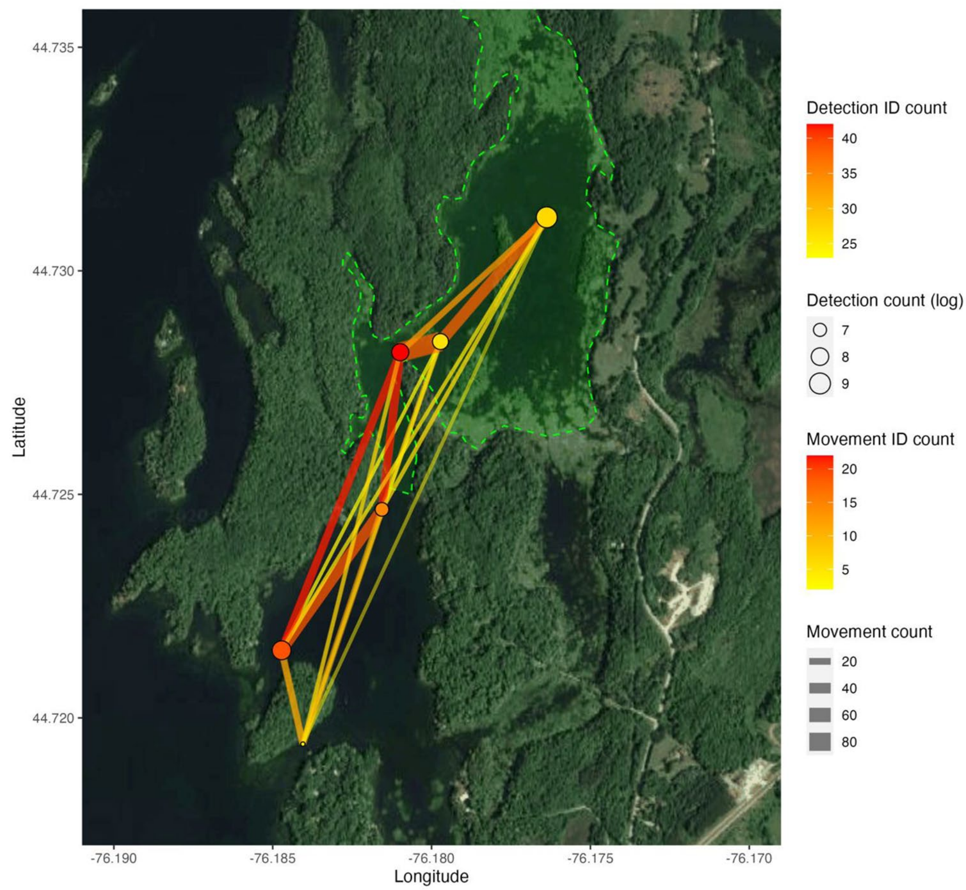

Fig. 2 Map depicting the aggregate detection and movement patterns of tagged largemouth within the study region on Big Rideau Lake. The freshwater protected area (FPA) is partly outlined by a green-dashed line. The acoustic receivers for tracking tagged largemouth bass are denoted as circles with movements between receivers connected by lines. The number of detections and movements are indicated by the size and colour of the circles and lines (Color figure online)

Table 1 Acoustic transmitter information implanted into 55 largemouth bass inhabiting the Big Rideau Lake protected area

Size range (mm), (sample size)	Transmitter weight (g)	Transmitter model	Expected life (*d*)
320–475 (25)	3.5	L-AMT 8.2	1522
240–449 (10)	1.1	L-AMT 5.2	568
130–449 (15)	0.28	L-AMT 1.416	131

Expected life of transmitters may vary by ± 5%, depending on environmental conditions

416.7 kHz, with a pulse repetition interval of 1 s minimum with 1 s increments, with a signal strength between 156 and 158 dB (re: uPA at 1 m). All experiments were conducted in accordance with the standards set by the Canadian Council of Animal Care (CCAC) under permit number BT-026 administered through the Carleton University Animal Care Committee.

Telemetry array setup and monitoring schedule

Six Lotek acoustic telemetry receivers (WHS 4250 4-Battery Delrin, Lotek Wireless Inc. ON, Canada) were set up in an array to detect residency and movement patterns of largemouth bass within the FPA area (inside and directly outside of the Big Rideau Lake FPA; see Figs. 1, 2). Three of the five receivers were aligned at or near the entrance to the FPA to provide directionality of movement (i.e. site was gated). Furthermore, two receivers were placed at the two narrow channels leading outward into the main lake basin, which were ~40 m and ~60 m wide at each constricting point (Fig. 2). Thus, if fish exited the FPA, we would be able to detect their movement(s) beyond the transition area, which separated the FPA from the main lake basin (see Zolderdo et al. 2019 for more detail). One receiver was placed deep within the FPA in a back-bay area, previously identified as a key spawning in brood rearing habitat (Fig. 2). Each receiver was powered by four Delrin batteries (Lotek Wireless Inc. ON, Canada), and provided a run time of approximately 150 days. As such, receivers were regularly visited to replace spent batteries and download detection data.

Data analysis

All statistical analyses were conducted using R (R Core Team 2018) via RStudio (RStudio Team 2016). Prior to analyses, data were first screened to remove erroneous detections that did not correspond to transmitter identification codes deployed in the study. This initial screening process was conducted using the Lotek software program (WHS Host × 64 Build, v1.5.2870.1, Lotek Wireless Inc. 2012). Largemouth bass detections were then filtered to remove any false detections prior to analysis (Simpfendorfer et al. 2015) including those that occurred prior to tag deployment, repeated detections that occurred within less than the minimum tag transmission delay and single detections that occurred within a 1 h time period at a given receiver (i.e. minimum lag filter). Detections were then visually examined to assess whether any mortalities or tag shedding occurred, which results in repeated detections of an individual tag at an individual receiver over extended periods of time, without any subsequent detections at other receivers (Klinard and Matley 2020). No transmitters appeared to exhibit this pattern. However, prior to assessing and modelling fish movements in relation to the FPA, the dataset was further filtered to include the time period where there was sufficient receiver coverage in the region, and ≥ 8 individuals were present in the tracking system (Supplementary Material I; Table 1, Fig. 3). Further, individuals were only included in the dataset if they had tracking periods ≥ 30 days and ≥ 10 detections.

The filtered dataset was used to assign fish locations (i.e. inside, outside the FPA) using a modified version of the last-observation-carried-forward (LOCF) method (Shao and Zhong 2003). The LOCF method is often used to assess general animal locations using passive acoustic telemetry arrays, where individuals are assumed to

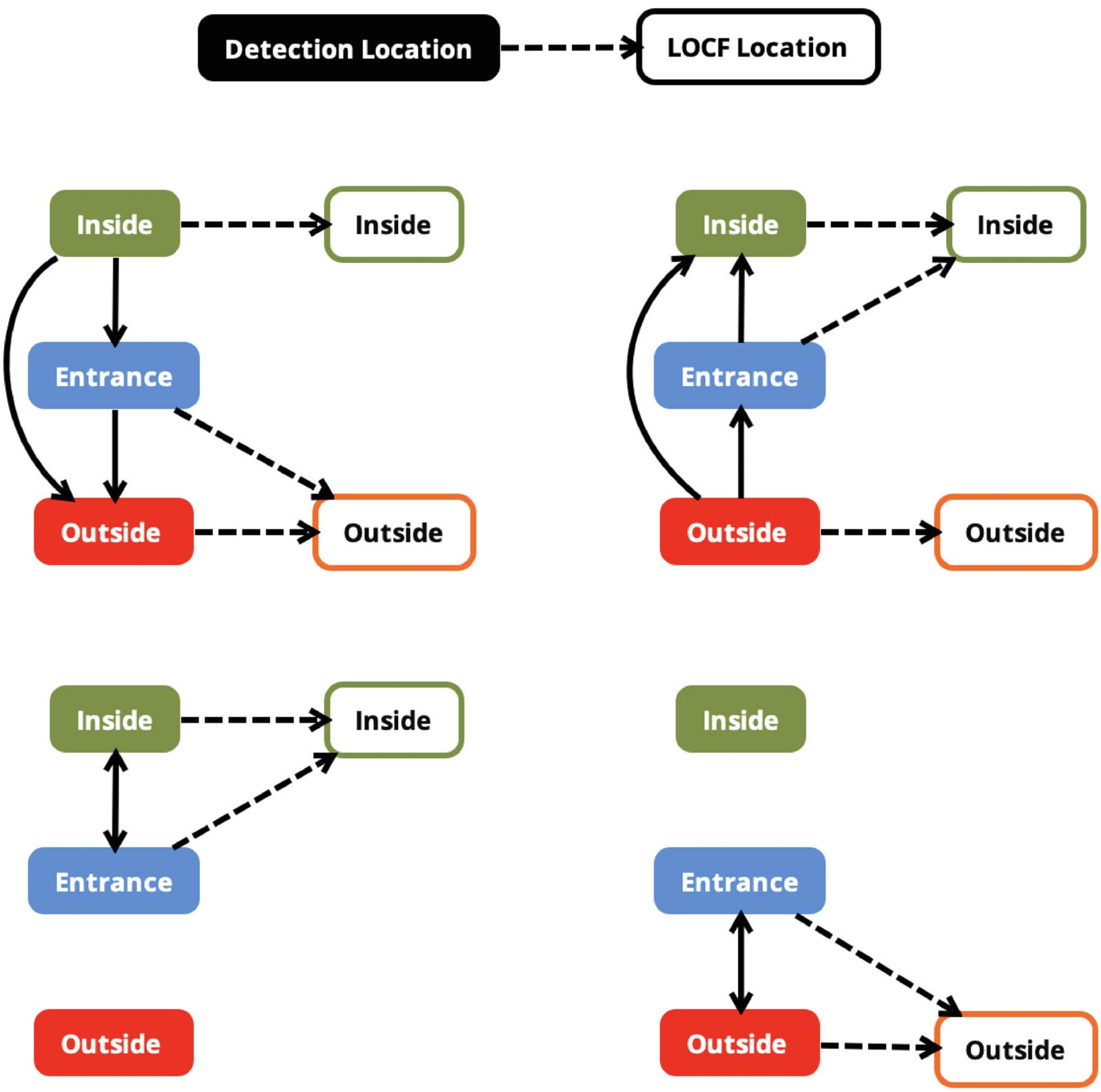

Fig. 3 Criteria used for a modified last-observation-carry-forward (LOCF) assignment of fish locations (inside/outside the freshwater protected area in Big Rideau Lake) based on detections at stationary acoustic receiver locations

be located in the discrete ecosystem segment where they were last detected until they are subsequently detected in another segment (e.g. Struthers et al. 2017; Kessel et al. 2014; Colborne et al. 2019). In this case, a modified set of decision rules were used (Fig. 3) because an acoustic receiver was located at the entrance of the FPA (Fig. 2). With this modified criterion, periods during and subsequent to detections at the entrance were considered either inside or outside the FPA depending on the location of the previous and subsequent detections. Using this criterion, positions for each fish were assigned (inside or outside the FPA) for every day from the tagging date to the date of the last detection for each tracked individual. In some cases, individual fish were assigned as both inside and outside the FPA on a given day due to intra-day movements.

To quantify the drivers of fish residency in relation to the FPA, daily fish positions assigned using LOCF were modelled using random forest (RF) algorithms (Breiman 2001). RF uses classification or regression trees to repeatedly create binary partitions in the data based on the predictors to optimize prediction of the response (Breiman et al. 1984; De'ath and Fabricius 2000). RF fits numerous trees using random subsets of data and predictors each time to minimize overfitting to training data and improve prediction accuracy (Breiman 2001; Cutler et al. 2007). The RF model was fit as a classification problem with daily fish location as a binary response (either inside or outside the FPA), and predictors included individual fish (FishID), fish total length (TLmm) and Julian day (dayJ). RF were fit with 1000 trees, and the dataset was split into ten folds, using a single fold at a time (repeated ten times) to train the model, and the remaining 90% of the data used to assess model fit. Model performance was assessed based on prediction accuracy and balance (relative balance of accuracy across response variable categories) in non-training data. Variable importance was assessed using mean decrease accuracy (MDA) and interaction importance using Friedman's *H*-statistic. Because the latter is scaled from 0 to 1, MDA was also transformed to the same scale by dividing MDA scores for each predictor by the total MDA score for all predictors in the model. Predictors and interactions were considered important when 95%. confidence intervals of MDA generated from tenfold cross validation did not overlap zero. Relationships between the predictors and the response, including predictor interactions, were assessed based on the marginal effects ($\hat{y}$; average relationship between the predictor and the response holding other predictors at their mean) using partial dependencies. Random forests were fit with the 'randomForest' package (Liaw and Wiener 2002), cross-validated model accuracy was assessed using the 'caret' package (Kuhn et al. 2019), predictor interaction importance was calculated with the 'iml' package (Molnar et al. 2018) and partial dependencies were calculated using the 'pdp' package (Greenwell 2017).

Results

After applying false detection filters, the final acoustic telemetry dataset consisted of 19,177 detections of 48 of 50 total tagged individual largemouth bass from 17 August 2016 to 27 September 2018 (Supplementary Material I; Table 1). Tracking durations were variable amongst individuals (227 ± 226 days; mean ± standard deviation; 1.3–744 day range). Of these individuals, 38 were detected for extended periods (≥ 30 days and ≥ 10 detections). All of these 38 individuals except for one were detected both inside and outside the FPA (Fig. 2), spending variable periods of time within the FPA (55 ± 32% of time; mean ± standard deviation; 1–100% range; Supplementary Material I; Table 1).

Most fish exhibited repeated movements in and out of the FPA (Fig. 2). Over time, the highest proportion of individuals were detected in the spring and summer seasons, with a sharp decline in occupancy (i.e. number of days inside the FPA boundaries) during the autumn that remained low through the winter (Fig. 4). After the tagging period in the summer and autumn seasons of 2016, the majority of individuals that were still being tracked in the system (see Supplementary Material; Fig. 3 for tracking numbers over time) returned to the FPA in the late winter and early spring of 2017 (Fig. 4). FPA residency remained high with some decline through the summer of 2017. This inter-annual occupancy pattern was repeated in 2016 and 2017. However, in the latter part of the study the number of fishes being tracked was steadily declining, likely biasing the proportion of individuals using the FPA upward.

Examining the drivers of largemouth bass space use in relation to the FPA, RF models were able to predict fish location (inside/outside the FPA) with 88% accuracy in non-training data, and 88% accuracy balance between the two response categories using individual fish, fish length and Julian day as predictors. All predictors were important and there were also important interactions between individual fish and Julian day, and fish length and Julian day (Fig. 5A). Marginal effects show clear patterns of occupancy amongst Julian day, with a rapid increase in FPA occupancy from days 60–100 (March–early April), sustained high occupancy through summer months and a decline in the autumn (Fig. 5B). The effect of fish length was more moderate, but with a clear pattern of increased occupancy for the largest individuals. Specifically, individuals > 430 mm total length had the longest continuous occupancy within the protected area boundary (Fig. 5C). There was also an important effect of individual and an interaction between individual and Julian day (Fig. 5D, F). Across fish sizes, the majority of fish tended to occupy

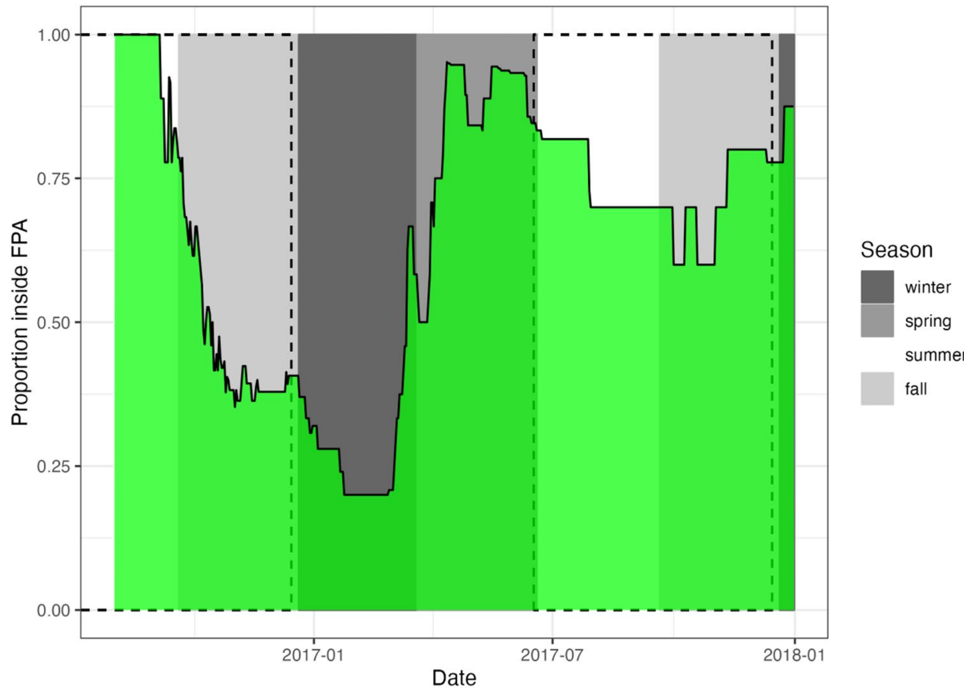

Fig. 4 Temporal patterns of occupancy of the Big Rideau Lake freshwater protected area by largemouth bass expressed as a proportion of tracked individuals (green area) from 3 August 2016 to 31 December 2017 when at least eight individuals were actively tracked in the system. Individuals were considered as being tracked in the period from the tagging date to the last detection. The dashed areas indicate open fishing seasons for largemouth bass in this system (Color figure online)

the FPA in the spring, summer and autumn months; however, the largest fish had a tendency to occupy the FPA for the most continual number of days in the spring months (Fig. 5E).

Discussion

Our findings show that largemouth bass captured in the FPA remained inside the protected area boundaries during a significant proportion of the open-access fishing season(s), suggesting that the spatial protection provided by the Big Rideau Lake (BRL) FPA is of value from a fisheries management perspective. However, all fish (with the exception of one individual) spent time both inside and outside of the FPA within a given year. Largemouth bass, like many potadromous species, are known to undergo seasonal movements at various temporal and spatial scales to access favourable habitat for feeding, reproduction and refuge (Fish and Savitz 1983; Waters and Noble 2004; Hanson et al. 2008). The BRL FPA is a shallow, heavily vegetated, littoral area, ideal for largemouth bass during the reproductive period as well as the growing season (Kramer and Smith 1962; Brown et al. 2009; Cooke pers obs). In spring, the early and accelerated macrophyte growth within shallow littoral habitats attracts various prey resources which, in turn, attracts largemouth bass due to increased foraging opportunities (Massicotte et al. 2015). Furthermore, shallow vegetated habitat provides ideal conditions to support offspring development and growth (Kramer and Smith 1962; Jennings 1997). In the BRL FPA, dense macrophyte growth continues into the summer and early autumn, creating highly complex habitat structure (Zolderdo et al. 2019), which is a key factor known to reduce home-range size in largemouth bass (Fish and Savitz 1983; Ahrenstorff et al. 2009). As water temperatures cool, largemouth bass transition to their overwintering habitat, which is offshore and deep water (< 10 m in depth) in structure (Hanson et al. 2008; Hasler et al. 2009). Previous research has shown that largemouth bass populations consolidate within select overwintering areas, and can travel significant distances (i.e. > 5 km) to occupy these locations (Carlson 1992; Raibley et al. 1997; Hasler et al. 2007). As the BRL FPA does not contain water depths greater then 2.5 m in depth, remaining inside the FPA overwinter may be impossible due to the potential of certain areas freezing solid, or experiencing otherwise adverse conditions due to low temperatures or dissolved oxygen concentrations. As such, it is not surprising that largemouth bass moved outward from the protected area boundary during the cold-water period. Together, the BRL FPA provides critical habitat for largemouth bass of all sizes to survive during the whole year, and also provides many months of protection from anglers by being a no-fishing zone.

Inter-annual variability in FPA occupancy between 2016 and 2017 may be linked to differences in environmental conditions between years. More specifically, record high-water levels occurred throughout the Rideau waterway system during the 2017 spring–summer season as a result of heavy snow melt coupled with extreme spring precipitation events (Zolderdo pers obs, 2017). The increased water level

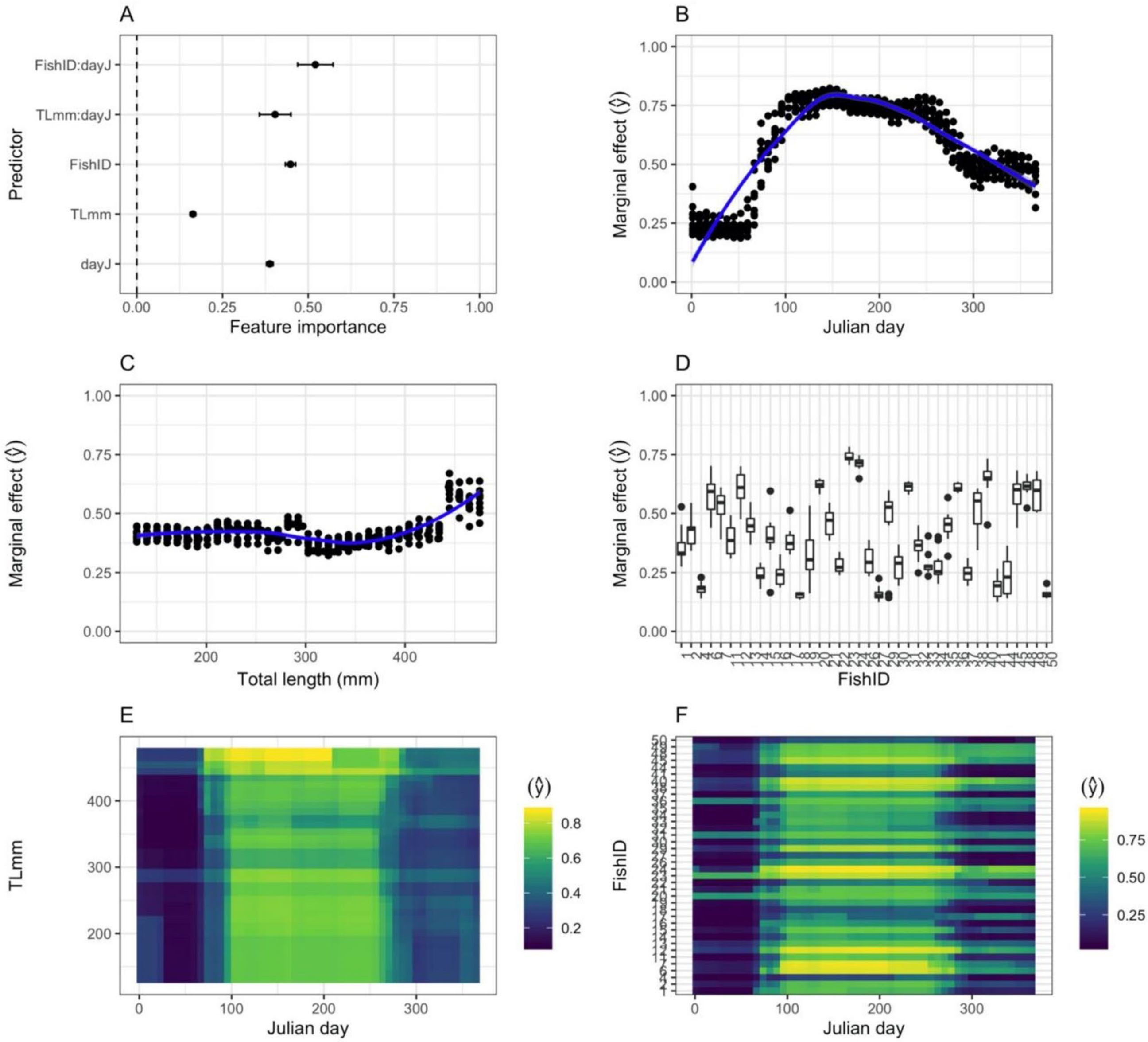

Fig. 5 Random forest model outputs predicting largemouth bass location (inside/outside Big Rideau freshwater protected area), **A** predictor (feature) importance scores ± 95% confidence interval, marginal effects ($\hat{y}$) of predictors **B** Julian day **C** fish total length, **D** individual fish, **E** interaction between Julian day and fish total length (TLmm), **F** interaction between Julian day and individual fish (FishID). Errors were generated by tenfold cross validation

within the BRL FPA during 2017 may have increased habitat availability which, in turn, may have increased largemouth bass residency time within the FPA. Higher water levels not only provide access to new habitat (i.e. flooded shoreline), but can also buffer water temperature fluctuations during dynamic weather conditions (Meals and Miranda 1991). Previous telemetry-based research has identified a negative correlation between habitat residency rates of largemouth bass and both water temperature and littoral zone water depth (Roy et al. 2018). Diurnal movement patterns have also been observed in largemouth bass, where telemetered fish have been observed to occupy deeper littoral habitats during daylight hours, and move into shallower areas during low-light conditions (Demers et al. 1996; Hanson et al. 2007). Thus, the increased water depth throughout the FPA area during 2017 may have resulted in higher residency through increased habitat volume. Furthermore, differences in residency rates between years may also be related to fish growth. As occupancy was positively correlated with larger body sizes, it may be that juvenile tagged individuals grew large enough between seasons to reach sexual maturity (i.e. reproduce) and/or successfully compete for home-range territories. Population density is known to be higher within the FPA, with density-dependent spillover occurring across the protected area boundary (Zolderdo et al. 2019). Natural population structuring relies on the senescence of older individuals to create niche space for younger, more fit individuals (Metcalfe 2006). Thus, it may be possible that the increased occupancy within the FPA for the 2017 year may, in part, be the result of natural population restructuring processes occurring with the FPA population.

Body size was observed to be an important factor influencing occupancy within the BRL FPA, with fish > 430 mm having the highest total number of days spent within the protected area boundaries (Fig. 5C) compared with smaller individuals. This increased occupancy amongst the largest telemetered fish could be related to condition factor following the overwintering period. More specifically, a larger body size enables a higher storage capacity for endogenous energy reserves (i.e. lipids; Cargnelli and Gross 1997) coupled with a lower size-specific metabolic rate (Norin and Clark 2015). This would enable larger fish to exit the overwintering period in better condition and make seasonal movements into the shallow littoral FPA habitat sooner relative to smaller individuals (Hanson et al. 2008; Midwood et al. 2017). Furthermore, the residency-body size relationship may also be related to the reproductive life-history of largemouth bass. As a result of exiting the overwintering period in better physiological condition, larger fish require less nutritional intake prior to spawning. This enables larger individuals to initiate spawning earlier in the season relative to smaller individuals (Iguchi et al. 2004). Furthermore, larger fish are able to engage in reproductive activities (i.e. parental care behaviours) longer due to their increased energy reserve capacity (Cooke et al. 2006; Suski and Ridgway 2007). Based on these factors, larger reproductively active individuals would remain within the spawning areas for longer durations of time relative to smaller fish which may, in part, be responsible for the increased occupancy amongst larger individuals observed within the FPA, especially during the spring–summer period (Fig. 5E). As such, our findings show that the protective capacity of the BRL FPA was greater for larger individuals, which may provide ecological benefits at the population level (i.e. increased reproductive output and recruitment).

Despite the small size of the BRL FPA (i.e. 0.57 km^2, 1.2% of lake surface area), it was sufficient in protecting tagged largemouth bass for 55 ± 32% of the year. However, fish did leave the protected area during portions of both the closed and open access fishing seasons. By this metric alone, the current FPA design does not provide uninterrupted, year-round protection as initially intended (Ontario Department of Game and Fisheries Monthly Bulletin 1939). However, the lowest occupancy period (i.e. < 25% of tagged fish present inside the FPA) occurred between January and March 2017, which overlapped with the closed fishing season for largemouth bass in the region (2021 Ontario Recreational Fishing Regulations Summary). Even if fish left the FPA boundaries, another protection measure against fishing was still in effect. Consequently, the mandated closed fishing season indirectly extended the BRL FPA's protective capacity. However, low occupancy still occurred during the open access fishing season (i.e. ~40–75%), largely during the autumn transition months of October–December. During this time period, FPA largemouth bass may have been vulnerable to angler capture, but angling for largemouth bass is greatly reduced, and may not be occurring at all during the October–December time period (Sheridan and Krishka 1995; Hogg et al. 2010). Thus, capture of FPA largemouth bass during the autumn transition period may be minimal as a result of reduced fisheries pressure associated with changes in angler behaviour. It is important to note, however, that these excursions outside of the FPA were most likely due to the lack of deep-water habitat within the BRL FPA, and occurred largely during the autumn transition and overwintering periods. This behaviour closely corresponds to previously identified seasonal movement patterns in largemouth bass (Carlson 1992; Hanson et al. 2008). The protective capacity of a FPA is a function of its size, as well as the habitat needs of the exploited species that occupy it (as reviewed in Acreman et al. 2020). Thus, to achieve a higher protective capacity for largemouth bass, FPAs will need to incorporate deep-water (overwintering) habitat.

Despite providing incomplete coverage of largemouth bass home ranges, the BRL FPA must still provide some degree of population-level protection, as previous research has observed greater abundance and biomass of largemouth bass within the FPA borders (Zolderdo et al. 2019). Differences in key physiological markers, which are indicative of fisheries-induced selection (i.e. high-vulnerability phenotypes; Philipp et al. 2015), have also been observed between the FPA and main-lake largemouth bass populations. For example, largemouth bass occupying the BRL FPA have been observed to have lower stress responsiveness to an angling and air exposure challenge, coupled with greater metabolic capacity compared with largemouth bass from adjacent main-lake areas (Zolderdo et al. 2023). As such, these population-level differences may be the result of increased protection specifically during the reproductive life-history stage. Despite the fact that a closed fishing season for largemouth bass occurs during the reproductive life-history period across all of the Rideau waterway lakes (i.e. 15 December–third Saturday in June), pre-season angling still occurs and has been increasing in prevalence since the 1990s (Philipp et al. 2023). Although it is illegal to target largemouth bass during the reproductive period, Philipp et al. (2023) observed hook wounding rates as high as 61% on nest guarding largemouth bass in two interconnected lakes within the Rideau Waterway system. This increased hook wounding is the direct result of pre-season angling, and resulted in significant reproductive failure (Suski et al. 2002). Angling-induced reproductive failure can reduce year-class recruitment, and lead to evolutionary change at a population level (Philipp et al. 1997, 2015). As observed in the current study, high occupancy within the FPA boundaries occurred during the critical reproductive life stage of largemouth bass. Thus, the protection afforded by the BRL FPA during the reproductive period may not only provide conservation benefits through protecting/promoting recruitment, but may also serve as an evolutionary enlightened management strategy to mitigate human-induced selection pressures on this heavily exploited sportfish population.

In conclusion, the current study highlights the importance of understanding the seasonal movements and habitat requirements of fishes across life stages to guide the establishment of effective FPAs (Acreman et al. 2020; Reyier et al. 2020). The BRL FPA appears to provide three season protection for largemouth bass, which was repeated across years, and protection was apparently better for large fish relative to small fish. However, largemouth bass have diverse seasonal habitat requirements, and individuals moved out of the FPA during the autumn, with low occupancy over winter, reducing the full protective capacity of the BRL FPA. Therefore, managers need to ensure that the goals of a protected area not only match the life history of a fish, but also must consider protection across all life stages. To ensure a higher protective capacity for largemouth bass, as with any species to be protected, a more thorough quantification of home-range size across seasons is needed, which requires a larger tracking array(s) then was established in the current study. Fortunately, advances in electronic fisheries tracking and monitoring technologies make it possible to evaluate the optimal location and coverage area(s) of future FPAs before they are established. However, largemouth bass have consistent summer habitat requirements, and protection for certain critical life-history periods (i.e. reproductive and active growing periods) can be achieved by setting aside ~1% of a lake area, which has resulted in significant population- and community-level benefits. For example, the small-scale spatial protection provided by the Rideau waterway FPAs, has amounted to physiological benefits in largemouth bass through the protection of high-performance metabolic and stress-resilient phenotypes (Zolderdo et al. 2023). Moreover, community-level benefits including increased population densities of both largemouth bass and other non-target fish species have also been observed (Zolderdo et al. 2019). Collectively, these results suggest that the current level of spatial protection provided by the Rideau waterway FPAs is of value from a fisheries management perspective.

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Author contributions AZ: Conceptualization, methodology, data collection and analysis, writing, editing. JB: Methodology, data collection and analysis, writing, editing, prepared all Figures 1–5. AA: Methodology, data collection, writing, editing. CS: Conceptualization, methodology, writing, editing. SC: Conceptualization, methodology, data collection, writing, editing.

Data availability All data are accessible upon request from the corresponding author.

Declarations

Conflict of interest The authors have no conflict of interest.

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