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Evidence of fish spillover from freshwater protected areas in lakes of eastern Ontario

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Abstract

1. Research has identified numerous conservation benefits attributed to the use of marine protected areas (MPAs), yet comparatively less is known about the effectiveness of freshwater protected areas (FPAs).
2. This study assessed multiple long-standing (>70 years active) intra-lake FPAs in three lakes in eastern Ontario, Canada, to evaluate their potential conservation benefits. These FPAs were intended initially to protect exploited populations of largemouth bass (*Micropterus salmoides* (Lacépède, 1802)), but since their establishment no empirical data have been collected to evaluate the effectiveness of FPAs for protecting bass or the broader fish community.
3. A comparative biological census of fish species abundance, biomass and species richness was conducted using snorkelling surveys within FPAs, along the bordering transition zones, and in more distant non-protected areas of the lake that had similar habitats to the FPAs.
4. In general, the FPAs yielded benefits that were most obvious (in terms of abundance and biomass) for the focal protected species (i.e. largemouth bass) as well as several shiner species. Largemouth bass and shiner abundance and biomass were highest in the FPA, lowest in the distant non-protected areas, and intermediate in the transition zone. Species richness was also highest in the FPAs in two of the three lakes.
5. Collectively, these results support the use of FPAs as a viable and effective conservation strategy that extends beyond simply limiting the exploitation of a target species. Beyond the benefits afforded to fish within the FPA, evidence of spillover in adjacent areas was also observed, which is promising. Additional research is needed on the effectiveness of FPAs in a variety of regions and water-body types facing various threats in an effort to understand when, where and how to best use FPAs to benefit aquatic biodiversity.

KEYWORDS

conservation evaluation, fishing, freshwater protected areas, habitat management, largemouth bass, littoral, recreation, spillover

1 | INTRODUCTION

Threats to freshwater habitats and the biodiversity they support are mounting in magnitude and complexity, making freshwater ecosystems among the most imperilled worldwide (Arthington, Dulvy, Gladstone, & Winfield, 2016; Jenkins, 2003; Ricciardi & Rasmussen, 1999). As such, immediate management action and regulatory intervention are needed to improve freshwater conservation and reverse current declining trends (Cowx, 2002; Nilsson, Reidy, Dynesius, & Revenga, 2005). One conservation strategy, commonly used within marine environments, is the establishment of marine protected areas (MPAs; Di Lorenzo, Claudet, & Guidetti, 2016). MPAs are considered largely beneficial as they reduce or eliminate human-mediated resource uses (e.g. overfishing), reduce adverse human impacts (e.g. habitat alteration or destruction) and allow the rehabilitation of ecosystems disturbed or damaged by human activities (reviewed in Di Lorenzo et al., 2016). Furthermore, MPAs can greatly benefit the biological communities that inhabit them (e.g. by increasing biodiversity), while providing economic benefits to local commercial and recreational fisheries through the export of recruitment subsidies (i.e. eggs and larvae) and spillover of harvestable fish to fishable waters (Ashworth & Ormond, 2005; Harmelin-Vivien et al., 2008; Tupper, 2007).

Despite the apparent benefits of protected areas (PAs) in marine systems, they remain comparatively uncommon in the freshwater realm (Abell, Allan, & Lehner, 2007; Cucherousset et al., 2007; Saunders, Meeuwig, & Vincent, 2002), particularly throughout North America. However, the use of PAs in European freshwater systems has received more attention and application in recent years owing to European Union directives requiring more rigorous habitat protection measures (Bouchet, Falkner, & Seddon, 1999; Council of the European Communities, 1992; Paavola, 2004). Nevertheless, the global application of freshwater protected areas (FPAs) as a conservation tool is still limited and, as a result, understudied. Indeed, there is relatively little research pertaining to the effectiveness of FPAs, which creates uncertainty regarding their application (Finlayson, Arthington, & Pittock, 2018; Harrison et al., 2016). With declining trends in freshwater biodiversity and the rapid degradation of pristine, intact freshwater ecosystems (Dudgeon et al., 2006; Reid et al., in press), action in the form of FPAs could be an effective conservation strategy (Abell et al., 2007; Harrison et al., 2016; Suski & Cooke, 2007).

Although the use of FPAs is relatively limited throughout inland lake and river systems in North America (Abell et al., 2007; Hermoso, Abell, Linke, & Boon, 2016), their application has resulted in successful outcomes (Suski & Cooke, 2007; Zuccarino-Crowe, Taylor, Hansen, Seider, & Krueger, 2016). Often the intention of FPAs is to protect biodiversity within entire ecosystems; however, resource-based FPAs that target a single species are common (Hedges, Koops, Mandrak, & Johannsson, 2010). Specifically, the establishment of FPAs to protect economically valuable species such as largemouth and smallmouth bass (*Micropterus dolomieu* [Lacépède, 1802]) in North America (Sztramko, 1985; Suski & Cooke, 2007; Twardek et al., 2017) are among the most common applications (Watson, Dudley, Segan, & Hockings, 2014).

The Rideau Lakes system (Eastern Ontario, Canada) is a unique freshwater system that comprises multiple lakes and rivers that stretch from Ottawa, Ontario, to the St Lawrence River system. The majority of lakes within the Rideau Lakes system support one or multiple long-term (>70 years) single-resource FPAs. These FPAs are closed to all fisheries activities 365 days per year and were initially established as an experimental means of protecting the viability of the largemouth bass fishery that was suffering from heavy exploitation through excessive catch-and-harvest (Ontario Department of Game and Fisheries, 1946). The FPAs were intended to provide an exclusion zone to promote growth and recruitment back into the declining largemouth bass populations. However, since their establishment, the effectiveness of these year-round FPAs in satisfying their primary objective (i.e. to protect largemouth bass and promote recruitment) has remained relatively unexplored. Furthermore, the utility of these FPAs to provide indirect benefits to other species of fish or the fish community as a whole has also largely been neglected. As a result, the Rideau Lakes FPAs provide a unique opportunity to investigate the direct effects of long-term protection on an economically and culturally significant fish species, as well as the potential indirect benefits of protection for the fish community as a whole.

One way to assess the benefits associated with protection is to quantify differences between the biological communities that reside inside and outside of designated PAs (Watson et al., 2014) and, as an example, spillover of fish species outside of PAs is often considered a biomarker of successful protection (Goñi, Hilborn, Díaz, Mallol, & Adlerstein, 2010). Previous research evaluating the effectiveness of MPAs has focused on quantifying various biological parameters including density-dependent spillover of fish biodiversity, abundance and biomass across a spatial gradient emanating outward from the MPA up to several kilometres from the protected area boundaries (Ashworth & Ormond, 2005; Rakitin & Kramer, 1996). Often, successful MPAs show gradient effects (i.e. spillover), where fish diversity, abundance and biomass decrease as distance from the MPAs increases (Harmelin-Vivien et al., 2008; Tupper, 2007). From a fisheries perspective, spillover of fish (juveniles or adults) is considered a key feature of an effective and successful protected area, where the export of economically valuable species of fishes outside of MPAs can result in continuous and renewable source populations for commercial and recreational fisheries (Di Lorenzo et al., 2016). Through direct comparisons of fish community parameters between PAs and adjacent non-protected areas, the benefits at the individual, population and community levels that may be linked, directly or indirectly, with the protection provided can be accurately quantified.

Employing techniques previously used to evaluate PAs in marine systems, the objective of this study was to evaluate the effectiveness of long-standing (i.e. since the 1940s) FPAs evidenced by direct assessment of spillover of species of fishes into fishable waters. We hypothesized that fish abundance, biomass and richness would be highest in the FPAs, lowest in areas of similar habitat but distant from FPAs, and intermediate in the areas immediately outside PAs, indicative of spillover effects similar to PAs in the marine environments. Assessments were replicated across three interconnected

lakes with similar fish communities, each containing a combination of PAs and non-protected waters.

2 | METHODS

2.1 | Study sites

Three interconnected lakes throughout the Rideau Lakes system, Ontario, Canada, were used for this study: Lake Opinicon, Newboro Lake and Big Rideau Lake. Each of these lakes has one or more long-standing (i.e. >70 year) intra-lake FPAs that provides year-round protection from fishing activity (Figure 1). The placement of the FPAs within each of the study lakes was based on historical knowledge of spawning locations for largemouth bass, provided from anecdotal observations by local fishing guides and resource managers (Ontario Department of Game and Fisheries, 1946). All lakes have active recreational fisheries (both catch-and-release and catch-and-harvest) for a variety of species of fishes including, but not limited to, black basses (a collective term for both smallmouth bass and largemouth bass), northern pike (*Esox lucius* (Linnaeus, 1758)), bluegill (*Lepomis macrochirus* (Rafinesque, 1810)) and yellow perch (*Perca flavescens* (Mitchill, 1814)). These lakes are also subject to intermittent small-scale commercial fishing activity that targets mainly 'pan-fish', e.g. bluegill and pumpkinseed (*Lepomis gibbosus* (Linnaeus, 1758)), yellow perch, black crappie (*Pomoxis nigromaculatus* (Lesueur, 1829)) and brown bullhead (*Ameiurus nebulosus* (Lesueur, 1819); Hogg, Lester, & Ball, 2010; Larocque et al., 2012) – all such fishing activities, both commercial and recreational, are prohibited inside the FPAs, and have

been since their inception. Lake Opinicon (~8.66 km²) houses two separate FPAs with an approximate combined protection area of 1.0 km². Newboro Lake (~17.01 km²) also has two separate FPAs with an approximate combined protection area of 3.33 km². Big Rideau Lake (~45.36 km²) has one designated FPA with an approximate protection area of 0.57 km² (Figure 1). These long-standing protected areas are easily identifiable from the water (i.e. well-maintained signage posted at each entrance way and along the bordering transition zones between the FPAs and neighbouring waters, as defined below), as well as from navigation and fishing maps. Furthermore, these FPAs are actively patrolled and enforced by the Ontario Ministry of Natural Resources and Forestry with assistance in reporting of infractions by the public to ensure that fishing activity does not occur within their boundaries.

2.2 | Visual censuses

Fish species richness, abundance and size (estimated to within a ± 2 cm error) were recorded by snorkellers conducting visual surveys along standardized transects within the littoral regions of each study lake. Transects were established within three zones of each lake. The three lake zones were designated as (1) entirely within the FPAs, (2) within the bordering transition zone immediately adjacent to the FPA boundaries, which we defined as the area of water/habitat extending outwards up to 2 km from an FPA border and (3) outside in fished areas, which we defined as the lake area that extended beyond the transition zone (i.e. >2 km from FPAs). Establishing the transition zones as 2 km lake/habitat areas enabled the home range

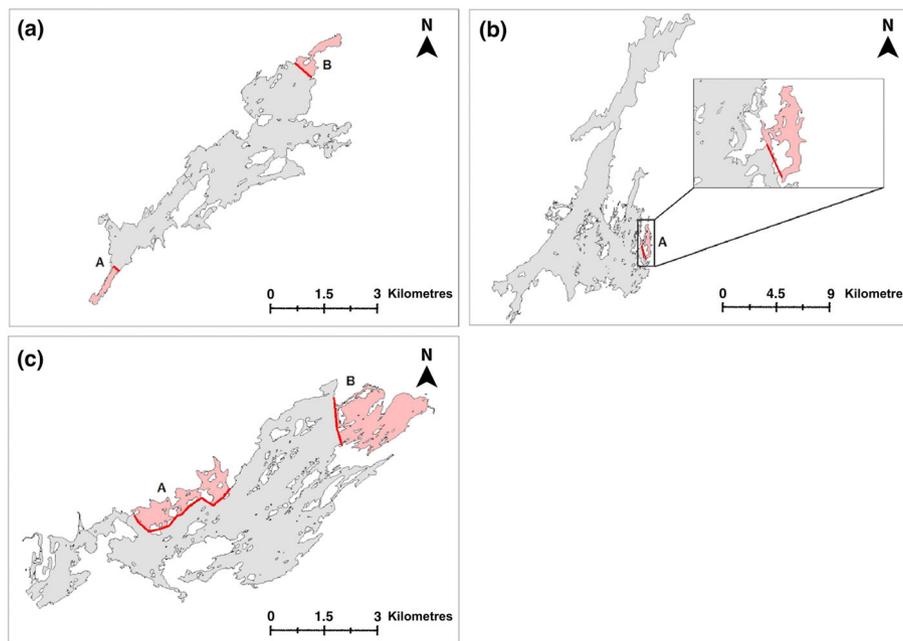


FIGURE 1 Maps of the three replicate study lakes: Opinicon Lake (OP) (a), Big Rideau Lake (BR) (b) and Newboro Lake (NB) (c). The freshwater protected areas (FPAs) are designated by red shading, with a solid red line delineating the FPA borders. For OP and NB that have two designated FPAs each (distinguished by 'A' and 'B', respectively), the data collected from each FPA were pooled together to provide a holistic representation of the protective potential provided by FPAs within each lake system

size of largemouth bass to be accounted for (i.e. $<1 \text{ km}^2$; Lewis & Flickinger, 1967; Ahrenstorff, Sass, & Helmus, 2009), reducing the potential confound of quantifying transient fish that may be long-term inhabitants of either the FPA or the outside fished lake zone. Establishing three distinct lake zones to survey in this manner allows informative evaluations of the effectiveness of these FPAs as a conservation tool, through the assessment of ecological spillover and/or changes in fish community structure between lake zones.

All snorkelling surveys were conducted within the month of July 2017. July was selected as the ideal period to evaluate the protective potential of the FPAs for two reasons: (1) largemouth bass have completed their spawning and parental care period by the end of June in the Rideau Lakes system (Cooke, Philipp, Wahl, & Weatherhead, 2006), reducing the potential bias associated with nest site habitat preferences (i.e. increased abundance of reproductively active fishes in the shallow littoral regions; Brown, Runciman, Pollard, & Grant, 2009) and associated nest-site fidelity (Twardek et al., 2017); and (2) recreational fisheries pressure is greatest during the month of July throughout the Rideau Lake system (Hoyle, 1990; Sheridan & Krishka, 1995), so the effect of protection afforded by the FPAs should be most detectable during this time period (i.e. catch-and-harvest and post-release mortality rates should be highest during July). To minimize any potential biases in sampling locations, all transects were established within the shallow littoral regions of each of the lake zones. Furthermore, survey times were systematically randomized between lake zones, following a specified temporal sampling effort per lake-zone approach. Specifically, lake zones were surveyed in 4 h time blocks: morning (08:00–12:00), afternoon (12:00–16:00) and evening (16:00–20:00), starting in a randomly selected lake zone and alternating through the remaining lake zones systematically. Randomizing survey times and locations in this manner reduces any potential spatial and temporal effects that may influence fish behaviour and habitat selection (Cooke, Steinmetz, Degner, Grant, & Philipp, 2003).

Collectively, 173 transects were surveyed across the three replicate lakes. In Big Rideau Lake, 62 transects were surveyed ($n = 25$ within the FPA, $n = 17$ within the transition lake zone, and $n = 20$ within the outside fished lake zone). In Lake Opinicon, 46 transects were surveyed ($n = 15$ within the FPAs, $n = 17$ within the transition lake zone, and $n = 14$ within the outside fished lake zone). In Newboro Lake, 63 transects were surveyed ($n = 24$ within the FPAs, $n = 23$ within the transition lake zone, and $n = 16$ within the outside fished lake zone). All surveys were conducted under strict, pre-set criteria to standardize observation effort and duration. Specifically, all transect dimensions were standardized to be 100 m in length and 5 m in width, snorkeller observation effort was restricted to 10 min per transect and the same snorkellers were used throughout the duration of the study. In addition, all snorkellers validated observations under 'practice' conditions which entailed comparative survey assessments of species identification, length estimations of fishes (various species) to within a $\pm 2 \text{ cm}$ error, vegetation complexity assessments to within $\pm 10\%$ variance, water depth to within $\pm 10 \text{ cm}$ variance and consistent substrate composition assessment.

During each transect survey, all fishes encountered were identified to species except for certain species of Cyprinidae that were too difficult to differentiate accurately under water from a distance (e.g. blackchin shiners (*Notropis heterodon* (Cope, 1865)) vs. blacknose shiners (*Notropis heterolepis* (Eigenmann & Eigenmann, 1893))). Based on the underwater visual identification difficulty of Cyprinidae and their known diversity within each of the study lakes, the identification of species of Cyprinidae was broken down as follows: shiner (including common shiner (*Luxilus cornutus* (Mitchill, 1817)), golden shiner (*Notemigonus crysoleucas* (Mitchill, 1814)), blackchin shiner and blacknose shiner), common carp (*Cyprinus carpio* (Linnaeus, 1758)), dace (*Chrosomus* spp.) and chub (*Semotilus* spp. & *Couesius* spp.). Grouping the members of the Cyprinidae family in this way allowed a coarse assessment of their diversity, abundance and biomass across lake zones. Furthermore, fishes that were observed during a transect survey, but were unable to be identified definitively to a genus or family group, were recorded and categorized as 'unknown'. This group of fishes was included in abundance analyses; however, they were not included in species richness or biomass assessments.

The numbers of fishes were counted and recorded individually, but when large schools of fish were encountered, snorkellers would estimate abundance using count intervals of 10, a method similar to that proposed in the literature (Harmelin-Vivien et al., 2008). The size of each fish observed was recorded to within a 2 cm error. Snorkellers calibrated fish size by estimating the lengths of fishes along practice transects (i.e. visually estimating stationary and mobile fishes) and estimating the lengths of known objects (e.g. PVC tubing, submerged logs, etc.). In addition, snorkellers drew measuring sticks (15 cm in length) on data slates (i.e. $\sim 30 \times 15 \text{ cm}$ CPVC sheets that enabled underwater data recording), to provide a reference for measurements during surveys if needed. Surveys only commenced once size estimation error was consistently within $\pm 2 \text{ cm}$ between snorkellers. Validating sampling error in this manner allowed for consistency in the fish parameter data collected, reducing any potential biases between snorkeller observations. Inherent biases and sampling error can arise from visual estimates of fish parameters (e.g. length and abundance), especially when fish are mobile or at a distance from the observer, making accurate visual assessments difficult (Jennings & Polunin, 1995). However, underwater visual census (UVC) can produce relatively accurate data (e.g. 86% accuracy in length measurements, and 91.6% accuracy in abundance counts; St. John, Russ, & Gladstone, 1990), especially when observers standardize visual sampling error and effort. Therefore, UVC methods can produce consistent and reliable data for comparative evaluations (Harmelin-Vivien et al., 2008; Macpherson, Gordo, & García-Rubies, 2002; St. John et al., 1990).

Owing to the high proportionality between length and weight within most freshwater fish (Schneider, Laarman, & Gowing, 2000), fish biomass for selected species was calculated using pre-established length-weight data generated from existing data from Rideau Lakes populations and Great Lakes populations (Lawrence, Godin, & Cooke, 2018; Schneider et al., 2000; see Appendix for details). Specifically,

weight (g) data for largemouth bass, pumpkinseed, bluegill, yellow perch and shiners was calculated for biomass comparisons. All shiners were grouped and analysed collectively for biomass and abundance assessments owing to difficulties in accurate underwater identification of certain shiner species. The length–weight ratio for common shiner was used as a proxy ratio to calculate shiner biomass (g) in order to provide a quantifiable, and comparable, index biomass score between lake zones. The length–weight ratio for the common shiner was chosen based on the ubiquity of this species throughout each of the replicate study lakes. It is important to note that the grouped shiner species are not monophyletic in origin. As such, grouping shiner species in this manner may create bias in the biomass values between lake zones depending on the true diversity of shiners observed within each transect or lake zone; however, the length–weight relationship for common shiner within the study region is well described in the literature (Schneider et al., 2000), whereas length–weight data for other shiner species (e.g. blackchin and blacknose shiners) were not available. Therefore, grouping and analysing the biomass data for the grouped shiner species in this manner, using the common shiner length–weight data as a proxy, enabled a coarse-scale evaluation of shiner assemblage biomass between lake zones.

Habitat structure and complexity was also assessed within each transect surveyed, as these factors can influence small-scale temporal and spatial variability of fish species (Randall, Minns, Cairns, & Moore, 1996). Several habitat features were measured, including vegetation complexity comprising emergent vegetation, submerged vegetation and coarse woody debris (CWD) cover (0–100%), water depth (m) and substrate composition. Substrate was categorized as organic matter (OM), rock (R), sand (S) and gravel (G). If mixed substrates were present during the survey, they were denoted to reflect the combination of substrate materials present (e.g. organic matter and rock = OM/R). All habitat features were measured at three standardized locations including 0 m (beginning of the transect), 50 m (middle of the transect) and 100 m (end of the transect) along each transect surveyed. At each of these locations, habitat parameters were measured within the immediate vicinity of the snorkeller (~5 m²); vegetation complexity and CWD were measured as the percentage cover of macrophytes, and CWD within the water column (e.g. 50% = half of water column filled by macrophytes and CWD). Substrate composition and water depth were analysed directly below the snorkeller.

2.3 | Data analysis

2.3.1 | Fish community composition and species richness

To define differences in fish communities between lake zones (i.e. FPAs, transition zones and outside fished zones), a multivariate approach was used. Owing to the potential differences in fish communities between each of the replicate study lakes (as a result of differing abiotic or biotic factors), community composition and species richness were analysed independently between lake zones within each study

lake. Specifically, non-metric multidimensional scaling (NMDS) ordination with analysis of similarities (ANOSIM) and similarity percentages (SIMPER) were used to compare fish community composition scores between lake zones (following similar methods used by Midwood et al., 2016). The mean abundance scores of observed fish species per transect per zone were used for community composition analyses. Using mean abundance scores can provide a reliable index of community composition, as species abundance can vary greatly as a result of density dependent or independent processes such as predator burden and exploitation. NMDS ordination allowed the visualization of the data, whereas ANOSIM determined whether there were statistically significant differences in community composition between lake zones. SIMPER provided a species-specific *post-hoc* analysis (except for shiner species as they were grouped together prior to analysis) to evaluate which species were driving the differences in community composition detected based on their mean abundance. Following the methodology of Midwood et al. (2016), only species that exhibited an arbitrary dissimilarity proportion >5% were interpreted and evaluated further, as this cutoff percentage reflected a meaningful dissimilarity proportion from an analytical perspective. A Bray–Curtis distance measure was applied to the non-transformed mean abundance data for all analyses conducted, as the Bray–Curtis function is designed to find a stable solution based on the global optima using numerous random starting points (Oksanen et al., 2013).

The input matrix contained the total abundance data for 13 species or species groups from each lake zone: largemouth bass, bluegill, pumpkinseed, yellow perch, shiner, black crappie, brown bullhead, dace, common carp, rock bass (*Ambloplites rupestris* (Rafinesque, 1817)), northern pike, chub, and unknown. For species of fishes that were determined to contribute to differences in community composition, a non-parametric Kruskal–Wallis (KW) test paired with a Mann–Whitney *post-hoc* analysis was conducted to determine if there were statistically significant differences in mean abundances between lake zones. Species richness between lake zones was analysed using a one-way analysis of variance (ANOVA) comparing the mean number of species detected per transect within each lake zone. A Tukey *post-hoc* analysis was used to differentiate statistically significant differences. The ANOSIM and SIMPER analyses were conducted using the statistical software package PAST 3.14 (Hammer, Harper, & Ryan, 2009), whereas the NMDS was completed using the metaMDA function in the *vegan* package (Oksanen et al., 2013) in RStudio (RStudio: Integrated Development for R. RStudio Inc., Boston, MA, USA). ANOVA, KW, Tukey and Mann–Whitney *post-hoc* analyses were completed using the statistical software package JMP 13 (SAS Institute, Cary, NC, USA). Statistical significance was set at (α) = 0.05 for all analyses and all values are reported as mean \pm standard error (SEM) where appropriate.

2.3.2 | Fish parameter evaluations

To evaluate the effectiveness and utility of the Rideau Lakes FPAs, fish abundance and biomass data were compared across zones (i.e. FPAs, transition zones, and outside fished zones) using a residual

maximum likelihood fitting of a mixed model regression. Separate models were run for fish abundance and biomass, and each model contained 'zone' as a single fixed effect (FPA, transition zone and outside fished zone), together with lake (Big Rideau Lake, BR; Newboro Lake, NB; and Opinicon Lake, OP) as a random effect. This use of 'lake' as a random effect allowed a comparison of patterns in response variables (e.g. fish abundance) across the three zones, while accounting for inter-lake differences (Zar, 1999). Post-hoc analyses using Tukey's test were conducted to differentiate statistical trends in the abundances and biomass of species of fishes between lake zones. Abundance data were analysed as a continuous data type with a Poisson distribution as abundance data were counted. Biomass data were analysed as a continuous data type with a normal (Gaussian) distribution. All analyses were completed using the statistical software package JMP 13 (SAS Institute, Cary, NC, USA).

2.3.3 | Habitat analyses

To understand the potential mechanisms underpinning differences in fish community parameters, it was necessary to determine whether habitat and temporal sampling effort were consistent across the zone-specific transects. Sampling time blocks within and between lake zones (within each replicate lake) were compared using a Wald chi-squared test. The proportion of vegetation (i.e. vegetation complexity) and water depth were compared within and between transects across lake zones using generalized linear models (GLMs). Nominal logistic regression analyses were used to analyse substrate composition between lake zones, because substrate composition was collected as categorical data. For these GLMs and nominal logistic regression analyses, lake zone (i.e. within the FPA, transition zone,

and outside fished zone) and location of habitat score (i.e. 0, 50 and 100 m) were entered as dependent variables, and the proportion of vegetation and transect water depth were entered as independent variables. Also, because the data types for vegetation measurements were proportions, GLMs for habitat analyses were run using a binomial distribution. Conversely, the data type for depth was continuous, and, therefore, depth GLMs were run under a normal distribution. Both habitat and depth GLMs were constructed to account for potential overdispersion in the datasets. All habitat data were analysed at an individual lake level owing to the habitat variability that occurs naturally between lake systems.

3 | RESULTS

3.1 | Fish community comparisons

The NMDS output suggests that there are distinct communities among replicate lakes, particularly Big Rideau Lake relative to Lake Opinicon and Newboro Lake (Figure 2). Within Big Rideau Lake, fish community composition was significantly different across all lake zones (ANOSIM, $P < 0.001$; $R^2 = 0.183$; Table 1), whereas no differences in community composition across lake zones were detected within Newboro Lake or Lake Opinicon (ANOSIM, $P > 0.05$ for all analyses). The SIMPER analysis for Big Rideau Lake suggests that fish species differences were mainly driven by the mean abundance of shiners, bluegill, yellow perch and pumpkinseed between all zone pairings, and mean abundance of largemouth bass only between the FPA and outside fished lake zone pairing (Table 1). However, statistically significant differences were only detected between shiners,

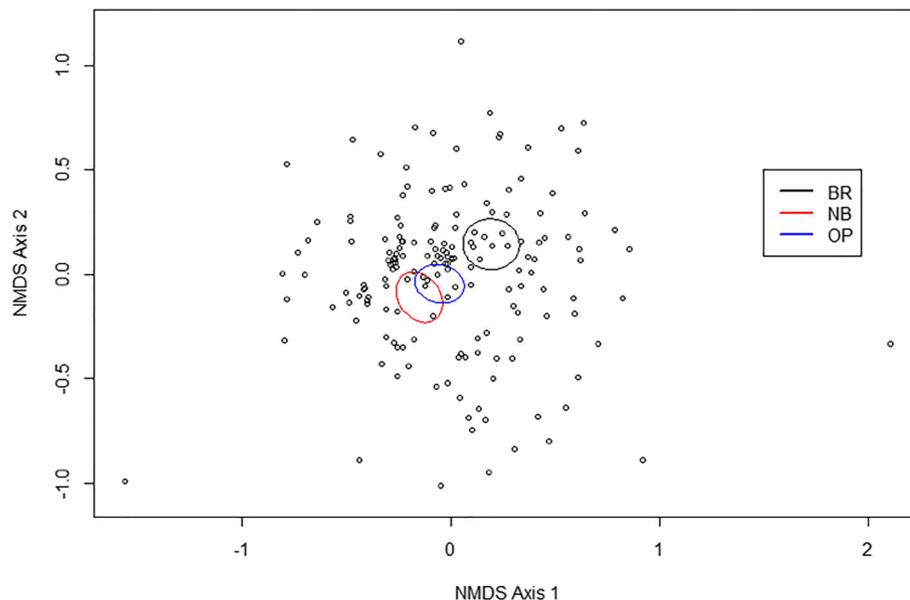


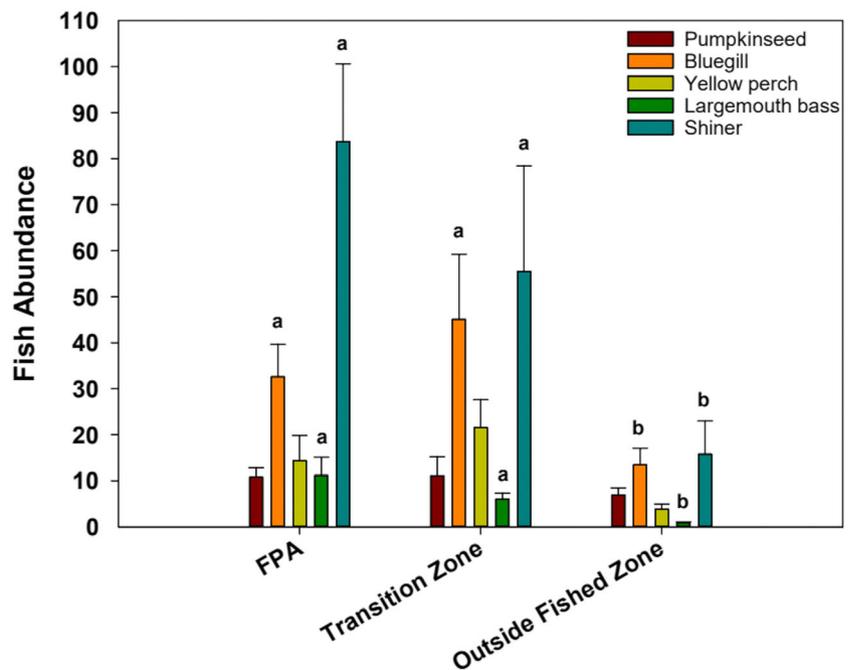
FIGURE 2 Non-metric multidimensional scaling output of fish community composition based on species abundance scores. The open circles represent the sample scores. Ellipses represent the 95% confidence intervals. The black ellipse represents the fish community composition score for BR, whereas the red ellipse represents NB and the blue ellipse represents OP. Note that ellipses that do not overlap represent distinct fish community compositions

TABLE 1 Output from similarity percentages (SIMPER) analyses for Big Rideau Lake showing overall dissimilarity of mean species abundances between each zone pairing. Note that only species with contributing dissimilarity values >5.0% are represented. Zone pairings are organized from highest to lowest for dissimilarity scores

Zone comparisons	Average dissimilarity	Species	Average A	Average B	Contribution
(A) Transition	72.97	Shiner	55.5	15.8	23.78
(B) Outside fished		Bluegill	45.1	13.4	19.46
		Yellow perch	21.5	3.85	17.43
(A) FPA	71.11	Shiner	83.7	15.8	35.85
(B) Outside fished		Bluegill	32.6	13.4	13.61
		Yellow perch	14.1	3.85	8.72
		Largemouth bass	11.2	0.9	6.65
		Pumpkinseed	10.8	6.95	5.42
(A) FPA	63.74	Shiner	83.7	55.5	28.98
(B) Transition		Bluegill	32.6	45.1	13.65
		Yellow perch	14.4	21.5	11.49

The average A represents the mean abundance for each species found in the specified zone listed first. The average B represents the same metric for the zone listed second. FPA, Freshwater protected area.

FIGURE 3 Differences in species abundances between lake zones within Big Rideau Lake. Lake zones include the FPA, the transition zone bordering the FPA (<2 km from a FPA border), and the outside fished lake area. The species represented in the figure were selected for Kruskal–Wallis analysis based on their contribution to the dissimilarity of community composition between lake zones within Big Rideau Lake. Error bars represent the standard error of the abundance means calculated from transect censuses within each zone; $n = 25$ within the FPA, $n = 20$ within the outside fished zone, and $n = 17$ within the bordering transition zone. Dissimilar letters (a and b) above the error bars denote statistically significant differences between groups ($P < 0.05$)



largemouth bass, and bluegill (KW; $\chi^2_{(3)} = 15.09$, $P < 0.0001$; $\chi^2_{(3)} = 36.17$, $P < 0.0001$; $\chi^2_{(3)} = 8.638$, $P < 0.05$, respectively). *Post-hoc* analyses indicate that shiner abundance was significantly higher within the FPA zone, compared with the outside fished zone. Similarly, both largemouth bass and bluegill abundance were significantly greater within both the FPA and the bordering transition zone, compared with the outside fished zone (Figure 3).

Species richness was found to be significantly different between lake zones across Big Rideau Lake, Newboro Lake and Opinicon Lake (ANOVA, d.f. = 2, $F = 9.447$, $P < 0.001$; d.f. = 2, $F = 4.210$, $P < 0.05$; d.f. = 2, $F = 3.252$, $P < 0.05$, respectively; Table 2). For Big Rideau Lake, *post-hoc* analyses indicate that species richness was significantly greater within the FPA and bordering transition zones, as compared

TABLE 2 ANOVA of mean species richness of fishes observed per transect within each lake zone across each of the replicate study lakes including Lake Opinicon (OP), Big Rideau Lake (BR) and Newboro Lake (NB)

Lake	Inside FPA	Transition zone	Outside fished zones	F	P
OP	4.800	4.588	3.930	3.252	0.048
BR	4.320	3.882	3.150	9.447	<0.001
NB	3.875	4.087	4.812	4.210	0.019

with the outside fished zone. Conversely, within Newboro Lake, *post-hoc* analyses show species richness to be greater within the outside fished lake zone compared with the FPAs. Within Opinicon

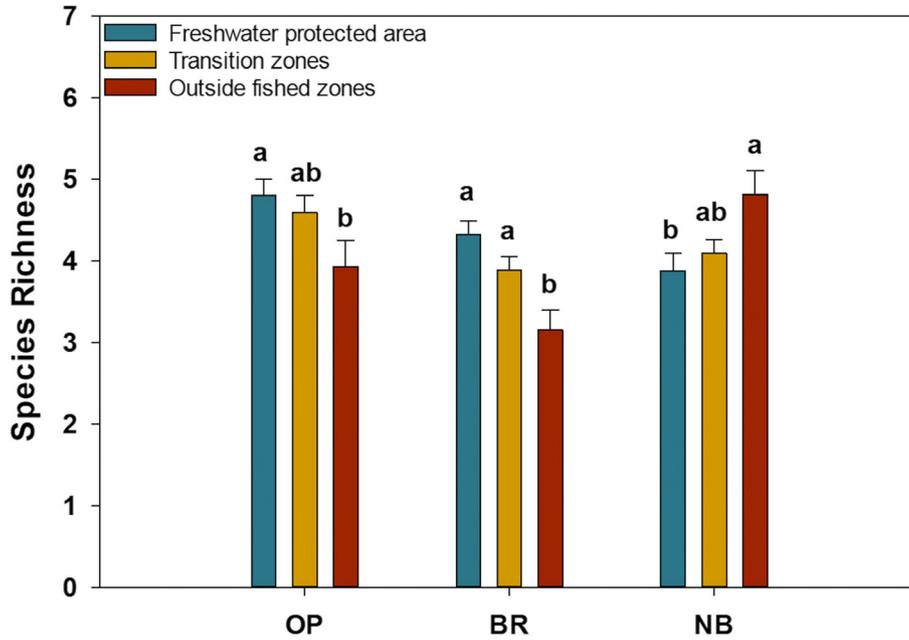


FIGURE 4 Differences in species richness between lake zones (i.e. outside fished zones, transition zones and FPAs) across each of the three replicate lakes: OP, BR and NB. Using real-time visual assessments from snorkelling censuses, 62 transects in BR, 63 transects in NB, and 46 transects in OP were evaluated. All transects were located within permanent FPAs (blue bars), outside of protected areas (red bars) or within bordering transition zones adjacent to FPAs (<2 km from an FPA border; yellow bars). Dissimilar letters (a and b) above the vertical error bars denote statistically significant differences between groups ($P < 0.05$)

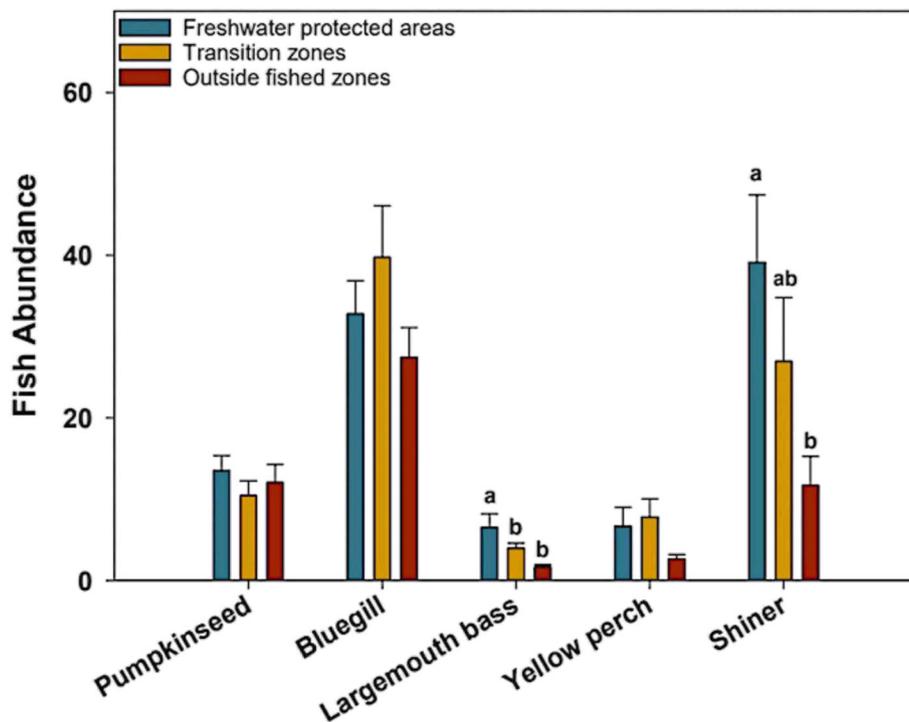


FIGURE 5 Differences in fish species abundance between lake zones (i.e. outside fished zones, transition zones and FPAs), based on pooled data from all replicate lakes: OP, BR, and NB. Error bars represent the standard error of the abundance means calculated from pooled transect data; $n = 64$ within FPAs, $n = 57$ within transition zones, and $n = 50$ within outside fished zones. Dissimilar letters (a and b) above the vertical error bars denote statistically significant differences between groups ($P < 0.05$)

Lake, *post-hoc* analyses reveal a greater species richness within the FPAs, compared with the outside fished lake zone (Figure 4).

3.2 | Fish abundance and biomass comparisons

Abundance and biomass of largemouth bass and shiners were found to be significantly different between FPAs and outside fished lake zones (fixed effect test, $F = 5.013$, $P < 0.01$; $F = 4.556$, $P < 0.05$ for abundance; $F = 10.993$, $P < 0.0001$; $F = 4.624$, $P < 0.05$ for biomass) across all replicate lakes. *Post-hoc* analyses indicate that largemouth bass abundance was significantly greater within FPAs, compared with outside fished zones (Figure 5). Similarly, largemouth bass biomass was found to be significantly greater within FPAs, compared with both the bordering transition zones and the outside fished zones (Figure 6). Shiner abundance and biomass were significantly greater within FPAs, compared with the bordering transition zones as well as the outside fished zones (Figure 5, 6). No statistically significant differences in abundance or biomass were detected between lake zones for pumpkinseed, yellow perch, or bluegill (fixed effect test, $P > 0.05$ for all analyses).

3.3 | Habitat and sampling effort comparisons

The results produced from the Wald chi-squared analyses found no differences in temporal sampling effort between lake zones within any of the replicate lakes ($P > 0.05$ for all analyses; Table 3). No differences were found in the proportion of vegetation cover between

TABLE 3 Output from the Wald chi-squared analyses testing for temporal differences in survey effort between lake zones within each of the replicate lakes including OP, BR and NB. Lake zones include the FPAs, the transition zone bordering the FPAs and the outside fished lake areas (>2 km from an FPA border)

Lake	Fixed effect	Degrees of freedom	Wald $\chi^2_{(3)}$	Prob > $\chi^2_{(3)}$	Significance
OP	Zone	2	3.509	0.173	n.s.
BR	Zone	4	8.516	0.074	n.s.
NB	Zone	4	8.794	0.066	n.s.

n.s., Non-significant.

lake zones within any lake ($P > 0.05$ for all analyses; Figure 7, Table 4). Furthermore, no differences in lake zone transect depths were detected within Big Rideau Lake ($P > 0.05$ for all analyses; Figure 8, Table 5); however, small differences in transect depth were detected within Newboro Lake and Opinicon Lake. Within Newboro Lake, transect depth was ~0.25 m greater within the transition zone compared with the depths within the FPA and the outside fished zones (GLM, $\chi^2_{(3)} = 17.002$, Prob > $\chi^2_{(3)} = 0.030$; Figure 8, Table 5). Within Lake Opinicon, transect water depth was ~20 cm deeper in the outside fished zones compared with the FPAs and transition zones (GLM, $\chi^2_{(3)} = 18.020$, Prob > $\chi^2_{(3)} < 0.001$; Figure 8, Table 5). Based on nearly all substrate measurements consisting of primarily OM, no differences were detected for substrate composition between lake zones ($P > 0.05$ for all analyses; Table 6).

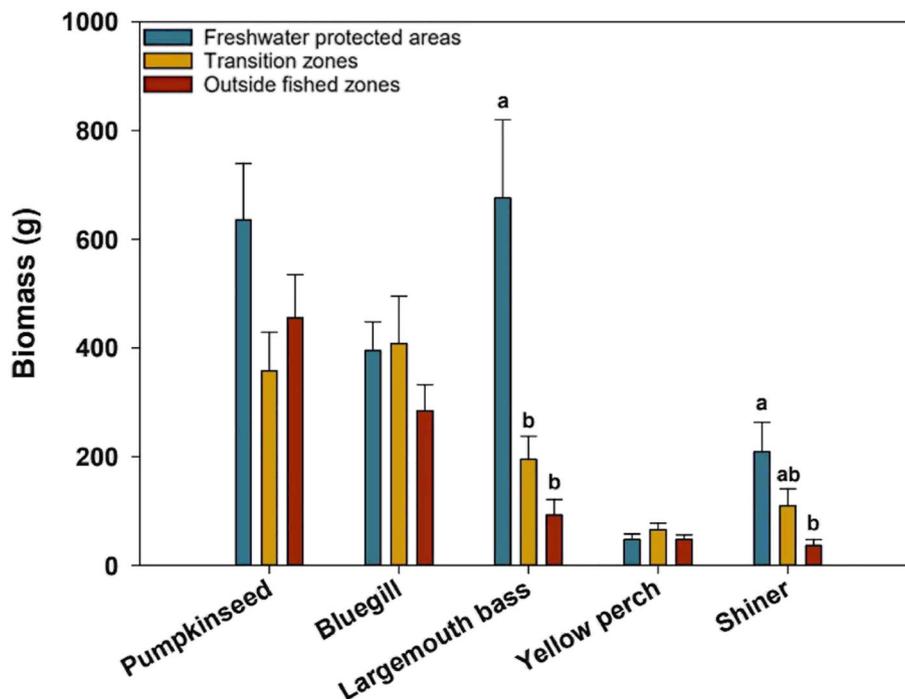


FIGURE 6 Differences in fish species biomass between lake zones (i.e. outside fished zones, transition zones, and FPAs), based on pooled data from all replicate lakes: OP, BR, and NB. Error bars represent the standard error of the biomass means calculated from pooled transect data; $n = 64$ within FPAs, $n = 57$ within transition zones, and $n = 50$ within outside fished zones. Dissimilar letters (a and b) above the vertical error bars denote statistically significant differences between groups ($P < 0.05$)

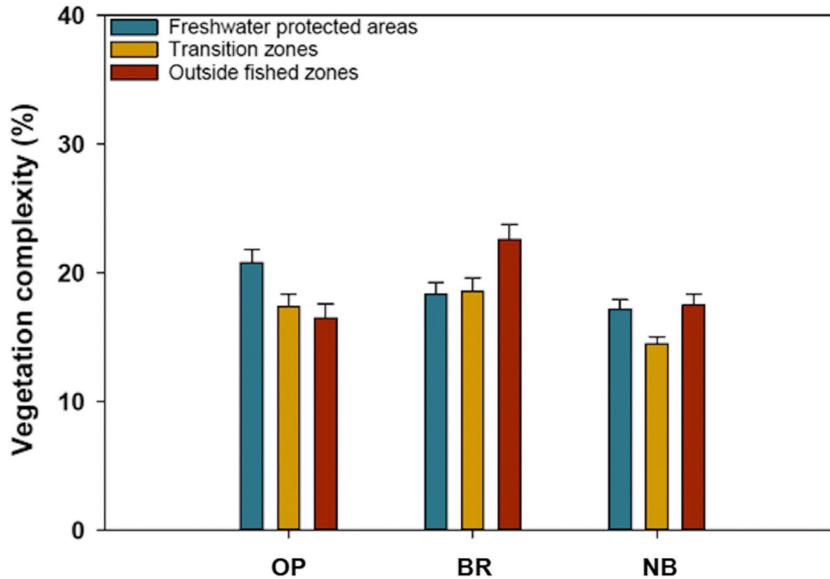


FIGURE 7 Mean transect vegetation complexity scores between lake zones (i.e. outside fished zones, transition zones, and FPAs) examined by snorkelling censuses across replicate lakes: OP, BR and NB. Using real-time visual assessments from snorkelling censuses, 62 transects in BR, 63 transects in NB, and 46 transects in OP were evaluated. All transects were located within permanent FPAs (blue bars), the transition zones bordering the FPAs (<2 km from an FPA border; yellow bars) or within outside fished zones (red bars). Dissimilar letters (a and b) above the vertical error bars denote statistically significant differences between groups ($P < 0.05$)

TABLE 4 Output from generalized linear model (GLM) analysis for differences in mean transect vegetation complexity per lake zone, across each replicate lake. For each of the replicate lakes, the model comparing transect vegetation complexity across zones and locations was not significant, thus no *post-hoc* analyses were conducted

Lake	Fixed effect	Degrees of freedom	$\chi^2_{(3)}$	Prob > $\chi^2_{(3)}$	Significance
OP	Zone	2	2.797	0.247	n.s.
	Location	2	0.627	0.730	n.s.
	Zone × Location	4	0.336	0.987	n.s.
	Whole model	8	3.722	0.881	n.s.
BR	Zone	2	2.890	0.236	n.s.
	Location	2	1.533	0.464	n.s.
	Zone × Location	4	0.711	0.950	n.s.
	Whole model	8	5.472	0.706	n.s.
NB	Zone	2	1.319	0.517	n.s.
	Location	2	0.599	0.741	n.s.
	Zone × Location	4	0.184	0.996	n.s.
	Whole model	8	2.053	0.979	n.s.

4 | DISCUSSION

4.1 | Fish community composition and species richness

The FPAs in the Rideau catchment were established in the 1940s to protect a subset of the largemouth bass population from fisheries exploitation and to promote recruitment, yet until recently there has been little effort to assess their effectiveness in protecting the initial focal species (largemouth bass) or the potential benefits afforded to the broader fish community. This study quantified the effectiveness of FPAs in three interconnected lakes within the Rideau catchment with the goal of defining the potential benefits of FPAs in freshwater temperate systems. The NMDS output suggested that there were distinct fish species assemblages among replicate lakes, particularly Big Rideau Lake relative to Lake Opinicon and Newboro Lake, which supported the independent assessment of fish species composition and

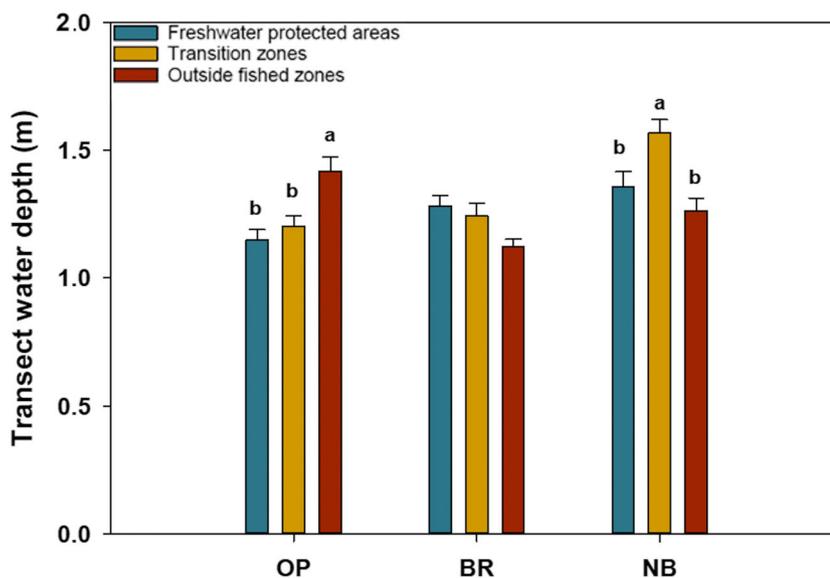


FIGURE 8 Mean transect depths between lake zones (i.e., outside fished zones, transition zones, and FPAs) examined by snorkelling censuses across replicate lakes: OP, BR, and NB. Using real-time visual assessments from snorkelling censuses, 62 transects in BR, 63 transects in NB and 46 transects in OP were evaluated. All transects were located within permanent FPAs (blue bars), the transition zones bordering the FPAs (<2 km from an FPA border; yellow bars), or within outside fished zones (red bars). Dissimilar letters (a and b) above the vertical error bars denote statistically significant differences between groups ($P < 0.05$)

TABLE 5 Output from GLM analysis for differences in mean transect water depth per lake zone, across each replicate lake. As the whole model tests for differences in mean transect water depth for both OP and BR were not significant, no *post-hoc* analyses were conducted. However, for NB the whole model test was significant, thus *post-hoc* analyses were conducted

Lake	Fixed effect	Degrees of freedom	$\chi^2_{(3)}$	Prob > $\chi^2_{(3)}$	Significance
OP	Zone	2	18.020	<0.001	***
	Location	2	0.607	0.738	n.s.
	Zone x Location	4	1.735	0.784	n.s.
	Whole model	8	20.063	0.010	*
BR	Zone	2	9.029	0.011	*
	Location	2	0.698	0.705	n.s.
	Zone x Location	4	1.525	0.822	n.s.
	Whole model	8	11.445	0.177	n.s.
NB	Zone	2	14.619	<0.001	***
	Location	2	2.457	0.292	n.s.
	Zone x Location	4	0.135	0.998	n.s.
	Whole model	8	17.002	0.030	*

*Significant at $P < 0.05$;

**significant at $P < 0.01$;

***significant at $P < 0.001$.

TABLE 6 Output from Nominal Logistic Regression analysis for differences in substrate composition per lake zone, across each replicate lake. For each of the replicate lakes, the whole model test for differences in mean transect vegetation complexity was not significant, thus no *post-hoc* analyses were conducted

Lake	Fixed effect	Degrees of freedom	$\chi^2_{(3)}$	Prob > $\chi^2_{(3)}$	Significance
OP	Zone	4	7.013×10^{-6}	1.000	n.s.
	Location	4	6.873×10^{-6}	1.000	n.s.
	Zone x location	8	9.701×10^{-6}	1.000	n.s.
	Whole model	16	8.868	0.918	n.s.
BR	Zone	6	8.696×10^{-6}	1.000	n.s.
	Location	6	9.843×10^{-6}	1.000	n.s.
	Zone x location	12	2.767	0.997	n.s.
	Whole model	24	16.187	0.881	n.s.
NB	Zone	6	5.254	0.511	n.s.
	Location	6	3.157	0.789	n.s.
	Zone x location	12	3.909	0.985	n.s.
	Whole model	24	20.590	0.662	n.s.

richness within each of the three replicate lakes. From the ANOSIM analyses, Big Rideau Lake was the only lake where species composition was significantly different between lake zones. Specifically, the abundance of shiners, bluegill and largemouth bass were significantly higher inside both the FPA and bordering transition zone, compared with the outside fished lake zone, despite there being no difference in habitat features measured across all sample locations (Figure 3). These results indicate a spillover of target fish species

(largemouth bass) and non-target species (bluegill and shiner) emanating outward from the Big Rideau Lake FPA. Given the relatively small home range sizes of largemouth bass and bluegill, these data suggest that these populations may be at their maximum density within the Big Rideau Lake FPA. A more holistic telemetry-based study tracking space-use patterns of fishes within FPAs would be invaluable in providing empirical data to confirm or track residency rates. For fish spillover to occur from a PA, it is a pre-requisite that the PA is 'filled' to facilitate the outflow of fish into non-protected zones (Goñi et al., 2010; Tupper, 2007). Spillover events are largely the result of density-dependent processes (e.g. intra-specific competition for resources) and can reflect, in part, the status and health of an ecosystem (Di Lorenzo et al., 2016).

As largemouth bass are one of the most highly targeted sport fish in Big Rideau Lake (Hogg et al., 2010; Hoyle, 1990; Sheridan & Krishka, 1995), the decline in fish numbers emanating outwards from this FPA could be a direct response to protection, which has been similarly observed in recreationally targeted marine fish (Westera, Lavery, & Hyndes, 2003). This trend could also be related to other factors not accounted for, including (but not limited to) increased forage availability (e.g. increased abundance of shiners and bluegill inhabiting the Big Rideau Lake FPA and the bordering transition zone). Similarly, bluegill are also popular sport fish within Big Rideau Lake (Hogg et al., 2010; Hoyle, 1990; Sheridan & Krishka, 1995), and the greater density of bluegill within the FPA and transition zone could be the result of protection. It is also possible that the higher numbers of largemouth bass and bluegill could be related to unique predator-prey interactions. Largemouth bass-bluegill assemblages are often held in check by both species, because of a balancing predator-prey dynamic (Hambright, Trebatoski, Drenner, & Kettle, 1986; Savino & Stein, 1982). More specifically, bluegill are a fundamental prey resource for largemouth bass, but are also a key nest-predator during their reproductive period (Cooke et al., 2006; Zuckerman & Suski, 2013). If the density of reproductively active largemouth bass is higher within the FPA and the transition zone, this could promote a greater abundance of nest predators (i.e. bluegill) owing to increased potential food availability. As nest-site fidelity is highly correlated with reproductive success in largemouth bass, coupled with relatively small home range sizes for both largemouth bass and bluegill (<250 m² for bluegill, and <1 km² for largemouth bass; Fish & Savitz, 1983; Ahrenstorff et al., 2009), relief from targeted fisheries pressure over time could allow for a greater proportional abundance of both species within the FPA, and also within the bordering transition zone as a result of density-dependent spillover (Abesamis, Russ, & Alcala, 2006; Halpern, Lester, & Kellner, 2010).

As shiners are not targeted by conventional recreational fisheries (i.e. rod-and-reel angling), only by commercial practices (e.g. collected using netting techniques for live-bait markets) within Big Rideau Lake (Hogg et al., 2010; Larocque et al., 2012), it is not certain why this grouped assemblage of species is more numerous within the FPA and the transition zone boundaries, especially when the risk of predation is significantly higher (i.e. with a greater density of largemouth bass within FPAs and bordering transition zones; Figure 4). In marine

areas, fisheries exploitation has been shown to alter community composition and species assemblages (Côté, Mosqueira, & Reynolds, 2001; Dulvy, Freckleton, & Polunin, 2004; Westera et al., 2003). Specifically, Watson, Harvey, Kendrick, Nardi, and Anderson (2007) found a variable response in the abundance of non-targeted prey fish species between MPAs and fished areas, indicating that fisheries exploitation of certain top-predator fish species can disrupt food web dynamics. It is also possible that differences in resource availability (e.g. food resources) may occur between these lake zones but were not accounted for in the present study.

The state of shoreline development could also potentially influence species composition and abundance, especially for species sensitive to habitat perturbations (Pusey & Arthington, 2003; Schneider, 2002). Degradation of the terrestrial riparian vegetation can reduce the shoreline buffering capacity to inhibit contaminated runoff (e.g. pesticide-laden rainwater) from entering lakes and rivers (Wenger, 1999). Extensive shoreline development is prominent throughout the Rideau Lakes area, largely caused by infrastructure development (e.g. construction of waterfront cottages). Through anecdotal observation, the focus of the shoreline development has been concentrated outside of FPAs, which could differentially affect species composition dynamics between zones (Bryan & Scarnecchia, 1992; Scott, 2006; Seitz, Lipcius, Olmstead, Seebo, & Lambert, 2006); however, the relationship between shoreline status (i.e. developed or natural) and fish community dynamics can be context- and species-dependent. Chu, Ellis, and de Kerckhove (2018) conducted a large-scale evaluation of the conservation benefits provided by terrestrial protected areas (TPAs) on fish communities inhabiting adjacent aquatic systems, and found that TPAs provide marginal benefits to lake fish assemblages. Furthermore, small-bodied fishes, including common shiner and golden shiner, were found in greater densities outside of TPA boundaries. Despite standardizing intra- and inter-transect habitat variables (vegetation complexity, depth and substrate composition) in the current study, shoreline development was not accounted for in the study design. Nevertheless, it is entirely possible that shoreline development is an important factor that indirectly influences differences in fish community assemblage dynamics between lake zones.

Species richness was also found to differ significantly between lake zones within each replicate lake. Within Opinicon Lake, species richness was highest inside the FPAs, intermediate within the bordering transition zones, and lowest within the outside fished lake zones (Figure 4). A similar trend was also detected in Big Rideau Lake, where species richness was significantly greater within both the FPA and the bordering transition zone, compared with the outside fished lake zone (Figure 4). Similar to community composition differences detected in Big Rideau Lake, it is likely that protection from fisheries afforded by the FPAs played a key role benefitting the fish communities in both Big Rideau Lake and Opinicon Lake. Greater species richness within PAs has been widely documented (Rodrigues et al., 2004), especially within marine environments (Côté et al., 2001; Edgar et al., 2014). Often the objectives of PAs are to promote habitat recovery, which enables populations and communities to re-establish a natural state (Abell et al., 2007; McLeod, Salm, Green, & Almany, 2009). Although

this can be particularly challenging to demonstrate, especially within the Rideau Lakes system owing to a lack of pre-FPA data, it is possible that the habitats within the FPAs both in Opinicon Lake and Big Rideau Lake have achieved a more naturalized state in the absence of fisheries activities, enabling these areas to support a greater, and more consistently diverse, community composition.

Differences in habitat features between lake zones may have influenced species richness within Opinicon Lake. Transect water depth was on average 20 cm deeper within the outside fished lake zone, compared with the FPAs and bordering transition zones (Figure 8). Therefore, it is possible that variation in species richness may be related to differences in mean transect water depth. Variation in water column depth can directly influence residence patterns of fishes, as shallow water is more easily influenced by abiotic and biotic processes (e.g. UV light exposure and avian predation; Cooke et al., 2003; De Haan, 1993), whereas deeper water can limit habitat complexity by reducing aquatic vegetation growth (Hudon, Lalonde, & Gagnon, 2000). Vegetation complexity, however, is considered a more influential driver of space-use and residency patterns of warmwater fishes, compared with water column depth (Hall & Werner, 1977; Keast & Harker, 1977; Keast, Harker, & Turnbull, 1978). Furthermore, it is important to note that transect water depth varied by a mere 20 cm, and no differences in vegetation complexity were detected between lake zones across any of the replicate lakes (Figure 7). As such, it is likely that the differences in mean transect water depth are not biologically significant in influencing the fish community parameters evaluated in Opinicon Lake.

Species richness was lowest within the Newboro Lake FPAs, intermediate within the bordering transition zones, and highest in the outside fished zones (Figure 4). The effect of protection was found to benefit the target species (largemouth bass) and specific non-target species (shiners) across all replicate lakes, as indicated from the multifactor analyses using the pooled fish parameter data (Figures 5, 6). It is possible, however, that the geographical location of the Newboro Lake FPAs may be unfavourable for certain fish species based on differences in habitat variables unaccounted for, including (but not limited to) unmeasured habitat complexity (e.g. dissolved oxygen) or microhabitat variables (e.g. finite differences in macrophyte communities between lake zones). These types of microhabitat features were not recorded in the present study, but may have influenced space-use dynamics of certain fish species – in particular, small-bodied fishes (e.g. small species or juvenile fishes; Paradis, Bertolo, Mingelbier, Brodeur, & Mignan, 2014; Massicotte et al., 2015; Stahr & Shoup, 2016). Similar to Opinicon Lake, differences in mean transect water depth were detected between lake zones within Newboro Lake and may have also influenced species richness between zones. Specifically, mean transect water depth was 25 cm deeper within the transition zone, compared with both the FPAs and the outside fished zones; however, it is important to note that the differences in transect water depth do not match the trend in species richness between zones (Figures 4, 8). Furthermore, no differences were detected in vegetation communities or substrate composition between zones. These habitat features are considered more important

in influencing space use and residence patterns in warmwater fishes, compared with water column depth (Keast et al., 1978; Keast & Harker, 1977; Werner et al., 1977).

Although collectively the Rideau Lakes FPAs have achieved their primary objective of providing effective protection of the largemouth bass populations, the indirect benefits of increased species richness (as observed through independent analyses in Opinicon Lake and Big Rideau Lake) is promising in terms of understanding and using FPAs for biodiversity conservation. Maintaining biodiversity is an essential component for optimal ecosystem functioning, as reduced biodiversity can impair essential ecosystem processes, such as nutrient cycling (Dudgeon et al., 2006; Loreau et al., 2001; Worm et al., 2006). As global freshwater biodiversity is currently in a state of decline (Reid et al., in press), FPAs may provide a useful tool to promote biodiversity conservation (Abell et al., 2007; Dudgeon et al., 2006; Pittock, Hansen, & Abell, 2008).

4.2 | Fish parameter evaluations

The effect of protection afforded by the Rideau Lakes FPAs was found to benefit largemouth bass and shiners significantly across all three replicate lakes. Specifically, the abundance and biomass of largemouth bass were 4- and 6-fold greater, respectively, inside FPAs compared with the outside fished lake zones. Similarly, shiner abundance and biomass were 4- and 6-fold greater, respectively, within FPAs compared with the outside fished lake zones (Figures 5, 6). These results provide evidence that protection offered by FPAs can increase the abundance and biomass both of target species (largemouth bass) and non-target species (shiners) within designated single-resource FPAs. Through direct assessments of species abundance and biomass across lake zones, the present study is one of the first to provide empirical evidence to allow a critically objective evaluation of FPAs. Indeed, these types of analyses are common in the marine realm (reviewed in Di Lorenzo et al., 2016), and are used as biomarkers to evaluate population health and status. However, there have been few quantitative investigations using these assessment metrics in FPAs (Hermoso et al., 2016), partly because of the limited use of PAs in fresh waters, and the scarcity of research data for those that do exist (Abell et al., 2007; Hedges et al., 2010; Hermoso et al., 2016). Pooling fish abundance and biomass data from all lake zones, from each replicate lake, enabled an objective, broad-scale, assessment to be made on the effectiveness and utility of the Rideau Lake FPAs. As this study is one of the first empirical evaluations of FPAs, understanding the broad-scale influence of protection on fish community parameters is an essential first step in understanding the variables that link conservation benefits to FPAs.

Largemouth bass remain one of the most highly sought-after sport fish in the Rideau Lakes system, and indeed in much of North America, with catch rates of black bass (i.e. largemouth bass and smallmouth bass) rising from 2,084,586 in 2005 to 3,145,829 in 2010 within the Rideau Lakes Wildlife Management Unit alone (Hogg et al., 2010). As such, selection for FPAs by largemouth bass

could be a response to growing angler pressure throughout the Rideau Lakes system, because the fish inhabiting the non-protected lake areas are subject to open, and increasing, exploitation. As discussed above, other abiotic and biotic factors that were not accounted for include (but are not limited to) specific resource availability, micro-habitat features, the state of shoreline development, and complex predator-prey interactions, all of which may have influenced these results. In particular, the methods used in the present study only evaluated coarse-scale habitat features (percentage vegetation cover, substrate composition and transect water depth) so it is possible that habitat variables that were not accounted for – such as water chemistry parameters, specific macrophyte communities, etc. – might have played an influential role in determining space-use and residence behaviour of the various species of fishes inhabiting the study lakes. In addition, because of the finite observation period, the lack of physical barriers isolating FPAs from the non-protected lake areas, and the variability of the home range size of largemouth bass (<1.0 km² depending on habitat complexity) relative to the total area covered by FPAs (OP ~1.0 km², NB ~3.33km² and BR ~0.57km²), the results may be limited to the observation period. It is possible, therefore, that the largemouth bass populations may indeed be transient between the lake zones, which further strengthens the need for telemetry-based research to evaluate the long-term residence and movement patterns of fishes within the FPAs. It is also important to note that the variation in FPA sizes between the replicate study lakes may also influence the occupancy rates of certain non-target species with large home range sizes (e.g. northern pike), consequently limiting the potential protective capacities of the FPAs for the broader fish community.

The results of this study support the initial mandate of the Rideau Lakes FPAs, which is to protect a subset of the largemouth bass population and to promote recruitment back into the main lake regions (Ontario Department of Game and Fisheries, 1946). Although these results suggest that not all Rideau Lakes FPAs are equal, with the Big Rideau Lake FPA providing the most detectable differences in measured community parameters, largemouth bass and shiner populations still benefitted from protection across all replicate lakes. As such, support for the continued management and use of the Rideau Lakes FPAs is merited. Although quantitative research pertaining to the effectiveness and utility of FPAs is scarce, examples are present in the literature to support the use of FPAs for conservation and fisheries benefits (Sztramko, 1985; Twardek et al., 2017; Zuccarino-Crowe et al., 2016). Specifically, seasonal FPAs have been designed and successfully used to protect nesting smallmouth bass from angler exploitation during the spawning and brood-care life-history stages, which has been shown to increase reproductive success at the population level (Suski, Phelan, Kubacki, & Philipp, 2002) while increasing angler catch-per-unit-effort (Sztramko, 1985). Furthermore, the use of FPAs to protect and rehabilitate lake trout (*Salvelinus namaycush* (Walbaum, 1792)) has proved successful within Lake Huron (Reid, Anderson, & Henderson, 2001) and Lake Superior (Schram, Selgeby, Bronte, & Swanson, 1995; Zuccarino-Crowe et al., 2016), increasing both adult and juvenile abundance within both

populations. The use of PAs has also positively benefited European eels (*Anguilla anguilla* (Linnaeus, 1758)) by increasing population size structure and migration rates in heavily fished waters (Cucherousset et al., 2007).

4.3 | Conclusion

The present study provided a unique opportunity to evaluate the effect of protection on fish community structure, through intra-lake evaluations of similar habitats that are managed under different fisheries management objectives (FPAs vs. fishable waters). The Rideau Lakes system allowed comparative, unbiased evaluations as each lake zone analysed consists of similar environmental and biological parameters. Thus, accurate and reliable inferences regarding the effectiveness and utility of these intra-lake FPAs could be derived, using comparative biological evaluations. Although fish community comparisons were not equal across all replicate FPAs, the effect of protection afforded by the Rideau Lakes FPAs was found to benefit both target (largemouth bass) and non-target (shiners) species through increased biomass and abundance. Current data regarding the effectiveness and utility of FPAs is lacking, and, given the present state of freshwater habitats and biodiversity, FPAs used in conjunction with other management tools may be an effective conservation strategy as evidenced from the present study. As protection is more economically viable compared with restoration, the use of FPAs by resource managers could provide a cost-effective means of promoting freshwater conservation (Abell et al., 2007, 2008). Beyond serving as a mechanism to maintain abundance, biomass, and biodiversity, FPAs may also serve to protect fish populations from fisheries-induced evolution (FIE; Kuparinen & Merilä, 2007; Twardek et al., 2017). FIE can occur as a result of intensive selection pressure on specific phenotypes (e.g. boldness) of a population (Heino & Dieckmann, 2009); as a result, the Rideau Lakes FPAs may provide refuge for fish populations against FIE. Given that the Rideau Lakes FPAs were established in the 1940s, obvious questions arise about the time that it will take for the conservation benefits of new FPAs to accrue. We encourage additional research on existing (especially long-standing) FPAs in different systems around the world to learn more about their potential role in aquatic conservation.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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