



Spatiotemporal ecology of juvenile Muskellunge (*Esox masquinongy*) and Northern Pike (*Esox lucius*) in upper St. Lawrence River nursery bays during their inaugural fall and winter

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Abstract

Understanding the spatial ecology of juvenile freshwater fish beyond summer months is an essential component of their life history puzzle. To this end, declines in the natural populations of sympatric Muskellunge (*Esox masquinongy*) and Northern Pike (*Esox lucius*) in the upper St. Lawrence River prompted study of spatiotemporal patterns and habitat requirements associated with earlier life stages of these congeneric, freshwater predators in fall and overwinter periods. Over 75 age-0 esocids were tagged and passively monitored using acoustic telemetry in four nursery embayments in fall and winter months from 2015 and 2017 months to elucidate spatiotemporal ecology and test hypotheses related to emigration. Presence, residency, space and habitat use were assessed and modelled against key environmental (i.e. water temperature and level) and biological (total length) covariates using mixed effect models. Muskellunge were found to spend more time in deeper, littoral regions with canopy-forming, submerged aquatic vegetation while Northern Pike aggregated in the deepest, highly vegetated region of their nursery embayment. Results suggest fish may exhibit transitional movements in fall months and may span outwards into nearshore regions along the main river channel. Studies informing coastal restoration initiatives to increase Muskellunge production are encouraged to assess sympatric habitat use relative to prominent embayment structures and further explore depth partitioning by these young predators. With a substantial influence from water-level regulation on use of nursery habitat, future studies must work in concert with management plans aimed at producing more natural riverine cycles and thus increased recruitment of *Esox* species.

KEYWORDS

esocids, habitat use, Muskellunge, Northern Pike, restoration, telemetry

1 | INTRODUCTION

For many freshwater species, little is known about their basic biology at juvenile life stages (see Cooke et al., 2016), though a prerequisite to protecting critical habitats and the corridors that connect them is understanding how fish distribute themselves in space and time at different stages of their life (Bond & Lake, 2003). To this end, fish–environment relationships are among the most fundamental to fish ecology, as they can constrain growth, fecundity and survival (Fry, 1971). To address widespread anthropogenic habitat alterations and noted declines in freshwater fish populations, both autecological and community-level management efforts to restore degraded fish habitats have increased (Cowx & Gerdeaux, 2004; Murry & Farrell, 2007), yet most of this work has focused on the creation of spawning habitat rather than ensuring that other key habitat features exist for all life stages. In particular, information on the ecology and seasonal habitat use of juvenile fish remains a significant research gap (e.g. Dombek, Menzel, & Hinz, 1986) and impedes management of coastal wetland ecosystems. Linking juvenile fish presence to specific physical and community habitat components is thus a useful tool when guiding habitat conservation and restoration activities (Murry & Farrell, 2007).

Substantial declines in self-sustaining yet naturally low-density populations of Muskellunge (*Esox masquinogoy*; Cook & Solomon, 1987; Farrell et al., 2007; Farrell, Getchell, Kapuscinski, & LaPan, 2017), and their sympatric congener Northern Pike (*Esox lucius*; Farrell, 2001; Smith, Farrell, Underwood, & Smith, 2007), have been detected in the upper St. Lawrence River. The proportion of Northern Pike inhabiting this region greatly exceed Muskellunge, which may be preyed on by their earlier spawning congener during their first year. Despite this sensitive period, and habitat modifications due to water-level regulation (Farrell, Holeck, Mills, Hoffman, & Patil, 2010), the Thousand Islands region is preceded by its reputation as a significant trophy Muskellunge fishery. Quantifying important habitat-by-esocid relationships may thus guide habitat enhancement projects and influence decisions regarding riparian and nearshore management (Murry & Farrell, 2007) to increase natural Muskellunge production.

Habitat partitioning between predatory *Esox* species during their juvenile years has been hypothesised to support sympatric populations. Farrell, Kapuscinski, and Underwood (2014) demonstrated that stocked and wild age-1 individuals exhibited interspecific habitat segregation at fine spatial scales, with Muskellunge concentrating in perimeter habitats, relative to deeper-dwelling Northern Pike (Cucherousset, Paillison, Cuzol, & Roussel, 2009; Hawkins, Armstrong, & Magurran, 2003, 2005; Pierce, Carlson, Carlson, Hudson, & Staples, 2013). Age-0 Northern Pike have been noted to aggregate in the deepest regions of their nursery habitat (Hawkins et al., 2003, 2005), particularly with decreasing water-levels (Cucherousset et al., 2009). Juvenile Northern Pike are well known for their individualistic behaviour, exhibiting a high degree of turnover in habitat use (Chapman & MacKay, 1984; Kobler, Klefoth, Wolter, Fredich, & Arlinghaus, 2008; Pierce et al., 2013). Indeed,

Pankhurst, Midwood, Wachelka, and Cooke (2016) noted age-0 Northern Pike exhibit three distinct behaviours: residing within a restricted area, moving between favoured areas, or using a large area with frequent shifts in habitat within a restricted area. Habitat availability may thus play a substantial role in the success of Muskellunge recruitment and survival within specific nursery embayments of regulated rivers, most notably during autumn emigration (Farrell et al., 2014). Without a better understanding of habitat use with respect to local variation (i.e. Cooper, Mead, Farrell, & Werner, 2008; Crane et al., 2015; Midwood, Kerr, Levick, & Cooke, 2015; Farrell et al., 2007), balancing the potential different habitat needs of sympatric, juvenile *Esox* sp. lacks precision.

Summer nursery habitat requirements for age-0 Muskellunge and Northern Pike are well understood; however, robust information on the critical habitats of either species, inclusive of the overwinter period, remains a significant gap in our understanding of juvenile esocids. These congeners indicate a preference for emergent vegetation in nearshore regions in their inaugural summer (e.g. Farrell, 1998; Hanson & Margenau, 1992; Owensby, Rice, & Aday, 2017); however, bottom-dwelling Northern Pike (Engstrom-Heg, Colesante, & Stillings, 1986) prefer dense, submerged aquatic vegetative [SAV] coverage (i.e. Casselman & Lewis, 1996; Cucherousset et al., 2009; Grimm & Backx, 1990; Pierce et al., 2013), while mid-column or surface-dwelling Muskellunge (i.e. Engstrom-Heg et al., 1986; Farrell, 1991; LaPan, 1985) are known to prefer intermediate SAV coverage throughout the water column (Murry & Farrell, 2007). Indeed, presence of fine-leaved, SAV in early summer periods and broad-leaved vegetation that grows close to the water's surface as summer progresses to autumn have been found important predictors for age-0 Muskellunge presence in large river systems (i.e. Crane & Kapuscinski, 2017; Farrell, 1998; Farrell et al., 2014; Farrell & Werner, 1999; Kapuscinski & Farrell, 2014; Murry & Farrell, 2007), whereas young Northern Pike may shift between patches and more pelagic areas (Kobler et al., 2008). Maximising edge habitat in littoral zones with moderate densities of SAV has thus been recommended to benefit multiple esocid life stages (Crane et al., 2015).

Habitat degradation throughout the St. Lawrence River system instigated the need for a long-term, science-based esocid monitoring programme through fish community research (Carmignani & Roy, 2017; Farrell, 2001; Farrell & Werner, 1999; Farrell et al., 2007, 2017). Recent relicensing of major power-producing dams on the St. Lawrence River then prompted timely negotiation of habitat restoration funds to better understand spatiotemporal ecology and habitat requirements of fishes impacted by management activities, including the earlier life stages of Muskellunge and Northern Pike (Kapuscinski & Farrell, 2014). The paucity of spatiotemporal information for the young-of-year *Esox* sp. had previously been hampered by technical limitations with telemetry (e.g. large tag size, short battery life); however, recent advances in telemetry technologies have now made it possible to tag and track small (i.e. <200 mm) fish over extended time periods (McMichael et al., 2010). To this end, preliminary research on this age-0 cohort using technological advancements supports primary use of coastal, nearshore habitats in fall (e.g. Farrell et al., 2014), followed by gradual movement by both

species to deeper, nearshore regions (Gallagher, Szekeres, Cooke, & Farrell, 2017). In this study, we continue work initiated by Gallagher et al. (2017) to elucidate intraspecific trends in age-0 Muskellunge and Northern Pike residency, spatial and habitat use during seasonal draw-down, and compare interspecific habitat use.

2 | METHODS

2.1 | Study location

This study took place in the Thousand Islands region of the upper St. Lawrence River (Figure 1), between Cape Vincent (43.30048 N, 79.80591 W) and Alexandria Bay, NY (43.30048 N, 79.80591 W). The upper St. Lawrence River is an oligotrophic system that is the effluence of eastern Lake Ontario and flows through the Eastern Great Lakes Lowland Forest (Thorp, Lamberti, & Casper, 2005). Water-levels in the upper St. Lawrence River are regulated by the International Joint

Commission under Plan-1958D at the Moses Saunders hydropower dam, a facility that has artificially suppressed the magnitude and periodicity of natural water-level fluctuation in the system (Farrell et al., 2010). The IJC has, however, implemented a new water-level regulation regiment, Plan-2014, which aims to better reflect natural hydrology of the system by permitting slightly greater variation (c. 6 in.) in water-level fluctuation to improve coastal wetland health (International Joint Commission, 2014). Such a plan may play an important role in alleviating changes in climatic variability that have driven fluctuations within the Great Lakes & St. Lawrence region, which experienced significant flooding during our study in 2017 and throughout 2019.

The Thousand Islands region is characterised by its complex archipelago (>1,800 islands), rocky shorelines, shoals, and extensive littoral community and coastal wetland embayments dominated by emergent and submerged vegetation (Farrell et al., 2010). The upper St. Lawrence River has also been the foci of a long-term monitoring programme for esocids (Farrell & Werner, 1999; Farrell et al., 2007, 2017), specifically, to inventory and evaluate critical early life habitats of Muskellunge and

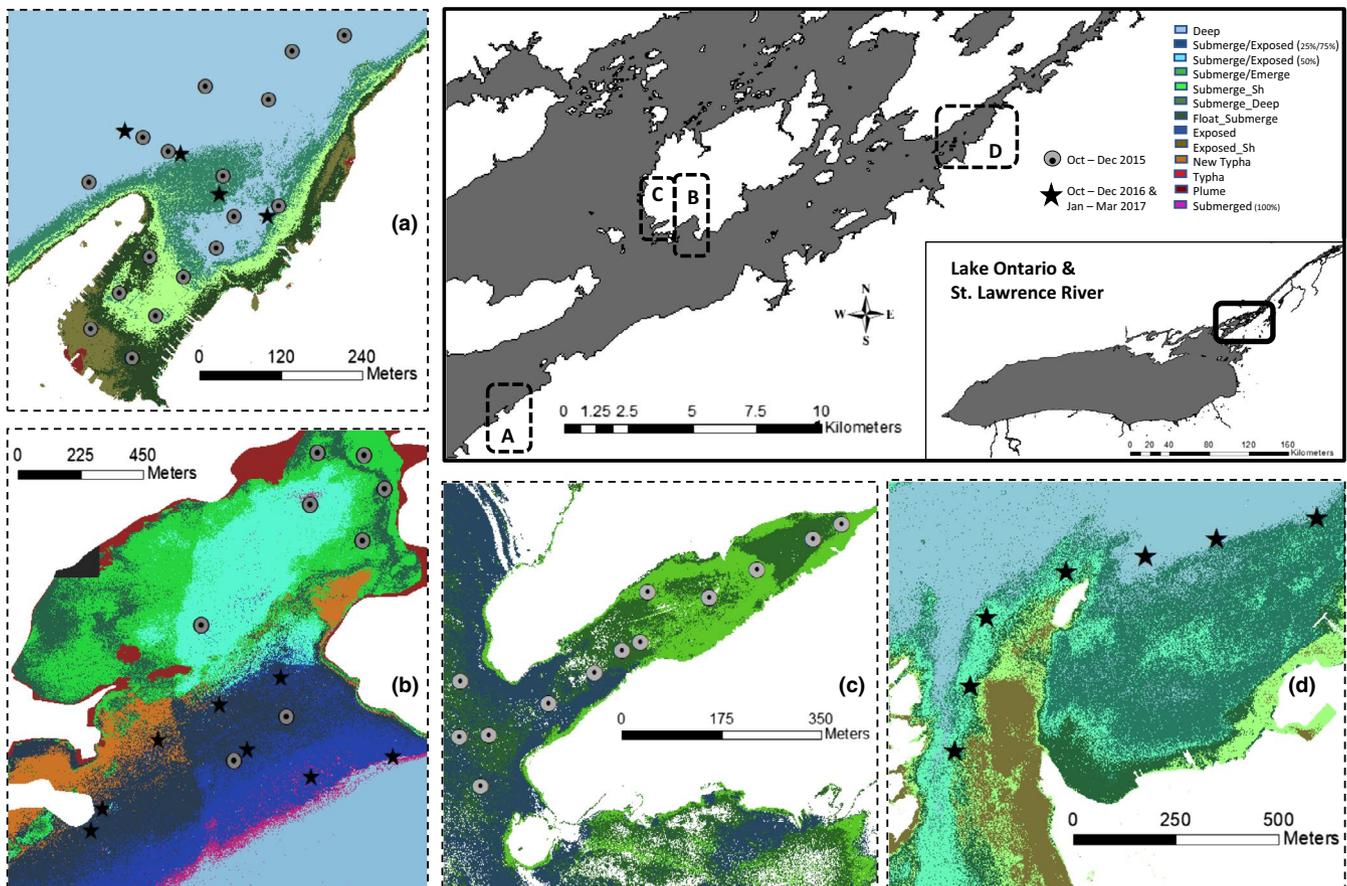


FIGURE 1 Map of the upper St. Lawrence River, and the study site, relative to Lake Ontario and the St. Lawrence River, where age-0 Muskellunge and Northern Pike were captured, tagged and tracked between 2015 and 2017. Embayment locations in which age-0 Muskellunge and Northern Pike were tagged and tracked are denoted by a dotted line indicating its location in the upper St. Lawrence River, with the associated letter. Embayments include (a) Rose, (b) Flynn, (c) Buck and (d) Grass Point bays. The receivers deployed in 2015 are denoted by a grey circle with a black dot, and those from November 2016 to March 2017 by black stars. Colours denote the habitat features selected through the Iso unsupervised clustering analysis in ArcGIS. Deep zones are those >3 m. Submerge/Exposed zones indicate regions with 25% or 50% exposed substrate. Submerge/Emerge zones include both SAV and emergent species in shallow waters, similarly to zones with both Floating and SAV. Exposed zones are exposed substrates in >3 m of water, and Exposed_Sh are similar zones in shallow waters. Note that *Typha* is only present in Flynn, while the Plume is only observed in the nearshore of Rose

TABLE 1 Detection and space use information for age-0 Muskellunge (MK) and Northern Pike (NP) monitored in the upper St. Lawrence River over two different years. Fish captured in 2015 were tracked between October and December, and those in September 2016 from October 2016 to March 2017. The no. of fish refers to the number of MK or NP considered "present" from tracking data. Core use (\pm SE) and extent (\pm SE) represent the mean 50% and 95% KUD (space range size) for each bay. Residency index (\pm SD) was calculated using the consecutive number of days fish were detected by the number of days the array was active

Year	Species	Bay	Size (ha)	No. of fish	Total Length \pm SD (mm)	Weight \pm SD (g)	Number of detections	Number of detections \pm SD	Core use (km ²) \pm SE	Extent (km ²) \pm SE	Number of days array active	Consecutive days present	Residency index \pm SD
2015	NP	Flynn	74	17	234 \pm 55.2	83 \pm 64.2	18,691	788 \pm 812	0.06 \pm 0.005	0.32 \pm 0.02	71	0-70	0.53 \pm 5.6
	MK	Rose	9	20	151 \pm 19.4	18 \pm 6.5	45,760	577 \pm 1 125	0.04 \pm 0.002	0.16 \pm 0.004	71	2-45	0.64 \pm 5.4
	MK	Buck	18	7	164 \pm 23.5	19 \pm 7.8	566	81 \pm 42	0.13 \pm 0.005	0.50 \pm 0.01	70	2-18	0.56 \pm 6.9
2016	NP	Flynn	74	7	227 \pm 38.3	85 \pm 47.2	1,074	80 \pm 102	0.18 \pm 0.01	0.62 \pm 0.008	178	9-165	0.05 \pm 0.9
	MK	Rose	9	4	182 \pm 45.5	35 \pm 28.5	761	143 \pm 127	0.02 \pm 0.008	0.06 \pm 0.002	180	31-86	0.17 \pm 0.5
	MK	Grass	47	5	174 \pm 33.5	32 \pm 11.9	661	98 \pm 102	0.11 \pm 0.004	0.49 \pm 0.01	170	0-12	0.00 \pm 1.0

Northern Pike. Like many coastal regions of the Great Lakes, those in the upper St. Lawrence River have experienced degradation of near-shore spawning and nursery habitats (Carmignani & Roy, 2017). As such, these coastal systems would benefit from science-based restoration initiatives and protection of critical habitat. Four embayments were selected for this study, based on past monitoring surveys where both age-0 Muskellunge and Northern Pike were known to be present. They included Rose Bay (44.185872°N -76.225169°E), Buck Bay (44.253241°N -76.136121°E), Flynn Bay (44.25324°N -76.136121°E) and Grass Point (44.283272°N -76.000774°E), embayments with a mix of open-water and vegetated nearshore coastal habitats.

2.2 | Embayment habitat descriptions

Rose Bay is a 9-hectare (ha) sheltered bay near Cape Vincent, New York, and its mouth slopes steeply into the main St. Lawrence River channel (Figure 1). Buck Bay (18-ha) is a narrow, shallow and sheltered bay that is adjacent to Flynn Bay, a 74-ha system off Grindstone Island with a drowned river mouth tributary (Figure 1; Farrell et al., 2014). Grass Point (47-ha), a New York State Park, was the least sheltered embayment that had a wide interface with the main St. Lawrence River channel (Figure 1). Although exposed to the main channel, Grass Point exposure to prevailing westerly winds was limited by outcrops of islands and mainland shoreline that extends north into the river.

2.3 | Fish capture

Age-0 Muskellunge and Northern Pike were captured using a standardised seining protocol where a 36.6-m seine net (6.4 mm mesh, stretch measure) with a 12.2-m bag was deployed in water depths <1.5 m for a distance of 18.3 m; one full transect encompassed 449 m² (Farrell & Werner, 1999). Muskellunge are monitored throughout the growing season, and those captured for tagging were within expected length for the age-0 range (J. M. Farrell, personal communications). The expected size range for Northern Pike captured was established a priori by checking scale samples for lack of annulus formation in prior studies (J. M. Farrell, personal communications). Captured age-0 Muskellunge and Northern Pike were transferred to a cooler that was held in a small dingy with aerated water from the site of capture until seining was complete. Cooler water was periodically exchanged to prevent thermal stress to fish.

A total of 38 Muskellunge were captured in all four bays studied over both seasons: 28 between 11 September 2015 and 15 September 2015, and 10 between 06 September 2016 and 06 October 2016 (Table 1). All age-0 Northern Pike ($n = 38$) were captured and tracked solely in Flynn over both seasons; 23 individuals were captured between 26 September 2015 and 28 September 2015, and 15 on 21 September 2016 (Table 1). The lone Muskellunge captured in Flynn in 2015 was translocated to Buck to bolster the sample size; however, upon consideration that this individual may

exhibit abnormal behaviour, it was not included in our spatial analyses, but its movement patterns are discussed.

2.4 | Tags and surgical implantation

Individuals were anaesthetised in an aerated basin using a concentration of 75 mg/L tricaine methanesulfonate (MS-222) until equilibrium was lost (i.e. opercular rates slowed, and fish were unresponsive to touch; see Carter, Woodley, & Brown, 2011; Wagner & Wahl, 2011; Wagner, Woodley, Seaburg, Skalski, & Eppard, 2014). Once anaesthetised fish were weighed (nearest 0.1 g) and measured for total length (TL; nearest 1 mm). Fish were placed supine on a small surgery table in a small tub with recirculating water and received a maintenance anaesthetic dose (75 mg/L MS-222) by placing a small-diameter (size) silicone rubber tube from a pump (in the recirculating tub) inside the mouth so water gently flowed over the gills. A c. 5 mm lengthwise incision was made with a No. 21 scalpel between the pelvic and pectoral fins and closed with one simple interrupted suture (PDS II, 3/0; Ethicon Inc.) following tag insertion. Tagged fish were implanted with a sterilised (betadine) mini-acoustic JSAT tag (2015 and 2016: Lotek Wireless, L-AMT-1.416, 0.28 g, 10.7 × 5.4 × 3.1 mm; 2016: PNNL JSAT, 0.20 g, 15.0 × 3.4 mm; Tables S3 and S4) into their coelom. Surgical tools were sterilised in a diluted solution of betadine between each surgery. Persistent opercular movement of anaesthetised fish was used to monitor their condition during surgery. Surgery time for both species ranged from under 3 to 12 min due to surgeons of varying expertise. Recovery time was not recorded. Both tag types emitted a coded signal frequency of 416.7 kHz, a pulse repetition interval (PRI) of 1 s minimum with 1 s increments, and signal strengths of c. 156–158 dB (re: uPA at 1 m). Fish recovered in the aerated basin until equilibrium was retained and were released in the bays where they were originally captured, except the translocated individual.

2.5 | Receiver deployment

In September 2015, 38 receivers (Lotek WHS4250 416.7 KHz, Newmarket, Ontario) were deployed in Rose, Buck and Flynn bays. A grid system in Rose and Buck bays was used to maximise residency and detection capacity with the assumption that fish remained in the shallow (<1 m) back portion of bays in the fall. A loose gate of receivers was positioned in deeper waters (1.5–3.0 m) of both bays to assess outward movement and residency as fall progressed to winter from October to December (Figure 1). Receivers in Flynn were deployed to assess the bay's shallow interior and deeper (>1 m) regions. All of these receivers were pulled and downloaded in December 2015. In October 2016, 21 receivers were redeployed in the nearshore region of Rose and Grass Point and the mouth of Flynn to assess fall residency. In November 2016, all receivers were downloaded and 24 (the original 21 plus

three additional) were redeployed in the mouth or perimeter of Rose, Grass Point and Flynn until March 2017 (Figure 1). In every instance that receivers were deployed, their location was recorded with a handheld GPS unit.

Receivers deployed in shallow waters were mounted using zip ties and electrical tape to rebar that was driven into the substrate. The receiver hydrophone tip sat several inches above the bottom to capture signals and to prevent attenuation issues. Receivers deployed in waters >2 m were secured between two sandbags filled with cobble-sized rocks and attached to twisted polypropylene rope that was connected to a buoy at the surface (Figure S1). Receivers set at depths >3 m were rigged so that the receiver was near the substrate and the connected buoy was 2 m below the water surface to ensure that water-level fluctuations would prevent adverse contact with boats and that ice did not form around the buoy and move the receiver.

The effective range at which implanted fish could be detected was calculated as the ratio of observed to expected detections captured by receivers from acoustic tags. Both implanted and sentinel tags deployed emitted a series of bursts (herein known as a ping) with a digital ID every 20 s; receivers were set to emit a similar ping every 60 s. To calculate the effective range, we divided the observed number of pings detected by the number expected ($n = 180$) per hour from sentinel tags, as well as the observed/expected number of pings from nearby receivers themselves ($n = 60$). Sentinel tags were placed 30, 70 and 120 m away from selected receivers in the nearshore region of Buck and Rose in 2015, to determine the furthest distance tagged fish would be detected 50% and 100% of the time. Manual range testing was also completed at 10, 30, 50, 70, 100 and 120 m from select receivers in Rose, Buck and Flynn in 2015. In 2016, range testing was not completed; rather, each receiver was set to emit a ping (known as a beacon signal) with similar power output to real tags (P. Wigglesworth, personal communications) every 60 s. Variation in pings/hour between signal sources (beacon vs. sentinel/manual tag) was accounted for by multiplying observed beacon signals by three.

2.6 | Environmental variable sources

A HOBO Pro v2 water temperature logger was attached to a receiver deployed in the interior, shallow region of each Rose and Buck in 2015, as well as a receiver deployed along embayment edge (before meeting the main channel) in each Rose, Grass Point and Flynn in 2016. New loggers were deployed in deeper waters associated with the winter 2016–2017 Rose array (>3 m) and waters c. 2 m deep in Flynn and Grass Point arrays. Mean monthly water-level data were sourced from the International Great Lakes Datum (Fisheries and Oceans Canada, 2017), where an average water-level is computed from a coordinated network of gauging stations throughout Lake Ontario. Water depths were documented in metres above sea level, as per IGLD 1985. Daily air temperature data were used as a proxy for water temperature in bays where temperature loggers were

not placed or failed to upload data, which included Buck and Flynn (2015) and Rose (2016/17). Air temperature data were sourced from Environment and Natural Resource Canada (2018) historical weather and climate data for October to December 2015 and October 2016 to March 2017. Hourly water temperatures for Rose (2015), Grass Point (2016/17) and Flynn (2016/17) were used to generate daily mean values and compared against daily mean air temperatures values using Pearson's correlation coefficient; the relationships were not strongly correlated ($p = <.70$). If they were highly correlated, water temperature from one bay (i.e. Grass Point) would have been used for another bay monitored within the same year (i.e. Rose).

2.7 | Analytical approach

Detection data were filtered so that double detections and detections <5 min apart at the same receiver were excluded. Detection data were then separated by year (2015 vs. 2016). Since the October arrays were a different design than November to March, October data were included to identify presence/absence and residency and omitted from space and habitat use analyses. Independent analyses were then performed on the age-0 cohorts tagged in 2015 and 2016/17, age-1 Muskellunge (captured in 2015) detected overwinter in Rose 2016/17, and age-1 Northern Pike (tagged in 2015) detected in Flynn 2016/17. Differences in overall body size, represented by total length, were compared for each species between years using a one-way ANOVA, with year as a fixed factor.

2.8 | Diel data

Detections over the full study period were categorised into four diel times: dawn (0500–0859), day (0900–1559), dusk (1600–2059) and night (2100–0459). Dusk and dawn were selected based on the earliest and latest hour that sunrise and sunset were observed in October. A generalised linear mixed model (*glm*, R package "lme4"; Bates, Maechler, Bolker, & Walker, 2015) with a Poisson distribution and a least regression test ("LR") were used to analyse the total number of detections per diel period from sentinel tags, beacon signals and tagged fish. Tagged data included the total number of detections per diel period from all receivers per embayment. Models included bay and year as fixed factors, with fish as the random factor. Pairwise comparisons were evaluated using a Tukey HSD test (*glht*, R package "multcomp"; Hothorn, Bretz, & Westfall, 2008). Significance was identified if $\alpha \leq 0.05$. All detection values are presented as mean \pm SD, and all residency and space range values are presented as \pm SE.

2.9 | Monthly residency

Abacus plots of acoustic detections were examined to visually assess spatiotemporal residency of fish in the arrays for the duration of

each study period (3 months 2015, 6 months 2016–2017; R package "glatos"; Holbrook, Hayden, & Binder, 2016). The presence/absence of a fish was identified on a monthly basis; a fish was considered present and assigned a value of one if it was detected ≥ 7 days in a given month. If not, they were considered absent and given a value of zero for that month. A monthly residency index ranging from 0 to 1 (where values close to 1 indicated high residency in the array; Espinoza, Cappel, Heupel, Tobin, & Simpfendorfer, 2014) was calculated for each fish classified as present by dividing the number of days a fish was detected within an array by the number of days the array was active during that month. To compare residency of fish detected from October 2016 to March 2017, monthly residency index values were divided by the number of receivers active each month to ensure a reduction in detections was not due to the reduction in number of receivers, and to confirm a natural pattern rather than an artefact of the array.

2.10 | Space range

Space range was calculated based on centre of activity (COA) locations and kernel utilisation distribution (KUD) values. COA locations were calculated using a method from Simpfendorfer, Heupel, and Hueter (2002), where mean fish positions (from all receivers within sequential 2-hr intervals) were calculated throughout the study period, to reduce spatiotemporal autocorrelation (Rooney, Wolfe, & Hayden, 1998). KUD values (50% core and 95% extent) were then estimated for individual fish by using the kernelUD function (R package "adehabitatHR"; Calenge, 2006). The kernelUD function included a smoothing parameter (h , which controls the width of the kernel functions), a grid size (on which the KUD should be estimated, and its resolution) and an extent value (the extent of the grid used for the estimation). The KUD considers the space use or range described by bivariate probability density based on relocation coordinates (the COA locations) and the kernel method (Wand & Jones, 1995), which averages the relocation values. The smoothing parameter was determined by calculating the " h " value for each fish within an embayment (per year) and using the median value (Hollensead, Grubbs, Carlson, & Bethea, 2016). The size of the grid was established by increasing grid values in increments of 250 (starting at 500) until the error message of "grid too small" no longer appeared, and extent values were increased starting at one. A consistent grid value of 1,000 (appropriate across all bays and years) and extent value of four were used. Finally, variation in core use and extent among individuals in the same embayment were assessed using linear models.

2.11 | Habitat features

Habitat types within each bay were determined using an image classification of raster files representing each bay in ArcGIS 10.5.1 (ESRI, 2017) to compare embayments in a consistent manner. NY GIS Clearinghouse orthoimage raster files from 2015 of each

embayment (NYS Information Technology Services, 2016) were merged using the *Mosaic Data Management* tool, and clusters associated with physical habitat types (e.g. vegetation, exposed substrate, depth) were identified for each embayment mosaic map using the *Iso unsupervised image classification* tool (20 classes), in which the Iso Cluster and Maximum Likelihood Classification tools are combined and classify individual pixels based on the raster bands (red, green, blue) associated with the raster files. Habitat types were established by comparing clusters to vegetation survey data in published literature (Farrell et al., 2014) and an Ontario submerged aquatic vegetation (SAV) shapefile, which provided coarse resolution of exposed sand regions, low and high SAV (Shuchman, Sayers, & Brooks, 2013). Mosaic maps for each bay were reclassified (*Reclassify* tool) based on like habitat features (see Figure 1 legend) and converted into polygon features (*Raster to Polygon* tool). To calculate the percent of each habitat type within each fish's core range per month, monthly core use (50% KUD) was first converted to ESRI shapefiles (*writeOGR*, R package "rgdal"; Bivand, Keitt, & Rowlingson, 2017) and then imported into file geodatabases (*Feature Class to Geodatabase* tool). Individual monthly core use ranges were intersected (each separately) to the habitat polygons, using the intersect tool. The percentage of each habitat type used within an individual's core use was divided by the total core area to calculate habitat proportions used.

2.12 | Mixed effect models

A series of mixed effect models (R packages "nlme," Pinheiro, Bates, DebRoy, & Sarkar, 2019; "lme4," Bates et al., 2015) were applied to focal bays, as recommended by Woodside (2009), to explore the influence of water-level, air and/or water temperature, and fish size (fixed factors which may elicit differences among response levels; Bolker et al., 2009) on spatial components (e.g. residency, space and habitat use within deployed arrays) for these *Esox* sp. between bays and years. Fixed factors were centred to simplify interpretation and facilitate comparison of their importance (Schielzeth, 2010). Fish ID was a random factor to enable population-level prediction and account for the repeated-measures nature of the data (Bolker et al., 2009). Collinearity between fixed factors was compared using Pearson correlation coefficients and variance inflation factors (*vif*, R package "car"; Fox & Weisberg, 2011), and residual and autocorrelation plots evaluated models' goodness of fit (Bolker et al., 2009; Zuur, Ieno, & Elphick, 2010). If autocorrelation was present, models were fitted to account for spatial (e.g. *corExp*) or temporal (e.g. *corAR1*, *corARMA*) correlations and heteroscedasticity. Akaike's information criterion (AICc) was calculated, and the models with the lowest AIC corrected for small sample sizes were selected (Burnham & Anderson, 2004; see Tables S7, S9, S11, S13, S15, S17, and S19). Linear models (LME) for space use were analysed using maximum likelihood, an "optim" *lmeControl* and a value of 10,000 for both *maxIter* and *msMaxIter*. Generalised linear mixed models (GLMM) were fitted with a binomial error distribution using a logit link and an *nAGQ* value of seven (e.g. Bolker et al., 2009). The *nAGQ* (Adaptive

Gauss-Hermite Quadrature) model is more accurate than Laplace estimations (Bolker et al., 2009) and increased the accuracy of the model's residency estimation (Pinheiro & Chao, 2006). Due to convergence failure, two separate optimisers were used as follows: the "bobyqa" for Flynn, Buck, and Grass Point and "nloptwrap" for Rose.

3 | RESULTS

3.1 | Descriptive

Over the course of the study, 98%–100% of age-0 fish tagged were detected on multiple receivers (2015:98% Muskellunge and 100% Northern Pike [Figures S2–S5, S7, S8, S11; Tables S1, S2]; 2016/17:100% Muskellunge and 98% Northern Pike [Figure S6, S9, S10, S12; Tables S3, S4]), indicating high survival in fall and overwinter periods. The average size of age-0 Muskellunge increased throughout our study (2015:154 ± 20.8-mm total length; 2016:177.0 ± 36.8-mm total length) but the difference was statistically indistinguishable ($F_{1,37} = 3.74, p = .06$). Similarly, Northern Pike did not statistically differ in total length between 2015 (234.0 ± 55.2-mm excluding 380-mm outlier) and 2016 (227.0 ± 38.3-mm; $F_{1,37} = 1.24, p = .27$), despite a slight (c. 7 mm) decrease in average size. Northern Pike tracked in 2015 exhibited high intraspecific overlap in range size and distribution, as did Buck Muskellunge, unlike the Muskellunge tracked in Grass Point and Rose bays in 2016. One Muskellunge originally caught and tagged in Rose in 2016 was subsequently recaptured 4 weeks later and had grown 78 mm and gained 49.3 g (Figure S13).

3.2 | Environmental variables

Water elevations in Lake Ontario (which directly influence our study site) decreased from 74.56 m IGLD85 (October 2015) to 74.47 m IGLD85 (November 2015) and increased in December 2015 to 74.74 m IGLD85. Levels increased substantially over the fall of 2016 through winter of 2017, nearly half a metre from 74.48 to 75.00 m IGLD85. For reference, 74.20 m IGLD85 is considered low water, while 75.40 m IGLD85 is considered high water for Lake Ontario.

Water temperatures were similar between bays (Rose 2015, Flynn 16/17 and Grass 16/17) between years in fall (October, 11.6°C to 15.1°C; November, 9.3°C to 9.5°C) and winter for Flynn and Grass (January, 1.3°C to 1.5°C; February 0.6°C; March, 4.0°C to 4.4°C); however, December water temperatures varied between years with warmer temperatures in Rose, 2015 (10.5°C) than Flynn or Grass Point in 2016/17 (4.2°C). Air temperatures were consistently lower than water temperatures (2015: October, 8.2°C; November, 6.2°C; December 3.7°C; 2016: January, -3.0°C, February, -2.2°C; March, -3.2°C). To this end, air temperature did not significantly influence spatial variables tested for either species, likely due to its unreliable predictive powers (i.e. lack of

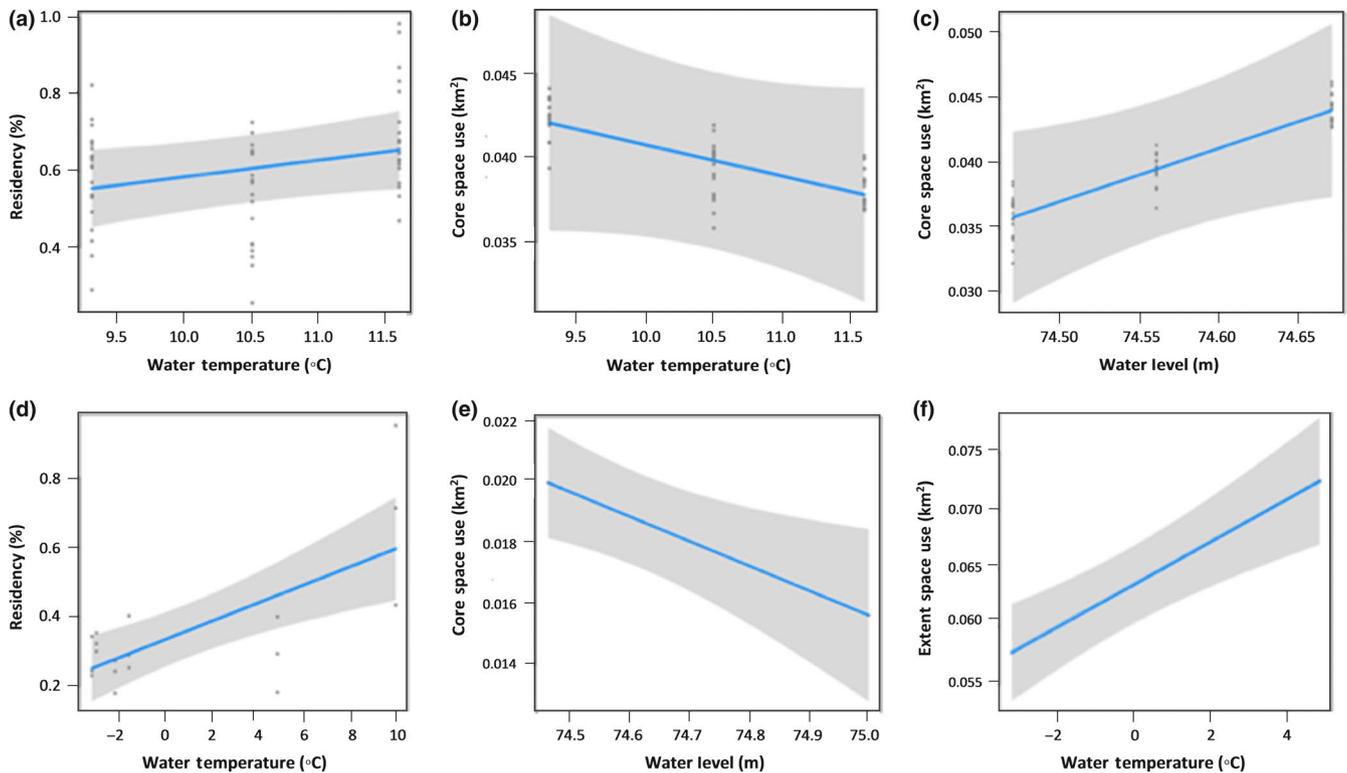


FIGURE 2 Variation in spatial variables of age-0 Muskellunge in Rose Bay from September to December, 2015 (a–c) and November 2016 to March 2017 (d–f); a) residency and (b) monthly core use are compared relative to water temperature, as well as (c) monthly core use against water-levels; (d) residency is compared against water temperatures, (e) core use against higher water-levels, and (f) extent against higher water temperatures

correlation with water temperature; inappropriate parameter for a coastal embayment study).

3.3 | Diel detections and range testing

A significantly greater number of sentinel pings were detected by receivers during night (33%; $z = 2.49$, $p = .01$) and day periods (30%; $z = 2.38$, $p = .02$) relative to pings detected at either dusk or dawn. The number of fish detections followed a similar pattern to sentinel tags between both years and all four bays; detections were noted for both species more so at night (30%–40%) and dawn (15%–32%) followed by dusk (14%–19%) and day (4%–19%) in their respective bays. Indeed, Muskellunge were detected significantly more often at night ($n = 18,279$; $z = 14.97$, $p < .001$), followed by day ($n = 10,321$; $z = 21.50$, $p < .001$) and dawn ($n = 9,649$; $z = 16.80$, $p < .001$), relative to dusk periods ($n = 7,444$; intercept, $z = 706.2$, $p < .001$). Though there was no significant difference in the number of detections captured from Northern Pike between diel periods (compared to Muskellunge), more detections occurred at night ($n = 8,195$) and dawn ($n = 7,113$) than day ($n = 3,407$) or dusk periods ($n = 3,593$). Significantly fewer detections were captured in 2016 relative to

2015 for both Muskellunge and Northern Pike ($\chi^2 = 19.40$, $df = 1$, $p < .001$), likely due to array location and Muskellunge sample size. Detection range for our JSAT tags were very low and varied by embayment and likely placement of receivers. For instance, in Buck Bay, 25% of pings from sentinel tags were detected at 50 m and manual tracking yielded 30% at 35 m. In Rose Bay, 100% of pings were detected at 30 m in the shallow back-bay, with 50% at 50 m, while manual tracking near the embayment mouth yielded 30%–75% of possible detections at receivers 65 and 75 m away respectively. It is evident that environmental influences (i.e. presence of canopy-forming vegetation, changes in bathymetry) likely played a role in fish detections as well as diel variation rather than fish movement between diel periods.

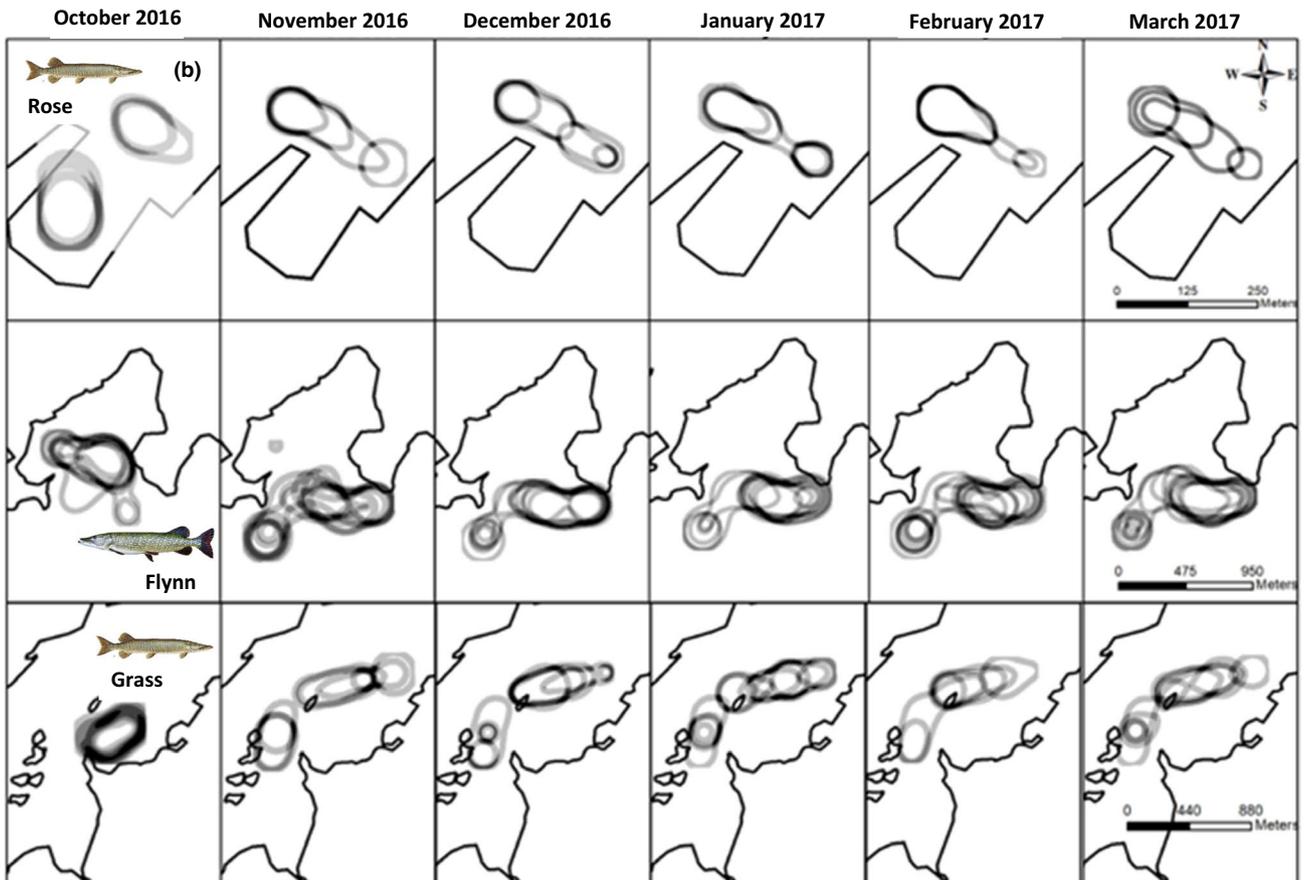
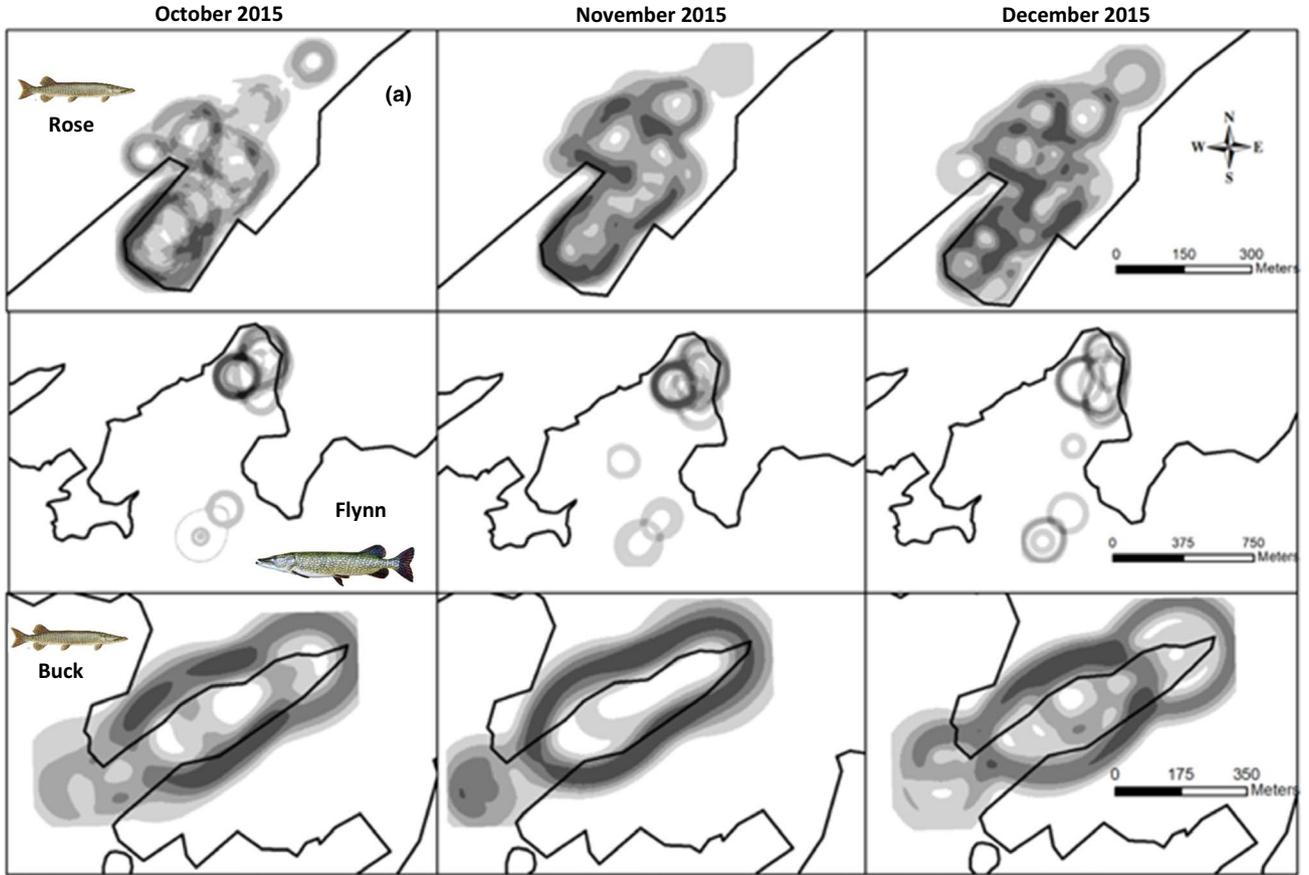
3.4 | Detections, residency & space range

3.4.1 | Muskellunge

Rose Bay

Of the 20 age-0 Muskellunge initially tagged in Rose in 2015, 16 fish were frequently detected ($577 \pm 1,125$ [mean number of

FIGURE 3 Core use range (km^2 –50% KUD) by age-0 Muskellunge and Northern Pike in the upper St. Lawrence River in (a) 2015 and (b) 2016 and 2017. Darker circles denote areas heavily used by fish based on a monthly analysis for (a) Rose (top), Flynn (middle) and Buck bays (bottom) and (b) Rose (top), Flynn (middle) and Grass Point (bottom)



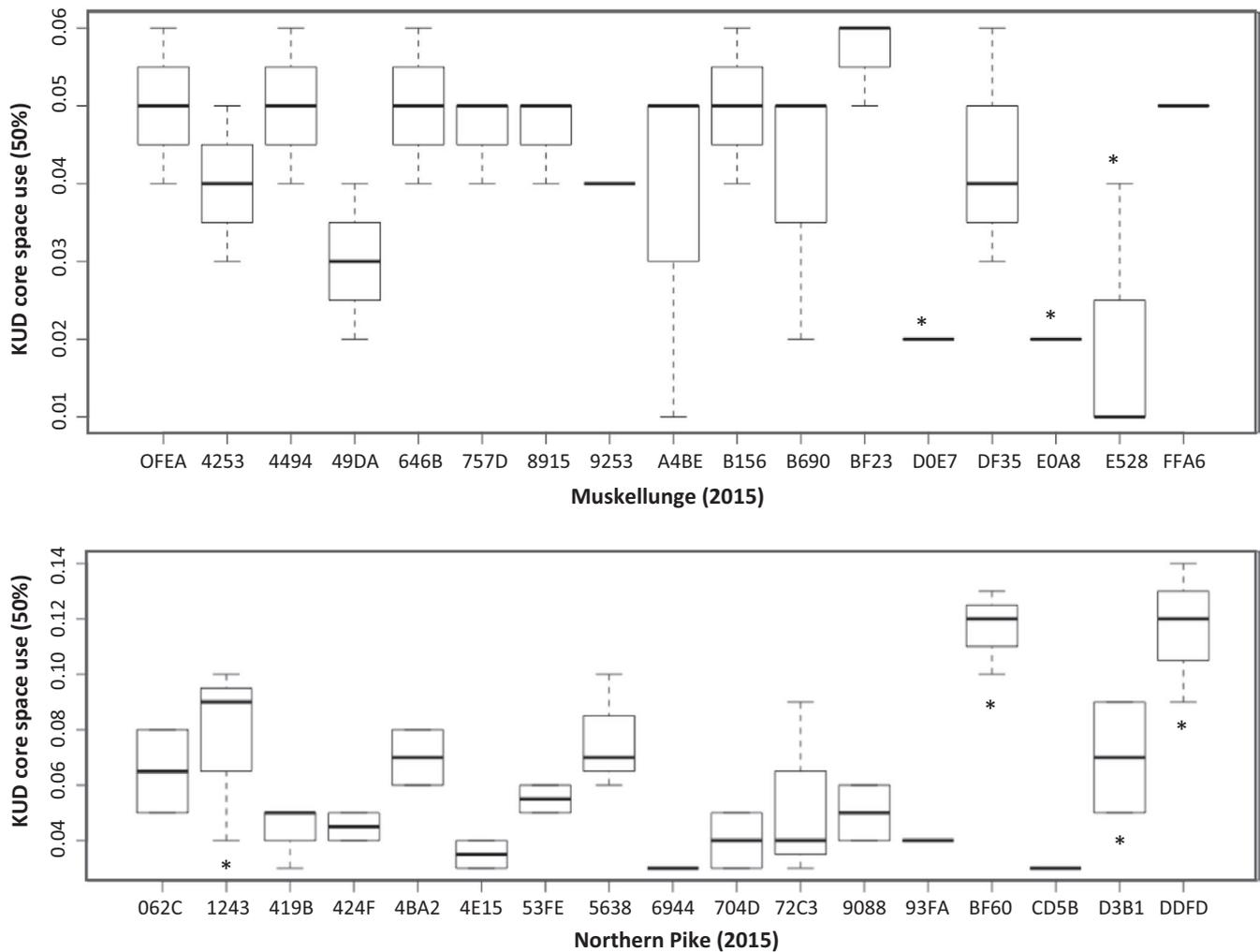


FIGURE 4 Differences in core use (km²–50% KUD) between Muskellunge in Rose, 2015, (top) and Northern Pike in Flynn, 2015 (bottom). Total length did not influence core use size between fish. Fish with significant differences in core space use are denoted by a star, above or below their boxplot

total detections per fish \pm SD], Figure S8, Table S1). In contrast, the five Muskellunge (including two recaptures) tagged in 2016 were detected less frequently over winter (143 ± 127), likely a product of differences in receiver array design and sample sizes between years. In 2015, residency index was highest during early fall (>0.50) and was significantly correlated with warmer water temperatures ($>10^{\circ}\text{C}$) in both 2015 and 2016 ($\chi^2 = 7.52$, $p = .006$, 2015, Figure 2a; $\chi^2 = 7.52$, $p = .006$, 2016, Figure 2d; see Tables S8 and S19). Larger fish were found to remain in the bay longer, as residency index was significantly higher with body size ($\chi^2 = 4.49$, $p = .03$) in 2016, but no effect was found in 2015. Covariates (i.e. temperature and water-level) had no effect on presence/absence in either season.

Three (out of 16) Muskellunge (D037, E0A8 and E528; 162–171 mm) detected in 2015 exhibited significantly smaller ($F_{19,56} = 3.33$, $p = .001$) core use range, relative to conspecifics (Figure 4), and were of intermediate size (range of 156–185 mm in Rose). The range size of individual fish was similar from September to December 2015 (core, $0.04 \text{ km}^2 \pm 0.002 \text{ SE}$, extent $0.16 \text{ km}^2 \pm 0.004$

SE; Table 1; Figure 3a, S16b,d). In 2016, all three Muskellunge detected shared the exact same core use size of 0.02 km^2 (Figure S17g, h), likely as a product of the array design, which drove small utilisation distribution outputs.

Water temperature and water-level were significant variables contributing to the fit of the data for core use range. In 2015, Muskellunge had smaller core use sizes as temperatures declined from 9.5°C to 11.5°C ($\chi^2 = 4.59$, $p = .03$; Figure 2b) and at water-levels below 74.70 m IGLD85 ($\chi^2 = 4.19$, $p = .04$; Figure 2c; Table S8). Over the 2016 winter season, Rose Muskellunge retracted their core use range in the small region of the embayment mouth monitored when water-levels increased substantially in early spring ($\chi^2 = 5.07$, $p = .02$, Figure 2e) and had larger extent sizes (95% KUD) when air temperatures were warmer ($>10^{\circ}\text{C}$) in early autumn ($\chi^2 = 14.36$, $p < .001$, Figure 2f; Table S8).

Buck, Flynn and Grass Point bays

All seven Muskellunge tagged in Buck were present within the bay in October and November, and their residency index remained high

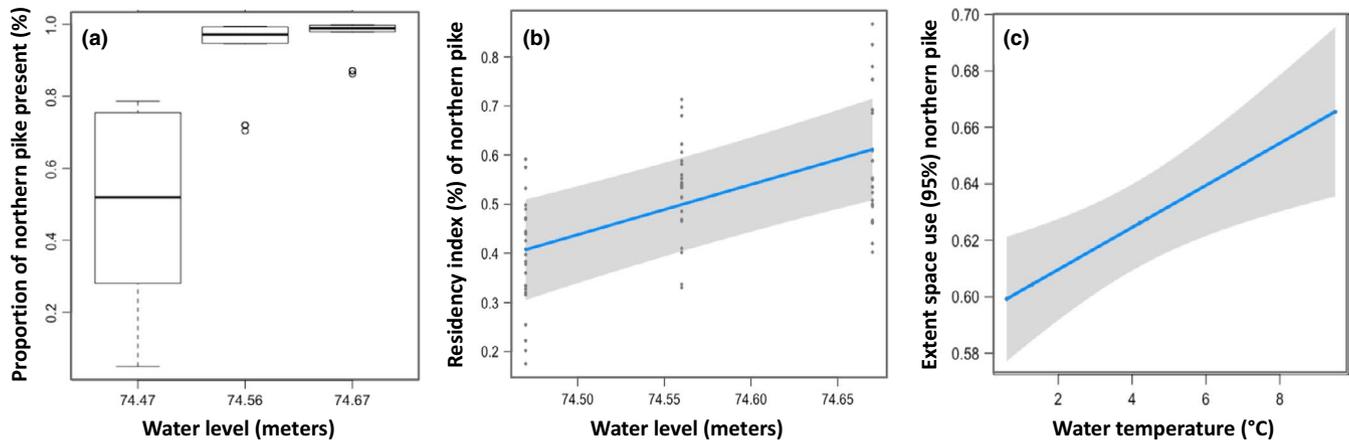


FIGURE 5 The effects of water-level and temperature on the spatial ecology of age-0 Northern Pike from September to December 2015, including (a) the proportion of individual Pike present, (b) their residency index relative to IGLD 1985 water-levels managed by the IJC, as well as their (c) extent range relative to water temperature in degrees Celsius

each month. Fish were not often detected (81 ± 42 , [mean detection of all fish \pm SD]); however, all fish exhibited extensive overlap in their use of Buck Bay (Figures 3a, S16a, b) with core use sizes of <0.15 km². Extent sizes averaged 0.50 km² \pm 0.01 SE (Tables 1, S1). Covariates had no effect on spatial responses among the factors examined (see Table S12). The lone Muskellunge tagged and transported to Buck from Flynn was infrequently detected in Buck ($n = 123$ detections) throughout the fall of 2015; however, it was detected in Flynn in 2016/17 for a brief period as an age-1 fish ($n = 43$ detections), demonstrating it migrated to its original site of capture. The sole Muskellunge captured, tagged and released in Flynn in 2016/17 was also infrequently detected over winter.

The five Grass Point Muskellunge tagged maintained a consistent presence within the embayment perimeter from November to March, indicated by moderate residency index values (0.38 ± 0.27 SD, Table S3). Space use was consistent (0.11 km² \pm 0.004 SE, core; 0.49 km² \pm 0.01 SE, extent) among fish, though their individual use of the embayment perimeter where waters drop off varied extensively; space range did not overlap visually (Figure 3b). No effects from biological or environmental variables on presence/absence, residency index or space occupied were observed (see Table S14).

3.4.2 | Northern Pike

All 23 age-0 Northern Pike tagged in 2015 were detected at some point, and 17 fish (788 ± 812 , [mean detection of 17 fish \pm SD]) were considered present (Table S2). Of these 17 fish, four (1,243, BF60, D3B1 and DDFD) were found to have significantly larger core ranges ($F_{16,39} = 4.22$, $p < .001$; Figure 4) relative to conspecifics. While DDFD and BF60 core use sizes were noticeably larger, these fish were conversely the largest and smallest captured, suggesting no relationship between physical size and size of core range. Core use range for all fish (0.06 km² \pm 0.005 SE, Figure S16c,e) was often restricted to the embayment interior (Figure 3a), while extent included both interior and mouth regions (0.32 km² \pm 0.02 SE). Residency index was higher

in the shallow interior of the bay (>0.50) relative to the deeper water habitat of the embayment's mouth (0.05).

Of 15 age-0 Northern Pike tagged in 2016/17, 100% were detected (80 ± 102 , [mean detection of fish \pm SD]), and 50% (seven) were considered present (Table S4). Core use (0.18 km² \pm 0.01 , Figure S17i) and extent size (0.62 km² \pm 0.008 , Figure S17j) doubled relative to age-0 fish monitored in 2015, likely due to the change in array size. Residency index was low (c. 0.05) indicating that fish used other regions (nearshore or deep waters) more often than the mouth.

Water-level-significantly contributed to the fit of the data for Northern Pike residency in 2015, as did water temperature for both residency and core range size in 2016 (see Table S10). Presence and residency index of Northern Pike were significantly higher (i.e. 96% of fish monitored) when water-levels remained at their regulated summer/autumn levels in 2015 than when levels receded below 74.50 m and 52% of fish monitored were present [$\chi^2 = 6.71$, $p = .01$, Figure 5a; $\chi^2 = 26.31$, $p < .001$, Figure 5b; Table S10), while in 2016, age-0 Northern Pike extent range (Figure 5c,d) significantly increased with warmer autumn water temperatures ($\chi^2 = 9.39$, $p = .002$, see Table S10).

3.5 | Age-1 Fish

3.5.1 | Muskellunge

Nineteen (95%) of the age-0 Muskellunge tagged in the fall of 2015 in Rose were detected at some point (31 ± 20 , [mean detection of fish detected \pm SD]) as age-1 fish in the fall and winter of 2016 in their natal embayment. Of these 19 Muskellunge, four fish were consistently present (Table S5) throughout the winter period of 2016/2017 (mean residency 0.48 ± 0.12 SE). Range size was restricted by array design; core use was tiny (0.02 km²), and extent (0.072 km² \pm 0.008 SE) included the entirety of the array (see Figure 1). The likelihood of an age-1 Muskellunge being present

in the array increased with total length at first capture ($\chi^2 = 4.70$, $p = .03$; Figure S14). Though temperature was found significant with respect to residency, the alternate model was not significant compared to the null model so this factor was not influential.

3.5.2 | Northern Pike

All 24 Northern Pike originally tagged in 2015 as age-0 fish were detected (75 ± 67 SD) in the 2016/17 array in Flynn as age-1 fish and 10 fish were present throughout the winter months (Table S6). Presence peaked in December with seven fish (63% of fish present) and declined as winter progressed (44%). Mean residency index was high (>0.55) for these seven fish, and mean core range (<0.2 km², Figure S17k) was concentrated on the western edge of the embayment mouth (Figure 3b). Average extent included all receivers located in the grid pattern within the embayment mouth (0.62 ± 0.005 SE, Figure S17l). As the alternate model was not significant compared to the null model, water-level was not indeed influential with respect to core use (see Tables S17 and S18).

3.6 | Habitat features

Flynn was the most diverse bay in terms of habitat including nine different habitat types. These included the following: established *Typha*, a mixture of SAV and emergent vegetation, SAV and floating vegetation, combination (50/50) of SAV and exposed substrates, newly developed *Typha* patches, exposed substrate, combination (25/75) SAV and exposed substrates, full (100%) SAV and deep waters (>3 m; Figure 1). The least diverse system was Buck which included only three habitat categories (i.e. floating vegetation, SAV and emergent vegetation, and exposed substrate); the array overlapped all three categories. Rose and Grass Point shared habitat features (Figure 1), except for deep, littoral waters with SAV and a small sediment plume observed along the shoreline that were unique to Rose (Figure 1).

Of the habitat features classified in each bay, the receiver array overlapped with four in Rose for the 2016/17 survey (i.e. deep waters, deeper littoral regions with SAV, and small proportions of both SAV intermixed with floating vegetation and exposed-shallow areas). In Flynn, the 2016/17 receiver array overlapped with seven of the nine habitat features (i.e. deeper waters, SAV, the combined [25/75] SAV and exposed region, exposed substrates, new *Typha* stands and regions of both submergent and emergent vegetation in shallower areas). The 2016/17 Grass Point fall survey overlapped with four of six features (i.e. deep waters, deeper littoral regions with SAV, regions with 50/50 exposed substrates and SAV among varying depths, and proportions of both SAV intermixed with floating vegetation), while the overwinter survey overlapped with all six features, which included shallow regions either exposed or support growth of SAV.

3.6.1 | Muskellunge habitat

In fall and early winter of 2015 and 2016/17, age-0 Muskellunge in Rose were found to disproportionately favour one habitat feature over others ($\chi^2 > 1.41$, $p < .001$, both years, see Table S8). Muskellunge frequented deep waters ($>90\%$ of habitat use within all core use range) relative to other available habitats (Tukey's, $z = -103.9$, $p = <.001$). Despite the availability of floating and SAV habitats, only 40%–45% of this habitat type was actively used ($>50\%$ of the time) in either October or November of 2015.

Buck Muskellunge more frequently occupied shallow waters characterised by exposed substrates (55%–85% of habitat use in core use range) and a mixture of SAV and emergent vegetation (30%–40%; $\chi^2 = 238.81$, $p = <.001$; Figure 6a) compared to floating vegetation. Muskellunge in Grass Point, however, appeared to occupy deeper waters (55%–75%) and deeper littoral waters with SAV (20%–80%) more often relative to habitats characterised by a 50:50 ratio of exposed water/substrate and SAV cover ($<20\%$) or floating vegetation with SAV ($<10\%$) ($\chi^2 = 52.94$, $p = <.001$; Figure 6b).

3.6.2 | Northern Pike habitat

Eight Northern Pike (TL = 213–275-mm) were nearly exclusively found in the vicinity of a receiver associated with 100% SAV cover and adjacent to habitat characterised by a 50:50 ratio of SAV cover and exposed substrates. Similar patterns were noted for all Northern Pike during both survey periods where fish disproportionately used different habitat types ($\chi^2 > 458.59$, $p < .001$, see Table S10). To this end, all 17 age-0 Northern Pike monitored in 2015 preferentially occupied one habitat over others ($\chi^2 = 252.7292$, $p = <.001$; Figure 6c); shallow nearshore region of Flynn, characterised by 50% SAV cover and exposed substrates, was preferred over exposed, shallow waters near the embayment mouth (Tukey test, $z = 4.69$, $p = <.001$; Figure 6d). In contrast, age-0 Northern Pike monitored overwinter in 2016/17 used significantly more exposed, shallow habitats (30%–55%) near the interior and southwest shore of Flynn Bay relative to deep water habitats (20%–35%) (Tukey test, $z = 14.97$, $p = <.001$; Figure 6d; see Table S10). Such a change in habitat preference from 2015 was likely influenced by the position of the 2016/2017 winter array.

3.6.3 | Age-1 habitat use

Age-1 Muskellunge detected in Rose in 2016/17 showed similar habitat use patterns observed during their first seasonal change; a greater proportion ($>95\%$) of all core space areas was comprised of deeper zones ($>95\%$), with little use of deeper littoral zones with SAV (3%–4%). Age-1 Northern Pike detected also showed similar patterns as their first year; individuals tended to use exposed

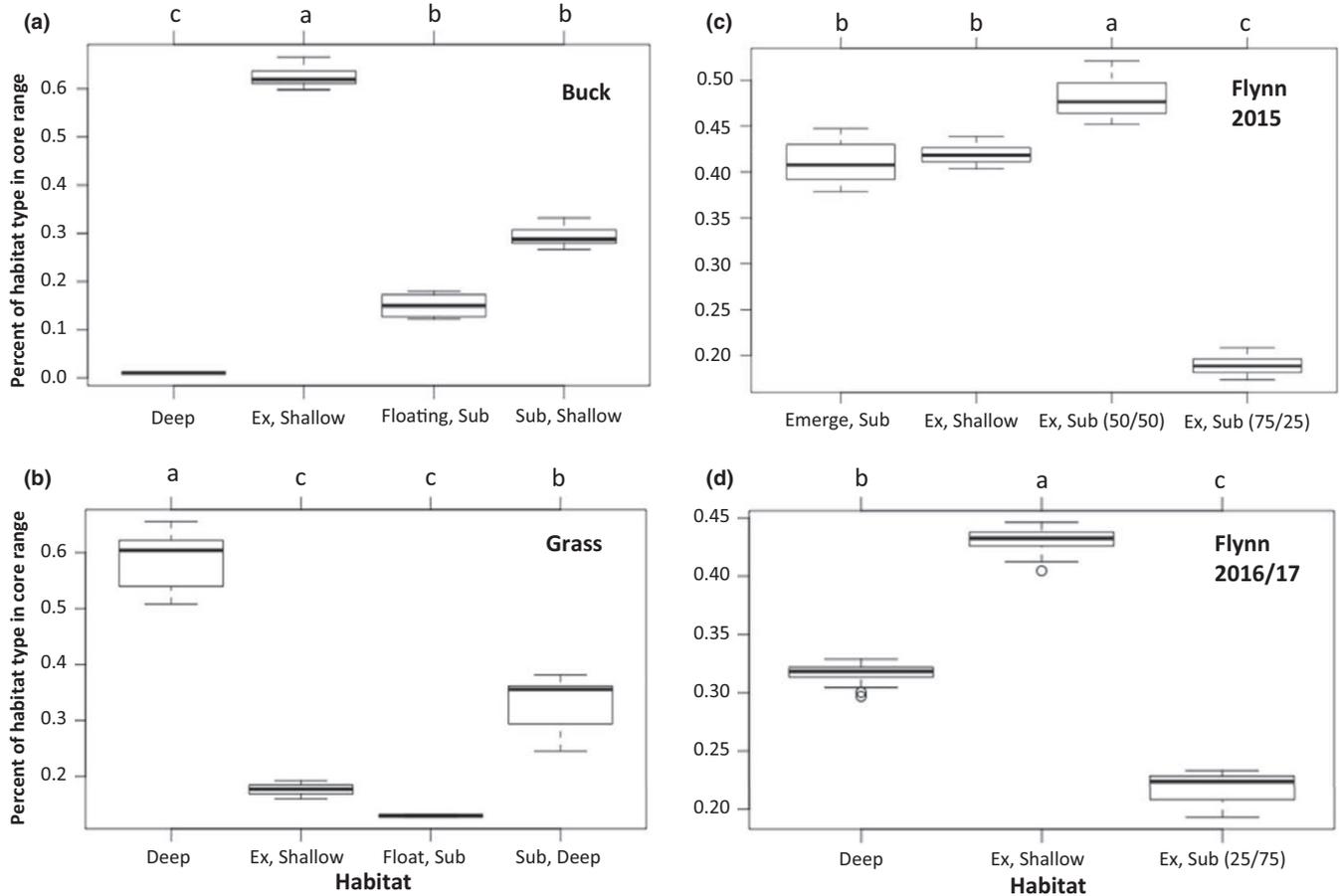


FIGURE 6 Boxplots indicating differences in proportional habitat use by age-0 Muskellunge in (a) Buck Bay in 2015, (b) Grass Point from 2016 to 2017), and for age-0 Northern Pike within (c) Flynn Bay for each 2015 and (d) 2016 to 2017. Habitat use categories include deep waters >3 m (Deep), exposed, shallow waters (Ex.Shallow), waters with 50% exposed substrate and 50% submergent vegetation (Ex. Sub (50/50)), waters with 75% exposed substrate and 25% submergent vegetation (Ex.Sub (75/25)), floating and submergent vegetation (Floating.Sub), emergent and submergent vegetation (Emerge.Sub). Letters indicate how habitats are grouped with respect to their level of significance; “a” is significantly different from “b,” “b” from “c,” etc. Deeper regions were most used by Rose Muskellunge (>90%) compared to Float, Sub

zones (35%–70%), but also used deeper zones (25%–45%) within small patches of SAV. Though habitat features (exposed, shallow waters, deeper zones [c. 1.5 m], and partially exposed waters with SAV, in rank order) were used in significantly different proportions ($\chi^2 = 252.73$, $p = <.001$, see Table S16) in 2016/17, the tendency for core use areas to include low proportions of available SAV within arrays either year may suggest core juvenile Northern Pike habitat is defined by specific ratios of available habitat features.

4 | DISCUSSION

Age-0 Muskellunge and Northern Pike gradually shifted their range to include deeper waters as winter approached (Gallagher et al., 2017); however, preference to reside in shallow regions of their natal embayments in fall months was species and embayment specific. Though individuals are hypothesised to seasonally emigrate from their nurseries as habitat relationships change across the first year of life (Murry & Farrell, 2007), our results suggest that

juvenile esocids may exhibit transitional movements. Though intraspecific core use size was comparable between individual Muskellunge within a bay, the locality (e.g. interior, mouth, full embayment) individual fish spent most of their time varied extensively between bays. This was likely attributed to when and where shelter-providing features (e.g. intermediate densities of surface-reaching vegetation that juvenile Muskellunge are known to occupy in late summer; Murry & Farrell, 2007) were distributed in the protected, nearshore embayments studied (e.g. Henning, Kapuscinski, & Farrell, 2014). For instance, large patches of SAV in deeper (2–4 m) regions, noted to persist throughout winter (Farrell, 2001), predominated the mouth of Rose Bay. In conjunction with a more stable temperature regime beyond the shallow bay (e.g. Jonckheere, 1994), this habitat may have enticed mid-column Muskellunge out of their nursery. Retracted core use sizes in Rose Bay as waters declined further support use of increased depths. Furthermore, fish notably hung out around prominent features such as sand bars, rocky points and offshore shoals dominated by emergent (i.e. *Scirpus* sp.) and SAV (e.g. *Potamogeton* and

Myriophyllum sp.) (e.g. Cook & Solomon, 1987), within Rose and Grass Point bays. Clearly, structures are an essential feature in nursery habitat (i.e. Owensby et al., 2017).

Fluctuating water-levels presumably has an influence on the density and diversity of senescing SAV species that reach the top of the water column and may play an important role in spatial overlap between congeneric predators such as esocids (Rosenfeld & Hatfield, 2006). Our study region experienced drought-like conditions in 2016 followed by intense flooding in early 2017; therefore, the lack of detections during winter months within the deeper embayment mouths may have been associated with continued use of the flooded nursery bay. We thus hypothesise that seasonal climatic events (e.g. water-level increase) influence whether young, newly recruited fish remain within their natal embayment their inaugural winter. As analytic tools may influence ecological interpretation, future exploration will evaluate age-0 Rose Muskellunge and Northern Pike captured in 2015 using network analysis to provide a more comprehensive picture of young esocid movement (i.e. bidirectional through vegetative corridors; Lédée, Heupel, Tobin, Knip, & Simpfendorfer, 2015), relative to physical habitat features.

Despite a shared affinity for similar habitats (Murry & Farrell, 2007), evident by increased use of areas that support growth of SAV, coexistence may indeed result from spatial partitioning. Use of different yet specific depths by congener species over a small depth gradient (i.e. one to three metres), as observed in sympatric juvenile skates (*Raja* spp.; Humphries, Simpson, Wearmouth, & Sims, 2016) and age-1 Muskellunge and Northern Pike (Farrell et al., 2014), likely plays a key role in local-habitat segregation the first winter season. As a result, Muskellunge may be able to effectively forage on preferred prey sources (i.e. fusiform-cyprinids; Engstrom-Heg et al., 1986; Kapuscinski, Farrell, & Murry, 2012) within canopy-forming vegetation and avoid predation by their competitively superior congener, despite lowered recruitment and reduced population health of Northern Pike (e.g. Cooper et al., 2008; Farrell, Mead, & Murry, 2006; Smith et al., 2007). Indeed, differences in position between species within canopy-forming vegetation may be the most critical component (Engstrom-Heg et al., 1986; Jonckheere, 1994). Monitoring fine-scale movement of age-0 Muskellunge and Northern Pike within manipulative habitat use experiments in a sympatric scenario, in situ or ex situ (e.g. Flynn Bay), is recommended (e.g. Farrell et al., 2014).

Habitat use by age-0 Muskellunge (i.e. deeper littoral zones where available) and Northern Pike (i.e. deep regions of their nursery bay with dense vegetation and littoral patches) in late fall notably contrasts habitat use patterns observed by Farrell et al. (2014) between radio-tracked, age-1 (wild-origin stocked and wild) Muskellunge (i.e. shallow, perimeter habitats) and age-1 (wild) Northern Pike (i.e. deeper, more exposed regions) in Flynn, two decades prior. Though such contrasts may have been associated with habitat delineation methods (i.e. fine-scale surveys vs. computer classification), telemetry tools employed (i.e. radio vs. acoustic), or the sympatric nature of Farrell et al.'s (2014) study opposed to embayment-specific comparisons, fine-scale habitat partitioning has been well-documented

between cohabitating species with similar ecological niches (i.e., Farrell, Werner, LaPan, & Claypoole, 1996). Congeneric spiny lobsters (*Panulirus* spp.) cohabit coral reefs by selecting different den locations based on predation risk and tolerance of environmental disturbance (Lozano-Alvarez, Briones-Fourzan, Osorio-Arciniegas, Negrete-Soto, & Barradas-Ortiz, 2007), and though *Octopus vulgaris* and its congener, *Macrotritopus defilippi*, exhibit high spatial overlap in shallow-water lagoons, each species selects differing den substrates (Bennice, Rayburn, Brooks, & Hanlon, 2019). Understanding how residency and space use fluctuate based on use of canopy-forming SAV for juvenile esocid cohorts their first winter with water-levels may thus offer insights and inform restorative actions to improve nursery habitat.

The importance of elevated water-levels and temperatures for juvenile Northern Pike was found to extend beyond their inaugural spring, posthatch (i.e. Hudon, Armellin, Gagnon, & Patoine, 2010). Hudon et al. (2010) found that ideal recruitment years for Northern Pike in the lower St. Lawrence River were characterised by higher water-levels (>4.9 m IGLD85) and high (>18.6°C) air temperatures in June, while Smith et al. (2007) noted negative associations between high winter water-levels and year-class strength. Our age-0 Northern Pike spatiotemporal patterns were highly influenced by higher water-levels (>74.60 m IGLD85) and water temperatures (>10°C), suggesting these conditions may act twofold: positive recruitment rates in spring months and favourable autumn nursery habitat conditions. Moreover, residence of age-0 Northern Pike was strongly associated with a deeper littoral region in early fall known to contain dense pondweed patches (*Potamogeton* spp.) from September to November; <30% of the detections occurred outside this region in the present study. Indeed, deeper regions may be more oxygenated and thus preferred compared to other regions of the natal embayment (i.e. Inskip, 1982). Similarly, age-0 Northern Pike in a France reservoir explored a limited area within their nursery bay (Cucherousset et al., 2009). Our results support notable behaviours documented for juvenile Northern Pike in other systems (Cucherousset et al., 2009; Hawkins et al., 2003, 2005), as well as by free-ranging, age-1 Northern Pike (391 ± 8.7 -mm) studied by Farrell et al. (2014). Considering this cohort is known to prefer dense (40%–90%) SAV among or near emergent aquatic plants (Casselman & Lewis, 1996), our results support use of specific nursery habitats throughout their juvenile stage. To this end, future spatiotemporal analyses which focus on the influence of variable water-level cycles authorised by the new Plan-2014 in the upper St. Lawrence River (International Joint Commission, 2014), in concert with fine-scale movement, are worthwhile.

The acoustic tags used in our initial season lasted substantially longer than anticipated, permitting spatiotemporal parameter evaluations of our tagged fish as age-1 individuals within two embayments; however, challenges associated with detection range prompted careful consideration of movement patterns for both species and age classes. Manufacturer specifications indicated a calculated lifespan of 87 days (L-AMT-1.416) and 131-days (L-AMT-1.421) with transmissions emitting at 20-s pings (Lotek, 2019); however, detections captured well into March 2017 suggest a lifespan of

more than 570 days. More research is required into the lifespan of mini-acoustic transmitters, to determine their validity in multi-year studies and the performance of an array with JSAT tags in various aquatic environments. Indeed, such environments pose challenges for passive acoustic monitoring as transmitter signals are attenuated by dense vegetation (Cooke et al., 2013). To this end, biased detections rates (i.e. diel period) may have influenced residency patterns and overestimated core range, and thus our interpretation of how regional variables (i.e. water-levels) may influence how long juveniles remain in their embayment and their motives to stay rather than move out. An increased rate of detections at night may be associated with maintaining a stationary position in denser vegetation, waiting for lower light levels before ambushing prey. Despite the opportunities mini-transmitter technology affords to study early life stages, trade-offs exist in battery size and the distance fish can be detected (e.g. Brownscombe et al., 2019); thus, we emphasise the need for array performance studies to reveal and compare range and detection efficiency of JSAT tags, particularly in lentic (i.e. wetland, large river, lake) environments.

Future studies are encouraged to focus on movement, core use range and habitat use of transitioning age-0 esocids in both shallow back-bays and deeper littoral waters by expanding arrays to include the nearshore region of the St. Lawrence River channel. The lone age-0 Muskellunge transported to Buck from Flynn in 2015 was briefly detected in the mouth of its natal embayment (i.e. Flynn, 1 km from Buck) during the winter of 2016. As spawning adults are known to exhibit strong site fidelity (e.g. LaPan, Schiavone, & Werner, 1996), this lone observation may provide a glimpse into site fidelity establishment during earlier life stages. As a complex corridor, made up of several islands, shoals and deep channels, exists between Buck and Flynn, we suspect this Muskellunge returned to its natal embayment by moving through continuous bands of deeper growing SAV present throughout this corridor. This may be similar to the movement of age-0 Muskellunge through dense bands of vegetation as observed in Georgian Bay wetlands (Craig & Black, 1986). Future spatiotemporal ecology studies may wish to transplant multiple juvenile Muskellunge from one natal embayment to another, close by, and track their movements to test the hypothesis that esocids exhibit site fidelity at an early age and establish their overwinter range near their natal embayment in their juvenile years.

Despite the sample size, the movement patterns of this transported fish may elucidate important ontogenetic similarities in spatial ecology between juvenile and subadult esocids, relative to adults. Moreover, array placement in deeper waters may minimise the influence of fluctuating environmental conditions that reduce attenuation issues encountered in shallow, heavily vegetated regions, and permit researchers to test the hypothesis that juvenile esocid core range extends beyond their natal bays to include nearshore, littoral corridors. Long-term tracking studies are encouraged to calculate whether use of specific habitat features by juvenile Muskellunge (i.e. deeper, littoral regions near embayment mouth) contributes to an above average number of adult recruits to the St. Lawrence River population on a per-unit-area basis, relative to other habitats used

(i.e. Beck et al., 2001). Increased contributions may then identify key habitats that promote survivorship of young fish to adulthood (e.g. Dahlgren et al., 2006). Studies may wish to further explore model extrapolation and transferability by studying transitory movement of age-0 esocids from their nursery embayments in Lake St. Lawrence, a reservoir created by the Moses Saunders dams that can experience drastic water-level change due to hydroelectric operations.

Results from our study identified spatial processes that correlate with water-level and temperature; however, fine-scale, manipulative studies within the upper river system may reiterate a causal process (e.g. predation) in space and habitat use between these predatory congeners. As such, quantifying habitat use from a seasonal perspective, relative to individual months (i.e. Woodside, 2009), may be tactful for fisheries managers to conserve and manage seasonal habitat features that enable Muskellunge to survive from a holistic view. Echoing Crane et al. (2015), protecting and/or re-establishing moderate densities of canopy-forming SAV to maximise littoral habitats and corridors between prominent features (i.e. rocky points, shoals) may aid juvenile Muskellunge meet basic biological needs overwinter. Manipulative studies are further required to test such autecological predictions associated with localised habitat use and overwinter behaviour, relative to Northern Pike. To this end, fisheries managers may wish to work with riparian landowners to appropriately manage canopy-forming SAV and mitigate its loss when juvenile fish are experiencing ontogenetic changes, which are known to play a crucial role in habitat segregation and existence of sympatry between juveniles and adult fish (e.g. *Rhinogobius* spp; Guo et al., 2014; Sone, Inoue, & Yanagisawa, 2001). Considering subadult Muskellunge are rarely observed, despite significant sampling effort (J. M. Farrell, personal communications), it is clear that spatiotemporal research on juvenile Muskellunge throughout the Great Lakes basin is a critical, yet understudied link.

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AUTHORS' CONTRIBUTION

JMF and SJC conceived and designed the investigation. SWR, JPL, PS, AJG and JMF performed field and/or laboratory work. SWR, EJIL and JPL analysed the data. JDM, AJG and JMF contributed materials, reagents and/or analysis tools. SWR, EJIL, JPL, AJG, JMF and SJC wrote the paper.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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