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Comparative spatial ecology of sympatric adult muskellunge and northern pike during a one-year period in an urban reach of the Rideau River, Canada

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Abstract The reach of the Rideau River that flows through Ottawa, Ontario supports a recreational fishery for northern pike (*Esox lucius*) and muskellunge (*Esox masquinongy*). The reach is unique not only because such a vibrant esocid-based recreational fishery exists in an urban center, but that these two species co-occur. Typically, when these species occur sympatrically, northern pike tend to exclude muskellunge. To ensure the persistence of these esocid populations and the fisheries they support it is important to identify key spawning, nursery, foraging and over-wintering locations along this reach, and to evaluate the extent to which adults of the two species exhibit spatio-temporal overlap in habitat use. Radio-telemetry was used to track adult northern pike ($N = 18$; length 510 to 890 mm) and adult muskellunge ($N = 15$; length 695 to 1200 mm) on 73 occasions over one year, with particular focus on the breeding seasons (early April until the end of May [56 % tracking effort]). For the two esocids, we observed 19–60 % overlap in key aggregation areas during each season and during the spawning period. The minimum activity (average linear river distance travelled between consecutive tracking events) and core range (linear river distance within 95 % C.I. of mean river position) were greatest in the winter and fall for northern pike and in the spring for muskellunge. On average, northern pike were considerably smaller than muskellunge and had lower minimum activities and smaller core ranges, which could be a result of thermal biology, limited suitable habitat, prey availability or predation. Results from this study will inform future management of these unique esocid populations and should be considered before any habitat alterations occurs within or adjacent to the Rideau River.

Keywords Radio telemetry · Minimum activity · Home range · Hotspots · Esocidae · Spatial ecology · Muskellunge · Northern Pike · Sympatry

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Introduction

Muskellunge (*Esox masquinongy*) and northern pike (*Esox lucius*) are the two largest members of the esocidae family and are often the apex predators of the freshwater systems they inhabit (Casselman et al. 1999; Baktoft et al. 2012). Muskellunge are found exclusively in North America and are known as a Great Lakes endemic species (Kerr 2011), while northern pike have a circumpolar distribution (Harvey 2009). Within their range, northern pike tend to be widely distributed while muskellunge populations tend to be more restricted in their distribution and occur in comparatively fewer systems (Scott and Crossman 1973; Casselman et al. 1999).

Despite reasonable overlap in their distribution, sympatric muskellunge and northern pike populations are rare. When they occur sympatrically northern pike are believed to be the superior competitor over muskellunge during the first year of life (Cooper et al. 2008). Possible explanations for the negative interactions between these two esocids include competition between young-of-year (YOY) fish for food and cover, predation of YOY muskellunge by YOY northern pike (Buss and Larsen 1961) and competition between adults for spawning sites (Inskip 1986). Northern pike are known to dominate in the first year because they spawn earlier in the season and as a result YOY northern pike are larger than YOY muskellunge. For this reason, successful sympatric populations of muskellunge and northern pike are of particular interest and this study was designed to help increase our understanding of these processes, as there are only a few studies on sympatric esocid populations.

Segregation of spawning and nursery habitat is believed to be an important characteristic of successful coexistence between esocid species (Inskip 1986). Spawning site segregation has been observed in many U.S. Lakes (Buss and Larsen 1961; Dombeck et al. 1986; Strand 1986; Diana et al. 2015) as well as in the Niagara River (Harrison and Hadley 1978). However, significant overlap of spawning habitat has also been observed in the St. Lawrence River (Werner et al. 1990; Farrell 1991; Farrell et al. 1996; Farrell 2001) and in the Ottawa River (Monfette et al. 1996). The presence of tiger muskellunge (hybrids of northern pike and muskellunge) is often regarded as evidence of spawning site overlap (Cooper et al. 2008).

Habitat selection and movement patterns of muskellunge have been reasonably well studied in lentic systems with the findings influenced by a variety of factors including size of the waterbody, temperature and prey abundance (Dombeck 1979; Younk et al. 1996; Casselman 2007; Murry and Farrell 2007). Telemetry studies have found that muskellunge are most active in the spring and fall transitional periods, with intermediate summer activity and minimal winter activity (Crossman 1956; Dombeck 1979; Younk et al. 1996). Similarly, monthly core range telemetry data suggests that muskellunge had the largest core ranges in spring and fall, with intermediate and small core ranges in the summer and winter, respectively (Dombeck 1979). On the other hand, habitat selection and movement patterns of northern pike have been well studied in both lentic and lotic systems with the findings influenced by the risk of predation by larger conspecifics as well as the factors reported above for muskellunge (Jepsen et al. 2001; Kobler et al. 2008). In previous studies, the peak activity of northern pike typically occurred in the spring and early winter (Cook and Bergersen 1988; Koed et al. 2006; Knight et al. 2008; Pauwels et al. 2014). One long-term telemetry study found that northern pike lack seasonal core ranges (Cook and Bergersen 1988). However, a more recent study (i.e., Jepsen et al. 2001) identified three distinct behaviours of northern pike: 1) staying in restricted areas, 2) moving between two or three "favourite areas" and 3) utilizing large habitat areas with frequent habitat shifts. To date, there have been no year-round studies evaluating the seasonal habitat use of sympatric esocid species. In this study, the year-round movement and interactions of sympatric populations of adult northern pike and muskellunge were characterized in the Rideau River, Ottawa, Canada using radio-telemetry.

The urban reach of the Rideau River in Ottawa, Ontario is home to sympatric populations of muskellunge and northern pike. Both species are targeted by recreational anglers within this reach. Muskellunge within the Rideau River and Rideau Canal are a unique population due to their successful propagation within a large urban centre (Gillis et al. 2010). However, there is some evidence that their spawning habitats may overlap, since hybrids have been found in the system (RVCA 2001). Regardless, the healthy native populations of northern pike and muskellunge within the Rideau River offer a unique opportunity to study sympatric esocids. Therefore, the objectives of this study were to compare: (1) the key aggregation hotspots (locations where detections occur significantly more often than a uniform distribution) of muskellunge and northern pike during spawning, nursery, foraging and over-wintering periods, (2) the seasonal minimum activity (average linear river distance travelled between consecutive tracking events) of both species, and (3) their seasonal core ranges (linear river distance within 95 % C.I. of mean river position) in the Rideau River. Results from this study will provide a better understanding of the characteristics of sympatric muskellunge and northern pike populations in a lotic system. Moreover, given that the Rideau River flows through a major urban centre, the study provides important information to resource managers about key habitats that need to be protected or restored to maintain or enhance these populations in the future.

Methods

Study site

Muskellunge and northern pike were tracked from 25 September 2013 through 18 September 2014, in the lower reach of the Rideau River (45°13′58.0″N, 75°63′60.63″W), located in Ottawa, Ontario, Canada (Fig. 1). This lower reach of the Rideau River spans approximately 11.5 km between Hogs Back Falls (45°22′14.87″N, 75°41′48.70″W) and Rideau Falls (45°26′28.04″N, 75°41′45.67″W; Fig. 1), both of which prevent upstream movements by fish. Due to logistical and access issues in the lower portion of this reach, the present study focused on an approximately 6.4 km stretch spanning from Hogs Back Falls to rapids under the highway 417 overpass (45°25′04.80″N, 75°39′46.38″W, Fig. 1). This section of the Rideau River has a mean width of approximately 90 m (14 m-185 m) and max depth of 9.1 m. Despite being located in an urban setting the majority of the system has natural cover in its riparian zone and there are extensive beds of aquatic vegetation in shallow-water sections of the river.

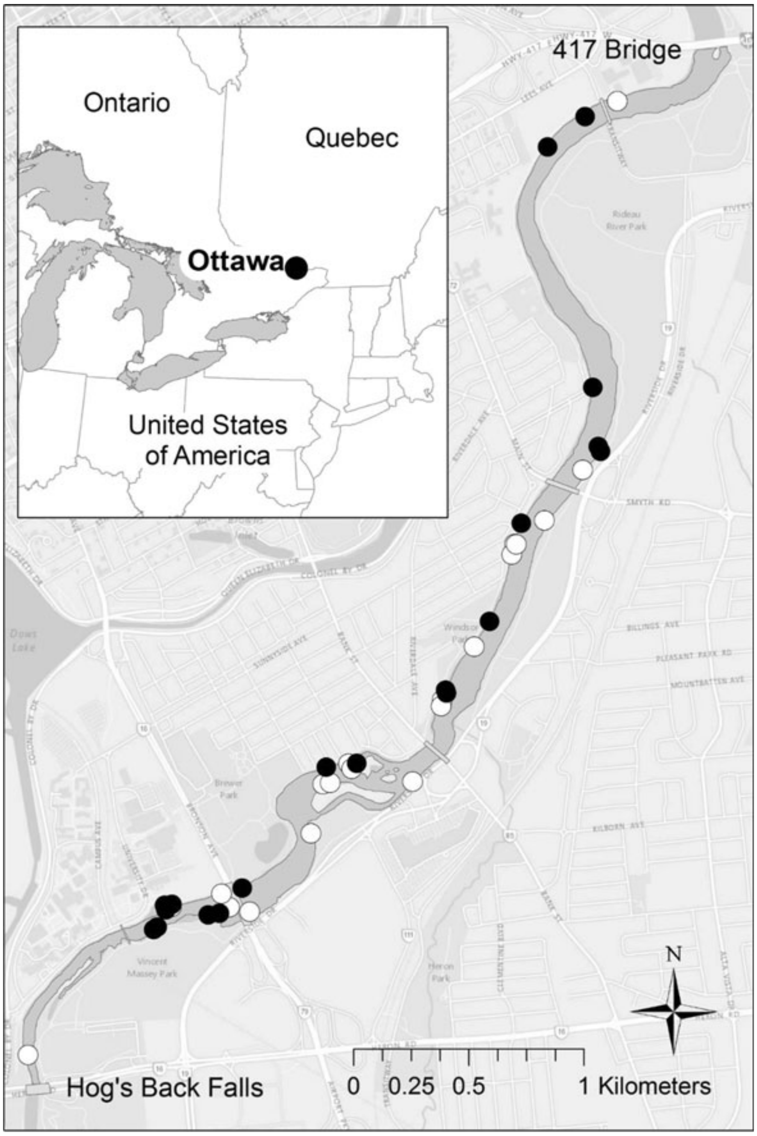

Fig. 1 Map of the urban reach of the Rideau River, Ottawa, Canada. The dots represent muskellunge (white) and northern pike (black) tagging locations. Inset shows the location of Ottawa relative to the Laurentian Great Lakes

Radio tagging

Esocids were captured between 13 May 2013 and 6 November 2013, by angling (a single fish) and electrofishing (32 fish). All electrofishing was done using an electrofishing boat (2.5 Generator Powered Pulser; Smith-Root, Inc., Vancouver, WA, USA) following techniques discussed in Landsman et al. (2011). Radio transmitters (Sigma Eight Inc. Newmarket, ON; TX-P5-1_1200, 43 × 16 mm. 15 g, repetition rate 3.0 s; estimated battery life of ~1 yr) with unique frequencies (148.317–149.788 MHZ) and passive integrated transponder tags (PIT; HDX PIT tag, Oregon RFID, Portland, OR, USA) were surgically implanted into 15 Muskellunge (mean 840 ± SD 141 mm, size ranges 695-1200 mm TL) and 18 Northern Pike (mean 623 ± 95 mm, size ranges 510–890 mm TL), following methods described in Cooke et al. (2003). Prior to surgery the fish captured via electrofishing were under electroanesthesia, which is a common state of anesthesia used for fish surgery as discussed by Jennings and Looney (1998). The single fish captured via specialized angling was anaesthetized in an induction bath of clove oil (60 ppm emulsified in ethanol; Anderson et al. 1997). After surgery, measurements of the total length (mm) and body depth at the pectoral girdle (mm) were recorded. The fish were provided a short period of recovery both in a trough, and then in the Rideau River, where they were held until they swam away at their own volition. All tagged fish were caught within the 6.4 km study reach (Fig. 1).

Tracking

Radio telemetry tracking was conducted on a roughly bi-weekly basis from 25 September 2013 until 9 January 2014 and on a weekly basis from 9 January 2014 until 18 September 2014. In order to evaluate their position during the spawning season northern pike were tracked on a daily basis from 9 April 2014 until 12 May 2014 and muskellunge were tracked daily from 23 April 2014 until 26 May 2014. These offset dates were selected to account for spawning of northern pike in slightly cooler waters, with muskellunge typically spawning two weeks later (Zorn et al. 1998). Northern pike typically begin spawning as soon as the ice melts (Pierce 2012); this occurred on 9 April 2014 in the Rideau River (ice was physically removed by the City of Ottawa ice removal crew). All tracking was done using a portable receiver (Biotracker, Lotek Wireless Inc., Newmarket, ON, Canada) and a three-element Yagi antenna (Model F150-3FB 11,653, AF Antronics, Inc. Urbana, IL, USA). Fish tracking was conducted from the western bank of the river by foot, rollerblade and bicycle. Fish positions were determined to be along transects perpendicular to the River bank, based on signal strength (Wagner and Wahl 2007). Once the strongest signal was found, the UTM coordinates from shore were recorded using a geographic positioning system receiver (Wildco 4110-G10 GPS, Garmin Ltd. Kansas City, MO, USA). Based on these UTM coordinates a fish was considered to be located along a transect perpendicular from the coordinate.

Data analysis

Following the methods of Teixeira et al. (2013) and Coelho et al. (2014), 2D HotSpot Identification analysis was performed using SIRIEMA (version 1.1, Laboratory of Ecology of Populations and Communities, Porto Alegre, RS, Brazil). Esocid positions were plotted on a geo-referenced map of the Rideau River centre line in SIRIEMA. Hotspots of species aggregation were determined during several time periods including: spawning seasons, spring, summer, fall and winter. In this analysis, hotspots were determined by dividing the river into 640 segments of equal length (10 m). A circle with a 100 m radius (which approximately reflects the tracking resolution) was then used to calculate the aggregation intensity value for each river segment. The circle was centered on the first segment and all tracking events inside the circle were summed. This sum was multiplied by a correction factor that considers the length of the river inside the circle area that was summed (Coelho et al. 2014). This procedure was then repeated for all 640 segments, resulting in an aggregation intensity value for each river segment. Each aggregation intensity value was then subtracted from the mean value of 100 Monte Carlo simulations of random distributions of the esocids to determine the significance of aggregation intensity. Values for aggregation intensity above the upper confidence limit (95 %) indicate significant esocid hotspots. These hotspots represent areas where detections were significantly more likely to occur relative to other regions of the reach. Once hotspots were calculated, the river locations of hotspots were compared between muskellunge and northern pike and the percent overlap of river locations (linear river distances [m]) was calculated. The beginning of spring was defined as the ice removal day (April 9), and the other seasons were defined by the winter (Dec. 21) and summer (June 21) solstices and the fall equinox (Sept. 21).

Esocid positions were plotted on a geo-referenced map of the Rideau River in ArcMap (version 10.2.2, Environmental Systems Research Institute, Redlands, CA, USA). Using the snap-to-line tool the points were snapped to the centre line of the Rideau River. For each tracking day the linear River position of each located fish was determined as the distance downstream from Hogs Back Falls. The minimum activities and core ranges were evaluated by calculating the linear movement of fish upstream and downstream. More specifically, the seasonal minimum activity is the average linear river distance travelled between consecutive tracking events and the seasonal core range is the linear river distance within 95 % C.I. of mean river positions in the Rideau River. The minimum activity and core range data sets were tested for normality and homogeneity of variance using Shapiro–Wilk and Levene's tests (Sokal and Rohlf 1995) and were rank-transformed to meet these assumptions where necessary (Conover and Iman 1981). Twelve individual t-tests were then applied to evaluate the differences between muskellunge and northern pike in each season. Six one-way ANOVA's (parametric test) were then applied to evaluate the differences of seasonal minimum activities and seasonal core ranges, within each species. When a main effect(s) term was significant, a Tukey–Kramer HSD post hoc test was used to compare the statistical significance of means. Bonferroni Corrections were applied (=α/18) to reduce the probability of committing Type I errors (Armstrong 2014), therefore the significance threshold was set to 0.002. All statistical tests were carried out using R Statistics (Version 3.1.2, R Statistical Computing, Vienna, Austria), means are reported as ±standard deviation (S.D.) where appropriate.

Results

Radio-telemetry was used to track adult northern pike ($N = 18$; length 510 to 890 mm) and adult muskellunge ($N = 15$; length 695 to 1200 mm; Table 1) on 73 occasions over one year, with particular focus on the spawning seasons (early April until the end of May). Over the course of this study the sample size decreased from 33 to 13 esocids. Three possible explanations for this were 1) the migration of esocids downstream into the Ottawa River (over Rideau Falls), 2) fish harvest and 3) tag failure/battery expiry. The latter was observed in two muskellunge re-captured by angling techniques in the fall of 2014. Both fish were found within 100 m of their last tracked location, but with expired radio tags. Esocids were found to traverse the rapids at Carleton and Bank street, indicating they were likely able to migrate downstream past the 417 rapids. However, no esocids were successfully located past the 417 rapids despite monthly extended searches to Rideau Falls in 2014.

Hotspots

The key aggregation hotspots of muskellunge and northern pike overlapped in each season and during the spawning period. During their respective spawning period's, hotspot overlap was similar to the spring hotspot overlap with 60.0 % for muskellunge and 45.7 % for northern pike (Table 2; Fig. 2). The lowest level of seasonal hotspot overlap occurred in the winter for muskellunge with 8.6 % of the linear distance of their hotspots overlapping with northern pike, while northern pike had 8.0 % overlap (Table 2; Fig. 3). Conversely, the most overlap occurred in the spring with 62.8 % for muskellunge and 45.5 % overlap for northern pike and these values were only slightly higher to the extent of overlap for both species in the summer (Table 2; Fig. 3). There was also relatively less hotspot overlap in the fall for both species, with 40.3 % for muskellunge and 26.0 % for northern.

Minimum activity

The seasonal minimum activities of muskellunge and northern pike were significantly different during the spring (T-test; $T_{30} = 9.759$; $P < 0.0001$; Fig. 4) and summer (T-test; $T_{24} = 5.700$; $P < 0.0001$; Fig. 4). More specifically, the minimum activities of 533 ± 303 and 327 ± 494 m for muskellunge were 12.9 and 7.8 times greater than northern pike in the spring and summer, respectively. The minimum activity of esocids in fall (T-test; $T_{17} = 2.106$; $P = 0.05$; Fig. 4) and winter (T-test; $T_{29} = -1.189$; $P = 0.2$; Fig. 4) were similar. The minimum activity of radio-tagged muskellunge varied seasonally (one-way ANOVA; $F_{(3,40)} = 9.279$, $P < 0.0001$; Fig. 4) as evidenced by increased activity in the spring relative to the winter (Tukey-Kramer HSD, $P < 0.002$; Fig. 4). Indeed, in winter, the minimum activity of

Table 1 Frequencies and total lengths of ecocids used in this study. The tagging date and number of days each fish was tracked is indicated

Muskellunge	Date Tagged	Total Length (mm)	Last Date Located	Total Times Located (days)	Times Located in Fall (/5)	Times Located Winter (/12)	Times Located Spring (/34)	Times Located Summer (/12)
1	28/05/13	720	10/07/14	39	3	9	24	3
2	03/06/13	715	18/09/14	53	3	10	33	7
3	03/06/13	723	16/06/14	30	0	6	24	0
4	22/07/13	1200	29/03/14	7	4	3	0	0
5	24/07/13	698	13/08/14	46	4	10	26	6
6	26/07/13	1016	30/06/14	40	3	8	27	2
7	06/11/13	907	18/09/14	49	1	10	26	12
8	13/05/13	744	18/09/14	48	1	4	34	9
9	16/05/13	860	30/07/14	35	1	5	26	3
10	16/05/13	695	25/05/14	27	2	9	16	0
11	14/05/13	770	23/07/14	49	3	9	33	4
12	04/06/13	925	18/08/14	28	0	8	16	4
13	04/06/13	865	06/09/14	53	2	10	31	10
14	23/07/13	908	06/09/14	57	3	11	33	10
15	24/07/13	856	18 09/14	48	2	3	30	12
Northern Pike	Date Tagged	Total Length (mm)	Last Date Located	Total Times Located (days)	Times Located Fall (/5)	Times Located Winter (/12)	Times Located Spring (/34)	Times Located Summer (/12)
1	13/05/13	690	11/09/14	62	5	12	34	11
2	13/05/13	684	6/08/14	58	5	12	34	7
3	13/05/14	510	18/08/14	59	4	12	34	9
4	14/05/13	552	11/09/14	62	5	12	34	11
5	14/05/13	728	18/09/14	59	5	9	33	12
6	14/05/13	634	30/07/14	56	5	12	33	6
7	14/05/13	580	30/07/14	56	4	12	34	6
8	14/05/13	585	26/05/14	22	2	20	0	0
9	14/05/13	663	23/07/14	52	5	8	34	11
10	13/05/13	604	30/06/14	52	5	11	34	2
11	13/05/13	515	23/07/14	53	4	11	33	5
12	13/05/13	547	16/07/14	52	2	12	34	4
13	13/05/13	576	18/09/14	61	3	12	34	12
14	16/05/13	723	18/09/14	55	1	8	34	12
15	16/05/13	890	18/09/14	58	5	8	33	12
16	14/05/13	527	18/08/14	58	5	10	34	9
17	16/05/13	628	18/09/14	62	5	11	34	12
18	16/05/13	578	30/07/14	52	0	12	34	6

muskellunge was an average of 114 ± 64 m a week, which is 4.7 times less than in spring. No significant differences in minimum activity were observed between the other seasons (Tukey-Kramer HSD, P's > 0.002; Fig. 4). The minimum activity of northern pike also varied seasonally (one-way ANOVA; $F_{(3,\ 60)} = 25.48$, $P < 0.0001$; Fig. 4) as a result of decreased activity in the spring and summer relative to the fall (Tukey-Kramer HSD, P's < 0.002; Fig. 4) and winter (Tukey-Kramer HSD, P's < 0.002; Fig. 4). In summer and spring the minimum activity of northern pike was an average of 42 ± 34 and 41 ± 32 m a week, respectively, which are 6.2–6.4 and 4.4–4.5 times less than in the fall and winter, respectively. No significant differences in minimum activity were observed between spring and summer or fall and winter (Tukey-Kramer HSD, P's > 0.002; Fig. 4).

Table 2 Summary of the number of hotspots identified for each species during each season as well as the total linear distance of hotspots. The distance of overlap between the species hotspots as well as the percent of the total hot spot area this overlap represents are also shown

Species	Season	Number of Hotspots	Hotspot Distance (m)	Hotspot Distance Overlap (m)	Overlap (%)
Muskellunge	Fall	7	632	251	40.3
	Winter	6	1063	90	8.6
	Spring	10	1223	762	62.8
	Spawning	10	1183	692	60.0
	Summer	5	982	511	53.7
Northern Pike	Fall	6	972	251	26.0
	Winter	11	1143	90	8.0
	Spring	11	1694	762	45.5
	Spawning	10	1624	742	45.7
	Summer	9	1273	511	40.5

Core range

The size of the core ranges of muskellunge and northern pike were significantly different during the spring (T-test; $T_{30} = 9.177$, $p < 0.0001$; Fig. 5) and summer (T-test; $T_{25} = 6.020$; $P < 0.0001$; Fig. 5). More specifically, muskellunge had core ranges of 928 ± 693 and 410 ± 466 m that were 20.1 and 7.1 times greater than northern pike in the spring and summer, respectively.

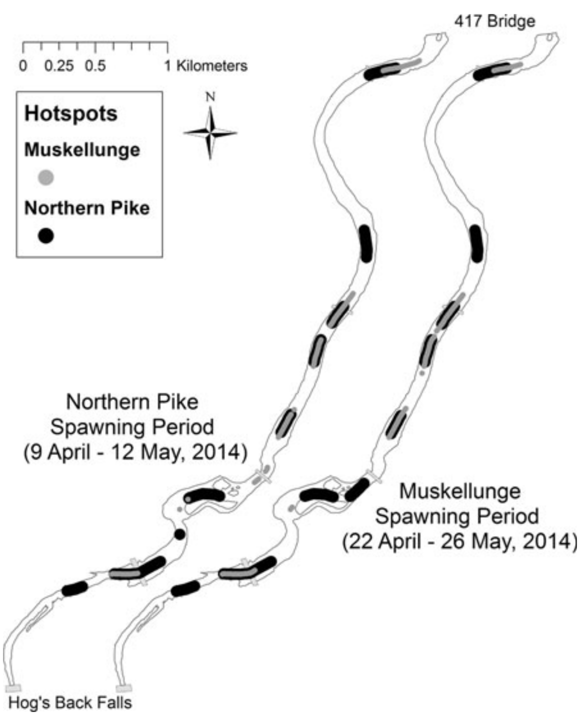

Fig. 2 Hotspot locations of muskellunge (*grey*) and northern pike (*black*) in the Rideau River, Ottawa, Canada during the northern pike spawning period and the muskellunge spawning period

The core range of esocids in fall (T-test; $T_{19} = 1.928$; $P = 0.07$; Fig. 5) and winter (T-test; $T_{30} = 0.0399$; $P = 1.0$; Fig. 5) were similar. The seasonal core ranges of radio-tagged muskellunge did not vary significantly (one-way ANOVA; $F_{(3,43)} = (5.804$, $P = 0.002$; Fig. 5). Meanwhile, the core range of northern pike did vary seasonally (one-way ANOVA; $F_{(3,\ 61)} = 44.64$, $P < 0.0001$; Fig. 5) as a result of decreased movement in the spring and summer relative to the fall (Tukey-Kramer HSD, P's < 0.002; Fig. 5) and winter (Tukey-Kramer HSD, P's < 0.002; Fig. 5). In fall and winter the average core ranges of northern pike were 639 ± 646 and 318 ± 364 m, respectively, while they were only 46 ± 38 and 58 ± 41 m in the spring and summer. No significant differences in core ranges were observed between spring and summer or fall and winter (Tukey-Kramer HSD, P's > 0.002; Fig. 5).

Discussion

Inter-specific comparison

Radio-telemetry using internally-implanted radio transmitters proved to be an effective method for studying the spatial ecology of muskellunge and northern pike in the Rideau River. During our study there was considerable overlap between muskellunge and northern pike throughout the year, particularly during spawning. Although the spatial segregation of esocids during non-spawning periods is not thought to be critical for populations to exist in sympatry, it was still interesting to note that there was extensive seasonal hotspot overlap for muskellunge and northern pike throughout the entire

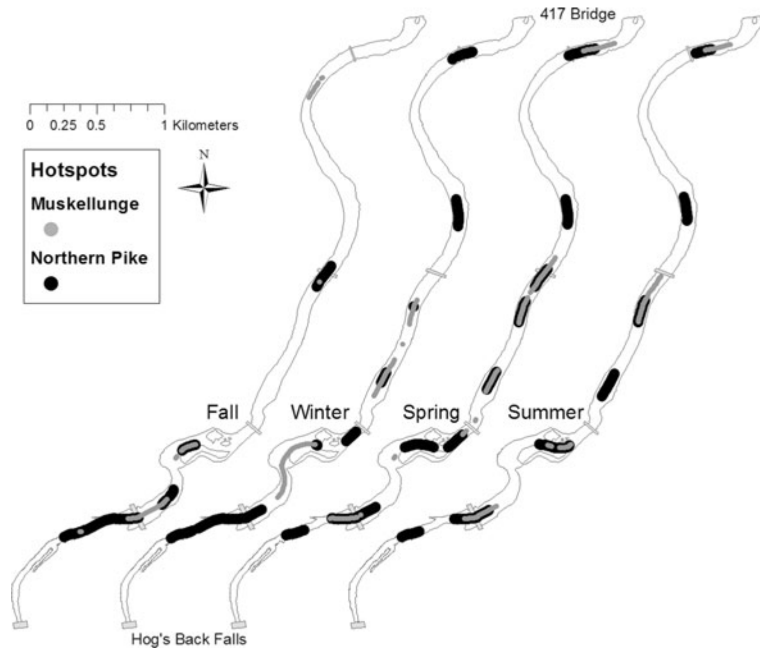

Fig. 3 Hotspot locations of muskellunge (*grey*) and northern pike (*black*) in the Rideau River, Ottawa, Canada during the fall, winter, spring and summer

year such that competitive interactions were possible. To our knowledge, this is the first study that has documented extensive range overlap between two esocid species during non-spawning time periods. Our finding of extensive hotspot overlap during spawning is consistent with previous studies in the St. Lawrence River (Werner et al. 1990; Farrell 1991; Farrell et al. 1996; Farrell 2001) and Ottawa River (Monfette et al. 1996). The observed overlap in the Rideau River occurred throughout the entire spawning period supporting the findings of Farrell et al. (1996) and Monfette et al. (1996) who observed spatial overlap of esocids for at least two weeks. Spawning site overlap can lead to predation of YOY muskellunge by YOY northern pike and increased competition between YOY fish for food and cover (Buss and Larsen 1961). Since northern pike spawn approximately two weeks prior to muskellunge they are typically the superior competitor over muskellunge during the first year of life (Cooper et al. 2008). However, the Rideau River adult muskellunge

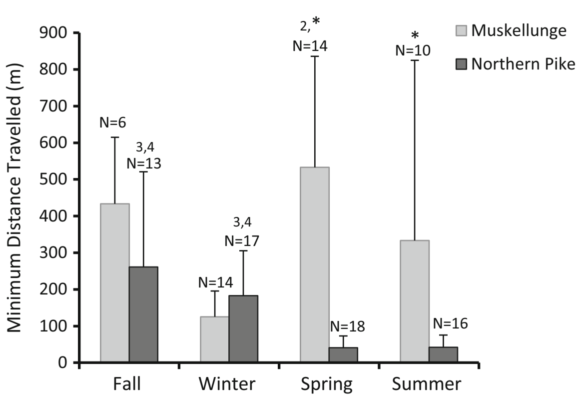

Fig. 4 Minimum activities of esocids in the Rideau River, Ottawa, Canada measured as linear river displacement travelled between consecutive tracking events (Mean ± SD) as recorded by radio telemetry for the representative seasons. 2-sig more than winter, 3-sig more than spring, 4-sig more than summer, *-sig more than northern pike

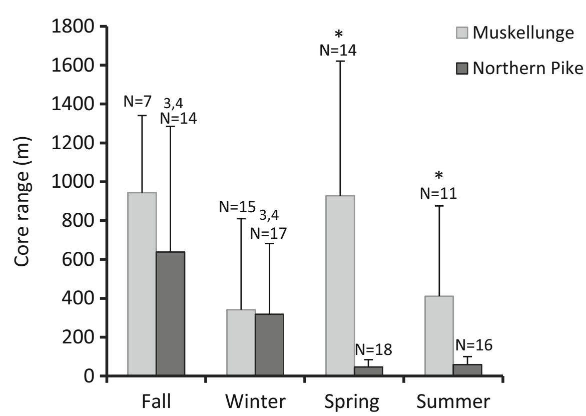

Fig. 5 Core ranges of esocids in the Rideau River, Ottawa, Canada measured using the 95 % confidence intervals of the mean river position (Mean ± SD) as recorded by radio telemetry for the representative seasons. 3-sig larger than spring, 4-sig larger than summer, *-sig larger than northern pike

population remains healthy despite extensive overlap in spawning locations.

In our study, we found that the minimum activities and core ranges of muskellunge in spring and summer were significantly greater than northern pike, while there were no significant differences between fall and winter. These differences may be related to the relative size of these species in the Rideau River where northern pike were on average smaller than muskellunge (623 mm and 840 mm, respectively). Since muskellunge are larger they likely out-compete northern pike for food and habitat and consequently occupy larger core ranges. Muskellunge do not feed often in winter and feed heavily in summer (Sternberg 1992), which could lead to predation of northern pike in the summer. This could explain why northern pike are significantly more active in the winter compared to the summer. Kobler et al. (2008) and Jepsen et al. (2001) found a positive relationship between size and movement of northern pike, which could be a result of cannibalism by larger northern pike in these systems (Eklov 1997). A positive relationship in the Rideau River between size and movement of northern pike would support the idea of predation by muskellunge (i.e., smallest northern pike move the least due to susceptibility to predation). However, during our study there was not a sufficiently large size gradient among the northern pike to test this theory; most fish ranged from 510 to 650 mm. Furthermore, muskellunge are also known to feed heavily in fall (Sternberg 1992) when northern pike were most active, which does not support the predation theory. Therefore, factors other than predation must also be considered, one of which is reduced competition.

The comparatively lower northern pike movement (relative to muskellunge) could be due to decreased competition for food in the spring and summer, as a result of increased prey abundance (Knight et al. 2008). In previous studies, increased prey abundance was found to lead to a sit and wait feeding behaviour of northern pike (Diana 1980; Webb and Skadesen 1980; Koed et al. 2006). The observed differences in core range size during the spring may also be linked to spawning habitat requirements. Northern pike prefer to spawn over submersed aquatic and terrestrial vegetation (Farrell et al. 1996; Farrell 2001; Cooper et al. 2008), specifically over sedge and grass dominated habitat (Monfette et al. 1996). By comparison, muskellunge are able to use a wider variety of spawning habitats and are less dependent on vegetation than northern pike (Farrell 1991; Monfette et al. 1996). Predation, food availability and the availability of spawning habitat may all contribute to the observed differences between these two species in terms of spring activity and core range. A more detailed evaluation of the types of habitat they select during the spawning season as well as an assessment of available prey would help to disentangle the relative importance of these components for both muskellunge and northern pike.

Spatial ecology of northern pike

Radio tracking revealed that the minimum activities and core ranges of northern pike were significantly smaller in spring and summer relative to the fall and winter. Some researchers have observed increased activity of pike in the spring (Cook and Bergersen 1988; Masters et al. 2005; Koed et al. 2006), but the elevated activity was associated with movement between spawning locations in larger waterbodies. In our study, all northern pike spawned in small concentrated areas that were located within their winter core ranges yielding well-defined spring core ranges. After spawning was complete, the minimum activity of northern pike in the Rideau River was reduced further and as a result core ranges remained restricted in the summer. Movement of northern pike is often linked to temperature, risk of predation and food demands (Kobler et al. 2008). Since peak activity in northern pike typically occurs between 8 and 10 °C (Lucas 1992; Pauwels et al. 2014), previous studies have suggested that restricted activity in the summer may occur with increased water temperatures (Headrick and Carline 1993). Indeed, Vehanen et al. (2006) observed lower summer activity when water temperatures exceeded 20 °C and higher activity when temperatures remain below 15 °C (Vehanen et al. 2006). For the Rideau River, water temperatures routinely exceed 20 °C in the summer, which may contribute to reduced summer activity. We cannot, however, discount the potential roles of predation by muskellunge and food availability in dictating seasonal activity and core range.

Our finding of greater minimum activities and core ranges in the winter and fall is consistent with previous studies of northern pike (Jepsen et al. 2001; Koed et al. 2006; Knight et al. 2008; Pauwels et al. 2014). These studies have suggested that the slightly increasing water temperatures that occur gradually during the winter result in increased activity (Jepsen et al. 2001; Koed et al.

2006) likely as a result of increased foraging (Diana et al. 1977; Cook and Bergersen 1988). In contrast, several studies reported minimal northern pike activity in the winter (Casselman 1978; Cook and Bergersen 1988; Vehanen et al. 2006), particularly when water temperatures were below 6 °C (Kobler et al. 2008). In winter, the majority of the Rideau River is covered in ice except for areas that experience high rates of flow. The winter of 2013–2014, when this study was undertaken, was one of the coldest in recent history; it was the coldest winter in 18 years and the third coldest in 35 years (EnviroCan 2014). The mean air temperature in Ottawa during the winter of 2013–14 was −9.8 °C (OWS 2015). Therefore, the increased activity of northern pike is somewhat unexpected with the exact mechanism unclear.

Several previous studies have suggested that northern pike lack defined core ranges (Diana et al. 1977; Chapman and Mackay 1984a, b; Cook and Bergersen 1988). Indeed, a recent study observed no differences in the activity of northern pike throughout the entire year (Baktoft et al. 2012); however, this study was completed in a small lake (~1 ha), which may have constrained activity. This was clearly not the case in the Rideau River where, despite seasonal differences in the size of their range, northern pike remained in the same core areas throughout the year and the outer boundaries of their core ranges expanded and contracted among seasons. Previous studies have documented a range of behavioural types within northern pike populations with some more sedentary individuals and others that are more mobile (e.g., Mann 1980; Jepsen et al. 2001; Masters et al. 2005; Vehanen et al. 2006; Midwood and Chow-Fraser 2015). It would appear that in the Rideau River, individual northern pike exhibit a variety of these behavioural types depending on the season with increased mobility during the fall and winter.

Spatial ecology of muskellunge

The minimum activity of muskellunge was greatest in spring and varied significantly from the minimum activity in winter, while the size of the core ranges of muskellunge did not vary significantly on a seasonal basis. Although, most muskellunge remained in the same core area throughout the year, the minimum activity increased in the spring leading to a trend towards larger core ranges. This is consistent with previous studies that found increased minimum activity and expanded core ranges during the spring as a result of spawning activity (e.g., Dombeck 1979; Miller and Menzel 1986a; Miller and Menzel 1986b; Strand 1986; Stronks 1996; Younk et al. 1996; Gillis et al. 2010). In our study, five muskellunge travelled more than 2000 m between daily tracking events during the spawning period, while an additional four muskellunge travelled more than 1000 m between daily tracking events. Minimum activity and core ranges of muskellunge tended to be lower in the winter, which supports previous studies that found muskellunge exhibited restricted winter movements and well-defined core ranges in the winter (e.g., Minor and Crossman 1978; Dombeck 1979; Strand 1986; Younk et al. 1996; Gillis et al. 2010). Minor and Crossman (1978) reported that muskellunge are least active between 0 and 2 °C. Therefore, we may hypothesize that reduced temperatures could be responsible for reduced activity and smaller core ranges of muskellunge in the winter.

The minimum activities and core ranges of muskellunge did not vary significantly among the spring, summer and fall seasons, a similar finding as previous studies by Miller and Menzel (1986b) and Stronks (1996). In the summer, after spawning was complete, the minimum activities of muskellunge were low and the core ranges of muskellunge were well defined, not unlike previous findings in both lentic and lotic systems (e.g., Crossman 1956; Dombeck 1979; Miller and Menzel 1986a; Miller and Menzel 1986b; Younk et al. 1996). Historically, the Rideau River shoreline has been heavily channelized, leaving little suitable habitat for muskellunge and northern pike during certain life stages, such as spawning. Moreover, fish in the urban reach of the Rideau River are restricted to an 11.5 km reach bounded on both ends by waterfalls. As a result, it is possible that the core range and minimum activities of muskellunge were similar in spring, summer and fall because of limited availability of suitable habitat for adult muskellunge.

Population status

Rust et al. (2002) suggested that systems that support self-sustaining muskellunge populations are surrounded by forested watersheds, whereas systems that have considerable shoreline development often require stocking. The latter would be expected for the Rideau River; however, results from seining and angling suggest that the Rideau River muskellunge population is healthy. During July 2014, 12 hotspots were seined as part of an ongoing study of fish communities in the Rideau River (data not shown); this resulted in the capture of 14 YOY muskellunge and one YOY northern pike. There are several explanations for the absence of northern pike from seven of the eight confirmed muskellunge nursery habitats including: esocid nursery site segregation, larger YOY northern pike migrating to deeper water, or northern pike reproductive failure. The last option is least likely since in the fall of 2014 30 YOY northern pike were removed from Brewer Park Pond (J. Lamoureux, pers. Comm.), which is located within the Rideau River floodplain and adjacent to some of the northern pike spawning hotspots. Northern pike eggs may therefore have entered the pond during the spring flood. Additionally, 54 muskellunge (5 recaptures) and 13 northern pike were caught as by-catch during 341 h of specialized muskellunge angling in the 2014 and 2015 fishing seasons, resulting in catch-per-unit-effort (CPUE) of 0.158, which is considerably better than the historical CPUE for muskellunge in the Rideau River (0.126; Kerr 2004). Furthermore, eight northern pike were captured in 24 h of northern pike angling in 2014 and 2015. Combined, these results suggest that the muskellunge population in the Rideau River is stable, despite extensive watershed development. Further research is needed to identify the most productive spawning hotspots in this reach of the Rideau River so they can be protected and used as reference sites for habitat remediation projects in the future.

Conclusion

In conclusion, our study indicates that seasonality has a significant impact on the interactions, core range and general movement patterns of adult muskellunge and northern pike in the urban reach of the Rideau River. Knowledge of the spatial ecology of muskellunge and northern pike obtained in this study should be considered before any habitat alterations occur within or adjacent to the Rideau River. Specifically, the identification of spawning and nursery habitats will help in promoting the reproduction of muskellunge and northern pike populations in this unique environment. Moreover, such efforts will assist with identifying future sites for habitat enhancement or restoration.

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