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Lake sturgeon (*Acipenser fulvescens*) spawning habitat: A quantitative review

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Abstract: The loss of spawning habitat has been identified as a limiting factor to population growth for lake sturgeon, *Acipenser fulvescens*, the most widely distributed species of the family in North America. While local information exists about lake sturgeon spawning habitat, a synthesis of all available data is needed across its range. Our study used meta-analytical techniques to describe the mean and range of critical spawning habitat characteristics based on data from 48 sites across all major watersheds in which lake sturgeon are found. Data were compiled into univariate habitat suitability indices to describe the spawning niche. Results indicate that peak suitability occurred at depth-averaged velocities of $0.6 \text{ m}\cdot\text{s}^{-1}$, depths of $0.55 - 0.85 \text{ m}$ in small rivers ($<100 \text{ m}^3\cdot\text{s}^{-1}$ annual average discharge) and $0.75 - 5.25 \text{ m}$ in large rivers ($>100 \text{ m}^3\cdot\text{s}^{-1}$), over cobble substrates ($64 - 256 \text{ mm}$) and that suitable water temperatures decreased with increasing latitude. This study provides a comprehensive review of critical spawning criteria from which future habitat suitability models can be adapted.

Keywords: Spawning, Rivers, Habitat Suitability, Environmental conditions, Lake Sturgeon

Introduction

Throughout North America, habitat loss and degradation are among the most significant threats to biodiversity (Wilcove et al. 1998; Venter et al. 2006). In freshwater environments, projected extinction rates are five times greater than those in terrestrial and marine settings, with habitat loss as one of the key factors influencing these declines (Ricciardi and Rasmussen 1999). In order to mitigate the threat of habitat loss, identifying the key threats and conditions of optimum habitats is of critical importance (Venter et al. 2006).

Of the 25 species of sturgeon (family *Acipenseridae*), 18 are classified as critically endangered (Thiem et al. 2013). Lake sturgeon (*Acipenser fulvescens*) is the most widely distributed species of the family in North America (Fig. 1), and is threatened or endangered across most of its range (COSEWIC 2006; NatureServe 2012). Of the many potential threats to lake sturgeon, spawning habitat has been identified as a limiting factor for population growth (Lytle 2008; Randall 2008; Bennion and Manny 2014). Unfortunately, the quality and quantity of existing habitat has been negatively affected by altered flow regimes, and reduced access to historic spawning grounds by dams (Haxton 2006; Bennion and Manny 2014). To counteract these effects, substantial effort has recently been dedicated to locating, restoring, and creating suitable lake sturgeon spawning habitat.

Over the past 20 years, spawning requirements have been described at specific rivers or sites, but a broad description of spawning habitat across its range is lacking (Auer 1996; Peterson et al. 2006; Daugherty et al. 2009). Lake sturgeon typically spawn in fast-flowing, main-channel river environments (Lyons and Kempinger 1992; Auer 1996), although there is anecdotal evidence of spawning in lakes (Harkness and Dymond 1961). Similar to other sturgeon species and to salmonids (Louhi et al. 2008), four habitat characteristics are considered critical for

spawning: flow velocity; water depth; water temperature; and substrate size (Threader et al. 1998; Dumont et al. 2011). Ideal ranges for lake sturgeon have been estimated as: flow velocities of 0.5-1.5 m·s⁻¹; coarse substrates of gravel to cobble with clean interstitial space; water temperatures of 11-15 °C; and depths of 1.1-3 m (Threader et al. 1998; Peterson et al. 2006; Dumont et al. 2011).

To describe the habitat requirements for lake sturgeon, we synthesized available data across the species range using meta-analytical techniques. The data were then used to create a Habitat Suitability Index (HSI), a quantitative tool to determine suitable conditions (Bovee 1982). HSIs have been applied in a variety of contexts to determine usable habitat in rivers (Haxton et al. 2008) or to assess habitat quality for re-introduction programs (Daugherty et al. 2009). Three main categories of HSI are defined as: (I) professional judgement via surveying experts; (II) habitat use data; and, (III) habitat preference data (Bovee 1986). Type I indices are most common, likely because they require no field sampling, but are considered to be of least value (Bovee 1986). Type II indices include presence-only data, whereas type III indices include presence-absence data (Hastie and Fithian 2013). In general, type III indices are thought to provide the most insight, and are most transferable throughout the range of the species (Moir et al. 2005), but also require more resources to create. Consequently, many researchers opt for type II indices (Moyle and Baltz 1985; Parsons and Hubert 1988), which can provide reliable results without the extra expenditures to produce type III preference indices (Moir et al. 2005).

While habitat suitability indices have been used extensively for lake sturgeon juvenile habitat (Jaric et al. 2014) and the spawning habitat of other sturgeon species (Wang et al. 2017), less work has been devoted specifically to spawning habitat for lake sturgeon. The best existing HSI for spawning requirements is unpublished (Threader et al. 1998), is limited by a lack of

available data, and is tailored to a specific region. The objectives of this study were to: (1) provide a quantitative summary of the four key spawning habitat characteristics from documented spawning events across four major drainage basins, and (2) develop univariate type II indices for each characteristic.

Methods

Data Compilation

Literature was initially retrieved from the Web of Science database using the search terms “lake sturgeon” and “spawning”. More information was then found by consulting the references within relevant articles. Due to a lack of peer-reviewed data, lake sturgeon researchers were contacted to contribute pertinent unpublished data. In total, 12 published and 22 unpublished reports representing 112 spawning events across 48 sites were analyzed (Fig. 1; Table 1).

Spawning sites were included in our analysis only if they had information regarding at least one relevant spawning habitat characteristic that was measured during or immediately following an observed spawning event. Spawning sites were classified by watershed (Mississippi, Great Lakes/St. Lawrence, Nelson, and James Bay), river magnitude (small = <100 m³·s⁻¹, large = >100 m³·s⁻¹) and whether or not data were from a peer-reviewed publication. Because the two Northern watersheds, James Bay and the Nelson River, had small sample sizes and were not significantly different for any variable in a preliminary assessment, they were pooled together and are hereafter referred to as the Northern Watersheds. The database was analyzed using ArcGIS, version 10.4. Distance to the nearest dam or other impediment to upstream migration (e.g. falls, rapids) was computed for each site using the distance tool in ArcGIS.

For all variables, when only ranges were given, the mid-point was used in our analyses unless a mean or mode was specified. If no range was given, it was assumed that any reported value was the mean. For sites that had data for more than one spawning event, the mean was calculated for each habitat characteristic and used in the analyses. Additionally, if multiple spawning locations were found to be within close proximity of one another (<500 m), they were classified as a single site.

For flow velocity, if the location within the water column where measurements were taken was specified, it was transformed to estimate the depth-averaged velocity (hereafter velocity), the average velocity across the vertical transect where the measurement was taken, using the logarithmic velocity profile (Knighton, 1998; Smart 1999). If the location in the water column was not mentioned, we assumed that the reported value represented the depth-averaged velocity.

All studies used in our analyses used or were converted to the Wentworth (1922) scale (sand: 0.06 – 2 mm, gravel: 2.1 – 16 mm, pebble: 16.1 – 64 mm, cobble: 64.1 – 256 mm, boulder: 256.1 – 4096 mm, bedrock: N/A). When proportions of substrate size classes at a specific site were not specified, classes were assigned hierarchically as primary, secondary, tertiary, or quaternary, if possible. For instance, if a given report stated a spawning bed was “mostly composed of substrate x and y, with some z”, substrate x and y would be considered primary and z would be secondary. When comparing substrate composition across watersheds, only the primary category was used.

Analyses

We first determined whether there were significant differences in velocity, substrate size and depth between watersheds. Due to small samples sizes, we used the non-parametric Mann-

Whitney U test. We used t-tests to verify if there were differences between published and unpublished data, and between river sizes. We also investigated the potential differences between sites less or greater than 10 km from dams, but it was dropped from our analysis because results did not differ. For temperature, significant differences between each major watershed made this habitat parameter inappropriate for a generalized suitability index. Instead, we explored latitudinal trends using a regression analysis.

Spawning habitat characteristics for velocity ($n = 24$), depth ($n = 34$) and substrate size ($n = 31$), were analyzed using simple arithmetic means and confidence intervals (95%). The mean or equivalent for each site was used as a datum in the analysis. We also calculated the mean minimum, and mean maximum value for each variable to quantify variability in spawning habitat used across the lake sturgeon range. Substrate size classes were then more thoroughly investigated by calculating the total proportion of each substrate type present across all sites, along with the confidence interval. For each substrate class, the proportion of times it occurred within each hierarchical classification (e.g. – primary, secondary, etc.) across all sites was calculated, as well as the respective confidence intervals.

Three approaches are typically used when analyzing suitability data: histogram analysis, nonparametric tolerance limits, or nonlinear regression techniques (Bovee 1986). Here, histogram analyses were used for the three key spawning parameters in order to fit type II indices (Bovee 1986). We fitted the suitability curve by manual interpolation, rather than using predetermined mathematical functions (e.g. quadratic, polynomial), which often do not describe the frequency distributions as precisely (Bovee 1986). Bin sizes to create frequency distributions were either in increments of 0.1 for velocity ($\text{m}\cdot\text{s}^{-1}$) and depth (m) in small rivers, and 0.5 for depth (m) in large rivers, or by existing substrate size classifications (Wentworth 1922). For each

habitat variable, each bin documented at a site was assigned a value of 1. The total frequency of each bin was then standardized to an index from 0 to 1.

Because our model relied heavily on data from the St. Lawrence/Great Lakes watershed, we tested that it performed well in the other major watersheds across the species' range. To do so we calculated the mean habitat suitability score for the parameters of velocity, substrate, small river depth and large river depth, and compared them to the scores of both the St. Lawrence watershed and the threshold for excellent quality habitat.

Results

Velocity

For velocity, the difference between watersheds (Supplementary Table 1), small and large rivers ($t_{22} = 0.1$, $p = 0.92$), and published and unpublished data ($t_{17} = 1.52$, $p = 0.15$) were all not significant. Across all 24 sites (Fig. 2; Table 2), the mean velocity was $0.85 \text{ m}\cdot\text{s}^{-1}$ ($\text{CI} = \pm 0.11$; Table 2). A type II curve, based on the frequency of use data (Fig. 3), indicated that suitability increased rapidly from a velocity of $0.1 \text{ m}\cdot\text{s}^{-1}$ until reaching a peak at $0.6 \text{ m}\cdot\text{s}^{-1}$. The curve slowly declined until reaching a value of 0 at $2.6 \text{ m}\cdot\text{s}^{-1}$.

Depth

The differences in depths between watersheds (Supplementary Table 1) and between published and unpublished data ($t_{19} = 1.08$, $p = 0.30$) were not significant. However, there was a significant difference ($t_{32} = 4.18$, $p = 0.0002$) between small and large rivers. The mean depth was 1.06 m ($n = 15$, $\text{CI} = \pm 0.33$) for small rivers and 5.7 m for large rivers ($n = 19$, $\text{CI} = \pm 1.99$) (Fig. 4; Table 2). A type II curve based on the frequency of use data for small rivers (Fig. 5) indicated that suitable depth increased rapidly from 0.26 m, until a peak between 0.55 – 0.85 m. The curve slowly decreased until 2.05 m, after which it decreased rapidly until reaching 0 at 3.15

m. In large rivers (Fig. 5), suitability increased rapidly until reaching a peak maintained between 0.75 and 5.25 m, after which suitability decreased steadily until reaching 0 at 26.25 m.

Substrate Size

For substrate size, the differences between watersheds (Supplementary Table 1), small and large rivers ($t_{32} = 0.8$, $p = 0.43$) and published and unpublished data ($t_{17} = 0.89$, $p = 0.38$) were not significant. Across all 34 sites with substrate size data, the mean was 117 mm (CI = ± 16.52 , Table 2), which corresponds to the size class cobble. Cobble was also the most common substrate size class observed across the 34 sites (Fig. 6), and was found at 85.3% of sites, followed by gravel at 67.7% of sites (CI = ± 15.7), pebble at 38.2% of sites (CI = ± 16.3), boulders at 26.5% of sites (CI = ± 14.8), sand at 5.9% of sites (CI = ± 7.9), and bedrock at 5.9% of sites (CI = ± 7.9).

A type II curve (Fig. 7) indicated that substrates finer than gravel or larger than boulders were not suitable for lake sturgeon spawning. In between these two extremes, suitability steadily increased from gravel to peak suitability at cobble.

Water temperature

Mean water temperature during spawning was significantly different between all watersheds (Supplementary Table 1), and decreased significantly as latitude increased (Fig. 8), as did the changes in minimum ($y = -0.37x + 28.66$, $p = 0.01$, $R^2 = 0.22$) and maximum water temperature ($y = -0.54x + 40.78$, $p = 0.006$, $R^2 = 0.25$). The mean temperature during spawning within each major watershed was 16.4 °C ($n = 5$, CI = ± 1.64) for the Mississippi, 14.1 °C ($n = 22$, CI = ± 0.66) for the Great Lakes/St. Lawrence and 10.5 °C ($n = 7$, CI = ± 0.51) for the

Northern watersheds. For the entire range, the mean water temperature during spawning was 13.72 °C ($n = 34$, $CI = \pm 0.78$) (Figure 9).

Model Validation

Mean habitat suitability scores (Supplementary Fig. 1) for velocity, substrate size, small river depth and large river depth within each major watershed were all above the threshold for excellent habitat. Additionally, even though most of our data came from the St. Lawrence/Great Lakes watershed, the mean scores for the Northern watersheds and the Mississippi were greater than those for the St. Lawrence/Great Lakes watershed for all variables.

Discussion

Our study indicated that velocity, small and large river depth and substrate size did not differ between watersheds or between published and unpublished sources of data. Not surprisingly, spawning depth was greater in large than in small rivers, but river magnitude had no effect on velocity, substrate type, or water temperature. Interestingly, there was a negative correlation between the temperatures at which spawning occurs and a site's latitude, suggesting local adaptation of different populations to climatic conditions. Our overall findings that suitability peaked at velocities of 0.6 m·s⁻¹, depths between 0.55 - 0.85 m in small rivers and 0.75 – 5 m in large rivers, substrate size class of cobble are similar to previous estimates, with one notable exception. In formulating a type I HSI for spawning habitat in slow moving Northern Ontario streams, Threader et al. (1998) stated that several survey respondents indicated that sturgeon preferred to spawn in velocities over 1 m·s⁻¹. High water velocities have been considered as critical habitat in much of the literature since (COSEWIC 2006; Pollock et al. 2015), with targets for spawning habitat restorations being as high as 0.8 – 1.5 m·s⁻¹ in Québec (Dumont et al. 2011). However, egg density at spawning sites decreases as current velocity

increases from $0.6 - 1.1 \text{ m}\cdot\text{s}^{-1}$ (LaHaye et al. 1992) and increases from $0.4 - 0.6 \text{ m}\cdot\text{s}^{-1}$ (Johnson et al. 2006). Our study supports these conclusions, suggesting that spawning habitat suitability peaks at $0.6 \text{ m}\cdot\text{s}^{-1}$, but can occur across a wide range of velocities.

Although the majority of our data was retrieved from within the Great Lakes/St. Lawrence watershed, our comparison of mean suitability scores for the parameters of velocity, substrate, small river depth and large river depth for each watershed shows that the model performs well for all regions within the lake sturgeon range. This conclusion is further supported by the lack of significant differences across watersheds for the key habitat variables.

Typically, excellent habitat is considered to include all sites with an HSI value greater than $0.75 - 0.8$ (Threader et al. 1998; Daugherty et al. 2009). However, there is no standard criterion, with most studies setting arbitrary index values as thresholds. Based on the average minimum and maximum values obtained in this study, we have adapted the threshold values to represent the closest velocity, depth, or substrate index score (see horizontal lines in Figs. 3, 5 and 7). Using this criterion, the most suitable habitat is defined by suitability index values greater than 0.7 for velocity, 0.9 for small river depth, 0.8 for large river depth and 0.8 for substrate size class.

In addition to the four criteria discussed, other factors can influence spawning site selection. Most importantly, lake sturgeon have high site fidelity to their native streams (Lyons and Kempinger 1992; Forsythe 2010), although individuals have been known to visit multiple sites within the same spawning season (Fortin et al. 1992). Furthermore, lake sturgeon prefer to spawn as river discharge is decreasing (Auer 1996; Forsythe 2010), and will cease spawning activity if discharge rapidly changes (Dumont et al. 2011). Spawning cessation has also been observed during periods of drastic changes in water temperature (Bruch and Binkowski 2002).

Additional cues may also predict timing of entry to spawning rivers. For example, spawning often commenced on the same calendar day over several years in the Black River (Forsythe et al. 2012), likely due to the effect day length has on the endogenous cycle of oocyte maturation (Doroshov et al. 1977; Forsythe 2010). Although grain size is known to influence spawning site selection, silt free interstitial space within the substrate may be even more important (Johnson et al. 2006; Dumont et al. 2011; Du et al. 2011). This space provides eggs with protection from predators and from being dislodged by water currents (Bruch and Binkowski 2002; Roseman et al. 2011), as well as acting as a refuge for newly hatched larvae (Auer 1999). Unfortunately, there is only one paper in our dataset (Manny and Kennedy 2002) describing this potentially crucial component of spawning habitat. Considerable attention has also been directed to the proximity of spawning areas to impediments to upstream migration such as dams, falls, or rapids (LaHaye et al. 1992; Auer 1999; Haxton 2006). We noted that 55% of sites were found within 1 km of a dam or impediment to upstream migration, with an additional 15% found within 10 km. These results may be biased however, because many studies in our data set focus on the effects of dams on local fish populations.

While it would have been ideal to synthesize data based on means, sample sizes, and standard deviations, such an approach would have excluded up to 79% of the available information. Instead we used data based on mid-points calculated from a given range to increase our overall sample size and the geographic representation of our sample.

Because critical spawning habitat may differ between drainage basins due to characteristics such as hydrology, geomorphology, anthropogenic disturbance, and climate (Moir et al. 2005), some authors recommend using site-specific habitat criteria whenever possible (Armstrong et al. 2003; Haxton et al. 2008). However, type II curves have shown good

transferability between streams with distinct hydrology, biotic composition, and geomorphology (Mäki-Petäys et al. 2002). For lake sturgeon, the only attempt to validate an ex-situ model showed poor-predictive power for juvenile habitat (Haxton et al. 2008). However, the quality of juvenile habitat may depend more crucially on local conditions, such as the quality and quantity of food available and the degree of interspecific competition (Moir et al. 2005). Ex-situ suitability indexes have proven to be valuable as reference points from which accurate river-specific models are developed (Daugherty et al. 2009; Krieger and Diana 2017).

Given the amount of resources that have recently been directed at restoring spawning habitat for lake sturgeon (Manny and Kennedy 2002; Dumont et al. 2011; Buszkiewicz et al. 2016), there is a clear need for a generalized index for reproductive habitat. Although the exclusive use of local data are preferred in formulating an HSI, such an approach can be resource intensive, and local models are typically supplemented with external data (Mäki-Petäys et al. 2002). This study provides a comprehensive review of critical spawning habitat which can be used in conjunction with hydrodynamic modelling to locate existing spawning sites for conservation, or establish areas with suitable conditions for restoration projects. In addition, it provides a baseline of data from which local-scale models can be adapted to mitigate or predict the effect of habitat loss.

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514 **Tables**

515 Table 1. Summary of data used to describe characteristics of lake sturgeon spawning habitat. Y =
 516 Yes, N = No, L = Large, S = Small, GL/SL = Great Lakes and St. Lawrence.

ID	Major drainage	River	Published	Dam within 10km	River magnitude	State/Province	Citation
1	Mississippi	Upper Mississippi	Y	Y	L	Mo.	Buszkiewicz et al. (2016)
2	Mississippi	St. Croix	N	Y	S	Wis.	Engel (<i>Pers. Comm.</i> 2016)
3	Mississippi	Red Cedar	N	Y	S	Wis.	Engel (<i>Pers. Comm.</i> 2016)
4	Mississippi	Yellow	N	N	S	Wis.	Engel (<i>Pers. Comm.</i> 2016)
5	Mississippi	East Fork White	N	Y	L	Ind.	Fisher (<i>Pers. Comm.</i> 2016)
6	GL/SL	St. Louis	N	Y	S	Minn.	Varian (<i>Pers. Comm.</i> 2016)
7	GL/SL	Sturgeon	Y	Y	S	Mich.	Auer (1996)
8	GL/SL	Kaministiquia	N	Y	S	Ont.	Friday (2005, 2013)
9	GL/SL	Wolf	N	Y	S	Wisc.	Koenigs (<i>Pers. Comm.</i> 2016)
10	GL/SL	Embarrass	N	Y	S	Wisc.	Koenigs (<i>Pers. Comm.</i> 2016)
11	GL/SL	Little Wolf	N	Y	S	Wisc.	Koenigs (<i>Pers. Comm.</i> 2016)
12	GL/SL	Upper Fox	N	N	S	Wisc.	Koenigs (<i>Pers. Comm.</i> 2016)
13	GL/SL	Big Manistee	Y	Y	S	Mich.	Chiotti et al. (2008)
14	GL/SL	Big Manistee	Y	Y	S	Mich.	Chiotti et al. (2008)
15	GL/SL	Lower Muskegon	Y	N	S	Mich.	Peterson and Vecsei (2004)
16	GL/SL	Menominee	N	Y	S	Mich.	Baker (<i>Pers. Comm.</i> 2015)
17	GL/SL	Muskegon	N	N	S	Mich.	Baker (<i>Pers. Comm.</i> 2015)
18	GL/SL	Grand	N	Y	S	Mich.	Baker (<i>Pers. Comm.</i> 2015)
19	GL/SL	Kalamazoo	N	Y	S	Mich.	Baker (<i>Pers. Comm.</i> 2015)
20	GL/SL	Peshtigo	Y	Y	S	Wisc.	Baker (<i>Pers. Comm.</i> 2011)
21	GL/SL	Upper Black	N	Y	L	Mich.	Baker (<i>Pers. Comm.</i> 2015)
22	GL/SL	Moon	N	Y	S	Ont.	Finucan and Chicoine (2008)
23	GL/SL	St. Clair	Y	N	L	Mich.	Manny and Kennedy (2002)
24	GL/SL	St. Clair	Y	N	L	Mich.	Manny and Kennedy (2002)
25	GL/SL	Detroit River	Y	N	L	Mich.	Manny and Kennedy (2002)
26	GL/SL	Detroit River	Y	N	L	Mich.	Roseman et al. (2011)
27	GL/SL	Richelieu	Y	Y	L	Que.	Thiem et al. (2013)
28	GL/SL	Des Prairies	Y	Y	L	Que.	Dumont et al. (2011)
29	GL/SL	St. Lawrence	N	Y	L	N.Y./Ont.	NYSDC (2012, 2013)
30	GL/SL	St. Lawrence	N	Y	L	N.Y./Ont.	NYSDC (2012)
31	GL/SL	St. Lawrence	Y	Y	L	N.Y./Ont.	Johnson et al. (2006)
32	GL/SL	St. Lawrence	N	Y	L	Que.	Environnement Illimite (1987)
33	GL/SL	Mille lacs	N	Y	S	Que.	Provost et al. (1982)
34	GL/SL	St. Lawrence	N	N	L	Que.	LaHaye et al. (2003)
35	GL/SL	Assomption	Y	N	S	Que.	LaHaye et al. (1992)
36	GL/SL	Ouareau	N	Y	S	Que.	Gauthier (2014)
37	GL/SL	Saint François	N	Y	S	Que.	LaHaye et al. (2015)
38	GL/SL	Saint Maurice	N	Y	L	Que.	GDG Conseil (2001)
39	GL/SL	Missisquoi	N	Y	S	Vt.	Mackenzie (<i>Pers. Comm.</i> 2015)
40	GL/SL	Lamoille	N	Y	S	Vt.	Mackenzie (<i>Pers. Comm.</i> 2015)
41	GL/SL	Winooski	N	Y	S	Vt.	Mackenzie (<i>Pers. Comm.</i> 2015)
42	Northern	Rupert	N	N	L	Que.	LaHaye et al. (2013)
43	Northern	Rupert	N	N	L	Que.	LaHaye et al. (2013)
44	Northern	Rupert	N	N	L	Que.	LaHaye et al. (2013)
45	Northern	Rupert	N	N	L	Que.	Guay and Gendron. (2011)
46	Northern	Little Fork	N	Y	S	Minn.	Aadland (<i>Pers. Comm.</i> 2016)
47	Northern	Winnipeg	N	Y	L	Man.	Man. Hydro (<i>Pers. Comm.</i> 2016)
48	Northern	Winnipeg	N	Y	L	Man.	Man. Hydro (<i>Pers. Comm.</i> 2016)

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Table 2. Quantitative summary of lake sturgeon spawning habitat.

Variable	$\bar{x}$	$\pm CI^{95\%}$	$\bar{x}$ min	$\pm CI^{95\%}$	$\bar{x}$ max	$\pm CI^{95\%}$	Range
Velocity ($m \cdot s^{-1}$, n = 24)	0.85	0.11	0.42	0.14	1.35	0.22	0.03 – 2.51
Depth – all (m, n = 34)	3.65	1.30	1.95	0.93	4.82	1.35	0.03 – 25
Depth small river (m, n = 15)	1.06	0.33	0.66	0.36	1.54	0.41	0.03 – 2.8
Depth large river (m, n = 19)	5.7	1.99	3.23	1.99	8.1	1.81	0.1 – 25
Substrate size (mm, n = 34)	117	16.5	31.8	16.5	202.2	23.8	0.01 – 256.1

Figure Captions

Figure 1. Lake sturgeon historic range adapted from COSEWIC, 2006; USGS, 2016; and NatureServe, 2012, with locations of spawning sites used in study and major watersheds within the range.

Figure 2. Mean (a), mode (b) or mid-point (c) of depth-averaged velocity at lake sturgeon spawning sites (ID number, $n = 24$) organized by major watershed. Error bars = the range of velocities observed per site; red dashed line = mean; and grey bar = mean range (i.e. mean minimum to mean maximum).

Figure 3. Type II utilization curve (black dashed line) for depth-averaged velocity at lake sturgeon spawning sites ($n = 24$), with bin sizes in increments of 0.1 and points showing the standardized frequency of velocity class occurrence. Grey bar = mean range of velocities; and black solid line = lower limit index score (0.7) of excellent habitat.

Figure 4. Mean (a), mode (b) or mid-point (c) of water depth at lake sturgeon spawning sites (ID number) organized by river magnitude (n small rivers = 15, n large rivers = 19) and major watershed. Error bars = the range of depths observed per site; red dashed line = mean; and grey bar = mean range (i.e. mean minimum to mean maximum).

Figure 5. Type II utilization curve for lake sturgeon spawning site water depth in small rivers ($n = 15$) and large rivers ($n = 19$), with bin sizes in increments of 0.1 for small rivers, and 0.5 for large rivers with points showing the standardized frequency of depth class occurrence. Light grey bar = mean range of depth in small rivers; dark grey bar = mean range in large rivers; solid grey line = lower limit index score of excellent habitat (0.9) in small rivers; and solid black line = lower limit index score (0.75) of excellent habitat in large rivers.

555 Figure 6. Percent occurrence of Wentworth substrate size class at lake sturgeon spawning sites (n
556 = 34) with the 95% confidence interval (red bars).

557 Figure 7. Type II utilization curve (black dashed line) for lake sturgeon spawning site substrate
558 size (n = 34) with bin sizes organized by substrate size class (Wentworth scale) and vertical bars
559 showing the standardized frequency of substrate size class occurrence. Transparent grey bar =
560 mean range of substrate size, and black solid line = lower limit index score (0.8) of excellent
561 habitat.

562 Figure 8. Linear regression ($y = -0.47x + 35.529$, $p < 0.005$, $R^2 = 0.38$) showing correlation
563 between mean water temperature and latitude at lake sturgeon spawning sites (n = 34).

564 Figure 9. Mean (a), mode (b) or mid-point (c) of water temperature at lake sturgeon spawning
565 sites (ID number, n = 34) and major watershed. Error bars = the range of water temperatures
566 observed per site; red dashed line = mean; and grey bar = mean range.

567

Figure 1. Lake sturgeon historic range adapted from COSEWIC, 2006; USGS, 2016; and NatureServe, 2012, with locations of spawning sites used in study and major watersheds within the range.

177x123mm (300 x 300 DPI)

Figure 2. Mean (a), mode (b) or mid-point (c) of depth-averaged velocity at lake sturgeon spawning sites (ID number, n = 24) organized by major watershed. Error bars = the range of velocities observed per site; red dashed line = mean; and grey bar = mean range (i.e. mean minimum to mean maximum).

219x157mm (300 x 300 DPI)

Figure 3. Type II utilization curve (black dashed line) for depth-averaged velocity at lake sturgeon spawning sites ($n = 24$), with bin sizes in increments of 0.1 and points showing the standardized frequency of velocity class occurrence. Grey bar = mean range of velocities; and black solid line = lower limit index score (0.7) of excellent habitat.

200x144mm (300 x 300 DPI)

Figure 4. Mean (a), mode (b) or mid-point (c) of water depth at lake sturgeon spawning sites (ID number) organized by river magnitude (n small rivers = 15, n large rivers = 19) and major watershed. Error bars = the range of depths observed per site; red dashed line = mean; and grey bar = mean range (i.e. mean minimum to mean maximum).

218x156mm (300 x 300 DPI)

Figure 5. Type II utilization curve for lake sturgeon spawning site water depth in small rivers ($n = 15$) and large rivers ($n = 19$), with bin sizes in increments of 0.1 for small rivers, and 0.5 for large rivers with points showing the standardized frequency of depth class occurrence. Light grey bar = mean range of depth in small rivers; dark grey bar = mean range in large rivers; solid grey line = lower limit index score of excellent habitat (0.9) in small rivers; and solid black line = lower limit index score (0.75) of excellent habitat in large rivers.

212x156mm (300 x 300 DPI)

Figure 6. Percent occurrence of Wentworth substrate size class at lake sturgeon spawning sites (n = 34) with the 95% confidence interval (red bars).

91x65mm (300 x 300 DPI)

Figure 7. Type II utilization curve (black dashed line) for lake sturgeon spawning site substrate size ($n = 34$) with bin sizes organized by substrate size class (Wentworth scale) and vertical bars showing the standardized frequency of substrate size class occurrence. Transparent grey bar = mean range of substrate size, and black solid line = lower limit index score (0.8) of excellent habitat.

91x65mm (300 x 300 DPI)

Figure 8. Linear regression ($y = -0.47x + 35.529$, $p < 0.005$, $R^2 = 0.38$) showing correlation between mean water temperature and latitude at lake sturgeon spawning sites ($n = 34$).

91x65mm (300 x 300 DPI)

Figure 9. Mean (a), mode (b) or mid-point (c) of water temperature at lake sturgeon spawning sites (ID number, n = 34) and major watershed. Error bars = the range of water temperatures observed per site; red dashed line = mean; and grey bar = mean range.

219x157mm (300 x 300 DPI)