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Title Page

Title: Evaluation and comparison of a habitat suitability model for post-drift larval Lake Sturgeon *Acipenser fulvescens* in the St. Clair and Detroit rivers.

Shortened Title: Habitat suitability model for larval Lake Sturgeon.

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Abstract

We evaluated composition and spatial distribution of riverine nursery habitat for larval Lake Sturgeon *Acipenser fulvescens* in Middle Channel of the St. Clair River, Michigan and Fighting Island Channel of the Detroit River, Ontario using habitat suitability modeling (HSM) and fish collections. Though model outputs indicated similar portions of high quality habitat in the Middle Channel (16.9%) and Fighting Island Channel (15.7%), both larval abundance and dispersal patterns varied between these systems. AIC analysis indicated the regression model using sand–silt substrate best predicted observed water volume standardized catch-per-unit-effort (VCPUE; number larvae * hr^{-1} * m^{-3}) in the Middle Channel. Of 93 larvae collected in the Middle Channel, most were found to cluster at three distinct areas of high and moderate quality habitat, which was composed predominately of sand–silt substrate. Lengths of larvae varied by as much as 9 mm and degree of yolk sac absorption also varied, indicating larvae in the Middle Channel remained within the channel after a short drift downstream. Of the 25 larvae collected in Fighting Island Channel, distribution was sporadic and occurrence did not significantly correlate with measured habitat variables. Larvae were relatively homogenous in size and yolk sac stage, indicating newly emerged larvae did not utilize available habitat in Fighting Island Channel, but drifted into the main channel of the Detroit River. Dispersal patterns indicate variability in young Lake Sturgeon ecology, which is dependent on local habitat conditions; most notably, substrate composition. Furthermore, modeled larval–habitat associations found in this study were compared to a similar study on larval Lake Sturgeon from the North Channel of the St. Clair River. Model outputs from all three systems accurately accounted for observed larval dispersal

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patterns among both rivers. This supports the transferability of an HSM parameterized for Lake Sturgeon from individual river reaches within two large river systems.

Introduction

The Great Lakes Connecting Channels (upper St. Lawrence, St. Mary's, St. Clair, Niagara, and Detroit rivers) contain some of the largest populations of Lake Sturgeon *Acipenser fulvescens* in the Great Lakes Basin (Thomas and Haas 2004; Bauman et al. 2011; Hayes and Caroffino 2012). Channel dredging (Bennion and Manny 2011), coastal development, wetland degradation and destruction, overfishing, and pollution have greatly reduced Lake Sturgeon abundance in all these systems (Peterson et al. 2007). These actions have resulted in a moratorium on commercial fishing for Lake Sturgeon in these rivers with exception of a fishery operating in the St. Lawrence River that allows an annual harvest of 80 tonnes (COSEWIC 2017).

Availability of and accessibility to suitable habitat is one of the greatest impediments to the recovery of Lake Sturgeon stocks in the Great Lakes (Hayes and Caroffino 2012; COSEWIC 2017). As Lake Sturgeon are prone to high rates of mortality through early development, efforts to identify quantity and quality of spawning and nursery habitat has become a top priority for resource managers operating in the Great Lakes Connecting Channels (GLFWRA 2006; Hayes and Caroffino 2012). In the St. Clair and Detroit rivers, Lake Sturgeon successfully spawn on artificial reefs that were constructed to enhance fish reproduction (Read and Manny 2006; Roseman et al. 2011a; Bouckaert et al. 2014); however, there are no documented accounts of increased abundance of young-of-year (YOY, 50 – 200 mm) and juveniles (200 – 500 mm) in these areas. While lack of documented increases in abundance may be attributed to poor sampling success or inefficient gear selection, it may also reflect high mortalities of larval fish.

Lake Sturgeon may experience a bottleneck early in life as a result of high predation rates or lack of suitable nursery habitat (Peterson et al. 2007; Daugherty et al. 2009); however, once larvae settle in nursery habitat and develop armored scutes along their bodies, predation pressure is greatly reduced (Peterson et al. 2007). Decreased predation pressure makes conditions experienced prior to this developmental milestone of particular importance. Assessments evaluating dispersal patterns and habitat preferences of larval Lake Sturgeon are essential in determining early-life stage survival and eventual cohort success.

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Lake Sturgeon larval drift studies have occurred in several systems throughout their range (Auer and Baker 2002; Smith and King 2005; Benson et al. 2006). Larvae emerge from their spawning source approximately 13 – 19 days post-hatch, at the onset of exogenous feeding (Peterson et al. 2007). Upon entering the current, larvae may disperse throughout the full vertical extent of the water column (D'Amours et al. 2001; Verdon et al. 2013), or drift predominately near the river bottom (Kempinger 1988; Caroffino et al. 2009; Roseman et al. 2011b). In the St. Clair River, Young (2015) used depth stratified conical drift nets deployed at varying depths downstream of known Lake Sturgeon spawning areas in the Middle Channel, and collected ~ 88 % of sampled larvae within 1 m of the bottom. Differences in larval drift patterns may be attributed to variation in hydrologic and hydraulic conditions among river systems (D'Amours et al. 2001; Caroffino et al. 2009; Verdon et al. 2013), though local habitat conditions may also influence larval dispersal, especially in systems where larvae drift close to the river bottom.

In a series of flume trials, Hastings et al. (2013) observed that when gravel substrate was present close to the initial larval release point, larval drift distance was short and larvae settled in these areas. When a different substrate was offered immediately downstream of the release point, larvae drifted longer distances to find gravel. These findings suggest larvae not only possess the ability to recognize suitable habitat when encountered, but also to orient and maneuver themselves to these locations. In fast flowing rivers such as the St. Clair River (> 1.5 m / s), larvae caught in the current could be transported out of the river in a single night of drift. Instead, Lake Sturgeon larvae are routinely collected up to several weeks after larvae initially begin to emerge and drift downstream (Bouckaert et al. 2014; Young 2015; Krieger and Diana 2017). If larvae are to remain in the river, they must seek refuge from the current using available substrate (Auer and Baker 2002; Benson et al. 2005) or find current shelters (e.g., rocks, logs, debris). Given this, quality and location of suitable habitat in relation to local spawning sources could also influence larval drift. Lake Sturgeon occur in dynamic systems that may differ in fluvial and ecological characteristics. This suggests early-life ecology of Lake Sturgeon is also variable among systems and that system specific evaluations are essential to understanding Lake Sturgeon behavior.

Krieger and Diana (2017) developed a habitat suitability model (HSM) using benthic habitat characteristics collected from a reach of the St. Clair River, the North Channel, to identify and characterize quality of habitat available to larval, YOY, and juvenile Lake Sturgeon. Results

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indicated significant associations between larval drift, locations of YOY collected from surveys, and areas of high quality habitat predicted by the HSM. Krieger and Diana (2017) were the first to develop a life-stage specific habitat model for Lake Sturgeon in the Great Lakes Connecting Channels, which will provide resource managers with insight into areas of likely YOY and juvenile residence. While HSMs have been extensively used to evaluate habitat for species management, the ability to transfer species – habitat associations from one system to another is uncertain (Morris and Ball 2006; Vinagre et al. 2006; Haxton et al. 2008). Assessments of the transferability of modeled species – habitat relationships across systems requires information on local habitat parameters and area specific information on animal dispersal patterns.

The purpose of this study was to parameterize and field test an HSM for larval Lake Sturgeon in the Middle Channel of the St. Clair River, Michigan, and the Fighting Island Channel of the Detroit River, Ontario. Further, we sought to demonstrate how an HSM developed for a particular Lake Sturgeon system, the North Channel of the St. Clair River (Krieger and Diana 2017), could be used to accurately describe larval drift patterns in systems with novel environmental characteristics. The objectives of this study were to (1) use an HSM parameterized with local habitat information in combination with dispersal patterns of larval Lake Sturgeon to identify relationships between local habitat characteristics and larval presence; and (2) assess how HSM modeled larval – habitat relationships translate across three river reaches in the Detroit and St. Clair rivers. Given the range in environmental conditions evident in these reaches and the variability in larval Lake Sturgeon behaviors as a function of local hydrologic conditions, we hypothesized larval Lake Sturgeon dispersal patterns in the St. Clair and Detroit rivers would vary in response to local habitat characteristics. We expected larvae collected from river reaches that lacked suitable nursery habitat would drift quickly from their hatching point of origin to locations outside the study areas, and individuals collected in reaches possessing more suitable habitat would congregate in high quality habitat areas within their respective river.

[A]Methods

[B]*Study sites*

We selected segments of the Middle Channel of the St. Clair River and Fighting Island Channel of the Detroit River for assessment (Figure 1). The St. Clair River is 64 km in length and drains water from Lake Huron into Lake St. Clair. It has an average annual discharge of

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5,150 m³/s, which remains relatively constant seasonally. Flow velocities in the St. Clair River range from ~ 0.3 to 1.7 m / s (Schwab et al. 1989), with mid-channel depth ranging from 13 – 15 m and scattered deep holes > 21 m. Within the St. Clair river, the Middle Channel is an 11.2 km long reach and at its head there is an artificial spawning reef (4,040 m^2) constructed in 2012 (Middle Channel Reef, Figure 1) where Lake Sturgeon eggs have been collected (Bouckaert et al. 2014). Larval fish from this reef are believed to remain in the lower river or drift into Anchor Bay (Young 2015).

The Detroit River is a 51 km long and drains water from Lake St. Clair into Lake Erie. Within the Detroit River, the Fighting Island Channel reach is located on the east side of Fighting Island in Canadian waters (Figure 1). The Fighting Island Channel is 5.5 km long, has an average annual discharge of approximately 5,300 m^3 / s and flow velocities range from ~ 0.2 to 0.9 m / s (Schwab et al. 1989), with mid-channel depth ranging from 7 – 11 m. In the channel, Lake Sturgeon eggs have been regularly collected from an artificial spawning reef (3,300 m^2) that was constructed in 2008 (Fighting Island Reef, Figure 1, Roseman et al. 2011a; Bouckaert et al. 2014).

[B]*Field data collection*

We conducted habitat assessments throughout the Middle and Fighting Island channels during summer and fall 2015 and 2016 following methodologies previously described by Krieger and Diana (2017). River habitat was characterized following an approach based on random-grids (0.1 km²; 889 total sampling locations). Water depth, benthic invertebrate composition, substrate composition, and longitude and latitude were collected at each sampling location. Longitude and latitude was recorded using a wide-area augmentation system (estimated positional accuracy < 3 m), and water depth was collected using a boat-mounted sonar and measured to the nearest 0.1 m. Benthic substrate composition was determined using a PONAR grab sampling device. This device consisted of two opposing semi-circular jaws (232 cm² jaw opening) that are held open by a steel trigger pin. The PONAR was lowered to the bottom where the jaws penetrated the substrate, causing the trigger pin to release and the jaws to shut; trapping a sample of the benthos. Two to three PONAR samples were taken at each location. Substrate composition of PONAR samples was determined by visual and tactile inspection following the Wentworth Sediment Classification Scheme (Wentworth 1922). Samples comprised of 50% or greater of a single substrate type (sand, silt, clay, cobble) were classified as that single substrate type.

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Samples with two substrate types, each contributing 35% to 50%, were categorized as a mixed substrate (e.g., sand-silt, sand-clay). All samples were washed through an elutriator and invertebrates were separated from sediment and other river debris. Invertebrate samples were preserved in 95% ethanol, transported to the lab, and sorted into one of six major taxa: Ephemeroptera (*Hexagenia*), Chironomidae, Hirudinea, Gammaridae, Dreissenidae, and Gastropoda. These taxa were selected based on their abundance and inclusion in Lake Sturgeon diets (Kempinger 1996; Nilo et al. 2006; Boase et al. 2011). Invertebrates not representing one of these taxa were discarded. Benthic flow velocities were measured to the nearest 0.1 m/s using a Sontek Acoustic Doppler Profiler (ADP, Model: M.78 #870-58-235) during each year of study. To collect benthic flow velocities, the ADP probe was attached to our research vessel, which was driven in a zig-zag pattern from bank to bank, throughout the entire study area. At each larval sampling location, a vertical velocity profile was measured while maintaining station in the river. Each profile consisted of 25 to 50 cells covering 0.3 m each. In some cases, return signal interference was generated in the bottom-most cell as ADP emitted wavelengths were absorbed, scattered, or reflected by benthic substrate. As such, benthic flow velocities were approximated based on the average reading from the two bottom-most cells and represent flows at depths from 0.1 to 0.5 m off the bottom. ADP data files containing velocity profiles were then exported into the software program Sontek Current Surveyor. Averaged readings taken from the last two cells in a given vertical velocity profile were extracted and converted into a GIS data layer in ArcGIS® 10.3.

Information on larval distribution of Lake Sturgeon was collected during their larval drift period using D-frame drift nets (area of opening = 0.3487 m^2, 1600 µm mesh), which sample the bottom 0.54 m of the water column. Beginning approximately eight days after eggs (minimum incubation time; Auer and Baker 2002) were collected on a reef by personnel from the U.S. Geological Survey (USGS), two nets were deployed approximately 50 m downstream of that reef, near mid channel. Once larval sturgeon were collected, nets were deployed in a fixed-stratified configuration with three levels of placement consisting of two nets per level. Each level of nets was placed approximately 0.3 km apart with the total array covering 0.6 km of the channel. Once larvae were collected in nets placed in the second level, we began to move the net array further downstream on a nightly basis to track the progression of drifting larvae. Nets placed at the third level were sufficiently downstream of second level nets to detect larvae

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drifting past our array. As such, collection of individuals in third level nets was infrequent. To assess dispersal patterns of drifting larvae, nets utilized throughout each study system were moved to a total of 25 – 40 locations (Figure 2), beginning approximately 50 m from each reef and continuing downstream 3 – 7.5 km to where the channels emptied into Anchor Bay or the main channel of the Detroit River. We assumed horizontal dispersal of larval Lake Sturgeon in the St. Clair River was restricted to mid-channel depths, where flow velocities were greatest and vegetation was limited, based on unsuccessful attempts to collect larvae closer to shore. Larval drift surveys in the Middle Channel took place from 10 June to 9 July in 2013 and from 5 June to 29 July in 2014. In the Fighting Island Channel, larval surveys took place from 28 May to 16 June in 2016. Nets were deployed at 20:00 hours each night and retrieved at 6:00 the following morning to capture the peak drift time of larval Lake Sturgeon (LaHaye et al. 1992; Auer and Baker 2002; Smith and King 2005).

Morphometric data from individual larvae were collected to assess differences in larval length and yolk sac stage. Variability in size and yolk-sac absorption of larvae collected from similar sites could indicate that larvae settled in those locations and highlight probable larval Lake Sturgeon nursery areas; while collections of larvae with more uniform size and yolk-sac stage could indicate larvae emerged from the reef and quickly drifted out of the study system. Similarly, higher proportions of larger larvae with smaller or fully absorbed yolk-sacs in individual areas could suggest larvae settled in nursery habitat to continue development. In contrast, higher proportions of smaller individuals with larger yolk-sacs could indicate larvae were still drifting through the system (Kempinger 1988; Peterson et al. 2007). Individual larvae were photographed at 60x magnification using a microscope with digital analysis software (Image Pro Plus 7.0). Total length (TL, mm) and yolk sac absorption stage (full, partial, or no-yolk sac) for each larva were measured from magnified images. Lake Sturgeon larvae with full yolk sacs were identified by a pronounced yolk sac extending to the pectoral fin and the lack of distinct pigmentation along the lateral portion of the head and trunk. Larvae with partially absorbed yolk sacs possessed less pronounced yolk sacs, which often appeared wrinkled or deflated, and had dark pigmentation along the head and trunk. Individuals with no-yolk sac lacked a yolk sac, had fully formed mouths, and possessed a prominent lateral band, which extended the entire length of the body (Wang et al. 1985; Kempinger 1988; Peterson et al. 2007).

[B]*Habitat modeling*

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The habitat GIS model followed methodologies detailed by Krieger and Diana (2017) and is summarized here. For each river reach, an extent map of the submersed channel was prepared using base layers delineating lake and river features (i.e. boundaries and islands), and was digitized using available satellite image basemaps of the study sites contained in the ArcGIS® 10.3 software package (Environmental Systems Research Institute [ESRI], Redlands, CA, U.S.A.). A river layer shapefile was created to establish study boundaries for each habitat model. Georeferenced depth (m) and benthic flow velocities (m / s) were converted into MS excel files and imported to shapefiles. Raster layers containing values for water depths and benthic flow velocities were interpolated for each study area using inverse distance weighting. Data on invertebrate density and substrate category from each sample location were also converted to georeferenced shapefiles. Thiessen polygons were created around each point to assign values across the entire study surface, and the resulting layer was clipped using the river layer shapefile and converted into a raster file.

For each area, a shapefile containing point values was created for locations where drift nets were placed. At each net location, longitude and latitude, net hours (total time a net was placed in a given location), and number of Lake Sturgeon larvae collected were recorded and imported into ArcMAP® 10.3.

The raster layer of each habitat variable was reclassified into habitat suitability index (HSI) values based on suitability criteria developed by Threader et al. (1998) for substrate, Benson et al. (2005) for benthic flow velocity, and Krieger and Diana (2017) for invertebrate density and depth (Table 1). As an example, if a polygon contained sand substrate, that location was assigned an HSI value of 1 for the substrate raster layer based on Threader et al (1998). If a point had a benthic current velocity of > 1.0 m /s it was assigned an HSI value of 0 based on Benson et al. (2005). In cases where substrate composition was found to include two or more substrate types, substrate HSI values were averaged for that location. The geometric mean of each reclassified layers was then calculated with the raster calculator in ArcGIS® 10.3 using the formula:

$$(Benthic\ Current\ Layer\ x\ Depth\ Layer\ x\ Depth\ \ Layer\ x\ Invert\ Layer)^{0.25},$$

to create a composite HSM throughout each system. Cells of the composite model with a value of 0 were defined as unsuitable habitat, whereas cell values ranging from 0.01 to 0.60 were

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defined as poor habitat, from 0.61 to 0.80 as moderate habitat, from 0.81 to 1.00 as high-quality habitat for larval, YOY, and juvenile Lake Sturgeon.

[B]*Data analyses*

Aside from information on habitat characteristics present in each of our study systems, we were also interested in comparing the number of Lake Sturgeon eggs that were deposited on a given reef during our study years. Estimations of egg deposition provides an approximation for the number of larvae expected to enter the drift in a given year and allows for a comparison of egg and larval survival between the Middle and Fighting Island channels. To estimate the input of Lake Sturgeon larvae into our study systems, we used information on average egg deposition (# / m^2) collected from various sites at each spawning reef, during years when larvae were also collected. We multiplied mean egg density by reef area to estimate total egg deposition by Lake Sturgeon at each reef location.

For both river reaches, we examined the relationship between larval Lake Sturgeon catch-per-unit-effort (CPUE; number larvae per hour) and combinations of habitat variables using multiple linear regressions (Table 2). To standardize CPUE between each sampling location, benthic flow velocity values were obtained for each net location from the interpolated raster layer. Since discharge in the Great Lakes Connecting Channels is relatively stable seasonally (Schwab et al. 1998; Hondorp et al. 2014), benthic flow velocities sampled over the course of several days during the larvae drift period were assumed to represent velocity values throughout the full drift period. Flow velocity values were multiplied by area of the drift net opening to estimate water volume passing through each net, giving a volume standardized CPUE (VCPUE) as number of larvae per hr per m^3 of water sampled. To allow for comparisons between river systems of variable size, we standardized VCPUE by dividing it by the total area of high, moderate, and poor quality habitat in each system. As such, VCPUE was calculated per km^2 of habitat.

Akaike information criterion (AIC) was used to measure relative fit of each regression and to assess the degree to which each habitat variable combination was useful in predicting VCPUE (Table 2). A One-Tailed T-Test was used to compare the relative amounts of high, moderate, poor, and unsuitable habitat between the Middle and Fighting Island channels. We used a One-Way ANOVA to compare yolk sac stage and length distributions of larvae between study systems. To assess the transferability of modeled species – habitat relationships across reaches,

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we compared larval Lake Sturgeon – habitat relationships modeled in this study to those of Lake Sturgeon in the NC modeled by Krieger and Diana (2017). CPUE values from Krieger and Diana (2017) were also standardized to account for differences in benthic flow velocities among net locations. All statistical analyses were performed using R-v 3.1.3 (R Development Core Team 2008). Model performance using AIC was tested using the "AICcmodavg" package (Mazerolle 2017). Alpha was set at 0.05 for all comparisons.

[A]Results

Observed larval Lake Sturgeon dispersal patterns in the Middle and Fighting Island channels indicate that although relatively similar habitat exists in both systems, subtle differences in one or more individual habitat features may have a large influence on larval dispersal. Further, the location of suitable habitat in relation to the individual spawning reef also influences local dispersal patterns and is an important consideration for successful recruitment of YOY Lake Sturgeon in the St. Clair and Detroit rivers.

The Middle and Fighting Island channels study areas were 18.66 and 7.07 km^2, respectively, and contained similar proportions of high, moderate, and low quality habitat between systems. (Figure 2). In the Middle Channel, 14.7% of modeled habitat ranked as high quality, while 76.8 % ranked as moderate quality. Similarly, 16.8 % of modeled habitat ranked as high quality in the Fighting Island Channel, with 79.3 % ranked as moderate quality. Areas designated as poor quality habitat comprised < 20 % of both study areas (Table 3). Benthic current velocity, invertebrate density, and depth were similar between systems (Table 3), while substrate composition was quite dissimilar. The Middle Channel was composed predominately of sand and silt substrate (sand – silt; 48% of total area), followed by sand (24%), and clay (15%). In contrast, clay was the most common substrate type (53%) in the Fighting Island Channel, followed by clay – silt (14%), and silt (10%).

Larval Lake Sturgeon abundance was considerably higher in Middle Channel than in Fighting Island Channel. If larvae were settling in these systems, we would expect to find individuals congregated in areas of high quality habitat, collections of individuals of variable length and yolk sac stage, and higher proportions of larvae with greater length and smaller yolk sac. During the summers of 2013 and 2014, 93 larvae were collected from 24 different locations downstream of the Middle Channel Reef, resulting from approximately 815 net hours of sampling. Larval TL ranged from 14.8 – 23.8 mm ($\bar{x}$ = 18.7 ± 2.01) with 79 % of individuals

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measuring between 16 – 20 mm (Figure 3), and lengths in individual nets differing by 2 – 6 mm. A partially absorbed yolk sac was evident on 27.9 % of larvae, while 57.4 % were found with no yolk sac, and 14.8 % were found with a full yolk sac. Larvae were collected in habitat of high quality (n = 15), moderate quality (n = 76), and poor quality (n = 2; Table 4). VCPUE was significantly higher in areas of high quality habitat (0.15) compared to moderate (0.11) and poor (0.09) quality habitat ($P < 0.05$).

Larval surveys in the Middle Channel indicate high larval concentrations occurred in three areas approximately 1.5, 3, and 4.5 km downstream from the Middle Channel Reef (Figure 2). The first two areas closest in proximity to the reef contained 51 and 14 larvae, respectively, and were in moderate quality habitat. The third area of high larval concentration occurred in high quality habitat and contained 15 larvae. All three areas of high larval yield occurred in areas comprised of sand – silt substrate. In addition to these three areas of high concentration, larval Lake Sturgeon were collected sporadically throughout the full extent of the system, with two individuals collected at the mouth of the channel (Figure 2).

In the Fighting Island Channel, total VCPUE of larval Lake Sturgeon was significantly lower (One-Tailed T-Test, P = 0.023). Larval Lake Sturgeon (n = 25) were collected downstream of the Fighting Island Reef during summer of 2016 from 16 different locations, resulting from approximately 400 net hours of sampling. Larval TL was similar to the Middle Channel, ranging from 12.5 – 19.7 mm ($\bar{x} = 17.7 \pm 1.9$; Figure 3); however, larvae collected in the Fighting Island Channel from a single net were homogenous in size (within 1.4 mm of each other), and a significantly higher portion were found with no yolk sac (77.8 %) compared to the Middle Channel (57.4%; P = 0.041). Six larvae were collected in areas of high quality habitat, 17 in moderate quality habitat, and 1 in poor quality habitat (Table 4). There was not a significant difference in VCPUE measured for nets located in areas of high, moderate, and poor quality habitat in the Fighting Island Channel. Larvae were collected throughout the full extent of the system; beginning 0.25 km downstream from the Fighting Island Reef to 5 km downstream at the mouth of the Fighting Island Channel.

Larvae in the Fighting Island Channel did not demonstrate areas of high larval concentration as observed in the Middle Channel. VCPUE in areas of poor quality habitat was significantly greater in the Fighting Island Channel than the Middle Channel (P = 0.03). No significant differences were found between VCPUE in areas of high or moderate quality habitat in the

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Fighting Island Channel compared to the Middle Channel (One-Tailed T-Test, $P > 0.05$ for both comparisons). Fighting Island Channel contained higher proportions of clay and clay – silt areas compared to the Middle Channel. Clay is a less effective medium for larvae to settle on and receives a HSI score of 0.2 (Threader et al. 1998; Table 1). In contrast, the most dominant substrate found in the Middle Channel (sand – silt) received a HSI score of 1.0.

Local habitat conditions also influenced the occurrence of larval Lake Sturgeon. AIC analysis combining catch and habitat parameters was used to compare 13 different multiple linear regressions describing VCPUE – habitat relationships in the Middle and Fighting Island channel (Table 2). The 13 different linear regression models were identical to those tested in Krieger and Diana's (2017) study of larval Lake Sturgeon dispersal in the North Channel to allow for comparisons between all 3 systems. In both the Middle and Fighting Island channels, only the top model is discussed as no other model was within 2 ΔAIC, with the exception of the "NULL" model for the Fighting Island Channel; suggesting there was a low probably of other models having the best fit (Burnham and Anderson 2002). In the Middle Channel, the highest ranked linear regression model predicted VCPUE using substrate, specifically locations composed of both sand – silt substrate ($df = 14$, $F = 2.38$, $P = 0.046$, $R^2 = 0.21$). For the Fighting Island Channel, AIC indicated the highest ranked linear regression model predicted VCPUE using benthic flow velocity, but this model was not statistically significant ($df = 12$, $F = 4.33$, $P = 0.072$, $R^2 = 0.11$); indicating that local habitat characteristics surveyed in this study did not significantly correlate with larval VCPUE in the Fighting Island Channel.

Though larval abundance was low in the Fighting Island Channel, estimated Lake Sturgeon egg density was considerably higher than in the Middle Channel. Lake Sturgeon egg sampling in the Middle Channel yielded 243 eggs / m^2 from egg mat gangs deployed immediately around the Middle Channel Reef during 2013 – 2014 (Prichard et al. 2017), while 1,367 eggs / m^2 were collected from gangs around the Fighting Island Reef during 2016 surveys (Craig et al. 2017). Total estimated egg deposition for each reef site was 9.8×10^5 for the Middle Channel Reef and 7.8×10^6 for the Fighting Island reef.

[A]Discussion

Variation in dispersal of larval Lake Sturgeon in relation to composition and spatial distribution of suitable habitat found in the Middle and Fighting Island channels supports our hypotheses on Lake Sturgeon – habitat interactions in the St. Clair and Detroit rivers. In the

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Middle Channel, high quality habitat consisted of areas composed of sand – silt substrate, and HSM output indicated presence of high quality habitat at variable distances downstream of the Middle Channel Reef where larval VCPUE was significantly greater compared to areas of moderate or poor quality habitat. In contrast, the Fighting Island Channel was composed predominately of clay and clay – silt substrate, larvae were found in low abundance, and there was no distinction in larval VCPUE between high, moderate, and poor quality habitat.

Given that high quality habitat in the Middle Channel did not occur until 4.5 km downstream from the Middle Channel Reef, we would expect low larval abundance immediately downstream from the reef and higher abundance closer to areas of high quality habitat further downstream. Our survey of larval Lake Sturgeon in the Middle Channel identified three areas of high larval concentration where 86% of larvae were collected at 1.5, 3, and 4.5 km downstream from the Middle Channel Reef. Only 3 larvae were collected within 1.5 km downstream of the reef and only 5 further than 4.5 km downstream. Furthermore, our AIC analysis indicated the presence of sand – silt substrate best described observed VCPUE values in the Middle Channel. While only one area of high larval concentration overlapped with high quality habitat in the Middle Channel, all three areas occurred in locations possessing sand – silt substrate.

These findings in the Middle Channel match well with and are supported by Krieger and Diana's (2017) study of larval Lake Sturgeon – habitat associations in the nearby North Channel. Their HSM output indicated an abundance of high quality habitat for larval sturgeon located in distinct patches approximately 0.25, 0.75, 1.25, and 2 km downstream of the Maslinka Reef, and 81 % of larvae (n = 283) were collected in these patches. Using AIC analysis methods analogous to ours, Krieger and Diana (2017) found the presence of sand substrate as the best predictor of larval CPUE in the North Channel, and that larvae were found in high densities in areas comprised of sand.

In contrast, no significant association between VCPUE and habitat quality was found for larval Lake Sturgeon in the Fighting Island Channel. In the North and Middle channels, larvae congregated in areas comprised of sand and sand – silt, which can provide refuge from high current velocities and potential predators (Auer and Baker 2002; Benson et al. 2005). However, the Fighting Island Channel possessed higher proportions of clay and clay – silt that is a less suitable medium for larvae to settle on (Benson et al. 2005; Krieger and Diana 2017). Indeed, of the four habitat parameters assessed in this study, substrate composition was the lone variable

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included in the best multiple linear regressions predicting abundance of larval VCPUE for both the North and Middle channels. As such, it is reasonable to assume that substrate would also influence larval dispersal in the Fighting Island Channel. Though while our model identified suitable larval habitat in the Fighting Island Channel, high HSI scores from non-substrate habitat parameters likely influenced HSM rankings. For instance, the HSM score for an area in the Fighting Island Channel composed of the median habitat values for depth, invertebrate density, velocity (Table 3), and clay – silt substrate would still receive a composite HSM score of 0.78; close to a ranking of “high” quality habitat in our study. Although depth, invertebrate density, and velocity values of the North, Middle, and Fighting Island channels are quite similar; the substrate composition of the Fighting Island Channel is markedly different. Since we gave equal weighting to all variables in our model, the similarities in some habitat characteristics could underestimate the importance of substrate composition in our HSM prediction. Given that larval Lake Sturgeon have been shown to drift greater distances when unsuitable substrate was not readily encountered (Hastings et al. 2013), prolonged time spent drifting could result in increased risk of predation and starvation (Auer and Baker 2002; Peterson et al. 2007), corresponding to high larval mortality rates, and relatively low abundance observed in our study.

In addition, even though estimated egg densities on the Fighting Island Reef were much higher than densities from the Middle Channel Reef, larval sampling in the Fighting Island Channel yielded far fewer individuals than were collected in the Middle Channel. This may indicate few larvae enter the channel due to high egg mortality, or larvae emerge from the reef and quickly drift through the channel. However, larval yield was low even in nets placed immediately downstream of the reef. Furthermore, if larvae were drifting quickly out of the Fighting Island Channel immediately after emergence we would expect higher catch rates during peak drift and a shorter overall drift period compared to Middle Channel; neither of which was observed. As such, while we believe egg deposition on the Fighting Island Reef is sufficient to produce similar numbers of drifting larvae as found in the North Channel by Krieger and Diana (2017; n = 283) and Middle Channel (n = 93); high rates of egg and larval mortality are likely responsible for low larval VCPUE in the Fighting Island Channel.

Differences in the physical characteristics of collected larvae further supports our assertion on variable drift patterns in larval Lake Sturgeon. In the Middle Channel, the majority of larvae collected were > 19 mm in length and were found with either a partial (62 %) or fully absorbed

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yolk-sac (33 %), indicating they were ending the yolk – sac stage and initiating consumption of food. Peterson et al. (2007) noted that larval Lake Sturgeon remain on their natal reef for periods of two to four weeks after hatch as they absorb their yolk sacs, then emerge from the reef with relatively similar length and a partially or fully absorbed yolk sac as they begin to drift downstream (LaHaye et al. 1992; Auer and Baker 2002). However, larvae collected downstream of Middle Channel Reef ranged in size by as much as 9 mm and showed considerable variation in both lengths and patterns of yolk sac composition from individuals collected in single nets. Variation in morphometric characteristics between larvae may indicate individuals entered the drift at different times with some possibly being dislodged from the reef due to turbulence or strong flow (Kempinger 1988; Peterson et al. 2007). However, if the majority of larvae were dislodged, downstream collections should contain higher proportions of small (12 – 16 mm) individuals with full yolk sacs, with more consistent numbers of larvae collected throughout the channel (as described in Smith and King 2005; Peterson et al. 2007). Instead, variability in size and developmental stage observed in larvae collected from the Middle Channel suggests individuals are residing in the river in areas of favorable habitat after drifting variable distances downstream from their spawning source.

While models describing species – environmental relationships have received much attention from scientific and resource management communities (Larson et al. 2004; Hirzel et al. 2006), the transferability of modeled relationships predicted by HSMs across systems is uncertain (Peterson et al. 2007; Haxton et al. 2008). Though more dispersed than larvae collected in the North Channel, we found that larval VCPUE in the Middle Channel was also significantly correlated with high quality habitat and was concentrated in three distinct areas. In the Fighting Island Channel, we found low abundance of larvae in high quality habitat and lack of a significant relationship between habitat parameters and larval VCPUE. Based on this, we conclude larvae exited the channel and dispersed into the Detroit River. Although variation in patterns of larval dispersal occurred across these river reaches, this variation was consistent with our predictions of larval dispersal in response to local habitat conditions in each system. Drifting larvae made use of and congregated around suitable habitat, most notably sand and sand – silt substrate in deep water with moderate currents, when it was available to them. If this habitat was not available, larvae remained in the water column and quickly drifted out of our study system. This is an important first step in linking HSI relationships across different reaches of river that

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support Lake Sturgeon and other species of interest, and emphasizes the importance of local habitat conditions in determining dispersal and habitat use of early life-stage fishes. While the Middle and Fighting Island channels are similar in many ways, there are dissimilarities that result in different patterns of larval Lake Sturgeon occurrence. System-specific models that incorporate a range of local habitat characteristics allows us to evaluate and compare habitat features between seemingly similar systems, and to determine subtle, yet important differences which have a profound influence on the distribution of local species.

[B]Limitations and Biases

While the findings and interpretations generated from this study are supported by available data and existing literature, some limitations and assumptions result from lack of available data. First, while predation on larval Lake Sturgeon has not been documented in the St. Clair or Detroit rivers, predators undoubtedly influence larval survival and subsequent dispersal to nursery habitat. Given that larvae were found to concentrate in areas at variable distances downstream of their spawning source rather than to continually decrease with downstream distance in the North and Middle channels, observed dispersal patterns in these systems cannot be explained by predator effects alone, but are instead the result of preferential habitat selection by larvae as well.

Additionally, there is a lack of knowledge in sources of larval Lake Sturgeon from locations upstream of our study sites. Young (2015) collected 54 larvae just upstream from the Middle Channel Reef; however, those larvae showed nearly identical proportions of stages with full, partial, and no yolk sacs to larvae collected from downstream in our study. In addition, lengths of larvae collected upstream and downstream from the reef in our study were not statistically discernible. Given the distinct concentrations of larvae in areas of high and moderate quality habitat downstream of the Middle Channel Reef, and the similarities in morphometric characteristics in upstream versus downstream collections, we believe larvae from upstream sources drifted past the Middle Channel Reef, mixed with larvae emerging from these reef, and used similar habitat downstream. Thus, the input of upstream larvae is not influencing larval distribution patterns found downstream.

[B]Conclusion

Observed larval dispersal and associations with local habitat quality support two main conclusions. First, larval Lake Sturgeon dispersal in the St. Clair and Detroit rivers varies in

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response to local habitat conditions and requires system specific evaluation in order to understand local larval – habitat associations. This conclusion is supported by variable patterns of larval dispersal in individual reaches of the St. Clair and Detroit rivers. Our second conclusion is that substrate is the most significant predictor of likely nursery areas for larval Lake Sturgeon in our study rivers and possibly for Lake Sturgeon in other Great Lakes Connecting Channels.

Although the North, Middle, and Fighting Island channels possess similar hydrological and ecological characteristics, they are still quite distinguishable. All three reaches have experienced varying levels of anthropogenic modifications, harvest and overfishing pressures, impacts from contaminants and invasive species, and have differences in specific habitat conditions. Subtle differences such as these are what distinguishes these as unique systems, and in part, drives the variation in larval Lake Sturgeon behavior highlighted in this study. Given this variation, we believe the mere presence of suitable habitat within a system is not sufficient for utility as nursery habitat. Rather, we believe the amount and location of this habitat in relation to sources of young Lake Sturgeon shapes early behavior and distribution by influencing larval drift and subsequent survival. Given the importance of early-life stage success in the recovery of Lake Sturgeon, future work should look to link available HSMs designed to identify candidate sites for spawning habitat in multiple rivers (such as the one developed for our study system by Bennion and Manny 2014) to models developed for identifying nursery areas. By understanding the connectivity between stages of early-life development, we can better understand the effects of proposed restoration activities and identify on-going impediments to stock recovery.

[A]Acknowledgments

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Tables

TABLE 1. Input values for the habitat suitability model for larval and juvenile Lake Sturgeon (from Krieger and Diana 2017).

Habitat Variable	**Suitability Index**	**Source**
Substrate Composition		Threader et al. (1998)
Clay	0.2	
Silt	1	
Sand	1	
Gravel	1	
Cobble	0.8	
Boulder	0.5	
Benthic Current Velocity (m / s)		Benson et al. (2005)
> 1.0	0	
0.6 - 1.0	1	
0.3 - 0.59	0.9	
0.0 - 0.29	0.5	
Water Depth (m)		Krieger and Diana (2017)
< 5.0	0	
5.1 - 10.2	0.8	
10.3 - 13.3	1	
>13.3	0.5	

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Invertebrate Density (# / m²)		Krieger and Diana (2017)
> 3000	1	
701 - 2999	0.7	
< 700	0.4	

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TABLE 2. Highest ranked regression models using AIC from the Middle Channel (MC) and Fighting Island Channel (FIC). Predictor variables are benthic current velocity, substrate composition, depth, and invertebrate density. Interaction terms are shown in parentheses. Relationships between larval VCPUE and HSM variables were modeled using simple and multiple linear regressions.

	Model Comparison Summary						
River	**Rank**	**K***	**AICc**	**ΔAICc**	**w_i**	**Cum. w_i**	**Model Variables**
MC	1	6	23.44	0	0.82	0.82	CPUE * Substrate
	2	7	29.37	5.93	0.11	0.93	CPUE * Substrate + Depth
	3	9	31.86	8.42	0.05	0.98	CPUE * Substrate + Velocity + (Velocity : Substrate)
	4	2	34.67	11.23	0.05	0.99	NULL
	5	3	36.28	12.84	0.01	1.00	CPUE * Velocity
	6	7	38.22	14.78	0.00	1.00	CPUE * Substrate + Invert
	7	9	39.94	16.5	0.00	1.00	CPUE * Substrate + Depth + (Substrate : Depth)
	8	11	41.33	17.89	0.00	1.00	CPUE * Substrate + Invert +Velocity + Depth (Velocity : Substrate)
	9	7	43.01	19.57	0.00	1.00	CPUE * Substrate +Velocity
	10	8	48.92	25.48	0.00	1.00	CPUE * Substrate + Invert + Depth
	11	8	49.22	25.78	0.00	1.00	CPUE * Substrate + Depth + Velocity
	12	9	51.34	27.9	0.00	1.00	CPUE * Substrate + Invert + Depth + (Invert : Substrate)
	13	9	53.41	29.97	0.00	1.00	CPUE * Substrate + Invert + Velocity + Depth
FIC	1	3	31.62	0	0.75	0.75	CPUE * Velocity
	2	2	33.49	1.87	0.23	0.98	NULL
	3	6	34.22	2.6	0.01	1.00	CPUE * Substrate
	4	9	38.94	7.32	0.00	1.00	CPUE * Substrate + Invert + Velocity + Depth
	5	9	39.43	7.81	0.00	1.00	CPUE * Substrate + Invert + Depth + (Invert : Substrate)
	6	11	42.33	10.71	0.00	1.00	CPUE * Substrate + Invert +Velocity + Depth (Velocity : Substrate)

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7	7	43.21	11.59	0.00	1.00	CPUE * Substrate +Velocity
8	9	45.11	13.49	0.00	1.00	CPUE * Substrate + Velocity + (Velocity : Substrate)
9	7	48.33	16.71	0.00	1.00	CPUE * Substrate + Invert
10	8	50.36	18.74	0.00	1.00	CPUE * Substrate + Invert + Depth
11	8	52.11	20.49	0.00	1.00	CPUE * Substrate + Depth + Velocity
12	9	54.33	22.71	0.00	1.00	CPUE * Substrate + Invert + Depth + (Invert : Substrate)
13	9	56.88	25.26	0.00	1.00	CPUE * Substrate + Invert + Velocity + Depth

* Number of model parameters (K).

TABLE 3. Median and range (in parentheses) for environmental variables collected in the Middle Channel (MC) and Fighting Island Channel (FIC) by habitat quality. Substrate composition is excluded from this table as it is a categorical variable.

Site	**Habitat Quality**	**Area (km^2)**	**Benthic Current Velocity (m / s)**	**Invertebrate Density (# / m^2)**	**Depth (m)**
MC	High	2.74	0.43 (0.36-0.47)	927 (905-1125)	13.26 (12.6-14.03)
MC	Moderate	14.14	0.38 (0.24-0.41)	1336 (129-4181)	12.19 (10.95-15.5)
MC	Poor	1.18	0.25 (0.12-0.56)	450 (124-2253)	4.7 (2.3-7.8)
MC	Unsuitable	0	0	0	0
FIC	High	1.19	0.42 (0.34-0.43)	882 (794-3312)	11.5 (8.9-11.86)
FIC	Moderate	5.61	0.37 (0.33-0.47)	794 (18-1588)	10.7 (8.9-11.28)
FIC	Poor	0.27	0.34 (0.29-0.51)	176 (0-265)	7.85 (8.93-9.24)
FIC	Unsuitable	0	0	0	0

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TABLE 4. Summary statistics of larval Lake Sturgeon catch from drift nets in each habitat quality type by river system.

Site	Habitat Quality	Larvae Collected	Net Hours	CPUE	VCPUE
MC	High	15	221	0.068	0.15
MC	Moderate	76	481	0.158	0.11
MC	Poor	2	112	0.018	0.09
MC	Unsuitable	0	0	0	0.00
FIC	High	6	105	0.057	0.048
FIC	Moderate	17	272	0.063	0.011
FIC	Poor	1	25.5	0.039	0.140
FIC	Unsuitable	0	0	0	0.000

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TABLE 5. Summary catch statistics in six locations that had high densities of larval Lake Sturgeon within the Middle Channel (MC). Area of each high density area is given along with (% area relative to total study area). Cluster ID corresponds to point locations on Figure 2.

Cluster ID	Habitat Quality	Area (km²)	Larvae Collected	Net Hours	VCPUE	Percent of Total
1-MC	High	0.041 (0.22 %)	15	220.33	0.12	16%
2-MC	Moderate	0.094 (0.52 %)	14	270.57	0.103	15%
3-MC	Moderate	0.098 (0.53 %)	51	120.13	0.59	54%

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Figure Captions

FIGURE 1. Map of study sites in the St. Clair and Detroit rivers. Stars show location of spawning reefs. Black arrows indicate flow direction. Map of the North Channel study site from Krieger and Diana (2017) is included for reference.

FIGURE 2. Map of net locations and Habitat Suitability Model output for larval Lake Sturgeon in the Middle Channel (MC) and Fighting Island Channel (FIC). Orange stars show locations of spawning reefs. Green triangles represent net sites where larval Lake Sturgeon were collected while red crosses represent sites where no larvae were collected. Black arrows indicate flow direction. Areas of high larval Lake Sturgeon densities are labeled and detailed in TABLE 5.

FIGURE 3. Length frequency histogram for larval Lake Sturgeon collected from the Middle Channel (MC) and Fighting Island Channel (FIC) from 2013 – 2016.

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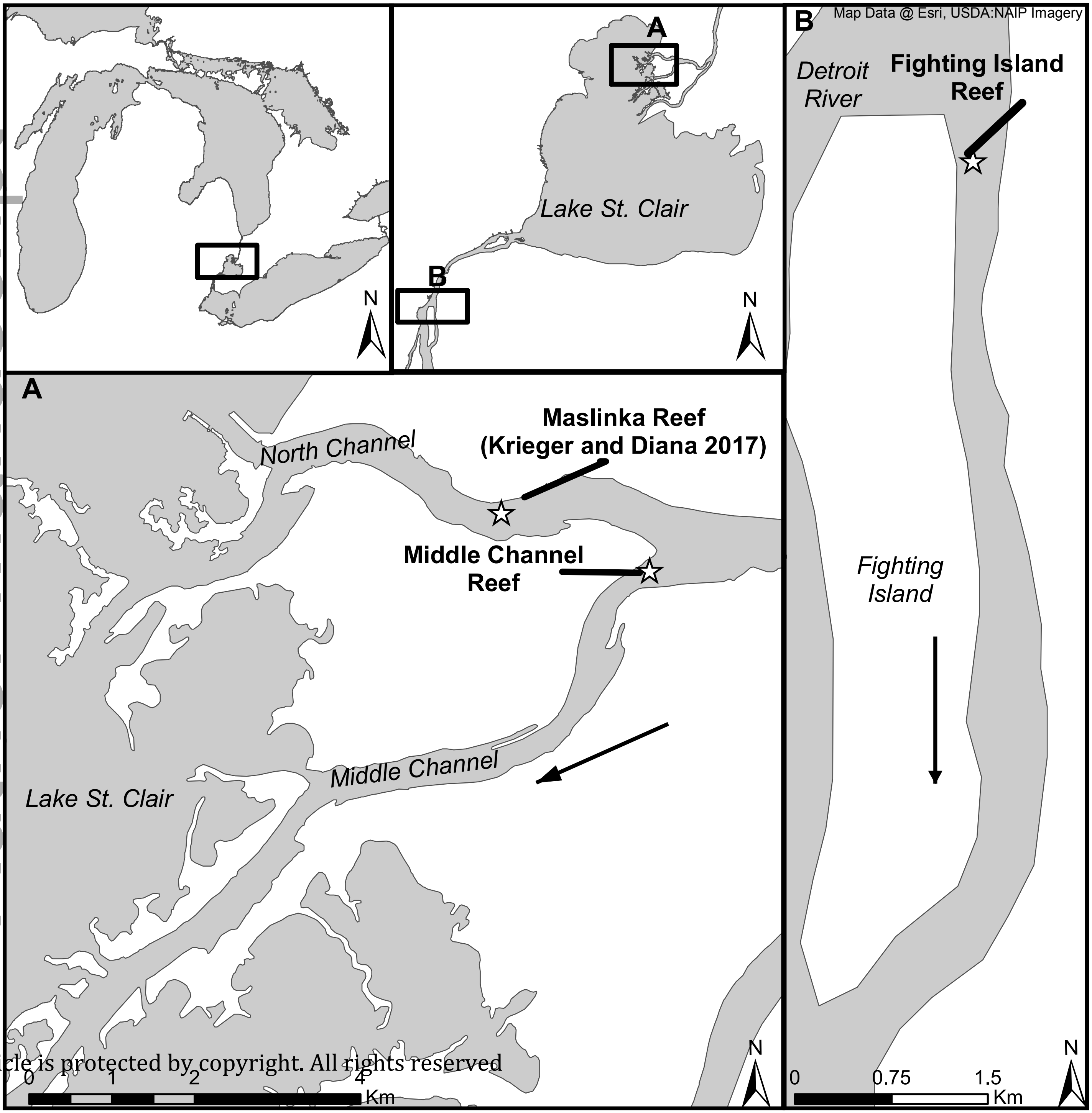

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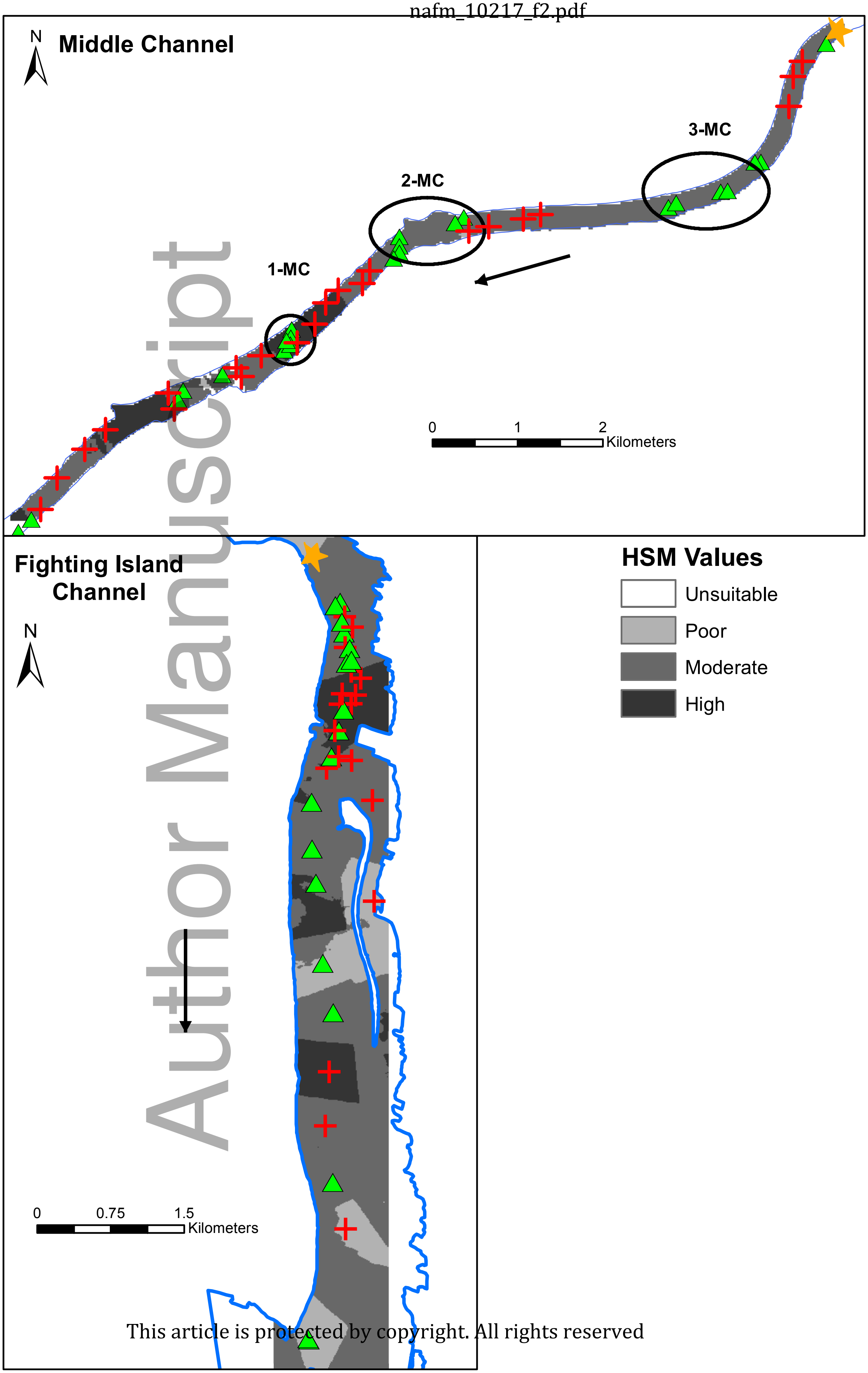

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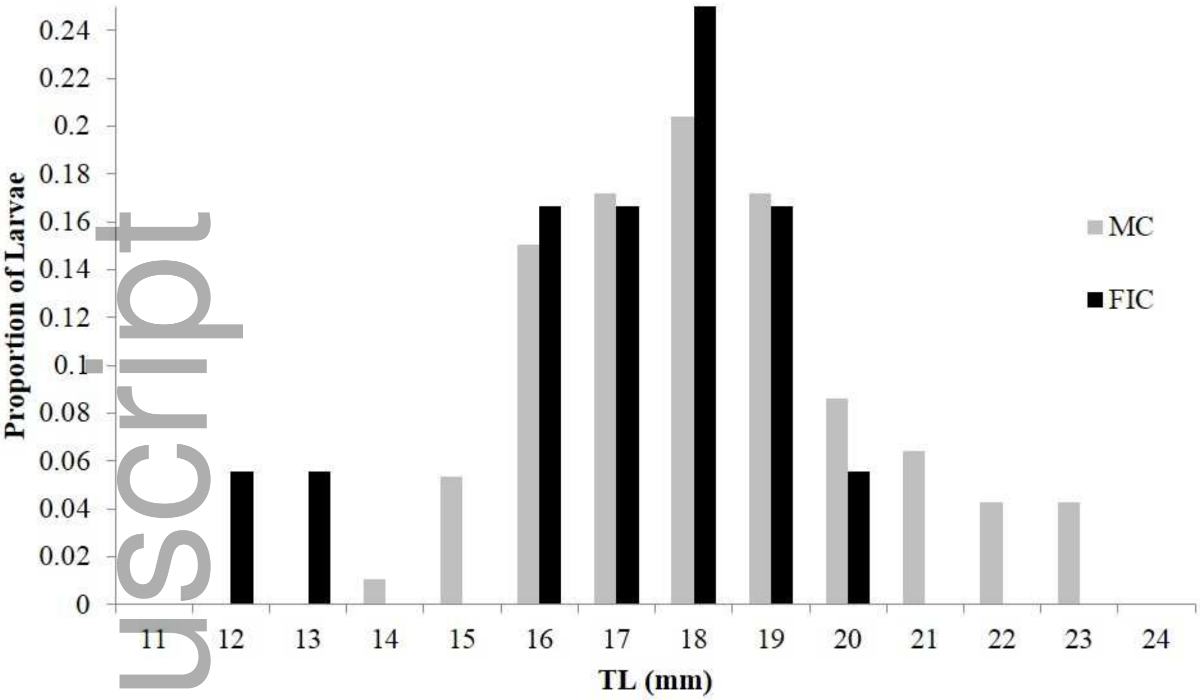

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