Journal of Great Lakes Research 41 (2015) 448–453

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Muskellunge egg incubation habitat in the upper Niagara River

Derek P. Crane [a,*], John M. Farrell [b]

[a] Lake Superior State University, 650 West Easterday Avenue, Sault Ste. Marie, MI 49783, USA
[b] State University of New York—College of Environmental Science and Forestry, 250 Illick Hall, 1 Forestry Drive, Syracuse, NY 13210, USA

ARTICLE INFO

Article history:
Received 14 November 2014
Accepted 30 January 2015
Available online 30 April 2015

Communicated by Stephen Charles Riley

Index words:
Muskellunge
Reproduction
Spawning habitat
Niagara River

ABSTRACT

Identification, conservation, and restoration of spawning and nursery habitats are essential for conserving the self-sustaining population of muskellunge (*Esox masquinongy*) in the upper Niagara River. The objectives of this study were to describe muskellunge egg incubation habitat, identify the most important habitat features associated with the presence of eggs, and make comparisons between spawning habitats identified through visual observation of spawning adults and collection of eggs. We conducted surveys for muskellunge eggs at four locations from 2012 through 2014 and used logistic regression to identify habitat features related to the presence or absence of eggs. We used Bayesian information criterion to select the most likely model and area under the receiver operating characteristic curve tests to determine variable importance and evaluate the model. One-hundred-thirty-six viable muskellunge eggs and two yolk-sac larvae were collected from 30 locations. The most likely model contained parameters for the percent rank of algae or aquatic macrophyte cover of the substrate and water depth. The percent rank of algae or aquatic macrophyte cover was the most important predictor of egg occurrence, and the odds of collecting a muskellunge egg increased by 100% for every 10 percentile increase in percent rank of cover. Spawning habitat features identified in this study were similar to those identified through visual observation of spawning adults. Muskellunge egg incubation locations and habitats should be protected from development and alteration to ensure the sustainability of muskellunge in the Niagara River.

Introduction

The muskellunge (*Esox masquinongy*) is the largest piscivore in the Great Lakes and provides unique fisheries for trophy-sized fish in all Great Lakes connecting channels and several areas of the Great Lakes proper. Most populations of muskellunge in the Great Lakes are self-sustaining. Early life stages of muskellunge are sensitive to habitat perturbations. It is hypothesized that loss or depletion of many muskellunge populations is due to alteration of spawning and nursery habitats (Trautman, 1981; Hanson et al., 1986; Kapuscinski et al., 2007; Kapuscinski et al., 2014). The sensitivity of muskellunge to alteration of spawning and nursery habitats is explained by three major factors: (1) increased biological oxygen demand of spawning substrates following anthropogenic eutrophication or artificial water-level regulation (Dombeck et al., 1984; Zorn et al., 1998), (2) the muskellunge is a scatter-spawning species and provides no parental care (Scott and Crossman, 1973), and (3) the propensity for muskellunge spawning habitats to be disturbed by human encroachment on aquatic ecosystems (e.g., shoreline armoring, removal of coarse woody debris, artificial water-level regulation, dredging of coastal embayments for marinas).

The vulnerability of muskellunge to environmental disturbance has resulted in an emphasis on study of spawning and nursery habitats. Three general methods have been used to identify muskellunge spawning habitats (see Crane et al., in press, for a review of these methods): telemetry (Strand, 1986; Pierce et al., 2007; Diana et al., 2015), visual observation of spawning (Zorn et al., 1998; Rust et al., 2002; Crane et al., 2014; Nohner and Diana, 2015), and egg collection (Farrell et al., 1996; Monfette et al., 1996; Farrell, 2001). Visual observation and telemetry provide information on habitat use by spawning adults, but may not provide information on egg incubation habitat if eggs are transported away from their initial deposition point by water currents. However, habitat descriptions based on collection of eggs may be misleading if eggs are redistributed to suboptimal habitats (Kelder and Farrell, 2009). Ideally, visual observation of spawning behavior or telemetry is validated by collection of eggs at points where fish were observed or believed to have spawned. In fluvial environments, where egg transport is likely, only including points validated by collection of eggs may result in a sample size that is prohibitive of rigorous quantitative analysis (e.g., Crane et al. (2014) only collected muskellunge eggs at 5 of 15 points where muskellunge were observed spawning). If eggs are likely to be transported away from their initial deposition point, results from separate surveys of spawning adults and collection of eggs should be considered together when describing habitat features that are associated with muskellunge reproduction.

* Corresponding author. Tel.: +1 517 643 1193.
E-mail address: dcrane1@lssu.edu (D.P. Crane).

http://dx.doi.org/10.1016/j.jglr.2015.03.019

Crane et al. (2014) presented a study of muskellunge spawning habitat in the upper Niagara River based on visual observation of spawning fish from 2011 through 2013. Fish were observed spawning in areas with moderate water currents (up to 32 cm/s) during the 2011 spawning period. It became apparent that there was potential for transport of eggs away from spawning points, and eggs were only collected at three of nine locations where muskellunge were observed spawning. Egg collection techniques were refined during the 2011 field season and a randomized survey for eggs was conducted from 2012 through 2014 (presented here) to complement the results presented by Crane et al. (2014) and provide a more holistic view of muskellunge reproductive ecology in the upper Niagara River. The objectives of this study were to describe muskellunge egg incubation habitat, identify important habitat features of locations where muskellunge eggs were collected, and make qualitative comparisons between spawning habitat documented through visual observation and egg collection.

Methods

Study area

The US waters of the upper Niagara River extend from the outlet of Lake Erie at Buffalo, New York to Niagara Falls at Niagara Falls, New York (about 32 km, as measured along the international border). The upper Niagara River supports a self-sustaining recreational fishery for muskellunge despite extensive in-water, riparian, and wetland habitat alteration (Kapuscinski et al., 2014). This investigation focused on four shallow water (≤2 m) locations that were identified by Harrison and Hadley (1978), Kapuscinski and Farrell (2014), and Crane et al. (2014) as important areas for muskellunge spawning and rearing (Fig. 1).

Habitat and egg data collection

Areas surveyed for muskellunge eggs and associated habitat features ranged in size from 8 to 42 ha and are henceforth referred to as "sites". Sites 2, 3, and 4, were nearshore locations with a gradient of increasing depth away from land; therefore, these sites were stratified into shallow (≤1 m) and deeper water zones (>1 – ≤2 m). Site 1 was a large mid-river shoal with no distinct habitat gradients, so it was not stratified. Site 1 was surveyed in 2012 and 2013, Site 2 was surveyed in 2013, and Sites 3 and 4 were surveyed in 2014. Sampling locations within each site (henceforth referred to as "points") were defined by a 1-m^2 quadrat and selected using the random point generator in ArcGIS (ArcGIS 10.1, Esri, Redlands, California). Surveys commenced when adult-sized muskellunge (about 80 cm; Harrison and Hadley, 1979) began congregating in the survey areas and finished when spawning activity was no longer observed.

The percent aerial cover of the substrate by algae or aquatic macrophytes, height of algae or aquatic macrophytes, dominant algae or

Fig. 1. Map of the upper Niagara River and four sites surveyed for muskellunge eggs and associated habitat features. Surveys were conducted from 2012–2014. Basemap from Esri Inc., 2014.

aquatic macrophyte taxa, water depth (cm), mean water column velocity (cm/s), and substrate characteristics were recorded for each point (see Crane et al. (2014) for a detailed description of methods). The methods for determining the proportion of mud and sand in the sediment deviated slightly in 2014 from the methods used in 2012–2013. The proportions of mud and sand were determined by wet sieving in 2014 and with an automated grain size analyzer in 2012 and 2013. The automated grain size analyzer was calibrated to report sieve-based grain size distributions, so classification of substrates should not have varied between methods. Standardized sampling for muskellunge eggs was conducted with a 500 μm d-frame net at each point. The d-frame net was gently swept across the substrate to dislodge and collect eggs. The entire quadrat was sampled during each egg sweep, and sampling continued until no eggs were recovered for three consecutive sweeps. All eggs 2.5–3.5 mm in diameter were retained for incubation (Fish, 1932, cited by Auer, 1982; Scott and Crossman, 1973; Farrell et al., 1996; Monfette et al., 1996) and positive identification of post-hatch larvae based on descriptions provided by Auer (1982) and Farrell (2001). The viability of all collected eggs was noted in the field. Translucent, amber-colored eggs were considered viable, whereas, opaque eggs were considered non-viable (Farrell, 2001).

Five continuous and two categorical independent variables were derived from the observed habitat data. Algae or aquatic macrophyte cover and height were converted to percent ranks (cover_rank, ht_rank) because algae and aquatic macrophyte growth can vary substantially among years. Percent rank was defined as the percentage of points in a year with a value less than a given point. The proportions of mud, sand, and gravel or larger size substrate particles were used to determine the substrate size class at each point according to Folk (1954). A quadratic term was added for water velocity because univariate plots suggested a unimodal relationship between water velocity and muskellunge egg presence or absence. Dominant algae or aquatic macrophyte taxa and water depth were analyzed as recorded in the field. Points with missing values for habitat features were not included in the data set ($n = 24$; 4% of the total sample).

Model development and evaluation

A series of logistic regression models were developed to identify the most important habitat characteristics that were associated with the presence of muskellunge eggs at a point. R statistical software was used to conduct all analyses (R version 3.0.2; R. Core Team, 2013), and the iteratively reweighted least squares method within the *glm* function was used to fit models.

The collection of at least one viable muskellunge egg at a point was used to determine presence in the response variable. It was assumed that all eggs were correctly identified as muskellunge eggs regardless of whether or not an egg successfully incubated and a post-hatch larvae was identified. We are confident that this is a reasonable assumption because (1) we observed muskellunge spawning activity at the sampling locations (see Crane et al., 2014), (2) there was limited spawning activity of other fishes in areas where muskellunge eggs were collected, (3) eggs that did not hatch were indistinguishable from eggs that hatched and were subsequently identified as muskellunge larvae, and (4) only 1 of 73 post-hatch larvae was not identified as a muskellunge (northern pike or muskellunge × northern pike).

Low ratios of presence locations to predictor variables may bias parameter estimates in logistic regression, particularly if the number of presence locations is <30 (Vittinghoff and McCulloch, 2007). Due to a small number of presence points in our sample ($n = 29$), we reduced the number of predictor variables by removing highly correlated variables ($|r| > 0.7$; Dormann et al., 2012) and variables that were unlikely to be important predictors of egg occurrence based on preliminary analyses.

After correlated and uninformative variables were removed, a series of eight models were fitted to test hypotheses about the relationships between the probability of muskellunge egg presence and the habitat variables (Table 1). Bayesian information criterion values (BIC; Schwarz, 1978) were used to select the most likely model from the eight models (i.e., lowest BIC; see Raftery, 1995). Mean BIC values were calculated for each model using a three-fold cross-validation process. Cross-validation was completed by partitioning the data into three equal subsets. Each model was trained using two subsets of data and tested using the third subset. The process was repeated so that each subset of data was used for testing once. Mean BIC values were then used to calculate information loss (ΔBIC; Raftery, 1995) and Schwarz weight (w_i; Wagenmakers and Farrell, 2004; Link and Barker, 2006) for each model. Information loss is the difference in BIC values between Model i and the model with the minimum value. Greater ΔBIC values correspond with increasing evidence against a model, relative to the model with the lowest BIC value (Raftery, 1995; Murtaugh, 2014). Schwarz weight is the probability that Model i is the true model, given that the true model is in the candidate set of models (Link and Barker, 2006).

Table 1
Ranking of eight competing muskellunge egg incubation habitat models, including terms for percent rank of algae or aquatic macrophyte cover of the substrate (cover_rank), water depth (cm; depth), and mean water column velocity (cm/s; vel). Cross-validated Bayesian information criterion (BIC), ΔBIC, and Schwartz weights (w_i) were used to rank the candidate models. The lowest BIC value and greatest w_i corresponded to the most likely model.

Model	BIC (SE)	ΔBIC	w_i
cover_rank + depth	124.12 (2.40)	0.00	0.77
cover_rank + depth + vel + vel^2	127.73 (2.56)	3.60	0.13
cover_rank + depth + cover_rank × depth	129.48 (2.74)	5.35	0.05
cover_rank	130.55 (5.77)	6.43	0.03
cover_rank + vel + vel^2	132.05 (5.59)	7.92	0.01
depth	144.37 (2.70)	20.24	<0.01
depth + vel + vel^2	148.34 (3.04)	24.21	<0.01
vel + vel^2	159.12 (2.67)	34.99	<0.01

The most likely model was evaluated by calculating the mean area under the receiver operating characteristic curve (test AUC) from a three-fold, cross-validated model run. Area under the receiver operating characteristic curve represents the probability that a randomly selected point where muskellunge eggs were present, has a higher predicted probability of egg presence than a randomly selected point where muskellunge eggs were absent (Hanley and McNeil, 1982; Franklin, 2009). Variable importance in the final model was determined by calculating the cross-validated AUCs for a series of models with each predictor variable withheld, and then comparing those values to the test AUC for the final model. The most important predictor of egg presence was indicated by the largest decrease in AUC when that variable was withheld from the model.

Results

Egg and habitat surveys were conducted from 23 May through 31 May 2012, 22 May through 6 June 2013, and 27 May through 17 June 2014. One-hundred-thirty-six viable muskellunge eggs were recovered from 28 points over the study period. Single eggs were collected at 13 points and >10 eggs were collected at four points. Seventy-two eggs, from 20 points were successfully incubated and identified as post-hatch muskellunge larvae. Additionally, individual yolk-sac larvae were collected at two points when sampling for eggs. Points where larvae were collected were classified as presence points because muskellunge larvae remain demersal until their yolk-sac is absorbed (Scott and Crossman, 1973). Therefore, these locations should be representative of egg incubation habitat. One point where eggs were collected was not included in the descriptive statistics and model development due to missing habitat data. Muskellunge eggs were most frequently collected in water 1–2 m deep with moderate current velocities (Table 2). Substrates at egg incubation locations consisted of muddy-

Table 2
Descriptive statistics (mean, SD) of habitat features at locations where muskellunge eggs were present and absent. Two points where recently hatched muskellunge larvae were collected were included in the locations classified as having eggs present. Dominant algae or aquatic macrophyte taxa and sediment size are reported as modes and the percentage of points they were dominant at. Percentages reported for the dominant algae or aquatic macrophyte taxa include locations where algae or aquatic macrophtye growth was absent.

	n	Algae/macrophyte cover (%)	Algae/macrophyte cover (% rank)	Algae/macrophyte height (cm)	Height (cm) Algae/macrophyte height (% rank)	Water depth (cm)	Water velocity (cm/s)	Dominant algae/macrophyte taxa	Dominant sediment size
Eggs present	29	90.4 (16.6)	78.8 (11.1)	8.5 (5.4)	83.3 (12.0)	143 (24)	13 (5)	Filamentous algae (96.6%)	Muddy-sand (68.9%)
Eggs absent	510	44.2 (31.7)	45.5 (27.8)	3.2 (4.4)	46.6 (29.8)	104 (37)	15 (8)	Filamentous algae (81.7%)	Muddy-sand (41.9%)

sand or sand that was covered with the greatest available growth of algae or aquatic macrophytes (Table 2).

Firm, sandy substrates and filamentous algae were the overwhelmingly dominant sediment classes and algae or aquatic macrophtye taxa at presence and absence locations. Sediment classes ranged from muddy-sand to gravelly-sand for 97% of presence points and 94% of absence points, and filamentous algae was dominant at 97% of presence points and 82% of absence points. Thus, there was a low probability of dominant sediment class and algae or aquatic macrophtye taxa being important predictors of muskellunge egg occurrence, and they were removed prior to constructing the set of candidate models. The cover_rank and ht_rank variables were highly correlated ($|r| = 0.76$). Ht_rank was removed from the dataset because preliminary modeling exercises indicated that cover_rank was more strongly associated with egg presence.

The model including terms for cover_rank and water depth was the most likely of the eight candidates (Table 1). The cross-validated AUC (mean = 0.87, SE = 0.02) for this model suggested strong predictive performance (Table 3). When all other variables were held constant, the odds of detecting a muskellunge egg increased by about 100% for a 10 percentile increase in cover_rank. A 10 cm increase in depth corresponded to a 29% increase in odds of detecting a muskellunge egg. Cover_rank was the most important predictor of egg occurrence. Average AUC decreased by 0.06 when cover_rank was withheld from the model, but only decreased by 0.03 when water depth was withheld.

Discussion

Logistic regression was effective in identifying key habitat features associated with the presence of muskellunge eggs in the upper Niagara River. Despite having a small sample size, we believe that the description of egg incubation habitat provided here is representative of the upper Niagara River because (1) the sites surveyed are the most important spawning areas for muskellunge in the river (Harrison and Hadley, 1978; Crane et al., 2014), and (2) a variety of habitats were surveyed within each site. Additionally, catches of age-0 muskellunge in the upper Niagara River suggest that eggs incubate successfully in these habitats (Kapuscinski and Farrell, 2014; Kapuscinski et al., 2014).

The limited collection of muskellunge eggs, despite sampling in known spawning areas, was intriguing but not surprising. Although female muskellunge generally produce >100,000 eggs (Scott and Crossman, 1973), collection of large numbers of naturally spawned eggs has proven difficult regardless of sampling method or habitat sampled. For example, Farrell (2001) only collected 63 muskellunge eggs during an intensive egg trapping effort in a St. Lawrence River bay, and Zorn et al. (1998) only collected 101 eggs during a two-year study of northern Wisconsin, USA lakes. Egg prevalence was about 5% in this study, and generally only one egg was collected at any given presence location (range: 1–39). Estimating total egg deposition was beyond the scope of this study, but rough estimates of egg deposition provide context for the low catches of muskellunge eggs sampled in natural environments. Ninety-nine eggs were collected from sampling 164 points at Site 1 (including points that were removed due to missing habitat data but were sampled for eggs) in 2013, yielding a collection rate of 0.604 eggs/m^2. When extrapolated to the 35.93 ha sampling area, the rough estimate of egg abundance for Site 1 was about 217,000 eggs in 2013. Hypothetically, this number of eggs could have been deposited by a single large female (Scott and Crossman, 1973). Farrell (2001) estimated that <90,000 eggs were deposited in a St. Lawrence River spawning bay in 1994 and <45,000 were deposited in 1995. Farrell (2001) hypothesized that the low estimates of egg deposition were due to muskellunge spawning in multiple adjacent bays. It is unlikely that the hypothesis provided by Farrell (2001) explains low egg collections at Site 1 in this study because numerous muskellunge were observed at this location during the spawning period, and it is one of the main muskellunge spawning areas in the upper Niagara River. Poor capture efficiency of the sampling gear may explain low egg catch rates; however, low catches are not unique to D-frame nets (Farrell, 1991, 2001).

Egg displacement by water currents or high rates of predation may also explain low catches of muskellunge eggs. Nohner and Diana (2015) documented muskellunge egg transport (eggs found at the water's edge and onshore) in a study of northern Wisconsin, USA lakes, but did not quantify this observation. Predation can be an important source of egg mortality for scatter-spawning fishes (Fitzsimons et al., 2002; Caroffino et al., 2010; Bajer et al., 2012). Nilsson (2006) estimated that three-spined stickleback (*Gasterosteus aculeatus*) consumed 22.5% of northern pike (*Esox lucius*) eggs deposited in Kalmar Sound, Sweden. Egg predators such as round goby (*Neogobius melanostomus*), brown bullhead (*Ameiurus nebulosus*), white sucker (*Catostomus commersonii*), *Moxostoma* spp., and crayfish (*Decapoda* spp.) were frequently observed during this study and may have consumed substantial numbers of muskellunge eggs.

Algae and aquatic macrophytes may provide some protection to incubating muskellunge eggs, and are probably important for successful egg incubation in bodies of water with strong currents and numerous egg predators, such as the upper Niagara River. Our study sites had moderate water velocities (up to 40 cm/s); therefore, any eggs deposited over bare sand would be transported downstream until they were trapped by algae or aquatic marcophytes or settled in low velocity depositional areas. Crane et al. (2014) occasionally observed muskellunge spawning over points relatively devoid of algae or aquatic macrophytes; however, no eggs were collected on bare substrates in this study and the majority of eggs were collected at points where 100% of the substrate was covered by algae or aquatic macrophytes. Furthermore, the only point where an egg was collected with <50% cover contained a large

Table 3
Parameter estimates, adjusted odds ratios, and mean cross-validated area under the receiver operating characteristic curve (AUC) for the final muskellunge egg incubation model. The odds ratio for percent rank of algae or aquatic macrophyte cover of the substrate (cover_rank) was based on a 10 percentile increase in cover. The odds ratio for water depth was based on a 10 cm increase in water depth.

Model term	Parameter estimate	95% CI	Odds ratio	AUC (SE)
Intercept	−10.8162	−14.7206 – −7.8632	NA	0.87 (0.02)
Cover_rank	0.0702	0.0428 – 0.1050	2.0168	
Water depth	0.0254	0.0131 – 0.0390	1.2885	

boulder that created a depositional area behind it. We did not examine the effects of habitat characteristics on consumption of muskellunge eggs by predators, but habitat characteristics have been found to affect the vulnerability of other fishes to egg predation. Predation on lake trout (*Salvelinus namaycush*) eggs by round goby is greater on bare and rubble substrates compared to gravel (Chotkowski and Marsden, 1999), and there is an inverse relationship between vegetation cover and risk of predation on centrarchid nests (Killourhy, 2013). Following an experiment examining predation on northern pike eggs, Nilsson (2006) concluded that lack of vegetation covering areas where eggs were dispersed led to unnaturally high predation rates. Muskellunge eggs incubating on bare substrates may be more vulnerable to predation than eggs covered by or entangled in the filaments and leaves of algae and aquatic macrophytes.

Growth of algae or aquatic macrophytes varied annually, and using the percent rank of algae or aquatic macrophyte cover allowed for standardization of this habitat characteristic among years. For example, the warmest average May water temperature for Lake Erie (at the head of the Niagara River) occurred in 2012; whereas, the average water temperature for May 2014 was the thirteenth coldest on record (National Weather Service; available online at: http://www.erh.noaa.gov/buf/laketemps/LakeTempsMay.php; accessed January 2015). Algae or aquatic macrophyte cover was $\geq$90% at 34% of points sampled in 2012, but only 8% of points in 2014. The inter-annual variability in growth of algae or aquatic macrophtyes may affect reproductive success of muskellunge and should be investigated further.

Eggs of scatter-spawning fishes are subject to transport by water currents, especially in fluvial ecosystems (Dustin and Jacobson, 2003; Kelder and Farrell, 2009; Nohner and Diana, 2015); therefore, habitat characteristics where eggs are released by spawning females may differ from where they settle to incubate (sometimes in low-quality habitat; see Kelder and Farrell, 2009). Consequently, the methods used to identify spawning habitats of fishes may affect study results. Water depth and velocity, substrate class, and dominant algae or aquatic macrophyte taxa were similar between muskellunge spawning points identified by collection of eggs and by visual observation of spawning pairs in the upper Niagara River (Crane et al., 2014). Algae or aquatic macrophyte cover and height and the percent ranks of both variables were slightly higher at spawning points identified by collection of eggs compared to visual observation. As described above, this was probably due to water currents displacing eggs or predators consuming eggs deposited in areas with minimal algae or aquatic macrophyte growth.

Conclusion

This study, along with studies of habitat use by spawning (Crane et al., 2014) and age-0 muskellunge (Kapuscinski and Farrell, 2014) have provided important information to guide habitat conservation and restoration for multiple life stages of muskellunge in the upper Niagara River. Based on Crane et al. (2014) and the findings of this study, muskellunge spawning and egg incubation generally occur mid-May to early-June in water 1–2 m deep. Substrates at spawning and incubation locations consist of muddy-sand or sand that is covered with the greatest available growth of algae or aquatic macrophytes. Collection of eggs and visual observation of spawning pairs were both reasonable methods for characterizing the spawning habitat of muskellunge in the upper Niagara River, but researchers should continue to consider egg transport when determining methods for investigating the reproductive habitats of fishes. A variety of native and non-native egg predators were observed in muskellunge spawning areas during this study, but it is unknown how egg predators affect the reproductive success of muskellunge. Future studies focused on predation on muskellunge eggs and determining how habitat mediates egg predation are warranted. A continued understanding of muskellunge ecology and habitat use in the upper Niagara River will be necessary for conserving this self-sustaining population in spite of human encroachment and a changing ecosystem.

Acknowledgments

This work was made possible by dedicated volunteers and technicians who aided in data collection and laboratory analysis. Alexander Karatayev and Mark Clapsadl provided substantial support through use of their facilities at the Buffalo State College—Great Lakes Center. Michael Wilkinson from the New York State Department of Environmental Conservation was instrumental in identifying locations for spawning surveys. Kevin Kapuscinski provided guidance during the study design process. Funding for this project was provided by the Niagara River Ecological Standing Committee, Fish and Wildlife Habitat Enhancement and Restoration Fund and the Niagara River Greenway Ecological Fund. Additional funding for sediment analysis was provided annually by the Niagara Musky Association.

References

Auer, N.A., 1982. Identification of Larval Fishes of the Great Lakes Basin with Emphasis on the Lake Michigan Drainage. Special Pub. Great Lakes Fishery Commission, Ann Arbor, MI, pp. 82–83.
Bajer, P.G., Chizinski, C.J., Silbernagel, J.J., Sorensen, P.W., 2012. Variation in native micro-predator abundance explains recruitment of a mobile invasive fish, the Common Carp, in a naturally unstable environment. Biol. Invasions 14, 1919–1929.
Caroffino, D.C., Sutton, T.M., Elliott, R.F., Donofrio, M.C., 2010. Predation on early life history stages of lake sturgeon in the Peshtigo River, Wisconsin. Trans. Am. Fish. Soc. 139, 1846–1856.
Chotkowski, M.A., Marsden, J.E., 1999. Round goby and mottled sculpin predation on lake trout eggs and fry: field prediction from laboratory experiments. J. Great Lakes Res. 25, 26–35.
Crane, D.P., Farrell, J.M., Kapuscinski, K.L., 2014. Identifying important micro-habitat characteristics of muskellunge spawning locations in the upper Niagara River. J. Great Lakes Res. 40, 325–335.
Crane, D.P., Miller, L.M., Diana, J.S., Casselman, J.M., Farrell, J.M., Kapuscinski, K.L., Nohner, J.K., 2015. Muskellunge and northern pike ecology and management: important issues and research needs. Fish in press.
Diana, J.S., Hanchin, P., Popoff, N., 2015. Movement patterns and spawning sites of muskellunge Esox masquinongy in the Antrim chain of lakes. Michigan. Environ. Biol. Fish. 98, 833–844.
Dombeck, M.P., Menzel, B.W., Hinz, P.N., 1984. Muskellunge spawning habitat and reproductive success. Trans. Am. Fish. Soc. 113, 205–216.
Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitaõ, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2012. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 35, 1–20.
Dustin, D.L., Jacobson, P.C., 2003. Evaluation of Walleye spawning habitat improvement projects in streams. Minnesota Department of Natural Resources, Investigational Report 502, St. Paul.
Farrell, J.M., 1991. Spawning ecology of sympatric northern pike and muskellunge in the St. Lawrence River. (M.S. thesis). State University of New York, College of Environmental Science and Forestry, Syracuse, NY.
Farrell, J.M., 2001. Reproductive success of sympatric northern pike and muskellunge in an upper St. Lawrence River bay. Trans. Am. Fish. Soc. 130, 796–808.
Farrell, J.M., Werner, R.G., LaPan, S.R., Claypoole, K.A., 1996. Egg distribution and spawning habitat of northern pike and muskellunge in a St. Lawrence River marsh, New York. Trans. Am. Fish. Soc. 125, 127–131.
Fish, M.P., 1932. Contributions to the early life histories of sixty-two species of fishes from Lake Erie and its tributary waters. Bull. U. S. Bur. Fish. 47 (10), 293–398.
Fitzsimons, J.D., Perkins, D.L., Krueger, C.C., 2002. Sculpins and crayfish on lake trout spawning areas in Lake Ontario: estimates of abundance and egg predation. J. Great Lakes Res. 28, 421–436.
Folk, R.L., 1954. The distinction between grain size and mineral composition in sedimentary-rock nomenclature. J. Geol. 62, 344–359.
Franklin, J., 2009. Mapping Species Distributions: Spatial Inference and Prediction. Cambridge University Press, Cambridge, UK.
Hanley, J.A., McNeil, B.J., 1982. The meaning and use of the area under the receiver operating characteristic (ROC) curve. Radiology 143, 29–36.
Hanson, D.A., Axon, J.R., Casselman, J.M., Haas, R.C., Schiavone, A., Smith, M.R., 1986. Improving musky management: a review of management and research needs. Am. Fish. Soc. Spec. Publ. 11, 335–341.
Harrison, E.J., Hadley, W.F., 1978. Ecological separation of sympatric muskellunge and northern pike. Am. Fish. Soc. Spec. Publ. 11, 129–134.
Harrison, E.J., Hadley, W.F., 1979. Biology of muskellunge (*Esox masquinongy*) in the upper Niagara River. Trans. Am. Fish. Soc. 108, 444–451.
Kapuscinski, K.L., Farrell, J.M., 2014. Habitat factors influencing fish assemblages at muskellunge nursery sites. J. Great Lakes Res. 40 (Supplement 2), 135–147.

Kapuscinski, K.L., Belonger, B.J., Fajfer, S., Lychwick, T.J., 2007. Population dynamics of muskellunge in Wisconsin waters of Green Bay, Lake Michigan, 1989–2005. Environ. Biol. Fishes 79, 27–36.
Kapuscinski, K.L., Farrell, J.M., Wilkinson, M.A., 2014. Trends in muskellunge population and fishery characteristics in Buffalo Harbor (Lake Erie) and the Niagara River. J. Great Lakes Res. 40 (Supplement 2), 125–134.
Kelder, B.F., Farrell, J.M., 2009. A spatially explicit model to predict walleye spawning habitat in an Eastern Lake Ontario tributary. N. Am. J. Fish Manag. 29, 1686–1697.
Killourhy, C., 2013. Predation on centrarchid nests in the St. Lawrence River following introduction of the round goby (Neogobius melanostomus). (M.S. thesis). State University of New York - College of Environmental Science and Forestry, Syracuse, NY.
Link, W.A., Barker, R.J., 2006. Model weights and the foundations of multimodel inference. Ecology 87, 2626–2635.
Monfette, R., Guénette, S., Dubuc, N., Fortin, R., Fourneir, H., 1996. Northern pike and muskellunge spawning ecology and reproductive success in the lower Ottawa River. In: Kerr, S.J., Olver, C.H. (Eds.), Managing Muskies in the '90s. Workshop Proceedings. OntarioMinistry of Natural Resources, Southern Region Science & Technology Transfer Unit Workshop Proceedings WP-007, pp. 55–65.
Murtaugh, P.A., 2014. In defense of *P* values. Ecology 95, 611–617.
Nilsson, J., 2006. Predation of northern pike (*Esox lucius* L.) eggs: a possible cause of regionally poor recruitment in the Baltic Sea. Hydrobiologia 553, 161–169.
Nohner, J.K., Diana, J.S., 2015. Muskellunge spawning site selection in northern Wisconsin lakes and a GIS-based predictive habitat model. N. Am. J. Fish Manag. 35, 141–157.
Pierce, R.B., Younk, J.A., Tomcko, C.M., 2007. Expulsion of miniature radio transmitters along with eggs of muskellunge and northern pike — a new method for locating critical spawning habitat. Environ. Biol. Fish 79 (1–2), 99–109.
R. Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (Available:http://www.R-project.org/).
Raftery, A.E., 1995. Bayesian model selection in social research. Sociol. Methodol. 25, 111–163.
Rust, A.J., Diana, J.S., Margenau, T.L., Edwards, C.J., 2002. Lake characteristics influencing spawning success of muskellunge in northern Wisconsin lakes. N. Am. J. Fish Manag. 22, 834–841.
Schwarz, G., 1978. Estimating the dimension of a model. Ann. Stat. 6, 461–464.
Scott, W.B., Crossman, E.J., 1973. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. 184.
Strand, R.F., 1986. Identification of principal spawning areas, seasonal distribution and movements of Muskellunge in Leech Lake Minnesota. Am. Fish. Soc. Spec. Publ. 11, 62–73.
Trautman, M.B., 1981. The Fishes of Ohio. Ohio State University Press, Columbus, OH.
Vittinghoff, E., McCulloch, C.E., 2007. Relaxing the rule of ten events per variable in logistic and Cox regression. J. Am. Epidemiol. 165, 710–718.
Wagenmakers, E.-J., Farrell, S., 2004. AIC model selection using Akaike weights. Psychon. Bull. Rev. 11, 192–196.
Zorn, S.L., Margenau, T.L., Diana, J.S., Edwards, C.J., 1998. The influence of spawning habitat on natural reproduction of muskellunge in Wisconsin. Trans. Am. Fish. Soc. 127, 995–1005.