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Identifying important micro-habitat characteristics of muskellunge spawning locations in the upper Niagara River

Derek P. Crane^{a,*}, John M. Farrell^{b,1}, Kevin L. Kapuscinski^c^a State University of New York, College of Environmental Science and Forestry, 104 Illick Hall, 1 Forestry Drive, Syracuse, NY 13210, USA^b State University of New York, College of Environmental Science and Forestry, 250 Illick Hall, 1 Forestry Drive, Syracuse, NY 13210, USA^c State University of New York, College of Environmental Science and Forestry, 304 Illick Hall, 1 Forestry Drive, Syracuse, NY 13210, USA

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ABSTRACT

Conserving and restoring muskellunge (*Esox masquinongy*) spawning habitat are essential for maintaining self-sustaining populations. A Maxent model was developed based on presence and background data to investigate the relationship between the occurrence of spawning muskellunge and habitat features in the upper Niagara River. Muskellunge spawning points ($n = 15$) were determined by direct observation of spawning pairs. Model inputs were based on micro-habitat features collected at each spawning point and a sample of 250 background habitat points. The full model was reduced to a four variable model to remove uninformative variables and reduce overfitting and redundancy. Model performance was evaluated based on the mean test gain of cross-validated models ($n = 15$). Model outputs identified aquatic macrophyte/algae coverage as the most important habitat feature at spawning locations. The relative probability of muskellunge spawning increased with the percent rank of total aquatic macrophyte/algae coverage, water velocity, and water depth and it was highest at points with muddy-sand to sand substrates. Mean test gain (0.68 ; $SE = 0.52$) of the cross-validated models indicated that the likelihood of an average muskellunge spawning point was nearly two times greater than an average background point. Results from this research advance our knowledge of muskellunge reproductive ecology, while providing scientists and managers with quantitative measures to guide habitat conservation and restoration.

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Introduction

The muskellunge (*Esox masquinongy*) is ecologically important as the apex native aquatic predator in the Niagara River and has supported a recreational fishery since at least the 1850s (Harrison and Hadley, 1978). The population is self-sustaining, and no stocking has occurred since 1974 (Kapuscinski et al., in press). However, habitat in the upper Niagara River has been substantially altered since the early 19th century, and the cumulative effects of habitat degradation and other ecosystem changes may limit the muskellunge population (Kapuscinski et al., in press). Muskellunge spawning habitat conservation and restoration are priorities for resource management agencies in several Great Lakes waters, including the upper Niagara River (Farrell et al., 2003, 2007; Kapuscinski et al., in press; Rowe and Hogler, 2012; Thomas et al., 2010). Additionally, restoration and protection of wetlands, including

vegetated shallow water habitat (<2 m), which is essential for spawning and early life stages of muskellunge (Craig and Black, 1986; Farrell, 2001; Farrell and Werner, 1999; Harrison and Hadley, 1978; Kapuscinski and Farrell, in press; Murry and Farrell, 2007) and other native fishes, are priorities for the $>\$1$ billion Great Lakes Restoration Initiative (Allan et al., 2013; Great Lakes Restoration Initiative Task Force, 2010).

Despite the substantial amount of money and effort being spent on nearshore and wetland habitat conservation and restoration in the Great Lakes, little information exists to guide actions that will benefit muskellunge. The few studies that have investigated muskellunge spawning habitat in the Great Lakes have only provided general descriptions (e.g., Haas, 1978; Harrison and Hadley, 1978), focused on populations that are not self-sustaining (e.g., Battige, 2011) or lacked predictive power beyond specific sites (e.g., Farrell, 2001; Farrell et al., 1996).

Acquiring information that can be used to bolster natural reproduction of muskellunge should be a primary research and management goal (Kapuscinski et al., 2007). Farrell et al. (2007) called for development of models that increase our understanding of the relationship between muskellunge reproduction and habitat, and can help guide habitat restoration. Contemporary muskellunge populations typically occur at low densities,

* Corresponding author at: 7808 119th Lane North, Champlin, MN 55301, USA. Tel.: +1 517 643 1193.

E-mail addresses: dpcrane@syrr.edu (D.P. Crane), jmfarrell@esf.edu (J.M. Farrell), klkapusc@esf.edu (K.L. Kapuscinski).

¹ Tel.: +1 315 470 6990.

which create challenges for researchers attempting to develop distribution or habitat models based on presence/absence data. Identifying true absences for species that occur at low densities can be difficult because individuals may go undetected and such detection errors may lead to bias in models and incorrect conclusions about habitat use (Baldwin, 2009). New technologies and modeling techniques are now available to develop habitat use models for fishes with presence-only data (Elith et al., 2006; Franklin, 2009). Presence-only methods may provide a means for effectively modeling habitat use by low density, cryptic aquatic organisms such as muskellunge. Nohner (2009) recently used presence-only methods to model muskellunge spawning habitat in self-sustaining northern Wisconsin lakes. Battige (2011) modeled spawning habitat and distribution of muskellunge in the lower Menominee River, Wisconsin, a tributary to Green Bay; however, this population is not self sustaining and was recently developed by stocking (Kapusinski et al., 2007). In order to develop a better understanding of muskellunge reproductive ecology in the upper Niagara River and provide information to guide habitat management, we (1) quantified micro-habitat features at muskellunge spawning locations in the upper Niagara River, (2) developed a Maxent model of muskellunge spawning locations based on habitat features at muskellunge spawning points and randomly selected background points, and (3) used model results to identify habitat features that were most important at muskellunge spawning locations.

Material and methods

Study area

This investigation focused on US waters of the upper Niagara River (Fig. 1). The Niagara River flows north from the outlet of Lake Erie at Buffalo, New York, to Lake Ontario. Niagara Falls divides the river into upper and lower sections about 32 km downstream from Lake Erie (measured along the international border). Despite being over 2.5 km wide at its widest point, water depths in the upper Niagara River are generally <6 m and the river contains many shallow shoals. The upper Niagara River and surrounding landscape have been extensively altered over the past 200 years by urban, residential, and industrial development, and about 60% of the US shoreline is artificially “hardened” (Wooster and Matthies, 2008). Additionally, gravel mining, dredging, and dumping of sediment have altered in-river habitat to an unknown extent. Despite its history of habitat alteration and degradation, the upper Niagara River still has areas of high quality habitat to support important native game (e.g., smallmouth bass (*Micropterus dolomieu*), largemouth bass (*Micropterus salmoides*), and muskellunge) and non-game fishes (e.g., emerald shiner (*Notropis atherinoides*), bluntnose minnow (*Pimephales notatus*), and *Moxostoma* spp.).



Fig. 1. Map of the upper Niagara River. Basemap from ESRI Inc., 2013.

Identification of spawning points and background habitat surveys

Visual observations (nighttime spotlighting) were used to locate spawning muskellunge following the methods of Zorn et al. (1998), Rust et al. (2002), and Nohner (2009) in May–June, 2011 and 2013. Sampling was attempted in 2012, but high winds during the peak spawning period limited our efforts and data from this year were not included in the study. Surveys began each night one-half hour after sunset and lasted until the sampling area (described below) was completely covered. Daytime survey efforts were also attempted, but water surface disturbance created by wind generally limited visibility. When a pair of spawning fish was observed the location was recorded using a Garmin Oregon 450 global positioning system (Garmin International, Inc., Olathe, Kansas), and an anchored float was placed at each spawning point to aid in returning to the location the following day for a detailed habitat survey.

Muskellunge spawning points were defined by a 1-m² point location where a spawning pair was first observed. This fine scale of habitat sampling was used to prevent possible bias caused by movement of muskellunge away from spawning habitat after being exposed to spotlights. Data describing the areal coverage of aquatic macrophytes and filamentous algae (SAV/algae), SAV/algae height, SAV/algae species composition, water velocity (m/s), depth (cm), and substrate within a 1-m² quadrat were collected at each identified spawning point. Aquatic macrophytes were identified to genus or species, and algae were classified as filamentous algae or macroalgae. Areal coverage of SAV/algae was visually estimated to the nearest percent. Additionally, the most dominant species based on areal coverage was recorded.

Standardized egg sweeps were conducted within the 1-m² grid at each spawning point using a 500 µm mesh D-frame net to confirm that the observation of paired muskellunge tended to correspond to a spawning event. The entire quadrat was swept three times, and if an egg(s) was collected additional egg sweeps were conducted until no eggs were recovered for three consecutive sweeps. Any eggs 2.5–3.5 mm in diameter (Fish, 1932, cited by Auer, 1982; Farrell et al., 1996; Monfette et al., 1996) were retained and incubated at the Buffalo State College Great Lakes Center for positive identification based on yolk-sac pigmentation of post-hatched larvae (Auer, 1982; Farrell, 2001). If substrates at a sampling point were determined to contain sediments ≥ 16.0 mm in the field, proportions of coarse to very coarse gravel, cobble, and boulder were visually estimated and accounted for when determining sediment class. Sediments < 16.0 mm were collected and sent to the lab for particle size analysis. Substrate samples sent to the lab were weighed (g) and sieved to separate particles < 2.0 mm in diameter and ≥ 2.0 mm in order to determine the fraction of each size class. Sieved particles ≥ 2.0 mm were classified as gravel (Udden, 1914; Wentworth, 1922). Particles < 2.0 mm were analyzed using an automated laser particle size analyzer to determine the fraction of sand and mud in each sample (2011, Malvern 2600 L laser particle size analyzer, Malvern Instruments, Worcestershire, UK; 2013, Beckman Coulter LS Series, Beckman Coulter, Inc., Brea, California). Sediments were assigned to 1 of 17 classes, ranging from mud to boulder. Sediments only containing mud, sand, and gravel were classified based on ternary plots of the fraction of mud, sand, and gravel in each sample (Folk, 1954). Two additional sediment classes were added to account for samples containing cobble and boulder size class sediments.

Sites to be surveyed for spawning muskellunge were chosen based on primary spawning areas identified by Harrison and Hadley (1978) and locations where age-0 muskellunge were collected during previous seining surveys (Kapusinski and Farrell, in press; Kapusinski et al., 2009, 2010). Each sampling site was pre-defined by a continuous polygon within the 1.5 m water depth contour in 2011; however, some water depths within individual polygons were slightly greater than these values due to depressions in the river bottom and changes in water level. The 1.5 m depth contour was selected based on previously reported muskellunge spawning depths (Dombeck et al., 1984; Farrell,

2001; Farrell et al., 1996; Nohner, 2009; Younk et al., 1996; Zorn et al., 1998), and our anticipated ability to accurately identify spawning pairs. In 2012, the pre-defined water depth contour was expanded to 2.0 m after observing muskellunge spawning in water depths exceeding 1.75 m during the 2011 spawning season and determining that water clarity would allow accurate identification of spawning muskellunge in water deeper than 1.5 m. All sample points > 2.0 m deep were excluded from the analysis to limit possible detection bias resulting from a decreased ability to identify spawning pairs.

Spawning survey locations encompassed a variety of aquatic habitat features. Site 1 was sampled for spawning pairs in 2011 and consisted of a 4.3 ha sand bar with emergent aquatic vegetation and adjacent shallow water habitat located about 150 m offshore of northeastern Grand Island, New York (Fig. 2). Site 2 was located along the southeastern shoreline of Grand Island, New York and was sampled in 2011 and 2013 (Fig. 2). Site 2 consisted of a nearshore area exposed to the main river currents and a restored wetland protected by rock breakwaters (Fig. 2). Sampling of the wetland was conducted in 2011, but low water prevented sampling this area in 2013. The area sampled at Site 2 was 7.5 ha in 2011. Including all water within the 2.0 m depth contour increased the sampling area at Site 2 to 7.8 ha in 2013. Site 3 was a large (35.9 ha) mid-river shallow water complex between Strawberry and Motor Islands, and was sampled in 2013 (Fig. 2).

A sample of background habitat points was collected at each site in order to provide information on habitat available to spawning fish. Background habitat sampling occurred each year a site was surveyed. A stratified sampling design, based on habitat features, was used at Sites 1 and 2. Site 1 was divided into three strata: (1) open water within the upstream facing “bay” of the *Typha* sp. stand, (2) a *Typha* sp. stand, and (3) a shallow sandbar upstream of the western edge of the *Typha* sp. stand. Poor water clarity precluded sampling the shallow water area west of the *Typha* sp. stand. Strata at Site 2 included: (1) a manmade wetland maintained by a series of breakwaters, (2) water outside of the wetland ≤ 0.75 m (2011) or 1.00 m deep (2013), and (3) water outside of the wetland 0.76–1.50 m deep (2011) or 1.01–2.00 m deep (2013). A simple random sample of background habitat points was collected at Site 3 because habitat strata were not clearly definable. Habitat sampling effort was standardized to about 4.5 points/ha at each site, and the same protocol for sampling habitat was followed at background points as was previously described for muskellunge spawning points. All background habitat data were collected during the muskellunge spawning period. Visual estimates of areal SAV/algae coverage were conducted by one individual in 2011; whereas, two different observers estimated SAV/algae coverage in 2013. Paired estimates of areal SAV/algae coverage at 42 background points sampled were used to test for differences between observers. The observer did not affect estimates of areal SAV/algae coverage (paired *t*-test, *t* = 1.0433, *df* = 41, *P* = 0.3029).

Model development, selection, and evaluation

Four continuous variables (water depth, water velocity, SAV/algae total coverage percent rank, and SAV/algae height percent rank) and two categorical variables (sediment class and dominant SAV/algae taxa), derived from the field data, were used to develop a model of muskellunge spawning habitat. The annual emergence of SAV and algae in the upper Niagara River generally coincides with the muskellunge spawning season. Because SAV/algae growing conditions can vary substantially from one spawning season to the next, absolute values of SAV/algae height and coverage may bias the Maxent model when pooling data over multiple years (i.e., habitat conditions that are considered background for one year may not be relevant to subsequent years). Therefore, SAV/algae height and SAV/algae areal coverage were converted to percent ranks (within years) to standardize these variables across years.

All modeling was conducted using the program Maxent (version 3.3.3 k; Phillips, 2008; Phillips and Dudík, 2008; see Elith et al. (2011)

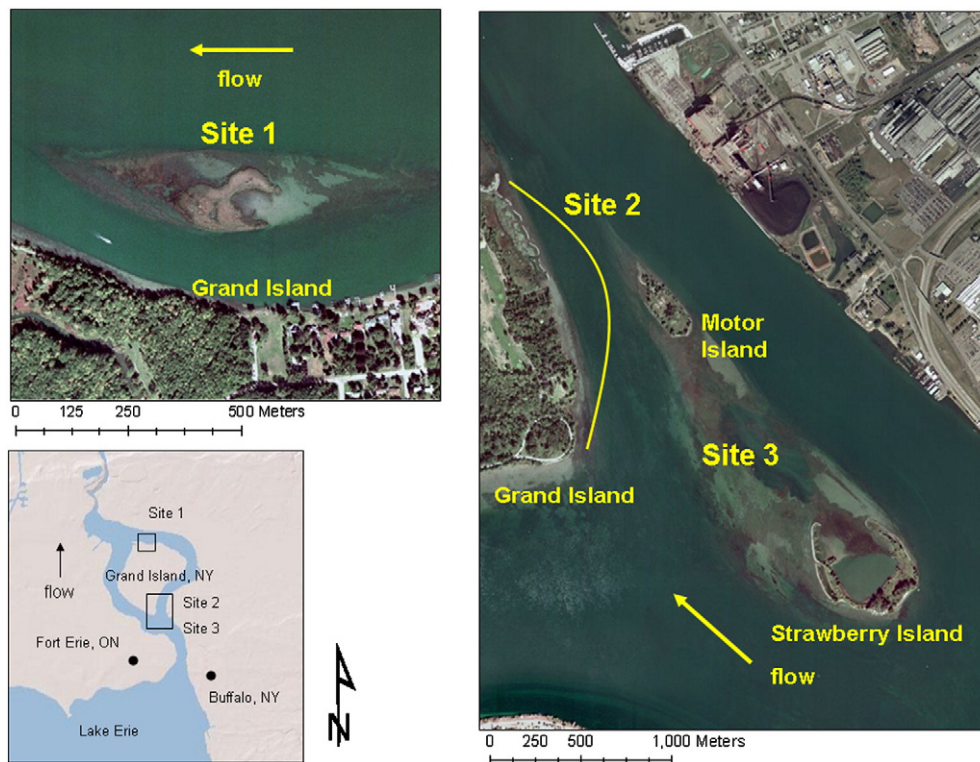


Fig. 2. Aerial imagery and map of sites surveyed for spawning muskellunge in the upper Niagara River during the 2011–2013 spawning seasons. Basemaps from Esri Inc., 2013.

for a detailed mathematical explanation). Maxent is a machine-learning method that is based on the principle of maximum entropy. Unlike traditional species distribution modeling methods that commonly use both presence and absence data, Maxent only requires presence and background habitat data. An important difference between the Maxent model and presence/absence models is that the Maxent model assumes that background data contains some presence locations. Therefore, model outputs do not represent the true probability of presence. Instead, Maxent allows users to choose from three outputs: raw, cumulative, and logistic. We used the raw output because the cumulative and logistic outputs are based on transformations of the raw output and rely on strong assumptions, such as the accuracy of user defined values for prevalence (Merow et al., 2013). The raw output is defined as the relative probability of presence at a point (re-scaled so values across all points within a defined landscape sum to one), given the species is present (Elith et al., 2011). The raw output is best used to rank the suitability of points given their habitat characteristics. The Maxent program was chosen to model muskellunge spawning habitat because, (1) “true” absences of spawning muskellunge are likely difficult to detect, and (2) Maxent has been successfully used to model habitat use and distribution for a variety of organisms (Elith et al., 2011; Franklin, 2009).

Maxent models were run using data derived directly from field observations in the Species With Data format to prevent modeling bias induced by error in interpolation of field collected data to GIS raster layers (i.e., habitat data were read directly into the modeling program from a Microsoft Excel worksheet instead of from a GIS file, which is more commonly used). Background and presence points with missing data were removed. Inter-variable correlation and results from Maxent's built-in jackknife tests of variable importance were examined to remove uninformative variables and prevent overfitting and redundancy (Parolo et al., 2008). Pairwise Pearson correlation coefficients for continuous variables were estimated in Microsoft Excel 2003 to identify and remove highly correlated variables ($|r| > 0.7$; Dormann et al., 2012) that may decrease model performance.

Maxent allows users to adjust a variety of settings within the model in order to customize the model based on study goals and taxon-specific

traits. Although the default settings for the Maxent model generally perform well (Anderson and Gonzalez, 2011; Phillips and Dudík, 2008), it is recommended that species-specific tuning be used to improve model performance and protect against overfitting (Anderson and Gonzalez, 2011; Halvorsen, 2012; Merow et al., 2013). Model settings for features and regularization parameters were adjusted in our model. Maxent automatically re-scales all predictor variables to 0–1 and fits a model based on transformed values of the predictor variables. Re-scaled predictor variables can be used to fit a Maxent model in six different ways, termed features: linear, quadratic, threshold, hinge, product, and categorical (Elith et al., 2011; Phillips and Dudík, 2008). Only linear, quadratic, and categorical features were modeled due to small sample size (Phillips and Dudík, 2008). Linear features take on the re-scaled values of the predictor variables, and quadratic features are equal to the re-scaled values of the predictor variables squared (Elith et al., 2011; Phillips and Dudík, 2008). Categorical variables are transformed to binary indicator values with one feature created for each class within a category. Except for categorical predictors, each environmental predictor can be used for multiple features.

Maxent has a built in regularization procedure to protect against overfitting (Phillips and Dudík, 2008). Values assigned to regularization parameters (β) “penalize” the model by shrinking feature coefficients (λ); coefficients from uninformative features are reduced to zero (Elith et al., 2011). We selected β values and predictors to include in the final model by fitting a series of models with β set to: default, 0, 0.05, 0.1, 0.25, 0.5, 0.75, 1.0, 1.5, 2.0, and 2.5. For each parameter value, we began by fitting a series of cross-validated ($n = 15$) models with decreasing complexity. Each model was trained leaving one presence sample out for testing, and each presence sample was tested once (i.e., leave one out method).

Results from jackknife tests of regularized training and test gain, averaged across cross-validated models, were examined to evaluate the models. Gain is similar to the goodness-of-fit measure of deviance for general additive and generalized linear models and is defined as the ratio of the penalized ln-likelihood of an average presence point, compared to an average background point (Phillips, 2008; Elith et al.,

2011). For example, a test gain of one in this study would indicate that the likelihood of an average muskellunge spawning point was about 2.7 times greater than the likelihood of an average background habitat point (Phillips, 2008). Gain was used to select β values and predictors because it is more sensitive to variable addition and removal compared to area under the receiver operating characteristic curve scores (Yost et al., 2008). The jackknife tests calculated average regularized training and test gains with each variable individually removed from the model (i.e., leave one out method) and with each variable as the only predictor (Phillips, 2008).

The full model was pruned by removing predictors in a backward stepwise fashion with a new set of cross-validated models created after each variable was dropped. First, we removed any variable that resulted in a negative test gain (i.e., the ln-likelihood of an average presence point < average background point) when using that variable as the only predictor during jackknife tests of variable importance. If more than two predictors resulted in a negative test gain, the predictor with the largest negative test gain was removed first. If no predictors resulted in a negative test gain, then the predictor that resulted in the smallest decrease in training gain when left out of the model during jackknife tests was dropped. A small decrease in training gain when a predictor is left out of the model during jackknife tests indicates redundancy in information contributed by the predictors. We compared average test gain values among the cross-validated models after fitting models with all combinations of β values and model complexity. We also examined test gain of individual models within each cross-validated model series. The number of negative test gain values in each cross-validated series was noted. The β value and predictors used in the final model were selected by balancing between maximizing average test gain and minimizing the number of individual models with negative test gain values within a cross-validated series. Once the final β value and predictors were selected variable response curves, created from the average of cross-validated models, were examined to investigate the relationship between habitat variables and relative probability of muskellunge spawning (Phillips, 2008). The final model was fit using all presence records, and all model λ values are reported as such.

To evaluate the muskellunge spawning habitat model we used the threshold-independent measure of average test gain for the cross-validated models (Phillips, 2008). Ideally models are fit using training data and evaluated with independent test data (Pearce and Ferrier, 2000; Pearson et al., 2007); however, this is not feasible when presence samples are small ($n < 25$) because it limits the information available for both training and evaluating the model (Pearson et al., 2007).

Results

Spawning and habitat surveys

Spotlighting surveys for paired muskellunge during the spawning season were conducted on 23 nights in 2011 (12 May–15 June) and 21 nights in 2013 (15 May–9 June). In 2011, nine pairs of muskellunge were observed between 30 May and 8 June. Six pairs were observed at Site 2 and three pairs were observed at Site 1. Eight of the pairs were observed during nighttime spotlighting efforts and one pair was observed during daytime habitat surveys. In 2013, six pairs of muskellunge were observed at Site 3 between 26 and 30 May. Five pairs were observed during nighttime surveys and one pair was observed incidentally during daytime habitat surveys. Pairs observed during the day were included in the model because spawning pairs and single fish observed during the day were located in the same general area as fish observed during nighttime spotlighting efforts and the relative rarity of observing spawning pairs. A muskellunge paired with a northern pike was observed in 2011; this pair was not included in model.

Successful collection of eggs from locations where paired muskellunge were observed and identification of post-hatch larvae in the lab confirmed that the behaviors (i.e. paired fish of mature size, positioned

side-by-side and touching or nearly touching) we observed in the field were part of the spawning act. Eggs were recovered and successfully incubated and identified as yolk-sac larvae muskellunge from three of nine muskellunge spawning points in 2011 and two of six spawning points in 2013. Eggs were also collected and identified as muskellunge post-hatching from 16 background points in 2013. Additionally, two yolk-sac larvae were collected at two background points in 2013.

Filamentous algae was the dominant SAV/algae taxa at 11 of 15 spawning points, and spawning generally occurred over firm muddy-sand substrate in areas with greater SAV/algae coverage and SAV/algae height compared to what was available (Table 1). Water depths at spawning locations ranged from 73 to 194 cm (mean = 142 cm; SD = 37), and water velocities ranged from 0.002 to 0.318 m/s (mean = 0.173 m/s; SD = 0.115; Table 1).

Background habitat data were collected at 250 points over the two year (2011 and 2013) sampling period. Filamentous algae was also the dominant SAV/algae taxa at the majority of background points, and it was dominant at nearly the same proportion of background points (77%) as spawning points (73%). Muddy-sand was the most common substrate class at background points, but it was dominant at a lower proportion of background points (55%) compared to spawning points (87%). Water depth at background locations ranged from 19 to 200 cm (mean = 115 cm; SD = 40), and water velocities ranged from 0.001 m/s to 0.401 m/s (mean = 0.131 m/s; SD = 0.076 m/s).

Model selection and evaluation

Model complexity was reduced from six predictors to four predictors to remove uninformative variables and limit overfitting and redundancy: SAV/algae total cover percent rank, sediment class, water depth, and water velocity. SAV/algae total cover percent rank and SAV/algae height percent rank were correlated (Table 2). SAV/algae height percent rank data were withheld from the modeling process because preliminary modeling efforts indicated that SAV/algae total cover percent rank resulted in a higher training gain when used as the only predictor. Dominant taxa data were removed because, when used as the only predictor in jackknife tests of variable importance, dominant taxa resulted in an average test gain of -0.19 . Trials varying β values indicated that $\beta = 0.1$ provided the best balance between average test gain (across cross-validated models) and number of individual models with negative test gain values (within cross-validated models; Table 3).

Jackknife tests of regularized training gain indicated that SAV/algae total cover percent rank contributed the most information to the final model (Fig. 3). Training gain decreased 33% when SAV/algae total cover percent rank data were withheld from the model, indicating that SAV/algae total cover percent rank contained substantial information that was not supplied by the other predictors. Maxent selected both linear and quadratic features for the SAV/algae total cover percent rank variable in the final model (Table 4). The variable response curve for SAV/algae total cover percent rank indicated that the relative probability of muskellunge spawning had a positive relationship with SAV/algae total cover percent rank when SAV/algae total cover percent rank was used as the only predictor (Fig. 4). Removal of water depth, water velocity, and sediment class predictors during jackknife tests of variable importance resulted in similar losses in average training gain (range: 10–16%); however using sediment class as the only predictor resulted in a higher average gain compared to using only water depth or water velocity. The raw output was highest for locations with sand or muddy-sand substrates (Fig. 4). Similar to SAV/algae total cover percent rank, water velocity and water depth displayed positive relationships with the relative probability of muskellunge spawning when used in isolation as predictors (Fig. 4). Maxent selected both linear and quadratic features for water velocity while selecting only a quadratic feature for water depth.

Mean test gain of the 15 cross-validated models was 0.68 (SE = 0.52), indicating that across models the likelihood of an average

Table 1

Habitat data from observed muskellunge spawning points in the upper Niagara River. Sediment classification was based on gravel–sand–mud grain size ternary plots (Folk, 1954). Mean (SD) values of SAV/algae total cover, SAV/algae total cover percent rank, SAV/algae height, SAV/algae height percent rank, water depth, and water velocity of muskellunge spawning and background points are reported in the final two rows. Modes are reported for the dominant SAV/algae taxa and sediment class.

Site (year)	Dominant taxa	Total cover (%)	Total cover % rank	SAV/algae height (cm)	SAV/algae ht % rank	Water depth (cm)	Water velocity (m/s)	Sediment class
2 (2011)	Fil. algae	75	96.9	2.0	90.5	165	0.300	Muddy-sand
2 (2011)	Fil. algae	85	98.6	1.0	84.2	167	0.318	Muddy-sand
2 (2011)	Fil. algae	50	84.5	1.0	84.2	177	0.291	Muddy-sand
2 (2011)	Fil. algae	80	97.9	0.8	81.1	149	0.270	Muddy-sand
2 (2011)	Fil. algae	21	69.8	0.0	50.9	73	0.125	Muddy-sand
2 (2011)	Fil. algae	95	100	6.0	91.8	165	0.263	Muddy-sand
1 (2011)	<i>Typha</i> sp.	14	61.5	9.4	93.9	81	0.016	Sand
1 (2011)	Fil. algae	51	84.7	1.0	84.2	104	0.011	Muddy-sand
1 (2011)	Bare substrate	0	0	0.0	0.0	90	0.002	Sand
3 (2013)	<i>Myriophyllum</i> sp.	99	84.1	5.0	76.4	143	0.155	Muddy-sand
3 (2013)	Fil. algae	71	68.4	4.8	75.9	160	0.130	Muddy-sand
3 (2013)	<i>Myriophyllum</i> sp.	60	57.4	9.2	94.6	194	0.295	Muddy-sand
3 (2013)	Fil. algae	40	48.2	0.8	31.7	165	0.230	Muddy-sand
3 (2013)	Fil. algae	100	84.6	4.8	74.8	135	0.095	Muddy-sand
3 (2013)	Fil. algae	100	84.6	6.6	83.0	157	0.090	Muddy-sand
Spawning points	Fil. algae	63 (33)	74.7 (26.1)	3.5 (3.3)	73.1 (26.3)	142 (37)	0.173 (0.115)	Muddy-sand
Background points	Fil. algae	42 (36)	47.7 (28.7)	3.3 (7.7)	46.6 (32.3)	115 (40)	0.131 (0.076)	Muddy-sand

muskellunge spawning point was nearly twice (1.97) that of an average background point.

Discussion

Muskellunge spawning habitat

We developed a Maxent model of muskellunge spawning habitat based on direct observation of spawning activity. Direct observation of muskellunge spawning pairs is relatively difficult and infrequently reported due to their low population densities. For example, Strand (1986) was unable to directly observe spawning fish despite frequent radio-tracking of adult muskellunge in Leech Lake, Minnesota. In our study, direct observation of paired muskellunge provided a rigorous criterion for identifying spawning locations and eliminated sampling bias associated with inferring spawning habitat based on the location of unpaired adult muskellunge during the spawning period or the capture of age-0 muskellunge. Direct observation of paired muskellunge also allowed us to describe spawning locations at the micro-habitat scale which had not been previously conducted in the upper Niagara River. Spawning activity of paired fish was confirmed with successful collection of muskellunge eggs and identification of post-hatch larvae. However, muskellunge eggs were not recovered from all spawning locations. Eggs may have been dispersed away from the point where paired fish were observed by river currents or consumed by predators, thus hindering our ability to collect eggs at all sampling locations. Alternatively, paired fish may not have always been actively spawning or spotlights may have disrupted spawning and gamete release.

Based on field observations and model outputs, substantial SAV/algae cover, relative to availability in a given spawning season, was an important characteristic of muskellunge spawning habitat in the upper Niagara River. Previous research has indicated that the importance of SAV/algae to muskellunge spawning varies among waters and

sometimes within a body of water. Descriptions of muskellunge spawning sites in bodies of water that support self-sustaining populations have included: bare substrate (Dombeck et al., 1984; Farrell et al., 1996; Haas, 1978; Monfette et al., 1996), dense beds of macroalgae (Dombeck et al., 1984; Farrell, 1991; Strand, 1986), decaying vegetation or leaf litter (Minor and Crossman, 1978; Younk et al., 1996), and emerging aquatic macrophytes (Farrell, 1991, 2001; Farrell et al., 1996). Methods for detection of spawning muskellunge and the spatial scales of previous studies have also varied and may have contributed to the inconsistent findings on the importance of SAV/algae coverage. However, lack of consistent findings on the importance of SAV/algae coverage to muskellunge spawning may also be indicative of their reproductive plasticity. Because muskellunge in the upper Niagara River frequently spawn in areas exposed to moderate water velocities, substantial SAV/algae coverage may be important for preventing egg redistribution. Additionally, SAV/algae may provide protection from numerous egg predators such as *Moxostoma* spp. (Johnson et al., 2006) and round goby (*Neogobius melanostomus*; Kornis et al., 2012).

Filamentous algae was the dominant SAV/algae taxa at muskellunge spawning points in the upper Niagara River, but reports of muskellunge spawning over filamentous algae in other waters are rare. Farrell et al. (1996) documented *Cladophora* spp. and *Spirogyra* spp. at muskellunge spawning sites in a St. Lawrence River bay, but *Potamogeton* spp., *Lemna* spp., and *Chara* spp. were the dominant SAV/algae taxa. Dombeck et al. (1984) documented muskellunge spawning over filamentous algae in Minocqua Lake, Wisconsin, but natural reproduction was poor. *Chara* spp., submerged macrophytes, such as *Potamogeton* spp. and *Myriophyllum* spp., and emergent aquatic vegetation, such as *Carex* spp., *Juncus* spp., and *Schoenoplectus* spp., are more frequently reported as common taxa at muskellunge spawning sites (Dombeck et al., 1984; Farrell, 1991, 2001; Farrell et al., 1996; Strand, 1986). Our model outputs indicated that the dominant species of SAV/algae at spawning points was a poor predictor of muskellunge spawning, and when used by itself performed worse than the null model. If SAV/algae coverage of the substrate is important for muskellunge spawning in the upper Niagara River as indicated by our model, filamentous algae may be the default habitat used by spawning fish because it is the first SAV/algae taxa to cover substrate at the beginning of the growing season. Although we observed some overwintering of *Myriophyllum* spp. in 2013, habitat dominated by SAV/algae taxa other than filamentous algae was largely absent until later in the spring/early summer. In order to create habitat to hold and protect incubating eggs aquatic vegetation plantings at muskellunge spawning habitat restoration sites should include species that emerge early in the growing season.

Table 2

Pearson correlation coefficients for quantitative habitat variables collected at muskellunge spawning points and background habitat points.

	Total cover % rank	SAV/algae height % rank	Water depth
SAV/algae height % rank	0.81		
Water depth	0.49	0.48	
Velocity	0.25	0.25	0.32

Table 3

β regularization parameter values used when tuning the model to optimize β values and prevent overfitting. The resulting test gain values and number of test gain values that were negative were used to identify optimal β regularization parameter values. A balance between maximizing test gain and minimizing the number of negative test gain values was used to select β regularization parameter values and the model. The environmental variables retained for each associated model that was evaluated during the β regularization parameter and model selection process are displayed on the right. β_c = the default β value for categorical features, β_{lqp} = the default β value for linear, quadratic, and product features. Only categorical, linear, and quadratic features were allowed. A regularization multiplier of 1 was used for all models.

β	Test gain	No. negative test gain values	No. variables
Default ($\beta_c = 0.357$, $\beta_{lqp} = 0.629$)	0.5481	3	3 (sediment, cover, and velocity)
0.00	0.6511	4	3 (sediment, cover, and velocity)
0.05	0.6829	5	4 (sediment, cover, velocity, and depth)
0.10	0.6793	4	4 (sediment, cover, velocity, and depth)
0.25	0.6560	4	4 (sediment, cover, velocity, and depth)
0.50	0.5531	5	2 (cover and velocity)
0.75	0.5001	3	3 (sediment, cover, and velocity)
1.00	0.4403	3	3 (sediment, cover, and velocity)
1.50	0.3584	4	2 (sediment and cover)
2.00	0.2977	4	1 (cover)
2.50	0.2152	3	1 (cover)

The quality of filamentous algae as egg incubation habitat is unknown and deserves more attention, considering its increased presence in the Great Lakes (Hecky et al., 2004; Auer et al., 2010). Dead or decaying filamentous algae can deplete dissolved oxygen in benthic habitats. However, the locations where we observed muskellunge pairs and collected eggs in the upper Niagara River had moderate water velocities which probably delivered water with adequate

dissolved oxygen for incubating eggs. Additionally, collection of late-stage eggs and yolk-sac larvae indicated that muskellunge eggs successfully incubated in these habitats. The dense web of filaments created by filamentous algae may make it difficult for predators to locate and consume incubating muskellunge eggs and demersal larvae. Conversely, there is a potential cost of spawning in filamentous algae associated with wind or boat-induced waves that can redistribute eggs and larvae

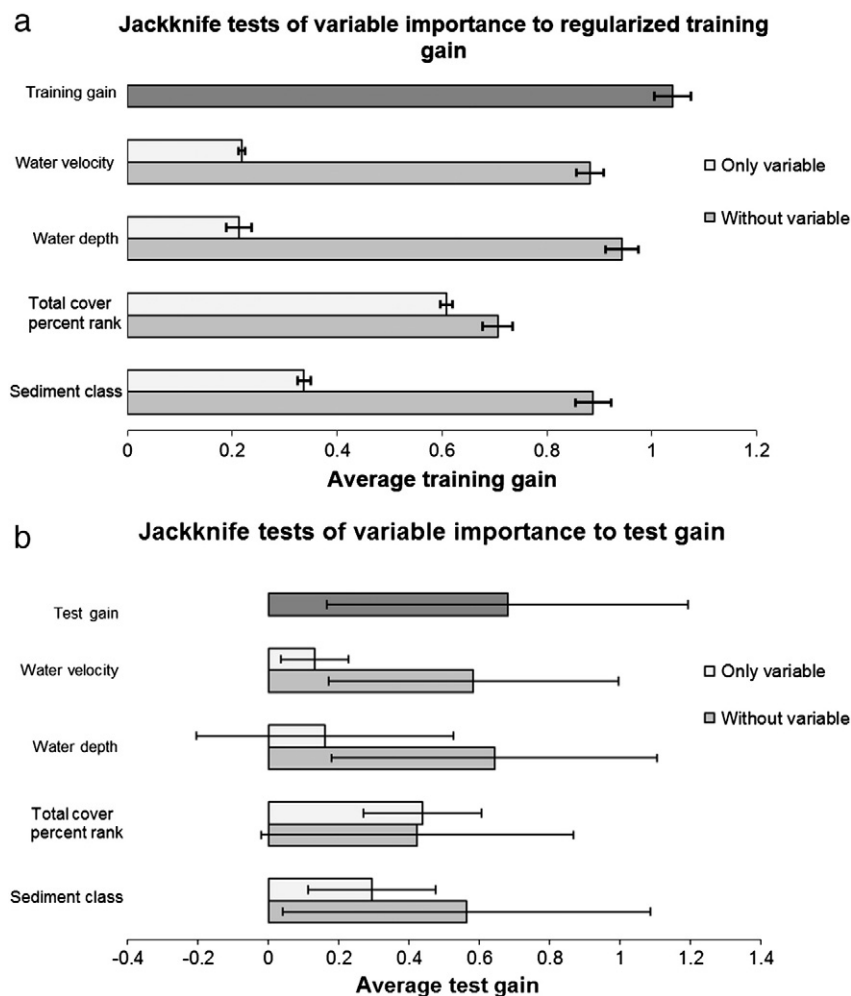


Fig. 3. Jackknife tests of 15 cross-validated muskellunge spawning habitat models. For each variable, the regularized training gain (a) and test gain (b) (mean \pm SE) are displayed for the model run with each variable withheld from the model and each variable used as the only predictor. Additionally, regularized training and test gain (averaged across the cross-validated models) for the full, four variable model, are displayed.

Table 4

Lambda (λ) values from the final Maxent muskellunge spawning habitat model. SD in parentheses are reported based on 15 cross-validated models. Categorical, linear and quadratic features of sediment class, total cover % rank, water depth, and water velocity variables were retained for the final model. The final model was based on $n = 15$ muskellunge spawning points and $n = 250$ background habitat points.

Variable	Lambda (SD)
<i>Categorical</i>	
Sediment class = sand	2.357 (0.216)
Sediment class = muddy-sand	2.656 (0.121)
<i>Linear</i>	
Total cover % rank	−4.474 (1.858)
Water velocity (m/s)	−3.526 (1.049)
<i>Quadratic</i>	
Total cover % rank	6.876 (1.571)
Water depth (cm)	2.192 (0.295)
Water velocity (m/s)	6.043 (0.926)

into suboptimal habitats. Filamentous algae are not rooted and can be more easily scoured from the substrate compared to rooted aquatic macrophytes.

In other waters muskellunge are frequently reported spawning over leaf litter or dead vegetation from the previous growing season (Minor and Crossman, 1978; Strand, 1986; Zorn et al., 1998). In the upper Niagara River, little submerged aquatic vegetation or leaf litter remains from previous growing seasons due to ice scour, shoreline armoring, loss of wetlands, and lack of large areas protected from

main river currents. Although submerged aquatic vegetation was largely absent in the Niagara River during our two years of study, new and previous season's growth of emergent *Typha* sp. was common in several areas of river. The majority of *Typha* sp. growth in the upper Niagara River occurs in dense monocultures along river margins. Farrell (2001) observed that muskellunge did not utilize habitat dominated by monocultures of *Typha* sp. for spawning in a St. Lawrence River bay but did spawn in areas with a mix of *Typha* sp. and other emergent vegetation. Similarly, we did not observe muskellunge spawning in dense monocultures of *Typha* sp., but we did observe muskellunge spawning within and along the margins of a *Typha* sp. "island" at Site 1. *Typha* sp. stems along the edges of the "island" were more sparsely distributed compared to the core area of the "island", allowing for fish to move easily between stems. The stem density in the core part of the "island" may have deterred fish from spawning in this area. Restoration efforts that create and sustain "islands" with low to moderate densities of emergent vegetation and maximize edge habitat may benefit spawning muskellunge.

Sediments at spawning locations in the upper Niagara River were firm and ranged from muddy-sand to sand. No muskellunge (paired or unpaired) were observed in the limited areas that were dominated by softer substrates. Muskellunge in waters with self-sustaining populations have been observed spawning over a wide variety of sediment types (Dombeck et al., 1984; Rust et al., 2002; Strand, 1986; Zorn et al., 1998). For example, within the Thousand Islands region of the St. Lawrence River, muskellunge successfully spawn in bays where the dominant sediments range from silt with high organic content to firm

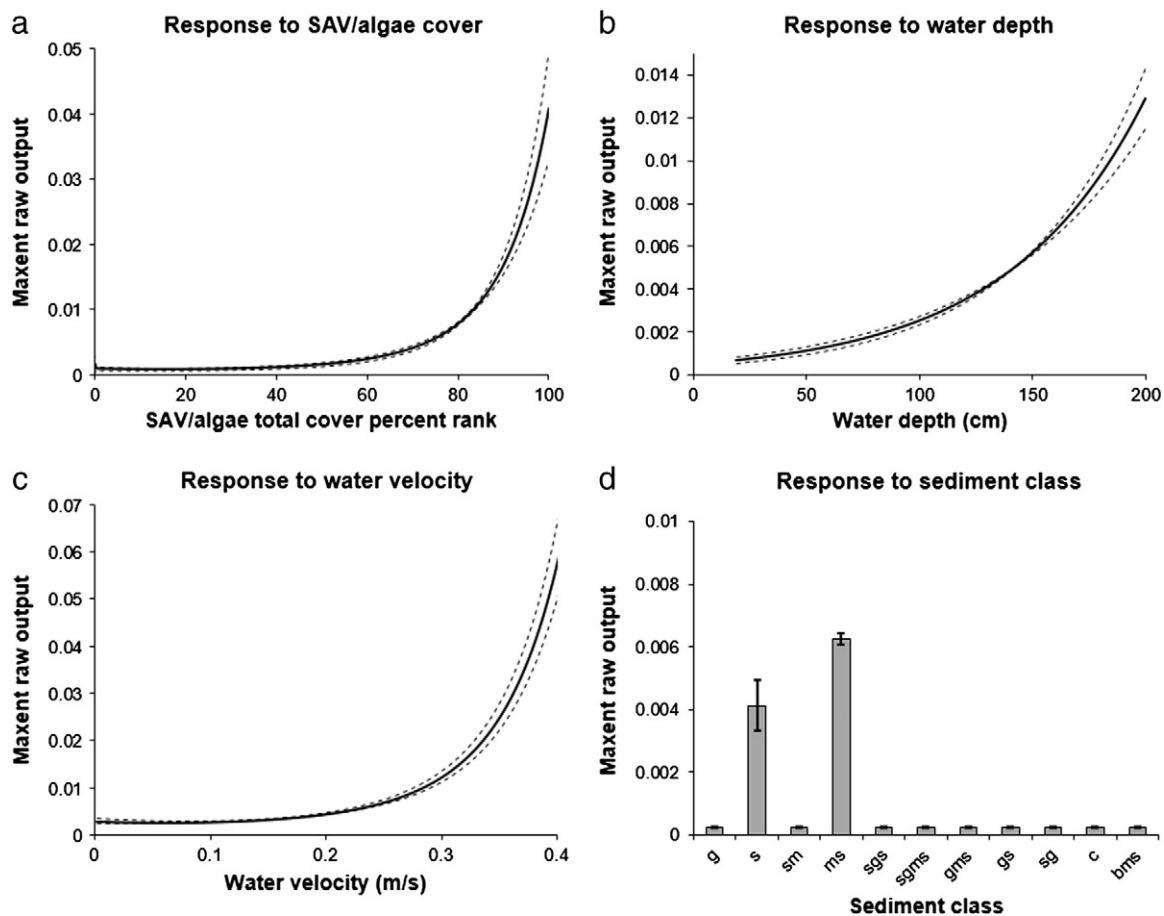


Fig. 4. Response curves (mean \pm SD), from 15 cross-validated muskellunge spawning habitat models, displaying the relationship between a) SAV/algae areal coverage percent rank, b) water depth (cm), c) water velocity (m/s), and d) sediment class and the Maxent raw output. Sediment classes for mud, sand, and gravel are based on ternary plots from Folk (1954): g = gravel, s = sand, sm = sandy-mud, ms = muddy-sand, sgs = slightly gravelly-sand, sgms = slightly gravelly-muddy-sand, gms = gravelly-muddy-sand, gs = gravelly-sand, sg = sandy-gravel, c = cobble, bms = boulder with muddy-sand. Response curves were created by using each environmental variable individually as the predictor. Solid line in a, b, and c is the mean while the hatched line gives the SD.

sand (Farrell et al., 2007). The muddy-sand substrates most common at muskellunge spawning sites in the upper Niagara River likely strike a balance between being coarse enough to facilitate movement of water rich in dissolved oxygen, and fine enough for supporting extensive aquatic macrophyte growth which is vital to newly hatched larvae and age-0 muskellunge (Murry and Farrell, 2007). Muskellunge spawning habitat restoration efforts in the upper Niagara River should incorporate sand and muddy-sand substrates and create conditions that sustain these substrates.

The importance of water velocity at muskellunge spawning locations varies over the geographic range of the species. We observed that muskellunge in the upper Niagara River generally spawned in areas with moderate water column velocities, and water velocity was an important predictor in the Maxent model. Similar to our study, Harrison and Hadley (1978) observed that water velocities of 0.2 m/s were typical of muskellunge spawning locations in the upper Niagara River. LaPan et al. (1996) noted that in the Thousand Islands region of the St. Lawrence River spawning stage muskellunge were most frequently collected in embayments with no measurable water current. Monfette et al. (1996) collected muskellunge eggs more frequently in areas with water velocities >0.1 m/s than <0.1 m/s in the Kinongne River, Quebec; however, little current was detected in two Ottawa River embayments where muskellunge eggs were collected. In a study of inland Wisconsin lakes, Zorn et al. (1998) noted minimal water velocities at all muskellunge spawning areas. As noted above, Dombek et al. (1984) documented muskellunge spawning over filamentous algae in a Wisconsin lake with poor natural reproduction. Dombek et al. (1984) also documented micro-stratification and low dissolved oxygen levels at these locations. Moderate currents in the upper Niagara River likely provide oxygenated water to eggs incubating in thick filamentous algae. Water velocity is also an important factor determining substrate composition in fluvial environments (Knighton, 1998). Moderate water velocities observed at muskellunge spawning points in the Niagara River likely maintained the firm muddy-sand to sand substrates that were also determined to be important predictors of muskellunge spawning.

Water depths at muskellunge spawning sites in the upper Niagara River were generally greater than what has been reported in the literature; however, spawning in depths similar to what we observed has been documented. For example, Haas (1978) suspected that muskellunge in Lake St. Clair spawned in waters >3 m deep, and muskellunge in Leech Lake utilized habitats 1–2 m deep for spawning (Strand, 1986). However, Haas (1978) and Strand (1986) inferred these values based on location or collection of adult muskellunge during the spawning season—actual spawning depths may have been different. Shallow, nearshore areas in the upper Niagara River were generally devoid of SAV/algae growth during the spawning season due to ice and wave scour; so muskellunge may have avoided spawning in shallow water areas due to lack of substantial SAV/algae coverage. Although most spawning locations identified in our study were located in water >1.5 m deep, spawning was observed in shallower locations, particularly at Site 1, where fish were observed spawning on the fringe of an offshore *Typha* sp. “island”. *Typha* sp. are robust enough to withstand ice and wave scour common to the Niagara River. The off-shore emergent vegetation growth at Site 1 provided an uncommon combination of SAV/algae growth in relatively shallow water (about 1 m) for muskellunge to use as spawning habitat.

The visual observation method used in this study was successful at identifying spawning locations, but, this method limited spawning surveys to waters <200 cm deep. Additionally, wind and low water clarity resulted in the loss of multiple survey nights. Future studies should consider coupling visual observation surveys with the recently developed technique of implanting transmitters in the oviduct of mature muskellunge prior to the spawn, and subsequent location of deposited transmitters that are assumed to be lost during expulsion of eggs (Battige, 2011; Pierce et al., 2007). This would allow for

identification of spawning habitats across a broader range of environmental conditions. Additionally, tracking of muskellunge in spawning condition would allow for faster identification of general spawning areas in large waterbodies. Coupling of the two methods may also increase the probability of obtaining adequate sample sizes for rigorous statistical testing and model development; small sample sizes have been reoccurring issues in studies of muskellunge reproductive ecology. However, we caution that the identification of spawning points should always be confirmed through direct observation of spawning or collection of fertilized muskellunge eggs.

Spawning habitat model

The Maxent modeling procedure was effective for modeling the relationships between muskellunge spawning occurrence and associated habitat features. Despite having a small presence sample size ($n = 15$), evaluation of our spawning habitat model indicated that it was capable of differentiating between potential muskellunge spawning habitat and background habitat. However, among-model variability in test gain was substantial even though our model demonstrated good performance when averaged across cross-validated models. Four of the 15 test points resulted in negative test gain values. Test points that resulted in negative test gain values had relatively low SAV/algae total cover percent rank scores and/or were in shallow water. However, three of the four points were located in close proximity (<1 m–20 m) to areas with substantial SAV/algae coverage. Hernandez et al. (2006) and Pearson et al. (2007) observed similar variability in model performance when using small sample sizes. Variability in model performance is an issue inherent to working with small sample sizes (Pearson et al., 2007) because each sample contributes a substantial amount of information to the model.

Model outputs indicated positive relationships between the relative probability of spawning and SAV/algae total cover percent rank, water depth, and water velocity. When water depth and water velocity were used individually as predictors, the highest relative probabilities of spawning occurred at the maximum values observed in the background samples (water depth = 200 cm; water velocity = 0.401 m/s). Because Maxent models are based on the frequencies that values for environmental covariates are observed at presence locations (i.e., probability densities) compared to background locations, the environmental response curves are heavily influenced by the distribution and range of values for target covariates in the background sample (Elith et al., 2011; Merow et al., 2013). Values near the observed maximums for water velocity and depth were not frequently sampled during background habitat surveys and may have influenced model outcomes. Although water depths of ≥ 190 cm (6 of 250 background samples) and ≥ 0.30 m/s (4 of 250 background samples) were rare at the sites surveyed for spawning muskellunge in our study they were not rare in areas adjacent to the study sites or in the upper Niagara River. Our visual observation method for detecting spawning muskellunge limited the conditions we could sample in, and therefore, the range and distribution of values in the background sample. It is possible that the response curves created by the Maxent model accurately reflect muskellunge spawning habitat use and the highest relative probability of spawning was in deeper and faster water than could be accurately surveyed. However, it is more likely that the observed patterns resulted from the combined effects of the relative rarity of background points with values near the observed maxima for water depth and velocity and a small number of presence locations with water depth and velocity values much greater than the means. The relationships between the relative probability of muskellunge spawning and water velocity and depth were likely uni-modal, with the highest relative probability of spawning occurring at water velocities and depths less than what was predicted by the model.

Over-estimation of the relative probability of spawning at water velocities and depths near the maximum values at background points

is supported by our field observations. First, spawning locations were relatively concentrated within a site and the greatest concentrations of unpaired muskellunge were observed in close proximity to these locations. Second, the highest water velocity observed at a muskellunge spawning point was 0.318 m/s and the average water velocity at spawning points was 0.173 m/s. Third, 14 of 15 spawning points were located in water <180 cm, and the mean depth at these points was 142 cm. Finally, the mean depth (144 cm) and water velocity (0.132 m/s) that muskellunge eggs were collected at during background habitat surveys were similar to the average water depth and velocity observed for spawning locations (D. P. Crane, SUNY-ESF, unpublished data). Expanded ranges of background habitat values for water velocity and depth as well as additional spawning locations may have resulted in uni-modal modal response curves.

Although model outputs identified percent rank of SAV/algae cover as the most important habitat characteristic at muskellunge spawning locations, percent rank of SAV/algae cover features had the most variability in λ values across cross-validated models. The percent rank of SAV/algae cover was >80% at 9 of 15 spawning points, but percent ranks ranged from 0 to 100%; thus contributing to the uncertainty in λ values. The lowest uncertainty in λ values was observed for sediment class features, which was not unexpected given that all muskellunge spawning points were located in areas with sand or muddy-sand substrates.

The ability of the muskellunge spawning habitat model to identify habitat features that were most often associated with muskellunge spawning can help guide habitat management in the upper Niagara River. For example, restoration efforts can focus on important features identified by the model and emphasize developing and sustaining habitat characteristics that are similar to those observed at spawning locations. Information from this study could also be used to prioritize areas for habitat conservation. Several areas of the upper Niagara River were identified as muskellunge spawning sites, and these areas could be designated as critical habitat and protected from development or degradation. A muskellunge spawning habitat model developed by Nohner (2009) was integrated with a geographic information system (GIS) and is currently being used to designate critical habitat in Wisconsin lakes. Unfortunately, GIS data related to the habitat variables used in this model are largely unavailable for the upper Niagara River. Creation of high resolution GIS data layers of physical and biological habitat features for the upper Niagara River should be a priority and would increase the number of decision support tools available to managers. Although our model could be coupled with a GIS and used to identify areas for conservation or as a tool to guide restoration, we caution that the potential bias in the response curves, as discussed above, may limit its capacity as a predictive model. Also, despite sampling a diversity of habitats to create the muskellunge spawning habitat model, neither the entire range of conditions available to spawning fish in upper Niagara River nor the range of possible conditions created by habitat restoration were encompassed. Extrapolating our model beyond the environmental conditions that were surveyed to develop it may result in spurious conclusions (Elith and Leathwick, 2009; Elith et al., 2011; Phillips et al., 2009).

Conclusion

Models for species distributions and habitat use are essential for conservation and habitat restoration planning (Franklin, 2009). We used a presence-only modeling process to identify habitat features associated with muskellunge spawning sites in the upper Niagara River. Developing a thorough understanding of the relationship between muskellunge spawning site selection and microhabitat characteristics is vital to preserving self-sustaining muskellunge populations. Continued collection of data encompassing greater environmental variability across space and time would increase the model's ability to generalize across a wider range of habitats. Future work that quantifies the quality of

habitat based on survival of muskellunge eggs and subsequent life stages would increase our understanding of muskellunge reproductive ecology and maximize effectiveness of habitat management for the species. Future research should also focus on linking models of spawning and rearing habitat to ensure that multiple early life stages are accounted for when applying these models to restoration initiatives. Such models would greatly enhance the ability of resource managers to set and achieve restoration targets.

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