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Index of Nursery Habitat Suitability for Muskellunge in Georgian Bay, Lake Huron

John Paul Leblanc*[1] and Patricia Chow-Fraser
Department of Biology, McMaster University
1280 Main Street West, Hamilton, Ontario L8S 4K1, Canada

Abstract.—To support Georgian Bay's self-sustaining Muskellunge *Esox masquinongy* fisheries, we developed two index of nursery habitat suitability (INHS) models that can be used to identify and monitor the quality of Muskellunge nursery habitats in coastal wetlands. The INHS models were based on habitat features found in wetlands with age-0 Muskellunge identified at two large embayments in northern Georgian Bay. One INHS model had five variables that included proportional abundance of Yellow Perch *Perca flavescens*, proportional abundance of cyprinids, fish species richness, the wetland's substrate slope, and a metric related to macrophyte abundance. The other INHS model included only three variables from the five-variable INHS, omitting information on macrophyte and fish species richness. When they were applied to an independent data set, both INHS models successfully tracked deterioration in nursery suitability after 15 years of sustained low water levels in Georgian Bay, but the five-variable INHS had higher overall accuracy and showed stronger discrimination between sites with and without young of the year. We applied the three-variable model to classify coastal wetlands in other regions of Georgian Bay and obtained a false-negative rate less than 13%. We also obtained a higher false-positive rate with the three-variable model compared with the five-variable model (54% versus 31%) because it required a lower threshold to indicate suitability (0.6 versus 0.70, respectively). These INHS models should allow managers to screen for suitable nursery habitat near current spawning sites across Georgian Bay and allow managers to predict how changes in water-level regimes might affect the suitability of spatially explicit wetland units.

Introduction

The Muskellunge *Esox masquinongy* fishery of Georgian Bay (Lake Huron) is well known for its trophy status and for producing large fish and is of great economic and ecological value to Ontario (Kerr et al. 2011). Since 2001, a restrictive harvest regulation that prohibits anglers from harvesting fish smaller than 137 cm (54 in) has been effective in keeping many of the spawning individuals alive in the population. Adult mortality is further minimized through voluntary catch and release by many dedicated anglers. Despite these conservation measures, which

* Corresponding author: johnpaul.leblanc@gmail.com
[1] Present address: Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, 1 Forestry Drive, Illick Hall, Syracuse, New York 13210, USA

have successfully limited the exploitation rate of adults in Ontario to less than 1% (Kerr 2007), the Muskellunge population in Georgian Bay could still be vulnerable to collapse if suitable nursery habitat that is near the spawning area becomes unavailable (Kapuscinski et al. 2014; Leblanc et al. 2014). That is why many Great Lakes jurisdictions, including Ontario, now focus on conserving habitat for early life stages as part of the overall management strategy of Muskellunge (Farrell et al. 2007; Liskauskas 2007).

To implement this aspect of the management strategy, agencies must be able to first identify nursery habitat. For Muskellunge, this has been difficult because only a few studies have been published to provide guidance. One of the earliest studies was conducted by Craig and Black (1986), who showed that age-0 Muskellunge are most often found in shallow portions of coastal wetlands from shore to approximately 1.0 m depth. More recent studies have provided further refinement by pointing out that suitable habitat must also include a structurally complex macrophyte community that allows age-0 Muskellunge to hide from predators (Murry and Farrell 2007; Kapuscinski and Farrell 2014; Wagner et al. 2015) while simultaneously allowing them to ambush their preferred prey (i.e., soft-rayed fusiform fish; Wahl and Stein 1988; Kapuscinski et al. 2012). With such information, it is now possible and desirable to develop an index that can be used to identify suitable habitat for age-0 Muskellunge before any shoreline modification can occur. Once a site has been identified as being suitable, a more detailed study can be carried out to confirm the presence of age-0 Muskellunge. This index could be philosophically similar to the standard habitat suitability index (HSI), except that the index should focus only on early-life habitat instead of habitat of all life stages (U.S. Fish and Wildlife Service 1981; Ahmadi-Nedushan et al. 2006; De Kerckhove et al. 2008). To differentiate it from the HSI, we refer to our index as an index of nursery habitat suitability (INHS).

The goal of this paper was to develop INHS models for age-0 Muskellunge specifically for Georgian Bay. We constrained this development to minimize false negatives (i.e., the incidence of nursery sites being misclassified as unsuitable) since we want to err on the side of conservation. To ensure that the INHS will be appropriate for biologists in most management agencies, we developed one of the models using only variables that are readily measured and available to fisheries biologists. It was not our goal to develop a habitat suitability model or species distribution model (SDM) that uses climatic or environmental features to predict species distributions over a large geographic region (e.g., Guisan and Thuiller 2005). Instead, the INHS is meant to be an indexing tool that can be used at the site level to screen for nursery habitat suitability within a wetland or wetland complex. The index could be especially useful for environmental agencies interested in restoring degraded habitat or creating new habitat to support age-0 Muskellunge.

Like the HSI scores, we wanted the INHS scores to be easily interpreted by setting the range from 0 (indicating completely unsuitable habitat) to 1 (indicating entirely suitable habitat) (U.S. Fish and Wildlife Service 1981), and that may be used to reflect the degree of change in suitability of a habitat that was positively or negatively impacted by natural (e.g., water levels of a lake) or human-induced disturbances (e.g., lakeshore modifications) (De Kerckhove et al. 2008). We also used a suite of suitability index (SI) variables similar to those in HSI that correspond to quantifiable dimensions of the habitat and that are scaled from 0 to 1. These SI variables will be based on habitat features that can discriminate between sites with and without age-0 Muskellunge in wetlands of Georgian Bay, including stem density of various groups of submersed aquatic vegetation (SAV), the proportional abundance and species richness of fish taxa, as well as the substrate slope of the wetland (Leblanc 2015). We will compare the performance of various INHS models and use independent data to validate the best one. These indices can be used to evaluate the impact of water-level changes on existing nursery habitat and complement existing efforts to protect the self-reproducing status of the Georgian Bay Muskellunge fishery.

Methods

Data and INHS Development

The data used for this study come from two large, hydrologically connected embayments in northern Georgian Bay that were selected because coastal wetland units have been minimally impacted by human disturbance (see Leblanc 2015 for detailed site description; Figure 1). Wetland units were operationally defined as contiguous areas of macrophyte cover from shore to the 1.0 m contour that varied in size from 0.2 to 11.0 ha with a mean area of 1.1 ha (SE = 0.17). In 2012 and 2013, we systematically surveyed all wetland units for seven key variables that had been identified as being significant discriminators between sites where age-0 Muskellunge had been caught (age-0 Muskellunge sites; $n = 16$) and a random selection of sites where they had not been caught (no-Muskellunge sites; $n = 39$) (Leblanc 2015). The presence or absence of age-0 Muskellunge was determined following the seining protocol described by Craig and Black (1986), where a standard seine net (15 × 1.2 m, 6.4 mm mesh) was hauled once through each wetland unit, at depths ≤1.2 m, in July of both years (Leblanc 2015). Approximately 18% of the wetland units seined in northern Georgian Bay found age-0 Muskellunge, which was similar to the capture rate reported by Craig and Black (1986), who surveyed a similar number of sites in an identical manner. The variables included were (1) stem density of canopy-forming SAV (Can SAV), (2) proportional abundance of Vallisneria americana in the Can SAV, (3) stem density ratio of substrate-covering SAV (Sub SAV) to Can SAV (Sub SAV : Can SAV), (4) the wetland's substrate slope, (5) proportional abundance of Yellow Perch *Perca flavescens*, (6) proportional abundance of cyprinid species, and (7) fish species richness. All plant community variables were calculated from information collected by surveying approximately 12 quadrats (0.25 m^2) per wetland unit at wetland depths between 0.5 and 1.0 m with the standard rake sweep method in August (Croft and Chow-Fraser 2009; Leblanc et al. 2014). The fish community variables were calculated from fish data collected from the standard seine haul from which age-0 Muskellunge had been excluded (Leblanc 2015).

To streamline the collection of data, we wanted to develop a simple metric that could be used to infer habitat complexity of the macrophyte community without having to count stems in the field. Macrophyte biovolume, which reflects the percentage of the water column occupied by SAV, can be estimated with hydroacoustic equipment or estimated in the field for which field-derived and remotely sensed estimates are highly correlated (Weaver et al. 1997; Valley et al. 2005). In the lower Great Lakes, investigators have used other similar indices and have

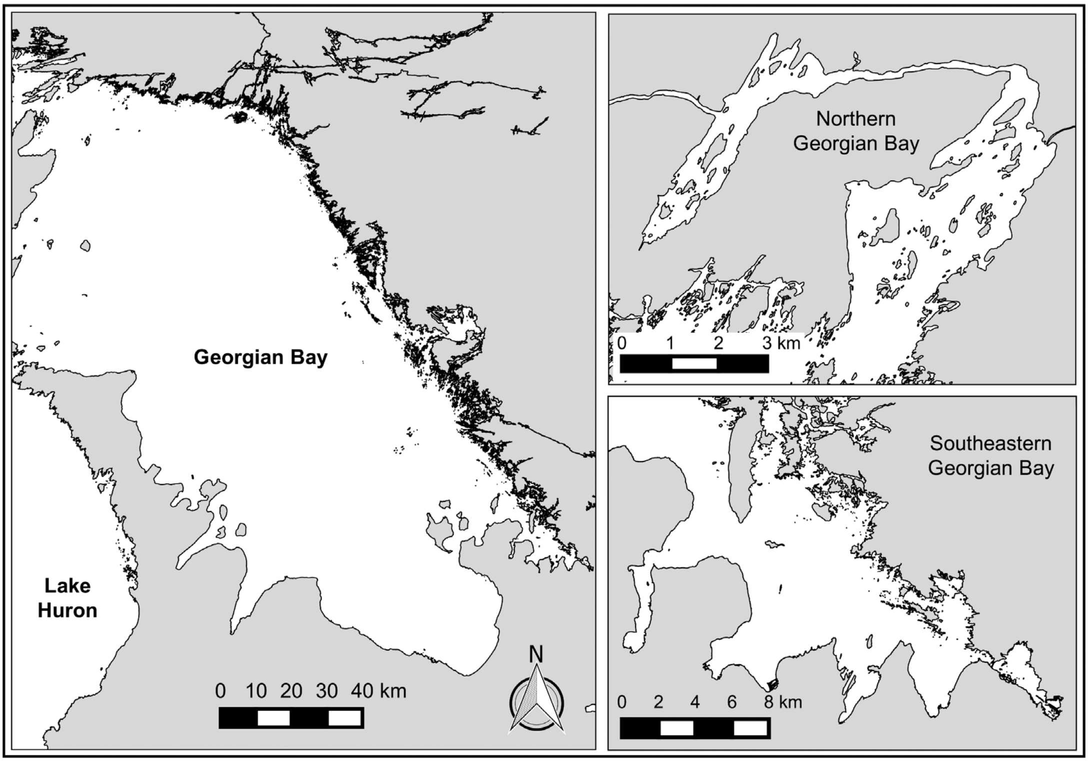

Figure 1.—Location of study sites in northern and southeastern Georgian Bay. Data collected in northern Georgian Bay were used to create the index of nursery habitat suitability (INHS) models (Leblanc 2015) and was applied to independent data from southeastern Georgian Bay (see Leblanc et al. 2014 for study site description) to determine the transferability of the INHS models throughout Georgian Bay. Embayments in northern Georgian Bay are hydrologically connected to Georgian Bay proper and to one another by a narrow channel. Like many embayments of Georgian Bay, both are oligotrophic and have been relatively undisturbed, except from the effects of 15 years of sustained low water levels.

shown that they are associated with intermediate densities of SAV in the water column (see Murry and Farrell 2007; Kapuscinski and Farrell 2014). At its simplest, biovolume can be derived by taking the mean SAV height, dividing it by the depth at which the SAV was measured, and then expressing it as a percentage (Valley et al. 2005). For each site with available data (n = 14 age-0 Muskellunge sites and n = 37 no-Muskellunge sites), mean SAV height (estimated to the nearest cm) was divided by the respective depth (cm) from which plants were found. These estimates of biovolume were restricted to the deepest quadrant of the three transects used during habitat assessments and a mean for each site was calculated. We restricted estimates of biovolume to this region of the wetland in order to make it consistent with data that would have been collected by hydroacoustic equipment (e.g., approximately 1.0 m; Weaver et al. 1997).

We derived suitability index curves for all variables mentioned above, based on the observed frequency distribution of age-0 Muskellunge associated with different levels of the SI variable (see Appendix A); the untransformed mean ± 2 SE was given an SI value of 1.0, while other values on both shoulders of the SE were given values between 1.0 and 0. Thus, SI curves are representative of habitat-use indices or comparable to a category-II HSI (Ahmadi-Nedushan et al. 2006). In many cases, the shoulders on either side of the mean were simply extended linearly from 1 to 0 to intercept the *x*-axis at locations that bracket observed distributions. When there were insufficient data, the line was subjectively broken or bent to reflect uncertainty of the relationship. As a result, SI curves should be considered hypotheses of suitable habitat relationships for age-0 Muskellunge that require further testing and refinement.

Suitability index scores for the relevant variables were calculated for each wetland unit. Based on the relatively low correlation between all SI variable pairs (i.e., $r \leq 0.30$), we have assumed that SI variables are statistically independent. Additionally, we assumed that the SI variables are compensatory and have not considered any single variable to be more important than others with regards to habitat suitability. Therefore, we created a composite INHS by calculating the arithmetic mean of all SI variables using the following formula:

$$\text{INHS} = \left(\sum_{i=m}^{n} V_i \right) / \, n, \tag{1}$$

where V_i is the SI value for the *i*th SI variable and n is the number of SI variables used to calculate the INHS score.

We could have used the lowest SI variable value as the criterion for overall suitability, but an arithmetic mean of the variables is less biased towards unsuitability (Ahmadi-Nedushan et al. 2006), something that we were aiming for, to minimize the number of cases in which age-0 Muskellunge sites would be misclassified as being unsuitable (i.e., a false negative). Furthermore, we wanted to ensure that all SI variables had equal weighting, since the SI curves were created with a small sample size that had high site-specificity.

To determine what combination of SI variables could effectively identify the suitability of age-0 Muskellunge sites, we carried out multiple logistic regression analyses and applied Akaike information criterion (AIC) model selection using the SI values for each variable in Statistica 8.0 (StatSoft, Inc., statsoft.com). The combination of SI variables that produced the best fit of the data (based on AIC values) and that were most consistent with the nearshore features hypothesized to promote suitable nursery habitat were used to populate the INHS (equation 1). Logistic regression analyses and AIC model selection included only those variables for which information on all sites were available (n = 7). Thus, biovolume was excluded as a candidate SI variable during model development and was substituted into the INHS as a surrogate measure of the macrophyte community after its relationship with other SAV-related SI variables was inspected to determine the degree of auto-correlation. Furthermore, knowing that data on wetland macrophyte community are time-consuming to collect and not readily available to fishery agencies, we also developed an alternate INHS model that only used fish-community variables and substrate slope information that may be less effective but still useful for screening purposes.

To aid interpretation of INHS scores, from the logistic regression output, we divided the range (from 0 to 1) into four categories that represented high, moderate, low, and no suitability (U.S. Fish and Wildlife Service 1981). The cut-off points separating these categories were optimized to minimize the false-negative rate while maximizing overall accuracy of classification. This was guided by the receiver operating characteristic (ROC) curve that compared the true-positive (sensitivity) and false-positive (1 – specificity) rates among all potential threshold points to discriminate between the age-0 Muskellunge sites and no-Muskellunge sites (Fielding and Bell 1997). The ROC curve was used to identify the cut-off that maximized the sensitivity at the lowest false-positive rate (i.e., sensitivity – false positive) that was independent of the prevalence of the species and potential threshold effects from presence–absence models (Pearce and Ferrier 2000; Manel et al. 2001). This allowed us to evaluate the usefulness or conservation value of the model (Fielding and Bell 1997; Pearce and Ferrier 2000).

The area under the curve (AUC) from the ROC was also used to evaluate the "discrimination capacity" of the INHS model (Fielding and Bell 1997; Pearce and Ferrier 2000). The AUC can be interpreted as an index of the probability that the model will correctly distinguish between a randomly selected age-0 Muskellunge and no-Muskellunge sites (e.g., AUC = 0.80 means that 80% of the time the model will correctly identify the age-0 Muskellunge site; Fielding and Bell 1997; Pearce and Ferrier 2000). Area under the curve values can range between 0.5 (no discrimination capacity) and 1.0 (perfect model with no overlap of the category's scores; Fielding and Bell 1997), and models can be ranked as having "poor" (AUC values between 0.5 and 0.7), "reasonable" (AUC values 0.7–0.9), and "very good" (AUC values ≥0.9) discriminating power (Pearce and Ferrier 2000).

Optimization and Evaluation of the INHS Models

We first evaluated the performance of the selected INHS model, derived from the seven variables, by applying it to an independent data set that consisted of published information corresponding to sites in southeastern Georgian Bay that no longer supported age-0 Muskellunge (Leblanc et al. 2014) but that had been confirmed as being nursery sites for Muskellunge during 1981 (Craig and Black 1986). We expected this model to correctly classify sites as being unsuitable in 2012 (Leblanc et al. 2014) but could not apply it to the 1981 data because information on stem densities was not available.

As part of model optimization for the alternate INHS models, those that excluded a measure of the macrophyte community, the ROC and AUC values were again used to determine precision of classification and to determine the cut-off point that could be used to maximize the sensitivity and, as much as possible, limit the false-positive rate among the various INHS models. Once an appropriate suitability threshold was determined, all of the INHS models that excluded a SAV related variable were applied to data from southeastern Georgian Bay (both the 1981 and 2012 data) to determine transferability of the models from region to region.

The alternate INHS model that yielded the lowest false-negative rate (i.e., highest sensitivity) when applied to data from southeastern Georgian Bay was further evaluated with data that had been collected in eastern Georgian Bay as part of a separate study (Cvetkovic et al. 2012). Fish species composition in paired fyke nets had been recorded during July 2007. We calculated the substrate slope by estimating the distance from shore to the 1.0 m contour (we assumed that the location of the large nets was at or near 1.0 m because this was a depth requirement for fyke-net deployment). We used relevant information from the two wetlands where an early life stage of Muskellunge had been caught and 22 other sites where age-0 Muskellunge had not been caught and the use of the sites by spawning Muskellunge was unknown.

Results

Multiple logistic regression and AIC model selection identified seven candidate INHS models within two units of the lowest AIC value (Table 1). The second ranked model consisted of five variables (i.e., proportional abundance of Yellow Perch, species richness of fish, proportional abundance of cyprinid species, substrate slope of the wetland, and stem density ratio of Sub SAV : Can SAV; Table 1). This five-variable INHS model yielded scores that had a highly significant logistic fit for the northern Georgian Bay data ($\chi^2 = 29.871$, $p < 0.001$; odds ratio = 36.0) and correctly classified 12 of the 16 (75%) age-0 Muskellunge sites and 36 of the 39 (92.3%) no-Muskellunge sites (Figure 2). Based on classification of cases from the logistic regression, the five-variable INHS also performed slightly better than the top-rated INHS model (Table 1) that classified 68.8% of age-0 Muskellunge sites correctly. Because more age-0 Muskellunge sites were classified correctly by the five-variable INHS model than the top-rated model and the ROC plot for the five-variable model indicated "very good" discriminatory capacity

Table 1.—Multiple logistic regression with Akaike information criterion (AIC) model selection of the suitability index (SI) variables used to predict the occurrence of age-0 Muskellunge. Ranks of models are sorted according to ascending AIC values, with the seven-variable model (i.e., Full) presented for reference. CYP = proportional abundance of cyprinids, RICH = fish species richness, Slope = substrate slope, Sub SAV : Can SAV= ratio of stem densities of substrate to canopy submersed aquatic vegetation (SAV), YP = proportional abundance of Yellow Perch, VALL = proportional abundance of Vallisneria americana, and Can SAV = stem density of canopy structuring SAV. Respective χ^2 and p-values are shown from the logistic regression for each index of nursery habitat suitability model.

	SI variables included										
Rank	CYP	RICH	Slope	Sub SAV : Can SAV	YP	VALL	Can SAV	No. of variables	AIC value	χ^2	p
1	✓	✓	✓	✓				4	46.72	29.61	<0.0001
2	✓	✓	✓	✓	✓			5	47.44	30.88	<0.0001
3	✓	✓	✓	✓		✓		5	47.54	30.78	<0.0001
4	✓	✓	✓	✓	✓	✓		6	48.42	31.90	<0.0001
5	✓	✓		✓	✓	✓		5	48.65	29.68	<0.0001
6	✓	✓		✓		✓		4	48.68	27.65	<0.0001
7	✓	✓	✓	✓			✓	5	48.71	29.61	<0.0001
16 (full)	✓	✓	✓	✓	✓	✓	✓	7	50.42	31.91	<0.0001

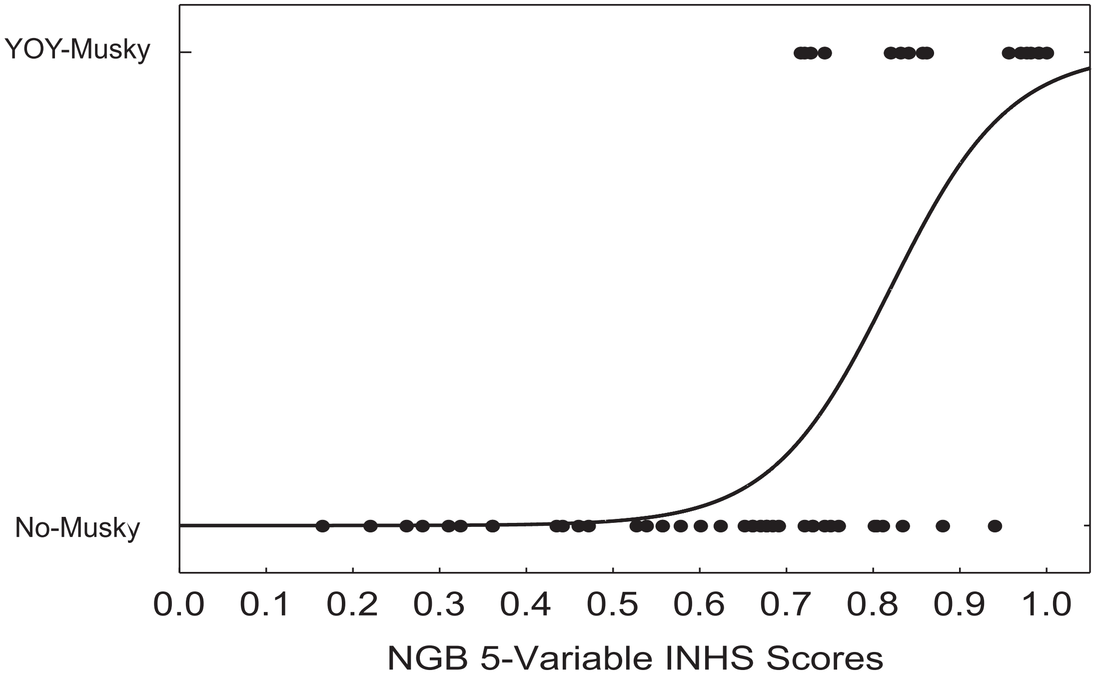

Figure 2.—Logistic regression of the scores associated with the five-variable index of nursery habitat suitability (INHS) model for the northern Georgian Bay (NGB) data. A significant logistic fit was observed ($\chi^2 = 29.871$, $p < 0.001$; odds ratio = 36.0), where 75% of the young-of-the-year Muskellunge (YOY-Musky) sites (12 of 16) and 92.3% of the no-Muskellunge (No-Musky) sites (36 of 39) were correctly classified. We interpret INHS scores ≥0.7 to have good to excellent suitability, scores 0.6–0.69 to have limited suitability, and scores ≤0.59 to have poor suitability. The No-Musky sites used for the analyses ($n = 39$) were randomly selected from the initial 67 sites that failed to capture age-0 Muskellunge (Leblanc 2015).

(AUC = 0.911), we decided to use the five-variable model to develop INHS suitability thresholds.

To optimize the performance of the various models, we manipulated the threshold from the logistic regression to classify age-0 Muskellunge sites (Figure 2). The ROC analysis indicated that a threshold of 0.70 was associated with the highest sensitivity and lowest false-positive rate among all threshold values. Given our overall objective was to minimize the false-negative rate, we came up with a lower suitability cut-off of 0.60 and break points at 0.70 and 0.80 to derive three suitability categories as follows:

≥0.8 high suitability
0.7–0.79 moderate suitability
0.6–0.69 low suitability
≤0.59 no suitability

This framework facilitated interpretation of the scores derived from the five-variable model so that all of the age-0 Muskellunge sites were correctly identified with at least moderate suitability (INHS score ≥ 0.70; Figure 3), while 12 of the 39 no-Muskellunge sites were assessed as being suitable (INHS score ≥ 0.70; Figure 3). In contrast, the top-rated model from AIC model selection failed to correctly classify three of the age-0 Muskellunge sites as suitable using this

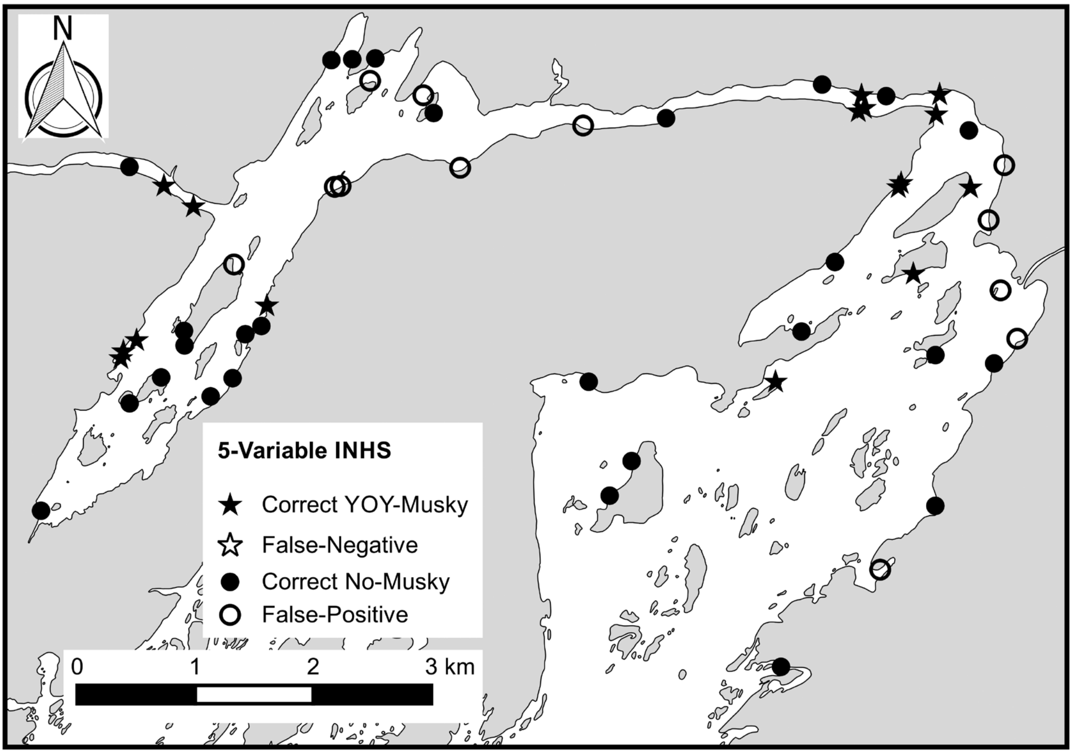

Figure 3.—Five-variable index of nursery habitat suitability (INHS) applied to northern Georgian Bay data. All young-of-the-year Muskellunge (YOY-Musky) sites were identified as such (habitat suitability index score ≥ 0.70). Twelve of 39 no-Muskellunge (No-Musky) sites were classified as YOY-Musky sites (i.e., false positive).

same framework (INHS ≥ 7.0) supporting our decision to select the five-variable INHS model. When we applied the five-variable model to the 2012 data corresponding to sites that had supported age-0 Muskellunge historically in southeastern Georgian Bay, we found that it successfully classified all of the 2012 sites as having "low" or "no" suitability for age-0 Muskellunge (mean INHS ± SE: 0.36 ± 0.036; minimum INHS = 0.13, maximum INHS = 0.62).

We also found that age-0 Muskellunge sites were associated with a significantly higher biovolume (mean ± SE: 49.0 ± 2.4%; n = 14) than no-Muskellunge sites (mean ± SE: 32.9 ± 1.9%; n = 37; t_{49} = 4.701, p < 0.001) and that age-0 Muskellunge were never found at sites with biovolumes less than 30% or greater than 70%. Additionally, we found that biovolume was significantly correlated with all SI variables related to macrophytes, positively related to stem density of Can SAV (r = 0.609, p < 0.0001), negatively related to stem density ratio (Sub SAV : Can SAV), and negatively related to the proportional abundance of *V. americana* SI variables (r < –0.464, p < 0.001). When biovolume was substituted into the five-variable INHS, in place of the variable for stem density ratio (Sub SAV : Can SAV), we found a significant logistic relationship (χ^2 = 23.302, p < 0.001, odds ratio = 20.6) that correctly classified 10 of the 14 (71.4%) age-0 Muskellunge sites and 33 of the 37 (89.2%) no-Muskellunge sites. The INHS with biovolume appeared to have very reasonable discriminatory capacity (AUC = 0.898) and the ROC plot indicated that a suitability threshold of 0.7 was still optimal for minimizing the false-negative rate. Using this threshold, 13 of the 14 age-0 Muskellunge sites (92.3%) were correctly classified while 9 of the 37 no-Muskellunge sites were assessed as being suitable in northern Georgian Bay (INHS ≥ 0.70; Figure 4). Thus, estimates of biovolume appeared an appropriate surrogate to infer the habitat complexity of the macrophyte community without the need to physically count stems of vegetation.

Development of Alternative INHS Model

Notwithstanding the relative importance of SAV as a component of suitable habitat for age-0 Muskellunge (minimum one SAV-related variable within all candidate INHS models; Table 1), stem density estimates are rarely available to fishery managers; therefore, we investigated whether an alternative INHS model could be developed that did not require use of stem counts (Table 2). We found that all logistic regressions of INHS scores resulting from models without a SAV variable were statistically significant ($\chi^2 \geq 14.60$, $p < 0.001$, for all INHS mod-

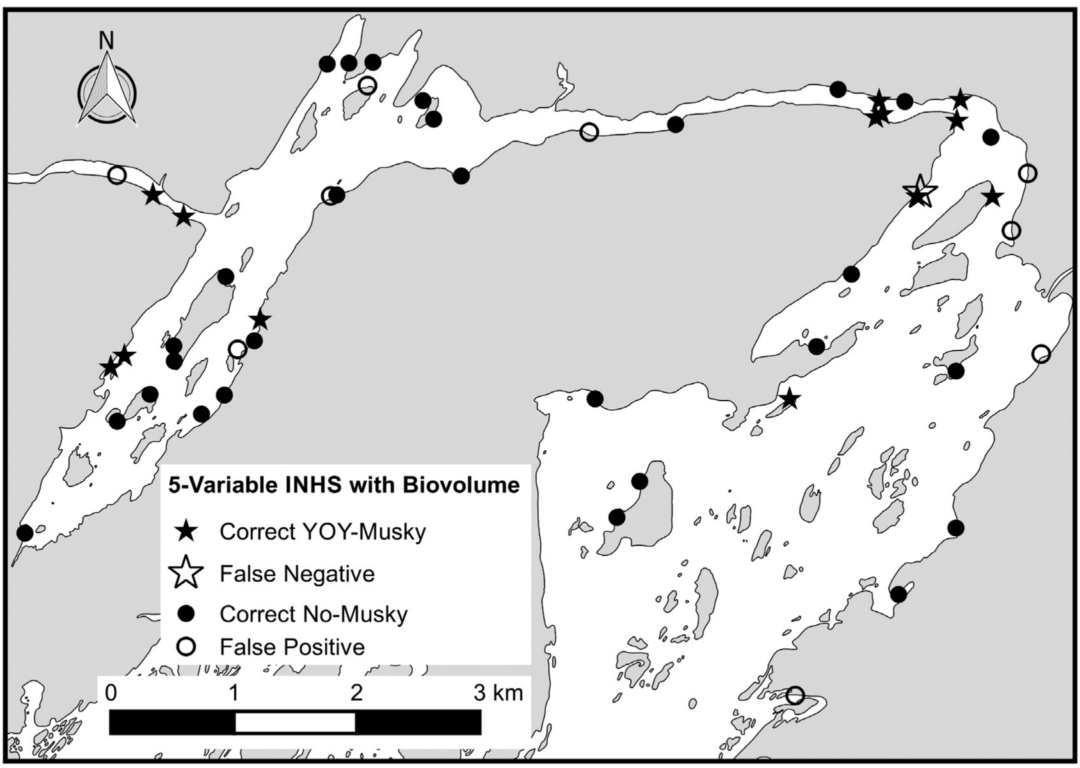

Figure 4.—Five-variable index of nursery habitat suitability (INHS) with biovolume substituted for the submersed aquatic vegetation variable applied to the northern Georgian Bay data. When an INHS score ≥0.70 was used to identify suitable nursery habitat, only 1 of the 14 young-of-the-year Muskellunge (YOY-Musky) sites was classified as a no-Muskellunge (No-Musky) site (false negative). Nine of the 37 No-Musky sites were wrongly classified as YOY-Musky sites (false positive).

Table 2. —Comparison of false negatives (i.e. nursery sites classified as not suitable) and false positives (i.e. nonnursery sites classified as suitable) associated with various index of nursery habitat suitability (INHS) models developed without submersed aquatic vegetation-related variables and applied to data collected in northern (i.e., calibration) and southeastern (i.e., validation) Georgian Bay. Receiver operating characteristic plots from the various INSH models from the northern Georgian Bay data was subsequently used to derive INHS scores to interpret suitable nursery habitat for Muskellunge (INHS ≥ 6.0). "Variables Included" identifies the specific variables used for the respective INHS models. Acronyms are defined in Table 1.

	INHS name	Variables included	False negative (%)	False positive (%)
Northern Georgian Bay	$INHS_{No\text{-}SAV}$	YP, CYP, RICH, Slope	0.0	51.3
	$INHS_{YP\text{-}CYP\text{-}Rich}$	YP, CYP, RICH	6.3	56.4
	$INHS_{YP\text{-}CYP\text{-}Slope}$	YP, CYP, Slope	12.5	53.8
	$INHS_{YP\text{-}Rich\text{-}Slope}$	YP, RICH, Slope	12.5	59.0
	$INHS_{CYP\text{-}Rich\text{-}Slope}$	CYP, RICH, Slope	18.8	43.6
Southeastern Georgian Bay	$INHS_{YP\text{-}CYP\text{-}Slope}$	YP, CYP, Slope	12.5	18.8
	$INHS_{YP\text{-}Rich\text{-}Slope}$	YP, RICH, Slope	25.0	12.5
	$INHS_{No\text{-}SAV}$	YP, CYP, RICH, Slope	31.3	18.8
	$INHS_{YP\text{-}CYP\text{-}Rich}$	YP, CYP, RICH	37.5	18.8
	$INHS_{CYP\text{-}Rich\text{-}Slope}$	CYP, RICH, Slope	56.3	12.5

els; Table 2). Nevertheless, only 10 of the 16 (62.5%) age-0 Muskellunge sites and 36 of the 39 (92.3%) no-Muskellunge sites were correctly classified in northern Georgian Bay, based on the logistic regression. Even so, the AUC value indicated that the models had reasonable discriminatory power (AUC < 0.840) when compared with the five-variable INHS. Based on the ROC of these various INHS models, we found that when the logistic regression threshold was manipulated, a suitability threshold value of 0.6 maximized the number of correctly classified age-0 Muskellunge sites. Using 0.6 as the cut-off to indicate suitability, the INHS model that included all fish variables as well as substrate slope of the wetland (i.e., $INHS_{No\text{-}SAV}$) identified all age-0 Muskellunge sites correctly but also had a correspondingly high false-positive rate of more than 50% (Table 2) compared to the five-variable INHS (Figure 5). All other INHS models (see Table 2) had relatively low false-negative rates and comparable false-positive rates as the $INHS_{No\text{-}SAV}$ when 0.6 was used to indicate suitability (Table 2).

To assess the transferability of the alternate INHS models, we applied them to an independent data set and compared their performance. We found that a three-variable model that included the proportional abundance of Yellow Perch, proportional abundance of cyprinids, and substrate slope (i.e., $INHS_{YP\text{-}CYP\text{-}Slope}$) was associated with the lowest false-negative rate (12.5%; Table 2; Figure 6). All other INHS models had false-negative rates ≥25.0% (Table 2), which is unacceptably high considering our conservation goals. Using this INHS model, we were successful

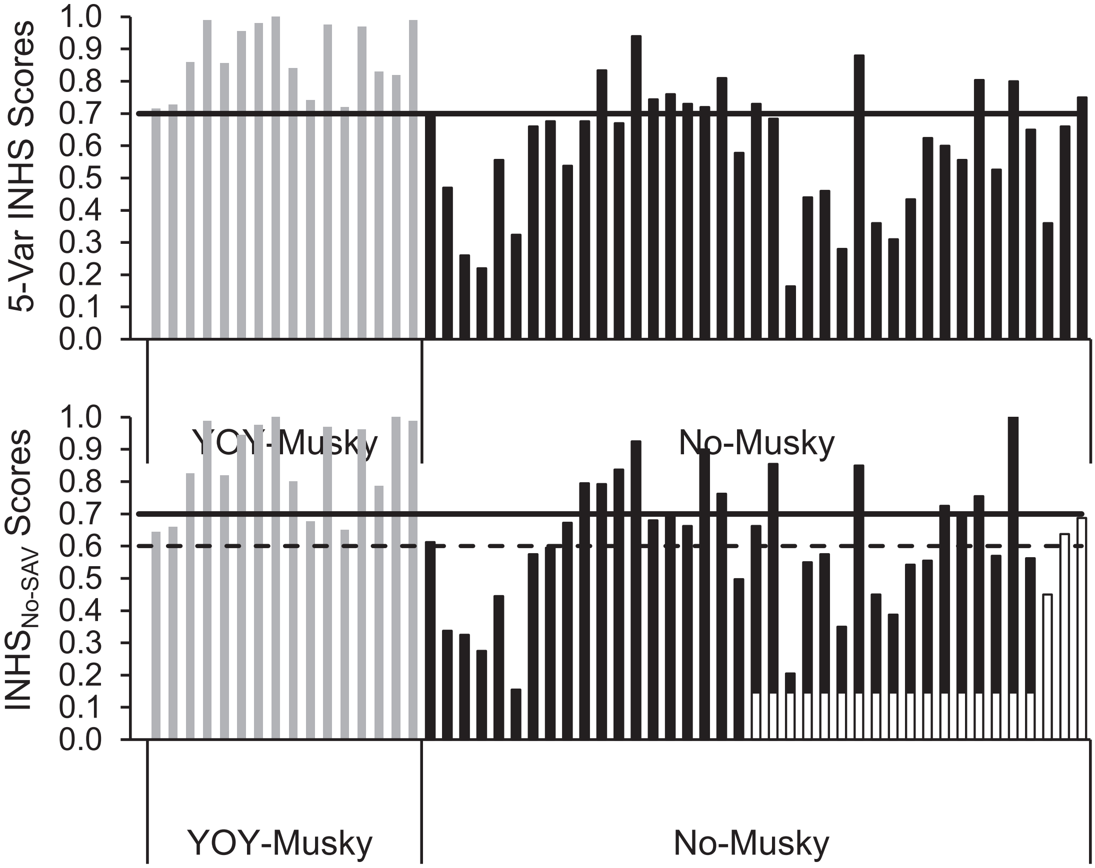

Figure 5.—Index of nursery habitat suitability (INHS) scores for the young-of-the-year Muskellunge (YOY-Musky) sites (solid gray bars; n = 16) and no-Muskellunge (No-Musky) sites (black and white bars; n = 39) from northern Georgian Bay determined with the (top) five-variable model and (bottom) $INHS_{No-SAV}$ model. Overlaying the figures are the INHS thresholds (solid black line = INHS ≥0.7 and dashed black line = INHS ≥0.6) used to identify suitable nursery habitat for both INHS models. Sites with INHS scores touching or above the respective horizontal lines were deemed suitable habitat for young-of-the-year Muskellunge. To minimize the false-negative rate for the $INHS_{No-SAV,}$ the threshold had to be lowered from 0.7 (solid line) to 0.6 (dashed line), but this elevated the false-positive rate.

in differentiating between age-0 Muskellunge sites and no-Muskellunge sites within northern and southeastern Georgian Bay (Tukey's honest significant difference [HSD], p < 0.001), but we also found a significant interaction between site type and region ($F_{1, 82}$ = 2.946, p = 0.029; Figure 7). In both regions, the mean $INHS_{YP-CYP-Slope}$ scores for age-0 Muskellunge sites were similarly high (INHS > 0.7: Tukey's HSD, p > 0.5), whereas the mean for no-Muskellunge sites was significantly higher for the northern sites than for southeastern Georgian Bay (Tukey's HSD, p < 0.001; Figure 7).

To further assess the transferability of the $INHS_{YP-CYP-Slope}$ model, we applied it to the two sites in eastern Georgian Bay that had supported age-0 Muskellunge and to

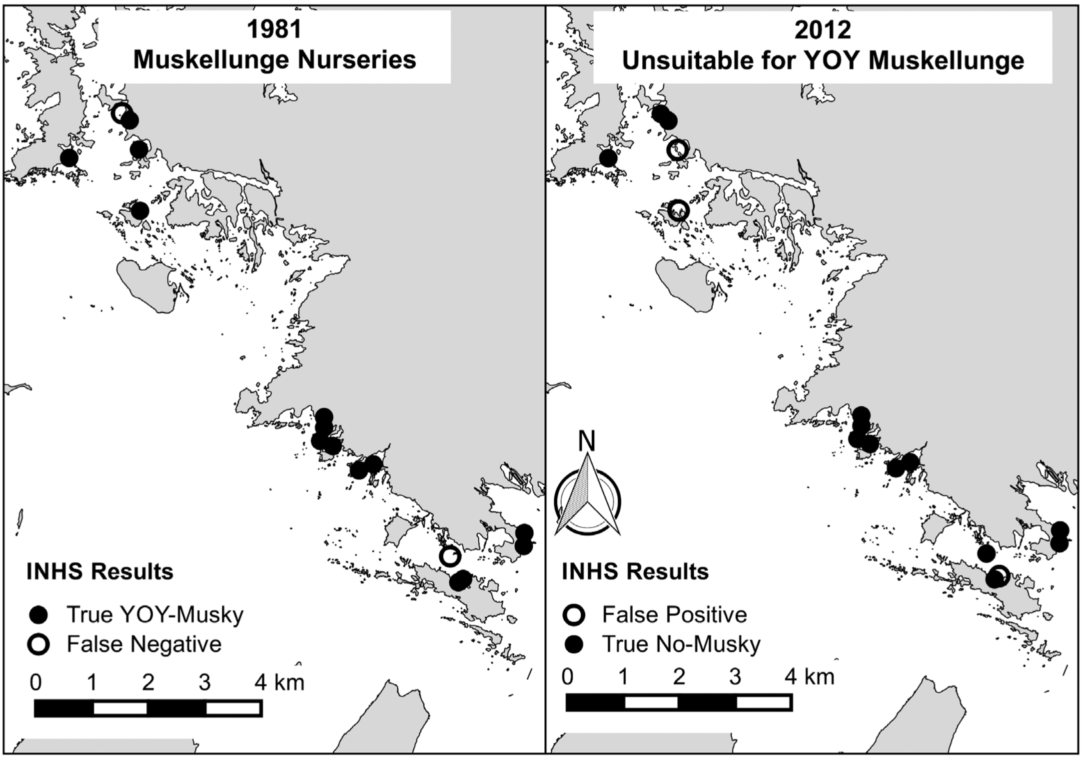

Figure 6.—Application of $INHS_{YP\text{-}CYP\text{-}Slope}$ to data associated with historic nursery habitat identified in 1981 (Craig and Black 1986) and to sites that were no longer deemed suitable and did not support young-of-the-year Muskellunge (Leblanc et al. 2014). False negative has an index of nursery habitat (INHS) suitability score of less than 0.60, whereas false positive has an INHS score ≥0.60.

22 other wetlands sampled in an identical fashion where age-0 Muskellunge had not been caught. The $INHS_{YP\text{-}CYP\text{-}Slope}$ correctly classified the two age-0 Muskellunge sites as being suitable ($INHS_{YP\text{-}CYP\text{-}Slope} > 0.65$), and the 16 of the other 22 wetlands in eastern Georgian Bay wetlands as being unsuitable ($INHS_{YP\text{-}CYP\text{-}Slope} < 0.60$).

Compared to all other INHS models that excluded SAV variables, we found the $INHS_{YP\text{-}CYP\text{-}Slope}$ to be the most accurate for classifying age-0 nursery habitat (14 of the 16 correctly classified). It was able to detect changes in habitat suitability for sites in southeastern Georgian Bay, even though it had been derived with data from northern Georgian Bay; however, because of the greater variability in INHS scores, we had to use a lower suitability threshold (0.6) than that used for the five-variable INHS (0.7). Nevertheless, this three-variable INHS failed to classify two age-0 Muskellunge sites as being suitable in both northern and southeastern Georgian Bay (Table 2; Figure 6).

Discussion

Of the models we tested, the five-variable model performed best, even when compared with models that included all seven variables. This five-variable INHS included three variables related to fish (proportional

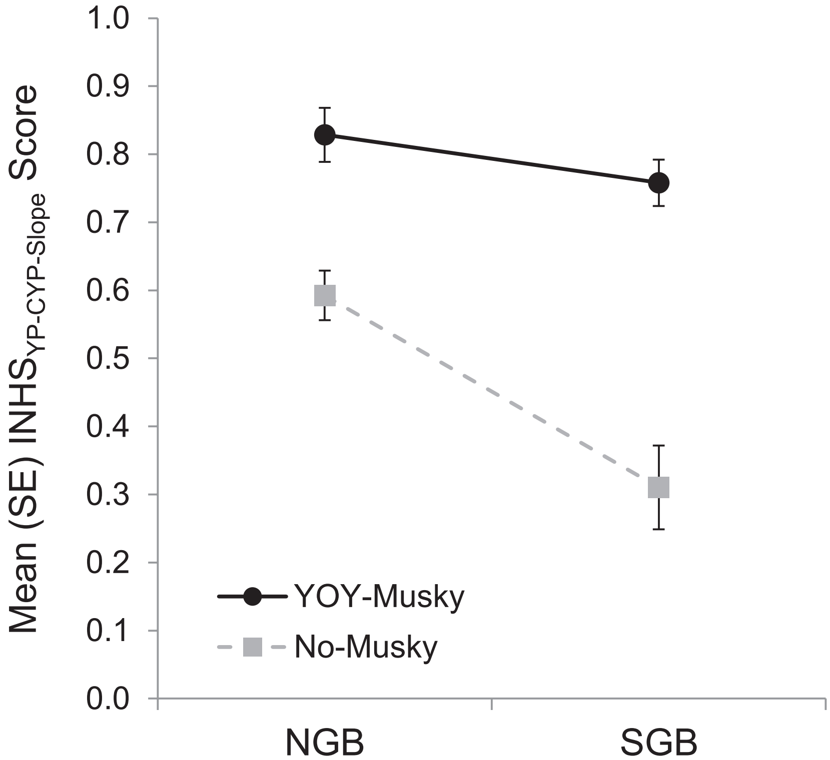

Figure 7.—Mean (±SE) INHS$_{YP\text{-}CYP\text{-}Slope}$ scores associated with young-of-the-year Muskellunge (YOY-Musky) and no-Muskellunge (No-Musky) sites from respective northern Georgian Bay (NGB) and southeastern Georgia Bay (SGB). A two-way analysis of variance indicated a significant interaction ($F_{1,82}$ = 2.946, p = 0.029). YOY-Musky sites did not differ between regions (Tukey's honest significant difference [HSD], p > 0.5), but both were significantly higher than the No-Musky sites, regardless of region (Tukey's HSD, P < 0.05). Southeastern Georgian Bay No-Musky sites had significantly lower INHS$_{YP\text{-}CYP\text{-}Slope}$ than did the No-Musky sites in northern Georgian Bay (Tukey's HSD, p < 0.05).

abundance of Yellow Perch, species richness of fish, and proportional abundance of cyprinid species), one related to site geomorphology (substrate slope) and one related to the macrophyte community (Sub SAV: Can SAV ratio). Information to populate the first four variables would have to be collected by fishery biologists in the field or, for substrate slope, from existing digital elevation models. The last variable, however, may require additional expertise and effort to collect, but since it can be substituted with biovolume, fisheries biologists can estimate this using hydroacoustic technology (Weaver et al. 1997; Valley et al. 2005) without having to count stems of plant taxa. Another reason why we recommend this five-variable INHS model is because it had very good discriminatory power (i.e., AUC value) when applied to the northern Georgian Bay data, being able to correctly classify all 16 of the age-0 Muskellunge sites. When we applied this model to the 2012 data from southeastern Georgian Bay, all of the no-Muskellunge sites were also correctly classified as being unsuitable (Leblanc et al. 2014).

The variables included in the five-variable INHS and $INHS_{YP\text{-}CYP\text{-}Slope}$ are based on ecological relationships previously identified as important when describing suitable nursery habitat for Muskellunge (Wahl 1999; Murry and Farrell 2007; Kapuscinski et al. 2012; Kapuscinski and Farrell 2014) but refined for Georgian Bay (Leblanc et al. 2014; Leblanc 2015). The components of the fish community we used likely reflect direct and indirect effects towards the classification of suitable nursery habitat. For instance, cyprinid species are a preferred forage of age-0 Muskellunge (Wahl and Stein 1988; Kapuscinski et al. 2012), and higher abundances of cyprinid species are expected to increase the growth and survival of juvenile Muskellunge (Szendrey and Wahl 1996). Yellow Perch, in contrast, are hypothesized to be a predator of Muskellunge eggs and larvae (Leblanc 2015) and would explain the antagonistic relationship between age-0 Muskellunge and Yellow Perch observed in Georgian Bay (Leblanc et al. 2014; Leblanc 2015) and the upper St. Lawrence River (Murry and Farrell 2007). Thus, both of these components of the fish community appear to influence early-life survival of Muskellunge (Murry and Farrell 2007; Leblanc et al. 2014) and helped drive the classification of suitable nursery habitat. Indirectly, high species richness of fish may help reduce predation on age-0 Muskellunge by providing alternative prey options for would-be predators (Wahl 1999) but could also be a surrogate measure of increased habitat complexity (Randall et al. 1996; Cvetkovic et al. 2010). Although habitat complexity undoubtedly benefits the early-life survival of Muskellunge (Murry and Farrell 2007; Kapuscinski and Farrell 2014; Leblanc et al. 2014), a direct metric of habitat complexity of the macrophyte community appears to be a more a sensitive measure for habitat suitability.

All things considered, the five-variable INHS is the one that we recommend to fisheries biologists to index suitability of habitat for age-0 Muskellunge. If, however, SAV information is unavailable, then we recommend the three-variable $INHS_{YP\text{-}CYP\text{-}Slope}$ because this was able to identify suitable nursery habitat with a respectable false-negative rate of less than 13% and correctly identified sites in southeastern Georgian Bay as being unsuitable when we were no longer able to find age-0 Muskellunge in any of the historic nursery sites in 2012. The $INHS_{YP\text{-}CYP\text{-}Slope}$ also correctly classified the two age-0 Muskellunge sites from eastern Georgian Bay as suitable. Although six of the sites from eastern Georgian Bay that did not catch age-0 Muskellunge were classified as suitable, the false-positive rate was similar to when the $INHS_{YP\text{-}CYP\text{-}Slope}$ was applied to data from southeastern Georgian Bay. While both models can correctly identify age-0 Muskellunge sites, addition of SAV-related variables decreased the false-positive rate by 23% (31% versus 54% for the five-variable INHS and the $INHS_{YP\text{-}CYP\text{-}Slope}$ model, respectively) in northern Georgian Bay, and this increased level of sensitivity is likely more acceptable in jurisdictions where development pressures are high.

Cook and Solomon (1987) developed an HSI that considered all life stages of the Muskellunge. This model was developed for both small inland lakes as well as larger coastal systems up to 1, 000 ha (Cook and Solomon 1987). It has not yet been applied to a system as large as Georgian Bay, with a surface area of ~15 000 km^2. We compared the usefulness of this HSI model against our two INHS models. According to Cook and Solomon (1987), habitat for adult life stages are rarely limiting in large systems, and therefore, we focused on their four proposed

SI variables for early life stages. The four SI variables were (1) a decline in water levels between April and June, (2) adequate dissolved oxygen concentration (DO) at the substrate–water interface, (3) abundance of coastal wetlands, and (4) adequate percentage cover of macrophytes. These four SI variables were difficult to apply to Georgian Bay. For example, the first SI variable could not be a limiting factor because water levels in Georgian Bay usually increase between April and early June, rather than decline, and are therefore suitable for promoting egg and larval survival (Cook and Solomon 1987). Dissolved oxygen at the substrate–water interface in wetlands of eastern and northern Georgian Bay are unlikely to be limiting because wetlands are at saturated oxygen concentrations (Cvetkovic and Chow-Fraser 2011), levels that should not interfere with the development of Muskellunge eggs (Dombeck et al. 1984; Cook and Solomon 1987; Zorn et al. 1998). Both of the last two SI variables are too coarse to be applied to Georgian Bay because virtually the entire eastern and northern shoreline of Georgian Bay are lined with abundant small wetlands (<2 ha; Midwood et al. 2012) that have high percent cover of macrophytes (Croft and Chow-Fraser 2007; 2009). Therefore, although some metric of the plant community is, no doubt, an important component of habitat for age-0 Muskellunge (Murry and Farrell 2007; Kapuscinski and Farrell 2014; Leblanc et al. 2014), prior to our INHS models there was no standardized way to quantify this for suitability assessment in Georgian Bay.

Since introduction of the HSI proposed by Cook and Solomon (1987), advances have been made to identify whole-lake (e.g., Rust et al. 2002) and within-lake features (e.g., Nohner and Diana 2015) that can predict the self-sustaining status of Muskellunge populations. Most efforts have focused on predicting the spawning locations selected by Muskellunge. For instance, Nohner and Diana (2015) developed a geographic information system-based model to predict spawning sites selected by Muskellunge within relatively small (50 ha) and large (1,500 ha) inland lakes of Wisconsin from remotely sensed information. Additionally, Crane et al. (2014) developed a model of the microhabitat features related to the spawning locations selected by Muskellunge in the Niagara River. Although specific features from the microhabitat of the spawning sites appeared to differ greatly between lacustrine and riverine systems, and among the trophic status of inland lakes (e.g., Crane et al. 2014; Nohner and Diana 2015), the suitability of spawning habitat is consistently interpreted to provide appropriate DO levels (Dombeck et al. 1984; Zorn et al. 1998; Rust et al. 2002; Crane et al. 2014; Nohner and Diana 2015), which, as mentioned earlier, does not appear limiting in Georgian Bay.

There is no doubt that DO is important for Muskellunge recruitment, and identifying locations used by Muskellunge for spawning is a necessary management strategy. The bottleneck, however, is likely the suitability for egg development and age-0 Muskellunge survival within wetland units used for spawning. This is consistent with observations of other investigators who have suggested that spawning and nursery habitats are spatially linked (LaPan et al. 1996; Farrell et al. 2007) and who found nursery sites occurring in close proximity (<30 m to 1 km) to their presumed spawning beds (Weller et al. 2016). Furthermore, adult Muskellunge have shown high fidelity to particular spawning areas within a large region (Jennings et al. 2011), including in Georgian Bay, where Muskellunge appear to have used a very specific spawning area within Severn Sound over a period of three decades (Weller et al. 2016), and continue to use wetlands that have nursery habitats with poor suitability (Leblanc et al. 2014). It remains unclear, however, if models developed to predict spawning-site selection can account for the requirements of spatially linked nursery habitats and site-fidelity behavior of Muskellunge in Georgian Bay. Thus, managers can more appropriately assess the self-sustaining capacity of Muskellunge in Georgian Bay by using the INHS models to inspect the suitability of nursery sites near Muskellunge spawning sites.

Because of the difficulties to catch age-0 Muskellunge and the presence–absence nature of the data, certain assumptions were used when developing the SI curves, the thresholds to classify habitat as suitable, and potential causal relationships between the variables and habitat suitability for age-0 Muskellunge. As a result, the SI curves required some subjectivity to develop and are considered hypotheses requiring further testing. The relationship between the variables and habitat suitability proposed by the SI curves, however, appear to agree with the framework and ecological relationships proposed by others that govern suitable nursery habitat for Muskellunge (e.g., Wahl 1999; Murry and Farrell 2007; Kapuscinski et al. 2012; Kapuscinski and Farrell 2014). Thus, we feel that the hypothesized SI curves likely capture underlying ecological relationships that define suitable habitat but could be refined when additional information is available.

The thresholds used to classify habitat as suitable were bias towards minimizing the false-negative rate. This would consequently increase the false-positive rate, but given the conservation concern for protecting early-life habitat of Muskellunge (Craig and Black 1986; Farrell et al. 2007), we felt that higher priority should be placed on identifying wetland units suitable for age-0 Muskellunge. Thus, by only using the age-0 Muskellunge sites when developing the SI curves, and biasing the threshold to minimize the false-negative rate, we assumed that the INHS models may classify some habitats not used by Muskellunge as suitable but would be less likely to classify suitable habitat as unsuitable.

Management Implications

The recent and unprecedented period of sustained low water levels in Lakes Huron and Michigan (Sellinger et al. 2008) is one of the main threats to the quality (i.e., less diverse macrophyte and fish communities; Midwood and Chow-Fraser 2012) and quantity (i.e., lost access to wetlands by fish; Fracz and Chow-Fraser 2013) of wetland habitat in eastern Georgian Bay. The low water levels are also likely impacting the suitability of other coastal wetlands used by Muskellunge for early-life habitats because the aquatic plant community depends in large part on water-level fluctuations (Keddy and Reznicek 1986; Wilcox and Meeker 1991; Midwood and Chow-Fraser 2012). With expected changes in water-level regimes within the Great Lakes over the next 50 years due to global climate change (Angel and Kunkel 2010), Great Lakes fishery managers everywhere, particularly those in Georgian Bay, are in urgent need of tools that can help them screen for suitable habitat for age-0 Muskellunge and assess how the suitability of the habitat would change in response to different water-level scenarios.

The INHS models proposed here provide a means to predict potential changes in the suitability of nursery habitat over time. By accounting for the response of macrophytes to water levels and the nearshore bathymetry, managers will have an indication of the potential suitability of nurseries near identified spawning sites under multiple water-level scenarios. Thus, managers can apply the INHS at locations with suspected declines in nursery suitability to determine if age-0 Muskellunge are present, the suitability status of the wetland, and potential efforts that can be carried out to rehabilitate the habitat. The labor-intensive requirement to calculate INHS scores and the vast distribution of small coastal wetlands in Georgian Bay (Midwood et al. 2012) likely makes it impractical to index the suitability of nursery habitat throughout the bay. It may therefore be more appropriate to establish sentinel sites at known early-life habitats used by Muskellunge to be monitored on a regular basis. By stratifying sentinel sites to reflect the gradient of nearshore bathymetries within Georgian Bay, the recruitment potential of the various subpopulations of Muskellunge in Georgian Bay can be assessed under different water level scenarios. Furthermore, the INHS models have the potential to promote restoration efforts by identifying and indexing wetlands with a higher likelihood of promoting early-life survival if stocking initiatives are deemed necessary.

To conserve critical habitat for a long-lived species, such as Muskellunge, managers will need to use broad-scale approaches (e.g., SDMs; Guisan and Thuiller 2005) in addition to site-specific assessment tools such as the INHS proposed here. Species distribution models typically require remotely sensed data that may or may not be easily accessible and include variables that indirectly reflect ecological relationships assumed to govern a species' distribution (Guisan and Zimmermann 2000). As a result, SDM models can be practical by providing an inventory of potentially suitable habitat (e.g., Nohner and Diana 2015), but may lack the precision and resolution needed to identify underlying ecological relationships operating at the site level that accommodate requirements most limiting to a species (Randin et al. 2006). For Georgian Bay, a useful Muskellunge SDM might include geomorphological variables that predict the type of macrophyte community in wetlands, as well as landscape features that might influence access of Muskellunge to spawning and nursery sites. In the absence of such an SDM, the INHS (though requiring field-derived data) should be a useful tool to guide rehabilitative actions in presumed degraded nursery sites (e.g., those in southeastern Georgian Bay; Leblanc et al. 2014) and become the foundation for development of a regional SDM model for Georgian Bay.

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Appendix A

The following are frequency distributions and derived suitability index curves for all variables used in developing the index of nursery habitat suitability (INHS) for Muskellunge. Suitability index (SI) curves were derived solely from the patterns observed with age-0 Muskellunge and ecological justification for the curves is provided. All estimates of the fish community were collected with the seining protocol described by Leblanc et al. (2014) in July of 2012 and 2013. All habitat variables were estimated from depths in the wetland between 0.5 and 1.0 m (Leblanc 2015) in August of the respective years, and habitat data were collected with the protocol described by Leblanc et al. (2014). Suitability index curves should be considered hypotheses that require further testing and refinement but are intended to reflect a continuum in suitability index scores. When data were insufficient, SI curves were bent or broken to reflect uncertainty in the relationships. Only those SI variables that contributed to the final INHS models are presented.

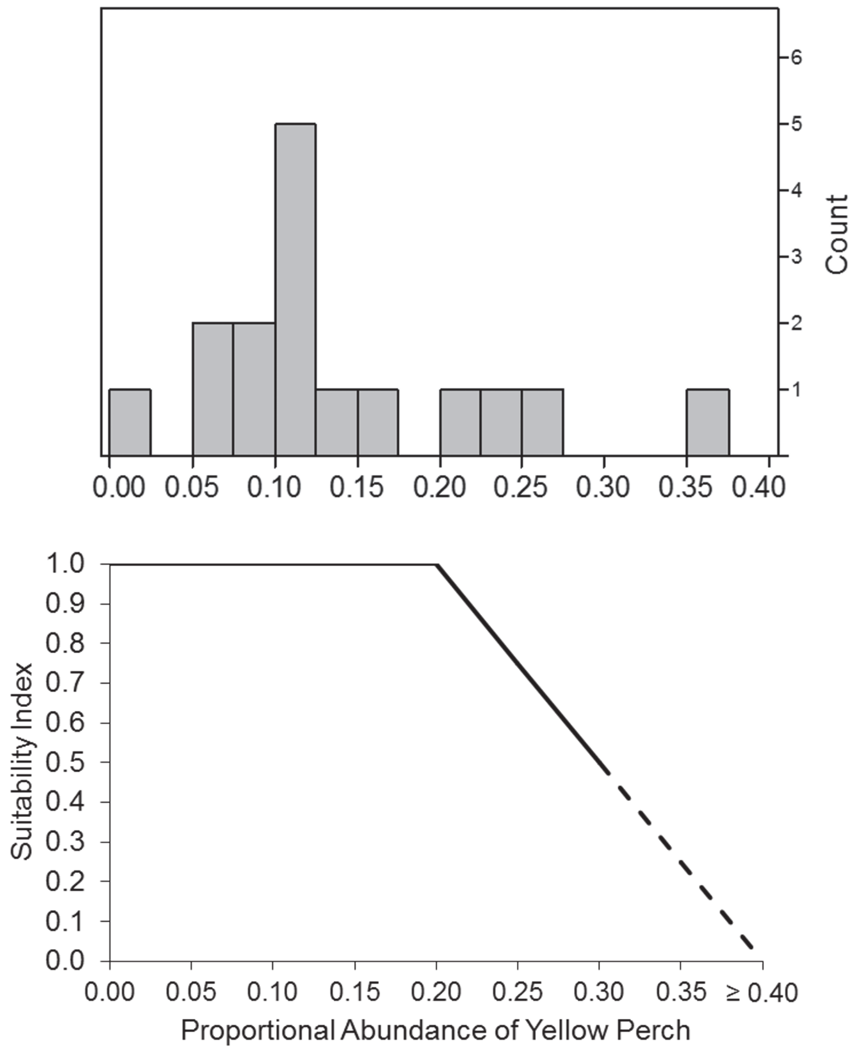

Figure A.1.—Frequency distribution and derived suitability index curve for the proportional abundance of Yellow Perch. Yellow Perch were identified as a source of Muskellunge early-life mortality (Leblanc 2015) and were never found in excess of 40% of the fish community with age-0 Muskellunge in northern Georgian Bay. Yellow Perch abundance has also been negatively related to the presence and abundance of age-0 Muskellunge from the lower Great Lakes (Murry and Farrell 2007; Kapuscinski and Farrell 2014).

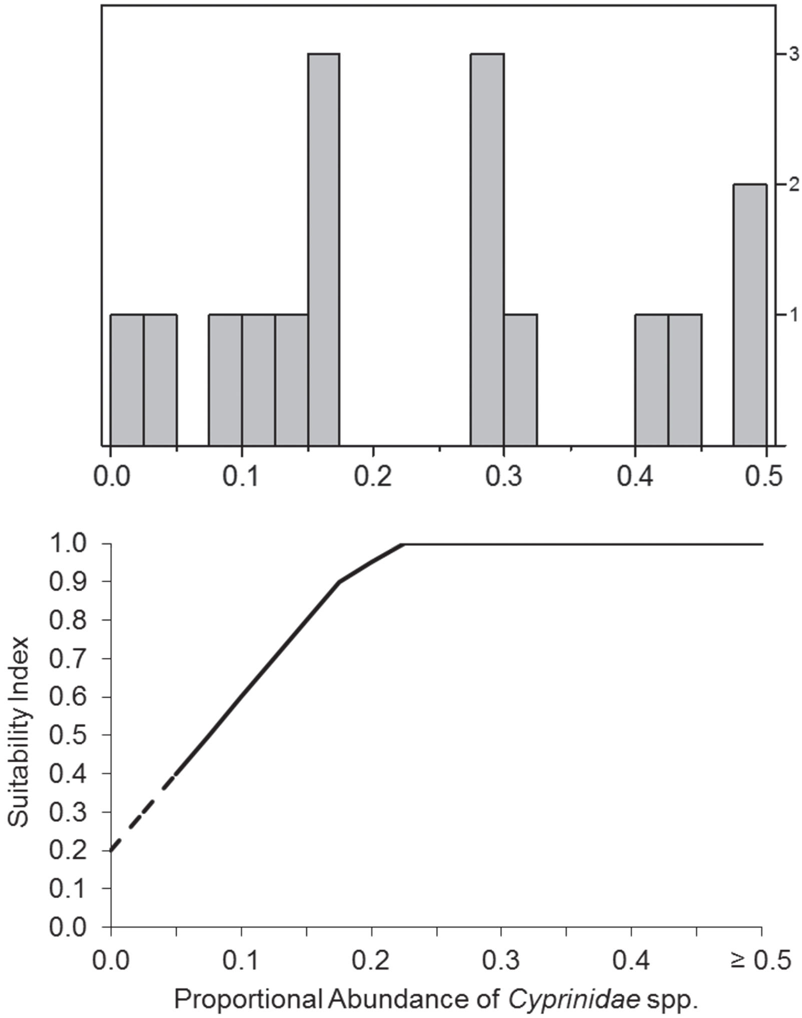

Figure A.2.—Frequency distribution and derived suitability index curve for the proportional abundance of cyprinid species. Cyprinids were considered preferred forage for age-0 Muskellunge (i.e., soft-rayed and fusiform species; Kapuscinski et al. 2012), and when at suitable abundances, that should translate into better growth and survival for the age-0 Muskellunge (Szendrey and Wahl 1996).

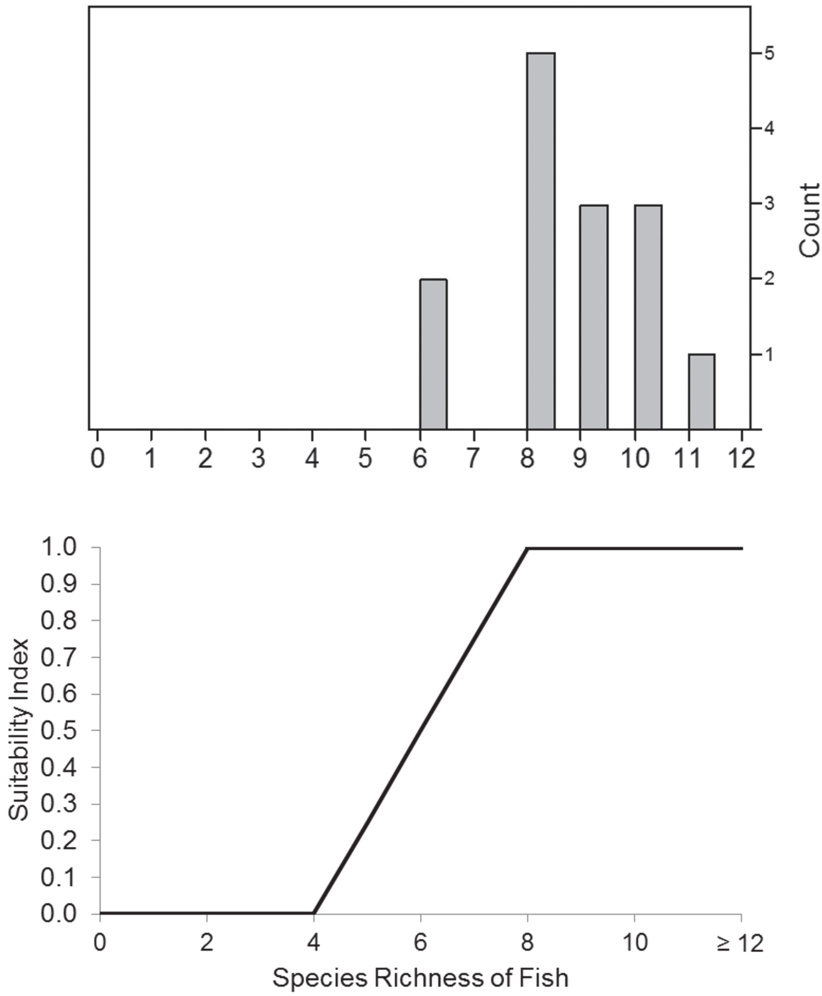

Figure A.3.—Frequency distribution and derived suitability index curve for the species richness of the fish community. Age-0 Muskellunge were found in wetlands with overall higher fish species richness than at sites where they were not found. High diversity in the fish community is also hypothesized to promote age-0 Muskellunge survival by providing alternative prey to predators of age-0 Muskellunge (Wahl 1999). Furthermore, high diversity in the fish community of a wetland is often related to greater habitat complexity that favours age-0 Muskellunge survival.

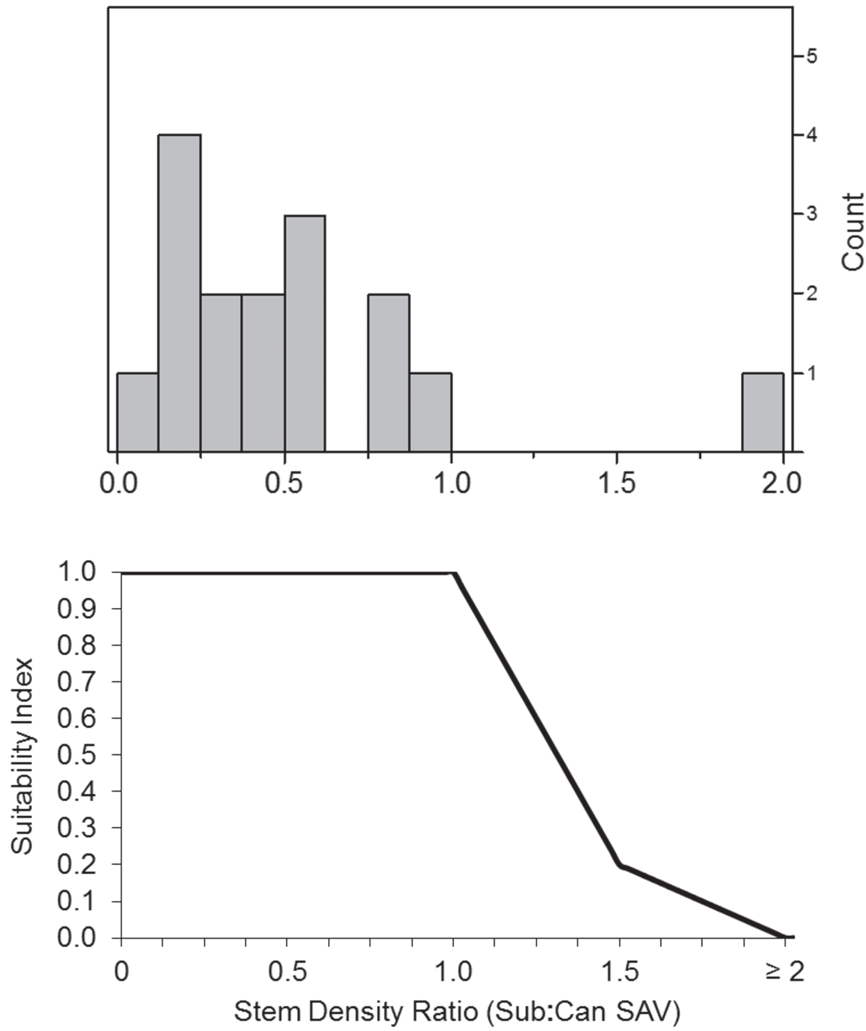

Figure A.4.—Frequency distribution and derived suitability index curve for the stem density ratio of substrate-covering (Sub) submersed aquatic vegetation (SAV) to canopy-forming (Can) SAV. Ratios less than 1 indicate a higher stem density count of Can SAV and limited contribution of Sub SAV. This variable was considered a metric of the combined contribution of different SAV growth forms in the water column. Age-0 Muskellunge have been negatively associated with high densities of Sub SAV while positively related with intermediate densities of Can SAV (Murry and Farrell 2007). Only one age-0 Muskellunge occurred in habitat where this ratio exceeded 1.

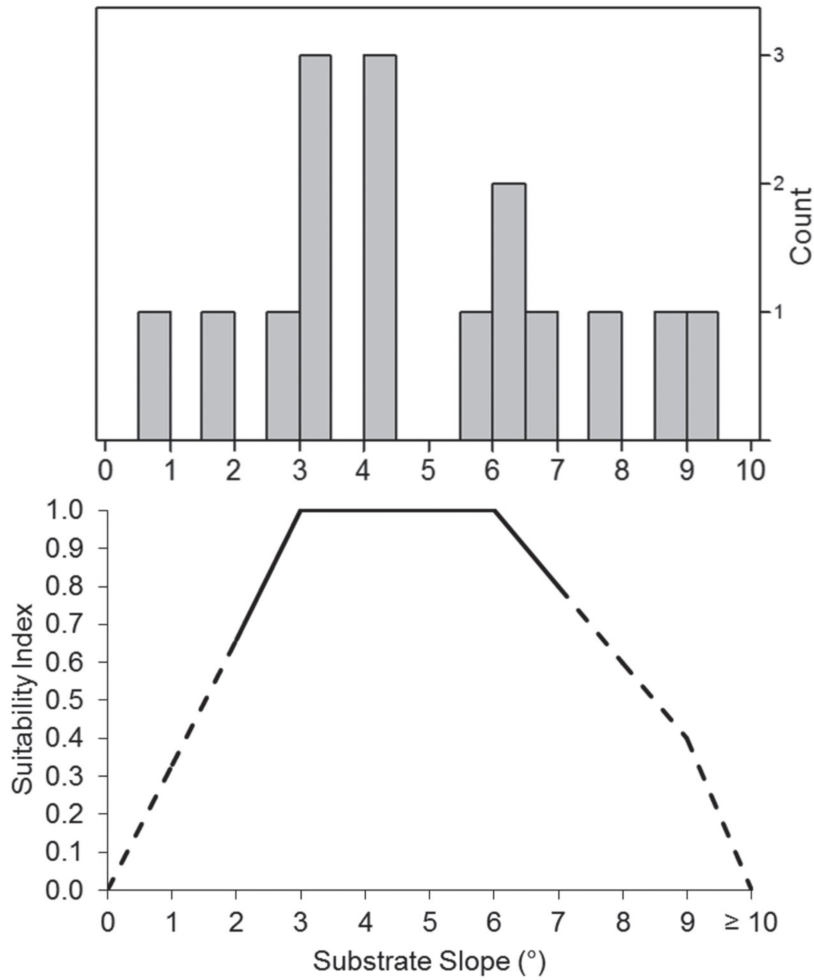

Figure A.5.—Frequency distribution and derived suitability index curve of the wetland's substrate slope, estimated between 0.5 and 1.0 m depth. The shallower substrate slopes that were exposed by the decade of low water levels appeared to be a primary cause for the change in nursery suitability for age-0 Muskellunge in southeastern Georgian Bay (Leblanc et al. 2014). Thus, substrate slope appears to be an important variable to infer how the suitability of a wetland changes in response to different water level scenarios in Georgian Bay for age-0 Muskellunge. Substrate slope explained some of the variation of the macrophyte community observed in the wetlands, where steeper substrate slopes promoted a more diverse community of canopy-forming submersed aquatic vegetation (SAV) and precluded the establishment of substrate-covering SAV (Leblanc 2015). Although age-0 Muskellunge were observed over a range of substrate slopes, most age-0 Muskellunge were found in wetlands with intermediate slopes (3° to 7°). Steeper slopes may also provide an additionally structural feature in the wetland and thus add to the structural complexity of the habitat.

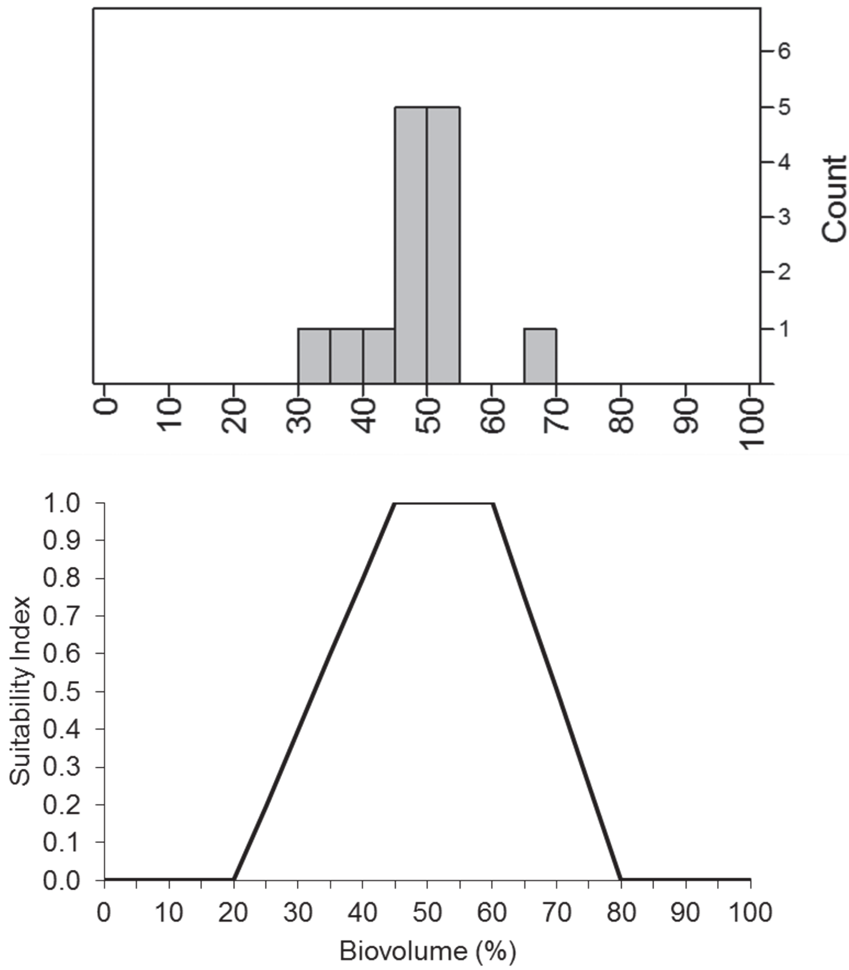

Figure A.6.—Frequency distribution and derived suitability index curve for submersed aquatic vegetation (SAV) biovolume. Biovolume is a measure of the percent contribution of SAV making up the water column and can be acquired with hydroacoustic techniques. It was measured as the mean height of the SAV divided by the depth of the water where the SAV was found (Valley et al. 2005). Thus, biovolume can be considered a surrogate metric of habitat complexity of the macrophyte community and would not require physical stem counts. Although our estimates of biovolume were made without hydroacoustic equipment, field-derived estimates are highly correlated with those acquired by remote sensing (Valley et al. 2005). Our estimates of biovolume appeared consistent with previous observations that suitable nursery habitat has intermediate densities of SAV in the upper water column (Craig and Black 1986; Murry and Farrell 2007). Additionally, biovolume has the potential to reflect multiple scales of habitat complexity of the SAV community composition (e.g., patchiness; Weaver et al. 1997), which may be more important when identifying nursery suitability for age-0 Muskellunge (Leblanc 2015).