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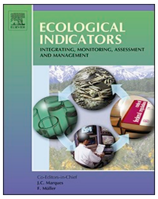

Development of a multi-scale wetland Resilience Index from muskellunge nursery habitat in Georgian Bay, Lake Huron

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ABSTRACT

In a 2012 study, no age-0 muskellunge (*Esox masquinongy*) were found in any of 16 historic nursery sites in coastal marshes of southeastern Georgian Bay (SEGB), and this was attributed to sustained low water levels (1999–2013) that had altered the vegetation structure of nursery habitat. In the same study, age-0 muskellunge were found in 16 coastal marshes surveyed in northern Georgian Bay (NGB), even though these sites had been subjected to the same water-level conditions. We hypothesize that hydrogeomorphic features of NGB sites made them resilient to effects of sustained low lake levels that made the SEGB sites unsuitable for age-0 muskellunge. Compared to their SEGB counterparts, the NGB nursery sites were significantly steeper, deeper, and less sheltered under low water levels. We used these hydrogeomorphic features to develop a multi-scale Resilience Index (RI) for identifying coastal wetlands that are resilient to stable low lake levels. The RI correctly classified the NGB and SEGB nursery sites, with an area-under-the-curve score of 0.973. Coarser-scale variants of the RI provide a regional screening tool in the identification of resilient wetland habitat (e.g. potential muskellunge nursery habitat), and a basin-wide approach to identify vulnerable wetland habitats. This multi-scale index, in conjunction with targeted field surveys, should provide managers a useful tool in the face of uncertain water level forecasts.

1. Introduction

Georgian Bay, Lake Huron supports a world-class, recreational muskellunge (*Esox masquinongy*) fishery. The eastern and northern shorelines in particular are characterized by thousands of islands and small embayments that support a diverse collection of habitat types, including many high-quality coastal wetlands (Cvetkovic and Chow-Fraser, 2011; Midwood et al., 2012). Coastal wetlands provide critical spawning and nursery habitat for many Great Lakes fish species (Jude and Pappas, 1992; Wei et al., 2004), including muskellunge, and those in Georgian Bay have remained largely unaffected by the types of anthropogenic disturbances that have been associated with loss or degradation of muskellunge habitat in other regions (e.g. Dombeck, 1986; Farrell et al., 2007; Rust et al., 2002). However, in 2012 age-0 muskellunge could no longer be found in nursery sites of southeastern Georgian Bay (SEGB) that had been identified from field surveys 30 years earlier (Leblanc et al., 2014). Evidence from radio-telemetry (Weller et al., 2016) and genetic studies (Wilson et al., 2016) indicate that the muskellunge of Georgian Bay exhibit spawning-site fidelity. Since spawning grounds were still active in SEGB (Weller et al., 2016), age-0 muskellunge should have been found at the historic nursery sites unless the habitat had ceased to be suitable.

Leblanc et al. (2014) hypothesized that changes in the wetland fish and vegetation communities resulting from the preceding decade of sustained low water levels in Lake Michigan-Huron had reduced suitability of nursery habitat at these sites for age-0 muskellunge. Mean annual lakes levels have typically fluctuated by over 1.0 m but from 1999 to 2013 remained below the long-term average with a range of less than 0.4 m. The low water levels, however, did not seem to affect nursery habitat suitability of coastal wetlands in northern Georgian Bay (NGB) since age-0 muskellunge had been found there in 2012 and 2013 (Leblanc, 2015). Given the differential responses of nursery sites in SEGB and NGB to the same lake levels, another variable must interact with water level to influence habitat suitability for age-0 muskellunge.

The "typical" muskellunge nursery habitat in southeastern Georgian Bay has been described by Craig and Black (1986) as wetlands with high stem densities of emergent vegetation at the shoreline, becoming less dense out to 1 m deep ($< 100\,\text{stems/m}^2$), and having 40–50%

Abbreviations: SEGB, southeastern Georgian Bay; NGB, northern Georgian Bay; NEGB, northeastern Georgian Bay; RI, Resilience Index; VIn, Vulnerability Index; REI, Relative Exposure Index; SAV, submersed aquatic vegetation

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cover of submersed aquatic vegetation (SAV) in more open water. Leblanc (2015) found that an important habitat features in nursery sites in NGB was a greater ratio of SAV stems within the upper water column relative to low-growing forms, such that almost 30–70% of the water column (i.e. biovolume) was occupied by SAV (Leblanc and Chow-Fraser, 2017). Such descriptions of moderate densities of wetland vegetation providing complex, three-dimensional structure within the nursery habitat are broadly consistent across other study areas in the Great Lakes basin (Murry and Farrell, 2007; Kapuscinski and Farrell, 2014; Werner et al., 1996). The habitat requirements for age-0 muskellunge appear to be highly prescribed and muskellunge are sensitive to habitat alterations (Dombeck, 1986; Farrell et al., 2007).

For age-0 muskellunge, suitable nursery habitat is a tradeoff between foraging efficiency and protection from predators (Crowder and Cooper, 1982; Diehl and Eklöv, 1995; Gotceitas and Colgan, 1989), factors that are critical for age-0 muskellunge, but that are also important for diverse fish communities (Eadie and Keast, 1984; Tonn and Magnuson, 1982). As such, suitable habitat for age-0 muskellunge is likely to be high-quality wetland that is suitable for a wide spectrum of other fish species. An essential condition for maintaining structural diversity of the wetland plant community in such wetlands is interannual fluctuation of Lake Huron water levels. Although ecologists agree that dampening or stabilization of these fluctuations could reduce or eliminate suitable habitat for wetland fish (Gathman et al., 2005; Midwood and Chow-Fraser, 2012; Wilcox, 2004; Wilcox and Meeker, 1991), sites can and do vary in response to these fluctuations depending on their geomorphology (Wei and Chow-Fraser, 2008).

Interactions between lake level and site geomorphology determine the hydrogeomorphic characteristics of a wetland. Since coastal wetlands can shift lakeward or landward with changing lake levels their hydrogeomorphic characteristics, like slope, can also vary with lake levels. Slope can influence the amounts and types of aquatic vegetation found in littoral areas (Duarte and Kalff, 1986; Duarte et al., 1986). Leblanc et al. (2014) reported that slopes at SEGB sites had been steeper under high water levels, and appeared to be more similar to those in NGB (Leblanc, 2015). In fact, slope emerged as the main predictor of habitat suitability for all sites studied in Georgian Bay (Leblanc and Chow-Fraser, 2017). Wind and wave exposure, which is subject to similar hydrogeomorphic drivers, also have documented effects on wetland vegetation (Duarte and Kalff, 1990; Jupp and Spence, 1977; Keddy 1982, 1984a, 1984b).

We hypothesize that differences in resilience (i.e. the persistence of suitable age-0 muskellunge habitat) of NGB and SEGB sites to sustained low water levels is primarily due to differences in local hydrogeomorphic features, in particular slope and wave exposure. An alternate hypothesis is that portions of SEGB wetlands had dried up or had become stranded by the low water levels, and were therefore no longer available as fish habitat (Fracz and Chow-Fraser, 2013; Lyon and Drobney, 1984). We will test these hypotheses by statistically comparing slopes, wave exposures, areal extents, and volumes of wetland habitats for both regions under high and low lake levels. We will identify hydrogeomorphic features that affect the resilience of muskellunge nursery habitat to stable low water levels and ultimately develop an index of wetland resilience to screen for age-0 muskellunge habitat. Since wetlands that provide suitable habitat for age-0 muskellunge should also be healthy wetlands suitable for a diverse fish community, we will apply this index more broadly as a management tool to identify regions of Georgian Bay with coastal wetlands vulnerable or resilient to water-level disturbances.

2. Methods

2.1. Multi-scale approach

Ecological processes can be influenced by factors at multiple spatial scales, which must be considered when developing and applying environmental indicators. Furthermore, the intended management applications of our Resilience Index each had unique objectives that span a broad range of spatial scales. As such, we have consciously developed several variants of the index to account for different spatial scales (and applications), rather than take a one-size-fits-all approach. We took this multi-scale approach to ensure that the index would be consistent across all spatial scales with respect to performance, feasibility and ability to provide meaningful information.

Index development and application were designed for three distinct spatial scales: **local**, **regional**, and **basin-wide**. The finest spatial scale we evaluated was at the **local** scale (~1 ha; i.e. a wetland unit); development of the **Resilience Index (RI)** at this scale was based on hydrogeomorphic features of nursery sites where age-0 muskellunge had been confirmed from field surveys. We scaled up the RI for application at the **regional** scale (1,000 – 10,000 ha; i.e. a large embayment), by employing coarser-resolution hydrogeomorphic data (primarily to reduce computational demands) that could be used as a screening tool to guide targeted field surveys. Finally, at the **basin-wide** scale (i.e. eastern and northern shorelines of Georgian Bay), we again scaled up the RI to identify regions in the Georgian Bay coastline where wetlands have been assessed as being vulnerable to stable low lake levels. Our goal was to use basin-wide RI scores to classify shoreline stretches into vulnerability categories that can be used as a scientifically defensible way to select sites for monitoring in the era of unpredictable water-level fluctuations.

2.2. Local scale: habitat characterization

Data for development of the local RI were obtained from published studies in two regions of Georgian Bay, southeastern Georgian Bay (SEGB) and northern Georgian Bay (NGB; Fig. 1), that had been sampled under two different lake-level scenarios. The two lake-level scenarios corresponded to 1981, when water levels had been relatively high (May to October monthly mean 176.8 m) and 2012, when water levels were almost a meter lower (May to October monthly mean 176.0 m). For context, with littoral slopes typical of Georgian Bay wetlands (1–7% rise; Weller and Chow-Fraser, 2019) a 0.8 m change in lake levels could result in a shift in shoreline position of 12–80 m that could have a major effect on wetland habitat. For RI development, we included 16 nursery sites in SEGB that had been identified in 1981 (Craig and Black, 1986) and that had been re-sampled in 2012 (Leblanc et al., 2014); we also included 16 sites in NGB which had been sampled in 2012 and 2013 (Leblanc, 2015). All studies used directly comparable seine-netting protocols to capture age-0 muskellunge (Leblanc et al., 2014). Note that the NGB sites had been sampled across two years (2012 and 2013) with similarly low mean water levels (approximately 8 cm difference).

We used a standardized protocol to delineate the boundary of a nursery site by applying a 100 m buffer around a capture location of an age-0 muskellunge (i.e. location of the seine haul), and excluding areas deeper than 2 m. We excluded areas below the 2 m contour because we assumed that age-0 muskellunge were using coastal wetlands as nursery habitat and the 2 m depth contour is the generally accepted lakeward boundary (Albert et al., 2005; Keough et al., 1999). If the capture site were located along a straight section of shoreline, then the nursery site would be delineated by a semi-circle with a 100 m radius, and exclude any area beyond the 2 m depth contour. We also assumed that age-0 muskellunge would use wetland vegetation for protection and stay within it, rather than move between spatially distinct wetland patches. Therefore, only contiguous areas within the 0–2 m depth zone surrounding the capture location were considered nursery habitat (Fig. 2; cross-hatching, zone 1). This ruleset was applied to all capture locations to delineate the boundaries for nursery sites under both the high-water and low-water scenarios.

We did not use an existing wetland habitat layer (e.g. the McMaster Coastal Wetland Inventory (MCWI) from Midwood et al., 2012; low-

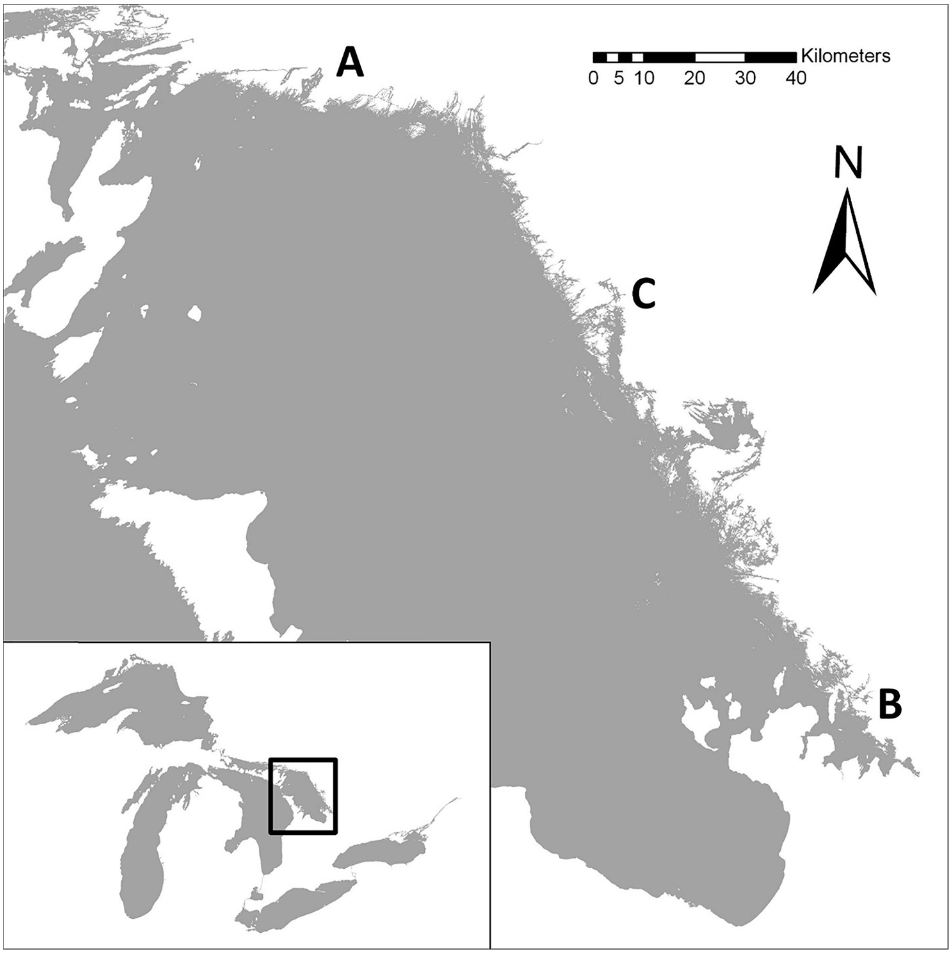

Fig. 1. Georgian Bay, Lake Huron (inset: location relative to Laurentian Great Lakes) with main study regions indicated: northern Georgian Bay (A), southeastern Georgian Bay (B), and northeastern Georgian Bay (C) .

marsh layer from Weller and Chow-Fraser (2019)) to restrict site identification, because several nursery sites used in this study occurred in areas that have not been classified as wetlands in available datasets. The misclassified wetlands were very small and we assume that these omissions in the independent wetland inventories were the result of detection limits or human error during manual delineation of wetlands (Midwood et al., 2012) or the coarse spatial resolution of modelling inputs (Weller and Chow-Fraser, 2019). We have confirmed that all nursery sites in this study occur in coastal wetlands.

All spatial data processing and analyses were completed with ArcGIS Pro v2.1 (ESRI, Redlands, California). We used a digital elevation model (DEM) built for each of the NGB and SEGB regions to derive hydrogeomorphic features at each nursery site. The DEMs were assembled with bathymetric data from the Canadian Hydrographic Service navigational charts and topographic data from the Ontario Contour (OMNR, 2009a) and Spot (OMNR, 2009b) elevation datasets. We used the Topo to Raster tool in ArcGIS Pro (based on the ANUDEM program; Hutchinson, 1989) to build a DEM for each region with a 5 m resolution.

We derived the shoreline and the 2 m depth contour for each region from its respective DEM. To improve calculation accuracy of nursery site area and the wave-exposure metric, we manually updated the shoreline using the most appropriate imagery to correct deviations from the true shoreline and to add small islands that had been missed in the DEM. In NGB, we used imagery from the Central Ontario Orthophotography Project (20 cm resolution; lake level ≈ 176.8 m) for the high-water scenario (176.8 m), and Quickbird imagery (60 cm resolution; lake level ≈ 176.2 m) for the low-water scenario (176.0 m). In SEGB, we used the digital terrain model (2 m resolution) derived from the South Central Ontario Orthophotography Project (SCOOP), which had been collected when the lake level was approximately 175.9 m, which is lower than both the low (176.0 m) and the high (176.8 m) lake-level scenarios. Therefore, the terrain model should accurately capture the shorelines for both scenarios since they would not have been obscured by water in the SCOOP imagery.

We classified our sites into four types: 1) **fringing** (occurring along a relatively straight section of shoreline) 2) **open embayment** (recessed into the shoreline with a large and exposed mouth), 3) **protected embayment** (embayment sheltered from most directions; i.e. accessible only through narrow channel(s) or protected by small islands), or 4) **archipelago** (amongst small shallow islands and lacking a clearly defined and persistent shoreline across lake levels). We measured five habitat features: area, volume, depth (volume/area), slope, and wave exposure at each nursery site corresponding to both lake-level scenarios based on boundaries of the nursery sites and the regional DEMs.

We derived hydrogeomorphic feature layers for water depth and slope from the DEMs and used the mean for all cells within the nursery-site boundary as a representative measure for each site. We calculated a Relative Exposure Index (REI; Fonseca and Bell, 1998; Murphey and Fonseca, 1995) as a metric of wave exposure. The formulation described by Malhotra and Fonseca (2007) was used to account for the effects of bathymetry on wave development. To determine fetch, lines radiating from sample points were extended until they intersected with the shoreline at increments of 11.25°. An inverse distance weighting function was then applied to each ray to account for the effects of

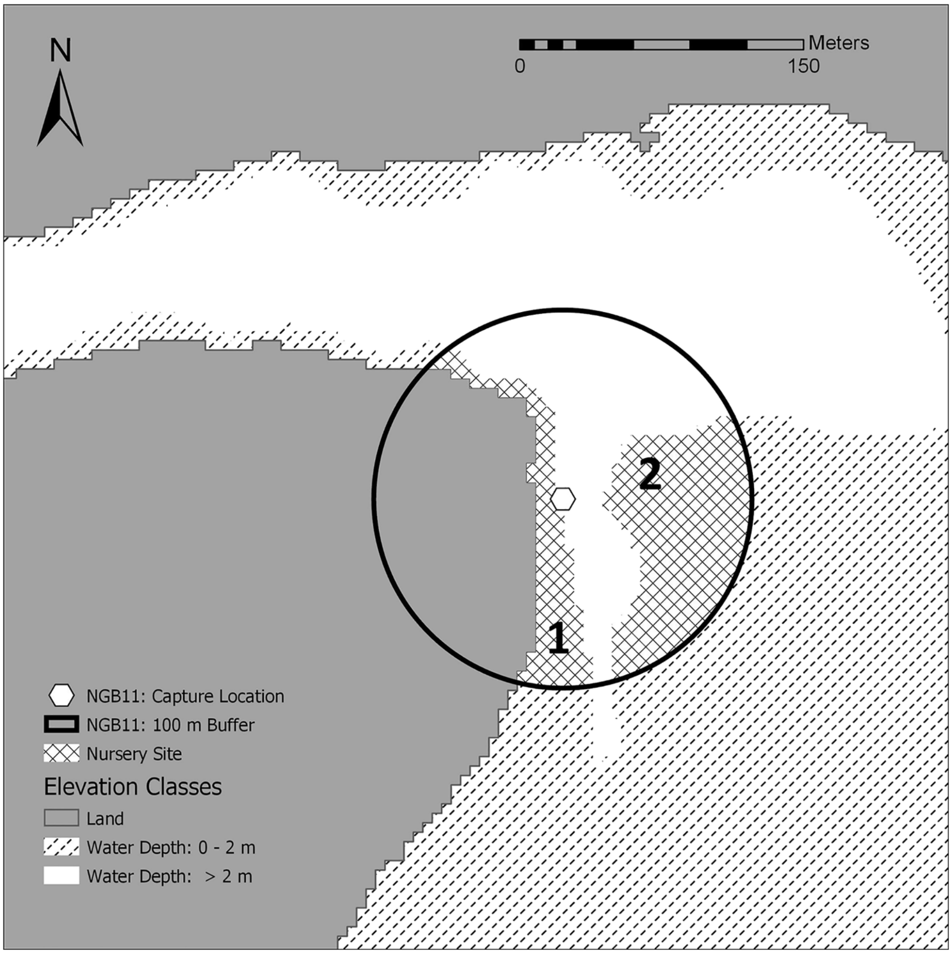

Fig. 2. Nursery site NGB11 is used to illustrate occasional discrepancies between hydrogeomorphic measurement at the local and regional scales due to difference in site areas. The regional-scale extent (cross-hatching: 1 and 2) consists of all area between 0 and 2 m deep within the 100 m buffer. The local-scale site extent (cross-hatching: 1) consists of area between 0 and 2 m deep within the 100 m buffer that contains the capture location; discontinuous patches (i.e. 2) are excluded.

bathymetry on wave development. A weighted average of neighboring rays was taken to determine effective fetch along eight bearings (N, NE, E…etc). The REI was calculated from the equation:

$$REI = \left(\sum_{i=1}^{8} E_i \times V_i \times D_i\right)/8$$

where E_i = effective fetch along the *i*th bearing, V_i = wind speed along the *i*th bearing, and D_i = duration of wind along the *i*th bearing. We used wind data from the US Army Corps of Engineers Wave Information Studies from Stations 93338 and 93370 for NGB and SEGB, respectively. Each station was approximately 10 km offshore of our nursery sites in each region and provided hourly hindcasts of wind speed and direction data from 1979 to 2014. We used wind data from a six month window (May to October) and only considered the highest 95% of wind speeds from each station (Fonseca and Bell, 1998). The REI calculation was computationally intensive so we distributed sample points in a 10 m grid pattern within each nursery site and took the median REI of the sample points as our wave exposure metric for the site.

All statistical analyses were performed with SAS JMP 13.0.0 (SAS Institute Inc., Cary, NC), unless otherwise indicated. Our goal was to evaluate how the hydrogeomorphic features of each site differed between regions and lake-level, particularly if there were changes between the high- or low-water scenarios, or regional characteristics that would explain the apparent resilience of the NGB sites to the period of sustained low lake levels. We used a Wilcoxon Signed Rank test to compare the median values of each hydrogeomorphic feature between the high- and low-water scenarios. We then compared hydrogeomorphic features of nursery sites by region and lake-level scenarios (i.e. SEGB high water, SEGB low water, NGB high water, NGB low water) using a Kruskall-Wallis test, with a Steel-Dwass post-hoc test for multiple comparisons. We did not exclude any sites for this test. A Bonferroni correction of α = 0.01 was applied to both tests.

2.3. Local scale: Resilience Index

We used results from our nursery-habitat characterization to develop an index to score areas based on their likelihood of supporting wetland habitat that is resilient to stable low lake levels. The development of this index was based on the assumption that suitable muskellunge nursery habitat (i.e. age-0 muskellunge were present) consisted of a structurally diverse aquatic vegetation community. Since age-0 muskellunge are very vulnerable to predators we expected them to only be found in areas with sufficient cover from predators and ample foraging opportunity, and not stray into less suitable habitat (e.g. open water, less cover). The aquatic vegetation communities described at confirmed muskellunge nursery sites (Craig and Black, 1986; Leblanc et al., 2014; Leblanc, 2015) were consistent with this expectation. We also assumed that under stabilized lake levels age-0 muskellunge would only be found in resilient wetlands. Therefore, all NGB sites were considered "resilient" since age-0 muskellunge had been found there under stable low lake levels. We selected the hydrogeomorphic variables that best differentiated the nursery sites in NGB from SEGB under the low-water scenario, and then developed a habitat suitability curve

(HSC) for each variable using measurements from the NGB low-water scenario. We fitted a suite of candidate distributions to the data for each variable to use as the basis for the HSC, and then selected the best-fitting one based on Akaike's Information Criterion (AICc) scores and goodness-of-fit tests. The probability density function from the best-fitting distribution was re-scaled to values between 0 and 1 to arrive at the HSC. A bootstrapping protocol in R (R Core Team 2018) was used to estimate the confidence intervals for each HSC (Som et al., 2016). We calculated the score of our RI as the mean of the HSC scores from each selected variable at a given site. We evaluated the performance of the RI based on its ability to correctly differentiate the NGB (i.e. "resilient") and SEGB (i.e. "not resilient") sites, using the area-under-the-curve (AUC) of a receiver operator characteristic (ROC) curve, a threshold-independent evaluation of the model's performance (Fielding and Bell, 1997), and a confusion matrix with a binary classification (i.e. "resilient" or "not resilient"). To be conservative for the binary classification and to minimize omission of "resilient" habitats, we set the threshold value so that all NGB sites would be classified as "resilient".

For operational use, we split the RI scores into three categories: "most resilient", "moderately resilient", and "least resilient". We maintained the same threshold as the binary classification such that the "least resilient" category did not contain any of the NGB sites. We set an upper threshold to separate between "moderately resilient" and "most resilient", so that only NGB sites were included in the "most resilient" category. Functionally, this meant that the "least resilient" and "most resilient" classes exclusively contained SEGB and NGB sites, respectively. The "moderately resilient" class was where the lowest NGB scores and highest SEGB scores overlapped.

2.4. Regional scale: Resilience Index

Our goal at the regional scale was to apply the local RI across a larger geographic area for use as a screening tool to identify broad areas (e.g. a large embayment) that support high proportions of resilient wetlands, and to guide targeted field surveys to identify muskellunge nursery habitat. The local-scale methods described previously were too computationally intensive to apply at the regional scale, so we developed an alternative protocol using coarser-scale hydrogeomorphic measurements for the Regional RI.

We worked from the same 5 m resolution DEMs as described previously but did not make manual corrections to the shoreline, using the lake elevation contour as derived from the DEM. We maintained the study space extent as the 0–2 m depth zone within each region, but opted for coarser-scale measurement of the REI. We applied a tessellation of 1 ha hexagons over the 0–2 m zone and used the centroids as sample points. Any centroids on land were shifted to the nearest point along the shoreline. This amounted to a maximum spacing between points of about 60 m. We then interpolated a regional REI layer using a Triangulated Irregular Network. We used the Focal Statistics tool, essentially a moving window, in ArcGIS Pro to calculate a mean value for each hydrogeomorphic feature at a given location. A circle with a 100 m radius was used as the focal window for consistency with the local-scale delineation of nursery site boundaries. We compared the hydrogeomorphic feature measurements and RI scores between the two scales (i.e. local and regional) for all NGB and SEGB sites (n = 32) to verify that the index scaled-up appropriately, and that the three operational resilience categories associated with the local RI had been conserved.

We applied the regional RI across the entire NGB and SEGB regions, and a third region in northeastern Georgian Bay (NEGB), Pointe au Baril. Within each region we quantified the area of each resilience category for the total study space (i.e. 0–2 m depth) and for wetland habitats, based on the MCWI (Midwood et al., 2012). There was one confirmed muskellunge nursery site in NEGB (Weller et al., 2016) and three sites suspected to be muskellunge nursery sites based on radio telemetry locations of adult muskellunge during spawning (Weller, 2018). We compared the regional RI scores and categories to the presumed status of these nursery sites as part of our index validation.

2.5. Basin-wide scale: Vulnerability Index

The **Vulnerability Index** (VIn) was essentially a coarser version of the regional RI with a reciprocal scoring system; an RI score of 0 would correspond to a VIn score of 1, indicating that a given area supported coastal wetlands that would be very vulnerable (i.e. not resilient) to wetland-community changes under stable low lake levels. Scaling up to a basin-wide RI required further simplification of the index. We excluded the wave exposure metric because it was the most limiting hydrogeomorphic feature with respect to computational demands. We checked the correlation between the regional RI and a version excluding wave exposure at all 32 nursery sites to confirm the appropriateness of this decision. We used a 10 m resolution DEM of Georgian Bay (see Weller and Chow-Fraser, 2019a for full details) and the same protocols as the regional RI for measuring depth and slope. The correlation of the basin-wide and regional-scale measurements was verified before proceeding. We calculated the RI for the 0–2 m depth zone across the eastern and northern shoreline of Georgian Bay (Severn Sound to MacGregor Bay) and subsequently considered only areas that had been identified as inundated wetland area in the MCWI (low marsh; Midwood et al., 2012). We applied a tessellation of 10,000 ha hexagonal tiles across the Georgian Bay shoreline and calculated a representative RI score for each hexagon as the mean RI score for the entire wetland area within the hexagon. The representative RI scores were then converted to the corresponding VIn scores. So a hexagon containing 60 ha of wetland would be represented by 6000 pixels with 10 m resolution (aligned to the DEM). The mean RI score of those 6000 wetland pixels would be the representative RI score for the hexagon, which would then be converted to the corresponding VIn score.

We developed a ranking system to prioritize areas for management focus based on their VIn scores and total wetland area, such that hexagons with more wetland area received higher priority. For example, we determined that a hexagonal tile with only 1 ha of wetland and a VIn of 0.95 should have a lower priority than a tile with 100 ha of wetland and a VIn of 0.7. We independently ranked the hexagonal tiles in descending order according to VIn scores and wetland area so that tiles with the lowest mean was designated highest management priority.

3. Results

3.1. Local scale: habitat characterization

Of the 20 SEGB sites, only one (SEGB 15) was classified as fringing and seven as open embayments, while the rest were protected embayments (n = 5) or archipelagos (n = 7). The shoreline configuration of the embayment sites afforded a greater level of protection from wave exposure than did the fringing site. The layout of the archipelago sites changed drastically with lake level; under the low-water scenario the sites were dominated by many small islands, which were fully or partially submerged under high water. This abrupt change in shoreline configuration resulted in less protection from wave exposure compared with that under the high-water scenario.

The SEGB sites had very gradual slopes under both high ($\bar{x}$ ± SE; 0.905% ± 0.151; n = 20) and low water-levels (0.778% ± 0.117; n = 16), and this resulted in an average lakeward shift in shoreline position of 20 m (± 0.17) between lake-level scenarios, and in some cases up to 80 m. The shallow nature of these sites meant that the nursery-site boundaries of all but two (SEGB15 and SEGB05) were delineated by the 100 m buffer. Under high water, the site area was relatively large (2.21 ha ± 0.14; n = 20), whereas under low water, the area shrank (1.50 ha ± 0.13; n = 16) as the shoreline shifted lakeward while the lakeward site boundary remained static. The pairwise

Table 1
Comparison of medians for hydrogeomorphic variables of muskellunge nursery sites in each region between high- (HIGH) and low-water (LOW) scenarios using Wilcoxon Signed Rank test. Measurements were derived from a DEM with manually corrected shoreline features. Bonferroni correction of $\alpha = 0.01$.

Variable	Region	HIGH	LOW	S	*p*
Area (m^2)	SEGB	22,311	14,387	−68	$< 0.001^*$
	NGB	4546	8852	60	$< 0.001^*$
Volume (m^3)	SEGB	22,168	4040	−68	$< 0.001^*$
	NGB	4917	7235	16	0.4332
Depth (m)	SEGB	1.00	0.27	−68	$< 0.001^*$
	NGB	0.99	1.04	−18	0.3755
Slope (%)	SEGB	0.63	0.62	28	0.1591
	NGB	8.46	5.84	−65	$< 0.001^*$
REI	SEGB	554.93	59.21	−68	$< 0.001^*$
	NGB	348.23	301.77	−68	$< 0.001^*$

Table 3
Summary of attributes and features of different Resilience Index scales, including target study area size (Size), resolution of digital elevation model used (DEM), included hydrogeomorphic features (HGM), and any other defining characteristics (Characteristics).

Scale	Size	DEM	HGM	Characteristics
Local	~1 ha	5 m	Depth Slope REI	Manually verified nursery site delineation REI samples: 10 m spacing
Regional	~1000–10,000 ha	5 m	Depth Slope REI	Automated nursery site delineation REI samples: ~60 m spacing
Basin-wide	> 10,000 ha	10 m	Depth Slope	Automated nursery site delineation Inverted scoring system for Vulnerability Index

Table 4
Specifications for the habitat suitability curves (HSCs) for hydrogeomorphic variables associated with muskellunge nursery sites. Local-scale data from the NGB sites under low-water (176.0 m) were used to fit a 2-parameter Weibull probability density function (Fitted PDF: α = scale parameter, β = shape parameter, W^2 = Cramér-von Mises goodness of fit) for each morphometric variable. The PDF was then re-scaled to values between 0 and 1, where 1 indicated the most suitable habitat (α and β parameters are from the original PDF, not the rescaled values). A Wilcoxon Signed Rank test ($\alpha = 0.05$) was performed to confirm median HSC scores were significantly different between SEGB and NGB sites.

Variable	Fitted PDF			Wilcoxon Signed Rank Test			
	α	β	W^2	NGB	SEGB	Z	*p*
Depth	1.124	3.791	0.25	0.80	0.05	4.315	< 0.001
Slope	6.924	2.221	0.25	0.90	0.13	4.353	< 0.001
REI	331.711	2.113	0.25	0.77	0.24	2.393	0.0167

comparison of SEGB sites ($n = 16$) from the high-water to low-water scenario indicated that sites experienced significant decreases in area ($S = -68.00, p < 0.001$), volume ($S = -68.00, p < 0.001$), and REI ($S = -68.00, p < 0.001$), while slope remained unchanged ($S = 28.00, p = 0.1591$; Table 1). This amounted to an average loss of 33.6% (SE = 3.7) in area and 81.6% (SE = 3.2) in volume. The REI fell from an average of 1692 (SE = 422) to 155 (SE = 66). The six sites with the most extreme decreases in REI were along the same stretch of shoreline. Most of these were archipelago sites, and the area offshore of the site boundaries was characteristically similar to the sites themselves (i.e. dominated by many small islands and shoals under low water, but submerged under high water).

By comparison, slopes of the NGB nursery sites were generally steeper and the sites occurred along relatively straight stretches of shoreline. Of the 16 sites, 12 were classified as fringing, three were protected embayments sheltered by small islands, and one an open embayment. Regardless of water levels, the NGB sites were much steeper than their SEGB counterparts (9.01% ± 1.20 under high water and 6.13% ± 0.75 under low water). Thus, the lakeward shift in shoreline position between lake-level scenarios was on average only 5.35 m (± 0.06) and no more than 35 m. The 2 m depth contour was encountered well within the 100 m buffer at almost all sites ($n = 13$), giving these the appearance of narrow bands along a straight shoreline. Areas of these nursery sites were relatively small regardless of water-level scenario (0.71 ha ± 0.14 vs 0.92 ha ± 0.12 in high and low water levels, respectively).

In pairwise comparison of NGB sites between high and low water

Table 2
Comparison of hydrogeomorphic variables for sites in all region-years (NGB or SEGB) at high- (HIGH) or low-water (LOW) levels. Kruskal-Wallis and the Steel-Dwass test were used to identify differences among groups. Groups sharing the same letter were statistically homogeneous.

Variable	Group	Mean	SE	χ^2; *p*	Statistical grouping		
Area (m^2)	SEGB HIGH	22,092	1431	37.034; < 0.001	A		
	SEGB LOW	15,037	1300			B	
	NGB HIGH	7150	1414				C
	NGB LOW	9176	1234				C
Volume (m^3)	SEGB HIGH	22,226	1517	38.964; < 0.001	A		
	SEGB LOW	4429	852				C
	NGB HIGH	8125	1821			B	C
	NGB LOW	8344	975			B	
Depth (m)	SEGB HIGH	1.01	0.03	35.184		B	
	SEGB LOW	0.29	0.05	< 0.001	A		
	NGB HIGH	1.11	0.05			B	
	NGB LOW	1.01	0.08			B	
Slope (%)	SEGB HIGH	0.91	0.15	48.966; < 0.001	A		
	SEGB LOW	0.77	0.12		A		
	NGB HIGH	9.01	1.20			B	
	NGB LOW	6.13	0.75			B	
REI	SEGB HIGH	1608.31	421.50	25.713; < 0.001	A		
	SEGB LOW	155.27	65.94			B	
	NGB HIGH	401.22	59.02		A		
	NGB LOW	292.61	38.31		A		

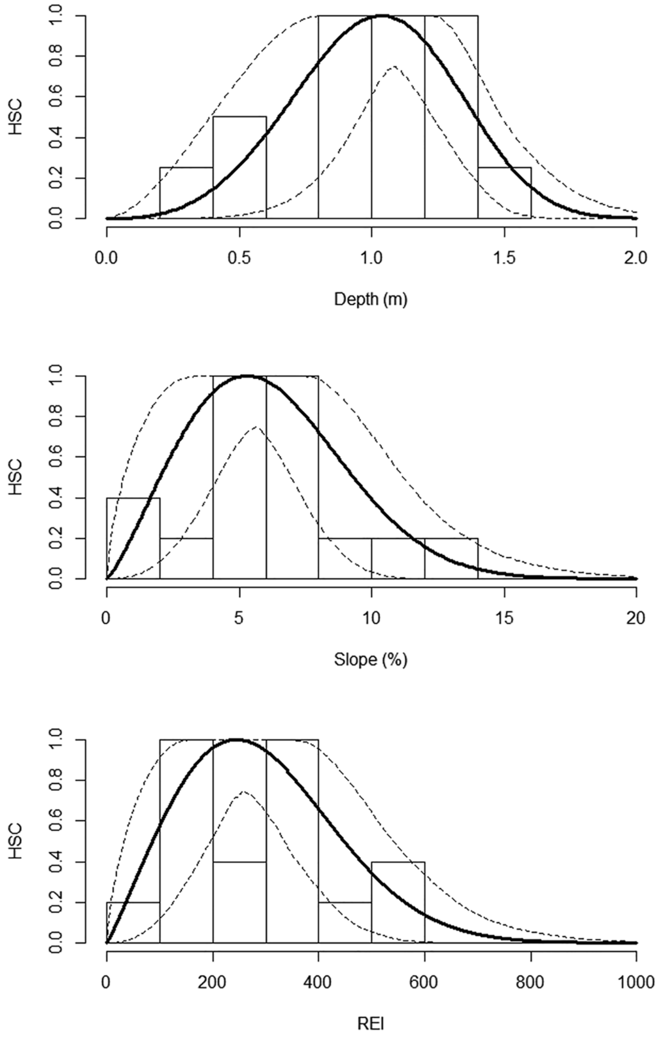

Fig. 3. Habitat suitability curves (HSCs; solid line) bounded by 95% confidence interval (dashed lines) for hydrogeomorphic variables associated with muskellunge nursery sites. A 2-parameter Weibull probability density functions was fitted to the data from northern Georgian Bay sites under low lake levels ($n = 16$). The HSC is the probability density function rescaled to values of 0–1.

levels, we observed a decrease in slope ($S = -65$, $p < 0.001$) and REI ($S = -68$, $p < 0.001$), an increase in site area ($S = 60$, $p < 0.001$), but no significant change in volume ($S = 23.00$, $p = 0.4332$; Table 1). The increase in area is consistent with the more gradual slope under the low-water scenario, while the volume remained the same because any increase in area was offset by a shift to shallower habitat. The shoreline configuration did not vary between lake levels, nor did it demonstrate the dramatic changes seen in parts of SEGB (i.e. emergence/submergence of many small islands), although the drop in lake levels dampened the depth-dependent component of REI calculations.

Slope was the most distinguishing feature between NGB and SEGB sites; however, slopes did not change between lake-level scenarios (Table 2). The shift in shoreline position between lake levels, essentially a function of the slope, and the use of a fixed lakeward extent for delineating site boundaries (i.e. 100 m buffer) explained the differences in area, volume, and depth, as described previously. Sites in the more steeply sloped NGB region (i.e., the 0–2 m depth zone) were able to shift lakeward from high to low water without encountering the 100 m buffer, whereas sites in the more gently sloping SEGB region shifted far enough lakeward to encounter the 100 m buffer. This effectively compressed some site boundaries under the low-water scenario. For example, the mean depth did not change significantly from high to low water in NGB (1.11 m vs 1.01 m; Steel-Dwass test: $Z = -0.508$, $p = 0.957$) but in SEGB the mean depth declined significantly (0.98 m to 0.27 m; Steel-Dwass: $Z = -5.078$, $p < 0.001$) as the more extreme lakeward shift compressed the site boundaries against the 100 m buffer. Also of note is that low water levels resulted in much lower mean REI scores for SEGB sites compared with high water levels, and lower than the REI scores of NGB sites, regardless of lake elevation (Table 2).

3.2. Local scale: Resilience Index

We selected slope, mean depth, and REI as the most appropriate hydrogeomorphic variables to develop the local RI for the muskellunge nursery sites under low lake levels (Table 3). Measurements of each of these features were able to differentiate between the NGB and SEGB sites under the low-water scenario (Table 2) and were consistent with our initial hypotheses regarding habitat suitability under low lake levels. We opted to exclude wetland area because several of the NGB sites were very small (< 0.5 ha) and this made us question the appropriateness of using area as a criterion of suitability. We did not find significant differences in wetland volume between NGB and SEGB sites

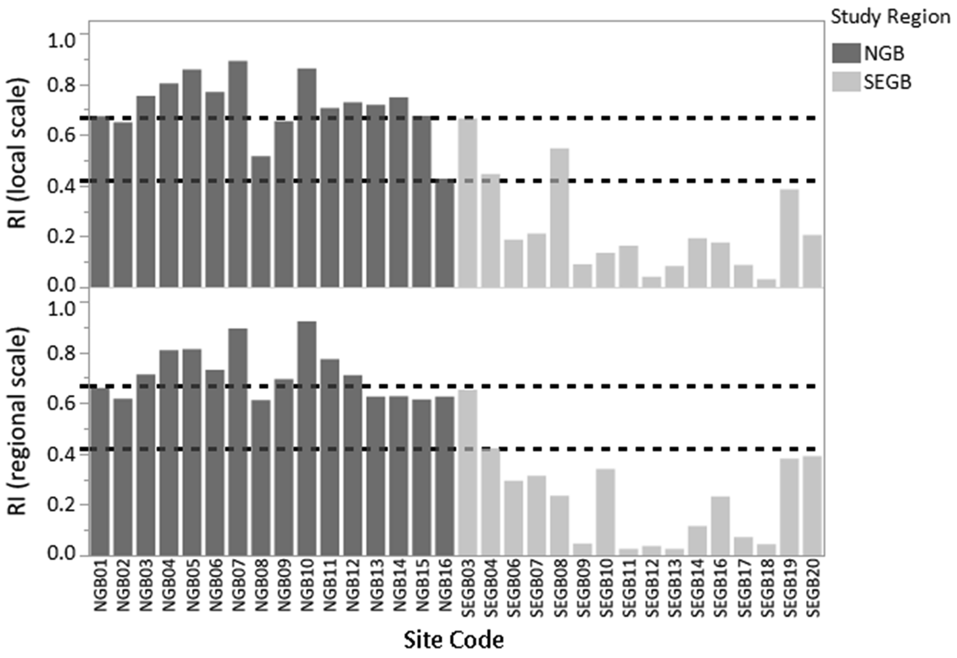

Fig. 4. Resilience Index (RI) scores for muskellunge nursery sites in southeastern Georgian Bay (SEGB; $n = 16$) and northern Georgian Bay (NGB; $n = 16$) using local-scale and regional-scale hydrogeomorphic variables. RI scores were calculated for each nursery site under the low-water scenario (lake level = 176.0 m). Dashed lines indicate the thresholds for defined categories: most resilient (> 0.67), moderately resilient (0.42–0.67), and least resilient (< 0.42).

Table 5
Percentage area in each region for three Resilience Index (RI) categories. Percent breakdown by the entire region (0–2 m Depth Zone) and subsequent application of a wetland mask layer (Wetland Mask). Total area of each region is included in brackets.

RI category	0–2 m Depth Zone			Wetland Mask		
	SEGB (2121 ha)	NGB (462 ha)	NEGB (236 ha)	SEGB (946 ha)	NGB (159 ha)	NEGB (66 ha)
Least Resilient	58	20	6	56	26	12
Moderately Resilient	28	50	32	27	47	33
Most Resilient	14	30	62	17	27	56

under the low-water scenario (Table 2). The HSC for each hydrogeomorphic variable was based on the probability density function of a 2-parameter Weibull distribution (Table 4), which had the lowest AICc score of the candidate distributions and acceptable goodness-of-fit (Cramér-von Mises W^2 test, $p > 0.05$). The probability density function fitted to the local measures (Fig. 3) seemed appropriate (i.e. optimal scores and shape of the curves were consistent with hypotheses) and significant differences between SEGB and NGB sites were maintained (Table 4). The slope HSC scores most clearly differentiated between the two regions (AUC = 0.953) with all of the SEGB sites having scores below 0.31, while 11 NGB sites had scores above 0.75.

The NGB sites had significantly higher HSC scores for depth and REI (Table 4) but there was greater overlap with SEGB scores at intermediate scores (AUC: 0.949 and 0.750, respectively). The local RI performed well with an AUC score of 0.973. The threshold for the binary classification scheme was set at 0.42 and three SEGB sites were misclassified (RI, local scale; Fig. 4). Of the 32 total sites, seven (three SEGB and four NGB) had intermediate scores, while the remaining sites separated out as expected (i.e. high NGB scores and low SEGB scores).

3.3. Regional scale: Resilience Index

The local- and regional-scale hydrogeomorphic measurements were highly correlated for depth (Spearman's $\rho > 0.97$) and slope ($\rho > 0.92$). Differences in HSC and RI scores were largely attributed to the different protocols used. NGB 11 was the most obvious outlier with an increase in mean depth (+0.52 m) and a decrease in slope (−6.93%) as product of the different rulesets (see Fig. 2). The REI correlation between site and region measures was weaker ($\rho = 0.37$) and attributable to the set of archipelago sites in SEGB which relied on manual shoreline updates to accurately capture the many small islands that directly affected their REI measures. Exclusion of these sites ($n = 5$) improved the correlation to $\rho = 0.83$. Correlations between local and regional HSC values were consistent with the

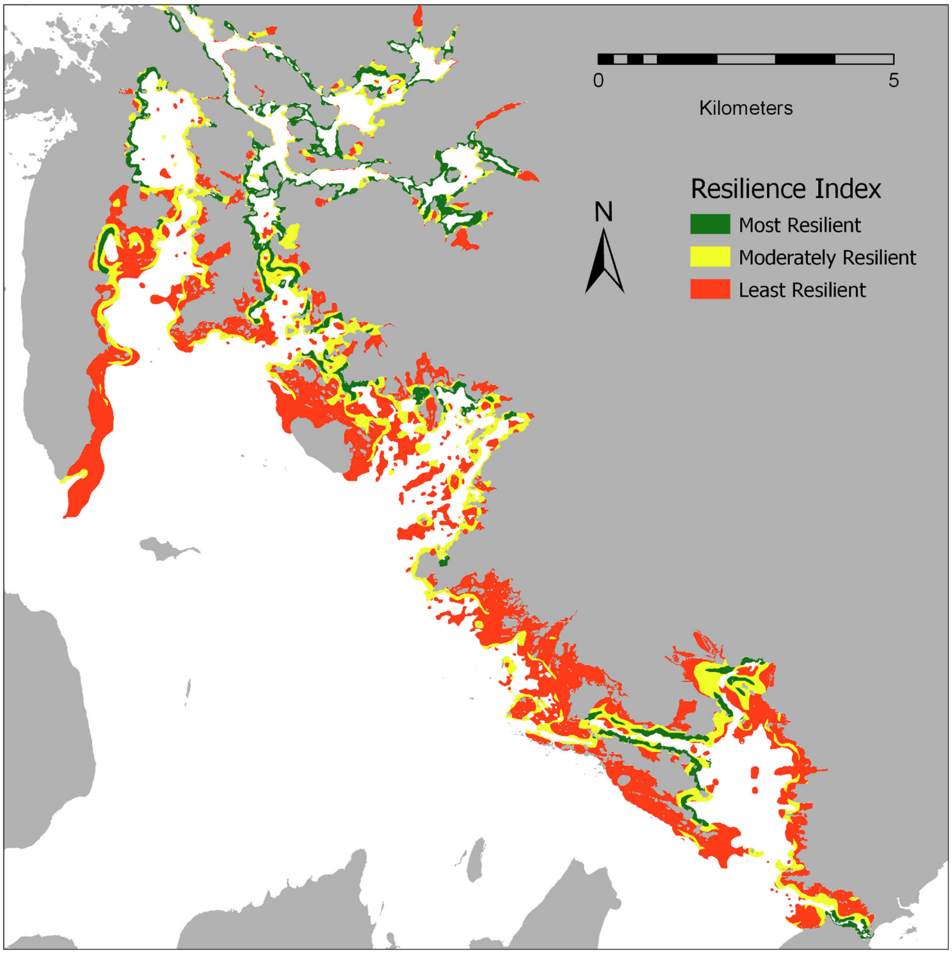

Fig. 5. Classification of wetland areas into three resilience categories for southeastern Georgian Bay.

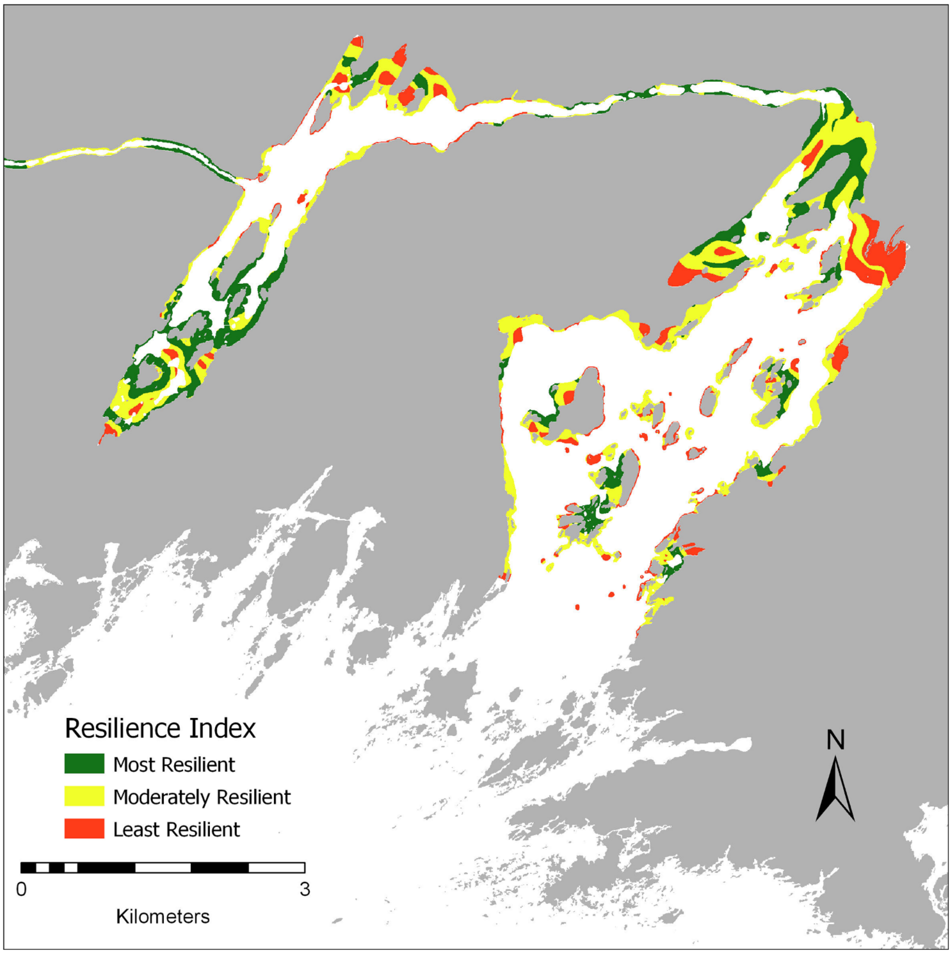

Fig. 6. Classification of wetland areas into three resilience categories for northern Georgian Bay.

hydrogeomorphic measurements for depth (ρ = 0.94), slope (ρ = 0.90), and REI (ρ = 0.72). Local and regional RI scores were highly correlated (ρ = 0.94).

The regional RI scores yielded an AUC of 0.975, and only one site was misclassified (SEGB03) based on the binary threshold, (Fig. 4; RI, regional scale). Overall, the RI performed well and consistently at both the local and regional scale. For simplicity, we used one set of threshold values to define the operational resilience categories for both the local and regional RI. We set the lower threshold at 0.42 (between "least resilient" and "moderately resilient") and the upper threshold at 0.67 (between "moderately resilient" and "most resilient"). This ensured that all NGB sites were classified as "most resilient" or "moderately resilient" while minimizing the misclassification of SEGB sites. No SEGB sites were classified as "most resilient".

Majority of SEGB was designated as "least resilient" (Table 5), with some narrow bands and small patches of "moderately resilient" or "most resilient" habitat towards the southern end of SEGB; the northern section of the region had a higher prevalence of resilient habitat where the nearshore slope was steeper (Fig. 5). NGB was primarily "moderately resilient" (Table 5) with only a few large wetland units that were considered "least resilient" (Fig. 6). Similarly, majority of the NEGB was classified as "most resilient" or "moderately resilient" (Table 5), and all of the suspected nursery sites were classified as "most resilient" (Fig. 7). The confirmed nursery site in NEGB had an RI score of 0.94.

3.4. Basin-wide scale: Vulnerability Index

The basin-wide RI (i.e. based only on depth and slope) was highly correlated with the regional and local RIs (ρ = 0.89 and ρ = 0.94, respectively) for the SEGB and NGB nursery sites. This provided adequate rationale to use the basin-wide RI to develop the Vulnerability Index (VIn). Majority of the eastern and northern Georgian Bay shoreline currently support wetlands that have low or moderate vulnerability to stable low lake levels (Fig. 8). The most vulnerable wetlands appear to be those in SEGB where there is a large amounts of wetland area with relatively high VIn scores (> 0.65). Isolated tiles with large proportions of highly vulnerable wetlands (VIn > 0.95) occurred along the northeastern and northern shoreline, but these tiles contained a very small total wetland area and therefore have low management priority (see area-vulnerability tradeoff; Fig. 8, Table A1).

4. Discussion

A growing body of work have confirmed the importance of structurally diverse, aquatic vegetation within muskellunge nursery habitat (Craig and Black, 1986; Kapuscinski and Farrell, 2014; Leblanc, 2015; Murry and Farrell, 2007; Werner et al., 1996). Previous studies have identified changes in the aquatic vegetation community as a probable cause of recruitment failure for muskellunge (Farrell et al., 2007; Leblanc et al., 2014), but we used well-established mechanisms related to aquatic vegetation communities to develop a habitat assessment tool. In this study, we have identified substrate slope, depth, and site exposure as key variables that are primarily linked to aquatic vegetation structure. We have shown that the interaction of these hydrogeomorphic variables with water level may explain how aquatic vegetation communities respond to changing water depth (i.e. a deeper site can support a more structurally complex SAV community than can a very shallow site).

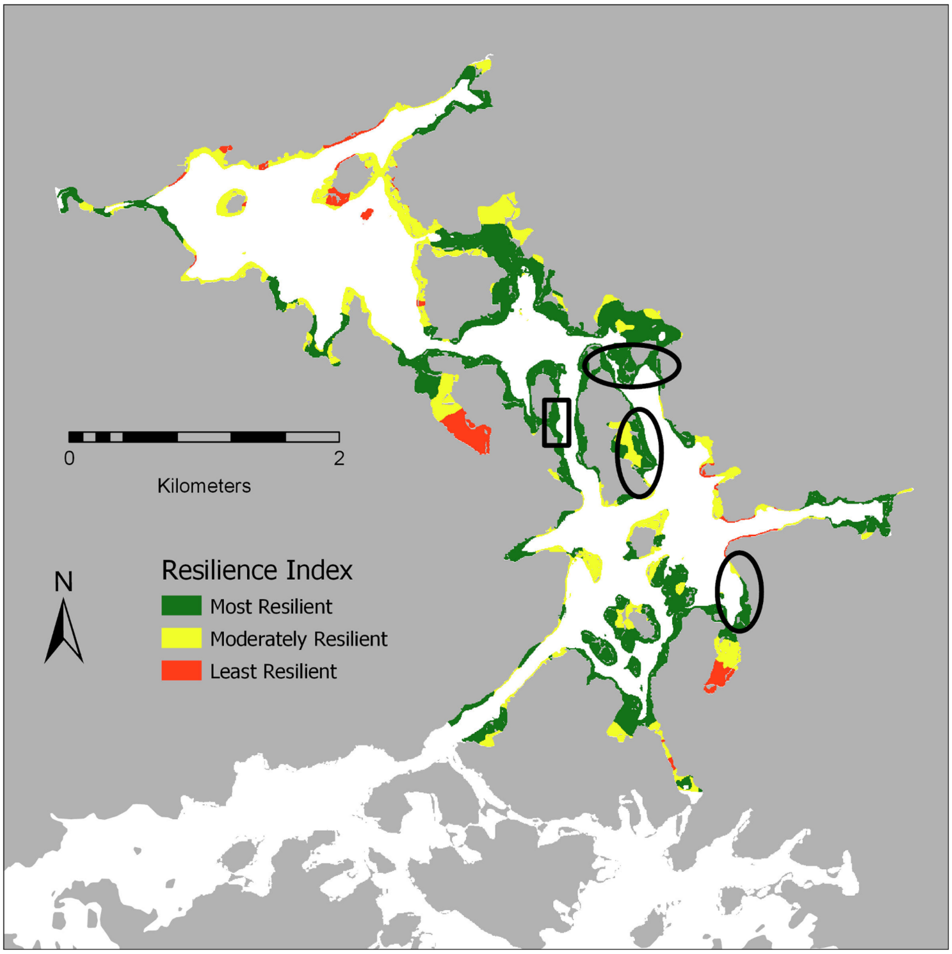

Fig. 7. Classification of wetland areas into three resilience categories for northeastern Georgian Bay. Rectangle indicates confirmed muskellunge nursery site (i.e. captured age-0 muskellunge) and circles are suspected nursery sites based on radio-tracking of spawning adult muskellunge.

We assume that under historical (i.e. typical) lake-level fluctuations, the continuous change in water levels acts as a disturbance regime, promoting a higher diversity of plant species (Keddy and Reznicek, 1986; Wilcox and Xie, 2007), and a greater structural diversity that provide optimal fish habitat. In the absence of fluctuating lake levels we should expect to see a homogenization of the plant community and a loss of diversity. The vegetation community essentially “catches up” to the lake level and the more competitive species become dominant. This in turn should be expected to result in a subsequent shift in the fish communities present in those habitats (Cvetkovic et al., 2010; Eadie and Keast, 1984; Midwood and Chow-Fraser, 2012; Smokorowski and Pratt, 2007; Weaver et al., 1997).

Our study confirms the importance of slope by showing this as the key distinguishing feature between NGB and SEGB sites (Leblanc et al., 2014; Leblanc, 2015). This also validates its use in development of a habitat suitability index for age-0 muskellunge (Leblanc and Chow-Fraser, 2017). We are also encouraged by the convergence of results at multiple spatial scales in this study. Steeper sites appeared to be more resilient to stable low lake levels but the exact mechanism by which this occurs is unknown. Based on the strong predictive relationship between littoral slope and maximum biomass of SAV found by Duarte and Kalff (1986), more gradual slopes are capable of supporting greater SAV biomass than steeper slopes. This suggests that when released from the typical disturbance regime of lake-level fluctuations (Keddy and Reznicek, 1986), our typically steeper NGB sites would have been unable to support as much SAV biomass as would the SEGB sites. We posit that the maximum SAV biomass supported by NGB slopes should correspond to a biovolume or structural configuration consistent with intermediate densities of aquatic vegetation. By comparison, when the SAV biomass increased in the SEGB sites, there was a corresponding increase in homogeneity and density of aquatic vegetation in some areas of Georgian Bay (Leblanc et al., 2014, Midwood and Chow-Fraser, 2012). Similar to biovolume as a proxy measure of density, SAV biomass may be considered a proxy for vegetation structure (Leblanc and Chow-Fraser, 2017; Valley et al., 2005).

We hypothesized that wave exposure promoted resilience of the NGB sites by acting as an alternative disturbance regime in the absence of fluctuating lake levels, essentially an example of the intermediate disturbance hypothesis (Grime, 1973; Keddy, 1984). Though there were differences between regions, slope is the most pronounced feature, and the SEGB sites had lower REI scores under the low-water scenario (Table 2). Exposure is a difficult metric to interpret as it encompasses a range of conditions that can affect aquatic plant growth, such as sediment sorting, physical damage to plants, or uprooting (e.g. physical disturbance; Jupp and Spence, 1977). Duarte and Kalff (1986) found that SAV biomass was negatively correlated with exposure (i.e. similar metric to the REI but without accounting for depth), but not at slopes in excess of 2.24%. This means that effects of exposure on vegetation may be a more important factor in SEGB than in NGB, and could in part explain the weaker discriminating power of the REI. The largest set of suitable nursery habitat with shallow slopes was from SEGB under the high-water scenario; nevertheless, we cannot draw conclusions because the typical lake-level fluctuation that prevailed during this period is a confounding factor.

It is difficult to assess if an alternative set of exposure HSCs tailored for gradual or steep slopes would have been useful. Under stable low

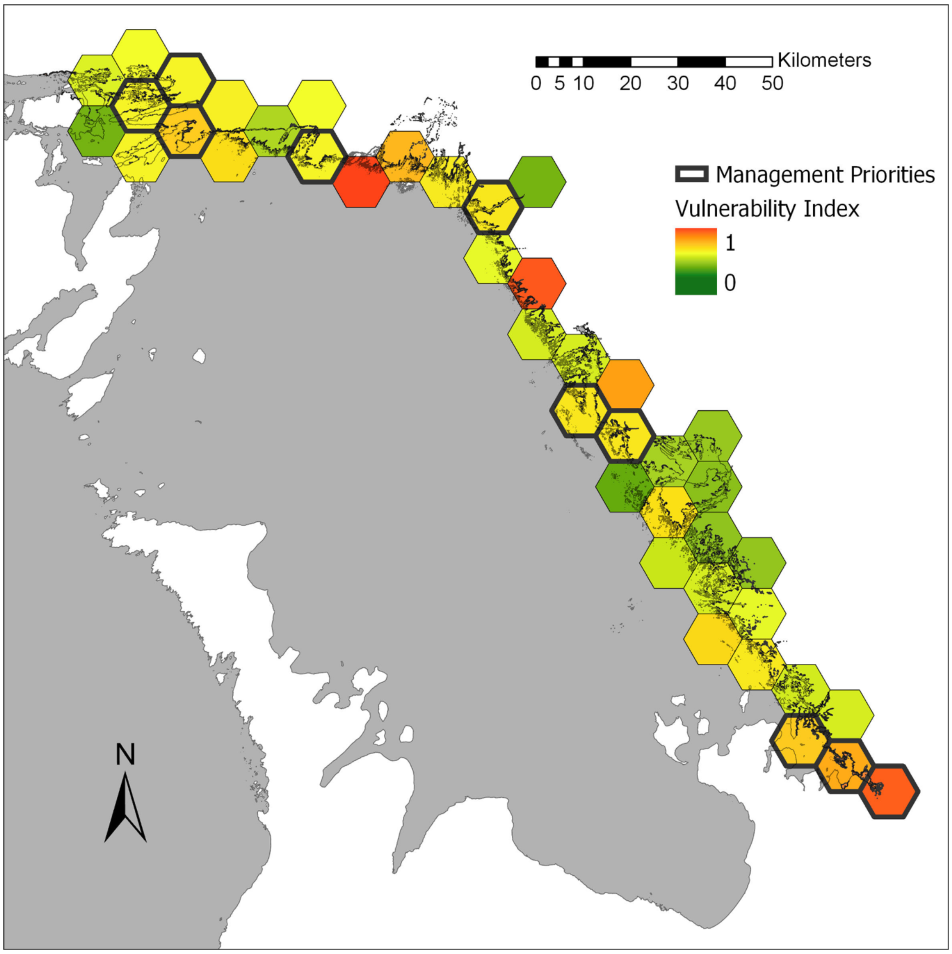

Fig. 8. Vulnerability Index (VIn) scores for the eastern and northern shoreline of Georgian Bay, calculated as the reciprocal of the mean basin-wide RI score for all wetland area contained within a hexagonal tile. Scores range from 1 (red) indicating most vulnerable to 0 (green) indicating least vulnerable. Priority tiles for management consideration (top 10, bold outline) were selected based on VIn score and total wetland area. Priority tiles support large wetland areas, many of which are considered vulnerable to community shifts under stable low water levels.

water levels, there were only two muskellunge nursery sites from NGB with gradual slopes (< 2.24%) and that had REI scores between 100 and 200; almost all of the SEGB sites (11/16) had REI scores of < 75. In shallow water (~1.0 m), wave exposure has been associated with SAV growth, presumably because the energy is required to remove fine sediments and to bring in associated nutrients (Duarte and Kalff 1986; 1990). This provides an alternative mechanism as to how physical disturbance of waves may act on SAV. The use of exposure is further complicated because the methods available to measure exposure are drastic oversimplification of complex processes including shoaling, breaking, and refraction (USCOE, 1977), and more accurate or appropriate measures involve the use of complex numerical models (e.g. SWAN, WeMo) which involve a level of computational power that can make them impractical to use at a large regional scale. While REI was not as useful in discriminating between our NGB and SEGB sites, we retained this variable in the RI because of its heuristic value; optimal values from its HSC made sense and we felt its ability to reduce scores at extremely high or low exposures was more evident when applied at a regional scale, and not just to the 32 sites that contributed to development of the index.

The significant decline in area and volume of nursery sites we found during low water levels (Table 1) are consistent with loss of wetland fish habitat reported by others for eastern Georgian Bay (e.g. Fracz and Chow-Fraser, 2013; Midwood and Chow-Fraser, 2012). However, we attributed this result to the nature of our site delineation, since we maintained a fixed buffer around the capture location as a maximum site extent. Recent models to simulate the response of coastal wetlands in Georgian Bay to low lake-levels suggest that the area of low-marsh actually increases under low lake levels but that volume decreases as shallower habitat becomes more dominant (< 0.5 m; Weller, 2018). Based on our knowledge of the region's bathymetry, we would expect a similar result if using a strictly depth-dependent site boundary, but difficulties associated with accounting for the often large lakeward or landward shifts in site position and extent precluded such an approach. Furthermore, Georgian Bay coastal marshes are typically quite small (< 2ha; Midwood et al., 2012), including those found in NGB which are known to support age-0 muskellunge. This supports our contention that the size of the available nursery habitat is less important than the types of structure within the habitat and its overall quality.

We stress the consideration of spatial scale when using the indices developed in this paper, particularly their respective purposes, limitations, and interpretations. The regional RI was one of the main products of this study, intended as a coarse-scale screening tool to remotely identify suitable muskellunge nursery habitat before more targeted surveys are conducted, similar to those carried out by Leblanc and Chow-Fraser's (2017) Index of Nursery Habitat Suitability. Of Leblanc and Chow-Fraser's (2017) 37 "no-muskellunge" sites used to develop the INHS, the regional RI only classified 5 as "least resilient" while the remained were evenly split between "moderately resilient" and "most resilient". We interpreted this poor classification of the "no-muskellunge" sites as evidence that resilient wetland habitat alone does not guarantee the presence of age-0 muskellunge and that other variables, hydrogeomorphic or otherwise, must be considered as well. Therefore we recommend using the regional RI to assess if a target region supports a high proportion of resilient wetlands that merit subsequent field surveys, or to prioritize sampling effort among larger wetland complexes (e.g. prioritizing based on resilience categories). Although the local RI provided finer resolution than did the regional RI, the much greater effort (both in terms of time and labor) required to produce the habitat layers are difficult to justify.

The VIn, and the priority rankings (Table A1), offers a relatively efficient means to identify the average vulnerability of wetlands over a broad area. We envision this being used in development of lake-wide sampling programs, possibly with subsequent, targeted use of the regional RI. We emphasize without hesitation, however, that such screening tools do not substitute for detailed field surveys that involve examining SAV structure and the fish communities, and that our hierarchy of indices must be used as intended (Table 3). The performance of these indices, particularly at the local and regional scale, depend on availability of fine-scale bathymetric information, which are currently lacking for most of Georgian Bay, and thus limits further improvements of the RI.

While the development and application of these resilience indices was limited in scope, they should prove useful in other regions and for purposes beyond muskellunge management. Our focus on age-0 muskellunge habitat allowed us to identify a much broader class of wetland habitat and assess its response to a specific water-level disturbance. The effects of lake levels on coastal wetlands in the Great Lakes is a concern with respect to both climate change and water-level regulation and tools to assess the resilience of these habitats would be a valuable asset to management agencies. Georgian Bay coastal wetlands are among the least disturbed in the Great Lakes (Cvetkovic and Chow-Fraser, 2011) so our habitat suitability metrics were derived under near-reference conditions with limited anthropogenic influences. Although the unique hydrogeomorphic setting of Georgian Bay coastal wetlands may limit the direct transferability of these indices to other regions, in the Great Lakes or elsewhere, the framework of this approach is broadly applicable: the use of an indicator species to identify target habitat and subsequent characterization of habitat suitability using hydrogeomorphic features.

5. Conclusion

Overall, we developed a set of indices that offers a relatively simple and effective means to gauge the resilience of wetlands water-level disturbance over multiple spatial scales. We recommend the RI be used to guide targeted field surveys or to identify areas that may be in need of restoration or protection as part of an overall strategy to sustainably manage the trophy muskellunge fishery in Georgian Bay. Further we propose the broader use of the RI and VIn in developing a management strategy for Great Lakes coastal wetlands subject to lake level disturbances.

Acknowledgements

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Appendix A

Table A1
Prioritized areas along the Georgian Bay shoreline for management focus due to vulnerability of wetlands to stable low lake levels. The study area is represented by 10,000 ha hexagonal tiles unique alpha-numeric identifiers (Tile ID). Latitude and Longitude (North American Datum of 1983) indicate position of tile center. Priority ranking was based off Vulnerability Index (VIn) score and total wetland area within the tile (Area). For example, tile I-3 had the highest VIn score but small wetland area so it is of lower priority than tile O-8, which has a lower VIn score but more wetland area. The number of spatially distinct wetland units (Units) is included for additional context.

Tile ID	Longitude	Latitude	VIn	Area (ha)	Units	Priority
T-15	−79.73680	44.77563	0.75	743.92	135	1
U-15	−79.62037	44.72591	0.94	127.76	4	2
S-14	−79.85343	44.82522	0.66	201.19	100	3
E-2	−81.51189	45.99053	0.65	191.53	79	4
O-8	−80.31737	45.40932	0.58	214.4	48	5
D-2	−81.63259	46.03829	0.54	117.05	208	6
H-3	−81.15127	45.94322	0.53	84.62	42	7
L-4	−80.67160	45.84613	0.57	58.71	65	8
N-8	−80.43581	45.45833	0.58	48.89	79	9
E-1	−81.51278	46.08724	0.53	62.89	63	10
J-3	−80.91115	45.94329	0.71	18.09	122	11
P-10	−80.20050	45.26347	0.60	31.74	78	12
O-7	−80.31620	45.50604	0.78	8.6	4	13
I-3	−81.03118	45.89496	0.99	4.11	9	14
Q-11	−80.08423	45.11751	0.44	68.99	135	15
R-13	−79.96854	44.97142	0.57	34.15	111	16
F-3	−81.39139	45.94265	0.60	16.09	23	17
S-13	−79.85151	44.92194	0.43	78.04	230	18
T-14	−79.73468	44.87234	0.44	65.27	81	19
N-7	−80.43484	45.55505	0.44	54.2	99	20
D-1	−81.63370	46.13499	0.51	36.28	44	21
F-2	−81.39207	46.03937	0.55	22.59	29	22
M-5	−80.55291	45.70065	0.95	0.09	3	23

(*continued on next page*)

Table A1 (*continued*)

Tile ID	Longitude	Latitude	VIn	Area (ha)	Units	Priority
C-1	−81.75351	46.08591	0.46	46.74	63	24
H-2	−81.15153	46.03994	0.50	36.09	29	25
P-9	−80.19914	45.36019	0.34	65.28	59	26
D-3	−81.63149	45.94158	0.53	24.24	38	27
K-3	−80.79127	45.89477	0.57	9.25	39	28
Q-10	−80.08267	45.21422	0.29	66.87	191	29
Q-12	−80.08577	45.02079	0.62	0.67	4	30
Q-8	−80.07955	45.40765	0.31	48.35	33	31
G-2	−81.27156	45.99136	0.36	44.4	48	32
R-12	−79.96680	45.06814	0.47	14.63	33	33
L-5	−80.67217	45.74942	0.48	7.2	25	34
Q-9	−80.08112	45.31094	0.28	34.92	67	35
M-6	−80.55368	45.60393	0.44	3.7	13	36
R-11	−79.96505	45.16485	0.30	8.08	18	37
M-3	−80.55136	45.89408	0.24	7.53	5	38
P-11	−80.20185	45.16675	0.41	0.45	2	39
C-2	−81.75219	45.98921	0.23	3.83	13	40
O-9	−80.31853	45.31260	0.21	2.51	12	41

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