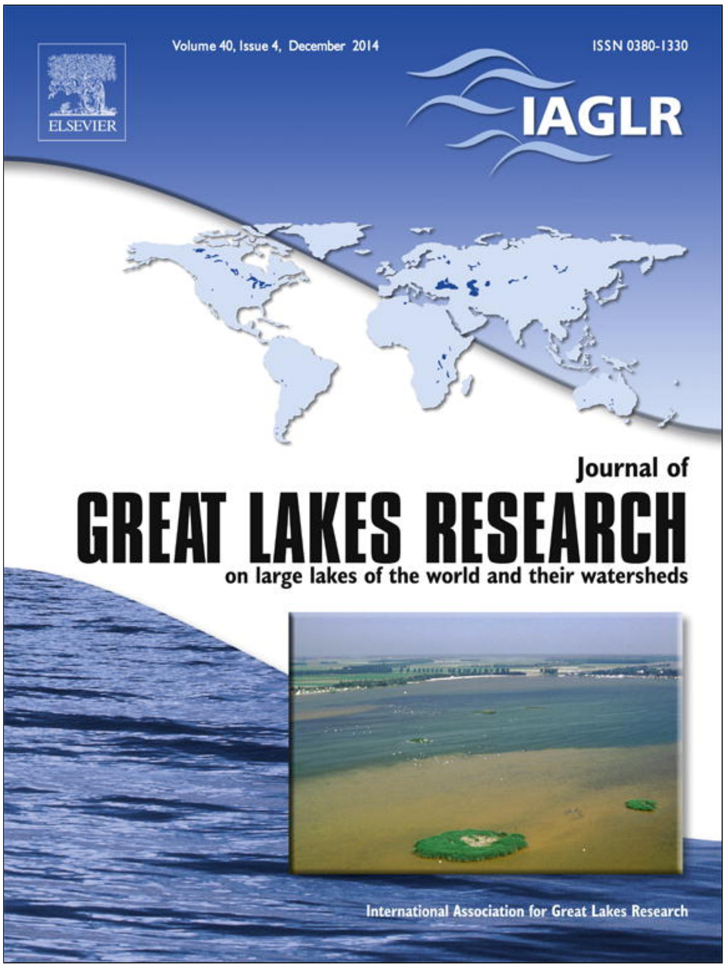
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Thirty-year update: Changes in biological characteristics of degraded muskellunge nursery habitat in southern Georgian Bay, Lake Huron, Canada

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ABSTRACT

Aquatic vegetation is a critical component of nursery habitat for young-of-the-year (YOY) muskellunge. The trophy status of the muskellunge fishery in southeastern Georgian Bay owes its reputation to the widespread distribution of aquatic vegetation in coastal marshes of this region. Unfortunately, wetland habitat has been in decline because of an unprecedented period of sustained low water levels since 1999. In this study, we strategically resampled 16 historic sites that supported YOY muskellunge in 1981. The sustained low water levels and increased shoreline modifications experienced by southeastern Georgian Bay may have contributed to the current disappearance of YOY muskellunge at those sites. These physical stressors appeared to have altered the habitat structure of the plant community and led to changes in fish communities, making them no longer suitable for YOY muskellunge. The precise mechanisms limiting survival to the YOY stage are unknown because spawning adults have been observed in the area in the spring of 2012 and 2013. These results corroborated previous sampling programs at the historic sites (2004–2005: $n = 8$ and 2007: $n = 16$) that employed other fishing gears and protocols as well as a supplemental YOY sampling in 2013 ($n = 26$ additional sites). If this muskellunge population is to remain self-sustaining, a complementary management strategy specifically developed for Georgian Bay is required. The strategy should identify and ultimately protect suitable muskellunge breeding habitat by accounting for the unique geomorphology, current physical stressors affecting Georgian Bay, and the biological links between suitable spawning and nursery habitats.

Introduction

Currently, many native muskellunge (*Esox masquinongy*) populations are no longer self-sustaining (Dombeck et al., 1986; Rust et al., 2002), the primary reason for which appears to be degradation and alteration of spawning and nursery habitat (Dombeck et al., 1986; Farrell et al., 2007; Inskip, 1986; Rust et al., 2002). Although the critical requirements of spawning habitat have been well defined (e.g., dissolved oxygen (DO) concentrations >3.2 mg/L at the substrate water interface; Dombeck et al., 1984; Zorn et al., 1998), relatively little has been established for nursery habitat (Farrell et al., 2007; Kapuscinski and Farrell, 2013; Kapuscinski et al., 2012; Murry and Farrell, 2007), particularly for self-sustaining populations. Newly hatched muskellunge and young-of-the-year (YOY) are assumed to require aquatic vegetation for protection since they are vulnerable to predation by fish, birds and even predaceous insects (Johnson, 1958; Wahl and Stein, 1989). As such, muskellunge nursery habitat in coastal wetlands has been found in close proximity to areas where adults spawn (LaPan et al., 1996). These areas tend to have intermediate densities of aquatic plants including emergent, floating, and submersed aquatic taxa, which structure the upper water column (Craig and Black, 1986; Murry and Farrell, 2007; Werner et al., 1996) and that support suitable abundances of soft-rayed fusiform fish that YOY muskellunge prefer (Kapuscinski et al., 2012; Kapuscinski and Farrell, 2013; Wahl and Stein, 1988). Despite these generalizations, large differences in eco-regions exist within the Great Lakes with respect to geomorphology, ecological characteristics and wetland conditions (see Chow-Fraser and Albert, 1999; Cvetkovic and Chow-Fraser, 2011), making it difficult to extrapolate from site to site in regard to specific habitat requirements for these early stages.

Since the mid-1990s, spawning habitats have been identified and monitored periodically throughout eastern and northern Georgian Bay (Liskauskas, 2007), but detailed inventories of nursery habitats have only been conducted in 1981 and only in southeastern Georgian Bay in the Severn Sound region (Craig and Black, 1986). Since 1999, water levels in the Bay have been extremely low (Sellinger et al., 2008) and in January 2013, they surpassed the previous record low level set in 1965. This period of sustained low water levels is unprecedented and has altered the habitat structure of many coastal wetlands in eastern Georgian Bay (Midwood and Chow-Fraser, 2012). Because the unique geomorphology of these coastal marshes appears to limit the lakeward migration of aquatic vegetation (Mortcsh, 1998), Fracz and Chow-Fraser

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(2013) estimated that almost 25% of the wetland habitat available to fish have already been lost between the historical high and the current low water levels; and greater losses are anticipated with continued water level declines due to global climate change (see Fracz and Chow-Fraser, 2013; Midwood and Chow-Fraser, 2012; Sellinger et al., 2008 for greater discussion). Such a magnitude of wetland loss and alteration is expected to have serious implications for the reproductive success of self-sustaining populations of muskellunge in Georgian Bay that use these wetlands as nursery habitat (Craig and Black, 1986). Along with this change, large stretches of shoreline in southeastern Georgian Bay have also been modified for cottage and recreational development over the past 30 years, alterations that include shoreline hardening, vegetation removal and dredging.

The goals of this study are multi-fold. First, we carried out a field survey in 2012 to determine the current status of historic muskellunge nursery sites in Severn Sound, southeastern Georgian Bay, an area that has not been re-examined for over 20 years (Leslie and Timmins, 1994). Secondly, using information collected by Craig and Black (1986; see Fig. 1) as reference conditions, we compared biotic characteristics between 1981 and 2012 to investigate whether the structural diversity of submerged aquatic (SAV) and emergent vegetation, an important determinant of the fish community (Kapuscinski and Farrell, 2013; Murry and Farrell, 2007), has changed. We speculate that declining water levels and shoreline modification are associated with altered habitat structure and have rendered the historic nursery habitats unsuitable for YOY muskellunge. Finally, we conducted an expanded survey to determine the location of nursery habitat for YOY muskellunge in the summer of 2013 by focusing on coastal wetlands associated with areas where adult muskellunge were found during the 2012 and 2013 spawning seasons. This is the first study conducted in Georgian Bay to investigate long-term changes in the habitat of early life stages of the muskellunge in Georgian Bay, and it will reveal important insights on the potential effects of sustained low water levels on the habitat suitability of historic nursery habitat for this economically and ecologically important muskellunge trophy fishery.

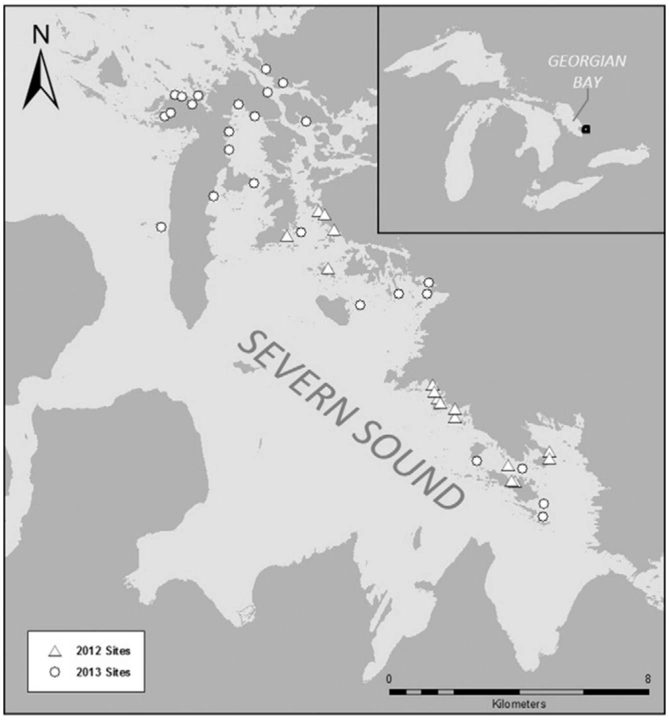

Fig. 1. Map of study area in southeastern Georgian Bay (inset shows location of Georgian Bay within the Laurentian Great Lakes). Triangles identify locations of 16 sites (corresponding to those sampled by Craig and Black, 1986) sampled in 2012, while open circles show locations of 26 additional sites sampled in 2013 (see Methods).

Methods

Study site

Our study sites occur in southeastern Georgian Bay, in the body of water known as Severn Sound (Fig. 1). This region has shallow contours, and is relatively warm and productive compared to the rest of the bay which has deep, cold, oligotrophic waters (Bennett, 1988; Weiler, 1988). Similar to the eastern and northern shores of Georgian Bay, the northern portion of Severn Sound occurs on Precambrian Shield where coastal wetlands are found among rocky outcrops, islands, and in protected bays (deCatanzaro and Chow-Fraser, 2011). Severn Sound began to experience nutrient enrichment by the mid-1980s that was attributed to agricultural and urban development within the watershed; this cultural eutrophication was sufficiently advanced that it was designated as an Area of Concern (AOC) by the International Joint Commission in 1987 and a Remedial Action Plan was enacted (Sherman, 2002). It was delisted as an AOC in 2003, and although the symptoms of eutrophication have disappeared (Croft and Chow-Fraser, 2007), water levels in the recent decade have remained extremely low and this may have exerted a different though equally adverse impact on the ecological integrity of the coastal wetlands in this region.

Historic data

In 1981, Craig and Black (1986) surveyed the fish communities of 103 coastal wetlands in the Severn Sound region in an effort to identify muskellunge nursery habitats. Twenty of the 103 sampled coastal wetlands were found to support YOY muskellunge. In this study, we will refer to these as “historic” sites and will consider them to have been suitable nursery habitat for muskellunge. The Ontario Ministry of Natural Resources (OMNR) provided field data from the 1981 technical report (Black and Craig, 1982) that was used subsequently for their 1986 publication. Data from both documents will be used here to compare with data collected in 2012 (see below).

Fish sampling

In 2012, we surveyed 16 of 20 historic sites sampled by Craig and Black (1986) using the same specifications of seine net (6.4 mm meshing × 15 m × 1.2 m) and same protocols they used (see Craig and Black, 1986 for seining details); only 16 sites were included due to time constraints. Although only a single seine haul per site was used in 1981, we opted to use two seine hauls per site in both the June and July sampling (i.e., 4 seine hauls per site) to increase sampling rigor. The bottom of the seine net was chained to prevent vegetation from rolling the net, and a third person trailed the seine haul with a dip-net to catch or identify any fish that passed through the net. The sampling also took place to match the original 1981 dates for at least one of the four seining efforts; all seine hauls within wetlands were always separated by at least 100 m. Water temperature was taken at a depth of 50 cm at each site after each seine haul. In June and July of 2013, we conducted additional YOY sampling in coastal wetlands where adult muskellunge congregated during the spawning period in 2012 and 2013. This approach has been successful at locating muskellunge nursery habitat in other studies (LaPan et al., 1996; Leblanc pers. obs.) and was expected to yield best-bet locations of current nursery habitat for YOY in Severn Sound. The same net described previously was used in single hauls at 26 sites. The 2012 and 2013 Severn Sound seining technique was identical to that used in a northern Georgian Bay study in 2012 and 2013, which successfully caught YOY muskellunge in both June and July (JP. Leblanc unpubl. data). All fish caught in these surveys were identified to species, counted and then released in the water where they had been caught.

Aquatic vegetation survey

We examined the habitat structure and other characteristics of the historic nursery sites during the first week of August 2012. Due to time constraints, habitat features were only characterized for 14 of the 16 sites sampled for fish in 2012; none of the sites sampled in 2013 were surveyed for vegetation. In 1981, Craig and Black placed quadrats ($0.25\ m^2$) at 2-m intervals along three transects that ran from the shore–water interface to the 1.0 m depth contour to survey the aquatic vegetation. In 1981, the average distance of these transects was 23.8 ± 2.1 m ($\bar{x} \pm 95\%$ CI) but due to the drop in water level (from 176.7 m to 175.92 m) and the bathymetry of Severn Sound, the mean length of the 2012 transects was three times longer (71.4 ± 18.6 m ($\bar{x} \pm 95\%$ CI)). This made it impractical to sample every 2.0 m along the transect in 2012. Therefore, consistent with the protocol of Craig and Black (1986) we ensured that the three transects were separated by at least 10 m, and extended them perpendicular to shore to the 1.0 m depth contour. Placements of the quadrats were, however, separated by intervals greater than 2-m, but we ensured that there were at least 10 equally spaced quadrats along each transect. For smaller wetlands, the start of the three transects were equally spaced along the shore but converged to a central point of the wetland at 1.0 m depth. Transect lengths were consistent within a site, but varied among sites, depending on substrate slope.

Craig and Black (1986) estimated the percent cover of the dominant taxon of SAV and identified all emergent and floating vegetation to species where possible, and counted their stems within each quadrat. We followed this procedure except we used a standardized rake-sweep method (see Croft and Chow-Fraser, 2009), where a garden rake was swept along the substrate-water interface within the quadrat boundaries and all the stems of SAV captured were identified and counted. This was required because high winds at the time of survey resulted in high sediment re-suspension that precluded a consistent visual estimation of SAV cover. We should note that clear water was normally observed throughout much of the season in 2012.

Shoreline modification

Our approach was to compare the number of docks present during 1981 and 2012 to determine if human development had significantly modified the physical condition of the shoreline between the two time periods; however, we were unable to find aerial photos of these sites acquired in 1981 and 2012. The closest approximation of these two time periods were orthophotos taken in 1987 (Forest Resource Inventory aerial photos, OMNR) and IKONOS satellite image (1-m resolution) acquired in 2009. We imported both sets of images into Geographic Information System (ArcMap 10; ESRI Inc., Redlands CA, USA, 2011) and for each site–era we delineated the perimeter of the wetland and counted the number of docks along the shoreline for the 16 sites. We calculated the number of docks per shoreline length ($\#\cdot km^{-1}$) for each period and compared them statistically.

Statistical analysis

All statistical analyses were conducted with the software package, STATISTICA 8.0 (StatSoft, Inc., 2007). We used a repeated measure statistical design to make comparisons between 1981 and 2012 data collected at the historic sites. Each site sampled (i.e. historic nursery wetland) was considered the sampling unit for both fish and habitat analyses. Thus, the data for each site from 2012 were matched with corresponding sites from 1981. When parametric tests were used, the data were transformed to satisfy parametric assumptions; however, if the data could not be normalized, then non-parametric equivalents were used. $Log_{10}(n + 1)$ transformations were used except for proportions, which were arcsine-square root transformed. The June 2013 fish community composition was only compared to the 1981 historic reference sites and not to the 2012 data. All data reported are in transformed units unless otherwise indicated.

Since we employed greater sampling effort in 2012 (4 samples per site) than in 1981 (one sample per site), one of the 2012 samples per site was randomly selected and used in direct comparison between time periods. Frequency of occurrence (percentage of sites where a fish species was present), mean proportional abundance, fish species richness, and Shannon's diversity index scores were calculated for each site and compared to those calculated for historic data. Beta diversity index ($\beta =$ gamma diversity–mean alpha diversity) was also calculated for each sampling period. Proportional abundances of all fish species that occurred in >65% of the sites were compared between time periods; those species occurring at <65% of the sites were first classified into functional guilds (see Table 1) and then grouped for comparison. Data collected in 2013 were treated in a similar manner and compared against data collected in 1981.

Emergent and floating vegetation were first classified into families. We standardized the data by dividing the stem counts for each family by total stem counts of all families (% total for each family). In order to make the 2012 data comparable to the 1981 data for SAV, we first had to convert the 2012 stem counts to an abundance category. Following the description of Craig and Black (1986) relative abundance ratings were calculated for each taxon within each site and their relative abundance ranks were compared to 1981 data. For all SAV taxa that occurred at >40% of the sites in 1981 and 2012, we compared median values of relative abundance ranks in the two time periods. To minimize potential Type-I errors, due to the large number of paired comparisons, a highly conservative Bonferroni correction of $\alpha = 0.005$ was used to test for significant differences between time periods. We also sorted SAV data according to two growth forms (i.e., "low growing" and "canopy growth" following Cvetkovic (2008)) and carried out a 2-factor repeated measures ANOVA (year *growth form as independent factors) to determine if there had been a significant change in habitat structure between 1981 and 2012 based on relative abundance ranks.

Craig and Black (1986) divided the nursery areas they sampled into four "depth zones" and provided a description of "typical muskellunge nursery habitat". They arbitrarily divided transects into these zones but did not indicate the actual depth associated with the upper or lower limits of each zone. In order to compare the depths at each zone between 1981 and 2012, we estimated a substrate slope that would have been present in 1981 and used that to approximate the upper limit of each depth zone and then applied these to the 2012 data. The boundaries of the four zones were determined as follows: Zone 1: 0.0 to 0.10 m; Zone 2: 0.11–0.53 m, Zone 3: 0.54–0.90 m and Zone 4: 0.91 to 1.0 m. Using these estimated depth zones we directly compare the 1981 and 2012 stem counts of emergent and floating vegetation for each site after first performing a square root transformation. We then performed a two-factor repeated measures ANOVA (time ∗ depth zones as independent factors) to determine if this vegetation type varied differentially among depth zones between time. For the 2012 data, we also determined the significant effect of depth zones and growth forms (i.e. low growing versus canopy) on stem densities of SAV using a two-factor ANOVA after first performing a $\log_{10}(n + 1)$ transformation. This analysis excluded depth zone 1 since no SAV was encountered there.

Results

Substantial changes in the fish community were noted between time periods; despite our intensive seining efforts in 2012, we found a complete absence of YOY muskellunge at all 16 historic nursery sites (Table 1; Fig. 2). There was a clear shift in the species composition of the fish community between years (Table 1): black crappie, smallmouth bass, and tadpole madtom (among others) that were common in 1981 were replaced with banded killifish, longear sunfish, and round goby in 2012 (i.e., ≥43%). As a result of these substitutions, we did not find

Table 1
Frequency of occurrence (%) and mean (±S.E.) relative abundance of fish sampled at 16 coastal wetlands in southeastern Georgian Bay (1981 and 2012; see Fig. 1) and the 2013 ($n = 26$) sampling of best-bet nursery habitat locations. Data for 1981 were obtained from Black and Craig (1982). Mean alpha species richness and Shannon Diversity index scores did not differ significantly between years ($p = 0.476$ and 0.958, respectively). Species presented alphabetically by common name within ecological guild group membership such that species occurring at >65% of sites sampled all years were considered "Standalone species". Species occurring at <65% of sites were classified as "Potential forage" for YOY muskellunge if body type could be described as soft-rayed and fusiform (Murry and Farrell, 2007; Kapuscinski et al., 2012) while all other species were classified as "Other species". Untransformed data displayed for presentation purposes.

Ecological guild	Common name	Scientific name	Frequency of occurrence (%)			Relative abundance		
			1981	2012	2013	1981	2012	2013
N/A	Muskellunge	*Esox masquinongy*	100	0	0	0.030 ± 0.007	0	0
Standalone species	Largemouth bass	*Micropterus salmoides*	75	69	69	0.297 ± 0.065	0.034 ± 0.088	0.077 ± 0.023
	Pumpkinseed	*Lepomis gibbosus*	88	88	88	0.258 ± 0.062	0.291 ± 0.063	0.366 ± 0.049
	Yellow perch	*Perca flavescens*	88	94	85	0.151 ± 0.034	0.341 ± 0.052	0.157 ± 0.035
Potential forage	Banded killifish	*Fundulus diaphanus*	0	50	27	0	0.027 ± 0.018	0.014 ± 0.089
	Blackchin shiner	*Notropis heterodon*	25	25	23	0.040 ± 0.045	0.048 ± 0.026	0.038 ± 0.031
	Blacknose shiner	*Notropis heterolepis*	0	0	15	0	0	0.013 ± 0.007
	Bluntnose minnow	*Pimephales notatus*	44	25	31	0.058 ± 0.028	0.033 ± 0.022	0.015 ± 0.007
	Brook silverside	*Labidesthes sicculus*	13	38	38	0.021 ± 0.019	0.055 ± 0.033	0.018 ± 0.008
	Central mudminnow	*Umbra limi*	<13	0	4	No data	0	0.001 ± 0.001
	Golden shiner	*Notemigonus crysoleucas*	<13	6	8	No data	0.003 ± 0.003	0.003 ± 0.003
	Iowa darter	*Etheostoma exile*	<13	6	8	No data	0.002 ± 0.002	<0.0001
	Johnny darter	*Etheostoma nigrum*	13	6	15	0.009 ± 0.006	0.001 ± 0.001	0.001 ± 0.001
	Logperch	*Percina caprodes*	<13	19	12	No data	0.022 ± 0.021	0.005 ± 0.004
	Spotfin shiner	*Cyprinella spiloptera*	0	25	19	0	0.010 ± 0.007	0.002 ± 0.002
	Spottail shiner	*Notropis hudsonius*	0	0	4	0	0	0.002 ± 0.002
Other species	Black crappie	*Pomoxis nigromaculatus*	44	0	0	0.014 ± 0.007	0	0
	Bowfin	*Amia calva*	<13	0	0	No data	0	0
	Brown bullhead	*Ameiurus nebulosus*	<13	25	4	No data	0.020 ± 0.012	<0.0001
	Longear sunfish	*Lepomis megalotis*	0	44	73	0	0.092 ± 0.035	0.100 ± 0.024
	Longnose gar	*Lepisosteus osseus*	<13	6	0	No data	0.007 ± 0.007	0
	Mottled sculpin	*Cottus bairdii*	<13	0	4	No data	0	<0.0001
	Rock bass	*Ambloplites rupestris*	<13	13	12	No data	0.002 ± 0.001	0.002 ± 0.002
	Round goby	*Neogobius melanostomus*	0	50	77	0	0.010 ± 0.004	0.165 ± 0.038
	Smallmouth bass	*Micropterus dolomieu*	<13	0	4	No data	0	0.001 ± 0.001
	Tadpole madtom	*Noturus gyrinus*	<13	0	19	No data	0	0.003 ± 0.002

significant differences in species diversity between time periods (i.e., mean species richness and Shannon's Index scores; $p > 0.4$).

Of the three most numerically dominant species present in both time periods, the relative abundance of yellow perch increased significantly between 1981 and 2012 (mean difference ± SE: 0.233 ± 0.070; Paired *t*-test, $t_{15} = 3.330$, $p = 0.005$), while that for largemouth bass decreased significantly (mean difference ± SE: −0.356 ± 0.101; Paired *t*-test, $t_{15} = -3.537$, $p = 0.003$; Table 1). Although we did not detect any significant differences between time periods for pumpkinseeds (Paired *t*-test, $t_{15} = 0.423$, $p = 0.675$), the combined catch of pumpkinseeds and yellow perch accounted for >60% of all the fish caught in 2012, compared with only 39% in 1981 (Table 1). Thus, consistent with a decline in beta-diversity between 1981 ($\beta = 14.56$) and 2012 ($\beta = 11.12$), the fish community appeared less diverse in 2012, dominated by yellow perch and pumpkinseed. We also compared the less common species between time periods (see Table 1). The mean relative abundance of the "potential forage guild" for 1981 was 0.276 ± 0.07 ($\bar{x} \pm$ SE), which was not significantly different from the mean for 2012 of 0.390 ± 0.081 (Paired *t*-test, $t_{15} = 1.100$, $p = 0.289$) (Table 1). Similarly, there was no significant difference between the mean proportional abundance of the "other species guild" 0.285 ± 0.077 ($\bar{x} \pm$ SE) calculated for the 1981 data, and 0.153 ± 0.033 calculated for 2012 data (Paired *t*-test, $t_{15} = -1.615$, $p = 0.127$; Table 1).

Physical features of the historic nursery sites differed significantly between time periods. In addition to a significant difference in median transect length between time periods (28.0 m vs. 59.3 m; Wilcoxon Matched Pairs Test: $z = 3.156$, $p = 0.004$), the median value of docks per shoreline km associated with the 1987 aerial photos was significantly lower than that associated with the 2009 IKONOS satellite images (0.0 vs. 6.05 docks $\cdot$ km^{-1}; Wilcoxon Matched Pairs Test: $z = 2.93$, $p = 0.003$, $n = 16$). No significant differences in water temperature were detected between sampling periods (Wilcoxon Matched Pairs Test: $p = 0.642$); however, water temperatures measured in 2012 showed greater variability (range: 17.4–30.5 °C) than those measured in 1981 (range: 21.0–28.0 °C).

Differences in the physical structure and taxonomic composition of the aquatic plant community were also evident. Average alpha richness of SAV was significantly lower in 1981 compared to 2012 ($\bar{x}$ difference ± SE: −3.714 ± 1.150, Paired-$T_{13} = -3.229$, $p = 0.007$), even though gamma richness did not differ between time periods (i.e., 17 species; Table 2). Due to differences in methods employed to survey the SAV community, (i.e. physically counting and identifying all SAV stems in 2012 vs. visual estimation of percent cover of SAV in 1981), we decided to only investigate differences between years with respect to the dominant SAV species present. We found relatively few differences on a species-by-species basis when relative abundance ranks were calculated for all of the common SAV species (encountered in >40% of the sites; Table 2). The only exceptions were *Myriophyllum spicatum* and *Potamogeton robbinsii* which were both more abundant in 2012 than in 1981 (Wilcoxon Matched Pairs Test: $p < 0.0025$; Table 2). Consequently, the relative abundance rank of pooled SAV growth forms was significantly greater in 2012 than in 1981 ($F_{1,\,26} = 11.137$, $p = 0.003$; Fig. 3), while low growth SAV had a significantly greater relative abundance rank than did canopy forms, when pooled within years ($F_{1,\,26} = 51.216$, $p < 0.001$; Fig. 3).

We wanted to know if mean stem densities for the two growth forms differed significantly among depth zones to describe present conditions of SAV at the historic sites (Fig. 4). Within each depth zone, low-growing taxa were noted consistently more frequently than were canopy taxa (Fig. 4). When pooled among depth zones, stem density of low-growing SAV was significantly greater than that of canopy SAV ($F_{1,\,78} = 35.760$, $p < 0.001$). There was also a significant main effect of depth zone (SAV growth forms pooled; $F_{2,\,78} = 11.921$, $p = 0.02$) with depth zone 2 having significantly lower stem densities than did depth zone 3 (Tukey HSD multiple comparison test; $p = 0.02$). The dominant canopy species in 2012 were *Elodea canadensis*, *Myriophyllum*

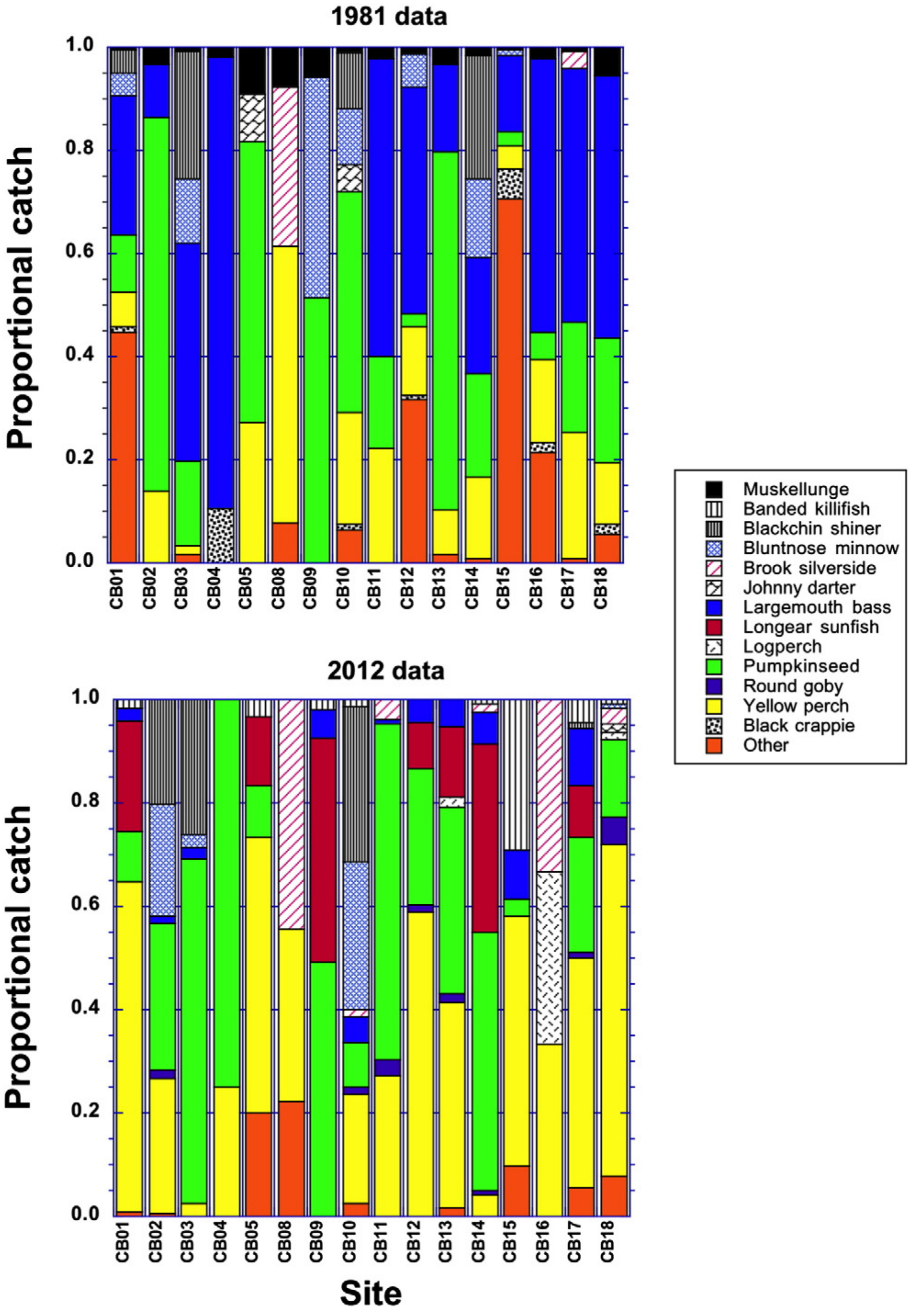

Fig. 2. Comparison of proportional abundance of fish caught in the 1981 and 2012 surveys. Untransformed data displayed for presentation purposes.

spicatum, and *Vallisnerias americana*, which accounted for >40%, >24% and >14% of all the stems counted in 2012, respectively while the dominant taxa of low-growing forms were *Najas flexilis*, *Chara* sp., and *Potamogeton robbinsii*, accounting for >85% of the stems counted for this growth form (see Table 2).

In 2012, we found fewer families of emergent and floating taxa per site than in 1981 ($\bar{x}$ difference ± SE: -3.928 ± 0.485, Paired-$T_{13} = 8.089$, $p < 0.0001$). Except for pipeworts (*Eriocaulaceae*), which was found more frequently in 2012 than in 1981, all other families were detected less frequently in 2012 than in 1981 (Table 3). Although we were unable to detect significant differences in percent composition of emergent and floating taxa at the family level, many families that had been present in 1981 were no longer present in 2012 (Table 3). We also compared stem densities of combined emergent and floating vegetation to determine significant differences between time periods and among depth zones. Although no significant interaction between time period and depth zone ($F_{3,\,78} = 2.3246$, $p = 0.081$) was detected, differential patterns of emergent and floating vegetation stem densities within years and among depth zones were found based on Tukey HSD multiple comparison tests. Within respective years, stem counts near the shoreline were significantly greater than those measured at all other depth zones (Tukey HSD; $p < 0.001$; Fig. 5); however, between years, stem densities in 2012 were always significantly lower than those in 1981 for all depth zones (Tukey HSD; $p < 0.03$ in all cases; Fig. 5). Whereas mean stem counts in 1981 were significantly higher in Zone 2 than in either Zone 3 or 4 ($p < 0.013$), we found no significant difference in stem densities of emergent and floating vegetation for depth zones 2, 3, or 4 in 2012 ($p > 0.191$; Fig. 5). These data are

Table 2
Frequency of occurrence (Freq occur; %) and mean relative abundance (Rel abund) with 95% Confidence Interval (CI) relative abundance of SAV sampled in 1981 and 2012. Common taxa are those occurring in >40% of the samples. A conservative Bonferroni correction of $\alpha = 0.005$ was used to test differences between median values between time periods. Untransformed data displayed for presentation purposes.

SAV taxa	1981			2012		
	Freq occur	Rel abund[d]	CI	Freq occur	Rel abund[e]	CI
Slender water nymph (*Najas flexilis*)[a]	92.9	6.21	1.07	100	6.00	0.91
Chara spp. (*Chara* sp.)[a]	85.7	4.50	1.56	92.9	5.71	1.07
Variable pondweed (*Potamogeton gramineus*)[b]	85.7	3.50	1.26	64.3	1.93	1.12
Water celery (*Vallisneria americana*)[b]	57.1	2.57	1.53	100	3.43	0.90
Common waterweed (*Elodea canadensis*)[b]	42.9	1.50	1.15	92.9	2.57	1.17
Coontail (*Ceratophyllum demersum*)[b]	42.9	0.57	0.44	71.4	0.71	0.27
Clasping-leaved pondweed (*Potamogeton richardsonii*)[b]	64.3	1.14	0.78	50.0	0.50	0.30
Milfoil sp. [b,c], *	42.9	0.43	0.30	100	2.64	1.12
Fern-leaf pondweed (*Potamegeton robbinsii*)[a], *	28.6	0.29	0.27	100	3.14	1.34
Flat-stemmed pondweed (*Potamogeton zosteriformis*)[b]	35.7	0.64	0.66	64.3	1.29	0.77

* Indicates median values are significantly different between time periods ($p < 0.0025$) based on a Wilcoxon Matched Pairs Test.
[a] Low growing SAV taxa.
[b] Canopy SAV taxa.
[c] Data for 1981 were not identified to species whereas 2012 data consisted only of (*Myriophyllum spicatum*).
[d] In decreasing mean relative abundance, those taxa occurring in <43% of sites in 1981 were: arrowhead spp. (*Sagittaria* spp.), pipewort (*Eriocaulon aquaticum*), bladderwort spp. (*Utricularia* spp.), Beck's water marigold (*Bidens beckii*), quillwort (*Isoetes* spp.), pondweed spp. (*Potamogeton* spp.), and large-leaved pondweed (*Potamogeton amplifolius*)
[e] In decreasing mean relative abundance, those taxa in the "Other" category in 2012 were: quillwort (*Isoetes* spp.), curly-leaf pondweed (*Potamogeton crispus*), Beck's water marigold, freshwater sponges, slender pondweed (*Potamogeton pusillus*), sago pondweed (*Stuckenia pectinatus*) and large-leaved pondweed (*Potamogeton amplifolius*).

consistent with the observation that the distribution of emergent and floating vegetation was less dense and more homogeneous in 2012 among all depth zones compared with those in 1981.

Twenty-six additional sites were sampled for YOY muskellunge in June 2013, in coastal wetlands where adult muskellunge had been caught during the 2012 and 2013 spawning period. Despite this increased effort, we did not find any YOY muskellunge in any coastal wetland. Although we found no significant differences in taxa richness between 1981 and 2013 ($t_{40} = 0.346$, $p = 0.731$), the beta diversity was slightly higher in 2013 ($\beta = 16.31$) than in 1981 ($\beta = 14.56$), and we found some differences in the species composition and community structure of the fish communities (Table 1). The proportional abundance of largemouth bass was significantly lower in 2013 ($\bar{x} \pm$ SE: 0.208 ± 0.041) than in 1981 ($\bar{x} \pm$ SE: 0.511 ± 0.094; $t_{40} = -3.380$, $p = 0.002$). By contrast, we found a higher proportion of fish that we grouped as "Other Species" (see Table 1) in 2013 (0.508 ± 0.055) compared with 1981 (0.285 ± 0.077; $t_{40} = 2.413$, $p = 0.02$; Table 1). This appeared to be driven by the presence of the invasive round goby. Since round goby had only colonized Severn Sound within the past decade, this species was absent in the 1981 samples, but it had been firmly established by 2013, accounting for approximately 60% of the catch. Once round gobies were excluded from the "Other Species" grouping, we no longer found a significant difference between time periods ($t_{40} = -0.1714$, $p = 0.865$).

Discussion

The current suitability of nursery habitats for YOY muskellunge in southeastern Georgian Bay is questionable. Despite the greater seining

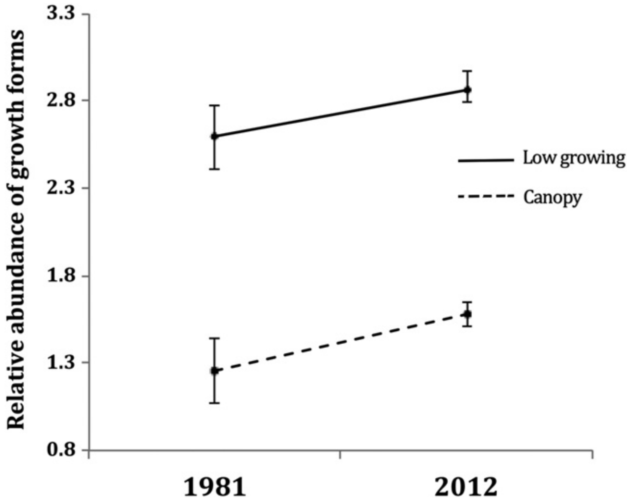

Fig. 3. Comparison of mean (±S.E.) relative abundance ratings of low growing and canopy growth forms surveyed in 1981 and 2012. Based on a 2-factor repeated measures ANOVA, no significant interaction was detected ($p = 0.880$) indicating that relative abundance ratings of SAV growth forms followed similar patterns between years. However, significant main effects of year ($F_{1,\,26} = 11.137$, $p = 0.003$) and SAV growth from ($F_{1,\,26} = 51.216$, $p < 0.001$) were detected.

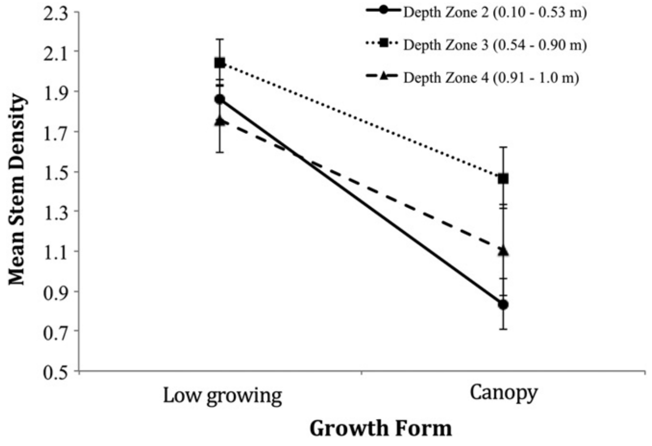

Fig. 4. Comparison of mean stem density ($\log_{10}(n + 1)$) of SAV for two growth forms sampled in 2012. Data are plotted separately for each depth zone (zones 2 to 4 inclusive). Two-factor ANOVA indicated no significant interaction between growth form and Depth Zone ($F_{2,\,78} = 1.191$, $p = 0.309$). Stem densities of canopy plants were consistently lower than those of low-growing forms irrespective of depth zone ($F_{1,\,78} = 35.760$, $p < 0.001$). When data was pooled by depth zone a significant main effect was noted ($F_{1,\,78} = 3.927$, $p = 0.02$) with depth zone 2 having significantly lower SAV stem densities than only depth zone 3 (Tukey HSD, $p = 0.02$).

Table 3
Comparison of frequency of occurrence, and percent composition with 95% Confidence Interval (CI) of families of emergent + floating vegetation sampled in 1981 and 2012. Data correspond to means for 16 sites. Overall family richness was significantly lower in 2012 (3.57 ± 0.562) than in 1981 (7.50 ± 0.416) (Paired *t*-test, $t_{14} = 8.089$, $p < 0.0001$).

Emergent and floating plant families	Frequency occurrence		% composition		±95% Confidence Interval	
	1981	2012	1981	2012	1981	2012
Grasses (Poaceae)	100	21	7	5	4.4	9.7
Arrowheads (Alismataceae)	100	<20	10	<3	12.1	–
Sedges (Cyperaceae)	93	86	54	42	13.8	20.3
Pickerelweed (Pontederiaceae)	79	21	9	4	4.9	5.6
Water lilies (Numphaeaceae)	79	50	7	13	4.6	13.0
Pondweeds (Potamogetonaceae)	79	43	5	3	3.8	3.7
Rushes (Juncaceae)	71	–	4	–	3.3	–
Burreeds (Sparganiaceae)	64	<20	2	<3	2.3	–
Pipewort (Eriocaulaceae)	–	64	–	17	–	15.4
Cattails (Typhaceae)	<20	29	<2	4	–	5.0
Others	71[a]	21[b]	3	3	2.4	6.2

[a] In decreasing frequency of occurrence are 7 families: irises (Iridaceae), cattails (Typhaceae), pipeworts (Eriocaulaceae), horsetails (Equisetaceae), arums (Araceae), parsley (Umbelliferae) and smartweeds (Polygonaceae).

[b] In decreasing frequency of occurrence are 2 families: burreeds (Sparganiaceae) and arrowhead (Alismataceae).

effort expended in 2012 compared with 1981, and an additional year (2013: 26 sites) targeting the "best-bet" nursery sites close to where adult muskellunge were found during the spawning season, we have not been able to find a single YOY. There have been significant changes in both the macrophyte and fish communities at the historic nursery sites, and at least some of these changes are related to the recent episode of sustained low water levels since 1999 (Midwood and Chow-Fraser, 2012) and some are due to modifications of the shoreline from human activities over the past 3 decades (D. Weller, unpub. data). The plant community has changed with respect to species composition and habitat structure. We noted an increase in the relative abundance ranks of *M. spicatum* and *P. robbinsii* in 2012 and a less diverse community of emergent and floating vegetation, and hence a less diverse vertical structure. Similarly, we observed a significant change in the fish community, with a shift in species composition (e.g., establishment of round goby) and a loss in beta-diversity through time. Compared with 1981, we observed a significantly lower catch of largemouth bass but a significantly higher catch of yellow perch in 2012 at the historic nursery sites.

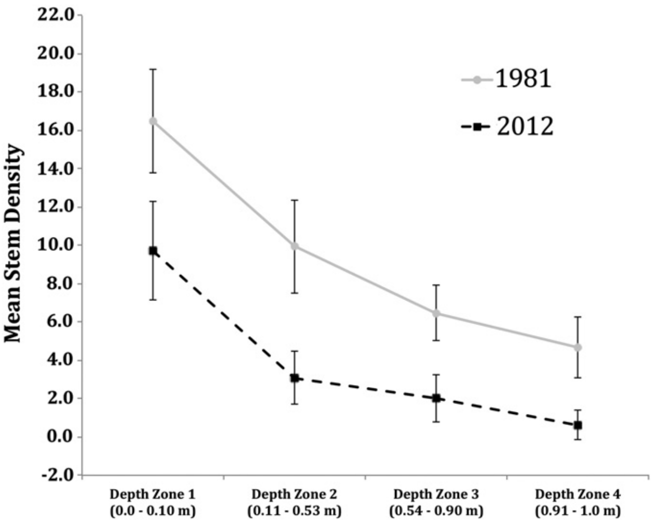

Fig. 5. Comparison of mean (±95% CI) stem densities (square root transformed) of emergent and floating vegetation measured at four depth zones in 1981 and 2012. There was no significant interaction between depth zone and time period (2-factor repeated measures; $F_{3,\,78} = 2.3246$, $p = 0.0813$); mean densities calculated in 2012 were all uniformly lower than those in 1981 (Tukey HSD multiple comparison tests; $p < 0.05$).

Because we only have data from two time periods, it is inappropriate to guess when the changes actually began. It is important to note that during the early 1990s, Leslie and Timmins (1994) found a few YOY muskellunge in southwestern Georgian Bay (i.e., in Sturgeon and Penetang Bays), which are located within an approximate 12 km radius from our furthest sites. By the following decade, however, Chow-Fraser (unpub. data) conducted electrofishing surveys and similar seining efforts in 2004, 2005 and 2007, and did not find any YOY muskellunge at 16 of the sites sampled by Craig and Black in 1981. In 2007, a shorter seine net (5.0 m × 1.0 m in 2007 versus 15.0 m × 1.2 m in 2012) with smaller mesh (4.0 mm in 2007 versus 6.4 mm in 2012) was hauled three times at each of 16 historic sites during June and July. In 2004 and 2005, day-time boat electrofishing surveys were used to sample eight of the historic sites opportunistically between mid-June and mid-August as part of a study to examine the effect of gear bias on sampling efficiency (see Cvetkovic et al., 2012). Because of these differences in methods, we were unable to make direct statistical comparisons with either the historic or 2012 data (Cvetkovic et al., 2012); but we can use these results to confirm that YOY muskellunge have not been present for at least the past decade. We are confident that if they had been present, the seining method we used in 2012 would have been able to catch YOY muskellunge in Severn Sound because we used this protocol successfully to sample YOY muskellunge in two embayments in northern Georgian Bay during 2012 (JP. Leblanc, unpub. data). These results confirm previous observations that the early life stages of muskellunge are highly sensitive to alterations of their breeding habitat (Dombeck et al., 1986; Farrell et al., 2007; Rust et al., 2002). This study is the first to show this same phenomenon in Georgian Bay, where the level of human activities is still relatively low compared to elsewhere in the Great Lakes.

Suitable muskellunge nursery habitat likely requires intermediate densities or cover of various macrophyte types (Cook and Solomon, 1987; Craig and Black, 1986; Murry and Farrell, 2007; Werner et al., 1996) sufficiently dense to provide cover from predation but not too dense to impede foraging activities (Crowder and Cooper, 1982; Diehl and Eklöv, 1995; Gotceitas and Colgan, 1989). Because YOY preferentially use the upper portion of the water column (Murry and Farrell, 2007; Werner et al., 1996), presence of canopy-forming SAV, floating and emergent vegetation are important structuring components of nursery habitat. Therefore, wetlands characterized by high densities of emergent vegetation (Craig and Black, 1986; Murry and Farrell, 2007) and canopy-forming SAV (Kapuscinski and Farrell, 2013; Murry and Farrell, 2007) should be considered high-quality nursery habitat, whereas wetlands dominated by low growth form SAV (e.g., macroalgae and *P. robbinsii*) with relatively low densities of canopy-forming SAV should be considered lower quality habitat (Kapuscinski and Farrell, 2013). Direct comparisons of emergent and floating macrophyte stem densities between 1981 and 2012 confirm that the historic nursery sites had become structurally homogeneous within the lower three depth zones. Furthermore, low-growing SAV taxa (primarily macroalgae), which are less suitable as nursery habitat than canopy forms, were consistently more abundant in all three depth zones. However, the mechanism(s) resulting in the altered macrophyte structure remains speculative. Interactions between low water levels, shoreline modification, and indirect physical processes such as increased ice-scour impacts from the shallower substrates, may act in tandem to facilitate currently observed macrophyte structure (i.e., diminished canopy vs. increased low SAV densities).

Differences in species composition and structure of the fish community likely followed changes in the macrophyte community at some point between 1981 and 2012 (Cvetkovic et al., 2010; Eadie and Keast, 1984; Smokorowski and Pratt, 2007; Weaver et al., 1997). Midwood and Chow-Fraser (2012) found a lag time of 5 years before both the plant and fish communities showed a significant response to sustained low water levels in eastern Georgian Bay. Therefore, it is likely that changes in the plant community did not facilitate a noticeable change in the fish community until the mid-2000s, at which point yellow perch began to increase at the expense of largemouth bass. This is consistent with the observation that largemouth bass prefer intermediate to high densities of aquatic vegetation (Scott and Crossman, 1998) and Midwood and Chow-Fraser's (2012) finding that there was a general reduction in abundance of largemouth bass following a decline in amount of "fish habitat" in wetlands of eastern Georgian Bay as a result of sustained low water levels. Havens et al. (2005) recorded a similar negative effect of water-level decline on largemouth bass recruitment and abundance in Lake Okeechobee, Florida. The increased abundance of yellow perch can also be explained by the literature. We know that this species can thrive in many habitat types from macrophyte dominated areas (Bryan and Scarnecchia, 1992; Fullerton and Lamberti, 2006) to rocky habitats (Janssen and Luebke, 2004), both of which are found at the historic sites. Past studies have also shown that habitats dominated by low-growing SAV, similar to what we currently see at the historic nursery sites, can lead to increased density of benthic macroinvertebrates (Hanson, 1990), which tend to favor yellow perch (e.g., Dettmers et al., 2003; Graeb et al., 2004; Romare, 2000).

It is interesting to note that the relative abundance of the preferred forage type for YOY muskellunge (i.e. soft-rayed fusiform species; Kapuscinski et al., 2012; Murry and Farrell, 2007) had not changed through time, even though some of the species had been replaced with ecological analogs (e.g., the reciprocal occurrence of bluntnose minnow in 1981 and banded killifish in 2012). Thus, it seems unlikely that availability of preferred forage was limiting muskellunge recruitment. Round gobies and yellow perch may be feeding on muskellunge larvae and eggs and thus limiting their recruitment (Fitzsimons, 1990; Nichols et al., 2003; Riley and Marsden, 2009; Steinhart et al., 2004). The negative association between yellow perch abundances and YOY muskellunge has been documented (Kapuscinski and Farrell, 2013; Murry and Farrell, 2007), and round gobies are known to be predators of eggs of many fish including other broadcast spawners (e.g., Lake Sturgeon (*Acipenser fulvescens*); Nichols et al., 2003). Nevertheless, this is pure speculation because the extent to which round gobies can limit muskellunge recruitment through egg depredation has not yet been studied (Kapuscinski et al., 2012). Given that muskellunge have a relatively low natural rate of recruitment (Scott and Crossman, 1998; Zorn et al., 1998; Farrell and Werner, 1999), continual exposure to increased egg and larval mortality could have dire consequences for the overall viability of the population (Nilsson, 2006). That adults returned to the same areas during the spawning season in 2012 and 2013, areas which are close to the historic nursery sites, suggests that muskellunge exhibit spawning-site fidelity (Crossman, 1990; Jennings et al., 2011; LaPan et al., 1996). If this is the case, then the sub-population in Severn Sound are inadvertently spawning in coastal wetlands that may be no longer suitable habitat for YOY, and protecting these spawning habitats may do little to ensure the reproductive success of this trophy muskellunge fishery.

There is currently insufficient data to point to a decline in the adult muskellunge population in Georgian Bay (Kerr, 2007); however, muskellunge populations in this region occur at low densities, and consist of genetically distinct sub-populations, including one from Seven Sound (Chris Wilson, OMNR, pers. comm.). Because muskellunge are long-lived and have slow growth, current monitoring programs (see Kerr, 2007; Liskauskas, 2007) do not provide sufficient information to resolve statistically significant change in populations over time for a particular sub-region of Georgian Bay (Brosi and Biber, 2009; Taylor and Gerrodette, 1993). When we examined data from the muskellunge Volunteer Angler Diary Program (VADP; see Kerr, 2007 and OMNR website: http://www.mnr.gov.on.ca) specifically for Severn Sound between 1995 and 2010, angler effort appeared to have been constant through time, while angler catch-per-unit-effort (CPUE; measured as the number of muskellunge angled per rod hour) showed a negative, albeit not statistically significant relationship with time (OMNR unpubl. data). This divergent pattern between angler effort and CPUE with time also casts doubt on the presumption based on VADP indices that the current muskellunge population is self-sustaining (Kerr, 2007; Mosindy and Duffy, 2007).

Despite the strong recommendations by Craig and Black (1986) that the breeding habitats in Severn Sound be protected from human development and the demonstrated association between shoreline modifications and muskellunge reproductive dysfunction elsewhere (Dombeck et al., 1986; Rust et al., 2002), the density of docks and development of marinas were permitted to increase along the shoreline between 1981 and 2012. This demonstrates clearly that we cannot rely on current planning regulations to protect critical fish habitat for this self-reproducing population in Georgian Bay, and there is urgency to educate local planning units on the tremendous value of coastal wetlands in this region (Brazner and Beals, 1997; Jude and Pappas, 1992; Wei et al., 2004).

We suggest that the observed change in macrophyte structure, in addition to shoreline modifications, may have been responsible for the disappearance of the YOY muskellunge. Thus, in addition to restricting the harvest of adults, an additional management strategy must include more stringent protective measures of both critically important spawning *and* nursery habitat. Novel tools that can efficiently and effectively identify suitable muskellunge spawning and nursery habitat must be developed specifically for Georgian Bay (e.g. Habitat Suitability Index model; Cook and Solomon, 1987). Our study shows that, in southeastern Georgian Bay, suitable muskellunge nursery habitat may be very limited; therefore, more detailed information regarding specific nursery habitat requirements for muskellunge, the processes that structure them, as well as linkages between spawning and nursery habitat must be elucidated (Farrell et al., 2007). If the southeastern Georgian Bay muskellunge population is to persist, complementary management strategies are needed, with greater emphasis on habitat protection.

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