Global Change Biology

Global Change Biology (2012) **18**, 93–105, doi: 10.1111/j.1365-2486.2011.02558.x

Changes in aquatic vegetation and fish communities following 5 years of sustained low water levels in coastal marshes of eastern Georgian Bay, Lake Huron

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Abstract

Aquatic vegetation in the relatively pristine coastal wetlands of eastern Georgian Bay provides critical habitat for a diverse fish community. Declining water levels in Lake Huron over the past decade, however, have altered the wetland plant assemblages in favour of terrestrial (emergent and meadow) taxa and have thus reduced or eliminated this important ecosystem service. In this study, we compared IKONOS satellite images for two regions of eastern Georgian Bay (acquired in 2002 and 2008) to determine significant changes in cover of four distinct wetland vegetation groups [meadow (M), emergent (E), high-density floating (HD) and low-density floating (LD)] over the 6 years. While LD decreased significantly (mean -2995.4 m^2), M and HD increased significantly (mean +2020.9 m^2 and +2312.6 m^2, respectively) between 2002 and 2008. Small patches of LD had been replaced by larger patches of HD. These results show that sustained low water levels have led to an increasingly homogeneous habitat and an overall net loss of fish habitat. A comparison of the fish communities sampled between 2003 and 2005 with those sampled in 2009 revealed that there was a significant decline in species richness. The remaining fish communities were also more homogeneous. We suggest that the observed changes in the wetland plant community due to prolonged low water levels may have resulted in significant changes in the fish communities of coastal wetlands in eastern Georgian Bay.

Keywords: change detection, coastal wetlands, Great Lakes, remote sensing, water-level regulation

Received 8 May 2011; revised version received 5 September 2011 and accepted 16 September 2011

Introduction

Global climate change is expected to greatly alter the hydrological cycle on a world-wide basis, resulting in drought, extreme precipitation events, and increases in sea level (Karl & Trenberth, 2003; Trenberth *et al.*, 2003). Predictions for large inland lakes, such as the Laurentian Great Lakes, have been highly variable, but majority point to an overall decline in lake levels for all five lakes, with much greater extremes than those experienced over the past century (Mortsch & Quinn, 1996; Magnuson *et al.*, 1997; Angel & Kunkel, 2010). These will be the result of predicted warmer winters, seasonal changes in precipitation, increased evaporation and water-surface temperatures, decreased ice cover, and earlier spring snow melt (Lenters, 2001; Quinn, 2002; Sellinger *et al.*, 2008; Hanrahan *et al.*, 2010). These modifications in hydrology will have far-reaching effects on the structure and function of coastal ecosystems, including a change in habitat ranges that may negatively impact artisanal, commercial and recreational fisheries, and allow for the introduction of invasive species (Ross *et al.*, 2001; Ficke *et al.*, 2007).

Unlike smaller inland lakes, water levels in the Great Lakes fluctuate naturally both seasonally and annually, and in multi-year cycles (Lyon *et al.*, 1986; Lenters, 2001; Quinn, 2002; Sellinger *et al.*, 2008; Hanrahan *et al.*, 2010). Such fluctuations govern the type of aquatic plant communities in coastal marshes that occur along the margins of these large lakes (Keddy & Reznicek, 1986; Quinlan & Mulamoottill, 1987; Grosshans *et al.*, 2004; Hudon, 2004; Gathman *et al.*, 2005; Wei & Chow-Fraser, 2005). Plants in these wetlands have a range of tolerance to depth and duration of inundation that allow them to dominate under different water-level scenarios (Gathman *et al.*, 2005). During periods of high lake levels, submerged vegetation typically dominate, whereas at low water levels, meadow species dominate (Burton, 1985; Hudon, 1997; Chow-Fraser *et al.*, 1998; Mortsch *et al.*, 2008; Wilcox & Nichols, 2008). This relationship is, however, complicated by the observed time lag between water level and vegetation type such that the distribution observed at any given time is determined by water levels experienced 2–5 years earlier (Quinlan & Mulamoottill, 1987).

Water levels in the Laurentian Great Lakes have a long history of human-induced regulation, which has

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disturbed the natural cycles of high and low water levels (Quinn, 2002). It is known that poor habitat conditions exist at extremely high (Gathman *et al.*, 2005) or low water levels (Quinlan & Mulamoottill, 1987), but the exact effects of a disruption in natural water cycles on coastal systems is not well studied. It is clear, however, that fluctuations are essential for maintaining healthy and functional coastal marshes because they prevent dominance by one type of vegetation community (Wilcox & Meeker, 1991; Wilcox, 2004; Gathman *et al.*, 2005).

Of the five Great Lakes, Lake Michigan–Huron is expected to undergo the greatest change in water levels, decreasing by as much as 2.5 m below base case (Mortsch & Quinn, 1996; Magnuson *et al.*, 1997). A drop of such a magnitude should have profound impacts on the plant communities of coastal marshes, but it is the loss of periodicity in the cycle of highs and lows that may be of a greater concern to ecologists. Early evidence of such a loss was documented by Sellinger *et al.* (2008), who showed that water levels have remained near record low levels since 1999, which has resulted in a period of continuous drawdown for almost 10 years, compared with a maximum period of continuous low levels of 5 years during the past century. Such a period of sustained low water levels may drastically alter the distribution of aquatic plants and lead to a more structurally homogeneous plant community.

Coastal wetlands of eastern Georgian Bay, Lake Huron, represent some of the most pristine systems in the Great Lakes (Chow-Fraser, 2006; Cvetkovic & Chow-Fraser, 2011). Because human-induced disturbance (e.g. agricultural and urban development) is minimal compared to other areas of the Great Lakes, the major threat to these wetlands is prolonged exposure to low water levels such as that experienced over the past decade. These coastal marshes form in small, shallow bays and are naturally oligotrophic due to low nutrient input from the surrounding granite bedrock and their connection to Georgian Bay (deCatanzaro & Chow-Fraser, 2011). Majority of these are still in pristine condition and they support a diverse community of aquatic macrophytes, typically with diverse vertical and horizontal structure (Croft & Chow-Fraser, 2007). This is important for the many wetland-dependent fish that use these areas for spawning and nursery habitat (Jude & Pappas, 1992; Randall *et al.*, 1996; Wei *et al.*, 2004; Jude *et al.*, 2005).

The ideal fish habitat must necessarily be optimized for both food availability and protection from predators (Savino & Stein, 1982; Werner *et al.*, 1983; Eadie & Keast, 1984; Killgore *et al.*, 1989). Many studies have shown a trade-off between dense aquatic vegetation, where fish are protected from predators but where fewer invertebrate prey exist, and the open water, where there is abundant food but where fish are much more vulnerable to predators (e.g. Werner *et al.*, 1983; Eadie & Keast, 1984; McIvor & Odum, 1988). This trade-off results in many species preferentially using areas along the edge of dense vegetation and open water, or areas with intermediate vegetation densities (Höök *et al.*, 2001; Jacobus & Webb, 2006). A complex landscape with numerous patches of vegetation is therefore ideal as it allows fish to move amongst patches in relative safety.

Structural complexity can be expressed in various ways, from a comparison of stem density and per cent coverage of species among sites (Trebitz *et al.*, 2009), to determination of patch size within wetlands (Jacobus & Webb, 2006), to a statistical measure of habitat variability across a region (Trebitz *et al.*, 2009). Jacobus & Webb (2006) found that when average patch size was reduced to <128 m^2, species richness of the fish community fell, rare species began to disappear, and overall, the fish assemblage became less diverse. We predict that the prolonged period of low water levels experienced over the past decade in Lake Huron has reduced the structural complexity of the plant communities in Georgian Bay wetlands, by allowing terrestrial meadow species to displace the emergent and submersed aquatic vegetation (Leahy *et al.*, 2005; Wei & Chow-Fraser, 2005). We also hypothesize that the alteration in structure and composition of the habitat would lead to a significant reduction in the species richness of the fish communities because high habitat complexity is essential for maintaining high fish diversity (reviewed in Smokorowski & Pratt, 2007; Cvetkovic *et al.*, 2010).

The large distribution of coastal wetlands in eastern Georgian Bay, coupled with difficulties in accessing many of them, prevents majority of wetlands from being surveyed *in situ*. Satellite imagery provides an alternate survey method because spectral information can be used to identify different plant groups that occur over a very large area (Bartlett & Klemas, 1980; Silva *et al.*, 2008; Midwood & Chow-Fraser, 2010). This approach has been used successfully to monitor changes in land-use (Dewan & Yamaguchi, 2009), and to map terrestrial wetlands (Houhoulis & Michener, 2000) and coastal wetlands (Leahy *et al.*, 2005; Baker *et al.*, 2007). We will examine changes in the habitat complexity by conducting a change-detection analysis of two IKONOS satellite images acquired in 2002 and 2008 for two regions of eastern Georgian Bay. The 6 year difference between acquisitions ensures that the 5 year lag time suggested by Quinlan & Mulamoottill (1987) is taken into consideration. We will determine significant changes in above-surface aquatic wetland vegetation (floating and emergent) and quantify changes in average patch size within wetlands. Our overall goal is to quantify changes in vegetation coverage and structure that have occurred during a period of sustained low water levels and determine how these changes in habitat have influenced the fish community. Understanding wetland vegetation dynamics is essential for making recommendations on future water-level regulation plans and understanding the potential response of the fish community to forecasted water levels.

Materials and methods

Study location

Georgian Bay is a large bay in northeastern Lake Huron. The shoreline of Georgian Bay is one of the longest and most complex in the world, allowing for the formation of thousands of coastal wetlands. On average, these wetlands are 1.4 (±12.0) ha in size (P. Chow-Fraser, unpublished data). Low levels of human development and watershed alteration have allowed these wetlands to remain in a relatively pristine state with high fish and plant species' richness (Seilheimer and Chow-Fraser, 2006, 2007; Croft & Chow-Fraser, 2007; Cvetkovic & Chow-Fraser, 2011).

Water levels

Water-level data were acquired from the Canadian Hydrographic Services, a Department of Fisheries and Oceans Canada. In order to account for the documented lag time in macrophyte communities, we compared water levels for the 5 years preceding the acquisition of our images, using only data from the growing seasons (April to September). Therefore, for 2002 imagery, we used mean water levels for the years 1997–2001, and for 2008 imagery, we used mean water levels for the years 2003–2007.

Process tree classification development and assessment

Midwood & Chow-Fraser (2010) developed a classification scheme for eastern Georgian Bay, called the process tree classification (PTC), that used 2002 IKONOS satellite imagery to map four distinct vegetation classes in wetlands: high-density floating (HD; covering >50% of the surface), low-density floating (LD; covering <50% of the surface), emergent (E), and meadow (M) as well as water (W) and rock (R). In this study, we chose two of the 2002 IKONOS satellite images covering the regions of North Bay and Tadenac Bay (collected on 1 July 2002 at 11:30 hours; Fig. 1). Images covering these same regions were acquired again on 16 July 2008 at 11:22 hours. For all images, bands were available in the visible (red, green and blue) as well as near-infrared spectra. All images were preprocessed by GeoEye (Dulles, VA, USA) using a proprietary procedure.

PTC2002 was designed specifically for use with 2002 IKONOS images and could not be applied to the 2008 satellite imagery (see methods in Midwood & Chow-Fraser, 2010). Instead, the procedure used to create and validate PTC2002 was repeated for the 2008 imagery, and ground truth samples collected concurrently with image acquisition were used to create the classification. This allowed us to quickly create PTC2008 using the structure of PTC2002. As was the case for PTC2002 (Midwood & Chow-Fraser, 2010), the minimum overall accuracy considered acceptable for PTC2008 was 85%. To verify the accuracy of PTC2008, ground truth samples for the six ground cover classes were collected in 10 wetlands (five wetlands in each Tadenac Bay and North Bay) during the summer of 2008. These 10 wetlands were selected because they were included in both the 2002 and 2008 IKONOS imageries (see below) and they had already been ground truthed and classified in the 2002 images with the process tree classification (PTC2002; Midwood & Chow-Fraser, 2010). Creation, validation and application of both PTC2002 and PTC2008 were conducted in DEFINIENS DEVELOPER 7.0 (Definiens®AG, Munchen, Germany).

Change detection

For this study, we opted to use a postclassification analysis, which involves mapping vegetation in two images separately and then compare the resulting maps (Coppin *et al*., 2004; Lu *et al*., 2004). The major disadvantage with this method is that the final accuracy of the change detection is the product of the initial classification accuracies and is therefore always lower (Coppin *et al*., 2004; Lu *et al*., 2004). Thus, the overall accuracy (comprising all six ground cover classes) of our change detection was calculated as the product between the overall accuracy in 2002 and the overall accuracy in 2008. Individual change-detection accuracies were also calculated for the six classes as the product of their individual accuracies in 2002 and 2008.

While not always ideal for change detection, postclassification analysis is more easily applied when reference maps are available, and it does not require radiometric calibration of the independent images (Coppin *et al*., 2004; Van Oort, 2007). This method has been used successfully to assess change in terrestrial environments (Mas, 1999), urban areas (Zhou *et al*., 2008; Dewan & Yamaguchi, 2009) and wetland cover (Macleod & Congalton, 1998; Zhou *et al*., 2010).

Macleod & Congalton (1998) identified four steps which are necessary for change detection analysis. First and most broadly, it must be determined if a change has in fact occurred during the dates of image acquisition. Next, the nature of the change should be determined so that specific classes can be identified and monitored during the analysis. Following class identification, changes in areal coverage should be identified. Finally, changes to spatial patterns of surface features should be determined. The assessment of areal change in these Georgian Bay wetlands will provide important information on how much vegetation is changing, and provide insight into the fish community.

To quantify changes that have occurred between 2002 and 2008, we selected 84 wetlands from both the Tadenac Bay and North Bay regions (Fig. 1). The McMaster Coastal Wetland Inventory (P. Chow-Fraser, unpublished data) was used to identify potential wetlands in the IKONOS images. We only

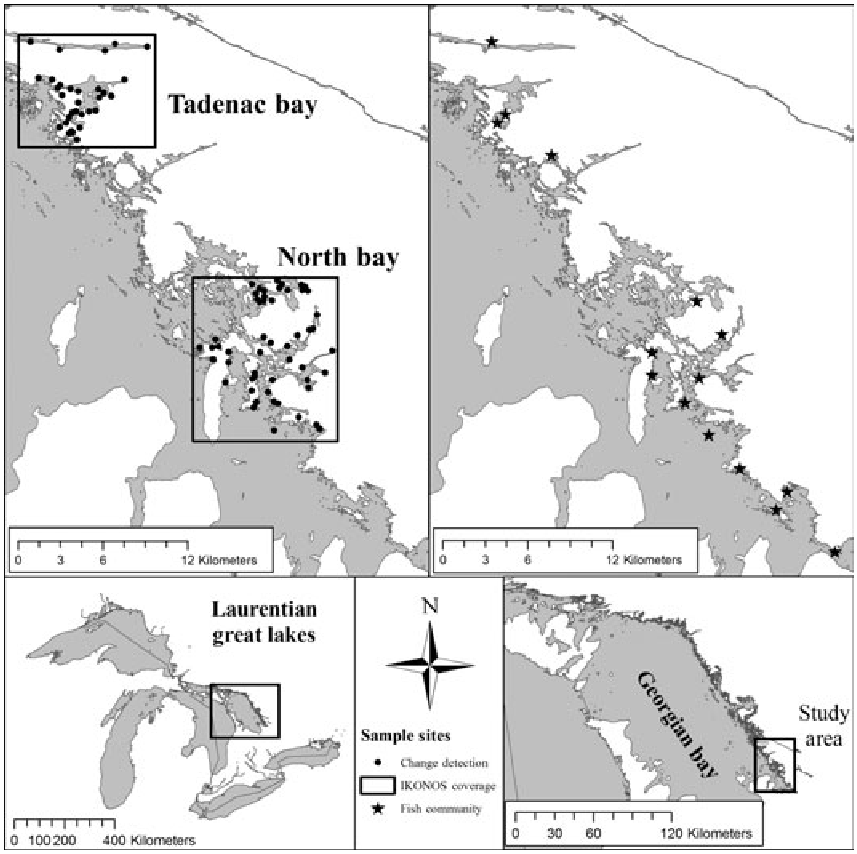

Fig. 1 Location of 84 wetlands (round dots) used in the analysis of change detection. Wetlands were located in two regions; Tadenac Bay is a relative pristine area with minimal human development. By comparison, North Bay is more densely populated and has greater boat traffic. IKONOS satellite images covering both regions were acquired in July 2002 and again in July 2008. Wetlands where fish data were collected (stars) partially overlap with wetlands used in the change detection analysis.

selected wetlands with minimum area of 0.25 ha and in which at least one class of aquatic vegetation was visible. Coastal marshes in both of these regions share a similar plant zonation that is dependent on water depth. Along the shoreline (shallowest water), there tends to be a small band of meadow vegetation. As depth increases, emergent vegetation becomes increasingly dominant until it begins to blend with floating vegetation out to a depth of approximately 1.5 m. Beyond this depth, submerged aquatic vegetation (SAV) is dominant out to a depth of between 4 and 6 m depending on water clarity (J. Midwood, personal observations).

We compared changes in patch size and areal extent of vegetation cover over the two time periods because these are known to influence fish communities in wetlands (Tonn & Magnuson, 1982; Dibble *et al*., 1997; Jacobus & Ivan, 2005; Jacobus & Webb, 2006). In addition to analysing classes individually, we combined the categories of E and LD into a single class of low-density-emergent (LDE) to minimize error due to misclassification (Midwood & Chow-Fraser, 2010). Changes in areal vegetation coverage were calculated in ARCMAP 9.2. (ESRI Inc., Redlands CA, USA, 2006) for all 84 wetlands in both Tadenac Bay and North Bay. This was accomplished by first using PTC2002 to classify the 2002 IKONOS images and then using PTC2008 to classify the 2008 imagery. Areal coverage (m^2) of each class (W, R, HD, LD, E and M) was then calculated for individual wetlands in each year. We also calculated the 'visible fish habitat' category (Midwood & Chow-Fraser, 2010), which is a combination of E vegetation with both LD and HD vegetation. To determine if patch size had changed from 2002 to 2008, we calculated mean patch size for the three classes that represent fish habitat (E, HD and LD). We also calculated the maximum polygon size for the three classes because mean patch size may obscure the presence of a single large patch.

Fish sampling

Fish sampling protocols followed those described in Seilheimer and Chow-Fraser (2006, 2007). In each wetland, three sets of paired fyke nets were used to sample the fish community. Nets were set parallel to the shoreline in beds of aquatic vegetation. Two pairs of large nets (4.25 m long, 1 m $\times$ 1.25 m front opening with 13 and 4 mm bar mesh) were set in approximately 1 m of water, and one pair of small nets (2.1 m long, 0.5 m $\times$ 1.0 m front opening with 4 mm bar mesh) were set in approximately 0.5 m of water. After 24 hours, the nets were removed and all fish were measured, counted and identified to species as per Scott & Crossman (1998). All fish were returned unharmed after processing.

Fish sampling sites in this study were chosen opportunistically based on availability of historical data (Table 1). Five of the 15 sites were not located in the same region as our change detection analysis (Fig. 1), but habitat changes should be transferable to other regions of Georgian Bay because sustained low water levels are a regional problem. Five sites had been sampled in 2003 (Green Island, Matchedash Bay, Musky Bay, Oak Bay and Quarry Island), five sites in 2004 (Green Island, Matchedash Bay, Moreau Bay, Oak Bay and Robert's Bay) and eight in 2005 (Ganyon Bay, Hermann's Bay, Lily Pond, North Bay, Ojibway Bay, Tadenac Bay 1, Tadenac Bay 2 and Treasure Bay). In 2009, all 15 wetlands were sampled once; surveys were conducted as close as possible to the date when the sites had been sampled between 2003 and 2005. The average time between sampling events was 8.3 ± 8.0 days earlier. In some instances, sampling in 2009 was conducted considerably earlier in the season (Lily Pond 81 days, Green Island 58 days, Moreau Bay 48 days, Musky Bay 34 days) or later (Ganyon Bay 48 days).

Statistical analysis and calculation of diversity

All analyses were performed in SAS JMP IN 5.1 (SAS Institute, Cary, NC, USA). An ANOVA was used to assess water-level changes between 2002 and 2008. A Wilcoxon *post hoc* test was used to compare the mean water level because of unequal variance in the 5 years preceding 2002 and 2008. We used paired *t*-tests to compare changes in the same wetland between 2002 and 2008, with respect to vegetation areal coverage and structure, and among years for changes in fish species richness. Paired *t*-test was also used to compare proportional changes of individual fish species, but to increase sample size, data from 2003 to 2005 were combined into a single category that we have designated as 'Earlier' and these were compared with data collected in 2009, which we have designated as 'Later'. By using a paired analysis, we were able to control for confounding variables such as latitude, climate, exposure, and anthropogenic development, which can influence the fish community (Brazner, 1997; Jude *et al.*, 2005; Seilheimer & Chow-Fraser, 2006; Latta *et al.*, 2008; Webb, 2008). To include rare species that could not be analysed individually, we created a *Cyprinidae* category that included all members of that family. Alpha-Beta-Gamma Diversity scores were calculated according to Whittaker (1956; reviewed in Veech *et al.*, 2002) for the 15 wetlands included in this study. Alpha-Diversity quantifies the diversity of the local community (within wetlands), Beta-Diversity quantifies diversity among local communities (among wetlands) and Gamma-Diversity quantifies diversity within a specific region (south-eastern Georgian Bay). Alpha and Gamma Diversity can be inferred from direct field sampling but Beta-Diversity must be calculated (Beta = Gamma − Alpha).

Results

Water levels

Between 2002 and 2008, there was a net decline in mean water level of 0.13 m during the growing season (Fig. 2). Mean water level (April to September inclusive) for the 5 years preceding 2002 was significantly higher than that corresponding to the 5 years preceding 2008 (Wilcoxon test; mean = 176.46 ± 0.45 m, 176.10 ± 0.13 m respectively, $P > \chi^2 = 0.003$, df = 1). The 5 year period preceding 2002 encompassed a rapid drop of 1.11 m, from a high of 177.10 m in 1997 to a low of 175.99 m in 2001; by comparison, water levels during the 5 year period preceding 2008 were uniformly low, varying by only 0.27 m from 176.23 to 175.96 m.

Change detection – accuracy

The overall accuracy of the change detection was 80.1% (product of 2002 overall accuracy = 87.4% and 2008 overall accuracy = 91.7%; Table 2). The classes with the lowest accuracy in both 2002 and 2008 were LD (74.6% and 59.0% respectively, 44.0% for the change detection; Table 2) and E (77.9% and 74.5% respectively, 58.1% for the change detection; Table 2). When these classes were combined into LDE (2002 accuracy = 86.9% and 2008 accuracy = 85.0%, 73.9% for the change detection; Table 2) the overall accuracy of the change detection increased to 85.9%. The most accurately classified feature was W (98.5% and 97.6%, 96.1% change detection; Table 2) followed by M (95.6%, 97.2%, 91.3% change detection; Table 2). Rock was the next most accurate variable (92.4%, 92.3%, 86.8% change detection; Table 2), followed by HD (88.4%, 83.8%, 74.0% change detection; Table 2).

Change detection – areal coverage/patch size

We used PTC to classify 84 wetlands included in both the 2002 and 2008 IKONOS images; these were located in both the Tadenac Bay and North Bay regions (Fig. 1). The change detection confirmed that significant changes in areal cover of the main vegetation categories had occurred between 2002 and 2008 (Table 3; Fig. 3). During this period, we saw a significant increase in the areal cover of M and HD, with an average increase of 2020.9 and 2312.6 m^2, respectively in each wetland (paired *t*-test, $P < 0.0001$, df = 83). There was a concomitant and significant decrease in cumulative areal cover of LD vegetation, with an average loss of 2995.4 m^2 (paired *t*-test, $P < 0.0001$, df = 83). There was also a trend towards a decrease in cover of E vegetation, with an average loss of 498 m^2 (paired *t*-test, $P = 0.0825$, df = 83), although this was not statistically significant. We combined the LD, HD and E to form the functional category 'fish habitat' and found a significant decrease in this feature between 2002 and 2008, with an average loss of 1181.5 m^2 in each wetland (paired *t*-test, $P < 0.0001$, df = 83). When only LD and

Table 1 Location (decimal degrees) and size of wetlands where the fish community was surveyed. Species richness and sampling dates (in brackets) for each year are also shown

Wetland name	Wetland code	Latitude	Longitude	Wetland size (ha)	2003 Species richness	2004 Species richness	2005 Species richness	2009 Species richness
Ganyon Bay	GY	44.91995	−79.81976	1.90	–	–	$8_{\text{(Aug 5)}}$	$6_{\text{(Jun 18)}}$
Green Island	GI	44.78574	−79.74797	4.90	$18_{\text{(Jul 9)}}$	$14_{\text{(Jun 3)}}$	–	$7_{\text{(Aug 18)}}$
Hermann's Bay	HRM	45.08662	−79.99669	2.90	–	–	$6_{\text{(Aug 31)}}$	$5_{\text{(Aug 18)}}$
Lily Pond	LY1	44.87076	−79.81547	3.20	–	–	$8_{\text{(Sep 1)}}$	$10_{\text{(Jun 12)}}$
Matchedash Bay	MB	44.75885	−79.69687	347.80	$17_{\text{(Jul 8)}}$	$15_{\text{(May 27)}}$	–	$12_{\text{(May 27)}}$
Moreau Bay	MO	45.01460	−79.94510	23.60	–	$17_{\text{(Jun 17)}}$	–	$6_{\text{(Aug 5)}}$
Musky Bay	MS	44.81197	−79.77945	19.40	$18_{\text{(Jul 9)}}$	–	–	$9_{\text{(Aug 12)}}$
North Bay	NB	44.89717	−79.79465	10.30	–	–	$13_{\text{(Jun 15)}}$	$6_{\text{(Jun 16)}}$
Oak Bay	OB	44.79466	−79.73221	50.20	$11_{\text{(Jul 8)}}$	$14_{\text{(Jun 9)}}$	–	$9_{\text{(Jun 9)}}$
Ojibway Bay	OJ	44.88786	−79.85587	1.70	–	–	$10_{\text{(Jun 15)}}$	$7_{\text{(Jun 24)}}$
Quarry Island	QI	44.83510	−79.80897	21.20	$20_{\text{(Jul 10)}}$	–	–	$7_{\text{(Jun 25)}}$
Robert's Bay	RB	44.85583	−79.83063	6.00	–	$15_{\text{(Jun 2)}}$	–	$4_{\text{(Jun 17)}}$
Tadenac Bay 1	TD1	45.03583	−79.99325	1.50	–	–	$10_{\text{(Jul 19)}}$	$5_{\text{(Jul 16)}}$
Tadenac Bay 2	TD2	45.03977	−79.98508	2.70	–	–	$5_{\text{(Jul 20)}}$	$7_{\text{(Jul 15)}}$
Treasure Bay	TB	44.87190	−79.86013	60.20	–	–	$15_{\text{(Jun 14)}}$	$8_{\text{(Jun 23)}}$

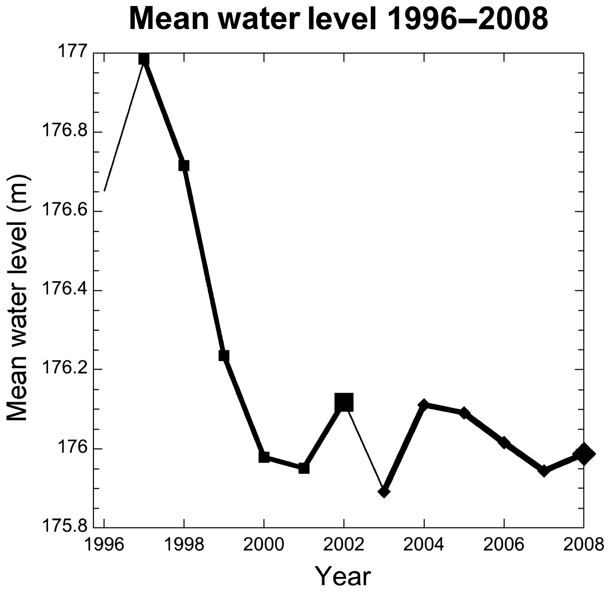

Fig. 2 Change in water levels of Lake Huron from 1996 to 2008 (data from Canadian Hydrographic Services, Department of Fisheries and Oceans). The large square and diamond represent the years IKONOS imagery was acquired (2002 and 2008, respectively). Thicker lines show the water levels in the 5 years preceding imagery acquisition.

Table 2 Combined accuracy for the change detection based on class. LD floating and emergent vegetation classes were combined during classification to form the LDE category

Class	2002 Accuracy (%)	2008 Accuracy (%)	Change detection accuracy
Meadow	95.6	97.2	91.3
HD floating	88.4	83.8	74.0
LD floating	74.6	59.0	44.0
Emergent	77.9	74.5	58.1
Rock	92.4	92.3	86.8
Water	98.5	97.6	96.1
Overall accuracy	87.4	91.7	80.1
LDE	86.9	85.0	73.9
Overall accuracy with LDE	94.1	91.3	85.9

E were combined, we still found a significant decrease in cumulative area with a mean loss of 3494.1 m^2 in each wetland (paired t-test, $P < 0.0001$, df = 83).

The change in areal cover of vegetation classes over the 6 years was also accompanied by a significant increase in the number of patches of E, HD and LD (Table 4). While the number of patches of E and LD increased in 2008 relative to that in 2002, the average patch size was significantly smaller in 2008 (Table 4). Although the average patch size of HD did not change significantly, they tended to be larger (Table 4). To ensure that mean patch size had not obscured larger changes associated with a few patches, we compared maximum patch size for these vegetation classes between years. There was a significant increase in the maximum patch size for HD [an average increase of 908.9 ± 322.5 m^2 (paired t-test, $P = 0.006$, df = 83: Table 4)] and a significant decrease in maximum patch size for E (an average loss of 390.5 ± 146.4 m^2; paired t-test, $P = 0.0092$, df = 83) and LD (average loss of 1945.0 ± 366.0 m^2; paired t-test, $P < 0.0001$, df = 83).

Fish community

The 15 wetlands we sampled for this portion of the study ranged from 1.5 ha (Tadenac Bay 1) to 347.8 ha (Matchedash Bay), with a mean size of 37.2 ha, but 75% of the wetlands were smaller than 24 ha (Table 1). Majority of the wetlands were located in the Severn Sound region of southeastern Georgian Bay. Exceptions include Hermann's Bay (within Twelve Mile Bay), Moreau Bay (within Go Home Bay) and Tadenac Bay 1 and 2 (within Tadenac Bay; Fig. 1).

A total of 40 fish taxa were identified in all surveys conducted between 2003 and 2009. Species richness corresponding to the Earlier survey (2003–2005) ranged from 5 to 20 species per wetland, compared with 4 to 10 in the Later (2009) survey (Table 1). The mean richness declined significantly from 13.2 in the initial survey to 7.2 in the more recent survey (paired t-test, $P < 0.0001$). We examined changes in the proportion of catch represented by some of the most common species sampled in eastern Georgian Bay (Table 5). Pumpkinseeds (*Lepomis gibbosus*) and bowfin (*Amia calva*) increased significantly as a proportion of our catch (paired t-test, $P = 0.0008$, and $P = 0.0009$, respectively) while tadpole madtoms (*Noturus gyrinus*), blackchin shiners (*Notropis heterodon*), black crappie (*Pomoxis nigromaculatus*), and the *Cyprinidae* family all decreased significantly as a proportion of our catch (paired t-test, $P < 0.05$). No significant changes in the proportion of catch were observed for brown bullhead (*Ameiurus nebulosus*), rock bass (*Ambloplites rupestris*), largemouth bass (*Micropterus salmoides*), yellow perch (*Perca flavescens*), longear sunfish (*Lepomis megalotis*), mimic shiner (*Notropis volucellus*), and bluntnose minnow (*Pimephales notatus*), although there were trends towards increasing proportions of brown bullheads and rock bass and decreasing proportions of largemouth bass, longear sunfish, and bluntnose minnows (Table 5; Fig. 4).

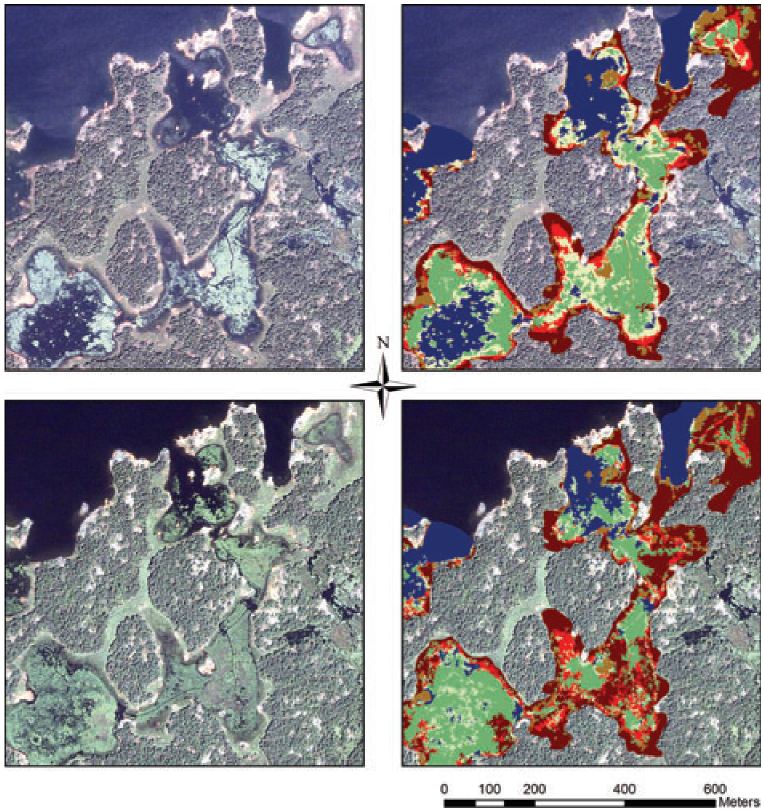

Fig. 3 Comparison of two original IKONOS images (a, b) with images that have been classified (c, d). Red = emergent vegetation, dark green = HD floating vegetation, light green = LD floating vegetation, maroon = meadow vegetation, blue = water and brown = rock. All images show Black Rock Bay in the Tadenac Bay region of eastern Georgian Bay. The top images were acquired on July 1st 2002 and the bottom images were acquired July 16th 2008. Comparing image c to image d it is clear that meadow vegetation (maroon) has colonized previously aquatic habitats.

Table 3 Areal change in vegetation coverage for 84 wetlands based on 2002 and 2008 IKONOS imagery. LD floating and emergent vegetation classes were combined during classification to form the LDE category

	Meadow	HD floating	LD floating	Emergent	LDE	Total area fish habitat
% Sites increasing	88.0	89.0	4.0	35.7	10.7	27.0
% Sites decreasing	12.0	11.0	96.0	64.3	89.3	68.0
Mean change	*2020.9 m^2	*2312.6 m^2	*2995.4 m^2	498.7 m^2	*3494.1	*1181.5 m^2

*$P > |t|$ = <0.0001; N = 84.

Table 4 Structural changes in wetland vegetation based on changes observed in 2002 and 2008 IKONOS images. The M, R and W class are not included because they are not considered components of fish habitat. LD floating and emergent vegetation classes were combined during classification to form the LDE category

	Δ # Patches	Δ Mean patch size (m^2)	Δ Max patch size (m^2)
Emergent	+22 ± 3*	−50.9 ± 7.7*	−390.5 ± 146.3**
HD floating	+39 ± 6*	+7.3 ± 3.9	+908.9 ± 322.5**
LD floating	+76 ± 14*	−92.5 ± 9.2*	−1945.0 ± 366.0*
LDE	+85 ± 14*	−165.9 ± 21.2*	−3584.9 ± 834.5*

*$P > |t|$ = <0.0001; N = 84.
**$P > |t| < 0.05$; N = 84.

We also observed declines in Alpha, Beta and Gamma Diversity between the Earlier and Later surveys, indicating an overall decline in species richness over the two time periods. The mean Alpha-Diversity (within wetlands) decreased from 13.2 in 2003–2005 to 7.2 in 2009. Gamma-Diversity (within a region) also decreased from 37 (Time 1) to 24 (Time 2), and, Beta-Diversity (among wetlands) decreased from 23.8 to 16.8 over time.

All wetlands were surveyed once in a calendar year and at different times during the season (Table 1). To account for the possible confounding effects of time of sampling between the initial (2003–2005) and latter (2009) surveys, we re-analysed the data by including only wetlands that varied by <2 weeks within the calendar year (n = 10). We still found significant differences for species richness between survey periods (paired t-test; $P < 0.0001$).

Discussion

This is one of the first studies to utilize remote sensing to analyse change over a large geographic area of the Laurentian Great Lakes, identify significant changes in wetland vegetation in response to a loss of hydrological variability, and link changes in the fish community to these habitat changes. Our results demonstrate that sustained low water levels have resulted in encroachment of meadow vegetation into previously aquatic habitat. This has led to a net loss of aquatic vegetation, which provides critical habitat for many fish species. The remaining aquatic habitat has become increasingly homogeneous due to increased patch sizes of dense floating vegetation. During a similar time period, we have also documented a decline in fish species richness in coastal wetlands that have been impacted by sustained low water levels.

Although there has been a net decline in water levels from 2002 to 2008, we do not believe that the observed change in the fish and plant communities can be attributed to a drop of 13 cm over this period. Instead, we attribute our observations to a change in periodicity of water-level fluctuation. The rapid decline in water levels of over 1 m between 1999 and 2002 would have resulted in wetlands in a state of disequilibrium. Without episodes of high water level in the intervening years, vegetation that colonized in 2002 would have persisted and become more dense. Consistent with previous studies, we observed a significant increase in meadow vegetation in response to lower, less variable water levels (Hudon, 1997, 2004; Wei & Chow-Fraser, 2008; Wilcox & Nichols, 2008). Thus, encroachment of meadow vegetation into areas of the marsh previously dominated by aquatic taxa has directly contributed to an overall loss of fish habitat in coastal wetlands of eastern Georgian Bay.

Of the aquatic classes, floating vegetation benefitted most from the sustained low water levels, covering more than 50% of the surface area of wetlands in dense patches by 2008, and this is consistent with findings of Quinlan & Mulamoottill (1987). Given that floating species such as *Nuphar variegata* and *Nymphaea odorata* tend to be limited to a depth of 170 cm in the coastal marshes of eastern Georgian Bay (J. Midwood, unpublished data), a drop of 13 cm would have little effect on their overall distribution. The favourable conditions, however, would have led to a transformation from primarily LD floating to HD floating over the 6 years of sustained low water levels.

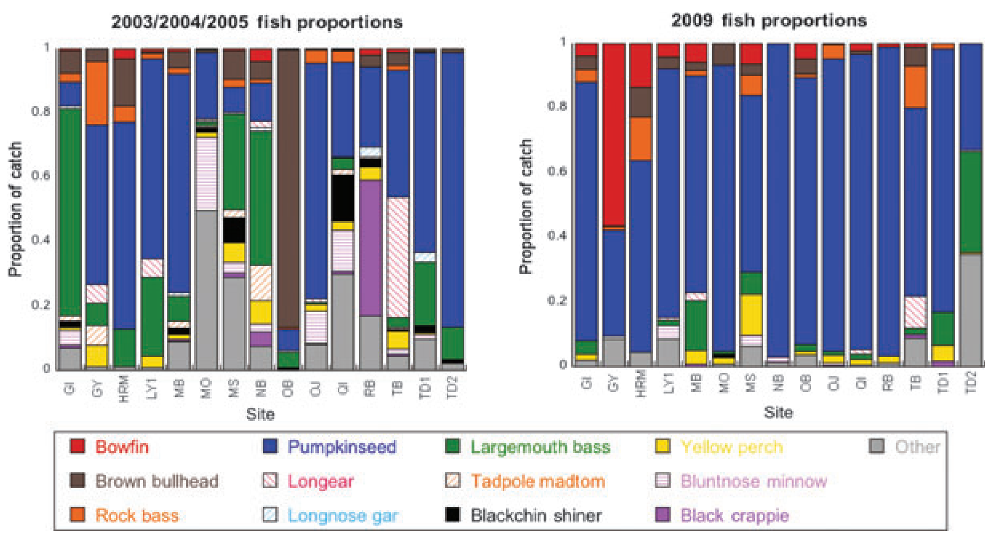

Fig. 4 Proportion of catch represented by each species, in each wetland for the 'Early' (2003–2005) and 'Later' (2009) sampling periods. There was a significant decline in species richness from the Early to Later time periods.

Table 5 Comparison of the proportion of the 13 most common fish species or groups between 'Earlier' and 'Later' sampling period (2003–2005 and 2009, respectively). *P*-values in bold indicate significant differences between survey periods

Common name	Scientific name	*P* value	Mean 'Earlier' proportion of catch	Mean 'Later' proportion of catch
Pumpkinseeds	*Lepomis gibbosus*	**0.0008**	0.37	0.69
Bowfin	*Amia calva*	**0.0009**	0.01	0.06
Tadpole Madtom	*Noturus gyrinus*	**0.0219**	0.02	0.00
Blackchin Shiner	*Notropis heterodon*	**0.0475**	0.02	0.00
Black Crappie	*Pomoxis nigromaculatus*	**0.0217**	0.03	0.00
Brown Bullhead	*Ameiurus nebulosus*	0.1080	0.13	0.06
Rock Bass	*Ambloplites rupestris*	0.7080	0.03	0.04
Largemouth Bass	*Micropterus salmoides*	0.1580	0.14	0.05
Yellow Perch	*Perca flavescens*	0.7423	0.03	0.03
Longear Sunfish	*Lepomis megalotis*	0.2242	0.27	0.01
Mimic Shiner	*Notropis volucellus*	0.0894	0.02	0.00
Bluntnose Minnow	*Pimephales notatus*	0.0810	0.05	0.01
Carps & Minnows	*Cyprinidae*	**0.0299**	0.15	0.02

In general, floating vegetation is not considered ideal fish habitat compared with emergent or SAV because it is less structurally diverse and supports fewer epiphytes (Höök *et al.*, 2001; Smokorowski & Pratt, 2007), and this is especially true when it occurs in dense patches. In addition, it is undesirable because it covers the water surface, and prevents SAV from becoming established (Parr & Mason, 2004), further reducing habitat structure. By comparison, suitable habitat structure is comprised of sparse patches of emergent and floating vegetation mixed with a diverse array of SAV. Therefore, conversion of LD vegetation into HD vegetation results in a net loss of desirable fish habitat.

The greatest change in coverage of HD vegetation occurred in the largest patch size, almost doubling from 2002 to 2008. The plant community changed from a heterogeneous patchwork, comprised of clusters of different vegetation, to one dominated by extensive areas containing homogeneous HD vegetation cover. This is similar to observations of Wilcox & Meeker (1991) who found that stabilization of water levels in a lentic system reduced vegetation diversity and structural complexity.

In accordance with the species–area relationship described by Arrhenius (1921), the observed decrease in the amount of available fish habitat from 2002 to 2008 resulted in lower fish species richness in coastal wetlands. Species richness not only changed at the scale of the wetland, we also observed decreases in species richness at the regional (Gamma Diversity) level, suggesting that declines in species richness may not be isolated to the 15 wetlands we sampled. While changes in the amount of habitat can explain the observed decline in species richness, the influence of concurrent changes in habitat structure on diversity must also be addressed.

Complex aquatic habitat contains numerous patches of vegetation that allow small fishes to move amongst them for foraging and protection from predators (Werner *et al.*, 1983; Killgore *et al.*, 1989). Large patches of contiguous dense vegetation can limit the amount of space in which prey fish can forage and force them to frequent edges of vegetation patches, where they are more vulnerable to predatory fishes, such as northern pike (*Esox lucius*), yellow perch (*P. flavescens*) and largemouth bass (*M. salmoides*), that hunt along the edge (Killgore *et al.*, 1989; Savino & Stein, 1989).

In a northern Lake Michigan–Huron coastal wetland, Jacobus & Webb (2006) predicted that a loss of vegetation patches with per cent coverage ranging from 15% to 25% would have the greatest impact on fish species diversity. They also found that species richness plateaued when patches reached 128 m^2. Consistent with this prediction, we found a decline in areal coverage of LD and E (<50% coverage) as well as a significant decline in their average patch size. This has important implications because significantly fewer tadpole madtom, black crappie, blackchin shiner, and *Cyprinidae* were associated with these small patches of LD. Because they are key diet items of muskellunge, northern pike and largemouth bass, loss of habitat for these small fish could negatively impact these large piscivores. By contrast, some species actually prefer dense vegetation (Jacobus & Ivan, 2005). For instance, we found a greater number of pumpkinseeds (*L. gibbosus*) and bowfins (*A. calva*) in the Later surveys, and this is consistent with the literature that pumpkinseeds prefer dense vegetation (Killgore *et al.*, 1989) and that bowfins utilize shallow water areas with dense vegetation (Mundahl *et al.*, 1998; Scott & Crossman, 1998).

Due to a net loss of desirable habitat for species other than pumpkinseeds and bowfin, we observed a decline in Beta Diversity. This indicates that wetland fish communities have become less heterogeneous in composition in recent years. Because water levels showed a net decline of only 13 cm during our study, we attribute the changes in diversity to the loss of interannual variability in water level rather than to the magnitude of water-level decline. From a management perspective, within a regulated system like the Laurentian Great Lakes it is critical to maintain as much of the natural variability in water levels regardless of the mean water levels.

The vegetation classes used in this study were formed at the level of resolution afforded by our satellite imagery. As such, we could not distinguish vegetation at the level of detail commonly used in published wetland work (i.e. species assemblages), but instead used a more simple functional taxonomy based on unique spectral signatures (Midwood & Chow-Fraser, 2010). Although this limits our ability to compare directly with findings in previous literature, this approach allowed us to conduct a regional study (84 wetlands across 194 km^2) that would otherwise have been impossible given the level of difficulty in sampling Georgian Bay wetlands. We are confident that as technology improves and more investigators choose satellite platforms to produce vegetation classes, we would eventually be able to match the taxonomic resolution of conventional studies.

Few published studies have examined the influence of water-level reduction on changes in the fish community in coastal wetlands of Lake Huron. Webb (2008) sampled five embayments in the Les Cheneaux Islands (Michigan) and found that a change of 1.2 m over a 9 year period (1996–2004) did not significantly affect the fish assemblages in the 'inner marsh' where hardstem bulrush (*Schoenplectus acutus*) dominated. We attribute this apparent discrepancy in conclusions between studies to the heterogeneous nature of Webb's study sites and to geomorphological differences between wetlands in the Les Cheneaux Islands and those in southeastern Georgian Bay.

The five sites in Webb's study were heterogeneous, and varied with respect to degree of exposure and human development along the shoreline, whereas the 15 sites in this study are much more homogeneous, and are primarily protected wetlands with minimal human impact (Cvetkovic & Chow-Fraser, 2011). Any effect of reduced water levels may have been masked by differences in exposure and human-induced disturbance. In addition, we argue that the cause of changes in the fish community in our study is the change in type and availability of wetland habitat resulting from the water-level decline and not merely the drop in water level itself. Hence, if the plant community in the Les Cheneaux wetlands had not changed significantly as water levels fluctuated, we should not expect a corresponding change in the fish community.

The type of aquatic vegetation in coastal marshes of the Great Lakes will depend on various factors including wetland geomorphology, bathymetry, exposure and substrate type (Keough *et al.*, 1999; Riis & Hawes, 2003; Albert *et al.*, 2005; Capers & Les, 2005). Webb (2008) sampled in a zone referred to as the 'inner marsh' that occurs closest to the shoreline where there are fringing stands of hardstem bulrush (*Schoenplectus acutus*), interspersed with patches of floating taxa [primarily yellow water lily (*N. variegata*)] and pondweeds (*Potamogeton* spp) and a 'well-developed understorey of floating or submerged swaying bulrush (*S. subterminalis*)' (Webb, 2008). By comparison, the coastal wetlands of southeastern Georgian Bay have a relatively expansive and diverse emergent plant community that include spikerush (*Eleocharis smallii*), Giant burreed (*Sparganium eurycarpum*), arrowheads (*Sagittaria cuneata and S. latifolia*), pickerelweed (*Pontederia cordata*) as well as different species of bulrush (*S. acutus, S. validus and S. americanus*). This does not tend to be a well-delineated zone such as the fringing bulrush zone but is often interspersed with pockets of floating taxa such as fragrant water lily (*N. odorata*), yellow water lily (*N. variegata*), floating hearts (*Nymphoides cordata*), watershield (*Brasenia schreberi*), floating burreed (*Sparganium fluctuans*) and wild rice (*Zizania palustris*). In water depths >50 cm, submergent taxa (too many to name here) are abundant and sometimes grow luxuriantly (see Croft & Chow-Fraser, 2007 for a complete list of aquatic plants). It is possible that changes in water level within this inner marsh zone did not lead to a similar change in the emergent-floating vegetation in the Les Cheneaux wetlands as they did in the Georgian Bay wetlands. Therefore, we suggest that low water levels may have differential impacts on wetlands depending on differences in geomorphology and dominant vegetation type.

To fully capture fish species richness in a wetland, investigators have suggested that a combination of different gear be used (Conrow *et al.*, 1990; Weaver *et al.*, 1993; Jackson & Harvey, 1997; Chow-Fraser *et al.*, 2006) and/or multiple sampling dates within a season be included (Pope & Willis, 1996; Brazner, 1997; Scott & Crossman, 1998). Because our initial data were limited to single-event sampling with fyke nets, it was necessary to be consistent with our effort (Breen & Ruetz, 2005) when comparing fish community assemblages between our 'early' and 'later' surveys. While fyke nets are known to preferentially capture small-bodied fishes (e.g. *Cyprinidae*; Ruetz *et al.*, 2007) and cause such schooling species to exhibit an all-or-none capture rate (Uzarski *et al.*, 2005), investigators have successfully utilized single-day fyke net sampling to create indices

(Uzarski *et al*., 2005; Seilheimer and Chow-Fraser, 2006, 2007; Bhagat *et al*., 2007) and to assess the fish community (Chow-Fraser *et al*., 2006; Uzarski *et al*., 2009). Brady *et al*. (2007) concluded that, for synoptic studies, it is better to sample more wetlands than increase effort per wetland. Therefore, despite the caveats we have mentioned here, we are confident that the changes presented in this paper are representative of the overall change in eastern Georgian Bay wetlands.

Cvetkovic *et al*. (2010) demonstrated that fish community composition in coastal wetlands is directly linked to aquatic macrophytes. To further elucidate this relationship, they recommended that studies be conducted to map habitat at a regional scale. In this study, we have demonstrated that changes in the fish community may be linked to habitat changes, identified through mapping and a change detection analysis. Our work suggests that use of remote sensing can be an effective strategy to track alteration in fish communities based on broad-scale changes in habitat structure and quantity in response to declining and/or increasingly stable water levels. The work presented in this study emphasizes the importance of maintaining water level variability, even over the short term. Stasis in water levels allowed vegetation to increase in density and the results were an overall loss of fish habitat and a reduction in coastal wetland fish diversity.

Acknowledgements

Funding for this project came from Georgian Bay Forever and the Ontario Ministry of Natural Resources through the Canada Ontario Agreement. J. Midwood received funding from the Ontario Graduate Scholarship. We are indebted to numerous summer students and other graduate students in the Chow-Fraser lab who helped to collect fields samples, especially Sarah Thomasen. We also greatly appreciate the work of both Maja Cvetkovic, Jeremy Lucyk and two anonymous reviewers who helped to edit earlier drafts of this manuscript.

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