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ARTICLE

Changes in water chemistry associated with beaver-impounded coastal marshes of eastern Georgian Bay

Amanda Fracz and Patricia Chow-Fraser

Abstract: Coastal marshes of eastern Georgian Bay contain unique water chemistry that reflects mixing between the relatively ion-rich waters of Georgian Bay and the relatively ion-poor water draining the Canadian Shield landscape. These unique chemical characteristics may be dramatically altered when wetlands become hydrologically disconnected from Georgian Bay through beaver activity. We sampled 35 coastal marshes in Georgian Bay, 17 of which had beaver impoundments built at the outlet of the coastal wetland. Impounded marshes had significantly higher total phosphorus (30.2 versus 15.3 μg·L^{-1}, p = 0.0015), soluble reactive phosphorus, (13.33 versus 3.7 μg·L^{-1}, $p \leq 0.0001$), total suspended solids (15.5 versus 2.1 mg·L^{-1}, $p \leq 0.0001$), turbidity (5.4 versus 1.6, p = 0.0004), and chlorophyll (6.2 versus 1.9 μg·L^{-1}, p = 0.0004), but significantly lower pH (5.57 versus 6.95, $p \leq 0.0001$), nitrates (0.03 versus 0.04 mg·L^{-1}, p = 0.0416), and conductivity (47 versus 134 μS·cm^{-1}, $p \leq 0.0001$), indicative of reduced mixing with Georgian Bay. The mosaic of chemical conditions and altered hydrological connectivity associated with beaver impoundments in coastal marshes of Georgian Bay may affect the distribution of other wetland biota, and further studies should be conducted to ascertain these impacts.

Résumé : Les marais littoraux de l'est de la baie Georgienne présentent une chimie de l'eau particulière qui reflète le mélange d'eaux relativement riches en ions dans la baie Georgienne et de l'eau relativement pauvre en ions s'écoulant du Bouclier. Ces caractéristiques chimiques particulières peuvent subir d'importants changements quand l'activité de castors entraîne l'isolement hydrologique de zones humides de la baie Georgienne. Nous avons échantillonné 35 marais littoraux de la baie Georgienne, dont 17 étaient caractérisées par la présence de barrages de castors à l'embouchure de la zone humide littorale. Les marais de barrage présentaient des valeurs significativement plus élevées de phosphore total (30,2 contre 15,3 μg·L^{-1}, p = 0,0015), de phosphore réactif soluble (13,33 contre 3,7 μg·L^{-1}, $p \leq$ 0,0001), du total des solides en suspension (15,5 contre 2,1 mg·L^{-1}, $p \leq$ 0,0001), de la turbidité (5,4 contre 1,6, p = 0,0004) et de la chlorophylle (6,2 contre 1,9 μg·L^{-1}, p = 0,0004), mais des valeurs significativement plus faibles du pH (5,57 contre 6,95, $p \leq$ 0,0001), des nitrates (0,03 contre 0,04 mg·L^{-1}, p = 0,0416) et de la conductance (47 contre 134 μS·cm^{-1}, $p \leq$ 0,0001), indiquant une réduction du mélange avec des eaux de la baie Georgienne. La mosaïque de conditions chimiques et de connectivité hydrologique associée aux barrages de castors dans les marais littoraux de la baie Georgienne pourrait avoir une incidence sur la répartition d'autres biotes de zone humide, et d'autres études devraient être menées pour établir l'importance de ces impacts. [Traduit par la Rédaction]

Introduction

Coastal marshes are some of the most threatened habitats in the Laurentian Great Lakes because they form in rivermouths, deltas, and protected embayments, where human development has also been concentrated (Maynard and Wilcox 1996). They are located at the interface between the land and water and have water chemistry that reflects both offshore processes and runoff from the watershed (deCatanzaro and Chow-Fraser 2011; Morrice et al. 2011). The extent to which each process can influence the water chemistry in a particular wetland will depend on the wetland's geomorphology. Wetlands that have a permanent and strong hydrologic connection with the Great Lakes (i.e., fringing wetlands, open embayments) will be heavily influenced by the chemical properties of lakewater, whereas those with a weak and intermittent connection (i.e., barrier beach, protected embayments) will be heavily influenced by runoff in the watershed and its associated land cover. The Canadian Shield of eastern Georgian Bay naturally exports large amounts of sediments, dissolved organic carbon rich in colour, and phosphorus to coastal marshes (Dillon and Molot 2005; Eimers et al. 2008; deCatanzaro and Chow-Fraser 2011). Its thin layer of acidic soils and granitic rocks contribute very few dissolved ions to its runoff (Weiler 1988). By contrast, the open water of Georgian Bay represents a source of conductivity, alkalinity, and nitrates owing to sedimentary bedrock at the southern and western portions (deCatanzaro and Chow-Fraser 2011). Therefore, based on characteristics of the water chemistry in these coastal wetlands, it is relatively easy to determine whether the water has a disproportionate contribution from Georgian Bay or from the watershed (see deCatanzaro and Chow-Fraser 2011).

There are over 6500 ha of coastal marshes in eastern Georgian Bay (Midwood et al. 2012), which contain some of the best water quality in the entire Great Lakes basin (Chow-Fraser 2006; Cvetkovic and Chow-Fraser 2011). The excellent water-quality conditions in many of these wetlands can be attributed to the absence of human disturbance in the adjacent landscape (Chow-Fraser 2006; deCatanzaro et al. 2009). Based on the research of deCatanzaro and Chow-Fraser (2011), we know that water chemistry in these wetlands is heavily influenced by the degree of connectivity between the coastal marsh and Georgian Bay. Fracz and Chow-Fraser (2013) has already shown that the hydrologic connection of coastal wetlands to Georgian Bay is a function of water level in Lake Huron. Owing to the convoluted landscape, the marshes of eastern Georgian Bay have formed in fringes along the shorelines and

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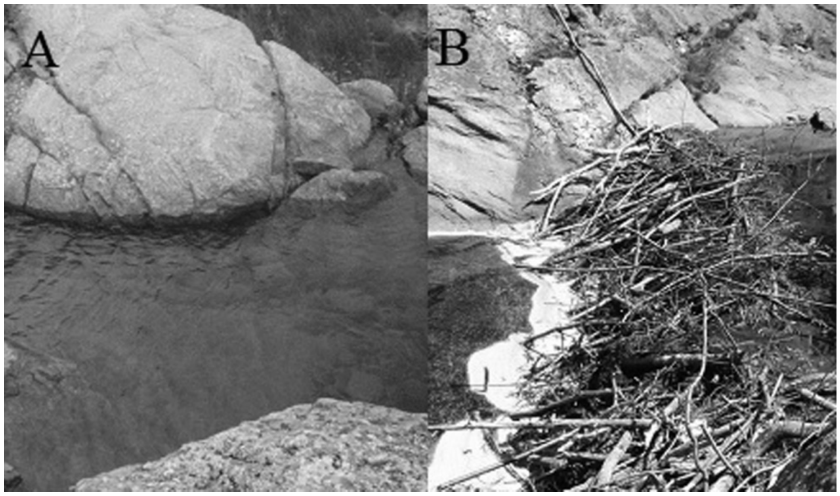
A. Fracz and P. Chow-Fraser. McMaster University, Department of Biology, 1280 Main Street West, Hamilton, ON L8S 4K1, Canada.
Corresponding author: Amanda Fracz (e-mail: amanda.fracz@gmail.com).

Fig. 1. Outlets of coastal marshes. (A) The narrow opening of an existing coastal marsh. (B) The narrow opening of a coastal marsh that has been disconnected by a beaver.



in protected embayments that have a narrow marsh outlet that limit hydrological connection (Fig. 1A). When water levels drop below the maximum depth of the outlet, many of these marshes can become hydrologically disconnected from Georgian Bay. Even if water levels do not drop below the depth of the outlet, a wetland may become cut off if a beaver dam is built across the outlet.

Water levels of Lake Huron, and therefore Georgian Bay, have been extremely low since 1999 (Assel et al. 2004; Sellinger et al. 2008). This decline has been attributed to several factors, including a change in conveyance of the St. Clair River (see IUGLS 2009) and hydroclimatic factors such as increased evaporation (see IUGLS 2009; Hanrahan et al. 2010). The International Joint Commission has acknowledged that anthropogenic activities have influenced natural fluctuations: human-induced climate change (Karl and Trenberth 2003) and dredging in the St. Clair River in 1962 led to erosion at the outflow of Lake Huron (IUGLS 2009). Lower water levels have led to shallower depths at marsh outlets and have created highly favourable conditions for beavers to build impoundments across them (Fig. 1B). Ideal wetlands to dam would have a small cross-sectional area at outlet (Barnes and Mallik 1997; Jensen et al. 2001), low gradient (Howard and Larson 1985; Beier and Barrett 1987; Jensen et al. 2001), and intermediate watershed size (Howard and Larson 1985; Barnes and Mallik 1997).

While previous studies have examined the role of water chemistry alterations of stream environments by beaver dams (Naiman et al. 1986, 1988), to our knowledge there are no studies that have examined impoundment within a coastal lentic environment. In this unique environment in Georgian Bay, beavers are impounding existing coastal marshes that have no riverine input and only receive watershed runoff. In this paper, we examine the water chemistry of beaver-impounded coastal marshes and compare it with other coastal marshes in eastern Georgian Bay. To avoid any confounding effects of human disturbance, we selected beaver impounded sites with no roads in the watershed, limited buildings directly bordering the marsh, and similar landscape properties. We predict that water chemistry in coastal marshes will be distinct from that of beaver-impounded marshes, as they are hydrologically connected to Georgian Bay and will be influenced by open water. Results from this study will fill an important gap in the literature concerning the role of beaver impoundments in shaping the water chemistry of coastal wetlands and will help managers anticipate ecosystem changes that may accompany the current period of sustained low water levels and future extreme low water-level scenarios associated with climate change in Lake Huron (Angel and Kunkel 2010).

Methods

Description of study area

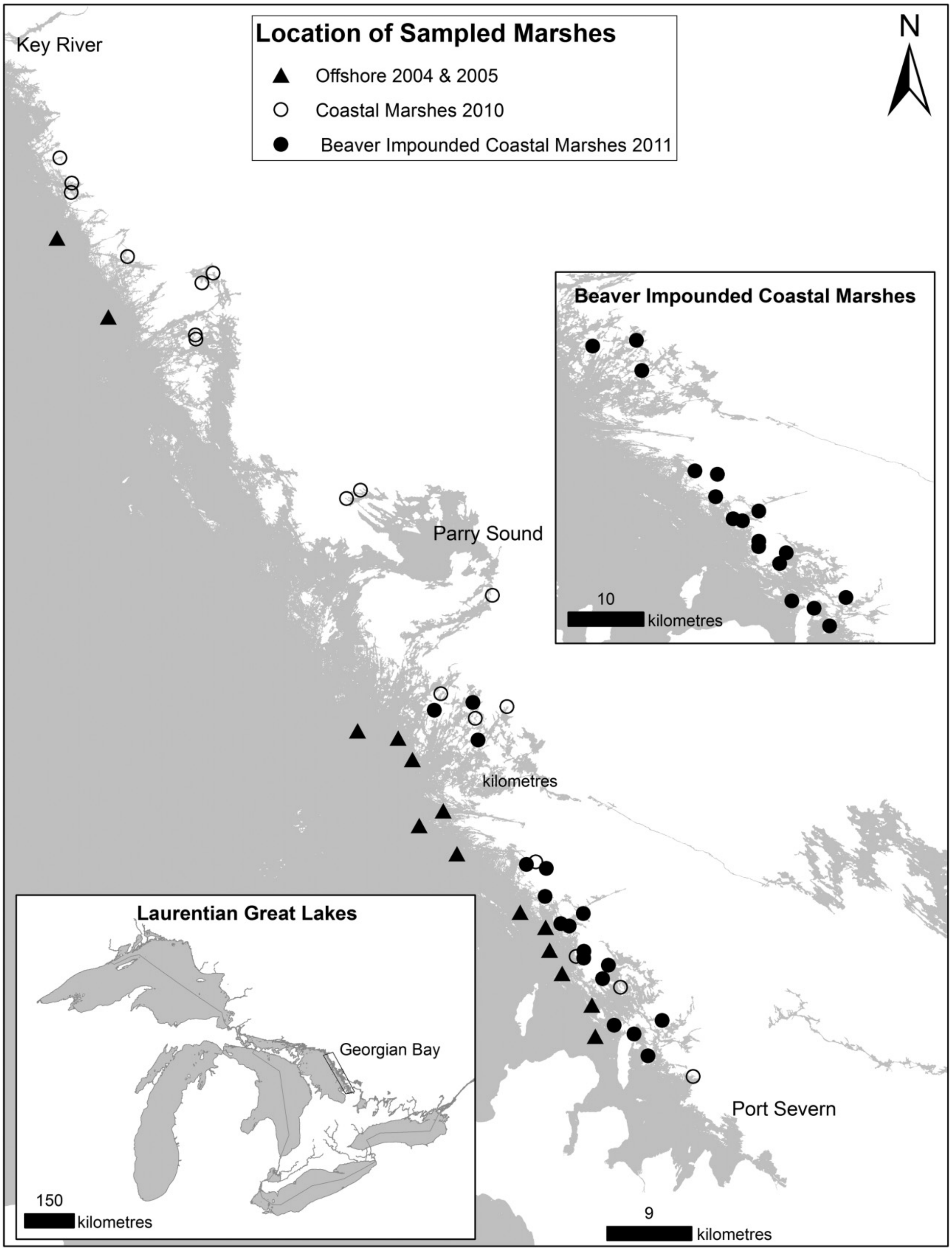
Coastal wetlands in eastern Georgian Bay are unique compared with that of other regions within the Laurentian Great Lakes drainage basin. There are two geologic regions: sedimentary limestone surrounds the southern and western portion, while Canadian Shield granitic rock underlies the remaining portion. Coastal marshes form along the convoluted shoreline, where there is enough sediment for vegetation growth and protection from wind and wave action. They often form in small embayments, with a narrow outlet connecting the marsh to open water. The dominant hydrological input is runoff from the watershed, often with no direct stream or riverine connection. Water chemistry is naturally oligotrophic owing to low nutrient inputs and the connection to Georgian Bay (deCatanzaro et al. 2009). The soils on the landscape are thin, sandy, acidic, and patchy (Weiler 1988). Vegetation on land is a mixture of second-growth deciduous and coniferous forest consisting of white pine (*Pinus strolobus*), red pine (*Pinus resinosa*), hemlock (*Tsuga canadensis*), white spruce (*Picea glauca*), sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), and beech (*Fagus grandifolia*) (deCatanzaro and Chow-Fraser 2011).

The mean density of dams in other regions has been estimated to be 5–19 dams·km^{-1} of stream for inland populations in Ekwan Point, northern Ontario (Woo and Waddington 1990), and 8.6–16 dams·km^{-1} of stream in southeastern Quebec (Naiman et al. 1988). In this study, however, we cannot make a similar estimate because dams are not situated along streams, and we cannot calculate dam density per kilometre, as this measurement assumes a distance over which damming is possible. It is not valid to calculate dam density per stretch of shoreline, since such an estimate would likely vary through time, as shorelines in Georgian Bay are known to shrink and expand depending on water levels. Therefore, damming opportunities would likely vary according to water levels. Nevertheless, we estimate that there are approximately 3 dams per 1000 ha in this region given our identification of dams from satellite imagery in 2002, when water levels had already begun to recede. This is likely an underestimate of current dam density, however, because more recently built dams associated with the recent episode of sustained low water levels are not included in this snapshot.

Selection of coastal marshes

In a previous study, Fracz and Chow-Fraser (2013) sampled 103 wetlands that had been randomly selected from 18 quaternary

Fig. 2. Sampling locations of coastal marshes sampled in 2010 (open circles, $n = 18$), beaver-impounded coastal marshes (solid circless, $n = 17$), and nearshore open water sampled in 2004 and 2005 (triangles, $n = 14$).

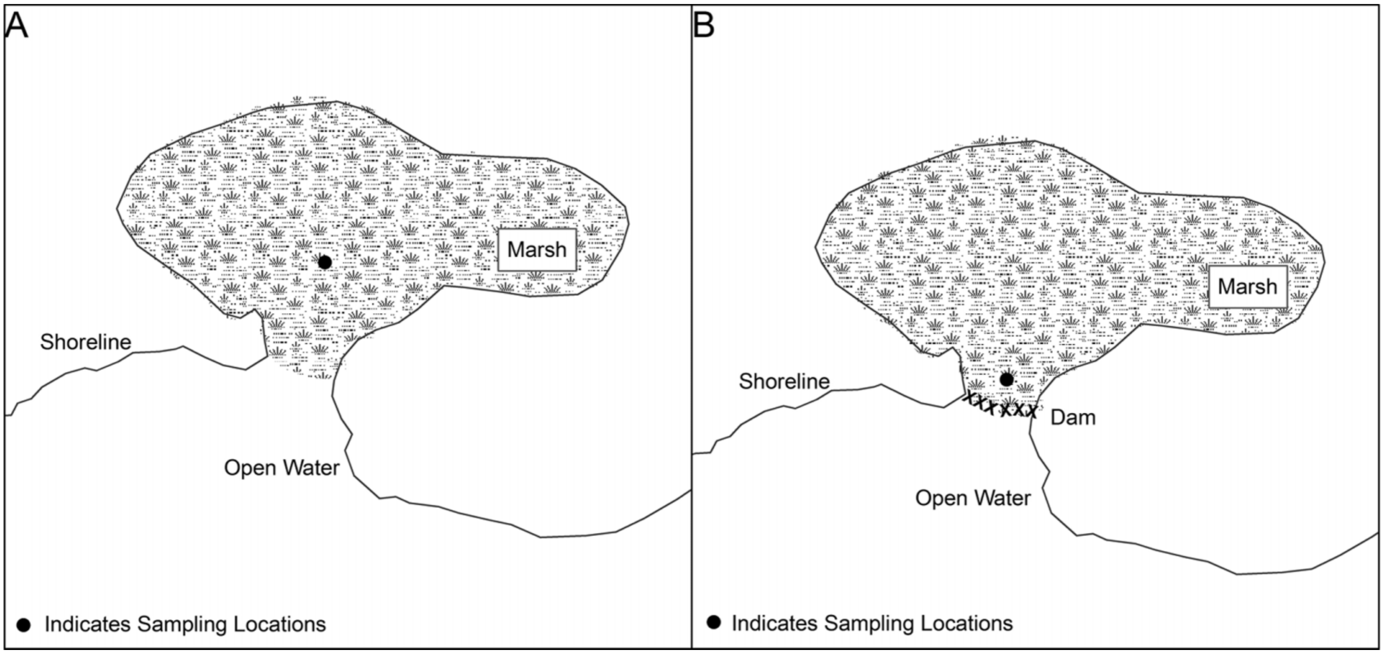


watersheds in eastern Georgian Bay in 2010. For this study, we randomly chose data from 18 of these coastal marshes (Fig. 2). All marshes were over 2 ha in size, which is the minimize size criterion used by the Ontario Ministry of Natural Resources to determine whether wetlands qualify for assessment under the Ontario Wetland Evaluation System (Ontario Ministry of Natural Resources 1993). An additional 17 beaver-impounded wetlands were also sampled in 2011 (Fig. 2). These were chosen from a list of 50 coastal beaver-impoundments that had been visually identified in a series of IKONOS satellite imagery acquired in 2002 (4 m resolution; Midwood et al. 2012). Based on the elevation of the maximum depth of the marsh outlet, we believe that all the beaver-impounded wetlands had at one point been connected to Georgian Bay but had become beaver-impounded by 2010.

Selection of open-water sites

We did not have the means to collect data in open-water areas of Georgian Bay for this study; however, we were given access to data that had been collected by the Ontario Ministry of the Environment during a synoptic survey of water-quality conditions at 131 locations in the nearshore zone of Georgian Bay between 2003

Fig. 3. A schematic of marsh geomorphology and sampling locations. The connection of the marsh to upland hydrological inputs is dominated by runoff from the watershed. The black dots indicate where water chemistry is sampled. (A) The typical shape and connection of a coastal marsh to open water. (B) An impounded coastal marsh whose connection has been altered.



and 2005 (Ontario Ministry of the Environment, unpublished data[1]). To choose appropriate data for inclusion in this study, we imported the locations of all 35 coastal marshes (17 beaver-impounded and 18 hydrologically connected wetlands) into a geographic information system (GIS). We then identified the closest offshore open-water station to our sites. In total, data from 14 stations were included in this study (Fig. 2).

Field sampling

The 18 coastal marshes (not associated with any impoundments) had been sampled between May and September 2010, and the 17 impounded wetlands between the end of May and mid-July 2011 (Fig. 2). Water samples in the latter were collected at mid-depth within 25 m above the beaver dam to determine the effect of the dam on water chemistry in the marsh (Fig. 3B). Emergent vegetation was generally lacking within this distance and as such was the best place for collection of water free from plant matter. Water from coastal marshes was collected at mid-depth in an area that appeared representative of the marsh (Fig. 3A). Effort was made not to disturb submergent vegetation or underlying sediment while collecting all water samples. We avoided sampling within 24 h of a noticeable (>5 mm) rain event. Timing of water collection varied between 0900 and 1630 h. In situ measurements of pH and conductivity (COND) were measured with an YSI 6600 multiprobe (YSI, Yellow Springs, Ohio, USA). Turbidity (TURB) was measured in situ with a Turbidimeter LaMotte 2020e (LaMotte, Chestertown, Maryland, USA).

We collected samples for determination of total nitrate nitrogen (NO_3-N), total ammonia nitrogen (NH_4-N), total suspended solids (TSS), total phosphorus (TP), and soluble reactive phosphorus (SRP). We processed all the NO_3-N and NH_4-N samples collected within 4–6 h of collection using Hach reagents and a Hach DR/890 colourimeter along with prescribed protocols. Preweighed GF/C filters with 47 mm diameter and particle retention of 1.2 μm were used to process water samples in triplicate for TSS; filters were dried in an oven at 100 °C, placed in a dessicator for at least an hour, and then weighed. The filtrate was frozen and used for SRP analysis. For TP analyses, whole water was first digested in the autoclave with addition of persulfate. Both SRP and TP samples were then analyzed in triplicate with the modified molybdenum blue method of Murphy and Riley (1962). Absorbance readings were measured with the Genesys 10 series spectrophotometer (GENEQ Inc., Montréal, Quebec, Canada). Similar filters were used for determination of chlorophyll *a* concentration (Chla) and processed in triplicate. Chla samples were extracted in 10 mL of acetone in a freezer for 2 h. The extract was then measured in a fluorometer and acidified with hydrochloric acid and remeasured to account for phaeophytin.

Data analysis and statistics

Statistical analysis was performed in JMP version 7.0.1 and R version 2.13.1, with results being considered statistically significant at α = 0.05. NH_4-N and NO_3-N values that fell below the detection limit (20 and 10 $\mu g \cdot L^{-1}$, respectively) were assigned half the detection limit value, a technique that has been used to treat data with concentrations below the limit of detection (see Trebitz et al. 2007; deCatanzaro and Chow-Fraser 2011). A nonparametric Wilcoxon test was used to determine statistically significant differences between water chemistry parameters measured in a coastal marsh and beaver-impounded coastal marshes (Fig. 3). Owing to processing and sampling errors, there were missing values for some of the variables (two for SRP and one for TURB). A principal component analysis (PCA) was completed to extract patterns among the large number of environmental parameters and to determine the effect of hydrologic connectivity. It was run with a correlation matrix that included $\log_{10}$ Chla, $\log_{10}$ TSS, $\log_{10}$ TP, $\log_{10}$ SRP, $\log_{10}$ NO_3-N, $\log_{10}$ NH_4-N, pH, and square-root COND for 15 beaver-impounded marshes, 18 coastal marshes, and 14 open-water sites collected by the Ontario Ministry of the Environment. Two beaver-impounded marshes were excluded because

[1]Contact at Ontario Ministry of the Environment: Ngan Diep, Ontario Ministry of the Environment, Great Lakes Unit of the Water Monitoring and Reporting Section, West Wing, 125 Resources Road, Etobicoke, ON M9P 3V6.

Table 1. Water chemistry variables measured within coastal marshes and marshes associated with beaver impoundments.

Parameter	Coastal marsh (n = 18)	Beaver-impounded marsh (n = 17)	p value
Total phosphorus (μg·L^{-1})	15.3±6.0 (4.7–29.7)	30.2±14.2 (4.5–55.6)	0.0015
Soluble reactive phosphorus (μg·L^{-1})	3.7±2.4 (0.6–10.8)	13.3±7.3 (6.2–30.1)	<0.0001
Total ammonia nitrogen (mg·L^{-1})	0.02±0.02 (0–0.07)	0.03±0.05 (0–0.23)	0.1888
Chlorophyll *a* (μg·L^{-1})	1.9±1.3 (0.6–3.8)	6.2±6.0 (1.2–26.3)	0.0004
Turbidity (NTU)	1.6±0.9 (0.3–3.5)	5.4±4.2 (1.4–17)	0.0004
Total suspended solids (mg·L^{-1})	2.1±1.6 (0.25–7.0)	15.5±7.9 (2.01–32.75)	<0.0001
Nitrate–nitrite nitrogen (mg·L^{-1})	0.04±0.02 (0.01–0.1)	0.03±0.02 (0.005–0.09)	0.0416
Specific conductivity (μS·cm^{-1})	134±48.3 (54–207)	47±38.9 (14–131)	<0.0001
pH	6.95 (6.19–8.97)	5.57 (4.76–7.52)	<0.0001

Note: Values are means ± standard deviation, with range shown in parentheses. n = 17 for all beaver-impounded sites except SRP (n = 15) and TURB (n = 16). The p values correspond to Wilcoxon tests comparing significant differences between coastal marshes and beaver-impounded marshes.

there were missing data. Data were either $\log_{10}$- or square-root-transformed to satisfy the assumption of normality. A Kruskal–Wallis test was used to determine significant differences among site types with respect to individual water chemistry variables. Nonparametric Wilcoxon tests were then used to conduct pairwise post hoc comparisons, and p values were compared with a Bonferroni correction value of 0.017.

Since all beaver-impounded marshes had been sampled in 2011, whereas coastal marshes had been sampled in 2010, we compared data for three beaver impoundments that had been sampled in both years in 2010 using a Wilcoxon signed-rank test. No significant differences (all $p > 0.05$) in water chemistry variables were found, consistent with Cvetkovic and Chow-Fraser (2011), who used coastal marsh data from multiple years to make comparisons in the same geographic locations. We also found no significant differences for water chemistry variables when sites were grouped for sites north of Parry Sound and south of Parry Sound (Wilcoxon test; $p > 0.05$). This was important, since the coastal marshes included in this study were distributed throughout eastern Georgian Bay, while the impounded marshes we included were distributed south of Parry Sound.

Results

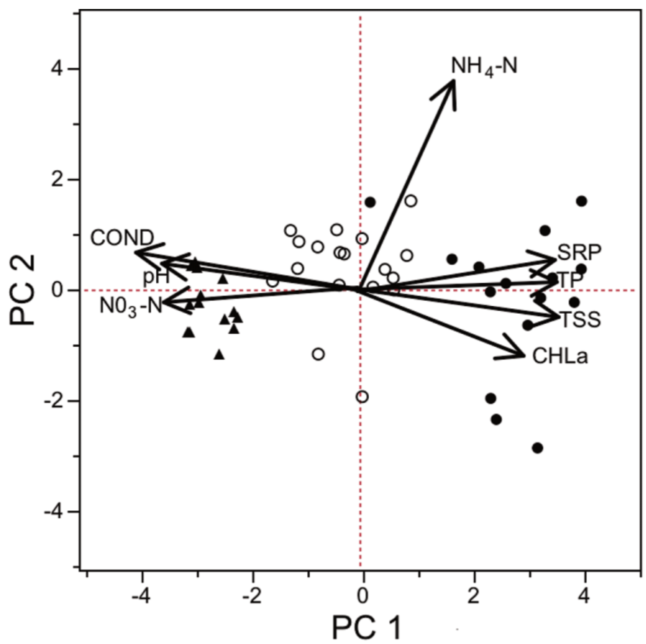
Coastal marsh versus beaver-impounded marsh

All water chemistry variables with the exception of NH_4-N differed significantly between beaver impounded marshes and coastal marshes (Table 1). Mean concentrations of TP, SRP, TSS, and Chla as well as mean TURB values were all significantly higher in the beaver-impounded marsh, whereas NO3-N, pH, and COND were all significantly lower. The only water chemistry variable that did not show significant differences was NH_4-N.

Open water versus coastal marsh versus beaver-impounded marsh

While our primary focus was to determine the effect of beaver impoundment on the water chemistry of coastal marshes, previous research by deCatanzaro and Chow-Fraser (2011) described a qualitative difference in water chemistry between the nearshore open water and the coastal marshes of eastern Georgian Bay. Open-water data provided by the Ontario Ministry of the Environment allowed us to formally test for quantitative differences between coastal marshes and open water, and to investigate the direction of the offshore-impoundment gradient for individual variables. We hypothesize that coastal marshes would have water chemistry that is more similar to that of open water than that of beaver-impounded marshes because they are hydrologically connected. We used a PCA to ordinate the three site types based on water chemistry variables. The first axis explained 67.5% of the variation in the dataset, while the second explained an additional 11.7%. PC1 was significantly and positively correlated with Chla, TSS, TP, and SRP and negatively correlated with pH, COND, and

Fig. 4. Principal component analysis (PCA) with impoundments (solid circles, n = 15), coastal marshes (open circles, n = 18), and nearshore open-water sites (solid triangles, n = 14). See Methods for explanation of abbreviations.



NO_3-N (Fig. 4), while PC2 was significantly and positively correlated with NH_4-N. Sites with positive PC1 scores corresponded with beaver impoundments that had high concentrations of phosphorus, suspended sediments, and algae in the water (solid black circles in Fig. 4), whereas those with negative PC1 scores were open-water sites located in the nearshore of Georgian Bay that corresponded with high NO_3-N concentrations, pH, and COND (solid black triangles in Fig. 4). Coastal marshes without any association with beaver dams had water chemistry that fell in the middle of the biplot and had intermediate concentrations (open circles in Fig. 4). Sites with positive PC2 scores had high concentrations of NH_4-N and included both types of coastal marshes.

A Kruskal–Wallis test indicated that there was a significant difference for all water chemistry variables when all three locations were compared (Table 2). Water chemistry differed significantly among water sample locations (NH_4-N, p = 0.0031; all others $p \leq 0.0001$). A post hoc analysis revealed that all comparisons were statistically significant among locations ($p < 0.017$ Bonferroni correction value), with the exception of Chla when comparing open water to coastal marshes (p = 0.7181), as well as NO_3-N and

Table 2. Comparison of mean water chemistry values associated with open water in Georgian Bay, coastal marshes, and beaver-impounded coastal marshes.

Associated with	Parameter	Open water (n = 14)	Coastal marsh (n = 18)	Beaver-impounded marsh (n = 15)	p value
Watershed	Total phosphorus ($\mu g \cdot L^{-1}$)	3.7a	15.3b	30.2c	<0.0001
	Soluble reactive phosphorus ($\mu g \cdot L^{-1}$)	0.7a	3.7b	13.3c	<0.0001
	Chlorophyll *a* ($\mu g \cdot L^{-1}$)	1.5a	1.9a	6.2b	<0.0001
	Total suspended solids ($mg \cdot L^{-1}$)	0.8a	2.1b	15.5c	<0.0001
	Total ammonia nitrogen ($mg \cdot L^{-1}$)	0.006a	0.01b	0.03b	0.0031
Lake	Total nitrate nitrogen ($mg \cdot L^{-1}$)	0.23a	0.04b	0.03b	<0.0001
	Specific conductivity ($\mu S \cdot cm^{-1}$)	184a	134b	47c	<0.0001
	pH	8.2a	6.95b	5.52c	<0.0001

Note: Values are means. The p value corresponds to a Kruskal–Wallis test comparing significant differences among the three sites. Similar letters denote the means are statistically homogeneous as determined by a nonparametric Wilcoxon test (α = 0.017).

NH_4-N when comparing coastal marshes to beaver-impounded marshes (p = 0.0526; p = 0.1260, respectively).

Discussion

Chemical constituents of water in coastal marshes of large lakes can come from both the watershed as well as from the lake (Morrice et al 2011). Variables such as phosphorus and suspended sediments originate from terrestrial sources and flow through the watershed into coastal marshes (Dillon and Molot 2005; Eimers et al. 2008; deCatanzaro and Chow-Fraser 2011) and thus can be classified as watershed-driven variables. Because of the well-known association between phosphorus and chlorophyll in lakes (Dillon and Rigler 1974), chlorophyll can also be considered to be influenced by the watershed. On the other hand, cations and anions in marshes of eastern Georgian Bay tend to come from mixing of lakewater during storm surges and seiches, since runoff from the weather-resistant rock of the Canadian Shield has low ionic strength (deCatanzaro and Chow-Fraser 2011). These are the lake-driven variables that include COND, pH, and NO_3-N.

We hypothesize that the presence of a dam across the outflow of a coastal marsh concentrates watershed-driven constituents while reducing inputs of lake-driven constituents. Hence, TP, SRP, TSS, and Chla were lowest in open water, intermediate in coastal marshes, and highest in beaver-impounded marshes. By contrast, COND, pH, and NO_3-N were highest in open water, intermediate in coastal marshes, and lowest in beaver-impounded mashes (Table 2). This hypothesis is further confirmed by the results of the PCA. The first principal component ordinated sites according to the degree of connection of the marsh with the open water of Georgian Bay; nearshore sites and beaver-impounded wetlands clustered at opposite ends of the PC1 axis. The coastal marshes that were not associated with beaver dams had intermediate conditions that reflected sources from both the watershed on the Canadian Shield as well as the open waters of Georgian Bay that have higher COND, pH, and NO_3-N. The nearshore data provided by the Ontario Ministry of the Environment clearly showed a trend towards higher levels of COND, NO_3-N, and pH from the open water to the beaver impoundments (Table 2). The degree of connection does not appear to influence concentrations of NH_4-N across the three site types as shown by the PCA analysis, and further research needs to be carried out to uncover the reason for this observation.

Many studies have documented the effects of size, slope, and proportion of wetlands in watersheds on the water chemistry (TP, TSS, and CHLa) of downstream wetlands (Curtis and Schindler 1997; Dillon and Molot 2005; Eimers et al. 2008; deCatanzaro and Chow-Fraser 2011). The coastal marshes and beaver-impounded wetlands that we included in this study had a similar range of watershed sizes (3.67–253.46 ha versus 3.80–367.66 ha, respectively), slopes (1.83%–13.11% versus 1.34%–13.25%), and amount of upland wetlands (0–35.69 ha versus 0–40.54 ha). There were two exceptions of coastal marshes that had watersheds >1000 ha. Since these marshes had strong upland hydrologic connection to the watershed, they should have had higher concentrations of watershed-driven variables. But rather than resembling beaver-impounded marshes, they were grouped together with other coastal marshes of smaller watershed size in the PCA biplot (Fig. 4). This indicates that watershed size did not confound the effect of hydrologic mixing in this study.

Few published studies include data on impounded coastal marshes of large lakes. Most studies have focused on lotic environments, and in these studies investigators have examined the effect of impoundment by comparing water chemistry of the stream above the dam with that of the stream directly below the dam (see Cirmo and Driscoll 1993; Margolis et al. 2001). In our system, however, the outlet of the impoundment flows into a lake rather than to a stream. Therefore, to determine the effect of the beaver impoundment on the preexisting coastal marsh, we sampled above the beaver dam. Sampling below the dam would have been more reflective of lake conditions, whereas in riverine systems, this tends to reflect the effect of the beaver dam due to the gradient and unidirectional flow of water. Despite this difference, when comparing the effects of the dam, there are many similarities between studies with respect to landscape context. Similar to our study, others have found that beaver dams can result in higher concentrations of TP (Klotz 1998), Chla (Błędzki et al. 2011), and TSS (Maret et al. 1987) within the impoundment. This reinforces the generally accepted assumption that impoundments are sinks for phosphorus and suspended particulates. Although we found a significantly lower pH in the beaver impoundment compared with the pH of coastal marshes, others have reported increased pH and high acid-neutralizing capacity in beaver ponds (Cirmo and Driscoll 1993; Margolis et al. 2001; Błędzki et al. 2011). This discrepancy is likely due to the location of our study; the Canadian Shield landscape is characteristic of ion-poor runoff and a thin layer of acidic soil (Weiler 1988), whereas other studies have taken place in different geologic environments such as the Adirondack Mountains, southwestern Pennsylvania, and Massachusetts.

The future creation or destruction of beaver-impounded marshes is difficult to forecast given our current imperfect understanding of climate change impacts. Global climate change is predicted to lead to further declines in water levels of Georgian Bay; one estimate is a 3 m decline by 2080 (Angel and Kunkel 2010). This could create more favourable conditions for beaver-impoundments, as the depths of the marsh outlet continue to decrease. Additional climate change predictions suggest that the frequency and intensity of storms will increase between periods of drought (Bates et al. 2008). Increased intensity of storms may result in discharge above the critical threshold value for a dam and thus cause it to collapse (Butler 1989; Hillman 1998; Butler and Malanson 2005). Beaver dams, however, are dynamic in nature. Regardless of climate, the number of beaver dams will naturally fluctuate along with beaver populations, resulting in temporal and spatial shifts in density of beaver-impounded areas (Naiman et al 1988). All these factors will contribute to the integrity of the dam, and the dam's integrity will consequently influence the hydrologic connectivity with Georgian Bay and the water chemistry of the impounded wetland.

This study has been the first to examine how water chemistry in the Great Lakes coastal marshes is altered by hydrologic disconnection owing to the biotic influence of the beaver. Beavers create landscape heterogeneity by producing a spatial mosaic of aquatic habitats (Johnston and Naiman 1990). The alteration of a coastal marsh by impoundment from a beaver modifies the hydrologic connectivity and influences the water chemistry by lowering the pH, lowering the amount of dissolved ions such as NO_3-N and COND, and increasing the amounts of phosphorus (TP and SRP), suspended sediments (TSS), and organic matter (Chla). Given that water quality in coastal marshes is an important determinant of fish and plant assemblages in wetlands of eastern Georgian Bay (Seilheimer and Chow-Fraser 2006; Croft and Chow-Fraser 2007), altered water chemistry and hydrologic connectivity in impoundments may shift species composition of the plant and fish communities. Little is known in this regard, and therefore further studies should be conducted to examine potential alterations in species assemblage due to impoundments as well as dam failures.

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