Environmental Research Letters

LETTER

Drying drives decline in muskrat population in the Peace-Athabasca Delta, Canada

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Keywords: ecohydrology, boreal ecology, hydrological remote sensing, habitat loss

Abstract
Empirical and anecdotal reports suggest that muskrat are in decline across North America, including in the Peace-Athabasca Delta (‘Delta’), Canada, one of the largest inland deltas in the world and part of a World Heritage Site with ‘in Danger’ status pending. Muskrat are a key ecological indicator in the Delta. We investigate whether the large-scale loss of critical habitat over the past half-century could be driving a decline in muskrat abundance in the Delta. To do this, we use the Landsat record (1972–2017) to construct a 46 year record of inundation, and compare changes in the extent of critical habitat to the survey record for muskrat (1970–2016) over this 5500 km² region. Results show that the declines in critical habitat and muskrat numbers in the Delta are synchronous: ~1450 km² of temporarily inundated regions that support critical habitat have diminished by ~10 km² yr⁻¹ over the past 46 years, while the muskrat population density (houses/km²) has also declined and is significantly related to critical habitat area (km²) ($R^2 = 0.60, P = 0.0001$). These findings have implications for the Delta, a Ramsar Wetland of International Importance in part for its role as a habitat for nearly 200 species of birds, many of which rely on the aquatic habitat considered here. Our results further suggest that the loss of wetland habitat is a primary driver of the decline of muskrat across the species’ native range.

Introduction
Canada’s Peace-Athabasca Delta (‘Delta’), the largest inland boreal delta in the world, is a Ramsar Wetland of International Importance and part of a UNESCO World Heritage Site with ‘in Danger’ status pending. Indigenous land users with decades of trapping experience in the Delta have reported ‘dramatic decline in the relative abundance of muskrat’ (Ondatra zibethicus), at least since ~1935 (Straka et al 2018). Recent work has shown that after years of known flooding (1972, 1974, 1996, 1997, and 2014), muskrat numbers recovered and then showed a short-term decline in subsequent years (up to 16 years since flooding) (Straka et al 2018), but does not evaluate drivers of the long-term trend reported by trappers.

For the first time, we investigate how a long-term disappearance in critical habitat is associated with long-term drying in the Delta that then drives the reported decline of the muskrat population.

Climate change and river regulation are driving drying in the Delta (Beltaos 2014). In the Delta, the paleolimnological record suggests drying has occurred since the late 1800s (Wolfe et al 2006), and analysis of the flood observational record since 1900 further indicates a 50% decline in flood frequency since 1968 (Beltaos 2018), when Peace River flows were altered for hydropower generation. Previous work has mapped Delta-wide drying for the brief episode 1996–2001, but does not address the long-term trend as we do here (Töyrä and Pietroniro 2005). The rate and spatial distribution of floodplain drying over the past half-century, which are crucial to muskrats, have not been quantified even though floodplain drying is often mentioned (Wolfe et al 2012, Beltaos 2014, 2018).
We quantify a severe long-term decline in abundance of the Delta’s muskrat, a key ecological indicator in wetland regions, a change also noted empirically and anecdotally across North America (Roberts and Crimmins 2010, Brietzke 2015, Ahlers and Heske 2017, Straka et al 2018). The causal mechanisms underlying the widespread population decline of muskrat across its native range have not been identified (Ahlers and Heske 2017). Studies of muskrat ecology across its native North American range indicate that they are highly sensitive to changing hydrologic conditions (Bellrose and Low 1943, Proulx and Gilbert 1983, Toner et al 2010). Here we investigate drying and the ensuing decreases in critical habitat of the 5500 km² Delta as a likely mechanism driving the decline in muskrat.

‘Critical habitat’ for muskrat in the Delta is comprised of hundreds of ephemeral water bodies that provide environments necessary for their sustainability in the Delta. This is because muskrat are semi-aquatic. Muskrat inhabit lakes, small ponds, streams, rivers and wetlands (Soper 1942), and they rely on emergent vegetation for food and to build houses (Westworth 1974). Muskrat must over-winter in their houses that are primarily anchored to stable near-shore features and overlie water deep enough for foraging under the winter ice covering lakes and ponds (Straka et al 2018).

Methods

Open water persistence mapping

We use Landsat (60 and 30 m resolution) satellite imagery (1972–2017) to quantify the spatial dynamics of open water on the Delta floodplain. Annual cloud-free composite scenes of the Delta were generated for the period 1984–2017 (except 2012) using the Google Earth Engine Landsat Simple Composite algorithm on images taken during the ice-free period between 15 June and 15 September. This default date range was customized for images where the default date range yielded cloud contamination and to avoid smoke from a 2015 fire in the northwest portion of the site (supplementary data table 1 is available online at stacks.iop.org/ERL/13/124026/mmedia). For years 1972–1983 and in 2012, cloud-free scenes of the Delta were selected from the GEE Landsat collections (supplementary data table 2). To minimize the effect of time of year on the measure of open water, images from June, July, and August were given priority over images from April, May, September and October, and images from July were given priority over images from June and August. For years with no single cloud-free image of the Delta, portions of multiple images were mosaicked to yield as cloud-free a view of the Delta as possible.

Open water mapping was performed using the JavaScript API and the GEE Landsat collections (supplementary data table 1) (Gorelick et al 2017). For each year, a water index was calculated for the TOA Reflectance image. For images with a shortwave infrared (SWIR) band, the modified normalized difference water index (NDWI) (Xu 2006) was calculated; for images without a SWIR band, the NDWI (McFeeters 1996) was calculated (supplementary data table 1). For 2012, the Landsat 5 Multispectral Scanner images’ Band 3 (NIR) was used rather than Band 4 (NIR) to calculate NDWI, as Band 4 data were not available.

Dynamic thresholding for each water index image was performed on the bimodal water index histogram using Otsu’s method, (GEE code developed by Nicholas Clinton), to yield a binary water/non-water image. Otsu’s method was used as it maximizes the inter-class variance of a bimodal distribution and has been applied for open water detection in GEE (Donchyts et al 2016).

Pixels in the water class were assigned a value of 1, and pixels in the non-water class were assigned a value of 0. Binary images in GEE API at zoom level 12 were corrected for misclassification. Misclassification of pixels occurred rarely and was due to contamination from clouds, cloud shadows, detector image errors (e.g. transmission striping), or unambiguous misclassification of water and land pixels.

The persistence map for the 46 year record (figure 1) was generated by adding pixel values of the binary images. A value of ‘0’ indicates continuously dry pixels, 46 indicates continuously inundated pixels, and intermediate values indicate an intermediate frequency of inundation. These values were converted to the percentages shown in the persistence map. The decadal inundation maps (supplementary data figure 1) were generated by adding pixel values of the binary images, with the pixel value indicating the number of years in the period that the pixel was inundated. Data to generate figure 2 employed GEE Image Pixel Area and Reducer Sum methods applied in succession to each binary map to calculate the total area of open water. The maximum region of critical habitat in at least one year was 1798 km².

Muskrat counts

We analyzed 21 years of muskrat count records since they were first collected in 1970 in the Delta. As mounds on ice-covered lakes, muskrat houses are counted during snowmobile ground surveys in winter and used as an index of population size, based on an average of five muskrat per house in the Delta (Ambrock and Allison 1972).

Muskrat house count data were from five survey reports during 1970–2005 and from the Peace-Athabasca Delta Ecological Monitoring Program during 2011–2016 (Surrendi and Jorgensen 1971, Ambrock and Allison 1972, Poll 1980, Westworth and Wiacek 2002, Westworth Associates Environmental Ltd 2006, Straka et al 2018). Data in hard copy were digitized. Each data point was manually verified to fix rare
Figure 1. Inundation persistence map. The persistence of water in the Delta, 1972–2017. Time inundated is expressed as the percentage of the Landsat record that a given location was classified as open water. The region that is ephemerally inundated is here assumed to correspond to critical Delta muskrat habitat. The black rectangle in the northwest quadrant of the Delta delineates the region of the representative Delta lake evaluated in figures 2(b)–(d).

Figure 2. Synchronous multidecadal declines of Delta muskrat and critical habitat. (a) The linear fit of muskrat population density versus time ($n = 14$, zero values excluded) has slope $= -0.17$, $R^2 = 0.46$, and $P < 0.01$. Critical habitat area over the period 1972–2017 is decreasing with linear fit (not shown) of $n = 46$, slope $= -10$, $R^2 = 0.32$, and $P < 0.001$. Gray shading shows 5 year intervals centered on years of local maxima in muskrat density for which there is satellite data: 1973–1977, 1996–2000, and 2013–2017. (b)–(d) show the reliability of local critical habitat at a representative Delta lake for each 5 year interval. Critical habitat is considered highly reliable if available for all five years, moderately reliable if available for four consecutive years out of five, and unreliable if available for four nonconsecutive years or three or fewer years out of five.
misreads. Survey areas for each count site were digitized in GIS using maps and GPS coordinates (supplementary data figure 2). Individual points were excluded if not associated with a verified survey site, or outside the Delta. Each count was normalized by its respective survey area, to obtain population density (houses/km²) (supplementary data table 3). Median densities observed in any given year served as our best estimate.

Ground survey muskrat count data provide a more accurate measure of house abundance than aerial surveys in the Delta (Poll 1980). In the absence of ground counts, we used aerial estimates for 1971, and converted values to ground count estimates using an empirical 1.9:1 ground to fixed-wing aircraft conversion ratio for the Delta (Ambrook and Allison 1972). The open water map for a given year was compared to the house count for the ensuing ice-bound period.

Given potential detection bias of years in which the median observed value of population density was zero, particularly since 2000, we excluded all years with zero median population densities from the linear fit of median population density versus time (figure 2(a)). Therefore, our estimate of declining population density over time is likely conservative.

Habitat reliability
The hydrologic landscape changes on a multi-annual basis during periods of flooding and drying (Peters et al 2006). Here we suggest that populations thrive when there is reliable local critical habitat for muskrat to establish their home range. We indicate critical habitat reliability as the number of years that a location is consistently suitable for muskrat occupation. We evaluate reliability at a representative Delta lake for three five-year periods centered around years of peak muskrat population density (figures 2(b)–(d)). The areas that are suitable during five consecutive years (high reliability) and four consecutive years (medium reliability) provide the most temporally reliable habitat (figures 2(b)–(d), dark and light purple). Fewer consecutive years of critical habitat area are mapped as low temporal reliability.

We focus on a representative lake in the northwestern quadrant of the Delta with a maximum reliable critical habitat area of 16 km² (figure 1). We examine the relation between critical habitat reliability and three sequentially lower local maxima in muskrat population density (1975, 1998, and 2015) (figure 2(a)). During these years, we inspected satellite images in a five-year window about each population density peak year.

Results
Inundation persistence, defined as the percent of the 46 years of record that any location appears as open water, is a simple measure of habitat viability (figure 1). The hydrologic landscape falls into three categories: regions that remain continuously dry, regions comprised mostly of the largest continuously inundated lakes, and periodically inundated or dry regions. The former two categories are either too dry or inhospitable, providing unsuitable habitat for muskrat. The latter ephemerally inundated region consists of hundreds of water bodies ranging in size from 100 to 0.1 km². For muskrat this set of ephemeral water bodies serves as ‘critical habitat’ that provides environments necessary for their sustainability in the Delta.

The critical habitat area has changed over time, exhibiting a decline over the past half-century and showing multi-annual wet and dry periods (supplementary data figure 1). The maximum area of critical habitat was 1445 km² (in 1974). Analysis of annual changes in critical habitat from the satellite record shows an overall decline from 913 km² (63% of the maximum) for the earliest period 1973–1977 down to 357 km² (25% of the maximum) for the period 2013–2017. Although there is tremendous temporal variation in critical habitat area, there is a general pattern of lower highs and lower lows, suggesting a decline over the entire period of 32% (a loss of 10 km² per year over the 46 year period 1972–2017; \( R^2 = 0.32, P = 0.001, \) figure 2(a)). While larger water bodies remain static features of the landscape, smaller hydrologic features comprising critical habitat are drying out (figure 1, figure 2(a)).

Since 1970, there has been a significant decline in muskrat population density \((n = 14, \) zero values excluded, \( R^2 = 0.46, P < 0.01).\) There were 19 years of survey records that overlapped with the satellite-derived critical habitat record (figure 3). On an annual basis, there is a positive correlation between muskrat
population density and critical habitat area (slope = 1.1 houses per km² for each added 100 km² of critical habitat, n = 19, R² = 0.60, and P = 0.0001, figure 3).

Considering five-year-long time windows during which critical habitat persisted, we see a decline in reliable critical habitat at the representative Delta lake (figures 2(b)–(d)). This decline in critical habitat corresponds to a decrease in muskrat population density. It is noteworthy that muskrat population density drops more precipitously from its peak value to low levels as the extent of reliable critical habitat diminishes, the drop taking >3 years after 1975, ~2 years after 1998, and just 1 year after 2015 (figures 2(a)–(d)).

Discussion and conclusions

Satellite imagery analysis of the Delta shows ~1450 km² of temporarily inundated regions that support critical habitat have diminished by ~10 km² yr⁻¹ over the past 46 years; a decline of ~32% over the last half-century. This environmental change corresponds to the severe decline of the muskrat population, a semi-aquatic mammal with cultural and economic importance for Indigenous communities in the Delta region, Canada and Alaska (Wilson 2014, Brietzke 2015, Straka et al 2018). The long-term loss of wetland habitat has implications for the ecological significance of the Delta landscape. There, hundreds of lakes and wetlands serve as habitat for nearly 200 species of birds, many migrating from across North America (Timoney 2013). With accelerating impacts of climate change at high latitudes and additional hydropower development underway on the Peace River, a continued decline in the Delta’s critical habitat is anticipated. In this case, the impacts of hydrologic change on Delta muskrat demonstrated here will likely worsen. Taken together with our findings, concurrent observations of widespread loss of wetland and aquatic habitat at sites across North America (Riordan et al 2006, McMenamin et al 2008, Davidson 2014) suggest that critical habitat loss is a likely causal mechanism responsible for the ongoing decline of muskrat across its native range.

Acknowledgments

We thank the Mikisew Cree First Nation, Athabasca Chipewyan First Nation, and Fort Chipewyan Métis Local 125 for helpful discussions about the Delta ecosystem; the Peace-Athabasca Delta Ecological Monitoring Program (PADEMP) for sharing their muskrat survey data and for bringing EMW on traditional territories in the Delta with the 2015 muskrat survey team; and Parks Canada for sharing historic muskrat survey data and logistical support in Fort Chipewyan. We appreciate discussions with Elizabeth Hadly and her lab members. We are grateful for financial support through an Environmental Venture Project Grant from the Stanford Woods Institute for the Environment, a George P Shultz Fellowship in Canadian Studies from the Stanford Freeman Spogli Institute for International Studies, and a Stanford Graduate Fellowship and McGee Grants from Stanford University.

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References

Ahlers A A and Heske E J 2017 Empirical evidence for declines in muskrat populations across the United States: muskrat population declines J. Wildlife Manag. 81 1408–16

Ambrock K and Allison L 1972 Status of Muskrat on the Peace-Athabasca Delta (Edmonton: Canadian Wildlife Service)

Bellrose F C and Low I J 1943 The influence of flood and low water levels on the survival of muskrats J. Mammal. 24 173

Beltaos S 2014 Comparing the impacts of regulation and climate on ice-jam flooding of the Peace-Athabasca delta Cold Reg. Sci. Technol. 108 49–58

Beltaos S 2018 Frequency of ice-jam flooding of Peace-Athabasca Delta Can. J. Civil Eng. 45 71–5

Brietzke C 2015 Muskrat ecology in the Mackenzie Delta: insights from local knowledge and ecological field surveys Arct. 68 527

Davidson N C 2014 How much wetland has the world lost? Long-term and recent trends in global wetland area Mar. Freshwater Res. 65 934

Donchys G, Baart F, Winsemius H, Gorelick N, Kwadijk J and van de Giesen N 2016 Earth’s surface water change over the past 30 years Nat. Clim. Change 6 810–3

Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D and Moore R 2017 Google Earth engine: planetary-scale geospatial analysis for everyone Remote Sens. Environ. 202 18–27

McFeeters S K 1996 The use of the normalized difference water index (NDWI) in the delineation of open water features Int. J. Remote Sens. 17 1425–32

McMenamin S K, Elizabeth A H and Wright C K 2008 Climatic change and wetland desiccation cause amphibian decline in Yellowstone national park Proc. Natl Acad. Sci. 105 16988–93

Peters D L, Terry D P, Pietroniro A and Leconte R 2006 Flood hydrology of the Peace-Athabasca Delta, Northern Canada Hydrol. Process. 20 4073–96

Poll D 1980 Muskrat Monitoring in the Peace-Athabasca Delta 1973–1979 (Edmonton: Canadian Wildlife Service for Parks Canada Prairie Region)

Proulx G and Gilbert F F 1983 The ecology of the muskrat, Ondatra Zibethicus, at Luther Marsh, Ontario Can. Field Naturalist 97 377–90

Riordan B, Verbyla D and McGuire A D 2006 Shrinking ponds in subarctic Alaska based on 1950–2002 remotely sensed images J. Geophys. Res.: Biogeosci. 111 G04002

Roberts N M and Crimmins S M 2010 Do trends in muskrat harvest indicate widespread population declines? Northeastern Naturalist 17 229–38

Soper J D 1942 Mammals of Wood Buffalo Park, northern Alberta and district of Mackenzie J. Mammal. 23 119–45

Straka J R et al 2018 ‘We used to say rats fell from the sky after a flood’: temporary recovery of muskrat following ice jams in the Peace-Athabasca Delta Arctic 71 218–28

Surrendi D and Jorgensen C 1971 Some Aspects of Muskrat Winter Ecology on the Peace-Athabasca Delta (Edmonton: Canadian Wildlife Service)
Timoney K P 2013 *The Peace-Athabasca Delta: Portrait of a Dynamic Ecosystem* (Edmonton: University of Alberta Press)
Toner J, John M F and Mead J V 2010 Muskrat abundance responses to water level regulation within freshwater coastal wetlands *Wetlands* 30 211–9
Töyrä J and Pietroniro A 2005 Towards operational monitoring of a northern wetland using geomatics-based techniques *Remote Sens. Environ.* 97 174–91
Westworth Associates Environmental Ltd 2006 *The Status of Muskrats on the Peace-Athabasca Delta 2002–2006 Surveys* (Edmonton: BC Hydro)
Westworth D A 1974 *Ecology of the Muskrat (Ondatra zibethicus spatulatus) on the Peace-Athabasca Delta, Wood Buffalo National Park* (Edmonton: Department of Zoology, The University of Alberta)
Westworth D and Wiacek R 2002 *The Status of Muskrats on the Peace-Athabasca Delta, 2000–2001 Survey* (Edmonton: BC Hydro)
Wilson N J 2014 The politics of adaptation: subsistence livelihoods and vulnerability to climate change in the Koyukon Athabascan village of Ruby, Alaska *Hum. Ecol.* 42 87–101
Wolfe B B, Roland I H, Thomas W D E and John W J 2012 Developing temporal hydroecological perspectives to inform stewardship of a Northern Floodplain Landscape subject to multiple stressors: paleolimnological investigations of the Peace-Athabasca Delta *Environ. Rev.* 20 191–210
Wolfe B B, Roland I H, Last W M, Edwards T W D, English M C, Karst-Riddoch T L, Paterson A and Palmini R 2006 Reconstruction of multi-century flood histories from oxbow lake sediments, Peace-Athabasca Delta, Canada *Hydrol. Process.* 20 4131–53
Xu H 2006 Modification of normalized difference water index (NDWI) to enhance open water features in remotely sensed imagery *Int. J. Remote Sens.* 27 3023–33