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2020

Original citation:

Turner, C. K., Lantz, T. C., & Fisher, J. T. (2019). Muskrat distributions in a changing Arctic delta are explained by patch composition and configuration. *Arctic Science*, *6*(2), 77–94. https://doi.org/10.1139/as-2018-0017

NRC Research Press
ARTICLE

Muskrat distributions in a changing Arctic delta are explained by patch composition and configuration

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Abstract: Climate change is altering Canada's western Arctic, including hydrology in the heterogeneous environment of the Mackenzie Delta, and these changes are impacting biotic communities. Muskrats are culturally important semi-aquatic rodents whose populations may respond to changing water levels in this region. We investigated the importance of patch configuration and patch composition — two properties affected by climate change — on muskrat presence and distribution in the Mackenzie Delta, using remote sensing and field-based surveys of lakes with and without muskrats. We tested multiple hypotheses about predictors of muskrat and forage biomass presence using a model-selection approach. We found that configuration and patch composition explained muskrat distribution in the Mackenzie Delta, with composition being of greater importance. Muskrats were more likely to occur in lakes with longer perimeters, higher amounts of forage biomass, and sediment characteristics that supported macrophyte growth. The latter two conditions are related to spring flooding regimes, which will likely be altered by climate change. This may result in a decrease in muskrat habitat in the Mackenzie Delta. Our research indicates that both patch composition and configuration are important for understanding species distributions in heterogeneous environments.

Key words: Arctic, muskrat, heterogeneity, Mackenzie Delta, hydrology.

Résumé : Les changements climatiques transforment l'ouest de l'Arctique canadien, en particulier l'hydrologie dans l'environnement hétérogène du delta du Mackenzie, et ces transformations se répercutent sur les communautés biotiques. Les rats musqués sont des rongeurs semi-aquatiques d'une importance culturelle, et leurs populations sont susceptibles de réagir à des changements des niveaux d'eau dans cette région. Les auteurs ont étudié l'importance de la configuration et de la composition des parcelles — deux propriétés affectées par les changements climatiques — sur la présence et la distribution du rat musqué dans le delta du Mackenzie, à l'aide de la télédétection et de relevés sur le terrain de lacs hébergeant ou non des rats musqués. Ils ont vérifié de nombreuses hypothèses quant aux prédicteurs de la présence de rats musqués et de biomasse fourragère à l'aide d'une approche de choix des modèles. Ils ont trouvé que la configuration et la connectivité des lacs, de même que la composition des parcelles, expliquaient la distribution du rat musqué dans le delta du Mackenzie, la composition s'avérant la plus importante. Les rats musqués étaient plus susceptibles de se trouver dans les lacs dont le périmètre est plus long, qui comportent une biomasse fourragère plus élevée et dont les caractéristiques sédimentaires favorisent la croissance de macrophytes. Ces deux dernières conditions sont liées aux régimes d'inondation printanière, qui seront vraisemblablement modifiés par les changements climatiques. Il pourrait en résulter une diminution de l'habitat du rat

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Received 16 June 2018. Accepted 20 November 2019.

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Arctic Science 6: 77–94 (2020) dx.doi.org/10.1139/as-2018-0017

musqué dans le delta du Mackenzie. Ces recherches indiquent que la composition et la configuration des parcelles sont importantes pour comprendre la répartition des espèces dans des environnements hétérogènes. [Traduit par la Rédaction]

Mots-clés : Arctique, rat musqué, hétérogénéité, delta du Mackenzie, hydrologie.

Introduction

Rapidly increasing temperatures and changing precipitation are altering the range and phenology of species, impacting population dynamics, and shifting community composition in the Arctic (Galbraith et al. 2002; Walther et al. 2002; Parmesan and Yohe 2003; ACIA 2004; Huntington 2006; Gilg et al. 2012; IPCC 2014). The Mackenzie Delta in Canada's western Arctic is currently experiencing a suite of changes, as temperatures have risen by approximately 3 °C from 1926 to 2017 (Lantz et al. 2019). Salmon abundance has increased in the last 20 years (Dunmall et al. 2013), and seasonal timing is changing, with river break-up occurring nearly 10 days earlier than in the 1960s (Lesack et al. 2014). The delta is an expansive alluvial plain dominated by thousands of lakes and interconnected channels that provide habitat for fish, birds, and mammals (Mackay 1963; Martell and Pearson 1978). Recent observations indicate that climate change is altering hydrological processes and lake flooding regimes in this region, and observed changes are likely to affect the distribution and conditions of lake habitat for many species (Lesack et al. 1998, 2014; Prowse et al. 2006; Déry et al. 2009).

Habitat for aquatic species in the Mackenzie Delta is heterogeneous and can be viewed as semi-connected aquatic resource patches surrounded by a matrix of less suitable (or possibly uninhabitable) habitat (Turner 1989; Kotliar and Wiens 1990; Tscharntke et al. 2012). In patchy environments like that of the Mackenzie Delta, a species' distribution is influenced by both the composition of resource patches and the configuration of these patches. Composition measures the biotic characteristics and resources within a patch, whereas configuration includes patch shape and connectivity, with the latter affecting species' ability to move through the matrix and access these resources (Taylor et al. 1993; Harrison and Bruna 1999; Goodwin and Fahrig 2002). Niche theory states that species can only persist when and where there are sufficient available and accessible resources, and suitable biotic and abiotic conditions, which vary based on species' requirements (Grinnell 1917; Hutchinson 1957). Taken together, composition and configuration offer a way to characterize complex habitats (Merriam 1995; Villard et al. 1995; Haines-Young and Chopping 1996; Drapeau et al. 2000), including the mosaic of water bodies within the Mackenzie Delta. For aquatic species, lakes are patches with varying habitat composition and configuration, embedded within a less suitable terrestrial matrix of variable connectivity dominated by spruce woodlands and alder and willow thickets (Gill 1971).

Most research on species' persistence in heterogeneous habitats focuses on the effects of anthropogenic fragmentation (Keitt et al. 1997; Kupfer et al. 2006; Prugh et al. 2008), but climate change will also affect species living in naturally heterogeneous environments (Opdam and Wascher 2004; Gilg et al. 2012). In the Mackenzie Delta, climate change will alter (1) patch configuration and connectivity, as some lakes and channels change shape, dry out, and the vegetation of the matrix changes (Myneni et al. 1997; Emmerton et al. 2007; Pisaric et al. 2007); and (2) patch composition, as some lakes become shallower and more acidic, and others receive more sediment and nutrients from increased sediment loads in the river (Marsh and Lesack 1996; Lesack et al. 1998; Prowse et al. 2006; Emmerton et al. 2007). A primary driver of these predicted changes is reduced flooding, as spring breakup dynamics shift and peak water levels decrease (Lesack et al. 2014).

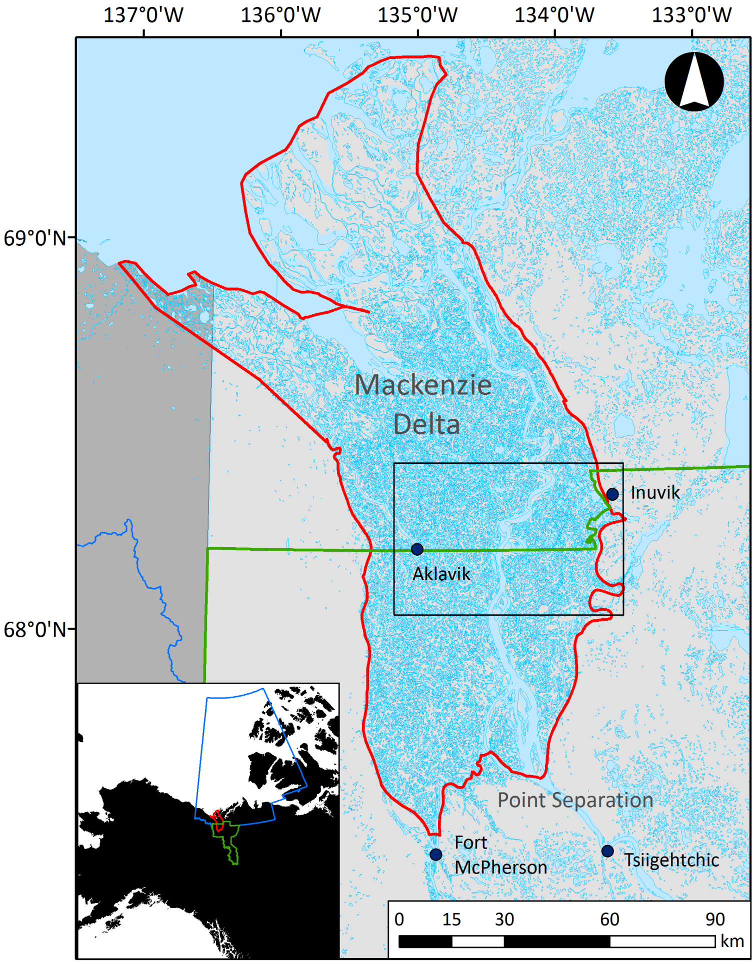
Research on the relative importance of patch composition versus configuration and connectivity is required to determine the mechanisms and magnitude of the impact of climate change on species (Wiens et al. 1993; Opdam and Wascher 2004). We investigated the importance of patch configuration and patch composition on the distribution of a semi-aquatic mammal, the muskrat (*Ondatra zibethicus* (Linnaeus, 1766)).

Muskrats are rodents with ecologically important roles in the food webs and communities of aquatic ecosystems; they are prey for numerous carnivores, primarily mink, eagles, and otter in the Mackenzie Delta, and can significantly impact the density and community composition of the plant foods they forage upon (Higgins and Mitsch 2001; Mott et al. 2013). Muskrat densities respond to lake water levels and they may serve as an important indicator species for changes in wetland ecosystems (Weller 1981, 1988; Straka et al. 2018). Muskrats are also culturally important in the Mackenzie Delta, in large part because of the role they played in the regional economy from the 1850s to the present (Gwich'in Elders 1997; Alunik et al. 2003; Turner et al. 2018). In recent decades, residents of this region have observed extended declines in muskrat abundance that are outside the normal range of variation (Arctic Borderlands Ecological Knowledge Society 2002, 2008; Bennett and Lantz 2014; Turner et al. 2018). This decline in muskrats is likely to have significant impacts on the delta communities that continue to rely on these animals for subsistence, trapping income, and overall well-being (Parlee et al. 2005; Turner and Turner 2008; Parlee and Furgal 2012; Gill et al. 2014; Turner et al. 2018).

Muskrats in the Mackenzie Delta live in bank burrows within lentic waterbodies. In summer they rely on emergent shoreline vegetation, and in winter they eat the roots and rhizomes of submerged macrophytes that persist on lake bottoms under the ice (Errington 1963; Jelinski 1984, 1989). Two factors that likely affect the ability of muskrats to effectively use and persist in lakes within the Mackenzie Delta are: (1) lake accessibility and shape (patch configuration), and (2) within-lake resource availability and abiotic conditions (patch composition) (Harrison and Bruna 1999; Goodwin and Fahrig 2002; Weyrauch and Grubb 2004; Schooley and Branch 2009; Thornton et al. 2011). In this study we investigated the relative importance of these factors on muskrat distributions. Specifically, we quantified patch configuration by measuring the connectivity of lakes to each other and to river channels (closure class, flooding distance, and interpatch distance between lakes), and the lake shape (perimeter, the ratio of perimeter to area, and area). We also characterized patch composition by measuring lake depth, submerged macrophyte biomass, water turbidity, and sediment nutrient content. We predicted that increased connectivity to river channels and other lakes, as well as lake size, would be positively related to muskrat presence, facilitating muskrat movement between resource patches (Jelinski 1984; Goodwin and Fahrig 2002). Within lakes, we predicted that muskrat presence would be positively correlated with edible macrophyte biomass, variables influencing the productivity of these edible macrophytes, and increasing lake depth (Stevens 1955; Jelinski 1989; Brammer 2016).

Although we categorized variables as patch configuration or patch composition, one mechanistically affects the other. Configuration variables measuring connectivity (closure class and flooding distance) influence lake accessibility for semi-aquatic animals and also directly influence patch composition variables by controlling sediment inputs from the river (Marsh et al. 1999; Squires and Lesack 2002, 2003*a*, 2003*b*; Squires et al. 2002). We sought to disentangle them to some degree by also investigating the drivers of submerged macrophyte presence (food availability) in individual lakes, and hypothesized that water depth, turbidity, and sediment organic matter content would be primary drivers (Squires and Lesack 2002, 2003*a*, 2003*b*). Overall, we expected that both patch composition and configuration would drive muskrat distribution within the shifting mosaic of the Mackenzie Delta.

Fig. 1. Map of the study region. The boundary of the Mackenzie Delta ecoregion (Ecosystem Classification Group 2007) is shown in red. The northern boundary of the Gwich'in Settlement Area (Gwich'in Tribal Council and Indian and Northern Affairs Canada 1992) and southern boundary of the Inuvialuit Settlement Region (Indian and Northern Affairs Canada 1984) is shown in green. Communities in the study area are marked with dark blue circles. Water bodies are outlined in cyan. Inset map shows location of study area in northwestern North America and the full extent of the Inuvialuit Settlement Region (blue) and the Gwich'in Settlement Area (green). The black box outlines the study area enlarged in Fig. 2. Map produced in ArcGIS (version 10.5).



Methods and materials

Study area

The Mackenzie Delta (hereinafter referred to as "the Delta") is a vast alluvial plain that extends from Point Separation 210 km north to the Beaufort Sea and covers an area of 13 000 km^2 (Fig. 1). The area contains hundreds of distributary channels and over 40 000 lakes that vary in size, depth, productivity, biodiversity, and flooding regimes (Hay et al. 2000; Squires and Lesack 2002, 2003*a*; Emmerton et al. 2007). The vegetation of the southern and central Delta is characterized by white spruce (*Picea glauca*) forest, and alder (*Alnus* spp.) and willow (*Salix* spp.) thickets, and the northern delta is dominated by sedge wetlands and tall shrub thickets (Gill 1971; Pearce et al. 1988; Burn and Kokelj 2009). Lakes in the Delta are strongly influenced by the annual spring flood, which is the main source of water, inorganic sediment, and nutrients (Marsh and Bigras 1988; Lesack et al. 1998).

We classified lakes into three categories: no-closure, low-closure, and high-closure, using data collected in 1992 (Marsh et al. 1999). This classification is based on flooding regimes, which are largely controlled by the height at which lakes are perched above distributary channels (Marsh and Hey 1989; Lesack and Marsh 2010). No-closure lakes are at the same height as the distributary channels and are connected to the river by a channel or small opening all summer; their levels rise and fall with river levels. Low- and high-closure lakes are perched above the channels, and they flood only in the spring when water levels are high during ice break-up. Low-closure lakes are perched at a height that high waters reach each spring, and are flooded every year. High-closure lakes are perched at higher elevations, and flood only every 2–4 years when spring flood waters are sufficiently high (Marsh and Hey 1989; Lesack and Marsh 2010). Biophysical differences in lakes among closure classes include lake transparency (Marsh et al. 1999; Squires et al. 2002), water solute chemistry, including pH and nutrient levels (Lesack et al. 1998), nutrient and organic matter content of sediment (Squires and Lesack 2003*a*), and macrophyte productivity and community composition (Squires et al. 2002; Squires and Lesack 2003*a*).

The Delta falls entirely within the traditional territories of the Gwich'in and Inuvialuit, as formalized by land claim agreements that established the Gwich'in Settlement Area encompassing the upper delta, and Inuvialuit Settlement Region extending across the lower delta to the coast (Indian and Northern Affairs Canada 1984; Gwich'in Tribal Council and Indian and Northern Affairs Canada 1992; Fig. 1). Residents of all four Delta communities — Invuik, Aklavik, Fort McPherson, and Tsiigehtchic — frequently travel in the Delta throughout the year by boat, automobile, and snowmobile for subsistence and income harvesting of many species (including muskrats), and to maintain extended social and family networks.

Data collection

To characterize spatial variation in muskrat occupancy and biophysical conditions among lakes with different hydrological regimes throughout the central Delta, we randomly selected 150 lakes from each of the closure classes defined by Marsh and Hey (1989). Closure class data were obtained from a database of approximately 3300 lakes in an area between Inuvik and Aklavik (Fig. 2) (Marsh et al. 1999). From this initial sample of 450 lakes, we retained all lakes with >50% ice coverage in imagery obtained for aerial muskrat push-up surveys, as described below. This stratified sample yielded 129 classified lakes (high closure = 44, low closure = 49, no closure = 36; Fig. 2). Although this sample may not be representative of the conditions in the entire Delta, by including a subset of lakes from each closure class, at a variety of distances from distributary channels, we contend that it effectively captures the variation among lakes throughout the central Delta.

Muskrats construct mounds of vegetation on the ice surface called "push-ups" that insulate and preserve an air hole in the ice that the animals use for feeding, breathing, and resting (Fig. 3) (Stevens 1955). Push-ups are constructed in the fall and are used throughout the winter, sinking into the lake when the ice melts in the spring. Push-up abundance on lakes is a useful indicator of muskrat presence in lakes over the winter, and of annual variation in muskrat abundance (Simpson et al. 1989). To document muskrat occupancy in individual lakes in the winter, we conducted an aerial photographic survey of muskrat push-ups from 21 to 22 May 2015. This date was prior to the breakup of the Mackenzie River and the melting of lake ice, when muskrat push-ups are most visible on ice-covered lake surfaces. Survey photographs were captured from a Cesna 172 with a camera mount in a bubble window. Vertical images with a resolution of 300 dpi were captured at an altitude of approximately

Fig. 2. Study region in the central Mackenzie Delta. The extent of this map corresponds to the area outlined in Fig. 1. Lakes are identified by closure class and muskrat push-up presence (polygon colour). Lakes that were surveyed in the field are shown as black dots. Map produced in ArcGIS (version 10.5).

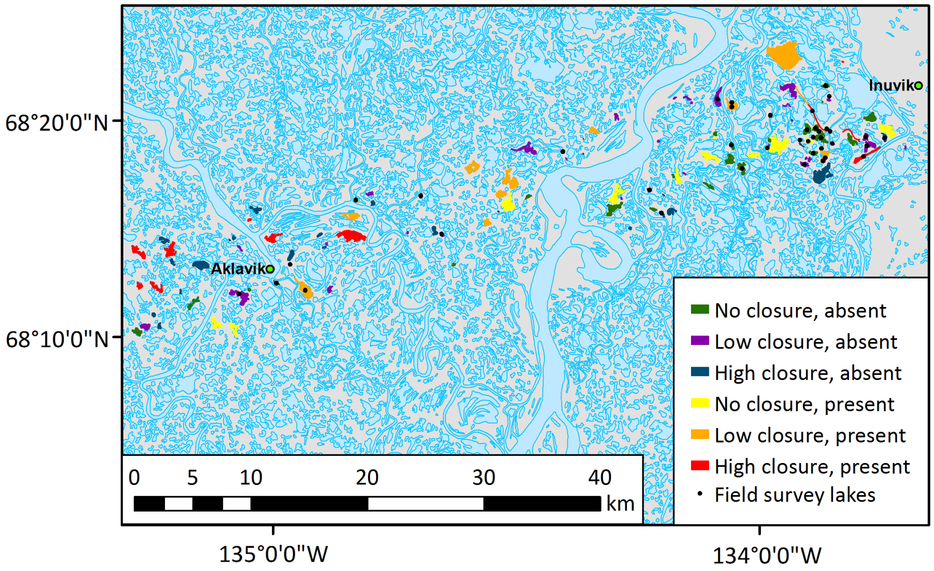
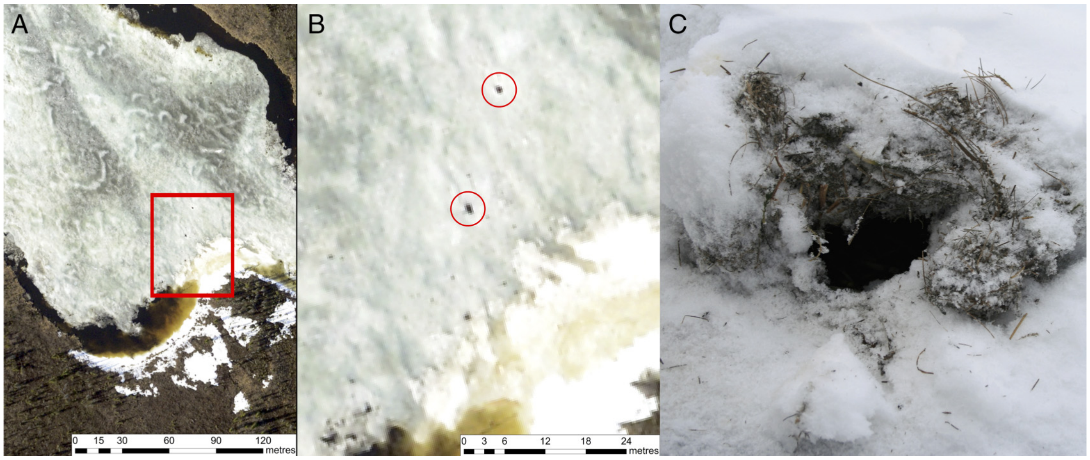


Fig. 3. (A) Example of an image of an ice-covered lake surface from aerial push-up survey. Red rectangle in (A) indicates enlarged region shown in (B). Push-ups are identified by red circles in (B). (C) Ground view of a muskrat push-up.



950 ft using a Nikon (Mississauga, Ontario, Canada) D800E camera equipped with a 28 mm lens. Individual push-ups were counted on all lakes by a single observer visually inspecting geo-referenced survey photos, based on the colour, size, shape, and context of the visible features on the ice surface (Fig. 3). Research in the Old Crow Flats Region of the Yukon (approximately 200 km west of our study area) showed that aerial surveys can be used to effectively estimate muskrat push-up density (Simpson et al. 1989). However, as the

relationship between the number of push-ups on a lake and muskrat abundance is uncertain (Simpson et al. 1989), we converted push-up counts in individual lakes to muskrat presence–absence data. As muskrats make more than one push-up, and multiple push-ups are hard to miss on aerial photos, we are confident that lakes without push-ups are reliably considered as being absent of muskrats throughout the entire winter. The presence of any number of push-ups is a reliable indicator of muskrat presence in the fall, although a lake's population may not persist throughout the winter because of predation or other causes of mortality.

We determined the area and perimeter of each lake using polygons digitized from 1:30 000 scale air photos taken in 2004. We measured flooding distance as the Euclidean distance from the lake edge to the nearest channel of the Mackenzie River and interpatch distance as the Euclidean distance between the shorelines of the nearest neighbouring lake. If lakes were connected by small channels or openings, the interpatch distance was recorded as 0. We also used these digital data to calculate the perimeter:area ratio for each lake (Supplementary Table S1-1[1]).

We conducted field surveys from 2 July to 24 August 2015 at 39 lakes accessible by boat and portage (high closure = 11, low closure = 17, no closure = 11) (Fig. 2). At each lake we measured turbidity and lake depth at multiple points along one or two transects extending across the lake. At the mid-point of each transect we collected a water sample at 0.5 m below the surface, which was analyzed for total phosphorus content (SM4500-P:D; APHA et al. 2012) by Taiga Environmental Laboratory (Yellowknife, Northwest Territories, Canada). We also collected a sediment sample at the midpoint of each transect using an Ekman (Wildco, Yulee, Florida, USA) grab sampler, which was analyzed for sediment chemistry (Ca, K, Mg, S, B, Cu, Mn, Mo, Na, Ni, P, Zn, N, organic C, and inorganic C) using microwave digest and inductively coupled plasma mass spectrometry methods (Beauchemin 1999). Sediment organic matter content was estimated using loss-on-ignition methods (Dean 1974). We collected submerged macrophyte standing crop samples from the lake bottom at three systematically selected points (the midpoint and halfway to the shore on either side) along each transect using a bottom rake method (Johnson and Newman 2011) with a circular swath (0.09 m^2). These samples were sorted by species, dried, and weighed to provide measures of overall biomass and community composition (Squires and Lesack 2003*a*; Johnson and Newman 2011). The biomass of edible macrophytes in each plot was also estimated by adding the total above-ground biomass of all edible macrophyte species. This variable was used as an index of the quantity of energy-rich roots or rhizomes preferred as winter forage by muskrats (Artimo 1960; Jelinski 1989).

Statistical analysis

To identify the combination of biophysical variables that best explained muskrat push-up and edible biomass presence in lakes we used a model-selection, information-theoretic approach to construct and compare models based on a priori hypotheses of the most ecologically relevant combinations of parameters (Burnham and Anderson 2002). We ranked support for competing hypotheses using generalized linear models (GLMs; Zuur et al. 2009*a*) and analyzed muskrat push-up presence with two datasets: (1) configuration variables among 129 lakes, and (2) configuration and within-lake (patch composition) variables among the 39 sampled lakes (Supplementary Table S1-1[1]). We also used generalized linear mixed models (GLMMs; Zuur et al. 2009*b*) to examine within-lake variables as predictors of the presence of edible biomass within 39 lakes (Supplementary Table S1-2[1]). All analyses were performed using R Statistical Software (R Core Team 2012).

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[1] Supplementary material is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/as-2018-0017.

To retain all possible data points for analysis, missing data were replaced with the mean of that variable across all 39 lakes. Although this method is not advisable when a significant portion of data is missing (Acock 2005; Graham 2009), we only applied mean substitution to three lakes (7.6% of the total) that were missing one or more measurements. This is not likely to substantially distort variance or correlations (Schafer and Graham 2002).

All variables were examined for outliers using Cleveland dotplots (Zuur et al. 2010). Collinearity was investigated with Pearson's correlation coefficient matrices for all variables, and variable pairs with r values >0.7 were not included in the same models to avoid high variance inflation factors (Graham 2003; Zuur et al. 2010). In the case of collinear variables, we retained variables with the strongest connection to the hypothesized relationships shown in Supplementary Tables S1-1 and S1-2[1]. All variables were standardized ($\mu = 0$, $\sigma = 1$) to more easily compare effect sizes among parameters with different measurement units and ranges.

To reduce the number of variables to consider in our candidate models, but retain information on the 18 sediment nutrient and trace element variables, we conducted principal component analyses (PCAs). PCAs reduce the dimensions of data by creating principal components (PCs) that each explain a portion of the overall variance in the data (Jolliffe 2013). The PC loadings measure the correlations between each PC and the original variables (Supplementary Table S2-1[1]). We ran three PCAs on sediment variables: one for muskrat push-up presence models (Analysis 1), and two for within-lake edible biomass presence models (Analyses 2 and 3) (see Supplementary Tables S2-1 and S2-2[1]). The first edible biomass PCA (Analysis 2) included all sediment variables and the second (Analysis 3) did not include organic matter and correlated variables. All three PCAs yielded similar results, and the loadings for Analysis 2 are provided as an example in Supplementary Table S2-2[1]. The two principal component scores explaining the most variance from each PCA (PC1 and PC2) were included as variables in model selection. In all cases, principal components were measures of sediment chemistry related to the relative importance of inorganic sedimentation (PC1) and nutrient enrichment from spring flooding (Barko and Smart 1986; Barko et al. 1986; Marsh et al. 1999; Squires and Lesack 2003*a*).

Our small sample size ($n = 39$) and high number of variables ($n = 12$) meant that fully saturated global models for all analyses were overfit or did not converge. Therefore, models were constructed with smaller sets of variables. Models were arranged in subsets to explore different hypothesized processes driving push-up and edible biomass presence (Supplementary Tables S3-1–S3-3[1]). We examined variance inflation factors (VIFs) to check for collinearity among covariates within models, and terms with VIFs >3 were dropped (Zuur et al. 2010) based on the process described above. Models combining the best predictors from each subset were added in a second stage of the model selection process, and should be considered exploratory rather than confirmatory (Burnham and Anderson 2002).

To examine the drivers of muskrat push-up presence, we constructed GLMs that transform non-normal response data using a log link function with a binomial error distribution (McCullagh and Nelder 1989) and a clog-log link function, which has an asymmetrical sigmoidal curve that is more accurate for samples with an imbalance of 0 and 1 s, as in our data (Hardin and Hilbe 2007; Zuur et al. 2009*a*). To test hypotheses about factors driving edible biomass, we used GLMMs to account for repeated samples within the same lake. GLMMs take into account correlation structures within the data by including a random effect variable identifying correlated measurements (Zuur 2009). We included lake as a random factor in all models.

For all models, we extracted model residuals and examined plots of the residuals versus predicted values, Q–Q plots using standardized deviance residuals, and an approximate Cook's distance to check for violations of assumptions (Zuur 2009). We compared models

Table 1. Model selection within the 129-lake patch configuration model set.

Model	Parameters	AIC_c	ΔAICc	AICc weight	Residual deviance[a]	*K*
5	**Perimeter**	**119.13**	**0.00**	**0.68**	**115.00**	**1**
8	Flooding distance + perimeter[b]	120.67	1.54	0.32	114.50	2
6	Area	132.88	13.74	0.00	128.80	1
7	Edge ratio	146.68	27.55	0.00	142.60	1
1	Interpatch distance + flooding distance + interpatch distance × flooding distance	152.79	33.66	0.00	144.50	3
2	Flooding distance	153.09	33.96	0.00	149.00	1
3	Interpatch distance	154.15	35.02	0.00	150.10	1
4	Closure class	156.62	37.49	0.00	150.40	2

Note: Models were ranked using the corrected Akaike information criterion (AICc). The best-fit model is bolded and indicated by ΔAICc = 0.00 and highest AICc weight. Additional information on each model is provided in the Supplementary Material.

[a] Null model deviance is 150.82 on 128 degrees of freedom.

[b] Model not considered competitive (Arnold 2010).

in each set using the Akaike information criterion corrected for small sample sizes (AICc). AICc scores generated by maximum likelihood estimation provide a measure of the fit and parsimony of each model in a set relative to one another, balancing optimal model fit with the number of parameters used (Burnham and Anderson 2002; Hocking and Reimchen 2009). We used the differences in AICc values relative to the best-fit model in each set (ΔAICc) and normalized AIC weights ($AICc_w$) to rank models in each set, with lower ΔAICc values and higher $AICc_w$ indicating better models. We did not consider models that included one additional variable that did not improve explanatory power enough to overcome the penalty for the added parameter of +2 AICc (Anderson and Burnham 2002; Burnham and Anderson 2002; Arnold 2010; Wenger et al. 2011), but these models are presented in model selection tables, and identified in the footnotes (Tables 1–3). We reported the magnitude and direction of parameter estimates for each individual covariate in the top ranked model of each analysis to evaluate their relative strength in predicting muskrat or edible biomass presence (Burnham and Anderson 2002).

Results

Model selection for patch configuration drivers of muskrat push-up presence

Push-ups were present in 27% of the sample of 129 lakes from which we collected remotely-sensed patch configuration data. Muskrat push-up presence was best explained by lake perimeter (model 5; ΔAICc = 0.00, $AICc_w = 0.68$; Table 1); longer perimeters were positively associated with push-up presence ($\beta = 0.376$, SE = 0.071, CI = 0.257–0.497, Fig. 4). Other patch configuration and connectivity characteristics, including area, edge:area ratio, interpatch distance, flooding distance, and closure class were relatively poor predictors of muskrat winter lake occupancy (Table 1).

Model selection for patch connectivity and within-lake drivers of muskrat push-up presence

At the 39 lakes where we conducted lake composition surveys, muskrat push-ups were observed in eight lakes (20.5%) (Fig. 2). For field-surveyed lakes, muskrat push-up presence was best predicted by a combination of variables describing patch configuration and within-lake patch composition (model 12; ΔAICc = 0.00, $AICc_w = 0.90$; Table 2), including lake perimeter ($\beta = 1.580$, SE = 0.555, CI = 0.634–2.959), PC2 values ($\beta = 1.430$, SE = 0.510, CI = 0.510–2.644), and edible biomass ($\beta = 1.098$, SE = 0.405, CI = 0.175–2.159). All of these variables had a positive effect size on muskrat push-up presence (Table 3).

Fig. 4. Predicted values from logistic regression (push-up presence as a function of perimeter) (blue line) with 95% confidence intervals (grey fill) and observed push-up presence and absence (black points) plotted against perimeter values.

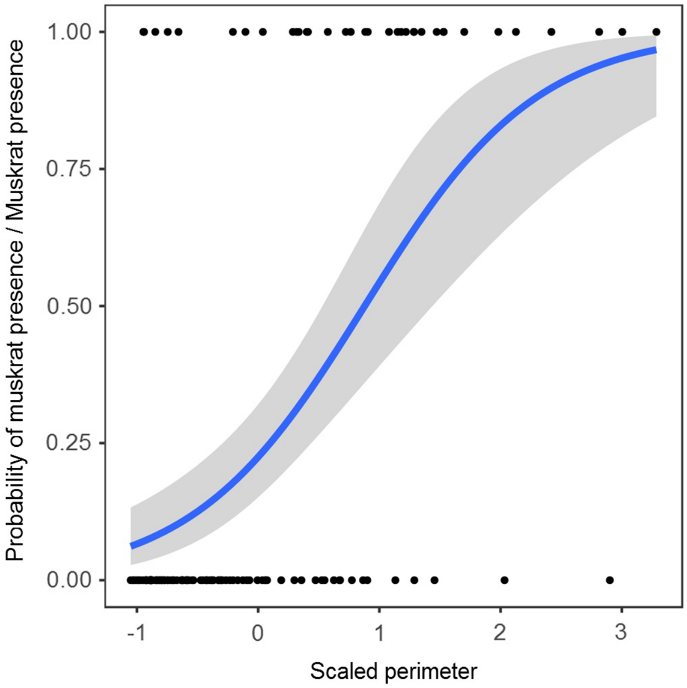

Table 2. Model selection from candidate models for muskrat presence based on combinations of patch configuration and composition variables from the field survey of 39 lakes in the Mackenzie Delta.

Model	Parameters	AICc	ΔAICc	AICc weight	Residual deviance[a]	K
12	**Perimeter + PC2 + edible biomass**	**31.64**	**0.00**	**0.90**	**22.46**	**3**
5	Perimeter	38.49	6.85	0.03	34.16	1
11	Perimeter + flooding distance[b]	39.27	7.64	0.02	32.59	2
13	Edible biomass + flooding distance + perimeter[b]	39.56	7.92	0.02	30.38	3
4	Area	40.73	9.09	0.01	36.4	1
7	Edible biomass	41.75	10.11	0.01	37.42	1
3	Flooding distance	42.6	10.96	0	38.27	1
14	Flooding distance + edible biomass[b]	43.16	11.52	0	36.48	2
2	Interpatch distance	43.33	11.69	0	38.99	1
6	Perimeter to area ratio	43.59	11.95	0	39.26	1
8	Edible biomass + depth	43.73	12.09	0	37.05	2
3a	Closure class	44.83	13.19	0	38.14	2
1	Interpatch distance + flooding distance + interpatch distance × flooding distance	45.96	14.32	0	36.78	3
9a	Edible biomass + PC1 + PC2 + depth^2	49.67	18.03	0	32.06	6

Note: Principal component values are from Analysis 1 and are measures of sediment nutrient and trace element content. Models were ranked using the corrected Akaike information criterion (AICc). The best-fit model is bolded and indicated by ΔAICc = 0.00 and highest AICc weight.

[a] Null model deviance is 39.58 on 38 degrees of freedom.

[b] Model not considered competitive (Arnold 2010).

Table 3. Estimated parameters for best model including perimeter, PC2, and edible macrophyte biomass (Model 12).

Parameter	Estimate	Standard error	*z*-value	*p*	2.5% profile likelihood confidence interval	97.5% profile likelihood confidence interval
Perimeter	1.580	0.555	2.847	0.004	0.634	2.959
PC2	1.430	0.510	−2.807	0.005	0.510	2.644
Edible biomass	1.098	0.405	2.712	0.007	0.175	2.159

Note: Note that parameter estimates are based on scaled values.

Table 4. Biomass presence-absence models by hypothesis sets: light attenuation, sediment, other variables, and post hoc combinations.

Model	Parameters	AICc	ΔAICc	AICc weight	Residual deviance[a]	K[b]
Set 1: light attenuation						
3	**Depth[c] + turbidity**	**79.15**	**0**	**0.80**	**70.6**	**3**
4	Depth + turbidity + depth × turbidity[d]	79.37	0.22	0.42	68.5	4
1	Depth	81.91	2.76	0.20	75.6	2
2	Turbidity	89.34	10.2	0	83.0	2
Set 2: sediment						
10	**OM + P**	**79.01**	**0**	**0.28**	**70.4**	**3**
7	**P + Ca + Mg + Mn + OM**	**79.20**	**0.19**	**0.26**	**66.1**	**6**
5	**PC1 + PC2**	**79.44**	**0.42**	**0.23**	**70.9**	**3**
9	**OM**	**79.81**	**0.8**	**0.19**	**73.5**	**2**
6	PC1a + PC2a + OM	82.63	3.62	0.05	71.8	4
8	P	91.49	12.47	0	85.1	2
Set 3: other variables						
12	**Phosphorus content in water**	**97.22**	**0**	**0.54**	**90.9**	**2**
11	Temperature	97.57	0.35	0.46	91.2	2
Set 4: post hoc combinations						
15	**Depth + P + OM**	**63.83**	**0**	**0.49**	**53.0**	**4**
16	Depth + turbidity + P + OM[b]	64.44	0.61	0.36	51.2	5
19	Depth + P + Ca + Mg + Mn + OM	67.88	4.05	0.06	49.7	7
17	Depth + OM	69.16	5.33	0.03	60.6	3
18	Depth + turbidity + OM	69.47	5.65	0.03	58.6	4
13	Depth + PC1 + PC2	71.15	7.32	0.01	60.3	5
14	Depth + turbidity + PC1 + PC2	71.44	7.61	0.01	58.2	5

Note: All models included a random effect of LakeID. PC1 and PC2 values are from Analysis 3, PC1a and PC2a values are from Analysis 2, and are all measures of sediment nutrient and trace element content. OM refers to sediment organic matter content. Models were ranked using the corrected Akaike information criterion (AICc). The best-fit models in each set are bolded and indicated by ΔAICc = 0 and the highest AICc weight.

[a] Null model deviance is 91.7 on 73 degrees of freedom.

[b] *K* values are one greater than number of estimated β parameters in the model because of the inclusion of a random effect for individual lakes in all models.

[c] Lake depth.

[d] Model not considered competitive (Arnold 2010).

Within-lake drivers of edible biomass presence

Edible biomass was present at 31% of transects ($n = 75$) in the 39 field survey lakes. The presence of edible biomass within lakes was best explained by variables related to light attenuation and sediment (model 15; ΔAICc = 0.00, $\text{AICc}_{\text{w}} = 0.49$; Table 4), and included negative correlations with lake depth ($\beta = -1.74$, SE = 0.71, CI = −4.49 to −0.78) and positive correlations with the concentration of organic matter ($\beta = 1.73$, SE = 0.83, CI = 0.46–5.19) and phosphorus ($\beta = 2.76$, SE = 1.65, CI = 0.53–8.26) in the sediment (Table 5). This post hoc model with a combination of the best parameters for multiple drivers was a much better fit than any a priori models based on only one hypothesized driver (Table 4).

Table 5. Estimated parameters for best-supported model of edible biomass including depth, and sediment organic matter (OM) and phosphorus (P) content (Model 15).

Parameter	Estimate	Standard error	*z*-value	Pr (>|*z*|)	2.5% profile likelihood confidence interval	97.5% profile likelihood confidence interval
Depth	−1.74	0.71	−2.43	0.015	−4.49	−0.78
OM	1.73	0.83	2.09	0.037	0.46	5.19
P	2.76	1.65	1.68	0.094	0.53	8.26

Note: Note that parameter estimates are based on scaled values.

Discussion

Resource availability within patches (composition) and patch configuration are both important drivers of muskrat occupancy of lakes in the Delta based on models that include both types of variables, with patch composition being more important. Based on previous research highlighting the importance of patch configuration for species colonization and persistence for animals in heterogeneous landscapes (Levins 1969; Hanski 1998; O'Brien et al. 2006; Haynes et al. 2007), we hypothesized that configuration and connectivity of water bodies would affect muskrat occupancy in the Delta. Perimeter was an important patch configuration variable but, overall, our models suggest that the movement and dispersal of muskrats among lakes is less important in the highly interconnected lakes of the Delta than patch composition. This is likely because: (1) the terrestrial matrix of the Delta remains permeable to muskrats and does not represent a detectable barrier to movement (Cook et al. 2004; Bender and Fahrig 2005; Kupfer et al. 2006), and (2) the high density of lakes and channels results in short distances between lakes not connected by water. Research on muskrats in agricultural areas in the United States (Errington 1939), and Europe, where this species is often considered invasive and managed as a pest (Artimo 1960; Bos and Ydenberg 2011; Skyrienė and Paulauskas 2012), indicates that they are highly mobile, effective dispersers. It is also possible that the closure class variable measuring patch connectivity was uninformative because it is an inadequate measure of complex flooding processes. The data used to classify lake closure class were collected during the spring of 1992 when water flow was the highest on record from 1973 to 2011 (Yang et al. 2015), and it is likely that in this dynamic system a 25 year old classification no longer describes variability in current processes.

The importance of composition and configuration variables including lake perimeter, edible macrophyte biomass, and inorganic nutrients suggests that these parameters are indicators of habitat quality. Perimeter is an important measure of patch composition as well as patch configuration, as lakes with longer perimeters provide more habitat for muskrat bank dens (Brammer 2016) and a greater abundance of emergent vegetation, which is an important food source for muskrats in the ice-free months (Errington 1963; Jelinski 1984). Local knowledge holders in the Old Crow Flats have indicated that muskrats prefer larger lakes (Brammer 2016). Edible macrophyte biomass and parameters impacting biomass (PC2 values) were important determinants of muskrat occupancy because submerged macrophytes make up >95% of muskrats' winter diet (Jelinski 1984), which we infer are a niche axis (Grinnell 1917). Edible macrophyte presence was positively associated with nutrient availability (sediment phosphorus (P) and organic matter (OM) content) and negatively associated with depth. The negative correlation with depth is likely related to the impact of light attenuation on photosynthesis at deeper depths (Squires et al. 2002; Squires and Lesack 2003*b*). We had expected that lake depth would be positively related to muskrat push-up presence, because muskrats require unfrozen water in the winter months (Stevens 1955; Jelinski 1984), and adequate depth was identified as an important habitat requirement by muskrat trappers in the Old Crow Flats (Brammer 2016). It is likely that depth was an uninformative variable because all the lakes sampled in our study were deep (>1.5 m) and large enough (>50 000 m^2) to not freeze to the bottom throughout their entire area, and would all have allowed muskrats access to submerged macrophytes throughout the winter.

We hypothesized that variables associated with lake flooding would explain variation in muskrat distribution. Although direct measures of flooding frequency were uninformative, patch variables influenced by flooding distance and frequency explained much variation in muskrat distribution. Three key variables measuring sediment nutrient content (PC2 scores, and P and OM in the sediment) were positively associated with either muskrat or edible biomass presence, and are largely controlled by the frequency of spring flooding, which deposits inorganic sediment from river water into flooded lakes (Marsh et al. 1999; Squires and Lesack 2003*a*). This suggests that interactions among patch composition and broader-scale processes like connectivity and flooding are critical components of population processes in complex heterogeneous environments. Numerous studies of other species in heterogeneous environments have also highlighted the importance of habitat composition in patches (Harrison and Bruna 1999; Goodwin and Fahrig 2002; Weyrauch and Grubb 2004; Thornton et al. 2011). However, in these systems, connectivity among patches is typically not a driver of patch composition. The Delta system is somewhat unique in this respect. Our results extend the assertion made by Schooley and Branch (2011) that research on populations in heterogeneous environments should not focus solely on patch configuration variables, but must also define habitat composition within the patches to accurately investigate habitat use and distributions.

The relationships among nutrients — maintained by regular flooding regimes (Squires et al. 2002; Squires and Lesack 2003*a*; Lesack and Marsh 2010) — and macrophyte and muskrat presence suggest that climate change is likely to impact future muskrat distribution in the Delta. Trends towards thinner ice, earlier snowmelt and break-up, and decreases in maximum spring flows are all likely to result in lower peak water levels during the spring flood (Lesack et al. 2014; Yang et al. 2015; Cooley and Pavelsky 2016). This is likely to decrease the number of low-closure lakes that flood annually, reduce water levels and alter lake shapes in high-closure lakes where evaporation becomes greater than water inputs (Marsh and Lesack 1996; Emmerton et al. 2007), and change the water and sediment chemistry of those that remain (Lesack et al. 1998). These changes are likely to reduce suitable muskrat habitat by negatively affecting biomass growth and the consistency of lake flooding regimes.

Conclusion

Our research indicates that patch composition is the primary determinant of winter muskrat distributions in the Mackenzie Delta, with some contribution from patch configuration. Connectivity among patches influenced several aspects of patch composition, which affected muskrat occupancy. The link between regular flooding and indices of patch composition suggests that climate-driven reductions in flooding in this ecosystem may reduce the abundance and composition of lakes that offer suitable habitat for muskrats. Future studies should explore the linkage between flooding and other broad-scale processes and the key habitat variables that we have identified to better predict how they will be altered in a changing climate. In this study we highlight the complexity of the drivers of species' distributions in dynamic environments where patch composition is a function of temporally variable processes. This points to the necessity of including both types of drivers, as well as their interactions, in studies of heterogeneous environments.

Acknowledgements

We would like to thank the many members of the Arctic Landscape Ecology Lab who assisted with this research: Paige Bennet, Kazlyn Bonnor, Kiyo Campbell, Emily Cameron, Maliya Cassels, Abra Martin, Nina Moffat, Becky Segal, and Will Tyson, as well as our collaborator Jeremy Brammer. We are very grateful to the many community members and staff of local organizations who facilitated project logistics, especially Doug Esagok. We also extend our thanks to the communities of Inuvik and Aklavik for their warm welcomes and extensive hospitality. Funding support for this research was provided by the W. Garfield Weston Foundation, Social Science and Humanities Research Council of Canada, Environment and Climate Change Canada, University of Victoria, Natural Sciences and Engineering Research Council of Canada, ArcticNet, The Canada Foundation for Innovation, Gwich'in Renewable Resources Board Wildlife Studies Fund, Polar Knowledge Canada Northern Studies Training Program, and Aurora Research Institute. This research was conducted with a Northwest Territories Scientific Research Permit (16322).

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