Springtime in the Delta: The sociocultural role of muskrats and drivers of their distribution in a changing Arctic delta

by

Chanda Kalene Turner
Bachelor of Arts, University of Victoria, 2012

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Supervisory Committee

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Abstract

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Climate change is altering environmental conditions in Canada's western arctic, including hydrology, permafrost, vegetation, and lake habitat conditions in the heterogeneous landscape of the Mackenzie Delta. The delta is an expansive alluvial plain dominated by thousands of lakes and interconnected channels that provide habitat for fish, birds, and mammals. Muskrats (*Ondatra zibethicus*) are a culturally important ecological indicator species found in the Delta. Throughout the 1900s, Gwich'in and Inuvialuit residents in the Delta relied heavily on the muskrat for food, fur, and culture, but as in other regions around the world, changing socioeconomic and ecological conditions are altering the land and Indigenous Peoples' access to it. This can strongly impact communities by affecting food security, physical health, and overall wellbeing. In the first part of this thesis, I investigated the role of muskrats in the cultural traditions and land-based livelihoods of the Gwich'in and Inuvialuit residents of the Mackenzie Delta by conducting interviews and meetings with over 70 community members. Although the role of muskrats has changed over the last 100 years, muskrat harvesting continues to offer Delta residents a meaningful way to remain engaged in, perpetuate, and strengthen their cultural identity and land-based traditions among generations, and ultimately, to foster individual and community wellbeing.

In the second part of this thesis, I investigated the importance of landscape connectivity and patch quality – 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 present in the winter. I tested multiple hypotheses about predictors of muskrat presence and biomass using a model-selection, information theoretic approach. My results show that patch quality related to specific habitat requirements is a more important driver of muskrat distribution than landscape connectivity in the Mackenzie Delta. Muskrats were more likely to occur in lakes with longer perimeters, higher amounts of edible submerged macrophyte biomass, and sediment characteristics that supported macrophyte growth. The latter two conditions are related to spring flooding regimes, which are likely to be altered by climate change. This may result in a decrease in the quality and quantity of preferred muskrat habitat in the Mackenzie Delta. My research indicates that patch quality and landscape-level processes are important for understanding species distributions in heterogeneous landscapes.

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Acknowledgments

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Dedication

To grandpa Gordon.

It’s a long ways from the farm.

Chapter 1 – Introduction

Climate change is altering species' ranges and interactions the world over (Galbraith et al., 2002; Gilg et al., 2012; Huntington, 2006; IPCC, 2014; Parmesan & Yohe, 2003; Walther et al., 2002). Development is also altering ecosystem structure and function (DeFries, Foley, & Asner, 2004; Foley et al., 2005), and affecting many Indigenous Peoples' access to their traditional territories (Colchester & Chatty, 2002; De Wet, 2006; Maldonado, Shearer, Bronen, Peterson, & Lazrus, 2013). Many rural and Indigenous communities are also experiencing changes in the way they interact with the environment as they move from hunting, fishing, or traditional agriculture livelihoods and become involved in mixed and wage economies (Berry, 2008; Nuttall, 2000; Usher, 1971; Wolforth, 1971). More and more, researchers and community members are recognizing the intensive and extensive cumulative effects of climate change and development on environments and land-based livelihoods (Duinker, Burbidge, Boardley, & Greig, 2012; Spaling, 1994).

In northern regions, these cumulative effects are especially evident and concerning as climate change is proceeding more rapidly in the Arctic than any other part of the world (ACIA, 2004; Duarte, Lenton, Wadhams, & Wassmann, 2012; Stern & Gaden, 2015). Low-lying Arctic deltas are expected to be especially impacted by the combined effects of both terrestrial and marine processes, which include warming ground temperatures, sea level rise, earlier spring breakup and melt, and increases in storm surge frequencies and magnitudes (ACIA, 2004; Burn & Kokelj, 2009; Fraser, Lantz, Olthof, Kokelj, & Sims, 2014; Kokelj et al., 2012, 2013; Lesack, Marsh, Hicks, & Forbes, 2014; Myers-Smith et al., 2011; Smith, Burgess, Riseborough, & Nixon, 2005; Walker, 1998).

The Mackenzie Delta (Figure 1.1) in Canada's western Arctic is the second largest Arctic delta in the world (Lesack & Marsh, 2010). It is a low-lying alluvial plain that contains thousands of small lakes (Emmerton, Lesack, & Marsh, 2007), which are highly productive (Squires & Lesack, 2003) and have diverse biotic communities (Hay, Michelutti, & Smol, 2000). Recent observations indicate that climate change is altering hydrological processes and lake flooding regimes in the Mackenzie Delta (Prowse et al., 2006; Wrona et al., 2006), which will affect resource availability and biotic and abiotic conditions in lakes (Déry, Hernández-Henríquez, Burford, & Wood, 2009; Emmerton et al., 2007; Lesack, Marsh, & Hecky, 1998; Lesack, Marsh, Hicks, & Forbes, 2014).

The Mackenzie Delta region is an important harvesting area for the Gwich'in and Inuvialuit peoples, as this wetland environment offers abundant habitat for fish, birds, and fur-bearing mammals, including muskrats (*Ondatra zibethicus*). Muskrats are semiaquatic furbearing rodents that supported a prolific fur and subsistence economy in the north throughout the 19th and 20th centuries (Stevens, 1953; Krech, 1976; Alunik, Kolausok, & Morrison, 2003). While participation in the fur trade has declined since the 1950s due to low fur prices and the high cost of trapping, muskrats remain important culturally and economically, and are still used for subsistence and income (Brietzke, 2015).

Like other northern mammals, muskrats exhibit periodic cycles in population size (Errington, 1963; Krebs, 1996). Research on fur returns from the Mackenzie Delta in the late 1800s to early 1900s indicates that population cycles in the Delta average around 10 years between highs (Clarke, 1944). In recent years, many residents of the Mackenzie Delta region have reported declines in muskrat abundance that are outside this normal range of variation (Arctic Borderlands Ecological Knowledge Society, 2002, 2008; Brietzke, 2015). This decline is likely to have significant impacts on local communities who rely on muskrats for subsistence, trapping income, and overall wellbeing (Parlee, Berkes, & Teetl'it Gwich'in, 2005). The impacts of environmental change on subsistence economies can be particularly intense when changing conditions limit access to species of exceptional cultural significance (Garibaldi & Turner, 2004; Moss, 2016) and will affect the entire the sociocultural system as it refers to a human population embedded within an ecological system. The term sociocultural refers to the combination of social and cultural factors defining individuals within a society, and the surrounding culture that shapes those individuals' actions, beliefs, and values (Nanda & Warms, 2013).

The objectives of my MSc are to explore the sociocultural importance of muskrats and determine the drivers of muskrat distributions in the Mackenzie Delta. To accomplish this, I used scientific and social scientific methods to conduct the independent but related projects presented in Chapters 2 and 3 of this thesis. A mixed methods approach is necessary for understanding changes in social-ecological systems, especially when culturally important species are being affected by change.

In Chapter 2, my objective was to *better understand the sociocultural role of muskrats in the Mackenzie Delta throughout periods of changing social, economic, and ecological conditions*. To address this objective, I conducted 20 semi-structured interviews with participants from Aklavik, Inuvik, Fort McPherson, and Tsiigehtchic, hosted community meetings about muskrats, and reviewed transcripts from 11 interviews conducted with 14 Inuvialuit participants from Aklavik and Inuvik.

In Chapter 3, I explored the question: *How do within-patch characteristics and landscape connectivity variables influence the distribution of muskrats in the Mackenzie Delta?* To answer this question, I conducted an ecological survey of lake conditions in 39 lakes and a remote-sensing survey of muskrat winter distributions and landscape connectivity characteristics in 129 lakes, and used an information theoretic model selection approach to determine the most important drivers of muskrat push-up presence in lakes.

In Chapter 4, I describe convergences and divergences between these two separate approaches. I also discuss directions for future research on muskrats in the Mackenzie Delta and other northern regions and discuss how my research may contribute to understanding the management and continued use of muskrats.

In the rest of this chapter, I provide critical background information not discussed in Chapters 2 and 3. Topics discussed include: ecological and hydrological conditions in the Mackenzie Delta, the Gwich'in and Inuvialuit land claims in the Mackenzie Delta region, the history of muskrat use by the Gwich'in and Inuvialuit peoples, community-based monitoring, and landscape and muskrat ecology.

Study Region: The Mackenzie Delta

The Mackenzie Delta is a vast alluvial plain that extends 210 km north from Point Separation to the Beaufort Sea and covers an area of 13,000 km^2 (Figure 1.1). The area contains hundreds of distributary channels and over 40 000 lakes that vary in size, depth, productivity, biodiversity, and flooding regimes (Emmerton et al., 2007; Hay et al., 2000; Squires & Lesack, 2003, 2002). The vegetation of the Delta is unique from the tundra areas that are immediately east and west of the alluvial floodplain. Where the surrounding regions are characterized by sparse black spruce (*Picea mariana*) and shrub tundra, the Mackenzie Delta is characterized by closed white spruce (*Picea glauca*) forest (Ecosystem Classification Group, 2007). In the delta the treeline sweeps north nearly to the coast of the Beaufort Sea, much further north than the areas immediately adjacent to it (Rampton, 1988).

The Mackenzie Delta is an important region of wetland habitat for numerous species, especially birds. At least 65 species of migrating birds, including numerous geese and duck species, shorebirds, and tundra swans use the Delta annually (Ecosystem Classification Group, 2007). The Kendall Island Bird Sanctuary in the outer delta encompasses one of the three largest snow geese breeding colonies in the Western Arctic (Ecosystem Classification Group, 2007). Many other wildlife species are found in the Mackenzie Delta region, including furbearers like beaver (*Castor canadensis*), mink (*Neovison vison*), marten (*Martes americana*), fox (*Vulpes spp.*), black bear (*Ursus americanus*), grizzly bear (*Ursus arctos*), moose (*Alces alces*), wolf (*Canis lupus*), wolverine (*Gulo gulo*), and muskrat, as well as many different species of fish (Berger, 1977). Other important animals in the region that are harvested for subsistence by the Gwich'in and Inuvialuit include caribou, snow geese (*Chen caerulescens*), beluga whales (*Delphinapterus leucas*), muskox (*Ovibos moschatus*), ringed seal (*Pusa hispida*), and bearded seal (*Erignathus barbatus*) (Joint Secretariat, 2003).

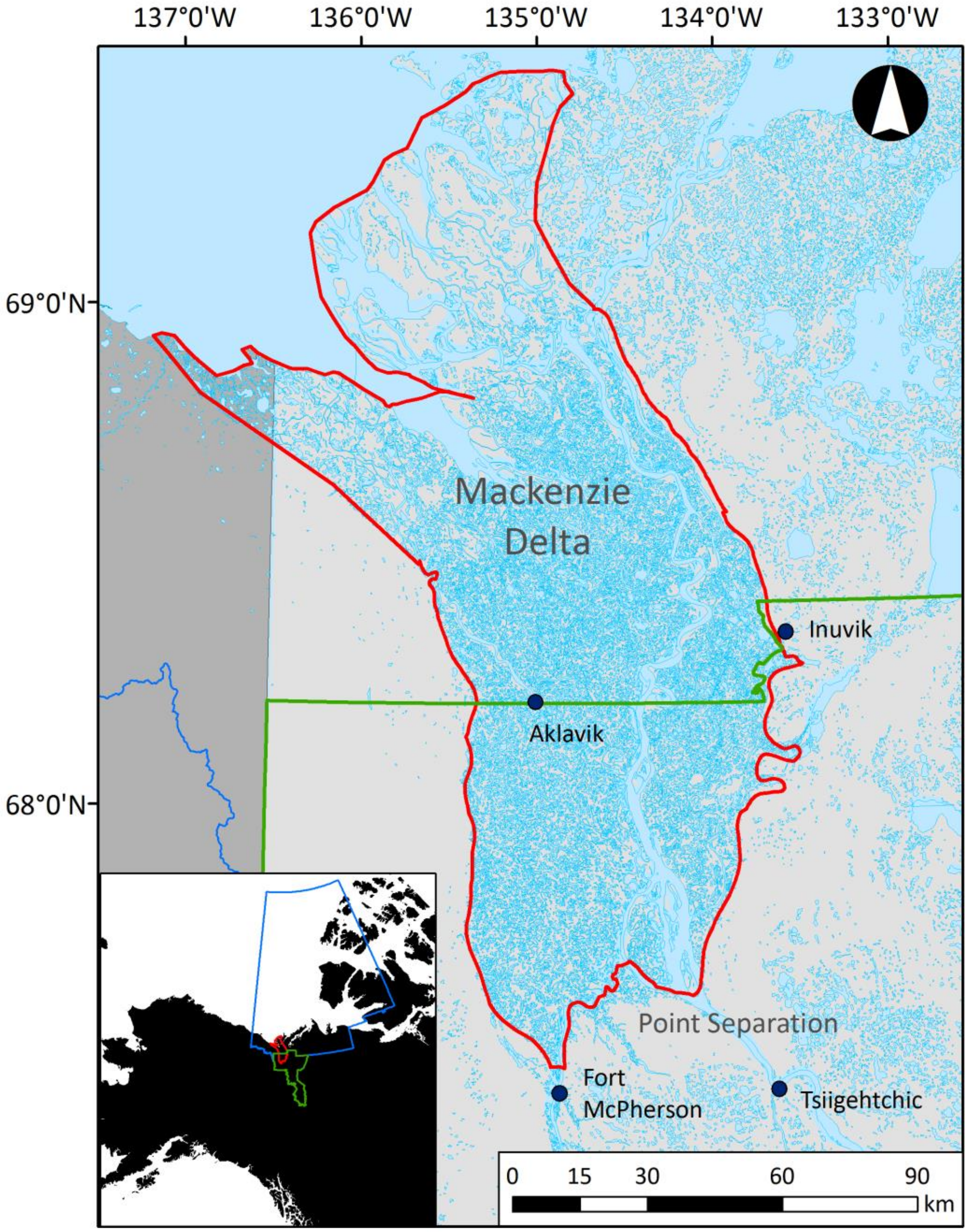

Figure 1.1 Map of study region. The boundary of the Mackenzie Delta Ecoregion (Ecosystem Classification Group, 2007) is shown in red. The northern boundary of the Gwich'in Settlement Area (Gwich'in Tribal Council & Indian and Northern Affairs Canada, 1992) and southern boundary of the Inuvialuit Settlement Region (Indian and Northern Affairs Canada, 1984) is shown in green. Communities involved in the study are marked with dark blue circles. Water bodies are outlined in cyan. Inset map shows

location of study area in northwestern North America and full extent of the Inuvialuit Settlement Region (blue) and the Gwich'in Settlement Area (green).

Hydrology

The ecology of the Mackenzie Delta lakes and surrounding vegetation is strongly influenced by flooding during spring break-up (Lesack, Marsh, & Hecky, 1998; Marsh & Hey, 1989; Squires & Lesack, 2002; Squires, Lesack, & Huebert, 2002). Break-up refers to the period of time when melt runoff water, termed the spring freshet, interacts with ice on channels throughout the Mackenzie Delta. Break-up timing and duration are controlled by hydroclimatic conditions, including the water level at freeze-up, the thickness of river ice, the amount and rate of spring melt, and spring temperatures (Goulding, Prowse, & Beltaos 2009; Goulding, Prowse, & Bonsal, 2009). Break-up events can be characterized as thermal, when warm air temperatures and low discharge levels result in the ice melting mostly in place, or dynamic, where air temperatures are cool, ice remains more intact, and river discharge is high (Goulding, Prowse, & Bonsal, 2009). Dynamic break-up events result in more ice-jamming, higher peak water levels as ice blocks the channels, and more extensive flooding than thermal break-up events (Marsh, 1998). Both types of break-up take place in the Mackenzie Delta, though some level of ice-jamming always occurs. Biotic and abiotic conditions in lakes in the Mackenzie Delta are strongly influenced by this spring flooding, and lakes are commonly categorized into classes based on the frequency of flooding (Marsh & Hey, 1989).

The flooding frequency of Delta lakes is primarily determined by a single physical feature: sill elevation (Marsh & Hey, 1989). Sill elevation is defined as "the highest point along the thalweg," which is the line of lowest elevation along a watercourse, “of the channel connecting the lake with the river, or in the absence of a connecting channel, the highest point along the route that floodwaters follow from a distributary channel to a lake” (Squires & Lesack, 2003, p. 334). Lakes with lower sill elevations will flood earlier, more often, and for longer periods of time than lakes with higher sill elevations. Three categories of sill elevation are defined as follows: no closure (lakes are connected to the river all summer); low closure (lakes flood in the spring, annually); and high closure (lakes flood in the spring, but not every year) (Marsh & Hey, 1989).

There are several important biophysical gradients that have been documented among these closure classes, including lake transparency and sedimentation rates (Marsh, Lesack, & Roberts, 1999; Squires & Lesack, 2003; Squires et al., 2002), amount of lake water renewal from the river (Lesack & Marsh, 2010), stability of water solute chemistry (Lesack, Marsh, & Hecky, 1998), the nutrient and organic matter content of sediment (Squires & Lesack, 2003), and macrophyte productivity and community composition (Squires & Lesack, 2003; Squires, Lesack, & Huebert, 2002). Lake transparency decreases with increasing flood frequency and, for lakes connected to one another, with decreasing distance to the river (Squires & Lesack, 2003). Sedimentation rates increase as lakes become more connected to the river (from high to no closure), although there is as much variation within no-closure lakes, which is likely related to factors such as proximity to main channels and type of connection to the river, as among all three lake closure types (Marsh, Lesack, & Roberts, 1999). The amount of lake water renewal through flooding is an important control on many factors related to lake water conditions; renewal is determined more by the amount of time that lakes are connected to the river for, rather than the frequency at which a lake floods (Lesack & Marsh, 2010). Variability in connection time increases with increasing sill height, and generally, lakes with lower sill heights are connected to the river for longer periods of time (Lesack & Marsh, 2010). Sediment nutrient (N and P) and organic matter (OM) content increase along with lake transparency (Squires & Lesack, 2003). Macrophyte productivity, measured by biomass, increases with increasing OM and N in sediment, and with increasing water transparency (Squires & Lesack, 2003). The community composition of macrophytes also varies with sediment nutrient levels and transparency, shifting from *Chara vulgaris* and *Ceratophyllum demersum*, at high transparencies and high sediment OM content, to *Potamogeton spp.*at lower transparencies and intermediate levels of OM (Squires & Lesack, 2003).

Changes in the Delta

Ecological change and development are ongoing in the Mackenzie Delta. Climate change is altering hydrological processes and lake flooding regimes. Peak water levels in the spring are decreasing as larger and faster spring floods remove thin ice from the river with minimal ice jams and flooding (Lesack, Marsh, Hicks, & Forbes, 2014), which will affect the distribution and conditions of lake habitat for many species (Déry, Hernández-Henríquez, Burford, & Wood, 2009; Lesack, Marsh, & Hecky, 1998; Lesack, Marsh, Hicks, & Forbes, 2014; Prowse et al., 2006).

The town of Inuvik was constructed as a planned community from 1956-1960, and incorporated as the Village of Inuvik in 1967. Development in the surrounding region began with seismic exploration for oil and gas in the 1960s (Burn & Kokelj, 2009) and the construction of the Dempster Highway in the 1970s (Gill, Lantz, O'Neill, & Kokelj, 2014). Most recently, a new all-weather highway was built from Inuvik to Tuktoyaktuk, in part to open up access to non-renewable resources (Scott, 2017). Other, more localized development on the landscape includes the construction of exploratory wells and sumps and the Ikhil Pipeline (Tyson, Lantz, & Ban, 2016).

Muskrat Ecology

Muskrats are widely distributed across most of North America, with the exception of the arctic tundra (Banfield, 1974). Like other northern mammals, muskrat population cycling is well documented (Errington, 1963), and the length of time between population highs and lows varies in different regions (Erb, Stenseth, & Boyce, 2000). It has been suggested that disease outbreaks and predator population cycles could cause these oscillations in numbers, but this process is poorly understood (Erb et al., 2000). Muskrat population cycles in the Taiga Plains ecozone, which includes the Mackenzie Delta, are estimated to have a periodicity of nearly eight years (Erb, Stenseth, & Boyce, 2000).

Muskrats live in bank burrows in lentic water bodies, including lakes, slow-moving rivers and streams, ponds, marshes, sloughs, and ditches (Banfield, 1974; Errington, 1963). They have varied diets throughout their range, but typically use the most available plant species in their habitat (Errington, 1963). Cattails form an important part of their diet in the southern part of their range (Errington, 1963), but they must rely on other species in the Mackenzie Delta. In the summer, they consume emergent shoreline vegetation (*Equisetum fluviatile*) and some submerged macrophytes (*Potamogeton spp.*), but in the winter their diet is restricted to the roots and rhizomes of submerged macrophytes that persist on lake bottoms under the ice (Jelinski, 1989). To survive long ice-covered winters, muskrats must have access to deeper water that will not freeze to the bottom and an abundance of submerged macrophytes for food (Jelinski, 1989; Stevens, 1955). Submerged macrophyte productivity and community composition vary significantly among lakes in the Mackenzie Delta (Squires & Lesack, 2003) and likely affect winter habitat quality. Factors influencing macrophyte productivity and community composition in Delta lakes are strongly related to the frequency and duration of spring flooding by the Mackenzie River (Squires & Lesack, 2003), as discussed above.

Muskrat Use in the Mackenzie Delta

Gwich'in, Inuvialuit, and other Inuit peoples occupying the Mackenzie Delta region have relied on subsistence fishing, whaling, hunting, and gathering foods for thousands of years, resulting in a high degree of reliance upon and connection to the land and ocean (Alunik, Kolausok, & Morrison, 2003; Heine, Andre, Kritsch, & Cardinal, 2007; Krech, 1984; Lyons, 2007). Many Inuvialuit are relative newcomers to the region, migrating from the North Slope of Alaska and further east of the Delta in the late 1800s and early 1900s (Lyons, 2007; Usher, 1971). The Gwich'in spent time in the Mackenzie Delta but did not use it intensively until the expansion of the fur trade in the mid-1800s and early 1900s (Wolforth, 1971). Socioeconomic change has been ongoing in the Mackenzie Delta Region for over 200 years: explorers, whalers, traders, missionaries, trappers, settlers, and oil and gas development have all impacted life in the Delta and altered traditional subsistence economies practiced by its residents (Alunik, Kolausok, & Morrison, 2003; Krech, 1976; Lyons, 2007; Usher, 2002). Chronologically, the main economies have included traditional subsistence harvesting, commercial whaling, the fur trade, militarization of the north and oil and gas development, and the rise of mixed wage economies (Lyons, 2007; Usher, 1971). The current economy in the region is mixed, with many people still engaged in subsistence harvesting and trapping, and some consistent wage labour opportunities, especially in Inuvik (Pearce et al., 2011; Usher, 2002).

In the early 1900s, Delta peoples seized the economic opportunity offered by the expanding and profitable fur trade (Alunik, Kolausok, & Morrison, 2003; Krech, 1984). By 1919, Aklavik had risen to prominence as the most important trading post in the Delta. From the 1920s to 1950s, when fur prices were very high, families involved in muskrat harvesting prospered (Alunik, Kolausok, & Morrison, 2003; Gwich'in Elders, 2001; Krech, 1976). In this time period, muskrat trapping and harvesting was extensive, with nearly the entire Delta partitioned off into registered traplines (Wolforth, 1971). Trapping was the primary source of income for many people, and also a substantial source of food for both people and dog teams. Many individuals or families often took in 2 000 to 3 000 muskrats in one season, with some larger families selling upwards of 10 000 pelts (Gwich'in Elders, 1997). During the 25-year period from 1930 to 1955, when harvest numbers are most reliable, there were only 5 years when recorded muskrat harvests in the Delta did not exceed 100 000 animals, and there were 8 years when there were more than 200 000 pelts sold from the Delta communities (including Aklavik, Fort McPherson, Tsiigehtchic, and Inuvik / Reindeer Station) (McTaggart Cowan, 1948; Wolforth, 1971).

Indigenous land use in the Mackenzie Delta: The Gwich'in Comprehensive Land Claim Agreement & Inuvialuit Final Agreement

The Mackenzie Delta is home to the Inuvialuit and Gwich'in Peoples, who both have settled land claims with the Canadian government (Gwich'in Tribal Council & Indian and Northern Affairs Canada, 1992; Indian and Northern Affairs Canada, 1984). The Inuvialuit Settlement Region (ISR) extends from subarctic forest in the Mackenzie Delta to High Arctic tundra on Banks and Victoria Islands (Indian and Northern Affairs Canada, 1984) (Figure 1.1). The Gwich'in Settlement Area (GSA) extends from the spruce woodlands near Inuvik, southward through the boreal forest to the alpine terrain of the Richardson Mountains at the Northwest Territories / Yukon border, and secondary use areas extend into the Yukon (Gwich'in Tribal Council & Indian and Northern Affairs Canada, 1992) (Figure 1.1).

The communities located in and around the Mackenzie Delta region include Inuvik, Aklavik, Tsiigehtchic, and Fort McPherson (Figure 1.1). Inuvik is the economic and administrative hub of the region, with numerous government and industry offices. It is also the largest community (pop. ~ 3 463) and is comprised Inuvialuit, Gwich'in, and non-Indigenous residents. Aklavik (pop. ~ 633) was the former economic and administrative hub of the Delta region, and is comprised of mostly Inuvialuit and Gwich'in residents. Fort McPherson (pop. ~ 792) and Tsiigehtchic (pop. ~ 143) are primarily Gwich'in settlements, with some Inuvialuit and non-Indigenous residents.

The Inuvialuit Final Agreement (IFA) was the second comprehensive land claim to be signed in Canada, in 1984. It was a landmark agreement between the Inuvialuit people and the Government of Canada that gave the Inuvialuit rights and a degree of control over a large area of their traditional territory, designated the Inuvialuit Settlement Region (ISR) (Indian and Northern Affairs Canada, 1984). The ISR encompasses more than 900 000 square kilometres and six communities in the Northwest Territories: Inuvik, Aklavik, Tuktoyaktuk, Paulatuk, Sachs Harbour, and Ulukhaktok (Figure 1.1). The IFA does not result in self-government for the Inuvialuit, but requires co-management of land and resources by the Inuvialuit and federal and territorial governments. The boards, councils, and committees established for wildlife and wildlife habitat co-management include one all-Inuvialuit body, the Inuvialuit Game Council, and five co-management boards, the Environmental Impact Review Board, the Environmental Impact Screening Committee, the Fisheries Joint Management Committee, the Wildlife Management Advisory Council Northwest Territories, and the Wildlife Management Advisory Council North Slope, that govern fish and wildlife management in the ISR. The Inuvialuit Game Council is comprised of representatives elected by members of the Hunters and Trappers Committees (HTCs) in each of the six ISR communities, and is responsible for appointing Inuvialuit members to the co-management boards listed above and represents the collective Inuvialuit interest in wildlife in the ISR (Indian and Northern Affairs Canada, 1984).

The Gwich'in Comprehensive Land Claim Agreement (GCLCA) set out the boundaries of the Gwich'in Settlement Area (GSA), which covers 56,935 km^2 in the Northwest Territories (Gwich'in Tribal Council & Indian and Northern Affairs Canada, 1992). There are primary and secondary use areas outside of the GSA within the Yukon Territory as well, encompassing much of the Peel River watershed and part of the Richardson Mountains. The GCLCA was signed in 1992 between the Gwich'in Tribal

Council, the Government of Canada, and the Government of the Northwest Territories. It includes provisions for land use planning, environmental impact assessment and review, regulation of land and water use, and co-management of resources by the Gwich'in peoples and governments within the GSA (Gwich'in Tribal Council & Indian and Northern Affairs Canada, 1992). The Gwich'in Renewable Resources Board (GRRB) is the main body responsible for the management of fish, wildlife, and forests in the GSA, and works closely with each community Renewable Resource Council (RRC) to set research priorities and implement management actions. There are four Gwich'in RRCs within the GSA: the Tetlit Gwich'in RRC (Fort McPherson), the Gwichya Gwich'in RRC (Tsiigehtchic), the Nihtat Gwich'in RRC (Inuvik) and the Ehdiitat Gwich'in RRC (Aklavik).

Community-based Research

Community-based research (CBR) is a practice that is increasingly becoming the standard for researchers, particularly in indigenous communities (Castleden, Morgan, & Lamb, 2012). Importantly, CBR involves community members at all stages of research, from conception to data analysis. The most effective community-based research is usually done in situations where researchers have long-standing relationships with the community they are working with (Castleden, Morgan, & Lamb, 2012).

In this MSc research, I was fortunate to begin working in the context of a relatively long-term involvement in the community. The Arctic Ecology Lab at the University of Victoria has been conducting research based on community involvement, needs, and requests in the Mackenzie Delta Region for over 8 years at the time of writing, and I have been involved for over 5 years. A community-based monitoring program was implemented in 2010 (Bennett & Lantz, 2014), and by 2016 had collected observations from over 60 Gwich'in and Inuvialuit monitors. These observations had many themes, but a major concern that was voiced by numerous monitors involved muskrat population declines and worries about the future of muskrat harvesting in the Delta. The identification of muskrat population declines as a research priority was the first step in the collaborative, community-based research methodology I employed throughout my MSc research (Castleden, Morgan, & Lamb, 2012). Subsequently, I developed research objectives and methods jointly with Gwich'in and Inuvialuit community organizations in Fort McPherson, Tsiigehtchic, Aklavik, and Inuvik through face-to-face meetings, phone calls, and emails. This process is described in more detail in Chapter 2.

Heterogeneous Habitat Use: Landscape Ecology & Niche Theory

Niche theory is an evolving concept that is based on identifying the factors that permit species persistence, and can be understood to include both a species' requirements from its habitat (ie. food) and its impact on this same habitat (ie. alteration of vegetation structure) (Chase & Leibold, 2003). Landscape ecology identifies heterogeneity and connectivity as important drivers of population dynamics and distribution: landscapes are comprised of patches of habitat that are more desirable for a certain species, which are interspersed among a mosaic that is less desirable or uninhabitable to that species (Goodwin, 2003; Kotliar & Wiens, 1990; Tscharntke et al., 2012; Turner, 1989). These patches can be functionally and physically connected to one another, to varying degrees. In these landscapes, a species' distribution is influenced by both the quality of resource patches and their ability to move through the matrix and access these resources (Goodwin & Fahrig, 2002; Harrison & Bruna, 1999; Taylor, Fahrig, Henein, & Merriam, 1993). For aquatic species, the Mackenzie Delta is a heterogeneous landscape comprised of patches of varying quality – small and large water bodies – embedded within a terrestrial matrix dominated by spruce woodlands and alder and willow thickets.

Most research on species' persistence in heterogeneous landscapes focuses on the effects of fragmentation and disturbance (ie. Keitt, Urban, & Milne, 1997; Kupfer, Malanson, & Franklin, 2006; Prugh, Hodges, Sinclair, & Brashares, 2008), but climate change will also affect species living in naturally heterogeneous landscapes (Gilg et al., 2012; Opdam & Wascher, 2004). In the Mackenzie Delta, changes driven by climate change may alter: 1) landscape connectivity, as some lakes and channels dry out and the vegetation of the matrix changes (Emmerton, Lesack, & Marsh, 2007; Myneni, Keeling, Tucker, Asrar, & Nemani, 1997; Pisaric, Carey, Kokelj, & Youngblut, 2007), and 2) patch quality, as some lakes become shallower and more acidic, and others receive more sediment and nutrients from increased sediment loads in the river (Emmerton et al., 2007; Lesack, Marsh, & Hecky, 1998; Marsh & Lesack, 1996; Prowse et al., 2006). It is necessary to understand species' interactions with their environment in order to determine the nature of their possible responses to climate change (Opdam & Wascher, 2004; Wiens, Stenseth, Van Horne, & Ims, 1993).

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Chapter 2 – Springtime in the Delta: The sociocultural importance of muskrats to Gwich'in and Inuvialuit trappers throughout periods of ecological and socioeconomic change

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> Doesn't quite feel like springtime in the Delta if you don't go out and get some rats… Therapeutic for Delta people.
>
> Trapper from Inuvik, NT

Introduction

Socioeconomic changes over the last two centuries have transformed Indigenous communities by introducing new economies, worldviews, political systems, and material goods (Berry, 2008; Freeman, 2000; Nuttall, 2000). Across the globe, Indigenous Peoples' traditional lifestyles have been altered as they have transitioned to permanent settlements, whether by choice or forcibly, and lost access to all or part of their traditional territories (Colchester & Chatty, 2002; Maldonado, Shearer, Bronen, Peterson, & Lazrus, 2013). Human relationships to ecological systems are also in flux, as communities who previously relied completely on hunting, fishing, or traditional agriculture have become involved in mixed and wage economies (Lu, 2007; Usher, 1971). The land itself is undergoing changes as industrial agriculture expands, global forest cover declines (DeFries, Foley, & Asner, 2004; Foley et al., 2005), freshwater resources become more vulnerable (Kundzewicz et al., 2008), and climate change creates more extreme and unpredictable weather (Coumou & Rahmstorf, 2012; Krupnik & Jolly, 2002).

The Arctic is currently experiencing the most rapid changes in climate of any region on earth (ACIA, 2004). These changes are affecting ecosystem structure and function, permafrost stability, and the abundance and distribution of wildlife (Post & Forchhammer 2008; Segal, Lantz, & Kokelj, 2016). Northern regions are also subject to intensifying human development, including the construction of roads, oil and gas infrastructure, and hydroelectric projects, which can alter physical conditions and ecosystem structure and function (Beltaos, 2014; Gill, Lantz, O'Neill, & Kokelj, 2014). In many northern communities there is growing concern about the cumulative effects of climate change and development on local ecosystems and land-based livelihoods (Schindler & Smol 2006; Tyson, Lantz, & Ban, 2016). Ongoing landscape change and shifts in peoples' ability to access their traditional territories strongly impact the health of northern communities by affecting food security, physical health, and overall well-being (Paci, Dickson, Nickels, Chan, & Furgal, 2004; Parlee & Furgal 2012; Receveur, Boulay, & Kuhnlein, 1997).

The impacts of environmental change on subsistence economies can be particularly intense when changing conditions limit access to species with exceptional cultural significance. For example, barren-ground caribou have been a primary food source for many peoples in Canada's north for thousands of years, but dramatic population declines and changes in accessibility in recent decades have resulted in lower harvests and increased reliance on store-bought foods (Canadian Wildlife Service, Parker, & Thomas, 1975; Festa-Bianchet, Ray, Boutin, Côté, & Gunn, 2011; Receveur, Boulay, & Kuhnlein, 1997). Similarly, camas, an important food species for Coast Salish Peoples in the Pacific Northwest, has been all but eliminated from people's diets through processes of environmental and social change and resulted in negative health and social implications for many Nations (Corntassel & Bryce, 2012). The significance of culturally important species in maintaining the continuity of knowledge and traditions and community health and wellbeing is increasingly being recognized (Joe, 1994), with other examples including western redcedar (Garibaldi & Turner, 2004) and riceroot (Joseph, 2012) in the Pacific Northwest, and tepary beans in southern North America (Nabhan &

Felger, 1978). In recent years, the term cultural keystone species has become prominent in the ethnoecological literature to describe species that shape the identity of a people (Garibaldi & Turner, 2004; Moss, 2016). These species provide a powerful lens through which to view impacts of socioecological change on indigenous communities.

Throughout the 1900s, residents of the Mackenzie Delta Region in the Northwest Territories relied heavily on a cultural keystone, the muskrat, for food, fur, and culture, but recent changes to ecological and economic conditions have altered the nature of this relationship. Like other northern mammals, muskrat population cycling is well documented and varies among regions (Erb, Stenseth, & Boyce, 2000; Errington, 1963). In recent years, many residents of the Mackenzie Delta region have reported declines in muskrat abundance that are outside the normal range of variation for this region (Arctic Borderlands Ecological Knowledge Society, 2002, 2008; Brietzke, 2015). It has been suggested that disease outbreaks and predator population cycles are the underlying cause of these oscillations in numbers, but the process is not fully understood (Erb, Stenseth, & Boyce, 2000).

In this study, our main objective was to better understand the role of muskrats (*Ondatra zibethicus*) in the cultural traditions and land-based livelihoods of the Gwich'in and Inuvialuit residents of the Mackenzie Delta throughout periods of rapid social, ecological, and economic change.

Study Region

The Mackenzie Delta of Canada's western Arctic lies within the Inuvialuit Settlement Region (ISR) (Indian and Northern Affairs Canada 1984) and the Gwich'in

Settlement Area (GSA) (Gwich'in Tribal Council and Indian & Northern Affairs Canada 1992) (Figure 2.1). The Mackenzie Delta ecoregion includes the alluvial terrain from Point Separation north to the treeline in the outer delta (Figure 2.1). The Delta is a productive environment that provides habitat for many species that are important contributors to the subsistence and fur economy in the region, including mink, marten, bear, wolf, wolverine, muskrat, and numerous fish and waterfowl species (Martell & Pearson, 1978).

The communities located in and around the Mackenzie Delta region include Inuvik (pop. ~ 3 463), Aklavik (pop. ~ 633), Tsiigehtchic (pop. ~ 143), and Fort McPherson (pop. ~ 792) (Figure 2.1). Inuvik, Fort McPherson, and Tsiigehtchic have year-round road access with the exception of freeze up and break up time, and Aklavik is only accessible by ice road in the winter months. Residents of all four communities frequently travel in the Delta throughout the year by boat, automobile, and snow machine for subsistence and income harvesting and to maintain extended social and family networks.

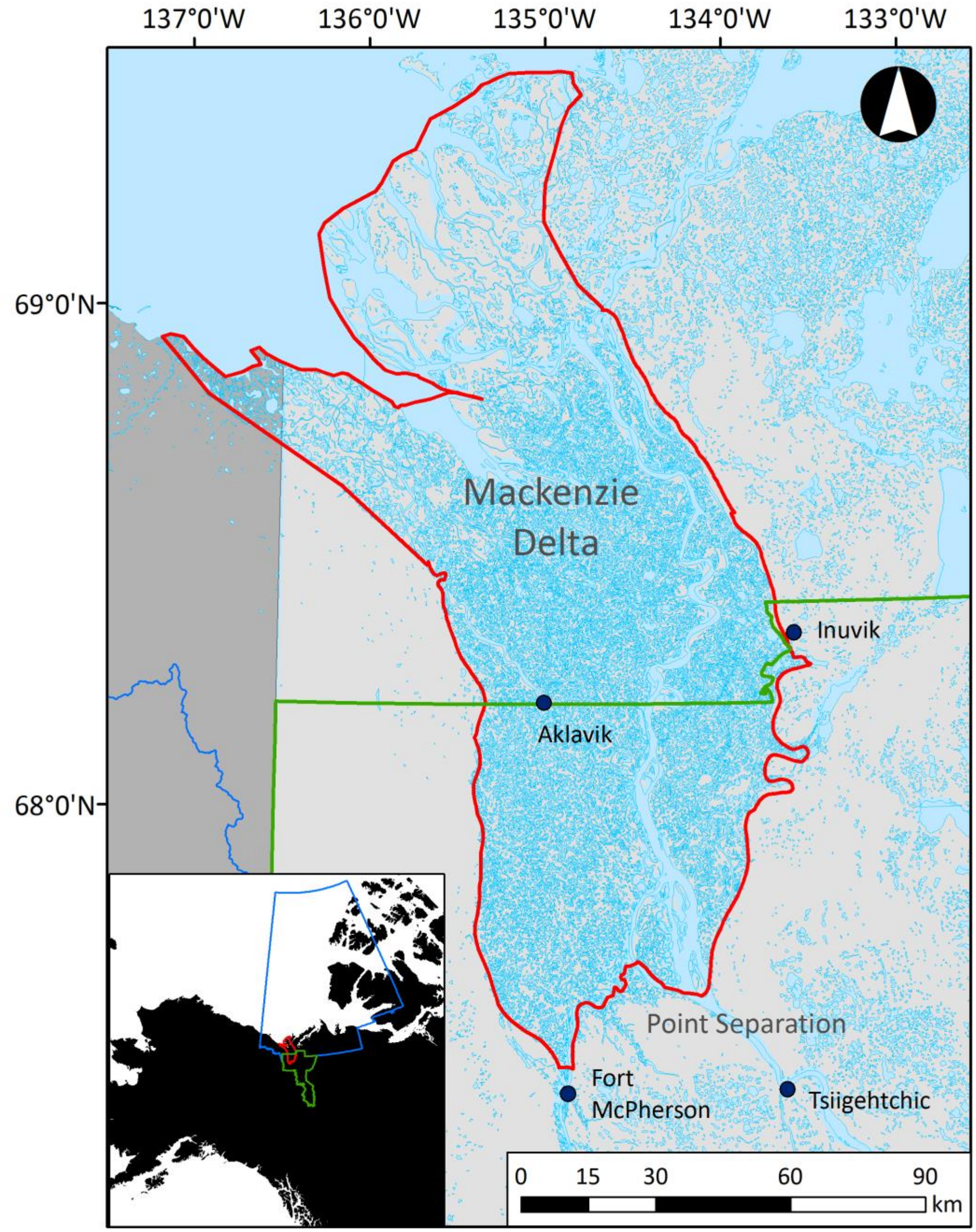

Figure 2.1 Map of study region. The boundary of the Mackenzie Delta Ecoregion (Ecosystem Classification Group, 2007) is shown in red. The northern boundary of the Gwich'in Settlement Area (Gwich'in Tribal Council & Indian and Northern Affairs Canada, 1992) and southern boundary of the Inuvialuit Settlement Region (Indian and Northern Affairs Canada, 1984) is shown in green. Communities involved in the study are marked with dark blue circles. Water bodies are outlined in cyan. Inset map shows

location of study area in northwestern North America and full extent of the Inuvialuit Settlement Region (blue) and the Gwich'in Settlement Area (green).

Gwich'in and Inuvialuit Peoples occupying the Mackenzie Delta region have relied on subsistence fishing, whaling, hunting, and gathering foods for hundreds of years, resulting in a high degree of reliance upon and connection to the land and ocean (Alunik, Kolausok, & Morrison, 2003; Heine, Andre, Kritsch, & Cardinal, 2007). Socioeconomic change has been ongoing in the Mackenzie Delta Region for over 200 years: explorers, whalers, traders, missionaries, trappers, settlers, and oil and gas development have all impacted life in the Delta and altered traditional subsistence economies practiced by its residents (Alunik, Kolausok, & Morrison, 2003; Krech 1976; Lyons 2007; Usher 2002). During a period of rapid transition in the early 1900s, fur prices rose and trade networks increased in scope and volume. Delta peoples seized the economic opportunity offered by this changing situation and many families prospered by harvesting muskrats in the early to mid-1900s (Alunik, Kolausok, & Morrison, 2003; Krech 1984). The current economy in the region is mixed, with many people still engaged in subsistence harvesting and trapping, and some working consistent wage labour jobs, primarily in Inuvik (Pearce et al., 2011; Usher, 2002).

Methods

In this project we employed a collaborative, community-based research methodology (Castleden, Morgan, & Lamb, 2012). This involved developing research objectives and methods jointly with organizations in four communities through face-to-face meetings, phone calls, and emails. These organizations included the Gwich'in

Renewable Resource Councils (RRCs) in each community, the Gwich'in Renewable Resources Board (GRRB), and the Gwich'in Tribal Council (GTC) Department of Cultural Heritage. A formal Research Agreement was signed with the GTC Department of Cultural Heritage, who administer the GTC's Traditional Knowledge Policy. Existing relationships with the Inuvialuit Joint Secretariat and the Inuvik and Aklavik Hunters' and Trappers' Committees were also fundamental to this project. Working closely with community organizations allowed us to hire community coordinators to arrange and conduct interviews in Fort McPherson, hire youth technicians in Fort McPherson and Aklavik, and ensured that we conducted interviews and site visits in a manner consistent with local expectations and cultural norms. The involvement of the authors in previous projects in the region (Bennett & Lantz, 2014; Gill, Lantz, & GSCI, 2014; Tyson, Lantz, & Ban, 2016) also allowed for continuity in the structure and content of interviews and built on respectful and productive relationships with key community members and organizations.

To explore the changing role of muskrats in the lives of Gwich'in and Inuvialuit residents of the Mackenzie Delta Region, we conducted 20 interviews with participants from Aklavik (n=5), Inuvik (n=3), Fort McPherson (n=10), and Tsiigehtchic (n=2) between June 2015 and April 2016. Interview participants were chosen based on recommendations made by staff members at the Gwich'in RRCs and GTC Department of Cultural Heritage, and the results of past studies of environmental change in the region (Bennett & Lantz, 2014; Gill, Lantz, & GSCI, 2014; Tyson, Lantz, & Ban, 2016). Several participants also contacted the lead author in order to take part. Participants had varying degrees of experience harvesting and utilizing muskrats in the past and present, and offered a broad array of perspectives on the social, economic and ecological significance of muskrats. Overall, we employed purposive sampling to recruit interview participants who were considered muskrat experts by their community or self-identified as such. This type of sampling is effective, efficient, and robust when investigating a specific aspect of culture (Tongco, 2007). We also reviewed transcripts from 11 interviews conducted with 14 Inuvialuit participants from Aklavik (n=6) and Inuvik (n=8) between 2012 and 2014 as part of regional community-based environmental monitoring projects that contributed to the identification of muskrats as a salient research topic (Bennett & Lantz, 2014; Gill, Lantz, & GSCI, 2014; Tyson, Lantz, & Ban, 2016). Most interview participants, including all young people, were active harvesters (n=25), while others, largely elders, were not currently active on the land (n=9). Overall, 7 interview participants were women, with the remaining 27 being men.

Interviews were semi-structured, and questions were designed to allow participants to share their experiences with and memories of muskrats, as well as their knowledge of muskrat ecology and habitat in the Delta. For a full list of interview questions, see Appendix 1. Some participants also used maps to identify specific locations where observations were made. All interviews were transcribed and transcripts were provided to participants, the majority of whom reviewed them for accuracy prior to analysis. Some participants consented to having their specific responses associated with their names, while others did not wish to be identified by name.

We also held public meetings in the spring of 2016 in Aklavik, Inuvik, and Fort McPherson. These meetings began with a brief update on research activities to date, which was followed by an extensive community-led discussion. Each meeting was attended by between 12 and 17 people, with 5 to 7 attendees actively participating in the discussion. Public meetings were attended by an approximately the same number of men and women, but male participants were the most active in discussions. All meetings were documented with comprehensive notes or recorded and transcribed with participants' permission. Meeting participants did not consent to being identified by name and are referenced by their community only.

Overall, transcripts and notes from 34 interviews and 3 meetings were reviewed as part of this study. Interview transcripts and meeting notes were analysed by iterative coding, which sought to identify key ideas present in participants' narratives. Subsequently, these codes were reviewed and used to develop broader topic categories that included closely related ideas. Associations among coding nodes were identified and used to create a smaller number of overarching themes for analysis (Richards & Morse, 2013), each of which included many of the topic codes previously developed (Appendix 2; Table A2.1). Observations were organized using these themes to explore similarities and divergence among participants and identify important intersections for discussion.

Results

Socioeconomic Importance of Muskrats

> That little animal has raised a lot of families.
>
> Fort McPherson community member

The majority of participants highlighted the economic and sociocultural importance of muskrats. Fred Koe, a trapper from Fort McPherson, explained that prior to the 1960s, trapping was "the only way people make a living [and] they were making a real good living." The late Inuvialuit Elder, James Rogers, recounted how important muskrats were as a source of income for his family in the 1940s:

> Every time [my dad] want something… he gives us 20 traps apiece, "go trap." Like that spring he wants a new outboard motor, "go trap." Trap enough muskrat for an outboard motor, finish.

From the 1920s to 1950s muskrats provided the primary income for families throughout the Delta, who were living in camps throughout the delta (Figure 2.2). Many interview participants reported families bringing in an average of 2 000 – 3 000 muskrat pelts each year in this time period (Gwich'in Elders, 1997), and sometimes a large family could have an annual harvest of up to 10 000 pelts!

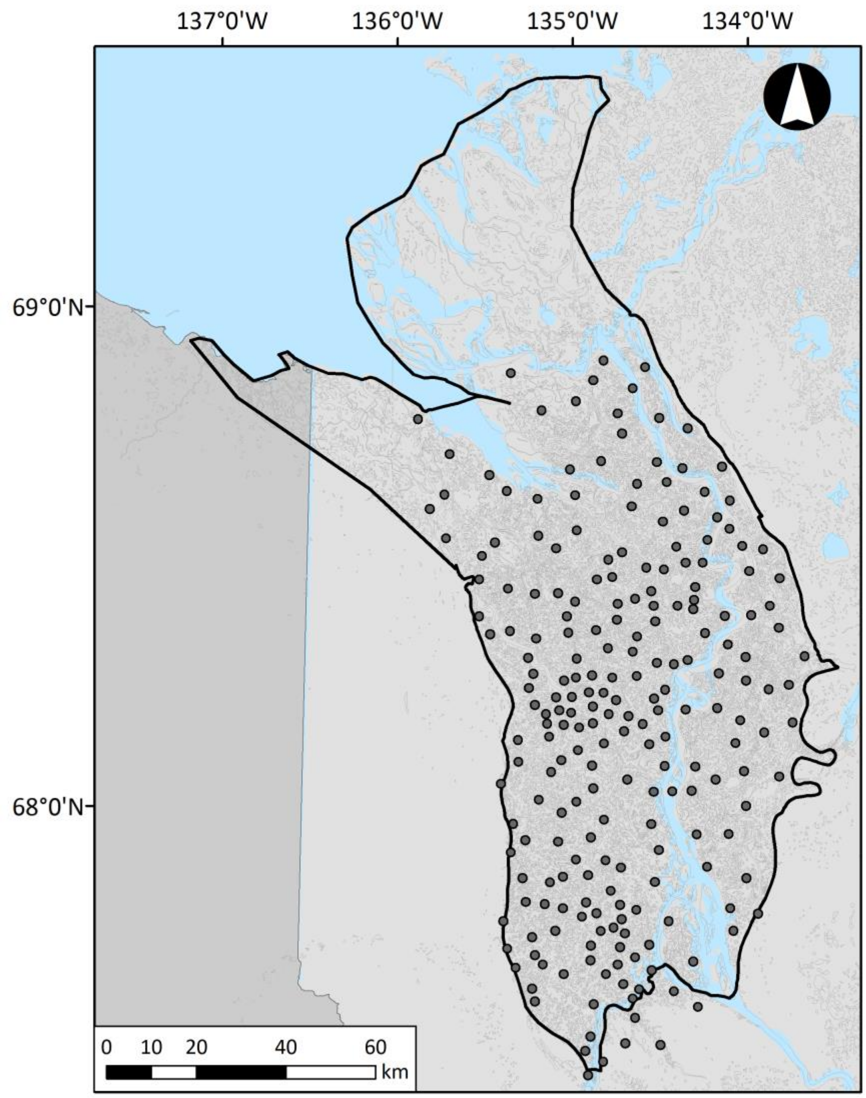

Figure 2.2 Map of trapping camps in the Mackenzie Delta in the 1950-51 season (data digitized from Wolforth, 1971).

In addition to muskrats being financially important, they were also an abundant source of food. One community member from Fort McPherson described how "we just lived on that muskrat because it's so good!" Dog teams were fed with the excess carcasses and the muskrats that were unfit for human consumption, which provided a source of energy for transportation.

Learning how to make a living on the land from parents and grandparents was a fundamental part of the subsistence harvesting lifestyle. As the late James Rogers put it, “what they taught us… you never forget.” A young trapper from Aklavik described learning the “majority of life lessons… in the bush. Stuff that could apply to everyday life… It was just as much of a[n] education as going to school.” This sentiment was echoed by several other interview participants (n=11).

People chose to harvest muskrats because they enjoyed it. Doug Esagok explained how his dad “made plenty of money, he didn’t have to trap. But he just loved it, so he always pulled us out [of school to go trapping.]”

Muskrat Ecology and Populations

Interview and meeting participants noted that there has been a large decline in muskrat abundance in the Mackenzie Delta in recent decades. Nearly every interview participant (29 of 34) reported that there are less muskrats than in the 1960s and 1980s, and there was consensus among attendees at each community meeting that populations had declined. Abraham Wilson was one participant who described the magnitude of this change: “certain lakes, you might see one or two rat houses; twenty years ago there was hundreds of them […] all on one lake.”

There was a clear consensus that muskrats are less abundant than they used to be throughout the Delta, but interviews also suggested that the rate of decline in population density has not been spatially uniform. Participants from Fort McPherson and Aklavik who trapped in the upper Delta between these two communities (n=11) described how muskrats have largely disappeared from this area in the last 5-10 years. However, Eddy McLeod from Aklavik asserted that "down below from [Aklavik] it's not too bad." Danny C. Gordon, an active trapper in the lower Delta, reported getting around 800 muskrats in 2014. This was significantly more than any other trappers reported, but he also emphasized that "for sure there's a decline of muskrats, we know that… and we don't know why they're declining."

Participants discussed potential causes of the decline in muskrat abundance, frequently citing changes to habitat and climate, interactions with other wildlife, and shifts in harvesting pressure. Declines were also often attributed to hydrological changes that made lakes unsuitable for muskrats, such as drained and drying lakes, changing water levels in the river and lakes, and changing flooding patterns.

Changing wildlife interactions may also be affecting muskrat populations, as participants discussed increases in the population densities of otter (*Lontra canadensis*) and beaver (*Castor canadensis*) in the last 20-30 years. Increasing beaver and otter populations are both seen as negative changes. Delta residents do not trap beavers or otters with the same enthusiasm or intensity as muskrats; there is little to no desire for their meat, both animals are larger, fattier, and harder to skin than muskrats, and the low value of these furs do not make up for the increased effort required to trap these species. Many participants (n=7) described how otters are extremely efficient predators of the muskrat with the ability to "clean the lake right out [of muskrats]," and asserted that they are likely influencing muskrat populations through predation. Numerous participants (n=13) also agreed that "the population of beaver is expanding, [and that there are] too many in the Delta." This change was concerning to trappers who noted that beavers may be affecting habitat conditions and food availability, or transmitting diseases or parasites to muskrats.

Participants also discussed the impact that reduced harvesting may have had on muskrat abundance. While most participants spoke about muskrat populations cycling between high and low in the past, many (n=15) specifically mentioned that they do not recall populations remaining so low for so long. Doug Esagok explained how "the year after [harvesting many muskrats], there'd be lots again… People always caught lots of muskrats." Eddy McLeod explained what happened in the 1980s:

> For awhile everybody just quit trapping and there was muskrats everywhere… nobody was trapping and then, after that was no muskrat. So […] maybe they got sick or cleaned the food out.

The shifting role of muskrats

Many participants indicated that muskrat harvesting has decreased considerably in recent years, and pointed to economic causes of this change in addition to the reduced populations. Fred Koe of Fort McPherson explained how the economic incentives have changed: "today I would say… it's better to just try to get a job and work in McPherson, because the Delta is not very good now." Some participants (n=7) described how trapping had become "just like kind of a hobby," rather than a lifestyle or means of making a living.

Residents of Fort McPherson who attended a public meeting discussed how fur prices declined in the 1980s, and subsequently "[they] all moved back to town and looked for jobs." Eddy McLeod, a trapper from Aklavik, described his personal situation:

> Well the fur price went down so I thought I'll work for a few years and if it comes back up I'll go back to trapping and hunting but it never did come back up enough so I just quit.

10 interview participants and several participants at public meetings described how low muskrat populations are a key factor that prevents them from trapping. Many Delta residents also expressed anger, resentment, and sadness at the low muskrat populations, and some didn't want to talk about it at all, saying merely "I don't get out there anymore" or "there's nothing there," in lieu of an interview. These sentiments were echoed by interview participants. Abraham Wilson, among others, was regretful that he could not trap because of the low populations: "You know, I wish I could trap this spring, but no muskrat houses ah?" Others, like Fred Koe, were frustrated with the way things are; "I told [my brother] the hell with it. You know, it's a bother. It's not worth it!"

Interview participants often discussed the prohibitively high cost of trapping in terms of gas prices. Doug Esagok of Inuvik explained "the price of gas is getting crazy […] and if you're not catching a lot of fur you're burning gas still anyway." Rising gas prices are part of the reason a young trapper from Inuvik said,

> [a]nd now, it's… a bit harder I guess to make a living doing stuff like that. So a lot of people have taken jobs in town and it's just not as common to see families going out anymore […] People still make time to go out, but […] not for the whole muskrat season right from March till June.

Many participants recounted with nostalgia and some sadness how it was 'long ago'. Neil Snowshoe explained that "*everybody* …[trapped] but nowadays nobody hardly goes." A trapper in Fort McPherson described the significance of the reduction in the number of people who spend time out on the land, "It's just so horrible you know, because our people used to *live* in the Delta," further explaining, "trapping muskrats was a *really big deal*, way back in the day. It was a big deal."

Numerous participants (n=11) expressed concerns about the processes of knowledge development and transfer being affected by people spending less time on the land. At a public meeting in Inuvik, a community member described how people in the past knew about animals and the environment because they spent long periods of time on the land, watching and learning. He lamented how this is changing as people spend more time in communities working wage jobs. An interview participant from Fort McPherson described the loss of knowledge transfer from "our parents… [and] grandparents where we learn all these things from[.] They're gone." The late James Rogers echoed this sentiment, saying "long ago, what our parents taught us… we're slowly losing it. And that's the sad part… It should be kept on you know." These observations were often accompanied by the perception that "the younger generation now, don't really care to do these things."

Continuity

Despite population declines, the increased cost of trapping, reduced trapping effort, and lower fur prices, most participants were not concerned about the continuity of muskrat harvesting as an important cultural tradition. The majority of participants expressed optimism and certainty that when the muskrat populations increase, people will return to the land. When community members at a public meeting in Fort McPherson were asked if they thought this would be the case, the response was a resounding yes, with one person describing how the community would be a “ghost town, everybody go out to bush camp.”

Participants gave a number of reasons why they continue to trap despite the changes in economic and ecological conditions. Many trap for food for themselves or family members. Muskrat meat has been described a “seasonal delicacy for Delta folks,” and carcasses are sold off to hungry friends and relations within days or even hours of returning from the bush. As Doug Esagok put it, “a lot of times people are beating down your door … asking to buy your muskrats.” This ‘craving’ for muskrat meat is part of what ensures the continuity of muskrat harvesting.

People also described a desire to continue to go out on the land to maintain traplines, even when there are few or no muskrats. A trapper from Aklavik explained how he still wants to “go out and check it out! You always think it might come back.” Similarly, Eddy McLeod from Aklavik described how “I don’t want to have no place to go so I keep a little area open yet, with trails and that.”

There are many people who continue to trap because of their emotional attachment to the experience and tradition. A trapper from Fort McPherson stressed the value of the tradition of muskrat harvesting: “I like seeing people go, whether they make a living out of it or not because it’s a tradition that we need to keep […] alive.” People frequently spoke about going on the land to trap in the spring as “liv[ing] that traditional time of year.” A trapper from Aklavik described trapping and shooting as something you “just look forward to […] every spring and you just want to go out there”. A trapper from Aklavik eloquently described his own personal connection: “it doesn’t quite feel like springtime in the Delta if you don’t get out and get some rats, [a]fter a long cold winter you get out there in the spring and … plants are growing back and all the birds are making noise, it's just good for you…therapeutic, for Delta people."

Discussion

Intensive muskrat trapping in the Mackenzie Delta from 1900-1950 created a regional economy based on this animal and fostered the development of Gwich'in and Inuvialuit cultural traditions rooted in this economy. While ecological and economic changes have led to a decline in muskrat trapping in the Mackenzie Delta, our analysis suggests that ongoing muskrat use provides communities with a way to support health and wellbeing and maintain cultural knowledge, traditions, and values in the face of ongoing socioecological change.

Cultural significance

Interview data, historical accounts, and contemporary observations all demonstrate that muskrats have been and continue to be a vital part of Gwich'in and Inuvialuit cultures, occupying the role of a cultural keystone species. A cultural keystone is defined as a species that shapes the identity of a people, and is important in traditional practices, food, and lifestyles (Garibaldi & Turner, 2004). Wolforth (1971) reported that in 1948 there were approximately 228 trappers with registered traplines in the Delta, only one year after the registration of traplines was introduced. Assuming each trapline was used by a family of 2-5 people suggests that 30-75% of Aklavik's 1953 population of 1 556 (Alunik, Kolausok, & Morrison, 2003, p. 211) was engaged in trapping at this time. The integrated economic and cultural significance of muskrat use is also evidenced by the inclusion of the springtime harvesting season in the Gwich'in Seasons Calendar and John

A. Snowshoe's clock of life (Loovers, 2010, pp. 155–156). Other indicators of the muskrat's cultural importance include oral traditions and stories about muskrats (Alunik, Kolausok, & Morrison, 2003; Gwich'in Elders 1997; Heine, Andre, Kritsch, & Cardinal, 2007).

Figure 2.3 Images showing the ongoing cultural importance of muskrats in the Mackenzie Delta. A – C) Muskrat jamboree and participants in the muskrat skinning contest 2016. Photos by Chanda Turner. D) Aklavik town flag. Photo by Sharon Farnel.

Every spring during traditional muskrat trapping time, each Delta community has a multi-day event, called a Jamboree, which includes skidoo races, old-time dances, feasts, games, and contests. These jamborees highlight the ongoing importance of muskrats by celebrating time spent out on the land in the springtime, people coming together, and the importance of this seasonal harvest. One of the highly anticipated events at all of the jamborees is the muskrat skinning contest, which brings this tradition off the land and into the community for a short time (Figure 2.3). Muskrat is one of the many important traditional foods offered at the opening feasts of these and other community events. The muskrat is also featured on the community of Aklavik's flag (Figure 2.3). The multifaceted importance of muskrats suggests that they can be considered a cultural keystone species in the Mackenzie Delta Region.

Decline in muskrat harvest

Despite the ongoing importance of muskrats, trapping effort has declined considerably since the 1980s. The conditions leading to the reduction in harvesting effort are interrelated and include the following economic and ecological factors: the increased cost of trapping, substantial reductions in fur prices, the proliferation of wage labour, and reduced muskrat populations.

Socioeconomic changes have reduced trapping effort by altering the cost:benefit ratio of muskrat harvesting for trappers in the Delta. Wolforth (1971) asserted that the decline in muskrat trapping began in the late 1950's following the 'Muskrat Period' from 1900-1950, when a drop in fur prices caused many trappers to transition to part-time trapping. By the 1960s very few people were supporting themselves solely on their trapping income. Wolforth (1971) speculated that this decreased harvesting effort may have also been partly caused by an increase in wage work associated with the construction of Inuvik. In the 1980s, the price of muskrat pelts declined further, when the anti-fur movement gained worldwide momentum and brought demand to a standstill (Alunik, Kolausok, & Morisson, 2003; Emberley 1997). Prices per muskrat pelt in the Yukon dropped from ~$20 in 1979 to less than $3 in 1989 (Brammer, 2016). For many people, including several interview participants, this reduction in income was the main stressor that brought them off the land and into the expanding wage labour market. Costs for fuel and equipment have also increased over time, especially as snowmobiles replaced dog teams and fuel became a necessary input for trapping. Participation in the wage economy has added an additional dimension of cost to trapping: people with full-time jobs do not always have the time and energy required to harvest traditional foods (Kuhnlein & Receveur, 1996). Conversely, those without jobs may have the time and energy, but not the financial opportunity, to go out harvesting.

Many of participants in this study also explained how reduced muskrat abundance has contributed to declines in their trapping efforts. Participants discussed many potential causes of this population decline, including changes to climate, habitat and hydrology, interactions with other wildlife, and shifts in harvesting pressure. The complexity of interactions among these factors makes it difficult for harvesters, researchers, and managers to assess which changes may be contributing most to the observed decline in muskrat abundance. Understanding muskrat population dynamics is further complicated by high spatial and temporal variability, associated with muskrat movement and cyclic populations (Clarke, 1944; Jelinski, 1984; Stevens, 1953). More long-term ecological research is needed to determine the magnitude of the decline throughout the Delta, and characterize the effect of the drivers noted above.

The cumulative effects of socioeconomic and ecological changes on the cost:benefit ratio of harvesting have led many people to characterize muskrat trapping as “not worth it!” Fewer trappers has resulted in a marked decrease in overall access to muskrats and participation in harvesting activities, which has a suite of potential implications for individuals and communities in the Mackenzie Delta.

Sociocultural impacts of a declining harvest

Interview participants identified several ways that reduced harvesting effort and decreased access to muskrats for food, fur, and culture may impact the health, wellbeing and cultural traditions and identity of communities in the Mackenzie Delta. Participants expressed their fear of the loss of cultural identity when they spoke about the sadness they felt because muskrats cannot provide a livelihood anymore. Reduced access to muskrats also means that they are not always available for personal consumption, feasts, and other important community gatherings. This can result in younger community members never developing a “taste” for this traditional food, and older community members losing this aspect of their cultural identity. Previous research indicates that wellbeing can be negatively impacted when self-reliance in attaining traditional foods is compromised, resulting in lowered self-esteem and reductions in cultural practices, identity, and pride (Kuhnlein & Receveur, 1996; Paci, Dickson, Nickels, Chan, & Furgal, 2004; Parlee & Furgal, 2012; Turner & Turner, 2008). These impacts can be intensified when access to a cultural keystone species like muskrats is reduced because of their more prominent role in people’s lives (Moss, 2016).

Decreased harvesting and consumption of traditional foods has also been shown to negatively affect the maintenance and development of traditional knowledge (Deur & Turner, 2011; Kuhnlein & Receveur, 1996). As wage jobs and school keep most families from being out in the bush for extended periods, there are less people engaged in the process of knowing, creating and recreating knowledge through observation and interaction with the environment (Berkes, 2012). Muskrat trapping was formerly an activity that most individuals were involved in, which meant that multiple generations were on the land together, teaching and learning from one another. It is likely that reduced trapping will result in decreased transmission of cultural traditions through these processes, especially as, in the words of a trapper from Aklavik, “it’s not as common to see families going out anymore.” The loss of this time spent on the land together may also affect the transfer of cultural values, including work ethic, respect for the land and other beings, feelings of pride and responsibility for trapping areas, and a willingness and desire to contribute to one’s community. Many elders expressed concerns about the decrease in the transfer of cultural values that are best learned and reinforced on the land in important places and through harvesting practices.

Continuity in muskrat use and significance

Despite concerns surrounding the reductions in muskrat harvesting and use in the Delta, our interviews with young and old, active and inactive harvesters all made it clear that muskrats still provide a vital connection to the land that engages people with their culture and the environment. Ongoing muskrat harvesting in the Delta provides a powerful focal point for sustaining cultural traditions and fostering healthy communities. The role of muskrat harvesting in mental, spiritual, and emotional wellbeing is shown by the words of many participants, including one who described spring trapping as “therapeutic.” In the Delta, the muskrat trapping and hunting seasons provide an opportunity for individuals to remain engaged in harvesting while continuing to be part of the wage economy. Trappers can take two to three weeks off of their regular job and participate in the traditional economy in the short-term, providing an important input of traditional food, emotionally-fulfilling time out on the land, and income from muskrat fur to balance out the majority of their year spent working in town. The inherent value of time spent on the land, away from town and its daily stressors, was also described as a key component of what makes berry picking important by residents of Fort McPherson (Parlee, Berkes, & Teetl'it Gwich'in, 2005). One berry picking participant explained how "even if I knew there were no berries there, I would still go visit those places" (Parlee, Berkes, & Teetl'it Gwich'in, 2005, p. 133). Many interview participants echoed this sentiment when they described how they continue to go out on the land and "check the lakes" even in the absence of muskrats. This indicates that being out on the land in the springtime is as important as the actual economic result of muskrat harvesting. Land-based activities including harvesting and environmental monitoring situated in important places out on the land can also reinvigorate cultural identities in youth (Brunet, Hickey, & Humphries, 2016; Cuerrier, Turner, Gomes, Garibaldi, & Downing, 2015) and many Delta residents are actively engaged in increasing cultural knowledge transmission. In all of the Delta communities, there are school programs and the GNWT's Take a Kid Trapping program which run each spring and ensure that youth attending school get these on the land experiences. Some young people in the Delta also still have the opportunity to get out and harvest muskrats with their grandparents and parents, and appreciate the intrinsic value of these experiences. A young trapper from Aklavik emphasized the importance of this continued knowledge transfer among generations: "all our knowledge we have of hunting and stuff is all useless if we don't hand it on to the next people."

Muskrats have an integral role in cultural events and the mixed economy of the Delta, which continues to connect individuals and communities to the land, and offers an experiential way for community members of all ages to remain active and engaged with their cultural practices and identity. The commitment of Delta residents to maintaining and reviving muskrat harvesting traditions contributes to individual and community health and wellbeing in tangible and intangible ways and highlights the potential role that muskrat harvesting traditions can play in efforts to maintain and strengthen cultural identity and knowledge transfer.

Conclusion

Our research investigated the impacts of ecological and socioeconomic changes on muskrat harvesting in the Mackenzie Delta. Muskrats have become less abundant in this region and make a smaller contribution to income and food than in the recent past. This has changed the nature of their role in these communities, but this species remains a vibrant and vital part of Gwich'in and Inuvialuit cultures in the Delta. We suggest that muskrats can be viewed as a link to the land and to the practices and traditions of the past, present, and future as ecological and socioeconomic conditions continue to change. Muskrats offer Delta residents a meaningful way to remain engaged in, to perpetuate, and to strengthen their cultural identity and land-based traditions among generations, as well as to foster individual and community wellbeing.

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Appendix 1 – Muskrat interview questions

1. Where did you grow up? In the bush, town?
2. Tell me about your experience with rats in the past.
    a. Timeframe
    b. Harvesting type
3. What are muskrats used for?
4. Why did people trap and shoot muskrats?
5. Do you still trap or hunt muskrats?
6. Why do people still trap? Or why don't they?
7. Do people still use the same traplines?
8. How are muskrats doing?
9. What do you think is going on with muskrats right now? 20 years ago? 50 years ago?
10. Have you seen changes in muskrat populations?
    a. What kinds of changes? When? Where? (map)
    b. What do you think is affecting them?
11. How widespread is this change?
12. What do you think the future of muskrat harvesting will be like?
    a. The future of muskrat health and populations?
13. Have you seen changes in muskrat lakes?
    a. Where? When? (map)
14. How do you know a lake has lots of muskrat?
    a. Observations (push ups), harvesting results, etc?
15. What are the differences between lakes that are good for muskrat and lakes that are not?
    a. Appearance?
    b. Location?
    c. Do all lakes have the same characteristics? Do some vary?
16. Are all lakes with lots of muskrat good for trapping?
17. Using a map, can you point out:
    a. Lakes that are good for trapping/have high muskrat populations
    b. Lakes that formerly had high muskrat numbers/were good for trapping. What happened?
    c. Lakes that have no or low populations of muskrat

Appendix 2 – Themes and topics from interviews

Table A2.1. Themes and their associated topics from interview transcript and public meeting notes iterative analysis, including the number of interviews or meetings where the topic was discussed. The total number of interview transcripts and meeting notes available was 37. Some topics also include an illustrative quotation from an individual interview.

Theme	Topic	No. of times observed
Ecological Observations		
	Habitat (food, flooding)	27
	Wildlife interactions	24
	Beavers	24
	Wildlife predation	20
	Otters	20
	Spatial variation	19
	Reasons for decline	17
	Effect of harvesting on populations	12
	Weather	12
	Overflow	11
	Climate change	10
	Ice conditions	9
Ecological Concern		
	Low populations: “There’s nothing!”	29

Theme	Topic	No. of times observed
Hard to make a living		
	Harder to get now (low populations)	29
	Fur prices	14
	Hard to make living now “Not worth it!”	14
	Wage work	12
	Cost of trapping	9
	Living in town	7
Social Concern		
	Lifestyle change	23
	Change in knowledge transfer	11
	Importance of observation: “Old people… they really got something”	9
	Loss of knowledge: “You just can’t know what happened”	5
	Nostalgia / Sadness: “It’s just so sad”	8
Optimism / Continuity		
	Harvesting for food: “beating down your door [for muskrat meat]”	21

Theme	Topic	No. of times observed
	Decline: "Something is happening"	17
Social Importance		
	Reasons to trap	25
	Living off the land / Traditional lifestyle	21
	Traplines (inherited)	19
	Cultural / personal importance	15
	Springtime: "therapeutic"	14
	Knowledge transfer	12
	Enjoyment	8
	Nostalgia / Sadness	8
	"The land always pulled me back"	4

Theme	Topic	No. of times observed
	Springtime: "therapeutic"	14
	Optimism: "everybody go out to bush camp"	10
	Youth harvesting: "they go out yet"	9
	Continuity of harvesting	8
Lifestyle Change		
	Lifestyle Change	23
	Changing attitudes / values	9
	Nostalgia / Sadness: "them days"	8
	"It's just like a hobby for me now"	7
Economic Importance		
	Economy / Income	23
	Harvesting for food	21
	Dog food	12

Chapter 3 – Patch quality matters more than landscape connectivity for muskrat distributions in a changing Arctic Delta

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CKT, TCL, JTF conceived the study; CKT conducted the research; CKT,TCL, JTF analyzed data; CKT, TCL, JTF wrote manuscript

Introduction

Rapidly increasing temperatures and changing precipitation are altering species' ranges and phenologies, impacting population dynamics, and shifting community composition in the Arctic (ACIA, 2004; Galbraith et al., 2002; Gilg et al., 2012; Huntington, 2006; IPCC, 2014; Parmesan & Yohe, 2003; Walther et al., 2002). The Mackenzie Delta in Canada's western Arctic is already experiencing these types of dramatic changes, as temperatures have risen by approximately 2ºC from 1926 to 2006 (Lantz & Kokelj, 2008), salmon have been increasing in abundance and distribution in the last 10-20 years (Dunmall et al., 2013), and seasonal timing is changing by nearly ten days in the springtime (Lesack, Marsh, Hicks, & Forbes, 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 & 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 (Déry, Hernández-Henríquez, Burford, & Wood, 2009; Lesack, Marsh, & Hecky, 1998; Lesack et al., 2014; Prowse et al., 2006).

The Mackenzie Delta is a heterogeneous landscape and can be viewed as resource patches that are surrounded by a matrix that is less suitable or possibly uninhabitable for a particular species (Kotliar & Wiens, 1990; Tscharntke et al., 2012; Turner, 1989). In such environments, a species' distribution is influenced by both the quality of resource patches and their ability to move through the matrix and access these resources (Goodwin & Fahrig, 2002; Harrison & Bruna, 1999; Taylor, Fahrig, Henein, & Merriam, 1993). Niche theory states that species can only persist when and where there are sufficient available resources and suitable biotic and abiotic conditions, which vary based on species' requirements (Grinnell, 1917; Hutchinson, 1957). Taken together, these two perspectives offer a way to characterize the water bodies within the Mackenzie Delta; for aquatic species, lakes are patches with varying habitat quality embedded within a terrestrial matrix dominated by spruce woodlands and alder and willow thickets (Gill, 2011).

Most research on species' persistence in heterogeneous landscapes focuses on the effects of fragmentation and disturbance (ie. Keitt, Urban, & Milne, 1997; Kupfer, Malanson, & Franklin, 2006; Prugh, Hodges, Sinclair, & Brashares, 2008), but climate change will also affect species living in naturally heterogeneous landscapes (Gilg et al., 2012; Opdam & Wascher, 2004). In the Mackenzie Delta, climate change will alter 1) landscape connectivity, as some lakes and channels dry out and the vegetation of the matrix changes (Emmerton, Lesack, & Marsh, 2007; Myneni, Keeling, Tucker, Asrar, & Nemani, 1997; Pisaric, Carey, Kokelj, & Youngblut, 2007), and 2) patch quality, as some lakes become shallower and more acidic, and others receive more sediment and nutrients from increased sediment loads in the river (Emmerton, Lesack, & Marsh, 2007; Lesack, Marsh, & Hecky, 1998; Marsh & Lesack, 1996; Prowse et al., 2006). A primary driver of the changes predicted above is reduced flooding as spring breakup dynamics shift and peak water levels decrease (Lesack et al., 2014). Research on the relative importance on patch quality versus landscape connectivity is required to determine the magnitude and extent of climate change's impacts on species (Opdam & Wascher, 2004; Wiens, Stensth, Van Horne, & Ims, 1993), so we investigated the importance of landscape connectivity and patch quality on the distribution of an aquatic mammal species, the muskrat (*Ondatra zibethicus*).

Muskrats are rodents with ecologically important roles in the food webs and composition of aquatic ecosystems; they are prey for numerous animals including mink and otter, and can significantly impact the density and community composition of the plant foods they rely on (Higgins & Mitsch, 2001; Mott, Bloomquist, & Nielsen, 2013). Muskrat densities respond to water levels and may serve as an important indicator species for changes in wetland ecosystems (PADEMP, 2014; Weller, 1981, 1988). Muskrats are also culturally important in the Mackenzie Delta because of the role they played in the regional economy throughout the 1900s (Alunik, Kolausok, & Morrison, 2003; Gwich'in Elders, 1997; Turner, Lantz, & Gwich'in Tribal Council Department of Cultural Heritage, in press). 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 & Lantz, 2014; Brietzke, 2015), and 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 wellbeing (Gill, Lantz, & GSCI, 2014; Parlee, Berkes, & Gwich'in, 2005; Parlee & Furgal, 2012; Turner, Lantz, & Gwich'in Tribal Council Department of Cultural Heritage, in press).

Muskrats in the Mackenzie Delta live in bank burrows within lentic waterbodies, and rely on emergent shoreline vegetation in the summer months and the roots and rhizomes of submerged macrophytes that persist on lake bottoms under the ice in the winter months (Errington, 1963; Jelinski, 1984, 1989). Two factors that could be driving muskrats' ability to effectively use and persist in lakes within the Mackenzie Delta are: 1) lake accessibility (landscape connectivity), and 2) within-lake resource availability and abiotic conditions (patch quality) (Goodwin & Fahrig, 2002; Harrison & Bruna, 1999; Schooley & Branch, 2009; Thornton, Branch, & Sunquist, 2011; Weyrauch & Grubb Jr., 2004). In this study we investigated the relative importance of these factors on muskrat distributions. Specifically, we quantified 1) landscape connectivity by measuring the physical connectivity of lakes to each other and to river channels (*closure class* and *flooding distance*), *interpatch distance* between lakes, *lake area*, *lake perimeter*, and the *ratio of perimeter to area*; and 2) patch quality by measuring *lake depth*, *submerged macrophyte biomass*, *water turbidity*, and *sediment nutrient content*. We hypothesized 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 (Goodwin & Fahrig, 2002; Jelinski, 1984). Within lakes, we hypothesized that muskrat presence would be positively correlated with edible macrophyte biomass, variables influencing the productivity of these edible macrophytes, and increasing lake depths (Brammer, 2016; Jelinski, 1989; Stevens, 1955). We also investigated the drivers of submerged macrophyte presence (food availability) in individual lakes, and hypothesized that water *depth*, *turbidity*, and *sediment organic matter content* would be the primary drivers (Squires & Lesack, 2003a, 2002, 2003b).

Methods

Study area

The Mackenzie 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 (Figure 3.1). The area contains hundreds of distributary channels and over 40 000 lakes that vary in size, depth, productivity, and biodiversity, and flooding regimes (Emmerton, Lesack, & Marsh, 2007; Hay, Michelutti, & Smol, 2000; Squires & Lesack, 2003a, 2002). Lakes in the Delta are strongly influenced by the annual spring flood, as it is their main source of water, inorganic sediment, and nutrients (Lesack, Marsh, & Hecky, 1998; Marsh & Bigras, 1988).

We classified lakes into three categories: no-, low-, and high-closure, based on their flooding regimes, which are largely controlled by the height at which lakes are perched above distributary channels (Lesack & Marsh, 2010; Marsh & Hey, 1989).

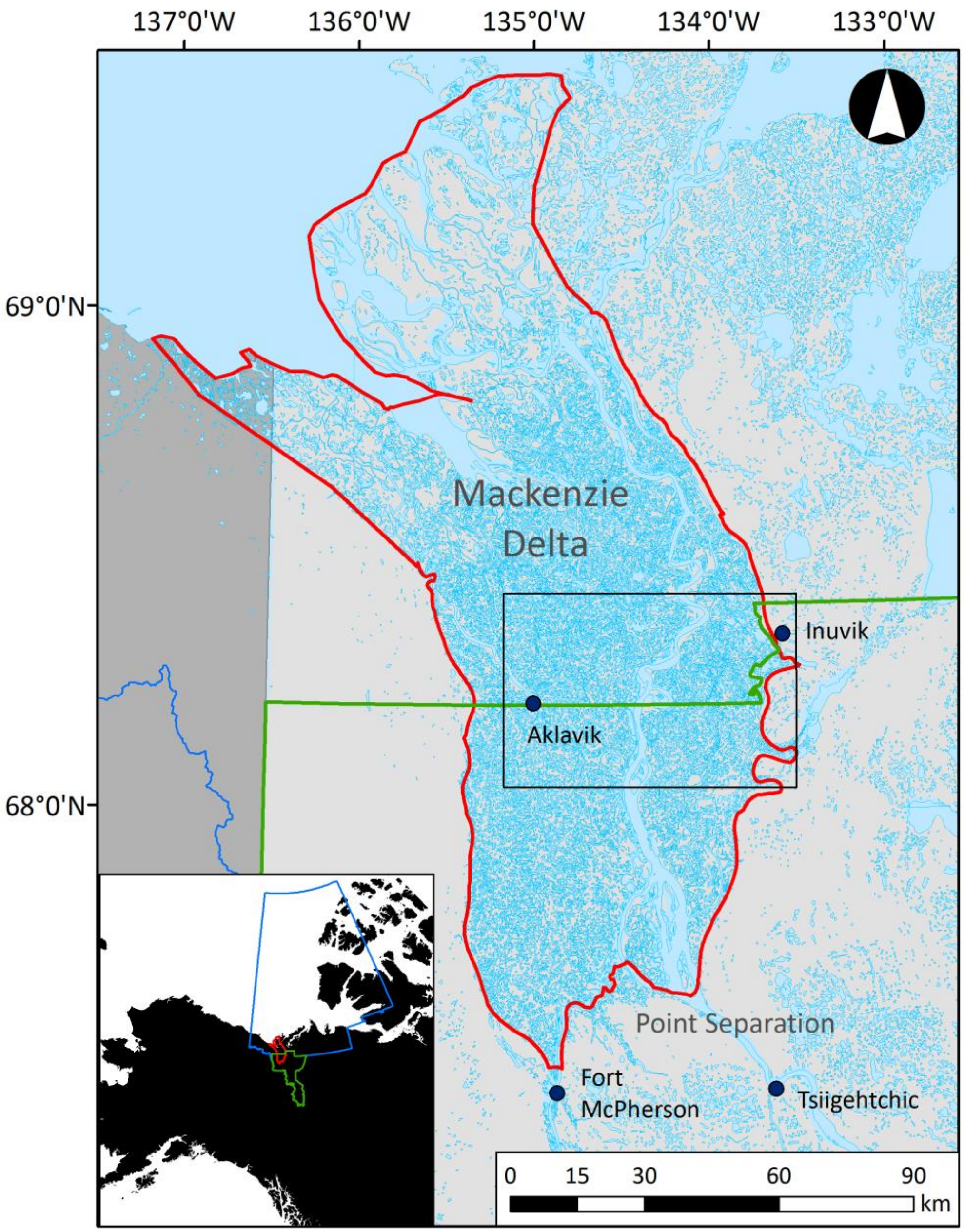

Figure 3.1 Map of study region. The boundary of the Mackenzie Delta Ecoregion (Ecosystem Classification Group, 2007) is shown in red. The northern boundary of the Gwich'in Settlement Area (Gwich'in Tribal Council & Indian and Northern Affairs Canada, 1992) and southern boundary of the Inuvialuit Settlement 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 full extent of and Inuvialuit Settlement

Region (blue) and the Gwich'in Settlement Area (green). Black box outlines study area enlarged in Figure 3.2.

No-closure lakes are at the same height as the distributary channels and are connected to the river all summer and 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 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 at higher elevations, and flood only every 2-4 years when spring flood waters are sufficiently high (Lesack & Marsh, 2010; Marsh & Hey, 1989). Biophysical differences among closure classes include lake transparency (Marsh, Lesack, & Roberts, 1999; Squires, Lesack, & Huebert, 2002), water solute chemistry, including pH and nutrient levels (Lesack, Marsh, & Hecky, 1998), nutrient and organic matter content of sediment (Squires & Lesack, 2003a), and macrophyte productivity and community composition (Squires & Lesack, 2003a; Squires, Lesack, & Huebert, 2002).

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 (Figure 3.1). Residents of all four Delta communities – Invuik, Aklavik, Fort McPherson, and Tsiigehtchic – frequently travel in the Delta throughout the year by boat, automobile, and snow machine for subsistence and income harvesting and to maintain extended social and family networks. 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 (Burn & Kokelj, 2009; Gill, 2011; Pearce, McLennan, & Cordes, 1988).

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 ~3300 lakes in an area between Inuvik and Aklavik, the bounds of which are indicated in Figure 3.2 (Marsh, Lesack, & Roberts, 1999) . From this initial large sample of 450 lakes, we retained all lakes with >50% ice coverage to allow for aerial muskrat surveys. This stratified sample produced 129 classified lakes (high closure = 44, low = 49, no = 36; Figure 3.2). Although this sampling 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 believe it effectively captures the variation among lakes throughout the central Delta.

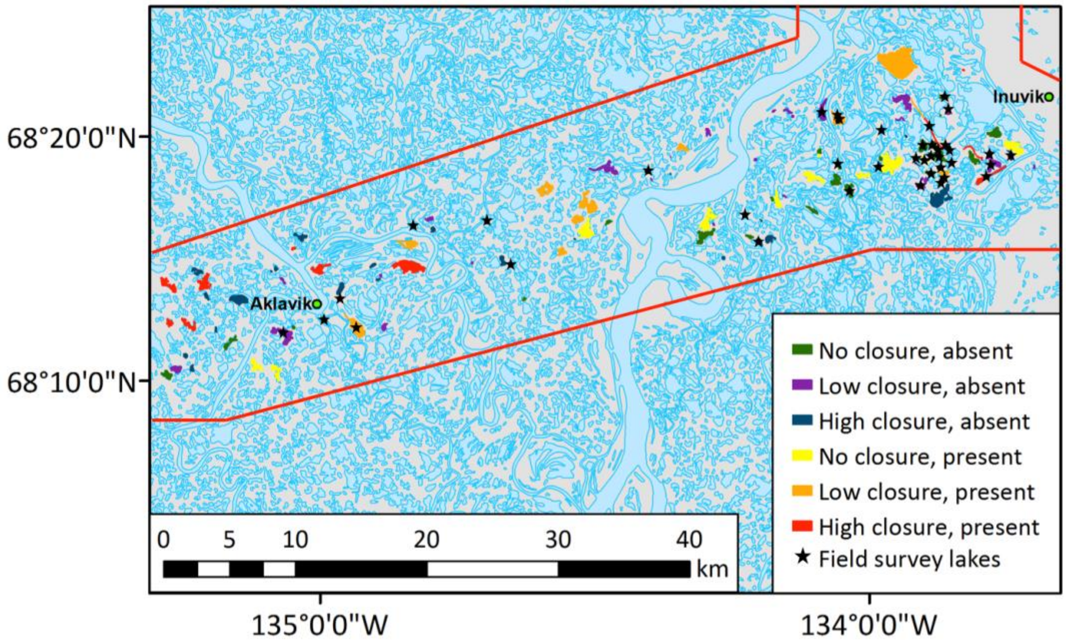

Figure 3.2 Study region in the central Mackenzie Delta. The extent of this map corresponds to the area outlined in Figure 1. The red polygon outlines the extent of the sampling frame where closure class surveys were done by Marsh, Lesack, and Roberts (1999). Lakes are identified by closure class and muskrat push-up presence (polygon colour). Lakes that were surveyed in the field are shown as black stars.

Muskrats construct mounds of vegetation on the ice surface called 'push-ups' that insulate and preserve an air hole in the ice which the animals use for feeding, breathing, and resting (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 & Boutin, 1989). To document muskrat occupancy in individual lakes in the winter, we conducted an aerial photographic survey of muskrat push-ups from May 21-22, 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. We identified individual push-ups by visual inspection of geo-referenced survey photos, based on the colour, size, shape, and context of the visible features on the ice surface (Figure 3.3). We converted push-up counts in individual lakes to presence-absence data, to account for uncertainties regarding the relationship between the number of push-ups on a lake and the number of muskrats in that lake, as well as variation in ice coverage among lakes. Lakes without push-ups are reliably considered as being absent of muskrats through the whole winter, and the presence of any number of push-ups is a reliable indicator of muskrat presence in the fall, if not the duration of the winter.

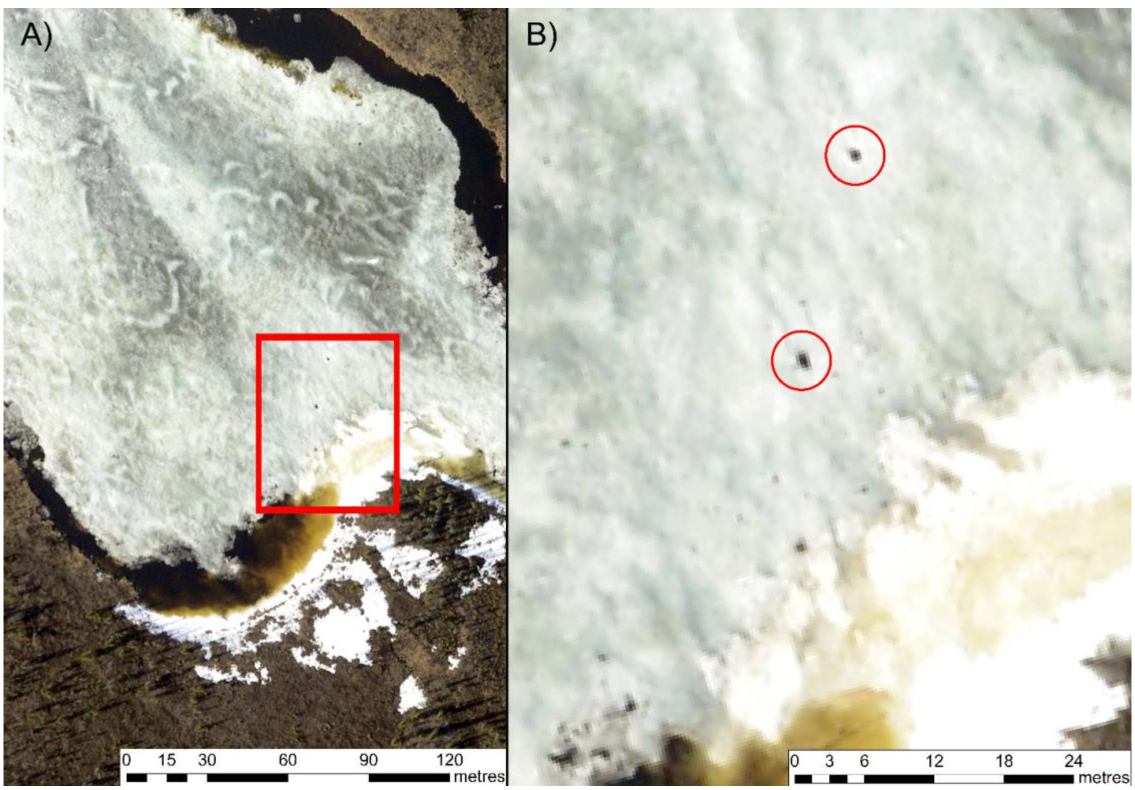

Figure 3.3 Example of an image of an ice-covered lake surface from aerial push-up survey. Red box in A) indicates enlarged region presented in B). Push-ups are identified by red circles on enlarged region (B).

We determined the area and perimeter of each lake using polygons digitized from 1:30000 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 (Table 3.1).

We conducted field surveys from July 2nd to August 24th 2015 at 39 lakes accessible by boat and portage (high closure = 11, low = 17, no = 11) (Figure 3.2). At each lake, we measured turbidity and lake depth at multiple points along one or two transects across the lake. At the mid-point of each transect we collected a water sample, which was analyzed for total phosphorus content (SM4500-P:D; APHA, AWWA, & WEF, 2012) by Taiga Environmental Laboratory (Yellowknife, NT, Canada). We also collected a sediment sample at the midpoint of each transect, which was analyzed for sediment chemistry (Ca, K, Mg, S, B, Cu, Mn, Mo, Na, Ni, P, and Zn, N, organic C, and inorganic C) using microwave digest and ICP methods. 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) on each transect using a boat rake method (Johnson & Newman, 2011) with a circular swath (0.08553m^2). These samples were sorted by species, dried, and weighed to provide measures of overall biomass and community composition (Squires & Lesack, 2003; Johnson & Newman, 2011). The biomass of edible macrophytes was also estimated for each lake by adding the biomass totals of all macrophyte species with energy-rich roots or rhizomes, which are preferred as winter food by muskrats (Appendix 2; Artimo, 1960; Jelinski, 1984).

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 & Anderson, 2002). Specifically, we used generalized linear models (GLMs; Zuur, Ieno, Walker, Saveliev, & Smith, 2009) in R Statistical Software version 3.3.3 (R Core Team, 2012) to analyse muskrat push-up presence with two datasets: 1) landscape connectivity variables among 129 lakes, and 2) landscape connectivity and within-lake variables among 39 lakes (Table 3.1). We also used generalized linear mixed models (GLMMs; Zuur, Ieno, Walker, Saveliev, & Smith, 2009b) in R Statistical Software (R Core Team, 2012) to examine within-lake variables as predictors of the presence of edible biomass within 39 lakes (Table 3.2).

To retain all possible data points for analysis, missing data were replaced with the mean of that variable. 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 & Graham, 2002).

All variables were examined for outliers using Cleveland dotplots (Zuur, Ieno, & Elphick, 2010). Collinearity was investigated with Pearson correlation coefficient matrices for all variables, and variable pairs with r values greater than 0.7 were not included in the same models to avoid high variance inflation factors (Graham, 2003; Zuur, Ieno, & Elphick, 2010). 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 principle 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 loadings of each variable for each PC indicate how much of the total variance explained by that PC is derived from each variable (Appendix 1; Table A3.11). We ran three PCAs on sediment variables: one for muskrat push-up presence models (P1), and two for within-lake edible biomass presence models (P2 & P3). The first PCA for edible biomass models included all sediment variables (P2) and the second did not include organic matter and correlated variables (P3). All three PCAs yielded similar results, and the loadings for P2 are provided as an example in Appendix 1 (Table A3.12). The two principal component scores explaining the most variance from each PCA were included as variables in model selection. In all cases, PCs 1 & 2 are measures of sediment chemistry that are related to varying inputs of river water and inorganic sedimentation controlled by flooding regimes (Barko, Adams, & Clesceri, 1986; Barko & Smart, 1986; Marsh, Lesack, & Roberts, 1999; Squires & Lesack, 2003a).

Table 3.1 Variables used in generalized linear model selection as predictors of muskrat push-up presence in lakes in the Mackenzie Delta. Variables are classified as landscape connectivity or within-patch variables and standard deviation is abbreviated as SD. Impact refers to the hypothesized direction of a variable's correlation with muskrat push-up presence.

Variable	Description	Mean ± SD	Range	Hypotheses	
				Impact	Rationale
Landscape connectivity variables					
Closure class	closure class	N/A	No, Low, High	No: + Low: + High: -	Higher flooding frequencies and durations (no and low closure) make lakes more functionally connected to dispersal corridors and increase nutrient inputs from the river.
Area	area of lake	0.19 ± 0.22 m^2	0.05 – 0.93	+	Larger lakes are easier to find in the landscape and are more likely to have higher abundances of small mammals (Fedriani, Delibes, Ferreras, & Roman, 2002; Goodwin & Fahrig, 2002).
Perimeter	perimeter of lake	2.34 ± 1.95 m	0.28 – 7.53	+	Lakes with longer perimeters are easier to find in the landscape (Goodwin & Fahrig, 2002) and are better habitat for muskrats (Jelinski, 1984).
Flooding distance	distance to nearest river channel	348.25 ± 540.81 m	0 – 2315	-	Lakes closer to the river are more functionally connected to dispersal corridors.
Interpatch distance	distance to nearest lake edge	34.15 ± 35.82 m	0 – 140	-	Lakes closer to one another are more functionally connected to one another (Goodwin & Fahrig, 2002).
Perimeter: area ratio	ratio of edge to area	21.33 ± 15.62 $km:km^2$	6.81 – 78.85	+	Proportionally more edge makes lakes easier to find in the landscape (Goodwin & Fahrig, 2002).
Within-lake patch quality variables					
Edible biomass	dry weight of energy-rich species	3.49 ± 3.46 m^2	0 – 18.59	+	Increased food availability supports species persistence and is an indicator of patch quality (Jelinski, 1984; Schooley & Branch, 2007).

Variable	Description	Mean ± SD	Range	Hypotheses	
				Impact	Rationale
Depth	average lake depth	1.50 ± 0.43 m	0.74 – 2.64	+	Deeper depths indicate the presence of unfrozen water required for muskrats' overwintering survival (Jelinski, 1989; Stevens, 1955)
PC1	measure of sediment nutrient content (see Appendix 1)	0 ± 1	-2.93 – 1.79	-	PC1 is primarily driven by increases in heavy metal concentrations (Cu, Ni, Zn) which are considered contaminants and decreases in Mg and inorganic carbon, which are beneficial for macrophyte growth (Barko, Adams, & Clesceri, 1986; Malec, Mysliwa-Kurdziel, Prasad, Waloszek, & Strzałka, 2011)
PC2	measure of sediment nutrient content (see Appendix 1)	0 ± 1	-1.51 – 2.90	+	PC2 is primarily driven by increases in Ca, S, Na, and inorganic carbon, all of which may be required in sediment for macrophyte growth (Barko, Adams, & Clesceri, 1986)
Organic matter (OM)	organic matter content in sediment	5.36 ± 2.96 %	2.15 – 17.44	+	Increasing levels of organic matter content in sediment support higher macrophyte biomass (Squires & Lesack, 2003a).
Turbidity	average turbidity of water	2.79 ± 1.47 %	0.85 – 6.70	-	Lower turbidity levels are related to lower light attenuation levels and higher macrophyte biomass (Squires, Lesack, & Huebert, 2002).

Table 3.2 Within-lake variables used in generalized linear mixed model selection as predictors of edible submerged macrophyte biomass presence in lakes in the Mackenzie Delta. Standard deviation is abbreviated as SD. Impact refers to the hypothesized direction of a variable's correlation with muskrat push-up presence.

Variable	Description	Mean ± SD	Range	Hypotheses	
				Impact	Rationale
depth	average lake depth	1.66 ± 0.63 m	0 – 3.21	-	Depth increases light attenuation (decreases light availability for photosynthesis)
PC1a	measure of sediment nutrient content not including organic matter (see Appendix 1)	0 ± 1	-2.53 – 1.99	-	PC1a is primarily driven by increases in heavy metal concentrations (Cu, Ni, Zn) which are considered contaminants (Fuentes, Disante, Valdecantos, Cortina, & Vallejo, 2007; Malec et al., 2011), and decreases in Mg, which are beneficial for macrophyte growth (Barko, Adams, & Clesceri, 1986)
PC2a	measure of sediment nutrient content not including organic matter (see Appendix 1)	0 ± 1	-2.44 – 1.97	+	PC2a is primarily driven by increases in Ca, S, Na, and inorganic carbon, all of which may be required in sediment for macrophyte growth (Barko, Adams, & Clesceri, 1986)
Organic matter	organic matter content in sediment	4.98 ± 2.75 %	1.55 – 17.44	+	Increasing levels of organic matter content in sediment support higher macrophyte biomass (Squires & Lesack, 2003a)
Turbidity	average turbidity of water	2.50 ± 1.99 NTU	0.6 – 12.7	-	Increased turbidity is related to decreased biomass (Barko, Adams, & Clesceri, 1986)
P	phosphorus content in sediment	820 ± 265 ppm	640 – 2034	+	Increasing sediment phosphorus content increases macrophyte growth (Barko, Adams, & Clesceri, 1986)

Variable	Description	Mean ± SD	Range	Hypotheses	
				Impact	Rationale
P_water	phosphorus content in water	0.012 ± 0.005 mg/L	0 – 0.029	+	Phosphorus is obtained primarily from the sediment, but some may be taken in from the water as well (Barko, Adams, & Clesceri, 1986; Smart & Barko, 1984).
PC1	summarized measure of sediment nutrient content including organic matter	0 ± 1	-2.92 – 1.89	-	PC1 is primarily driven by an increase in Cu, which is considered a contaminant (Fuentes, Disante, Valdecantos, Cortina, & Vallejo, 2007; Malec, Mysliwa-Kurdziel, Prasad, Waloszek, & Strzałka, 2011), increases in K and Na, and decreases in Mg, which are all beneficial for macrophyte growth (Barko, Adams, & Clesceri, 1986)
PC2	summarized measure of sediment nutrient content including organic matter	0 ± 1	-2.70 – 2.40	+	PC2 is primarily driven by increases in Ca, S, and inorganic carbon concentrations, which are beneficial for macrophyte growth (Barko, Adams, & Clesceri, 1986), and decreases in Zn concentrations, which is considered a heavy metal contaminant (Fuentes, Disante, Valdecantos, Cortina, & Vallejo, 2007; Malec, Mysliwa-Kurdziel, Prasad, Waloszek, & Strzałka, 2011)
Ca	calcium content in sediment	3.72 ± 1.44 %	0.84 – 7.47	+	Calcium in the sediment is taken up by macrophytes (Barko, Adams, & Clesceri, 1986)
Mg	magnesium content in sediment	1.33 ± 0.28 %	0.76 – 2.00	+	Magnesium in the sediment is taken up by macrophytes (Barko, Adams, & Clesceri, 1986)
Mn	manganese content in sediment	389.1 ± 98.6 ppm	215.5 – 792.1	-	Mn in high amounts is toxic to plants (Barko, Adams, & Clesceri, 1986)

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 (Tables 3.3 – 3.5). We examined variance inflation factors (VIFs) to check for collinearity among covariates within models, and terms with VIFs > 3 were dropped (Zuur, Ieno, & Elphick, 2010). 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 & Anderson, 2002).

To examine the drivers of muskrat push-up presence, we constructed generalized linear models (GLMs). GLMs are models that allow response variables to be non-normally distributed by transforming response data using a log-link function with a specific error distribution (McCullagh & Nelder, 1989). We used logistic linear models, which are used for response variables that are binomially distributed, as in the case of presence-absence data (McCullagh & Nelder, 1989). We used a clog-log link function, which has an asymmetrical sigmoidal curve that is more accurate for samples with an imbalance of 0s and 1s, as in our data (Hardin & Hilbe, 2007; Zuur, Ieno, Walker, Saveliev, & Smith, 2009a).

To test hypotheses about factors driving edible biomass, we used generalized linear mixed models (GLMMs) to account for possible correlation among measurements 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 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 & Anderson, 2002; Hocking & Reimchen, 2009). We used the differences in AICc values relative to the best-fit model in each set (ΔAICc) and the weight of evidence ($AICc_w$) to rank models in each set, with lower ΔAICc values and higher $AICc_w$ indicating better models. We did not consider models which included one additional variable that did not improve explanatory power enough to overcome the penalty for the added parameter of +2 AICc (Anderson & Burnham, 2002; Arnold, 2010; Burnham & Anderson, 2002), but these models are presented in model selection tables, and identified in the footnote (Tables 3.6 – 3.8). They are not discussed in the text further. 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 & Anderson, 2002).

Table 3.3 List of *a priori* candidate models for landscape connectivity drivers of muskrat presence models for 129-lake dataset.

Model	Model variables	Muskrat presence is predicted by
1	interpatch distance + flooding distance + interpatch distance * flooding distance	Distance between lakes, flooding distance, and the interaction between these variables.
2	flooding distance	Flooding distance only.
3	interpatch distance	Distance between lakes only.
4	closure class	Closure class only.
5	perimeter	Lake perimeter only.
6	Area	Lake area only.
7	edge ratio	Ratio of lake perimeter to area only.
8	flooding distance + perimeter	Lake perimeter and flooding distance.

Table 3.4 List of candidate models for muskrat presence based on combinations of landscape connectivity and within-lake patch quality variables in 39-lake dataset. PC values are from P1.

Model	Model variables	Muskrat presence is predicted by
set 1: landscape connectivity		
1	perimeter	Lake perimeter only.
2	interpatch distance	Distance between nearest lakes only.
3	flooding distance	Flooding distance only.
3a	closure class	Lake closure class only.
4	area	Lake area only.
5	perimeter	Lake perimeter only.
6	perimeter:area	Ratio of lake perimeter to area only.
11	flooding distance + perimeter	Lake perimeter and flooding distance.
set 2: patch quality		
7	edible biomass	Edible biomass productivity only.
8	edible biomass + depth	Edible biomass productivity and lake depth.
9[a]	edible biomass + PC1 + PC2 + organic matter + depth^2	Edible biomass and sediment nutrients (PC1, PC2, and OM) and intermediate depth
9a	edible_bio + PC1 + PC2 + depth^2	Edible biomass and sediment nutrients (PC1 and PC2) and intermediate depth.
set 3: post-hoc combinations		
10[a]	perimeter + flooding distance + PC2 + edible biomass	The combined effect of two best-supported landscape (lake perimeter and flooding distance) and within-patch variables (summarized sediment nutrient content (PC2) and amount of edible biomass.)
12	perimeter + PC2 + edible biomass	The combined effect of the best-supported landscape connectivity variable (lake perimeter) and two best-supported within-lake variables (summarized sediment nutrient content (PC2) and amount of edible biomass).
13	flooding distance + perimeter + edible biomass	The combined effect of the best-supported covariates from the landscape connectivity (flooding distance, lake perimeter) and within-patch (amount of edible biomass) subsets.
14	flooding distance + edible biomass	The combined effect of the best-supported covariate from the landscape connectivity (flooding distance) and within-patch (amount of edible biomass) subsets.

[a]Models contain collinear variables and were not considered in model selection.

Table 3.5 List of candidate models for within-lake models of edible biomass presence. PC values are from P2 and P3.

Model	Variables	Edible biomass presence is predicted by:
set 1: light attenuation		
1	depth	Water depth.
2	turbidity	Water turbidity.
3	depth + turbidity	Water depth and turbidity.
4	depth + turbidity + depth * turbidity	Water depth and turbidity, and the interaction between them.
set 2: sediment		
5	PC1 + PC2	Summarized sediment nutrient variables including organic matter (P3)
6	PC1a + PC2a + organic matter	Summarized sediment nutrient variables not including organic matter and correlated variables (P2) and sediment organic matter content.
7	P + Ca + Mg + Mn + OM	Phosphorus, calcium, magnesium, and manganese concentrations in sediment, and sediment organic matter content.
8	P	Phosphorus concentrations in sediment.
9	OM	Sediment organic matter content.
10	OM + P	Phosphorus concentrations in sediment and organic matter content.
set 3: other variables		
11	temperature	Water temperature.
12	water phosphorus	Total phosphorus in water.
set 4: post-hoc combinations		
13	depth + PC1 + PC2	The combined effect of the most parsimonious model from the light attenuation subset (depth) and the summarized sediment variables (PC1 + PC2).
14	depth + turbidity + PC1 + PC2	The combined effect of the best supported covariates from the light attenuation subset (depth + turbidity) and the summarized sediment variables (PC1 + PC2)
15	depth + P + OM	The combined effect of the most parsimonious model from the light attenuation subset (depth) and best-supported sediment variables (P + OM).
16	depth + turbidity + P + OM	The combined effect of the best-supported covariates from the light attenuation (depth + turbidity) and sediment (P + OM) subsets.

Model	Variables	Edible biomass presence is predicted by:
17	depth + OM	The combined effect of the most parsimonious models from the light attenuation (depth) and sediment (OM) subsets.
18	depth + turbidity + OM	The combined effect of the best-supported covariates from the light attenuation subset (depth + turbidity) and most parsimonious sediment model (OM).
19	depth + P + Ca + Mg + Mn + OM	The combined effect of the most parsimonious model from the light attenuation subset (depth) and well-supported sediment variables (P + Ca + Mg + Mn + OM).

Results

Model selection for landscape connectivity drivers of muskrat push-up presence

Push-ups were present in 27% of the sample of 129 lakes we collected remote-sensed data in. Muskrat push-up presence was best explained by lake perimeter (model 5; ΔAICc= 0.00, $AICc_w$ = 0.68; Table 3.6); longer perimeters were positively associated with push-up presence (β = 0.376, SE = 0.071, CI = 0.257 – 0.497, Figure 3.4). Other landscape connectivity characteristics, including *area*, *edge:area ratio*, *interpatch distance*, *flooding distance*, and *closure class* were relatively poor predictors of muskrat winter lake occupancy (Table 3.6).

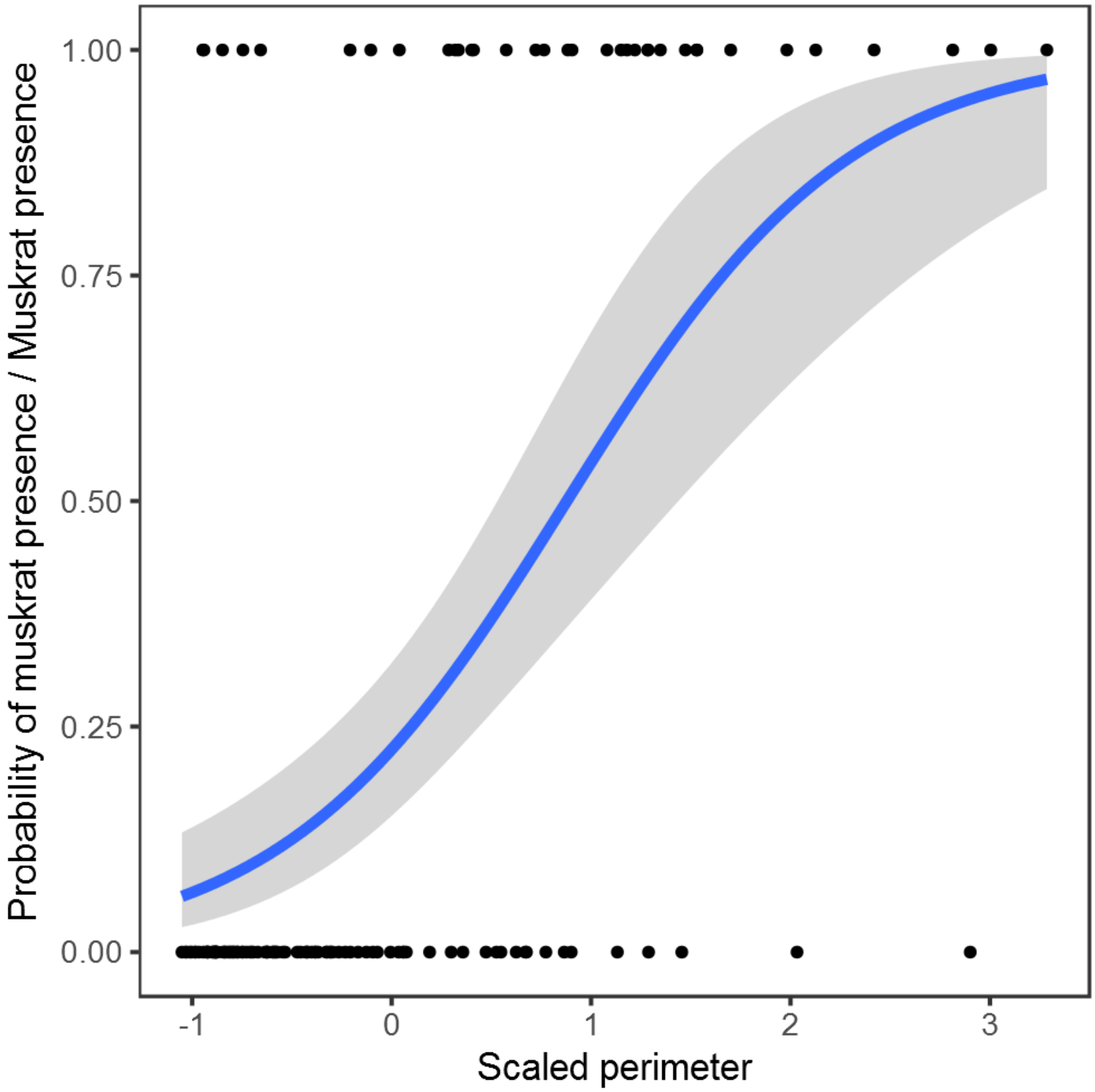

Figure 3.4 Predicted values from logistic regression (push-up presence ~ perimeter) (blue line) with 95% confidence intervals (grey fill) and observed push-up presence and absence (black points) plotted against perimeter values.

Table 3.6 Model selection within the 129-lake landscape connectivity model set. Models were ranked using AICc, corrected Akaike information criterion. The best-fit model is bolded and indicated by ΔAICc = 0.00 and highest AICc weight.

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

[a] Null model deviance is 150.82 on 128 degrees of freedom
[b] Model not considered competitive (Arnold, 2010)

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

At the 39 lakes where lake quality surveys were conducted, muskrat push-ups were observed in 8 lakes (20.5%) and not observed in 31 lakes (79.5%) (Figure 3.2). For field-surveyed lakes, muskrat push-up presence was best predicted by a combination of variables describing landscape connectivity and within-lake patch quality (model 12; ΔAICc= 0.00, $AICc_w$ = 0.90; Table 3.7), including lake perimeter (β = 1.580, SE = 0.555, CI = 0.634 – 2.959) and PC2 values (β = 1.430, SE = 0.510, CI = 0.510 – 2.644) and edible biomass (β = 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 3.8).

Table 3.7 Summary of all model subsets: 1) landscape connectivity, 2) patch quality, and 3) post-hoc combinations. PC1 & PC2 values are from P1. Models were ranked using AICc,

corrected Akaike information criterion. The best-fit model is bolded, and indicated by ΔAICc = 0.00 and highest AICc weight.

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

[a] Null model deviance is 39.58 on 38 degrees of freedom (df)
[b] Model not considered competitive (Arnold, 2010)

Table 3.8 Estimated parameters for best model including perimeter, PC2, and edible biomass (Model 12). Note that parameter estimates are based on scaled values.

Parameter	Estimate	SE	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

Within-lake drivers of edible biomass presence

Edible biomass was present at 31% of transects (n=75) in 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, $AICc_w$ = 0.49; Table 3.9), and included negative correlations with lake depth (β = -1.74, SE = 0.71, CI = -4.49 – -0.78) and positive correlations with the concentration of organic matter (β = 1.73, SE = 0.83, CI = 0.46 – 5.19) and phosphorus (β = 2.76, SE = 1.65, CI = 0.53 – 8.26) in the sediment (Table 3.10). 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 3.9).

Table 3.9 Biomass presence-absence models by hypothesis sets: light attenuation, sediment, other variables, and post-hoc combinations. All models included a random effect of 1|LakeID. PC1 & PC2 values are from P3, and PC1a and PC2a values are from P2. OM refers to sediment organic matter content. Models were ranked using AICc, corrected Akaike information criterion. The best-fit models in each set are bolded, and indicated by ΔAICc = 0 and the highest AICc weight.

model	parameters	AICc	ΔAICc	AICc weight	Residual deviance[a]	K[b]
set 1: light attenuation						
3	**depth + turbidity**	**79.15**	**0**	**0.80**	**70.6**	**3**
4	depth + turbidity + depth* turbidity[b]	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

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

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

[c] K values are one greater than number of estimated β parameters in the model due to the inclusion of the random effect 1|LakeID in all models

Table 3.10 Estimated parameters for best-supported model of edible biomass including depth, and sediment organic matter (OM) and phosphorus (P) content (Model 15). Note that parameter estimates are based on scaled values.

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

Discussion

Patch quality matters more than landscape connectivity for muskrat distributions in the Mackenzie Delta

Our results indicate that resource availability within patches is a more important driver of muskrat occupancy in the Mackenzie Delta than landscape connectivity. Previous research shows that connectivity is important for patch colonization and species persistence for a range of animals in heterogeneous landscapes (Hanski, 1998; Haynes et al., 2007; Levins, 1969; O'Brien, Manseau, Fall, & Fortin, 2006), and we hypothesized that connectivity of water bodies in the Delta, measured by *lake closure class* and *interpatch distance*, would affect muskrats' ability to colonize and persist in individual patches (lakes). However, our findings suggest that the movement and dispersal of muskrats among lakes are less important in the highly interconnected landscape of the Mackenzie Delta than patch quality. This is likely because the terrestrial matrix of the Mackenzie Delta is easily permeable to muskrats and does not represent a barrier to movement (Bender & Fahrig, 2005; Cook, Anderson, & Schweiger, 2004; Kupfer, Malanson, & Franklin, 2006), and the high density of lakes and channels results in short terrestrial distances among lakes not connected by water. Muskrat mobility and effective dispersal has been observed in variable landscapes around the world, including agricultural landscapes in the United States (Errington, 1938), and in numerous European countries, where they are often considered invasive and managed as pests (Artimo, 1960; Bos & Ydenberg, 2011; Skyrienė & Paulauskas, 2012). It is also likely that one of these variables (closure class) 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 1973-2011 (Yang, Shi, & Marsh, 2015), and it is likely that in this dynamic system a 25 year old classification no longer measures variability in current processes.

However, while our direct measures of flooding frequency were uninformative predictors, the positive correlation between key determinants of muskrat habitat and flooding distance indicates that muskrat habitat quality is linked to flooding frequency. Three key variables (sediment nutrient contents (*PC2 scores*), and *P* and *OM* in the sediment) that are positively associated with either muskrat or edible biomass presence are largely controlled by the frequency of spring flooding, which deposits inorganic sediment from river water into flooded lakes (Marsh, Lesack, & Roberts, 1999; Squires & Lesack, 2003a). Numerous studies focused on other species in heterogeneous landscapes have also highlighted the importance of habitat quality in patches (Goodwin & Fahrig, 2002; Harrison & Bruna, 1999; Thornton, Branch, & Sunquist, 2011; Weyrauch & Grubb Jr., 2004), but have not considered how connectivity among patches can affect the patch quality itself. Our results support Schooley & Branch's (2011) assertion that research on populations in heterogeneous landscapes should not focus solely on landscape configuration variables, but must also define habitat quality within the patches in order to accurately investigate habitat use and distributions. However, our results also indicate that the interactions among patch quality and landscape processes, including connectivity, must be considered when doing research in complex heterogeneous landscapes.

Basic muskrat habitat requirements are relevant predictors of muskrat presence

Our results indicate that intrinsic lake characteristics – lake *perimeter*, *edible macrophyte biomass*, *inorganic nutrients important for macrophytes* – are the most important determinant of muskrat presence in the Mackenzie Delta. 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 also indicated that muskrats prefer larger lakes (Brammer, 2016). *Edible macrophyte biomass* and parameters impacting biomass (*PC2 values*) were important predictors, because submerged macrophytes make up >95% 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 & Lesack, 2003b; Squires, Lesack, & Huebert, 2002).

We had expected that depth would be positively related to muskrat push-up presence, because muskrats require unfrozen water in the winter months (Jelinski, 1984; Stevens, 1955), 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 enough (>1.5m) to not freeze to the bottom throughout their entire area, and would all have allowed muskrats access to submerged macrophytes.

Implications for muskrat distributions in the face of climate change in the Mackenzie Delta

Flooding processes in the Mackenzie Delta control lake sediment and nutrient dynamics, impacting numerous aspects of individual lake ecology and patch quality (Lesack & Marsh, 2010; Squires & Lesack, 2003a; Squires, Lesack, & Huebert, 2002). The relationships among nutrients, as maintained by regular flooding regimes, and both 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 (Cooley & Pavelsky, 2016; Lesack, Marsh, Hicks, & Forbes, 2014; Yang, Shi, & Marsh, 2015). This is likely to decrease the number of low-closure lakes that flood annually, reduce water levels in high-closure lakes where evaporation becomes greater than water inputs (Emmerton, Lesack, & Marsh, 2007; Marsh & Lesack, 1996), and change the water and sediment chemistry of those that remain (Lesack, Marsh, & Hecky, 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 quality is the primary determinant of winter muskrat distributions in the Mackenzie Delta. The landscape connectivity processes we measured did not directly control muskrat distributions, but were related to many aspects of patch quality that were useful predictors. The link between regular flooding and indices of patch quality suggests that climate-driven reductions in flooding in this ecosystem may reduce the abundance and quality of lakes that offer suitable habitat for muskrats. Future studies should further explore the linkage between flooding and other landscape-level processes and the key habitat variables that we have identified, to better predict how they will be altered in a changing climate. This study highlights the complexity of the drivers of species' distributions in dynamic landscapes where patch quality is a function of landscape processes and points to the necessity of including both types of drivers, as well as their interactions, in studies of heterogeneous landscapes.

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Appendix 1 - Principal Component Analysis Results

Table A3.11 Variance explained by first five principal components summarizing sediment chemistry in three PCAs (P1, P2, & P3). P1 was run on the data summarized by lake (n=39), and P2 and P3 were run on data summarized by transect (n=72). P2 included all sediment variables, and P3 did not combine sediment nitrogen, carbon, organic carbon, or organic matter concentrations.

Principal Component	**Proportion of variance explained**		
	P1	P2	P3
PC1	0.471	0.427	0.477
PC2	0.214	0.253	0.162
PC3	0.092	0.070	0.091
PC4	0.069	0.065	0.076
PC5	0.055	0.056	0.073

Table A3.12 Loadings for Principle Components 1 & 2 for P2. Mean values >|0.30| are italicized.

Variable	**PC1 mean**	**PC2 mean**
Ca	-0.151	*0.373*
K	*0.313*	-0.063
Mg	*-0.322*	0.109
S	0.213	*0.308*
B	0.235	-0.108
Cu	*0.330*	-0.138
Mn	0.043	-0.219
Mo	0.188	0.017
Na	*0.301*	0.046
Ni	0.238	-0.253
P	0.070	-0.020
Zn	0.272	*-0.300*
CIN	-0.193	*0.325*
N*	0.293	0.282
C*	0.187	*0.397*
CORG*	0.261	0.299
OM*	0.277	0.288

*Variables are only included in P2

Appendix 2 – Edible biomass species list

(Based on Artimo, 1960; Jelinski, 1984)

Callitriche hermaphroditica

*Eleocharis acicularis**

*Equisetum fluviatile**

Pocaeae

Lemna trisulca

Myriophyllum sibiricum

Potamogeton filiformis

Potamogeton friesii

Potamogeton gramineus

Potamogeton pectinatus

Potamogeton praelongus

Potamogeton richardsonii

Potamogeton zosteriformis

Ranunculus aquatilus

*Sagittaria cuneata**

*Sparganium sp.**

*Denotes uncommon species

Chapter 4 – Conclusion

Summary

Environmental conditions in Canada's western Arctic are being impacted by climate change and increased industrial development (ACIA, 2004; Schindler & Smol, 2006; Stern & Gaden, 2015; Tyson, Lantz, & Ban, 2016). The Gwich'in and Inuvialuit residents of the Mackenzie Delta have relied on the resources in this environment for centuries, and changing ecological conditions and altered access to the land can affect their well-being (Parlee, Berkes, & Gwich'in, 2005; Usher, 1971). Muskrats are an important semi-aquatic furbearer and have been harvested for food and fur in great numbers since the 1800s (Gwich'in Elders, 2001; Krech, 1984). Gwich'in and Inuvialuit trappers have observed a decline in the abundance of this species since the 1980s, when fur prices also declined rapidly. The overall goal of this research was to investigate and contextualize the economic and cultural importance of muskrats and assess the determinants of muskrat habitat selection in the Mackenzie Delta. My thesis consisted of two separate but related projects where I: 1) used social science methodologies to explore changing human and muskrat interactions and the ongoing importance of these animals to Gwich'in and Inuvialuit residents; and 2) conducted an observational ecological study to explore the drivers of muskrat distributions. In this chapter I consider how the findings of these separate but related projects informed one another and suggest future directions for research on muskrats.

The first part of my thesis explored the role of muskrats in the lives of Inuvialuit and Gwich'in residents of the Mackenzie Delta, in the context of changing socioeconomic and ecological conditions. I conducted interviews and meetings with over

70 community members and identified key themes in participant responses. Although the role of muskrats has changed over the last 100 years, muskrat harvesting continues to offer Delta residents a meaningful way to remain engaged in, to perpetuate, and strengthen their cultural identity and land-based traditions among generations, and ultimately, to foster individual and community wellbeing. This is consistent with the findings of other studies showing that Indigenous communities around the world continue to practice traditional activities and rely upon the land, despite changing access and environmental conditions (Corntassel & Bryce, 2012; Garnett et al., 2009; Kuhnlein, Erasmus, & Spigelski, 2009; Loring & Gerlach, 2009).

In the second part of my thesis, I investigated the influence of landscape connectivity and patch quality – two properties affected by climate change – as drivers of on muskrat presence and distribution in the Mackenzie Delta, using remote sensing and field-based surveys of lakes with and without muskrats present in the winter. I tested multiple hypotheses about the predictors of muskrat presence and macrophyte biomass in lakes using a model-selection, information theoretic approach. The results of this study indicate that within-patch habitat quality has a larger influence on muskrat distribution than landscape connectivity variables. Specifically, muskrats were more likely to occur in lakes with longer perimeters, higher amounts of edible submerged macrophyte biomass, and sediment characteristics that supported macrophyte growth. The latter two conditions are related to spring flooding regimes, indicating that this process has an indirect effect on the within-patch factors influencing muskrat distributions. Since climate change will alter the nature of individual lake conditions, it is likely that warming temperatures will alter the quantity and quality of available habitat for muskrats in the Mackenzie Delta.

This research highlights the importance of considering landscape connectivity and patch quality, as well as the interactions among them, in studies of complex heterogeneous landscapes.

Divergence and convergence of different approaches

Both sub-projects of my master's research addressed community concerns about changing muskrat populations and were guided by conversations with individual community members, the Tetlit and Nihtat Gwich'in Renewable Resource Councils, the Inuvik and Aklavik HTCs, and the Gwich'in Renewable Resources Board. The methodologies I used yielded different perspectives, and influenced the nature of the conclusions drawn.

The two projects diverged in their spatial and temporal score: the scientific study targeted a small set of lakes in a single year, while land users' observations were applied to a larger part of the Delta over a longer time period. These observations encompassed an understanding of this system throughout and in some cases, prior to, their lifetimes. These sub-projects also diverged in their goals and priorities: the ecological study was designed to identify specific drivers and quantify their effects on muskrat distributions, while documenting land user observations did not focus on quantifying the effects of specific drivers, but rather on identifying the myriad of conditions, processes, and change, ecologically, economically, and socioculturally, that have been observed and experienced by individuals.

The results of these two separate projects did, however, converge on many conclusions about the nature of processes and conditions that determine muskrat distributions in the Mackenzie Delta. Local knowledge holders and the scientific study both indicated that flooding was an important process in the Delta because of the way it influences conditions in lakes. Some of the specific drivers, including the abundance of food in lakes where muskrats are present, were identified separately by both studies. The importance of the Delta ecosystem as a whole was also brought up in both studies, albeit in different ways. Local knowledge holders brought this type of understanding to all conversations regarding muskrats, whereas the scientific study identified the importance of understanding heterogeneity at multiple scales as an area of further research required to fully understand changes in muskrat distributions.

These sub-projects were also mutually informative and contributed to the direction of one another. For example, speaking with local knowledge holders gave me a better understanding of long-term trends in muskrat abundance and the distribution of muskrats in the Delta. This knowledge highlighted the need for research into potential drivers of observed declines, which led to my research exploring the factors influencing distribution (Chapter 3). Understandings of long-term dynamics held by local land users and traditional knowledge holders, especially in scientifically data-poor systems, are increasingly being used to inform resource management (Brewster, Neumann, Ostertag, & Loseto, 2016; Eckert, Ban, Frid, & McGreer, 2018; Mallory, Gilchrist, Fontaine, & Akearok, 2003).

The scientific methods used in Chapter 3 also provided insights into specific aspects of the Delta environment that were mentioned, but not quantified, in interviews with land users. While land users are well aware of the broad-scale effects of a warming climate and are observing many changes on the land when they are out harvesting, there is some uncertainty regarding the magnitude and impact of specific changes that will directly affect muskrats. The research I conducted for Chapter 3 indicates that changes in flooding patterns driven by climate change will affect sediment and nutrient delivery and submerged macrophyte productivity in lakes, which will influence muskrat distributions in the Delta. Furthermore, remote-sensing methods allowed for a broader and more systematic spatial analysis of muskrat presence than could be gleaned from discussions with land users, because information could be obtained for lakes that were largely inaccessible to land users or researchers on the ground, and encompassed multiple trapping areas that would only be accessed by individual harvesters.

Limitations and biases

The extensive and sustained harvest of a species may result in population declines or crashes when the harvest exceeds the carrying capacity of the species (ie. Atlantic cod: Hutchings & Myers, 1994). Wildlife researchers and harvesters may differ in their perceptions of the effects of harvest on wildlife populations, and the causes of population declines (Parlee & Caine, 2018). In the Delta, local knowledge holders consistently do not consider harvesting to be a possible driver of the observed declines in muskrat populations. From a population ecology perspective, the drastic decline in muskrat populations observed from the 1980s onwards is not likely due to the intense harvest pressure during the Muskrat Period (1900-1950). The intensive and extensive harvest pressure began to ease in the 1960s and especially after the 1980s when the population decline became very pronounced. The long lag between the highest intensity of harvest and the observed decline is not supportive of harvest as the driving factor of the decline. Additionally, numerous life history characteristics of muskrats lend themselves to adequate compensatory response to harvest pressure (Clark, 1990), including their early breeding maturity (<1 year), high fecundity (10-20 young / year), and rapid population expansion and growth (Errington, 1963; Stevens, 1955). These assumptions were not rigorously evaluated in this study, and better understanding of population dynamics and response to harvest is an area of potential future study.

There can be selection bias in participant selection for qualitative research, as it is not a random selection of the population and is influenced by both participant and researcher subjectivity. In this study, we purposively selected muskrat experts as identified by local management organizations and some self-identification, in order effectively and efficiently elicit robust information and conclusions (Tongco, 2007). One bias that could result from this participant selection approach would be a type of 'non-response bias' (Hill, Roberts, Ewings, Gunnell, 1997), where only community members who agreed that muskrats were declining took part in order to voice their concerns, while those who were not concerned did not. While this type of bias may significantly skew the outcomes of studies that rely on small numbers of key participants engaged in a single point of contact (one interview), or if researchers are not careful to be neutral and keep assumptions out of questions or the framing of the project, my own reflexivity led to the engagement of a large number of participants through an iterative process of results-sharing and knowledge-creating in open-ended conversations, which offers greater certainty in the validity of the conclusions I drew (Creswell & Miller, 2000). While selection bias is important to consider in all fields of inquiry, using rigorous social science methods ensured that I came to accurate conclusions representative of the majority of participants in this study.

Future research priorities

My interviews with local knowledge holders highlighted that additional research is required to address their overarching concern: “how and why are muskrat population cycles changing?,” as this broader question was not fully addressed in this thesis. In order to identify drivers of cyclic populations, a variety of conditions and the species’ population must be recorded over time; a Master’s project does not afford the longitudinal continuity to do this. Furthermore, local knowledge holders frequently discussed the cumulative effects of changing environmental conditions and the effects of interactions with other species (otters, mink, and beavers). These are not currently captured in environmental or wildlife monitoring datasets being produced by academic or government researchers in the region, but there is recognition among co-management bodies and other institutions that these issues need to be explored. Some of the environmental changes that are widely acknowledged by local knowledge holders and scientific researchers that should be investigated in more detail include: 1) changing interactions among muskrats, beavers, mink, and otters; 2) quantifying the variation among lakes in the availability of emergent vegetation for summer food; and 3) monitoring changing environmental conditions including overflow on top of the ice, decreasing water levels, and changing flooding patterns.

All of the priorities identified above can be pursued using both scientific methods and by documenting local knowledge on an ongoing basis; continued collaboration will lead to a more complete understanding of this species. There is widespread recognition that ongoing community-based monitoring provides individuals with more opportunities to be out on the land together connecting with traditional practices, and can address concerns regarding knowledge transfer to youth (Cuerrier et al., 2012; Krupnik & Jolly, 2002; Wolfe et al., 2011), as were identified by many participants in this study. Research on species that are culturally significant provides a particularly powerful focal point for collaboration, as the research and knowledge-sharing is relevant and meaningful for all participants. Future projects should involve youth, expert land users, and Elders in all components of muskrat research, including biological, ecological, and local knowledge studies.

The Mackenzie Delta is not the only region where muskrats play a key role in the ecological, economic, and cultural systems of local people. They are similarly situated in the lives of the Vuntut Gwich'in First Nation in Old Crow Flats, Yukon (Brammer, 2016) and the Athabasca Chipewyan First Nation in the Peace-Athabasca Delta, Alberta (PADEMP, 2014; Straka, Gray, & MacMillan, 2014). Bringing together local knowledge from multiple communities can provide "cross-scale insights" (Berkes, 2012, p. 175) that assist in formulating a clearer picture of the ecological status of muskrats in Canada's north. Future research endeavours should involve collaboration within and among researchers and community members from all three regions.

Conclusion

My thesis research arose out of community concerns regarding changes in muskrat populations and use in the Mackenzie Delta. Ecological and local knowledge studies were developed with extensive input from community members and local co-management organizations. Local knowledge indicates that muskrats continue to be important to highly adaptable Delta residents, and provides insight into changing ecological conditions that may be adversely affecting muskrats. An observational ecological study identified some of the lake-specific characteristics driving muskrat distributions, and the landscape processes affecting these lake conditions.

Local land users may not only observe changes before scientists or managers, but they are also likely to observe and experience change in different ways than science. Local people make observations and conclusions based on what is relevant to their use of and experiences on the land. Scientific inquiry targets a specific relationship among conditions or processes and attempts to quantify the nature and magnitude of this relationship. Science can answer questions regarding processes that people on the land cannot or do not observe, and local knowledge can provide a better understanding of conditions over time and space because of the longitudinal aspect of observations, which may be missing from scientific datasets. These two ways of knowing and gathering information can each stand on their own and provide insight into a system, and they can also inform one another, sometimes resulting in a deeper and more nuanced understanding of the system being observed.

Further study of the complex Delta ecosystem should continue to involve multiple ways of knowing and explore changing hydrology, species interactions, abiotic conditions affected by climate change, and the cumulative effects of these changes on muskrats, other culturally important animals, and the peoples who rely on them.

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